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Sensory Horizons and the Functions of Conscious Vision

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Short Abstract: We discuss the functions and evolution of conscious vision. Conscious vision, we argue, operates too slowly to be suited for immediate actions, but instead evolved for offline cognition. We trace the emergence of conscious vision to the water-to-land transition, where larger terrestrial sensory horizons allowed animals to benefit from model-based planning. This shift drove the evolution of "reality monitoring"—the capacity to determine whether internal signals reflect external reality or endogenous activity uncoupled from sensory input. Following higher-order theories of consciousness, we associate consciousness with this reality monitoring function and discuss novel empirical predictions.

Long Abstract: It is not obvious why we are conscious. Why can't all of our mental activities take place unconsciously? What is consciousness for? We aim to make progress on this question, focusing on conscious vision. We review evidence on the timescale of visual consciousness, showing that it is surprisingly slow: postdictive effects reveal windows of unconscious integration lasting up to 400 milliseconds. We argue that if consciousness is slow, it cannot be for online action-guidance. Instead, we propose that conscious vision evolved to support offline cognition, in tandem with the larger visual sensory horizons afforded by the water-to-land transition. Smaller visual horizons typical in aquatic environments require fast, reflexive actions of the sort that are guided unconsciously in humans. Conversely, larger terrestrial visual horizons allow benefits to accrue from "model-based" planning of the sort that is associated with consciousness in humans. We further propose that the acquisition of these capacities for internal simulation and planning provided pressures for the evolution of reality monitoring—the capacity to distinguish between internally and externally triggered signals, and to solve "Hamlet's problem" in perception—the problem of when to stop integrating evidence, and fix a particular model of reality. In line with higher-order theories of consciousness, we associate the emergence of consciousness with the emergence of this reality monitoring function. We discuss novel empirical predictions that arise from this account, and explore its implications for the distribution of conscious (vs. unconscious) vision in aquatic and terrestrial animals.

Introduction

It's not obvious why we are conscious[1]. Your mind often operates 'in the dark'. While standing or walking, for instance, your body maintains balance by relying on the unconscious integration of sensory inputs to keep you upright without your direct awareness. If you accidentally touch a hot plate, you'll remove your hand before consciously experiencing pain. You might also have experienced leaving a difficult problem aside, only for the solution to suddenly pop into your awareness a moment later—perhaps a result of unconscious cognitive processes operating behind the scenes. But why can't all of our mental activities take place 'in the dark'? What is consciousness good for? We aim to make progress on this question—focusing for now on conscious vision[2].

Understanding the function of consciousness is crucial for gaining insights into its evolutionary origins and its distribution among species. Despite extensive research on this question since at least the 19th century (Michel, 2019), one aspect has been relatively neglected: what the speed of consciousness reveals about its function. Every conscious percept is preceded by a cascade of unconscious sensory processes. The speed of consciousness is how fast one becomes conscious of objects and events in one's environment following sensory input (Dainton, 2023; Herzog et al., 2020). We review the empirical literature to show that **visual** consciousness is surprisingly slow. Yet, we are capable of fast and accurate responses to visual stimuli. We argue that if consciousness is slow, fast

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[1] We follow the standard way of explaining the term 'consciousness' in the philosophical literature (Nagel, 1974). Consciousness is 'subjective experience'. A mental state is conscious if there is 'something it's like' for the subject to be in that state. There is nothing it's like for a subject to perceive a subliminal stimulus. Seeing a stimulus unconsciously doesn't feel like anything—it feels like not seeing it. By contrast, there is something it's like to see a stimulus presented supraliminally—one consciously experiences shapes, colors, etc. This is the contrast we focus on. See Schwitzgebel (2016) for a definition by examples.

[2] **Our focus on vision is in large part due to the fact that there is much more available evidence on the functions of conscious vision (as opposed to unconscious vision) compared to other sensory modalities. In particular, consciousness research has learned a lot from phenomena like blindsight (Weiskrantz, 2009) and work on dorsal stream vision (Milner & Goodale, 2006). Furthermore, while we believe that our analysis can shed light on the evolution of consciousness *simpliciter*, there is also the possibility that other types of sensory and affective states became conscious earlier or later than visual states in evolutionary history. For example, there is the possibility that vision operates unconsciously in otherwise conscious animals—in organisms with *other* types of conscious sensory or affective states.**

responses have to be triggered and guided by unconscious sensory states (Milner & Goodale, 2006). When searching for the role of **visual** consciousness in our mental lives, we have to look for mental processes that do not suffer from its relative sluggishness—visual consciousness is not for immediate reactions.

We build on this point and on evidence from sensory ecology to propose an account of the evolution of visual consciousness. We show the importance of sensory horizons for thinking about the evolution and distribution of visual consciousness. The sensory horizon of an organism is how far it can sense a change in its environment. A limited sensory horizon imposes immediate reactions to most ecologically relevant visual stimuli—such as predators or prey. We review studies in sensory ecology showing that animals differ radically in their sensory horizons. In particular, the fact that light is rapidly scattered in water severely limits the visual horizon of aquatic animals such as fish (MacIver et al., 2017; MacIver & Finlay, 2022; Nilsson et al., 2014). We believe that an analysis of the water-to-land transition and the hundred-fold increase in visual range associated with it can provide new insights into the evolution of visual consciousness[3].

We then argue that an increase in sensory horizon provides pressures for the evolution of a cognitive function called reality monitoring—the capacity to **determine whether internal signals reflect external reality or endogenous activity uncoupled from sensory input** (Dijkstra et al., 2022; Johnson & Raye, 1981; Lau, 2022; Simons et al., 2017). This function arises in response to two computational problems. First, organisms that evolved the capacity for internal uses of sensory processes for cognition face the problem of having to differentiate between **internal signals that reflect reality and endogenous activity uncoupled from sensory inputs**. Second, organisms that can afford to wait to accumulate more reliable perceptual evidence face what we call Hamlet's problem in perception—the problem of determining when to stop accumulating evidence before committing to a perceptual decision. We suggest that a reality monitoring system evolved to flexibly solve these

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[3] Malcolm MacIver has expressed a similar view in a blogpost (https://tinyurl.com/mum6pbkt). The work of MacIver and collaborators on the functional constraints posed by sensory horizons inspired us to explore connections to the timescale of human consciousness (MacIver & Finlay, 2022; Mugan & MacIver, 2020). We thank him for invaluable comments and discussions.

problems. In line with higher-order theories of consciousness, we associate the emergence of consciousness with the emergence of this reality monitoring function (Fleming, 2020; Lau, 2022).

Consciousness is slow

Suppose that an apple is unexpectedly thrown at you. You are not visually conscious of the apple as soon as the light reflected from it hits your retina. Instead, a cascade of sensory processes transforms this input into a conscious percept. These sensory processes occur before the conscious percept emerges. And as any other physical process, they take time. So, your conscious percept lags behind reality. The question is: how much time does it take for conscious perception to emerge? How long between the moment a change in sensory information is registered on your retina and the moment you consciously experience the apple? This is the question of the speed of (visual) consciousness.

Answering that question is relevant for determining what consciousness is for. Take an extreme scenario where it takes you a full second to consciously perceive the apple. That speed would indicate that consciousness is not directly involved in any of the vision-involving functions that can be performed relative to the apple before one second. Suppose that you catch the apple or duck to dodge it in less than a second. A speed of consciousness of one second would mean that the visual information that triggered and guided your reaction was unconscious. Meanwhile, suppose that conscious perception occurs within 50 milliseconds (ms). In that scenario, your action might have been triggered and guided by your conscious percept. This simple example shows how the speed of consciousness is informative with respect to the functions that conscious perception might be involved in (Figure 1A). This is why the question of the speed of consciousness matters.

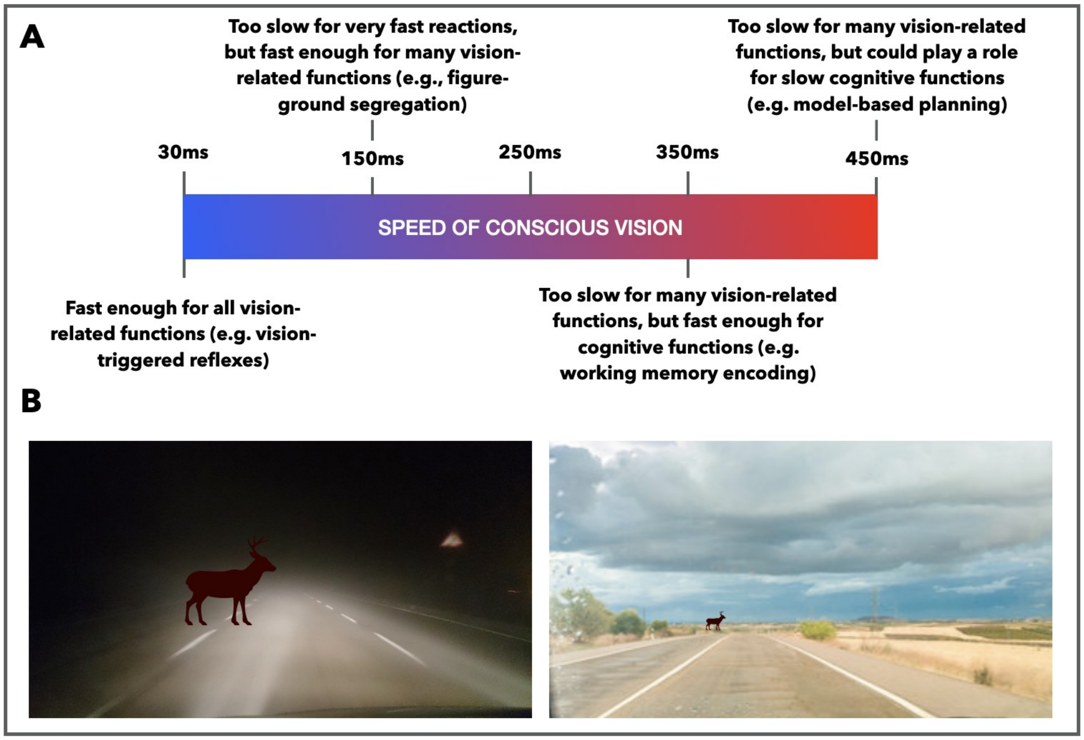

Figure 1. A) How the speed of visual consciousness is relevant for studying its functions. Mental functions that operate based on visual inputs and which are faster than the timescale of conscious vision must operate based on unconscious visual inputs. B) Illustration of the relationship between the distance at which visual objects are detected and the speed at which a response is required. When driving on a foggy road at night, visual objects are detected at the last moment, prompting fast vision-based reactions but precluding the execution of slow vision-based functions. When viewing objects at a distance, slower mental functions (e.g., model-based planning) can operate based on the visual input.

How could we begin to address the question of the speed of consciousness? One way would be to identify the chain of neurocognitive processes leading to consciousness and then determine how fast those processes can occur. In the case of vision, information takes about 50ms to travel from the retina to the first stage of visual cortical processing in the primary visual cortex (Ducati et al., 1988; Foxe & Simpson, 2002; Schmolesky et al., 1998). After that, the first feed-forward sweep of visual cortical processing is generally believed to occur unconsciously (Fahrenfort et al., 2007; Pascual-Leone & Walsh, 2001; Silvanto et al., 2005), and complex feedback processing does not seem to shape perception before around 120ms (Boehler et al., 2008; Koenig & Ro, 2019; Koivisto et al., 2011). For this reason, there is relatively wide agreement that conscious perception does not occur before about 120ms (although see Zeki, 2003; Zeki & Bartels, 1999).

But different theories make widely different predictions from there. For instance, the local recurrence theory of consciousness hypothesizes that consciousness emerges within 150ms after stimulus onset with feedback loops from higher- to lower-level perceptual areas (Lamme, 2006, 2016). Meanwhile, the global neuronal workspace theory claims that consciousness only occurs once visual representations are globally broadcast to a variety of neurocognitive modules around 350ms after stimulus onset (Dehaene & Naccache, 2001; Mashour et al., 2020). Past a certain point, theories of consciousness are too uncertain to settle the question of the speed of consciousness on their own.

Another related method might be to look for the time of emergence of the first markers of conscious perception: how early can we tell whether a stimulus will be consciously perceived or not just by looking at brain activity? Studies to date have provided conflicting results with electroencephalography (EEG) and magnetoencephalography (MEG) markers anywhere between 130ms and 350ms (e.g., Dembski et al., 2021; Gaillard et al., 2009; Railo et al., 2011; Salti et al., 2015; Sergent et al., 2021). The problem is that it is exceedingly difficult to identify whether any of these markers are precursors of consciousness, genuine correlates of consciousness, or consequences of consciousness (Aru et al., 2012; Block, 2024; De Graaf et al., 2012). Just because some activity predicts consciousness does not mean that consciousness emerges at the time of that activity. The activity of a barometer can predict rain while also occurring before the rain itself. Instead of deferring to a particular theory or specific markers of consciousness, we next turn to evidence that directly bears on the question of the speed of consciousness.

Postdiction and the speed of consciousness

The strongest kind of evidence on the speed of consciousness comes from psychological effects called 'postdictive effects'—in which the way one consciously perceives a stimulus presented at time *t* changes because of events occurring at *t+1*. Let us use visual masking as a simple example to illustrate this. In metacontrast masking, presenting a mask 70ms after a target—a 70ms stimulus-onset asynchrony (SOA)—can make the target invisible (Breitmeyer & Ogmen, 2006). This is a postdictive effect. Had the target been processed consciously within 70ms, the mask would have arrived too late to make it invisible. So, this effect indicates that conscious perception takes at least 70ms **(assuming that the target is processed equally fast irrespective of whether or not the mask is presented)**.

We can use psychological effects of this kind to identify a *lower bound* for the speed of consciousness. Emphasis on '*lower bound*'. The fact that the mask is ineffective when presented 130ms after stimulus onset, but effective at 70ms, does not show that conscious perception occurs within 130ms. Why? Because it does not show that no method could make the target invisible (or retrospectively change its subjective appearance) more than 130ms after its onset. It just shows that we cannot achieve this using a metacontrast mask alone[4]. With this caveat in mind, the important point is that we can investigate a lower bound for the speed of consciousness using postdictive effects of this kind.

How far have psychologists pushed the lower bound of the speed of consciousness? Postdictive effects in the 50-200ms time range have been studied for decades (Eagleman & Sejnowski (2000); Kolers & Von Grünau (1976); see Hogendoorn (2022); Shimojo (2014) for reviews). For example, in the Poggendorff illusion, a straight line interrupted by a shape (such as a rectangle) appears misaligned, even though the line segments are actually collinear. Sugita et al. (2018) showed that presenting the rectangle up to 200ms after the line segments causes subjects to perceive the lines as misaligned (Figure 2A). Since presenting the rectangle 200ms after the lines determines the perceptual fate of the lines, conscious perception of the lines must have waited at least 200ms.

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[4] Visual masking must imply a lower bound for the speed of conscious perception that is in fact much higher than the maximal SOA at which the mask can still achieve an effect. This is because processing the mask itself takes time. The easiest way to show this is through the phenomenon of 'target recovery'—which happens when the mask is masked (Öğmen et al., 2006). For instance, Amassian et al. (1993) suppressed the perception of three letters by presenting a mask 100ms later. They then discovered that applying transcranial magnetic stimulation to the visual cortex 100ms after the mask suppressed the mask, and thus led to a recovery of the target letters. The target must have been processed unconsciously for 200ms, since a TMS pulse 200ms after its onset could still determine whether or not the target was perceived (see also Ro et al. (2003); see Gale et al., (2024) for target recovery in mice using optogenetic suppression of the mask). **It is also important not to confuse the speed of consciousness with the minimal duration of *exposure* required to consciously perceive a stimulus. Psychophysics studies using a modern-day tachistoscope have shown sensitivity to stimuli presented for less than a millisecond (e.g.** Lanfranco et al., 2024)**. This does not imply that the target is *processed*—much less *consciously* processed—in a millisecond or less. One might become conscious of a target presented for less than a millisecond long after the target itself has disappeared.**

We can go further with 'long-lasting' postdictive effects (see Herzog et al. (2020) for a review). Many of the relevant experiments involve visual stimuli called 'Vernier'—two vertically superimposed bars with an horizontal offset (Figure 2B). These stimuli fuse remarkably well (Scharnowski et al., 2007). When a Vernier is followed by an anti-Vernier (a Vernier with the opposite offset), the two stimuli fuse into a neutral Vernier—the offsets cancel one another. This effect is postdictive in nature. Integration also happens for Verniers presented in a moving stream of Verniers (Figure 2B). Notably, if a Vernier is presented at the start of the stream, subjects perceive its offset as transported along the stream even if all the following stimuli do not have an offset.

A striking discovery from Drissi-Daoudi et al. (2019) is that presenting an anti-Vernier in the stream up to 450ms after the first Vernier can postdictively change the appearance of the entire stream (Figure 2B). Doing so brings discrimination performance for the Vernier offsets from 75% to *chance level*: if the first Vernier in the stream has an offset to the right, subjects who would otherwise be able to discriminate it at 75% accuracy become totally unable to do so when it is succeeded by a Vernier with the opposite offset 450ms later. This integration seems mandatory: it is not disrupted by saccades during the stream (Drissi-Daoudi et al., 2020) or by the presentation of distractors (Vogelsang et al., 2024). The other remarkable aspect of the sequential metacontrast paradigm (SQM) is that there is a *discrete* time window during which Verniers integrate. A Vernier presented 100ms in the stream does not integrate with an anti-Vernier presented 550ms after the start of the stream (that is, 450ms after the Vernier). The window of integration closes about 450ms after the start of the stream, and the anti-Vernier is now outside of this discrete window.

Motion does not have to be involved to obtain long-lasting postdictive effects with Verniers. Scharnowski et al. (2007) discovered that Vernier dominance in Vernier fusion can be manipulated up to 350ms after the presentation of a Vernier by Transcranial Magnetic Stimulation (TMS) to the early visual cortex. That is, the way in which subjects perceive the fusion of two Verniers depends on whether or not a TMS pulse will be delivered 350ms later.

Several long-lasting postdictive effects involve attention. In a series of experiments Sergent et al. showed that attracting exogenous attention to a stimulus location up to 400ms after its offset can postdictively improve its discriminability and reported subjective visibility—a phenomenon called ‘retro-perception’ (Sergent et al., 2013; Thibault et al., 2016; Xia et al., 2016). Importantly, in a Gabor orientation discrimination task, Thibault et al. (2016) found that the retro-cue does not affect the precision of the representations, but mainly changes the ‘guess’ rate. This suggests that the retro-cue does not simply consolidate the representation of an already visible target, but instead postdictively determines the target’s conscious or unconscious fate. Other postdictive attentional effects include distortions of visual space by retrospective attentional cues (Ono et al., 2023; Ono & Watanabe, 2011). In the attentional repulsion effect, attending to a location makes a stimulus next to that location appear further away than it really is (Lawrence et al., 2020). Ono & Watanabe (2011) showed that the attentional repulsion effect can occur postdictively and found that it is preserved even when the attentional cue is presented up to 400ms after stimulus offset.

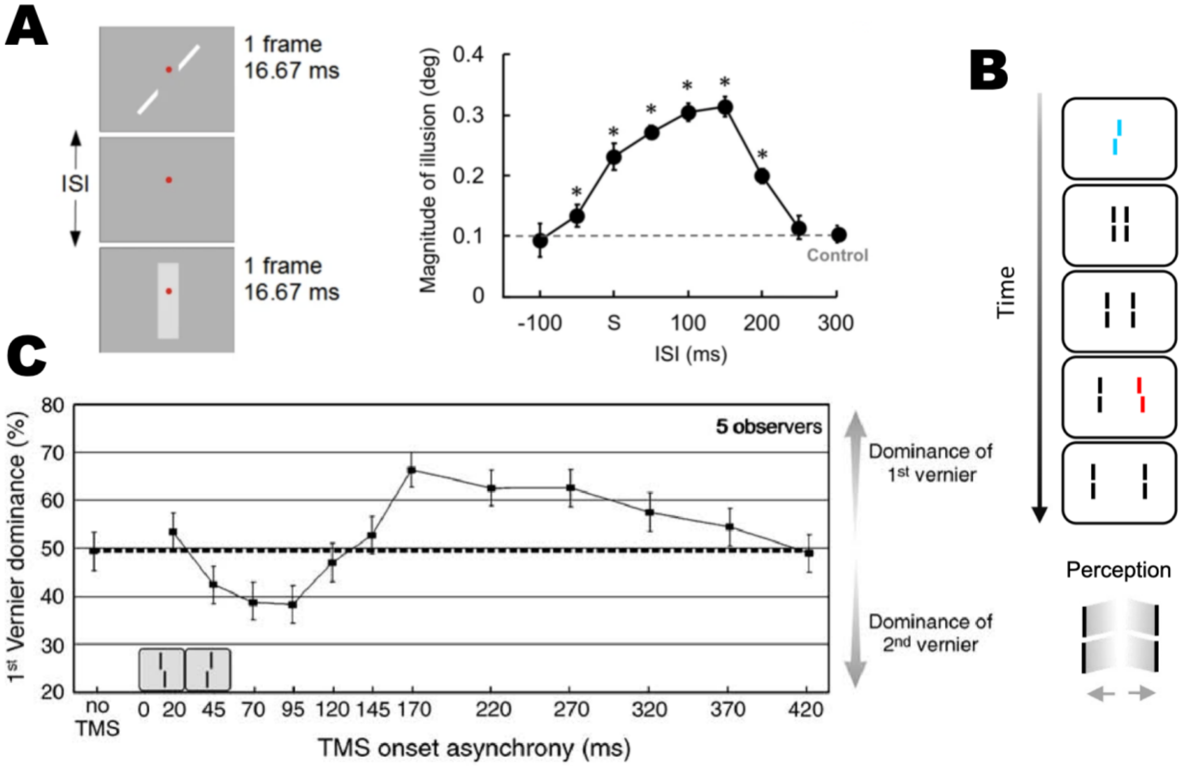

Figure 2. Postdictive effects. A) Asynchronous presentation of the elements creating the Poggendorff illusion. Presenting a rectangle up to 200 milliseconds after collinear line segments changes the perceived colinearity of the lines. Source: adapted from Sugita et al. (2018). B)

Sequential Metacontrast paradigm (SQM). A Vernier (with an offset to the right) and an anti-Vernier (offset to the left) fuse into a neutral Vernier (no offset) when presented in rapid succession. This is true even when the Vernier and anti-Vernier are presented within a stream composed of neutral Verniers. In those conditions, presenting an anti-Vernier up to 450ms after the start of the stream postdictively changes perception of the entire stream, such that no Vernier or anti-Vernier is consciously perceived at all. Source: Adapted from Drissi-Daoudi et al. (2019). C) A Vernier and anti-Vernier presented in succession normally fuse into a neutral Vernier. However, applying transcranial magnetic stimulation to early visual cortex up to 320ms after the presentation of the Vernier and anti-Vernier can postdictively change what participants consciously experience.

Postdictive effects also occur in other modalities. One of the most famous effects is the cutaneous rabbit illusion—a tactile illusion in which the perceived location of a tap on the skin is affected by the location of a subsequent tap. This postdictive effect is robust in the 300ms range (Flach & Haggard, 2006; Geldard & Sherrick, 1972; Kilgard & Merzenich, 1995). One can also find postdiction across modalities (Stiles et al., 2022), although effects have so far only been demonstrated under 200ms. For instance, the McGurk effect can be induced with an asynchrony between sound and movement, suggesting a window of 200ms for the integration of sound and visual information (Van Wassenhove et al., 2007). As another example, Stiles et al. (2018) have shown that sounds postdictively affect vision. In the audio-visual rabbit illusion, observers presented with a sequence of spatially separated flashes paired with sounds perceive an illusory flash located between the real flashes if a sound occurs between the flash-sound pairs. That is, the location of an illusory flash depends on whether a flash-sound pair will be presented 130ms after the onset of the first flash-sound pair.

We have reviewed long-lasting postdiction effects in the 350-400ms range. These effects suggest that conscious perception does not generally occur before 350ms after stimulus onset. If conscious perception occurred before that, manipulating post-stimulus processing would be too late to change it. The fact that the fate of a percept can still be changed in that time frame indicates that it was not already conscious. This means that consciousness is slow. It is preceded by a window of unconscious sensory integration that can last up to 450ms in the most extreme cases (Herzog et al. 2020). We now answer some objections to this interpretation.

What long-lasting postdiction shows

Let us address two objections. A first objection is that subjects might be phenomenally conscious of the real sequence of stimuli, but can only cognitively access the integrated sequence. That is, phenomenal consciousness overflows cognitive access. In the SQM, for instance, subjects *are* phenomenally conscious of the offset of the first Vernier, but by the time they start *thinking* about what they saw, this information is no longer available for report (this is similar to what Dennett (1991) called an 'Orwellian' account). Call this the 'overflow gambit', because the response says that phenomenal consciousness overflows cognitive access (Block, 1995, 2007).

There are two main problems with the overflow gambit. The first problem is that it is *ad hoc*. To see why, consider the fact that the worry overgeneralizes: one could say the same to deny that **short-term postdictive effects like visual** masking **have** an effect on phenomenal consciousness. **Just like visual masking, long-lasting postdiction experiments include not only introspective reports but also forced-choice discrimination tasks. For example, in the SQM, participants cannot discriminate the orientation of the first Vernier when a Vernier with an opposite offset appears 300ms later in the stream (Drissi-Daoudi et al. 2019). This effect persists even when researchers explicitly inform participants about the paradigm and instruct them to focus on the first Vernier. The evidential standard used to assess perception in long-lasting postdictive effects matches the standard used to demonstrate the effectiveness of visual masking. This means that maintaining the overflow gambit requires non-question-begging reasons to claim that long-lasting postdictive effects involve phenomenal overflow while shorter postdictive effects like visual masking do not.**

Admittedly, cases of phenomenal consciousness without cognitive access are plausible in the (near) absence of attention. And it is indeed in those cases that phenomenal overflow is usually posited (Block, 2007; Lamme, 2003, 2010). **But when no attentional manipulations are involved, and working memory is not otherwise overloaded, phenomenal overflow seems much less plausible. This is why proponents of the overflow thesis like** Lamme (2016) **believe that there is no overflow in cases like visual masking:**

> It is safe to assume invisibility in masking, because there is no conceivable reason that could prevent the subject from reporting his visual percept, had he had one: the subject is sitting there, focussing his full attention to the target location, ready to push the button as soon as he sees the target. The not-seeing can therefore not be attributed to the absence of attention, to a lapse of memory, or to any other cognitive function sitting between a potentially conscious sensation and its report. (Lamme, 2016, p.35)

The same is true in many of the effects reviewed above (Michel & Doerig, 2022). Participants do attend to the relevant stimuli in long-lasting postdictive effects. **They have nothing else to do but to identify the relevant stimuli. Yet, they still fail to identify them and deny seeing them. Given this, we see no theory-independent reason to maintain that they nevertheless consciously experience the relevant stimuli.** If one wants to maintain that there is inaccessible phenomenal consciousness in long-lasting postdiction when all the available indicators suggest unconscious processing instead, the burden of proof is on them.

The second problem with the overflow gambit is that one of its predictions is incompatible with the evidence, at least in the case of relatively fast postdictive effects. Cowan & Greenspahn (1995) conducted an experiment where subjects viewed an apparent motion display. In half of the trials, a target appeared to move continuously from left to right, though it was actually presented first on the left and then on the right with a 100ms delay. On the other half of the trials, the target was shown on the left twice, making it impossible for participants to predict whether apparent motion would occur. The experiment had two conditions. In one condition, Cowan & Greenspahn instructed subjects to respond as fast as possible when they saw the target moving through the midpoint of the display. In the other condition, subjects had to respond when they saw the target reach the end point. The overflow gambit predicts that subjects should respond faster in the end point condition. Indeed, according to this view, subjects should *first* perceive the target at the end point, and *then* perceive the apparent motion only after this. This is not what Cowan & Greenspahn (1995) found. Reaction times were the same in both conditions, suggesting that the whole perceptual episode was released at the same time (See White (2024) for an in-depth discussion). Further experiments of this kind could be carried out with long-lasting postdictive effects, but for now there is at least one postdictive effect in which the overflow gambit is wrong.

A second possible objection to the view that consciousness is slow is that the lag between consciousness and reality should be noticeable. You might wonder how it is possible for consciousness to be that slow, and even think that you have good introspective data indicating otherwise. Take a sport like baseball, for instance. A ball thrown at 100mph (161 km/h) reaches the batter in about 375 milliseconds. If it took 350ms for the batter to construct a conscious percept of the ball, the batter would consciously perceive it far behind its actual location (Nijhawan, 2008). The batter would have to hit the ball when their conscious percept is as of the ball leaving the pitcher's hand. But this obviously contradicts introspective evidence: the batter presumably feels like they are hitting the ball as the ball is approaching towards them. So, one might think that a lag of 350ms between action and conscious perception should be noticeable.

This objection confuses the properties of mental states and the properties *represented* by mental states. A mental state might represent that something is green without itself being green. This distinction applies to temporal properties as well. We need to distinguish between a mental state occurring at a time *t*, and a mental state *representing* events occurring at a time *t* (Dennett & Kinsbourne, 1992). Just because the batter's experience *represents* the ball approaching at time *t* does not mean that the experience itself occurred at *t*. All that is needed to account for the feeling that one hits the ball at the time one sees the ball approaching is an experience that *represents* those two events occurring at the same time. The experience itself might occur at a later time. A temporal gap between an event and an experience of that event need not imply an experience that *represents* the temporal gap—an experience *of* the gap. This view—according to which the temporal character of experience is explained by temporal properties *represented* by mental states instead of being entirely inherited from the temporal relations between mental states—is increasingly gaining in popularity (Dennett & Kinsbourne, 1992; Droege, 2022; Herzog et al., 2016, 2020; Hogendoorn, 2022; Lee, 2014; Prosser, 2018; White, 2023). For our purposes, its main advantage is that it can explain why we do not notice the lag between consciousness and reality despite the fact that consciousness is slow: **our introspective access is limited to the contents represented in experience—which feature no temporal gap.**

Before we continue, let us add two clarifications. First, we do not claim that perception in general is slow. Perception is fast, especially for superordinate categories (e.g. ‘animal’ vs. ‘non-animal’). For instance, when presented with two pictures, only one of which is an animal, subjects can initiate a saccade to the correct image in less than 150ms (Kirchner & Thorpe, 2006). In the same way, subjects can initiate saccades towards faces in just a 100ms (Crouzet et al., 2010). The fact that sports like ping-pong and badminton are even possible is an existence proof that skilled actions can be triggered remarkably fast based on visual cues. But this does not imply that *conscious* perception is fast. Our claim is that those fast responses are likely triggered by unconscious sensory information. **We survey empirical evidence for this claim in the next section.**

Second clarification: above, we discussed the fact that experimental evidence from postdictive effects can only provide us with a *lower bound* for conscious perception. This does not imply that the lower bound is always the same across contexts. We do not claim that conscious perception always takes 450ms, as in the SQM. This might be an extreme case. Consciousness could be faster in other contexts and may even vary within a given visual scene depending on factors such as visual eccentricity or attention (Jovanovic & Mamassian, 2019, 2020a, 2020b). We discuss how the speed of consciousness might be somewhat flexible in the section ‘The emergence of Reality Monitoring’. Our claim is: the fact that visual consciousness is typically slow—and sometimes very slow—reveals something about the kinds of functions it might be involved in. The relative sluggishness of visual consciousness gives us a clue as to what visual consciousness might be for. In particular, it is incompatible with a role in immediate reactions to stimuli.

Sensory Horizons

A key constraint on the usage of perceptual information for the guidance of action is the concept of “sensory horizon”. To a first approximation, an organism’s sensory horizon is the spatial limits of a particular sensory modality—for instance, vision is a long-range sense, whereas the range of haptic sensing is typically limited to bodily space (at least in the absence of tool use; Miller et al., 2023). More precisely, the sensory horizon is the distance over which an agent can detect new information, keeping the agent's location constant (e.g., without moving). As we will see, sensory range is important for function as it allows the *flexible* guidance of action by representing the world beyond the agent. The key insight is that the sensory horizon determines the utility of different timescales of perception. We aim to show that combining the finding that perceptual consciousness is not for immediate reactions with the constraints imposed by the limits of sensory horizons provides a fruitful framework for understanding the evolution and distribution of visual consciousness.

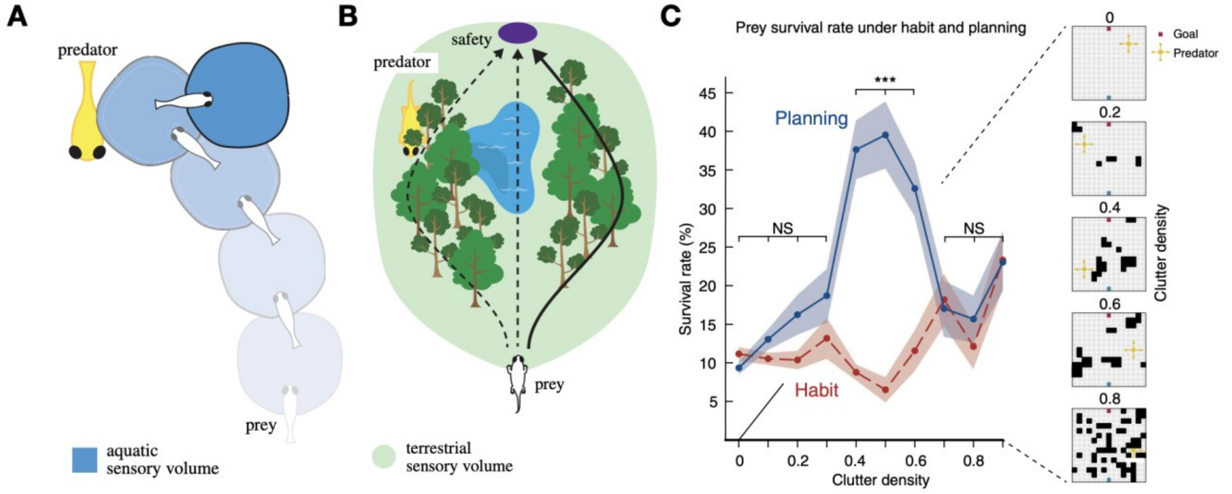

Figure 3. Sensory horizons. A) The aquatic visual sensory volume is limited, and the fish sees the predator just in time to attempt an escape manoeuvre. B). The terrestrial sensory volume is vastly larger owing to a ~100-fold increase in visual range. The enlarged sensory horizon allows the prey to inspect future trajectories to safety while hiding from a predator, affording longer-timescale planning. Source: adapted from MacIver & Finlay (2022) and MacIver (2009). C) Computational modeling of predator–prey interactions occurring within a 'grid world' environment (column on right; prey, blue; predator, yellow) in which the density of occlusions was varied (Mugan & MacIver, 2020). Prey used either habitual or model-based action selection to get to the safety (red square) while being pursued by the predator. The plot shows the survival rate of the prey as a function of the clutter density of the environment for both model-based (blue solid line) and habitual action selection (red dashed line). The benefit of model-based planning peaks when the environment is moderately cluttered. This patchy terrestrial structure, in combination with enhanced visual range, can reveal and hide predators as a function of their movement and creates a

selective benefit for selecting among possible future scenarios. Line indicates the mean ± s.e.m. across randomly generated environments. NS, not significant; $P > 0.05$, ***$P < 0.001$. Source: adapted from Mugan & MacIver (2020).

Consider the following example. For a fish in murky water, the sensory horizon of vision is limited, and any predator encroaching on the fish will be detected relatively late, leaving the only option for escape being a rapid and reflexive defensive maneuver (Bhattacharyya et al., 2017; Catania, 2009; Figure 3A). One could compare this to driving on a foggy road at night (Figure 1B)—visual objects are detected at the last moment, forcing one to rely on fast reflexive processes. In contrast, for a terrestrial animal, the sensory horizon of vision is typically much larger, and predators (or prey) can be sensed remotely, over a distance (Figure 3B). Critically, this sensory (spatial) distance creates the opportunity for slower timescale sensorimotor processes (Hunt et al., 2021; MacIver & Finlay, 2022). If the sensory horizon is small, actions have to be fast and reflexive—akin to the unconscious processes we considered in Section 1. It is only when the sensory horizon is larger that the slower timescale of conscious integration becomes both relevant and useful for the guidance of behavior. In what follows, we explain how the sensory horizon of vision underwent a dramatic transition in evolutionary history.

The water-to-land transition in vertebrate life occurred around 400 million years ago, with two of the largest radiations of land animals (mammals and birds) eventually acquiring around 10-fold larger brains relative to body size compared to fish. As MacIver and colleagues have argued, because natural selection operates over adaptations to an environment, studying what this change in ecosystem encouraged in terms of sensory, motor or cognitive adaptations provides a rich testbed for theories of brain function in general (MacIver & Finlay, 2022). A salient transition was the acquisition of much larger sensory horizons on land.

Because light is rapidly scattered and absorbed in water, the visual range of aquatic organisms is of the order of tens of meters in the best conditions—leading to a rapid fall-off in detection sensitivity for ecologically relevant objects. This can be measured by the "beam attenuation length", defined as the distance over which a parallel beam of light of a given wavelength loses 63% of its light. For bluish wavelengths, this distance can be up to 24m in clear ocean water but reduces to 2-7m in coastal or fresh water. Because of this, the “aquatic sensory volume” for objects ecologically relevant for fish such as predators is just around one or two body lengths away (any further away, and detection becomes limited by the watery environment) (MacIver et al., 2017; Nilsson et al., 2014). Escape responses need to be very fast, and any delay incurred between registering the presence of a predator and the subsequent escape response can be the difference between life and death (Figure 3A).

Once an organism is seeing on land however, the picture is literally very different (Figure 3B). As mentioned by MacIver & Finlay (2022), the beam attenuation length for similar wavelengths in air is over 25,000m, with the longest line-of-sight photograph taken from a mountain in Spain to a mountain in France being over a distance of 443km! For this reason, a terrestrial sensory volume can be approximately a million-fold larger than the aquatic sensory volume due to the ~100-fold increase in visual range[5]. In such volumes, predators and prey can be registered at a distance, and slower mental processes can be leveraged to avoid and pursue them, respectively.

Qualitative differences in conscious control

What might those slower mental processes be? A fruitful perspective, grounded in both animal learning theory and reinforcement learning, is that different “controllers” can drive behavior (Daw & O’Doherty, 2014; Dolan & Dayan, 2013; Hunt et al., 2021). A *Pavlovian* controller enables reactive responses to biologically significant events by associative learning (classical conditioning). These responses are rapid, stereotyped and reflexive. A *habitual* controller enables **more flexible learning than afforded by Pavlovian control**, by reinforcing **stimulus-response linkages** that previously led to reward (obeying Thorndike’s “law of effect”; Thorndike, 1911). However, the habitual (or “model-free”) controller is still relatively inflexible, in that if new information comes to light that makes it unwise to pursue a previously rewarded action, it is unable to make use of this information. As noted

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[5] Sensory horizons are constrained by the properties of both the organism’s sensory apparatus and the environment. Eye socket volume has substantially increased in terrestrial animals compared to fish, presumably in order to benefit from increased sensory volume (MacIver et al., 2017; though see Nilsson, 2017). Intriguingly, measurements of eye sockets, combined with evolutionary simulations, show that eyes nearly tripled in size just before vertebrates began living on land. The idea is that, having moved into shallower waters, larger eye sockets moved dorsally to enable aquatic-dwelling tetrapods such as *Tiktaalik* to begin benefitting from terrestrial visual range.

by LeDoux (2023), model-free processes are rigid because “they are controlled by the past” (p.163). This is famously shown in studies of devaluation—if a rat is trained that a lever gives it a food reward, but this food is then devalued (by feeding to satiety, or making it subjectively aversive), then the habitual controller will not “know” the food is now not wanted, and the lever may continue to be pressed (Adams & Dickinson, 1981; Dickinson, 1985; this over-expression of habitual responding is a canonical model of addiction, Everitt et al., 2008).

Many of these simpler forms of learning and behavioral control may proceed unconsciously. A well-studied example is provided by fear conditioning. Studies in animal models have described subcortical pathways that elicit rapid (reflexive or Pavlovian) defensive responses to threatening stimuli (LeDoux & Pine, 2016). In humans, similar pathways can be activated by subliminal stimuli (Morris et al., 1998; Whalen et al., 1998) and may support affective blindsight (De Gelder et al., 1999; Tamietto & De Gelder, 2010), leading to the potential for nonconscious forms of threat learning (Hamm, 2003; Raio et al., 2012; Taschereau-Dumouchel et al., 2018). Subliminal stimuli may also elicit positive motivational responses accompanied by heightened activation in the ventral striatum, a key target of midbrain dopaminergic projections (Pessiglione et al., 2008)[6]. Some of these simple forms of learning also do not even require a brain: associative learning is found in animals such as jellyfish (Bielecki et al., 2023), learning can occur independently of inputs from the brain in spinalized rats (Grau et al., 1998; Liu et al., 2005), and even trace conditioning can be achieved in decerebrate animals, such as decerebrate guinea pigs (Kotani et al., 2003). Finally, a core psychological feature of habits is that they may proceed independently of conscious control processes (Wood & Rünger, 2016). In summary, “model-free” learning and behavioral control can occur unconsciously.

In contrast to Pavlovian and habitual control, *model-based* or *goal-directed* control chimes with our usual conception of what it means to consciously control an action. We know things about our environment, and can use this information to reach our goal. Briefly, the current state of the art in

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[6] **Some subliminal effects on behaviour have been subject to high-profile replication failure, notably social priming studies** (Nosek et al., 2022)**. Our focus here is on the psychophysics of unconscious influences on immediate action which have a firmer grounding in neuroscience** (Mudrik & Deouell, 2022)**. However, these subtle effects remain controversial and are in need of further replication in light of methodological developments** (Newell & Shanks, 2023; Stein et al., 2024)**.**

computational neuroscience proposes that the brain maintains and updates an internal model of the world, and uses this to rapidly compute how hypothetical actions in the world would or would not lead to reward (Doll et al., 2012; Hunt et al., 2021; Mattar & Lengyel, 2022). Model-based control is thought to depend on inferring transitions through (sensory) states. For instance, a plan for how to obtain coffee may include transitioning between my office, the street, and the coffee shop, prior to obtaining the coffee. Computing transitions between states is flexible—because if the route to my favorite coffee shop is blocked, I can plan around it (in the form of a different set of state transitions, such as walking around the block). There are many candidate algorithms for planning which are outside the scope of this article. However, core to all planning algorithms is an *internal model* of the environment: an agent's representation of how the environment is affected by the agent's actions, allowing counterfactual computations of the form "what would happen if I do X?" (Battaglia et al., 2013; Craik, 1943; Mattar & Lengyel, 2022; McNamee & Wolpert, 2019).

Notably, this "planning" process is distinct from the effortful thought characteristic of conscious deliberative planning (although this would also be an example of higher-level model-based control). Instead, the online "planning" that is achieved through rapid simulation of future sensory states is intuitive and (relatively) fast. A focus of current neuroscientific research on online planning is on replay (or "preplay"; Foster, 2017; Hunt et al., 2021; Mattar & Daw, 2018; Singer et al., 2013). Here, neural representations of different points in an internal model of the environment (such as positions in a maze or elements of a connected graph) are sequentially activated prior to acting. Neural replay might support internal "searches" through possible future paths that the agent could take, and has been documented in both rodents and humans (Dragoi & Tonegawa, 2011; Gupta et al., 2010; Liu et al., 2019; Ólafsdóttir et al., 2015) with a time lag of around 20-50ms between sequentially activated states (Kay et al., 2020; Liu et al., 2021). The entire replayed sequence is compressed into a time window of <200ms, consistent with online planning taking up time—but not that much time (Hunt et al., 2021; Liu et al., 2019). For instance, Kay et al. (2020) found neural activity in the rodent hippocampus encoding two possible future scenarios (two upcoming maze paths) in constant alternation at 8 Hz: one scenario per 125ms cycle. Importantly, this fast replay activity might also involve sensory representations when relevant (Doll et al., 2015; Kurth-Nelson et al., 2016; Y. Liu et al., 2019; Schwartenbeck et al., 2023; Wittkuhn et al., 2024).

It is likely that the use of internal models to navigate external environments (and associated neural replay) occurs routinely in the background, in the absence of conscious awareness (see the “Reality monitoring” section below; Wittkuhn et al. 2024). However, there is nevertheless a general assumption that switching from habitual to model-based control involves conscious experience of the relevant sensory information—an experience of what the internal model represents (Butlin, 2020; Frith, 2021; Pennartz, 2018). For instance, the global workspace model of consciousness proposes that consciousness is associated with the flexible usage of perceptual information in a global workspace, where perceptual states can be flexibly mapped onto a variety of possible actions (Baars, 1988; Dehaene & Naccache, 2001). Some of the clearest evidence for this link comes from the process-dissociation procedure (PDP), in which model-based and habitual responses are placed in opposition to each other and their influences on subjects’ behavior measured (Jacoby, 1991). In the classic version of this paradigm, subjects are provided with a prime stimulus (e.g. referee) and asked to complete a word stem (e.g. ref……) with any word that comes to mind, *except* the prime word. When the prime word is visible / conscious, then this is straightforward, and subjects are able to flexibly refrain from completing the stem with the prime, exhibiting goal-directed control (in which the goal is “don’t use the prime”). But when the prime is subliminal, the frequency of wordstems completed by the prime is higher than expected by chance—showing inflexible, habitual responding (See also the ‘Perruchet effect’ for a similar effect; Perruchet, 1985).

Similar dissociations have been identified in blindsight—a phenomenon caused by lesions in primary visual cortex, in which patients can perform visual tasks in the absence of reported conscious visual experiences (Weiskrantz, 2009). Persaud & Cowey (2008) presented blindsight patient GY with a grating stimulus in either the upper or lower quadrant of his visual field. Crucially, the required response was to say the opposite of its location (e.g. reporting “Down” if the stimulus was in the upper quadrant). GY had no trouble following exclusion instructions in his normal, sighted field, but tended to erroneously respond with the real location when the grating appeared in his blind field. Strikingly, this pattern of erroneous responding actually *increased* as the grating contrast was increased—

suggesting that the impact of blindfield stimuli on behavior is mediated through inflexible, habitual responses rather than flexible model-based control. This same logic has been used to argue for a qualitative dissociation between unconscious and conscious usage of visual information in macaque monkeys (Ben-Haim et al., 2021). In summary, there is growing evidence that switching to model-based control requires consciousness of the relevant sensory information (see also Tsushima et al., 2006).

Conversely, the online control of action can be guided by largely unconscious sensory information. A famous example of this is the distinction between dorsal and ventral visual streams (Goodale & Milner, 2018; Milner & Goodale, 2006, 1993). Damage to the ventral visual stream in patient DF led to impairments in conscious shape perception, but left the online guidance of action intact (Goodale et al., 1991). Similar dissociations between conscious perception and action guidance have been observed in healthy observers. For instance, in the hollow mask illusion, prior knowledge of faces creates a powerful visual illusion that a concave mask is a normal convex 3D face. And yet when observers are asked to "flick" targets on the surface of the mask, the flicking movements are directed at the real, not illusory locations of the targets (Króliczak et al., 2006; for dissociations using other illusions, see Aglioti et al., 1995; Chen et al., 2015; Ganel et al., 2008; Ozana & Ganel, 2020). Dissociations have also been identified between online eye movements and explicit perceptual reports (e.g., Wong & Mack, 1981; see Spering & Carrasco, 2015 for a review). In general, eye movements provide a fast orienting system to stimuli which are yet to reach conscious perception (Crouzet et al., 2010; Kirchner & Thorpe, 2006). Finally, the existence of masked priming effects on behavior, discussed above, is a prima facie example of short-timescale unconscious influences on action (Vorberg et al., 2003).

As Goodale & Milner (2013) write, "...the dorsal (action) stream works in real time and stores the required visuomotor coordinates only for a very brief period... The ventral (perception) stream, on the other hand, is designed to operate over a much longer time scale." (p. 81-82). This longer time scale enables the ventral stream to create the mental furniture that allows us to think about the world and plan our actions.

Computational perspectives on the timescale for consciousness and control

As noted above, model-based planning requires an internal model of the world in which to plan. This can be a model retrieved from memory—for instance, I can "install" a model of my home office, and consider whether the desk I am thinking of buying would fit into that space. In humans, planning is often oriented towards **goals that are relatively distant in the future**: for instance, we take a shopping bag when leaving the house because we plan to pick up groceries (Suddendorf et al., 2022). But it is arguably much more common (particularly in the evolutionary history of land animals) to need to plan in the here-and-now**, for the immediate future**[7]. I see a predator moving behind some trees, and I need to rapidly—in a few tens of milliseconds—figure out an escape route (Figure 3B). It is easy to see that an agent with a large sensory horizon has an advantage here—because a larger (albeit still partially observable) state space is immediately available to it.

The problem is that the here-and-now is always changing—the predator is here *now,* but it wasn't a few seconds ago. There is thus a tension between engaging in model-based simulation within a stable model of the world, and losing our dynamic coupling with a constantly changing environment. An attractive proposal is that the temporal window of integration of conscious experience provides this model of the world, allowing us to imagine and plan in the immediately remembered present—what the world was like in the past 300-500ms. This window of integration provides a stable platform for imagination and simulation, while also remaining sensitive to important changes in the environment. This architecture could be further finessed by making the window of integration itself sensitive to important environmental changes and/or to natural "boundaries" between events—a point we come back to in the next section (J. M. Zacks, 2020).

This view is compatible with (but does not assume) specific predictive processing views of brain function (Clark, 2013; Hohwy, 2013). Predictive processing holds that perception is realized by a process of inference on the causes of sensation, mediated by a continual interplay between background expectations and beliefs and current sensory inputs. When the internal model and the sensory input fail to match, a 'prediction error' ensues, and our hypotheses are subtly altered to better approximate

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[7] It is debatable whether the heavy-duty term "planning" remains appropriate here—but we follow its conventional usage in the reinforcement learning literature on model-based control. We are focused on a particular type of model-based planning algorithm that conditions future possibilities for action on the current (inferred) state of the agent (Mattar & Daw, 2022), underpinning percept-guided behavior.

reality. Predictive processing accounts themselves do not distinguish between unconscious and conscious perception. However, extensions of this framework suggest that a key property of **the sub-personal inferences leading to conscious perception** is identifying a sufficiently reliable world model for use in the service of mental simulation and planning (Fleming, 2020; Hohwy, 2013). Hohwy explicitly ties conscious perception to “active” aspects of inference (Parr et al., 2022), suggesting that the brain is engaged in a dynamic interplay in which a model of the world is selected and “fixed” for subsequent planning, before a new model is built, and so on. It is intriguing to speculate that the timescale of this alternation between perceptual and active inference is similar to that identified for the window of conscious perception, around 300-500ms. Recent discoveries in animals also indicate that the neural correlates of current versus hypothetical experience can alternate within a theta cycle (Kay et al., 2020).

In summary, in this section we have argued that conscious vision is closely associated with the capacity for model-based planning, and that the timescale of conscious perception allows for the processes of (covert) active inference and mental simulation that are thought to subserve model-based behavior. In contrast, a wealth of evidence supports the view that online action control can be achieved unconsciously.

One important clarification before we close this section. In what follows we will argue that the expanded sensory horizons characteristic of terrestrial animals underpin the utility of conscious perception and model-based control. This does not mean, however, that we are only conscious of objects that are at a sensory distance. Engaging in perceptual inferences over longer timescales becomes advantageous for larger sensory horizons. But once slower conscious perception is acquired, it can incorporate any sensory input into its world model—including inputs from the agent’s own body, and peripersonal space. On this view, while online action control may be achieved unconsciously, we can still be conscious of our unconsciously-guided actions.

Sensory horizons and consciousness

Returning to our evolutionary analysis, in recent computational studies of how organisms escape from predators, Mugan & MacIver (2020) have shown that in reduced sensory volumes typical of an aquatic environment, there is simply no time for planning, and instead fish escape from predators by relying on habitual, model-free responses. Such rapid control of online action, pervasive prior to the water-to-land transition, does not require consciousness. In contrast, in terrestrial conditions, with much greater visual range, there is (some) time for planning—and such planning significantly boosts predator avoidance especially in cluttered environments where the predator might disappear behind occluders, and then appear again. As discussed in the previous section, the timescale of human consciousness is consistent with a central role in fixing a perceptual model of the world that is then used for internal simulation and planning (we will argue in a subsequent section on reality monitoring that the simulations themselves are largely unconscious).

This argument leads naturally to the view that organisms that evolved prior to the water-to-land transition, and which predominantly rely on small aquatic motor volumes, do not need either model-based control or conscious visual experience. If it were possible to do the kind of visual psychophysics we describe in Section 1 on fish, then we would predict that the temporal window of integration of postdictive effects on discrimination would scale with the sensory horizon. In other words, aquatic organisms would not be susceptible to long-lasting postdictive illusions, because they have no need to integrate sensory information over ~3-500ms to enable a stable world model in which to control their actions. They are rooted in the present, constrained by small sensorimotor volumes.

Most aquatic animals are not part of the "Buena Vista Sensing Club" (MacIver, 2009), and therefore might not have developed model-based planning. There are exceptions to this general view. Most notably, land mammals that have returned to the water and use long-range echolocation, such as dolphins and whales, may retain the benefits of larger sensory horizons for planning (MacIver & Finlay, 2022). Another key variable influencing the benefits of model-based planning in simulation is the presence of occlusions, making clues to adversaries cryptic. Terrestrial habitats such as savannahs provide selective benefits to planning over large sensory horizons (Mugan & MacIver, 2020). But there may be aquatic species and environments for whom similar benefits emerge. **The cluttered terrestrial-like environments of coral reefs and tide pools may be unusually rich environments for the evolution of model-based visual cognition. For instance, collaborative hunting where fish indicate the location of prey hiding in the reef has been documented in bluefin trevally-**

krait teams (Somaweera et al., 2023) **and grouper-moray eel teams** (Vail et al., 2013)**, and experiments indicate that tide-pool dwelling gobis can rapidly form cognitive maps of shallow waters to enable one-shot learning of tide pool location when jumping from one to another** (Aronson, 1971)**. The octopus is also unusual in developing sophisticated deception strategies to deceive predators and conspecific competitors over an intermediate visual range** (Godfrey-Smith, 2024)**.** Finally, as noted in footnote 5, species which are aquatic dwelling but have the ability to take advantage of terrestrial visual range may have developed model-based control and conscious **visual** experience. These species may include extinct transitional tetrapods at the water-to-land transition (such as *Tiktaalik*) and/or the archerfish which hunts insects above the water's surface using water jets (Volotsky et al., 2024).

Because consciousness (as measured in humans, which is the natural starting point; Bayne et al., 2024) is associated with slow temporal windows of integration (Section 1), the evolutionary pressures to create such states would in general only manifest for larger sensory horizons. In contrast, organisms with restricted sensory horizons may only require model-free control, acting on the sensory present, rather than the remembered present. We have argued that these aspects of control are unconscious in humans. It is parsimonious to think that they would also be unconscious in other animals[8]. Aquatic

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[8] Zacks & Jablonka (2023) also propose that simpler forms of stimulus-response learning (limited associative learning) may proceed unconsciously. However they diverge from our account in suggesting that consciousness emerged along with "unlimited" (model-free) associative learning (Birch et al., 2020; Ginsburg et al., 2019) within a global workspace, prior to the emergence of the capability for model-based control. Another theory from which we diverge is Merker's view (Merker, 2007; see also Barron & Klein, 2016), according to which **the function of consciousness is to integrate interoceptive and exteroceptive signals in midbrain structures for target selection, action selection, and the ranking of needs (the 'selection triangle'). We converge on the idea that consciousness involves building a model for determining "what to do next" (Merker, 2007, p.71), but Merker's focus is on target selection for immediate action rather than model-based planning. This is in tension with evidence of target selection without conscious perception in blindsight (Weiskrantz, 2009) and dissociations between conscious vision and targeted eye movements** (Carrasco & Spering, 2024; Spering & Carrasco, 2015) **or hand movements** (Bridgeman, 1986; Goodale & Milner, 2018)**. Alongside evidence that conscious vision is slow, this suggests that vision-based target selection for immediate action does not require consciousness. Like other 'local theories' of consciousness (e.g. local recurrence theory), Merker's view also faces difficulties accounting for the postdictive effects mentioned above** (Michel & Doerig, 2022)**. Nevertheless, Merker's view could align with ours if integration occurs in two stages: an unconscious stage driving immediate reactions and a second stage enabling model-based planning.**

animals with restricted sensorimotor volumes therefore have no evolutionary need for conscious visual states. **This might especially be the case for animals in the 'pelagic zone'—away from the shores or coral reefs—who do not live in cluttered environments.** Instead, we propose that a **major discontinuity** in the evolution of visual consciousness occurred at the water-to-land transition.

The emergence of reality monitoring

So far we have given a descriptive account that links two key empirical features of human visual consciousness: its slowness, and its role in model-based planning. We propose that the co-evolution of both features is a response to the need to plan over larger sensory horizons. In this last section, we offer an argument that seeks to explain, rather than merely describe, this co-evolution of model-based planning and consciousness. In particular, we suggest that conscious vision might have evolved as a response to two computational problems arising from the water-to-land transition: the problem of reality monitoring, and what we call 'Hamlet's problem in perception'. We discuss these two problems in turn.

Reality monitoring

Larger sensory horizons afford time to use the perceptual system both online (for building a model of the world) and offline (for simulation, planning and imagination). This presents a deep computational problem. For conscious perception to be a useful basis for planning and simulation, the percept should not itself be changed by the simulation[9]. If I imagine (simulate) an aggressive dog jumping over the fence next to me, I should not now perceive the dog jumping over the fence. The simulation allows me to realize it's not a good idea to stand near the fence. It should not lead me to start running away from an (hallucinated) dog. A rational agent needs to keep apart its representation of the world, and its simulations or (active) inference through this representation of the world. This is known as "reality monitoring" (Dijkstra et al., 2022) .

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[9] The values of states in the world model *will* be changed by simulation—this is what the simulation is for (Mattar & Daw, 2018). But the model itself should not be changed.

One solution to perceptual reality monitoring (PRM) is to develop a system of higher-order representations indicating which first-order representations are reliable reflections of the world as it is now (Cortese & Kawato, 2024; Lau, 2019, 2022; Michel, Forthcoming). Under the PRM theory of consciousness, conscious representations are the result of the process of selecting reliable perceptual signals for use in the rational (model-based) control of action (see also Gershman, 2019). The machinery for reality monitoring tags perceptual signals as reflecting the outside world as it is now—flagging the present (Droege, 2022; Gregory, 1996). In other words, conscious experience is the platform on which further cognition and planning is built—it cannot itself be changed by cognitive operations.

An empirical prediction of this view is that if the current world model is conscious via the operation of PRM, then the accompanying internal simulations should be largely unconscious. This is plausible—it seems unlikely that the rapid neural signatures of replay discussed above hypothesized to underpin model-based planning are consciously experienced. After all, these bursts of internal simulation are compressed in time, with individual trajectories through future possible states (for instance, possible routes through a maze, or courses of action to avoid a predator; Figure 3B) typically being completed in less than 200ms (Kay et al., 2020; Y. Liu et al., 2019). If we experienced such replay bursts, then they would constantly be in competition with perception itself. Consistent with this view, a recent study using fMRI in humans suggest that replay of previous visual experiences serves to update task representations, but is independent of conscious experience (Wittkuhn et al., 2024). There is also evidence that predictions about future visual stimuli are encoded in the visual cortex (Ekman et al., 2023; Kok et al., 2017; Kurth-Nelson et al., 2015; Turner et al., 2023). Yet, those predictions are not consciously experienced, or at least not always. Otherwise one wouldn't be able to experience the *omission* of a stimulus from a predictable sequence (Li et al., 2024). This hypothesis is ripe for future empirical investigation.

One obvious counterexample is conscious visual imagery, which is often used to motivate the need for reality monitoring (Dijkstra et al., 2022). **According to our account, visual imagery occurs consciously as a result of being tagged by the reality monitor as reliably representing the**

world. This predicts that conscious mental imagery does not wear its unreality on its sleeve, so to speak. Instead, it has some level of 'assertoric force' (Siegel & Sillins, 2015)**, perhaps proportional to its degree of vividness. It is first taken at face value, and this impression is then overridden post-facto based on non-perceptual signals (reviewed in Dijkstra et al. 2022).** This hypothesis is supported by studies showing that external and internal (imagined) signals are intermixed during near-threshold perception, with their combined strength determining judgments of reality and confidence (Dijkstra et al., 2021, 2024; Dijkstra & Fleming, 2023). **Hyperphantasia (which is characterized by vivid conscious mental imagery) also seems associated with the experience of hallucinations** (Oertel et al., 2009)**, thus indicating that those who experience more vivid imagery tend to confuse it with genuine perceptual representations.** This view would also suggest that far from being dysfunctional, aphantasics (individuals who do not experience mental imagery) may in fact be optimal, **when considered** from a reality monitoring standpoint—consistent with their ability to perform well in tasks requiring offline visual processing (Keogh et al., 2021; Pounder et al., 2022). **Of course, this is not to say that conscious visual imagery does not play a functional role. It undoubtedly does (just think of using visual imagery to determine whether a couch will fit through a door). But the extent to which this functional role depends on visual imagery occurring consciously (as opposed to unconsciously) is an open question, especially given emerging evidence suggesting functional unconscious visual imagery in aphantasia** (Michel et al., 2025; Nanay, 2021; Pounder et al., 2022; Weber et al., 2024)**.**

In sum, the capacity for model-based planning promotes the development of reality monitoring capacities allowing organisms to distinguish, among all mental representations, which representations should impact one's beliefs about what is happening in the world right now. Unconscious mental models do not compel us to believe that the world is as they represent it to be right now. Conscious experiences do. This epistemic contrast is explained if conscious representations are those selected by a reality monitoring system—an account that is also consistent with a long tradition in philosophy of mind and epistemology positing an essential tie between conscious perceptual experiences and perceptual beliefs (Armstrong, 1968; Byrne, 2016; Glüer, 2009; Lyons, 2009; Smithies, 2019).

Hamlet's problem in perception

Fodor (1987) noted that cognitive systems face Hamlet's problem—a version of the frame problem in artificial intelligence:

> Suppose that, in pursuit of rational belief fixation, you undertake to subject whichever hypotheses might reasonably be true to scrutiny in light of whatever evidence might reasonably be relevant. You then have the problem of how to determine when demands of reason have been satisfied. You have, that is to say, Hamlet's problem: How to tell when to stop thinking. (Fodor, 1987, p.26)

Thinking more and exploring relevant options is generally beneficial. But thinking has to end at some point. How to know when to stop thinking (for instance, planning) is Hamlet's problem. A similar problem arises in the case of perception. Indeed, when engaged in model-based control, the timescales for planning and perception need to be considered jointly. In order to act in a timely manner, one needs to curtail unnecessary planning; in order to plan in a timely manner, one needs to curtail unnecessary evidence gathering when forming an internal model of the environment[10].

Suppose that an organism has a limited sensory horizon, like that of an electric fish (Snyder et al., 2007). With a short sensory horizon, the environment itself imposes a strict limit to how long the organism can afford to wait before reaching a decision and initiating a response. Organisms with short sensory horizons are not free to flexibly determine how much sensory evidence they should get. But animals with large sensory horizons have that luxury: with more time comes the freedom to wait for more sensory evidence to build more reliable internal models. Animals with large sensory horizons have also developed mechanisms to flexibly control evidence search—the most obvious of which are the evolution of the neck in early tetrapods (Carstens, 2023), and a drastically increased capacity for

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[10] One might argue that it would be more adaptive for a system to engage in a continuous and dynamic process of perception and planning, with no discrete switches between the two. Further theoretical work will be required to understand whether and how the temporal windowing of perception implied by postdictive effects in perception is adaptive for the control of behavior. One possible advantage is that a slower temporal oscillation of perception and (active) inference allows for the comparison and selection among distinct counterfactual action plans, all conditioned on the same (comparable) world model (Hohwy, 2019; Kay et al., 2020).

targeted eye movements (Land, 2015). **Not only that, but long sensory horizons also afford time to integrate sensory information with background beliefs: animals can now take time to *think* about what they see before acting, potentially leading them to decide whether or not to gather more evidence.**

Since the environment itself does not dictate when the search for evidence should end, and since organisms following the water-to-land transition have more time and more flexible means for scanning large sensory horizons, they face Hamlet's problem in perception: how to know when to stop searching and accumulating sensory evidence. We argued above that humans sometimes integrate evidence during a 400ms window before reaching a conscious perceptual decision. Hamlet's problem in perception is the problem of determining how long this window should be.

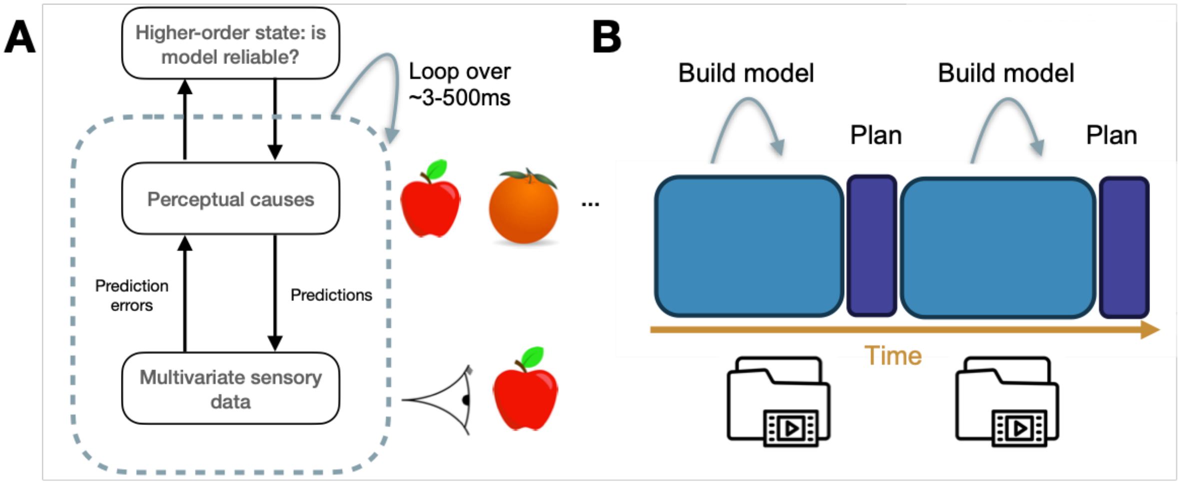

Figure 4. Reality monitoring and windows of integration. A) Higher-order states in generative models of perception can provide information about the reliability or precision of a world model (Fleming, 2020). B). The timescale of conscious perception allows a reliable world model to be built over a given time window of integration, and then be used for offline simulation and planning. Source: adapted from Herzog et al. (2020).

We suggest that a metacognitive mechanism monitoring the reliability of one's own perceptual states—such as the reality monitoring system hypothesized above—could be repurposed for flexibly opening and closing windows of sensory integration. As a first approximation, this mechanism could simply operate by tracking the signal-to-noise ratio of sensory representations, essentially applying the principles of signal detection theory (Green & Swets, 1966) on the sensory representations themselves (Lau, 2022; Morales, 2024). Whenever a signal is judged reliable enough, the monitoring system closes the window of sensory integration, thereby settling on a given interpretation of the way the world is over a given time window (Figure 4A).

The view that a higher-order mechanism is partly responsible for flexibly closing windows of sensory integration makes a central prediction: evidence accumulation in animals with large sensory horizons should be (at least in part) under metacognitive control.

There is preliminary evidence to confirm this prediction. For starters, information-seeking behavior seems guided by metacognitive states. Desender et al. (2018) designed a visual task where accuracy was matched across conditions that differed in confidence levels. By giving subjects the opportunity to take a second look at the evidence, they showed that information seeking is guided by confidence, and not just accuracy (see also Schulz et al., 2023). Another dissociation between performance accuracy and metacognition in information seeking behavior is found in blindsight monkeys. Kato et al. (2021) trained blindsight monkeys to search for a hidden target in their blind visual field. Although monkeys were able to perform a saccade right on target in the blind field, they then kept looking for it. A speculative interpretation could be that since monkeys were not metacognitively sensitive to the success of their visual search in the blind field, they did not properly terminate the visual search.

Evidence accumulation itself might also be partly under metacognitive control. Balsdon et al. (2020) designed a task in which participants could stop evidence accumulation whenever they wanted to reach a certain level of performance. They showed that the capacity to appropriately set a bound on evidence accumulation was strongly related to metacognitive efficiency. This prompted Balsdon et al. (2020) to suggest that “confidence decisions are not the result of some inert post-decisional process, but reflect an online control process that moderates sensory evidence accumulation” (p.7). According to this model, confidence is computed before the decision is fully reached, as seems plausible given recent results indicating that confidence signals are computed relatively early in the prefrontal cortex

(Brosnan et al., 2020; Gherman & Philiastides, 2018; Xue et al., 2023). Similar models have been proposed in the case of value-based decision making (Bénon et al., 2024; Lee et al., 2023), and this work is also in line with other well-established online modulations of visual processing by prefrontal cortex (e.g., Duan et al., 2024; Kar & DiCarlo, 2021; Yan et al., 2023).

The fact that evidence gathering is partly[11] under metacognitive control in humans does not mean that information-seeking behavior in conditions of uncertainty is evidence of metacognition, or that metacognition is the only way to set a decision boundary for evidence accumulation. What we tried to show instead is that evidence accumulation is under partial metacognitive control, in line with the view that a metacognitive mechanism helps solve Hamlet's problem in perception.

Temporal windows of integration

The computational solutions to reality monitoring and Hamlet's problem sketched above are two sides of the same coin. Terrestrial animals with long-range sensory horizons need to build a reliable model of the world in which to plan, but not dawdle over doing so—otherwise they risk becoming dynamically uncoupled from their environment, and rooted in the past. This is a tradeoff with reliability at its core. Too little sensory evidence accumulation, and the internal model will be too impoverished to enable useful model-based control. But too much evidence accumulation and the model will never get built in the first place. We suggest that metacognitive signals tracking the reliability of a first-order world model provide a natural computational basis for managing this tradeoff. Once one's confidence is increased to a particular threshold, an internal model can be "fixed" and used for rapid offline simulation. The temporal window of conscious experience is the result of this delicate balance achieved from simultaneously solving perceptual reality monitoring and Hamlet's problem.

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[11] To be clear, we do not claim that all information-seeking behavior is evidence of metacognition or that evidence accumulation is always guided by metacognitive states. That would be wrong (see Edwards-Lowe et al. (2024) for an empirical dissociation). To see why, suppose that a robot with a camera tracks rectangular objects by attributing a probability of being rectangular to objects in its environment. One could implement a simple 'information-seeking' rule in this robot such that whenever a stimulus is ambiguous, the robot moves its camera around the object to get multiple angles. This rule can be implemented without metacognitive representations. For instance, one could design the robot such that representing an object with a 50% chance of being rectangular automatically triggers the evidence gathering process until the probability is sufficiently high or sufficiently low.

Our view makes novel empirical predictions. First, it predicts a link between metacognitive confidence and the timing of bursts of neural replay (assuming that the latter provides a neural substrate for online planning)—with replay only occurring only once a subject is confident enough[12]. This view also predicts a link between reality monitoring and confidence, with recent studies of the interplay between perception and imagination suggesting that judgments of reality are tightly coupled to fluctuations in confidence (Dijkstra et al., 2024). Another prediction is that reality monitoring capacities should only be found in animals with larger sensory horizons and capable of internal simulation. Finally, it predicts that the window of integration of conscious experience discussed above should be in part governed by the reliability of sensory signals—with longer windows of integration being adopted in lower-reliability environments.

Consciousness and reality monitoring

The view that consciousness emerges with a reality monitoring system, as described above, has significant explanatory benefits. Support for this 'perceptual reality monitoring theory of consciousness' (PRM) comes from an inference to the best explanation (Lau, 2022; Michel, Forthcoming). Let us finish by listing some of the explanatory benefits that are most salient given the hypothesis developed in this article.

First, we often take the remarkable coherence of our conscious experiences for granted. But given the discussion above, one would not necessarily expect this from considering what sensory areas represent at any given time. Again, it is striking that our conscious experiences remain coherent despite the fact that several sensory representations coexist at any given moment, fulfilling multiple roles for perception and cognition, from the maintenance of sensory information over time to sensory activity involved in learning, planning, and predicting (Ekman et al., 2023; Kay et al., 2020; Kok et al., 2017; Liu et al., 2019; Wittkuhn et al., 2022). For instance, King & Wyart (2021) showed that images presented in a rapid visual stream can be robustly decoded from brain activity up to one second after

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[12] Note here the relevant confidence is in one's entire first-order representation(s) of the environment rather than confidence in a particular aspect of the representation, such as an individual stimulus element —in simple psychophysics experiments these two types of confidence are often correlated.

stimulus presentation. Yet, subjects presumably feel like they are experiencing a single image at a time—**perhaps together with a sense of the relations between this image and the previous image(s)**. There is an apparent tension between long-lasting parallel encoding and the apparently serial nature of the contents of experience. A recent focus in neuroscience of identifying neural activity related to a state other than the agent's current state is prima facie evidence that the brain contains a multitude of internal processes that do not correspond to our current experience (Liu et al., 2021; Mattar & Lengyel, 2022). If conscious experiences are constituted by representations selected and tagged as reliably reflecting the world as it is *now* by a reality monitoring mechanism, this explains why our conscious visual experiences are coherent, instead of being meaningless jumbles of represented features.

A second advantage of the account is that it explains the unique epistemic profile of conscious representations. For our purposes, there are three relevant epistemic features that seem to separate conscious perceptual states from unconscious perceptual states. The first is the apparent connection between conscious experiences and belief justification. Conscious perceptual experiences justify perceptual beliefs—for instance, a conscious experience of an apple justifies the belief that there's an apple. A common view in epistemology is that unconscious representations do not likewise justify beliefs (Byrne, 2016; Huemer, 2006; Smithies, 2019). This epistemic asymmetry is explained if conscious representations are precisely those that are selected by a reality monitoring mechanism to have a direct impact on belief formation. The same hypothesis accounts for the second epistemic feature: conscious experiences lead to *stubborn* tendencies to believe (Lau, 2022). As noted by Armstrong (1968) when discussing this idea:

> If a thing looks to be a certain way, although we know on independent grounds that it cannot actually be that way, we may still half-believe, or be inclined to believe, that it is as it looks. And this inclination to believe can persist even when we clearly recognize that the inclination is irrational. (Armstrong, 1968, p.239)

By contrast, unconscious perceptual states do not seem to result in a stubborn propensity to believe—for instance, blindsight subjects never insist that the world is as their unconscious states represent it to be (Weiskrantz, 2009). This contrast is explained if a function of a reality monitoring system is to select which perceptual states should impact our beliefs (partly for the purpose of model-based planning). A third relevant epistemic feature of consciousness is that conscious perceptual decisions are available for explicit metacognitive evaluation, whereas unconscious perceptual decisions are not (Persaud et al., 2007, 2011; Vlassova et al., 2014). That is, explicit metacognition seems *consciousness-selective* (See Michel (2023) for a review). This feature is explained if the representations selected by the reality monitor also become available for metacognition, which can then re-use reality monitoring capacities (i.e. assessing signal-to-noise ratio) for explicit confidence ratings.

The perceptual reality monitoring theory, coupled with the account developed here, also provides a principled explanation for why vision used in the online guidance of action is not conscious—as supported by the influential two visual stream hypothesis (Kozuch, 2023; Milner & Goodale, 2006; Wu, 2013). Vision for action is unconscious because it needs to be fast. The visual system responsible for vision for action—the dorsal visual stream—does not face the reality monitoring problem and Hamlet's problem, which the reality monitoring system evolved to solve. The reality monitoring system is not meant to assess the reliability of visual representations in the dorsal visual stream—which is why those representations are unconscious.

This is just a relevant subset of the explanatory benefits of the hypothesis that consciousness is linked to the activity of a perceptual reality monitoring system (for more, see Lau, 2022; Michel, Forthcoming)[13]. If this view is on the right track, visual consciousness comes online with the emergence of perceptual reality monitoring capacities. In turn, reality monitoring capacities emerge in response to the reality monitoring problem and Hamlet's problem in perception—computational problems that arise for animals with large sensory horizons.

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[13] A relevant prediction not mentioned in these reviews is that patients with reality monitoring deficits should typically show deficits in conscious, but not unconscious, processing. This prediction can be tested in some patients with schizophrenia (as well as neurotypical subjects with low doses of ketamine). A study by Grandgenevre et al. (2015) is particularly important here. In change blindness tasks, eye movements generally move to the changing feature before the conscious, explicit detection of the change (eye movements themselves are largely guided by unconscious visual information, see Spering & Carrasco, 2015). Grandgenevre et al. showed that patients with schizophrenia are not impaired for *implicitly* detecting the changing feature (their eyes move to the target even faster than neurotypical subjects), but are significantly slower for *explicitly* detecting it. This finding is generally consistent with an elevated consciousness threshold in patients with schizophrenia (See Berkovitch et al. (2017) for a review). The perceptual reality monitoring theory accounts for these results.

Let us nevertheless emphasize that our account is compatible with a variety of alternative views. Instead of going through the list, let us paint with broad strokes. One of the main dividing lines in consciousness research is between those who think that consciousness fulfills a perceptual role (as in the local recurrence theory; Lamme, 2016), and those who think that consciousness is for cognition (as in the global workspace theory; Mashour et al., 2020, or **the attention schema theory**; Graziano, 2015). Our account is compatible with 'cognitivist' theories of all kinds, as long as they hypothesize that the kind of cognition that consciousness supports is model-based.

Beyond vision

The current paper has focused on vision, which affords a particularly precise connection between sensory horizons, evolutionary biology, and the speed of consciousness. In future work it would be of interest to develop this theoretical project for other sensory modalities—for instance, drawing on empirical work on postdictive phenomena in conscious audition (e.g., Alais & Burr, 2003). More broadly, we envisage a generalization of our argument that encompasses world models in general, regardless of their sensory origins. We would expect that the capacity for flexible model-based planning would scale with the organism's (multimodal) sensory horizon. Such a prediction could potentially be tested by imposing artificial restrictions on the sensory horizon in one modality (such as introducing visual fog) and asking how another modality may be prioritized to compensate. Also relevant here are nascent investigations of multimodal perceptual metacognition, and theoretical models that posit domain-general forms of confidence (Deroy et al., 2016; Masset et al., 2020; Morales et al., 2018).

What about sensory modalities for which the idea of sensory horizon does not straightforwardly apply, such as touch, and affective states, such as fear or pain? Our view is that those states do not occur consciously if they are only recruited for model-free processes. From here, there are two possible paths to extend our account. One possibility is that model-based planning (and reality monitoring) are tied to large sensory horizons (including but not restricted to *visual* horizons). If this is correct, our account predicts that organisms with short sensory horizons do not have conscious states. But there is another possibility consistent with our hypothesis: organisms that are otherwise conscious (e.g., consciously

experience pain) might operate with unconscious vision as long as vision is not recruited for model-based planning. After all, it is possible for one type of state (i.e. vision) to occur unconsciously while other types of states occur consciously—as in blindsight subjects. Which of those possibilities turns out to be correct depends on future research on the origins and functions of model-based planning for other sensory modalities and affective states (e.g., in the case of fear, see LeDoux, 2019, 2023).

Conclusion

We developed an account of the functions and evolution of visual consciousness, starting from the claim that consciousness is slow and thus unlikely to play a role in immediate reactions to visual stimuli. By considering both the relative sluggishness of conscious vision and the hypothesis that limited sensory horizons constrain the speed at which organisms must react to visual information, we surmised that most aquatic animals do not consciously experience vision. Instead, visual consciousness evolved following the water-to-land transition, which expanded sensory horizons and enabled organisms to afford slower model-based planning. While model-based planning came with significant benefits, it also created challenges. The first challenge was to distinguish reality from simulation. The second challenge was Hamlet's problem in perception: how to know when to stop accumulating sensory evidence and settle on a given interpretation of the way the world is. A reality monitoring mechanism provides a solution to both problems by monitoring sensory representations and acting as a router between perception and cognition. We suggest that, by selecting a coherent set of representations among the myriad representational activities the mind is engaged in, a reality monitoring mechanism grants those representations the epistemic profile that is typical of our conscious representations. Through this lens, reality monitoring and the capacity for model-based planning are deeply intertwined, offering a new perspective on the functions of conscious vision.

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Competing interests

None.

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