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Mindful awareness as a mechanism of change for natural childbirth in pregnant women with high fear of childbirth: a randomised controlled trial

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Behavioural and Neural Evidence for Conscious Sensation in Animals

An Inescapable Avenue towards Biopsychism?

Abstract: Evidence for all sorts of cognition in animals is mounting. But is this accompanied by conscious sensation or phenomenology? To answer that question, it is noted that consciousness to us presents itself as a contrast: we are asleep or awake, we either see something or we don't, each state or condition accompanied by distinct neural correlates. The contrast implicitly holds there is conscious sensation; you cannot lose what you didn't have to begin with. So if there is similar behavioural and neural evidence for a conscious–unconscious contrast in any animal, there should be some sort of difference in the 'what it is likes' between the two extremes — for the animal in question. Findings from sleep, anaesthesia, blindsight, masking, and rivalry present unequivocal evidence for such a dichotomy in monkeys and — surprisingly — possibly insects. For other animals (mammals, birds, reptiles, fish) the situation is less clear, although mostly due to a lack of evidence rather than evidence to the contrary. Implications for theories of consciousness, and the role of neural versus behavioural findings, are discussed.

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1. That Devious Mosquito in My Room

I am in Italy. It's warm and pleasant. Night has fallen, and I am trying to read a bit before falling asleep. But there's this mosquito. I heard it humming around my head already a few times. There seems to be a pattern to it: whenever I read a few pages it's approaching, to go away as soon as I look up from the book. It is as if the annoying beast can sense my state of vigilance. When I look for it, trying to smack it so that I can quietly enjoy the last part of this day, it stays away. Only when my attention really drops, and I go back reading, does it try to attack. So, I decide to lure it towards me, not really reading but attentively monitoring my surroundings while keeping a reading posture. To no avail, it stays away. Until, again, I drop my guard. The animal is a mind reader. I give up. There is little I can do against so much dedication and intelligent tactics. The next morning, I have three itchy bumps.

Can mosquitos really sense the state of vigilance of their victims? And if so, how? Do they really have the intelligence to only approach a victim that is off guard? Mosquitos sense their prey via a complex set of mechanisms, detecting CO_2, body odour, visual cues, movement, and possibly more (Zhan *et al.*, 2021). And they do seem to notice when you're on the attack (Vinauger *et al.*, 2018). But am I right in ascribing a little 'mind' to the animal, anthropomorphizing behaviour that may just be simple reflexes (Wynne, 2004)? Animal cognition is getting ever more attention, and with that, it is getting increasingly clear that animals share many cognitive functions with us (Edelman and Seth, 2009). However, there seems to be a last 'bastion' here: in our heads, many of these cognitive operations are accompanied by a mysterious 'extra': consciousness. When we process sensory input, we see, hear, and feel. When we use this information, we know. When we make a decision, we think. When animals do these things, do they also see, hear, feel, know, and think? Is that mosquito in my room seeing that I'm reading, does it know the coast is clear, does it put any conscious thought — non-verbal of course — into its decision to attack?

2. To See or Not to See

Consciousness is a multifaceted phenomenon, ranging from having conscious sensations to higher-order forms such as self-consciousness, as addressed in studies like the Gallup mirror test. According to these, self-consciousness seems limited to quite a few species. The test and

its interpretation are, however, not without controversy (Gallup and Anderson, 2020). It's akin to the studies of animals having theory of mind (Penn and Povinelli, 2007), or possessing some form of language (Fitch, 2020), to name some other hornets' nests, in that they are all issues with a long history of experimentation and sometimes fierce debate. What I would like to address here is some more basic aspect of consciousness, that of having conscious sensations (Block, 2005).

This topic — although seemingly simpler — has received relatively little attention (Edelman and Seth, 2009; Pennartz, Farisco and Evers, 2019). That is maybe because the field of consciousness science dealing with sensation is riddled with issues like hard problems, explanatory gaps, inverted spectra, qualia, and other philosophical conundrums (Havlík, Kozáková and Horáček, 2017) that make it seem impossible to know 'from the outside' whether someone or something else has conscious sensations. So how on earth can we know whether there is conscious sensation in a mosquito, a lizard, a dog, or an ape?

There are ways to answer this question, I will argue here. A key starting point is that consciousness is a contrast. A contrast with unconscious processing. Almost all consciousness science builds on paradigms where consciousness is somehow manipulated (Klink *et al.*, 2015; Kim and Blake, 2005), looking for functions or neural processes that suffer from such manipulations and that do not. The prime goal of such experiments is to find the 'neural correlate of consciousness' (NCC) (Koch *et al.*, 2016). But note how this endeavour rests on the assumption that there *is* a conscious–unconscious contrast. My suggestion is to turn this around. If we can find behavioural or neural contrasts in animals that are like the ones we find in human studies on consciousness, shouldn't the conclusion then be that there is consciousness — of some sort — in these animals too?

For example, the critical distinction in blindsight (Weiskrantz, 1996) is that between yes-no responses — indicative of the presence or absence of conscious experience — and alternative forced choices — allegedly possible without conscious experience. If such a behavioural contrast is also found in animals (and there is a strong case for that in macaque monkeys — Supèr, Spekreijse and Lamme, 2001 — see below), granting them a conscious–unconscious contrast (and hence conscious experience) seems inevitable. Other examples would be looking at the effects of anaesthesia, masking, or rivalry, which are widely recognized as key manipulations as well. By systematically investigating to what extent these manipulations yield conscious–

unconscious contrasts in animals, one can paint an image of the similarity of sensory experience between animals and humans.

In short, I will take an 'if it looks, swims, quacks like a duck' approach to the matter, not unlike Edelman and Seth (2009) and Pennartz, Farisco and Evers (2019), but focusing on the conscious–unconscious contrast as an indicator. Also, the approach will allow for a comparison between behavioural and neural indicators, seeing if they converge or diverge, and arguing which we should 'believe' more.

3. The Case of Sleep and Anaesthesia:
Biopsychism Right Off the Bat

The phenomenon that is probably most strongly inspiring us to study consciousness at all is that it gets turned off for eight hours or so every day. If this were not the case, our fascination with the subject would maybe never have arisen. Consciousness exists by virtue of its contrast with unconsciousness. And what a ubiquitous contrast this is. Despite the obvious dangers associated with being (more or less) defenceless for such a long time, there is no animal that does not sleep (Cirelli and Tononi, 2017). Some have clever strategies, some sleep in turns, some let their brain hemispheres take turns (Kelly *et al.*, 2019), but, either way, every animal just has to sleep, goes through the contrast between being awake and not.

Yet will it experience the contrast? Sleep in all animals is accompanied by a generally immobile posture[2] and an elevation of sensory thresholds. Even cockroaches and flies 'lay down' when sleeping. Human sleep is characterized by different stages, the most prominent being REM and non-REM sleep. These separate stages are present in all mammals and birds, possibly in reptiles and (cuttle)fish (Rattenborg *et al.*, 2017; Kelly *et al.*, 2019). Sleep–wake cycles are controlled by neural structures in species ranging from mammals to insects that have similar genetic and molecular signatures and use similar neurotransmitters (Helfrich-Förster, 2018). One of the leading hypotheses for the need for sleep postulates that it is necessary for the

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2 Some animals cannot stay immobile. Ram ventilating — as opposed to pumping — sharks must maintain swimming to keep the flow of oxygen-rich water through their gills going. Whether they sleep is controversial. Some diurnal change in swimming pattern is sometimes observed (Kelly *et al.*, 2019). In captivity they sometimes accidentally bump into objects such as aquarium walls while what seems to be sleeping.

proper reorganization of memory traces, in that synapses that are strengthened or created during the day get pruned during sleep (Tononi and Cirelli, 2014). Interestingly, also in fruit flies, synapses increase in size and number during the day and decrease during sleep. Effects of sleep deprivation on memory, activity, and alertness are similar between mammals and fruit flies (Helfrich-Förster, 2018). All in all, sleep in animals looks, swims, and quacks like sleep in humans.

One is forced to an even more 'panpsychistic' — or rather 'biopsychistic'[3] — conclusion when we look at the artificial equivalent of sleep: anaesthesia. Isoflurane and halothane inhibit responses to nociceptive stimuli in animals as different as worms, flies, goldfish, ducks, rats, horses, monkeys, and man. Most strikingly this happens at comparable end-level concentrations of these volatile anaesthetics. In all these species, 'higher'-level cognitive functions such as exploration, mating, or coordinated movement 'go' before more primitive, reflex-like reactions such as withdrawal (Zalucki and van Swinderen, 2016). This doesn't stop at animals. Plants such as the Venus flytrap or Mimosa pudica no longer respond to stimulation of their trigger hairs (normally excited by prey insects), decrease chlorophyll synthesis, and induce seed dormancy when 'anaesthetized' with ether (Yokawa, Kagenishi and Baluška, 2019), one of the earliest anaesthetics used in humans. These effects are reversible and the effect on movement is caused by an inhibition of calcium spikes (Yokawa *et al.*, 2018). Plants produce their own volatile anaesthetics when under stress (Fammartino *et al.*, 2010; Loreto *et al.*, 2006), not unlike the endorphins that mammals produce. The unicellular eukaryote Tetrahymena pyriformis stops swimming (Nunn *et al.*, 1974) and luminous bacteria stop shining when exposed to volatile anaesthetics of various sorts, again at comparable doses as required to anaesthetize humans (White and Dundas, 1969). Some have therefore argued that sentience started when life made a difference between 'inside' and 'outside', and the need arose to keep this difference stable, or defend it against disturbance (Cook, Carvalho and Damasio,

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[3] Traditionally, the term 'panpsychism' is reserved for the idea that everything ranging from humans to thermostats or even stones or single atoms have some sort of 'mind'. Previously, I have used the term in a somewhat less lenient way, to indicate that some form of consciousness may be present in all *living* (or biological) organisms (Lamme, 2018). Later on, I learned that the correct term for this would be 'universal biopyschism' (SelfAwarePatterns, 2020; Fulda, 2020). I here therefore adopt the short version 'biopsychism'.

2014). Arthur Reber bites this bullet completely by granting conscious sensation to all that lives (Reber, 2018).

Sleep is accompanied by clear neural correlates. Already the first EEG recordings by pioneer Hans Berger (Tudor, Tudor and Tudor, 2005) showed the typical characteristics of sleep: a gradual increase in low frequency content, accompanied by a decrease in high frequency oscillations. All mammals and birds show this pattern, but it should be noted that EEG and behavioural signs of sleep may dissociate (Rattenborg *et al.*, 2017). Even in zebrafish, sleep is accompanied by an increase in slow oscillations between subcortical and 'cortical' structures, together with a decrease in spiking activity (Leung *et al.*, 2019). In the fruit fly, however, sleep causes a more general decrease of neural activity over all frequencies (Nitz *et al.*, 2002), most likely due to the absence of thalamocortical circuits in the fly, which are the main generators of slow wave activity in the mammalian brain.

In addition to looking at frequency content, it may be informative to look at the extent, directionality, and complexity of neural inter-actions. One such measure, perturbational complexity index (PCI), shows clear correlations with states of wakefulness, being lowest during anaesthesia and deep sleep (Sarasso *et al.*, 2015), indicative of a loss of meaningful long-range recurrent interactions between neurons. In that sense, slow EEG waves, although large in amplitude, seem to go along with a loss rather than an increase of integration of information across the brain (Tononi and Massimini, 2008). PCI has been used to quantify consciousness and successfully predict out-comes in unresponsive patients with disorders of consciousness like vegetative state (Rosanova *et al.*, 2012), so holds great potential for 'measuring' consciousness in animals. A recent study applied a similar analysis to neural recordings in the fruit fly (Leung *et al.*, 2021) and found that anaesthesia is accompanied by a collapse of neural integration, normally present during wakefulness and supported by recurrent neural circuitry.

A major distinction in the directionality of neural interactions is that between feedforward and feedback connections (Lamme, Supèr and Spekreijse, 1998). Where feedforward connections flow from the senses towards central or output regions, feedback flows in the oppo-site direction. In the monkey brain, feedforward processing remains present during anaesthesia, as many sensory (visual) neurons keep responding to input, and in a highly specific way (Lamme and Roelfsema, 2000). Feedback signals are selectively suppressed (Lamme, Zipser and Spekreijse, 1998). This difference may be due to

the fact that feedforward and feedback processing in part depend on different neurotransmitter systems (Self *et al.*, 2012), feedback systems relying more on the NMDA receptor. Some have even argued that the final common pathway of all anaesthetic effects is the NMDA receptor (Flohr, Glade and Motzko, 1998), which is widespread among the animal kingdom and present in species ranging from mammals to nematode, fruit flies, and sea anemones (Wudick *et al.*, 2018).

Also, both in the human and monkey visual cortex, Granger causality analysis revealed that feedforward signals are carried by high frequency (gamma) local field potentials, whereas feedback signals by lower frequency (alpha/beta) oscillations (Michalareas *et al.*, 2016; van Kerkoerle *et al.*, 2014). Anaesthesia selectively blocks these lower frequency feedback signals, while leaving high frequency feedforward signals relatively intact, as has been shown in humans, monkeys, ferrets, rodents, and the fruit fly (Cohen, van Swinderen and Tsuchiya, 2018).

In sum, studies on sleep and anaesthesia show a striking similarity of their effects on behaviour and neural activity between all animals (and maybe even plants and bacteria). Upon anaesthesia, all animals seem to go through a (possibly non-linear) transition of states, going from a state of recurrent and integrated neural exchange (awake) to a state where processing is feedforward and localized (anaesthetized/asleep). This strongly supports that there is a conscious–unconscious dichotomy in all of them. One may keep asking 'what it feels like' to be a fly, and that question remains difficult to answer, given the differences in sensory organs, neural structures, and behaviour (but see Lamme, 2018, for an attempt). Yet that it feels different *to the fly* to be awake or to be asleep is a conclusion that is fully supported by the current data. In that sense, the fly may be just as 'surprised' at the new dawn as we are in the morning waking up.

4. Now You See It, Now You Don't: Blindsight

The easiest way of knowing whether someone has a conscious sensation seems to be by simply asking: 'Did you see that?' Well, it depends. Patients with lesions to the primary visual cortex respond 'no' to the question 'did you see that?' when shown a stimulus in their blind hemifield, yet guess (~75%) correctly when asked 'was it a triangle or a square?' (for instance). Also, localization of these stimuli, by pointing or saccadic eye movement, is well (~80%) above chance

level. This phenomenon of blindsight was one of the pivotal findings of the 1970s, sparking a renewed interest in consciousness science (Weiskrantz, 2004). Again, it shows consciousness as a contrast, between what is consciously reported to be seen and what is apparently unconsciously processed by the visual system given the correct forced-choice guessing. Some controversy still surrounds the phenomenon, such as that it may all come down to response criteria differences (Phillips, 2021), but these objections have been tackled by rigorous signal detection analyses (Michel and Lau, 2021; Azzopardi and Cowey, 1997).

Blindsight is well established in monkeys (macaques), using paradigms that mimic the questions asked to human subjects. Monkeys are trained to either respond with a touch to the location of a stimulus or a touch to a 'I didn't see anything' location, which is first learned by presenting 50% trials with targets and 50% without. The alternative 'forced-choice' task is to guess with a touch to a potential target location in every trial. After a unilateral V1 lesion, stimuli in the blind field are classified as 'I didn't see anything' in the first task, yet ~95% correctly localized in the second (Cowey and Stoerig, 1995). Findings were replicated using a paradigm where saccadic eye movements were made to localize targets, and the 'I didn't see' response was made by maintaining fixation (Moore *et al.*, 1995; Supèr, Spekreijse and Lamme, 2001).[4] Signal detection analysis showed that in monkeys there is a strong difference in sensitivity for yes/no versus forced-choice tasks in the blind hemifield, which is independent of response criterion, and which is not there for stimuli at near-threshold (Yoshida and Isa, 2015). In that sense, the case for blindsight may be even stronger in monkeys than in humans.

Blindsight is generally believed to be mediated by a visual pathway that bypasses V1, via the colliculus superior and pulvinar (Kinoshita

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4   A somewhat similar paradigm to gauge conscious perception was used in crows. They were trained to report presence or absence of a grey square by either pecking at a subsequent blue or red square or not. Importantly, the relation between response (pecking vs. no-pecking) and perception (presence or absence), as well as stimulus saliency, was flexibly varied on each trial. Neural recordings revealed that many neurons in the birds nidopallium caudolaterale of the telencephalon responded to the stimulus intensity, regardless of report, but that an important subset of neurons reflected the upcoming report during the delay between grey stimulus and coloured target, indicating neural correlates of perception (or at least impending report) to be present in birds (Nieder, Wagener and Rinnert, 2020). The findings do, however, not pertain directly to the issue of whether these birds experience a conscious–unconscious contrast.

et al., 2019). On that ground, blindsight may be expected in other mammals with similar circuitry, such as rodents (Beltramo and Scanziani, 2019). A Long Evans rat with bilateral V1 lesion could approach salient targets, yet not discriminate complex images, optic flow, or orientation (Petruno, Clark and Reinagel, 2013). This seems less impressive than the famous monkey Helen, studied at the Cowey lab, who seemed able to navigate space quite well on the basis of visual cues only, despite a double-sided ablation of V1 (Stoerig, 1997). This was, however, after training.[5]

Another way to tell blindsight from conscious vision is to measure subjects' confidence in their discrimination choice (Ko and Lau, 2012). Typically, when stimuli are consciously perceived, better performance goes along with higher confidence. Unconscious processing will result in performance unrelated to confidence (Robichaud and Stelmach, 2003). This type of metacognition seems present in bees that were trained to discriminate between a target presented either above or below a reference point, one of which was rewarded with sucrose, the other punished with quinine. When the discrimination became difficult, they often opted for an exit to a second chamber where another choice was available — in other words choose the 'I didn't see it' button when possible (Perry and Barron, 2013).

5. You Don't See It, But Your Brain Does

The search for a distinction between conscious and unconscious processing without lesions to the visual cortex has a long history. Typically, stimuli are rendered 'invisible' by manipulations such as backward masking, dichoptic masking, continuous flash suppression (CFS), binocular rivalry, or one of many other ways (Kim and Blake, 2005). A key finding supporting the presence of a conscious–unconscious contrast is that of impaired detection while other behavioural responses to stimuli remain possible, or while neural signals still express selective responses.[6]

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[5] Humans with bilateral lesions to V1 report being fully blind, yet responses to looming objects can be recorded from the temporal and parietal cortex (Hervais-Adelman *et al.*, 2015).

[6] Considerable controversy lies in what 'counts' as evidence for these manipulations revealing unconscious processing. Do we take a subject's word for it when he says, 'I didn't see it' (a so-called 'subjective' threshold), or do we only believe there was no conscious percept when there is chance performance (or $d' = 0$) in a detection or discrimination task (an 'objective' threshold)? The extent of unconscious processing

Best studied in different species is the effect of (backward) visual masking. Two types are distinguished, one in which the target and mask overlap (as in pattern masking), the other where they don't but they share contours (metacontrast masking). While pattern masking typically yields so-called 'type A' curves, with the strongest drop in visibility of the target when immediately followed by the mask, and less effect with longer delays, metacontrast masking may give so-called 'type B' curves, with the strongest drop in visibility of the target when it is followed by a mask some 40 milliseconds later, and less effect when the mask has a short or long delay to the target. Studies of masking in monkeys typically yield type A curves (Lamme, Zipser and Spekreijse, 2001; Kovács, Vogels and Orban, 1995); type B curves following metacontrast masking have been reported but are variable (Bridgeman, 1980). Note however, that also in humans, whether type B curves show up is dependent on individual traits (Maksimov *et al.*, 2013). One study (Kovács, Vogels and Orban, 1995) directly compared pattern masking functions between man and monkey using the exact same stimulus and found remarkable overlap.

In alignment with earlier results (Rolls and Tovee, 1994), it was found that successfully masked stimuli still evoke specific activation of shape-selective neurons in the monkey temporal lobe, indicating that feedforward neural tuning remains intact despite invisibility (Kovács, Vogels and Orban, 1995). Further corroboration of masking selectively disrupting feedback, but not feedforward processing, was found in a study where textured figure-ground stimuli were either masked or unmasked. A sigmoidal masking function was found, going along with a sigmoidal suppression of recurrent figure-ground signals with more effective masking. Feedforward tuning properties (orientation selectivity) were not affected (Lamme, Zipser and Spekreijse, 2001). Similar results were later obtained in human subjects (Fahrenfort, Scholte and Lamme, 2007).

While consensus is that macaque monkeys show similar behaviour and neural effects upon masking as humans, results are more mixed for other animals. Visual orientation discrimination in rats does not seem impaired by masking, although it must be noted that behaviour is quite variable, also because rats have poor visual acuity (Dell,

seems much smaller (or even absent) in the latter case (Stein *et al.*, 2020). These issues are beyond the scope of this paper (yet see Lamme, 2020), but given this difficulty it is no surprise that studies looking for unconscious processing in animals using such paradigms are rare.

Arabzadeh and Price, 2019). Neural responses in V1 are, however, suppressed by masking, suggesting that these rats base their behaviour on other (non-cortical?) pathways (Dell, Arabzadeh and Price, 2018). So while there is clear evidence for a conscious–unconscious dichotomy induced by masking in humans and monkeys, this is less clear for other mammals, let alone non-mammals.

6. Now You See This, Then You See That

In binocular rivalry, stimuli remain constant, while the conscious percept spontaneously switches from one to the other. The search for neurons whose activity switches along with perception, rather than following the physical stimulation, played an important role in the early days' search for the NCC (Logothetis, 1998). These results, mainly obtained from the monkey visual cortex, showed that early neurons in visual areas mainly follow the stimulus, while higher-level neurons in the temporal lobe most often followed the conscious percept. More recent work, combined with work in human subjects, and also looking at other bistable perceptual phenomena (Donner *et al.*, 2008), paints a picture where rivalry is mostly a matter of dynamic competition between neurons throughout the visual system, and that which neurons get involved depends on stimulus characteristics (Tong, Meng and Blake, 2006).

Of relevance to the present discussion is mostly to what extent rivalry is a sign of a conscious–unconscious dichotomy and whether it is present in animals. The suppressed — unseen — stimulus during rivalry may evoke selective activation of even high-level regions (*ibid.*), arguing for the case that rivalry reveals a dichotomy between conscious and unconscious representations. However, others view rivalry as a potentially low-level mechanism of competition between neural assemblies, not necessarily related to consciousness. For example, neural signs of rivalry may occur for stimuli that are unseen (Zou, He and Zhang, 2016; Bahmani *et al.*, 2014). To argue for a conscious–unconscious dichotomy based on the presence of rivalry in animals is therefore contentious.

Either way, rivalry, in the sense of competition between alternative sensory inputs, seems widespread in the animal kingdom. The similarity in the dynamics of rivalry (distribution of dominance times, dependence on contrast, etc.) between man and monkey is striking (Logothetis, 1998). Monkeys also seem to experience spontaneous perceptual switches for other bistable stimuli such as the random dot

rotating sphere (Leopold, Maier and Logothetis, 2003). In our heads, rivalry occurs because perception must 'choose' between the overlapping inputs from the two eyes. Yet many other animals do not have binocular vision with front facing eyes, but instead have eyes that face opposite directions (many birds, reptiles, and insects, but also quite a number of non-predatory mammals), or even move totally independently (think chameleons). In these animals, rivalry between the two eyes is not so much competing for perception but rather for action. Clear signs of such rivalry for action are present in insects such as flies, that spontaneously switch flight direction when the two eyes are confronted with competing directions of motion, or in chameleons that follow and catch prey with saccadic movements of one eye, while the other eye is motionless (Carter *et al.*, 2020). It is unclear to what extent this is accompanied by similar neural correlates as seen in primates.

In sum, the characteristics of perceptual switching seen in human subjects seem also present in a range of phylogenetically distant species. Whether this is a sign of switches between conscious percepts, i.e. the dominant one emerging from the unconscious into the conscious, the to-be-suppressed one fading away, remains to be determined in species other than primates.

7. Who Qualifies:
The Remarkable Position of Insects

Table 1 summarizes the findings of this review. For each of the 'manipulations' sleep, anaesthesia, blindsight, masking, and rivalry, which in consciousness research are used to study the conscious–unconscious contrast, it is summarized whether there is evidence for such a contrast or not, either from a behavioural or neural perspective. Note that the table takes a conservative view, in the sense that if evidence is absent (mostly because there are no data about it — or I couldn't find any), the box is ticked red, and the summary flag denies the existence of a conscious–unconscious contrast in that (class of) species.

BEHAVIOURAL AND NEURAL EVIDENCE FOR A CONSCIOUS - UNCONSCIOUS CONTRAST

		man	monkey	mammal	bird	reptile	fish	insect	other	
SLEEP	*Behavioural*									
	immobility									
	higher sensory thresholds									
	Effects of sleep deprivation									
	Neural									
	Genetics and molecular biology									
	REM vs non-REM stages									
ANAESTHESIA	*Behavioural*									
	Inhibition of nociception									
	selective loss of (higher) function									*1
	Neural									
	Low vs High freq EEG effects									
	Complexity index going down									
	Feedback going before feedforward									
	NMDA receptor									*2
BLINDSIGHT	*Behavioural*									
	Classical yes/no vs 2AFC distinction									
	Metacognition									
	Neural									
	'Blindsight' parallel pathways									
MASKING	*Behavioural*									
	Type A (pattern) masking functions									
	Type B (metacontrast) masking functions									
	Neural									
	Feedback disrupted, feedforward not									
RIVALRY	*Behavioural*									
	Competition between sensory inputs									
	Competitition between 'overlapping' inputs									
	Neural									
	Some neurons follow dominant, others don't									

*1 Plants, eukaryotes, prokaryotes
*2 Sea anemones

Legend:
- evidence present
- some (or mixed) evidence found
- no evidence found yet
- evidence found to the contrary
- con - unc contrast present
- con - unc contrast possibly present
- no evidence (yet) of con - unc contrast

Table 1. Behavioural and neural evidence for a conscious–unconscious contrast in animals. Boxes are checked green if evidence is found in at least one or some representative animals of that class (underlying value then = 1). Boxes are red if no evidence has been found (yet) (box = 0), red on a yellow background if evidence to the contrary is found. Boxes are yellow if the evidence is scarce or mixed within the class of species (box = 0.5, for example, some fish sleep, others don't seem to). For each condition, the findings are 'summarized' into the 'behavioural' or 'neural' rows, where the results from the boxes below are 'averaged': average value < 0.33 = red tick mark, 0.33–0.66 = yellow tick mark, > 0.66 = green tick mark.

Several conclusions are possible. First, many data points are missing. This is no surprise, given that consciousness research has been a 'no-go area' for cognitive and neural science for quite a while, from which it has escaped only some 25 years ago (Koch *et al.*, 2016). Also,

studying awake animals in the lab (let alone in the field) requires complex set-ups, particularly when combined with neural measurements. Some species have been used a lot (monkeys, rodents, insects), others much less.

Second, the conclusion seems fully warranted that monkeys share so many aspects of the conscious–unconscious contrast with us — both behaviourally and neurally — that granting them the presence of consciousness seems fully warranted. Note that I talk of sensory consciousness here, as that is what most of the research discussed here is about. To what extent other mammals qualify is mostly a matter of lack of evidence than evidence to the contrary (although the effects of masking in rats seem somewhat at odds). And although high-level aspects of consciousness, such as self-awareness, intelligent problem solving, or language, have been documented in birds, relatively little is known about the criteria for a conscious–unconscious dichotomy other than effects of sleep and anaesthesia. A recent paper showed that crows could report presence or absence of a stimulus by either pecking at a target or not, and could flexibly adjust their response mode (Nieder, Wagener and Rinnert, 2020). Importantly, neurons in the telencephalon modulated their activity according to the bird's reported percept. Taken together, the presence of conscious experience seems likely. Somewhat more caution is in order for reptiles and fish — so far.

Third, it is quite remarkable that insects (of which the most studied species is the fly) tick so many boxes. Their behaviour and sensory (visual) systems are vastly different from ours, which makes granting them conscious experience feel quite a stretch. Yet based on the effects of sleep, anaesthesia, and the presence of rivalry and metacognition, some sort of conscious–unconscious dichotomy is clearly present. Insects having conscious experience was already inferred on the grounds of neural architecture before (Barron and Klein, 2016). They also tick many boxes when considering to what extent they qualify for having the necessary ingredients for consciousness from the perspective of various theories of consciousness, such as global workspace theory (ants and bees have 'access' and flexibly manipulate sensory information), integrated information theory and recurrent processing theory (fly brains show all neural signatures required, see above), and higher-order thought theory (e.g. bees have metacognition) (Lamme, 2018). Common ancestors between insects and humans are more than 500 million years old. The similarities therefore could be a matter of parallel evolutionary convergence or of highly

conserved mechanisms. Common regulatory genes determine the development of mid- and forebrain structures, suggesting that all animals that possess a brain share highly conserved mechanisms for sensory integration and coordinated behaviour (Bridi *et al.*, 2020). The conscious–unconscious contrast may just be very old.

The findings together, and the insect findings in particular, suggest that if sufficient research would be devoted to it, all boxes of Table 1 would probably get ticked, implying that all animals share some sort of conscious–unconscious dichotomy. And according to the rationale of this paper, we should then also conclude that they all have some sort of conscious experience. Or to be more precise, will somehow 'feel different' between their conscious or unconscious states, between their conscious and unconscious experiences. That is not to say that it feels the same to be an awake fly as it feels to be an awake human or monkey. Conscious experience is naturally determined and constrained by the make-up of sensory equipment, its neural processing, and the neural architecture underlying it. Elsewhere (Lamme, 2018), I have argued that what the fly sees is most likely an amalgam of motion and colour without the strong notion of 'objects' that dominates human vision, which may be similar to what blindsight patients experience. And that hence conscious vision in flies may be more similar to what humans would call unconscious vision. Yet this doesn't deny conscious vision in the fly — in the sense of a contrast with its unconscious vision (which is even more 'in the dark'). Conscious vision in mammals is probably much more like ours, although there too differences in colour pigments, being predator or pray, having binocular vison or not, circular fovea or visual streak — which in turn make visual brains differ too — will make a difference as to 'what it is like'. What we share is the transition, going from visual processing 'in the dark' (Chalmers, 1995) to conscious seeing.

8. State versus Content:
Erring on Which Side of Caution?

Another look at Table 1 may yield quite a different conclusion. A first objection may be that most of the positive evidence comes from manipulations of state — sleep and anaesthesia — rather than content. And both sleep and anaesthesia are — at their core — defined by behavioural evidence, like absence of movement or responsiveness. And we know that, in human subjects, the conscious state and having conscious sensation may diverge. Examples are the sometimes vivid

(and painful) sensations that people experience under anaesthesia (Kotsovolis and Komninos, 2009), conscious sensation during vegetative state (Laureys, 2005), and of course dreaming or sleepwalking and other sleep disorders (Oudiette *et al.*, 2009). Some caution towards taking behavioural or even neural signs of sleep and anaesthesia as evidence for a conscious–unconscious dichotomy seems in order. Combined with the absence of evidence for such a dichotomy from blindsight, masking, or rivalry in many species other than primates, a universal biopsychistic conclusion as drawn above may seem unwarranted.

On which side of caution should we err then? That may depend on the goal of the classification of species. If that goal is an ethical one, it seems natural to err on the side of biopsychism until we have clear evidence to the contrary.[7] Yet also if the goal is scientific, as in trying to understand the origins of consciousness, I think there are good reasons to err on the side of biopsychism: many — if not all — current theories of consciousness are so simple that they endorse a high degree of biopsychism and even panpsychism. They need additional 'missing ingredients' to move away from it (Lamme, 2018; Northoff and Lamme, 2020). Laying the burden of proof on those denouncing biopsychism or panpsychism therefore poses a healthy challenge for improvement of these theories.

9. The Role of Neural Evidence

One may also question what the findings from blindsight, masking, or rivalry bring exactly. They show a behavioural dichotomy, alright, but do they present evidence for a conscious–unconscious dichotomy *per se*? Other (behavioural) dichotomies exist that are not taken as such evidence: short- vs. long-term memory, global vs. local processing, what vs. where, and many more. Blindsight, masking, and rivalry are taken to reveal a conscious–unconscious dichotomy in humans in part because of introspective intuitions and verbal report: to us, a masked, suppressed, or degraded stimulus is (sometimes) not seen and *hence* not reported. This implies a sort of three stage process: 1. sensory processing; 2. conscious perception of it (or not); 3. behavioural response

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7   Only if having conscious sensation would have ethical consequences, which it will most likely not have for many people. I believe the animals I kill (like that mosquito) or eat (I eat meat) have conscious sensation. I do not feel particularly bad about that. Maybe I'm a psychopath…

based on 2 (rather than on 1). Could it be that, in the animal, it is just not reported? So that there is a direct link between stimulus and report, without any intervention of conscious perception? The case has been made that blindsight in monkeys is just that: a difference in stimulus–response behaviour for yes-no versus forced-choice localization or discrimination, possibly mediated by attention (Allen-Hermanson, 2010). Even a signal detection analysis showing different d' for the two behaviours (Yoshida and Isa, 2015), or showing that neural pathways for the two types are different (Kinoshita *et al.*, 2019), cannot in principle counter such objections.

What may help to surpass such objections is evidence that the animals base their behaviour on an 'intermediate' state, a state between purely sensory processing and behaviour. Combining neural data with signal detection analysis of behaviour may provide such evidence. Supèr had monkeys view textured figure-ground stimuli of varying saliency (Figure 1a) and at random locations. Their task was to make a saccadic eye movement to the location of the textured square to indicate perception (a 'YES' response). Twenty percent of trials contained no figure, and were rewarded when the monkey then maintained fixation, to indicate absence of perception (a 'NO' response). On a number of figure present trials, however, monkeys also maintained fixation, as if indicating absence of perception. This number of NO responses — logically — increased (from ~8% to ~58%, Figure 1c) with decreasing saliency. Note that the behavioural paradigm is identical to the one used to demonstrate presence or absence of perception in blindsighted monkeys (Moore *et al.*, 1995). Also note that the behavioural data alone do not provide strict evidence for a state between sensory processing and behaviour. Neural data recorded during the experiment showed a remarkable pattern, however. Feedback signals from higher-level cortical areas back to V1 (showing up as a delayed (>100 ms) modulation of responses, and previously shown to reflect figure-ground organization — Lamme, 1995; Zipser, Lamme and Schiller, 1996 — Figure 1b)[8] followed neither the stimulus nor the behavioural response (Figure 1c): for high saliency figures it was present when monkeys reported YES, yet absent when they reported NO. For low saliency figures, this relation

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[8]   These modulations are also selectively absent during anaesthesia and masking (Lamme, Zipser and Spekreijse, 1998; 2001), and have been theorized to reflect a neural correlate of conscious perception (Lamme, 2006; 2010).

decreased, up to the point where feedback modulation was almost the same for YES and NO figure present trials. How could this be explained?

A model where the modulation reflected a stage *between* strictly sensory processing and the behavioural response could fully account for the data (Figure 1d). In the model, sensory processing in most instances (say 90%) results in recurrent feedback, and hence modulation signals in V1. In some instances (say 10%), however, recurrent feedback does not arise.[9] The recurrent feedback signal is then taken

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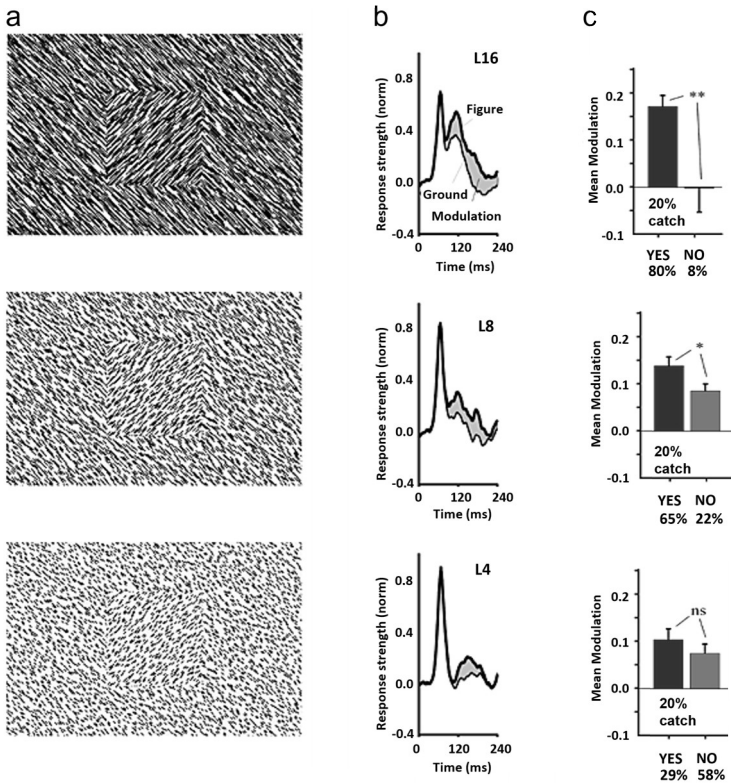
9   It appears that the occurrence or non-occurrence of recurrent interactions depends on the state of the visual cortex at the moment the stimulus arrives (Supèr *et al.*, 2003).
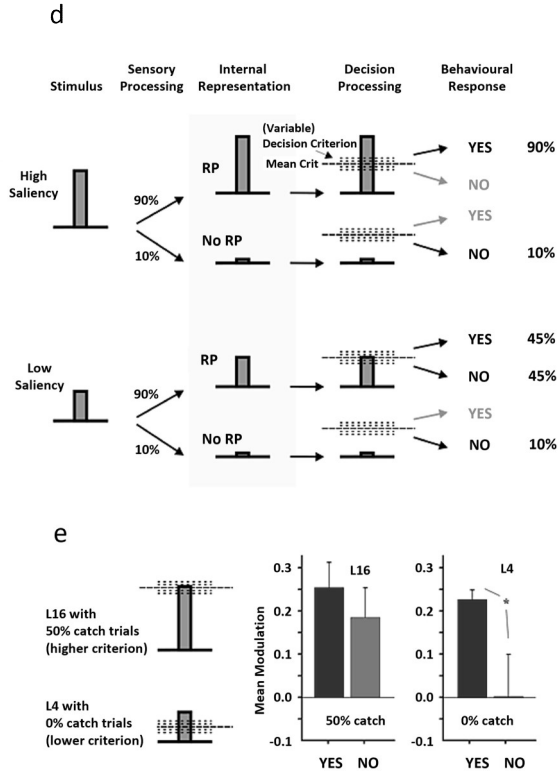
Figure 1a–e. Summary of an experiment in monkeys showing neural evidence for a stage between strictly sensory processing and behaviour (Supèr, Spekreijse and Lamme, 2001). See text for details.

as the internal representation that is fed into a classical signal detection model with a set (but somewhat variable) decision criterion. When the modulation signal is above this criterion, the monkey responds YES, otherwise it responds NO. This can fully account for the relation between YES/NO responses and feedback modulation at all saliencies. Moreover, the model was tested by changing decision criteria for high and low saliency stimuli (Figure 1e). Elevating the decision criterion for the high saliency (L16) stimulus (by increasing number of catch trials) resulted in a watering down of the relation between modulation and behavioural response; lowering the decision criterion for the low saliency (L4) stimulus (by lowering percentage of

catch trials) increased the relation between modulation and behavioural response, just as predicted by the model.

In sum, the combined behavioural and neural data (and their combination only!) provided strong evidence for an internal signal that sits between purely sensory processing and decision processing. The animals base their response on this intermediate stage. These kinds of findings, where neural data recording is combined with manipulation of stimulus and decision variables, can offer a window into the mechanics of the animal mind. I believe it is even stronger evidence for conscious perception than any verbal report will ever be; it objectifies an internal state that we would otherwise just have to 'believe' to exist when we base it on introspection or verbal report.

And that has been the goal of this paper: to find objective criteria for conscious experience in animals, either from behaviour, from neural evidence, or from both.

So that mosquito in my room, it doesn't have to tell me it's conscious. I just know.

References

Allen-Hermanson, S. (2010) Blindsight in monkeys, lost and (perhaps) found, *Journal of Consciousness Studies*, **17** (1–2), pp. 47–71.

Azzopardi, P. & Cowey, A. (1997) Is blindsight like normal, near-threshold vision?, *Proceedings of the National Academy of Sciences USA*, **94** (25), pp. 14190–14194. doi: 10.1073/pnas.94.25.14190

Bahmani, H., Murayama, Y., Logothetis, N.K. & Keliris, G.A. (2014) Binocular flash suppression in the primary visual cortex of anesthetized and awake macaques, *PLoS ONE*, **9** (9), e107628. doi: 10.1371/journal.pone.0107628

Barron, A.B. & Klein, C. (2016) What insects can tell us about the origins of consciousness, *Proceedings of the National Academy of Sciences USA*, **113** (18), pp. 4900–4908. doi: 10.1073/pnas.1520084113

Beltramo, R. & Scanziani, M. (2019) A collicular visual cortex: Neocortical space for an ancient midbrain visual structure, *Science*, **363** (6422), pp. 64–69. doi: 10.1126/science.aau7052

Block, N. (2005) Two neural correlates of consciousness, *Trends in Cognitive Sciences*, **9**, pp. 46–52. doi: 10.1016/j.tics.2004.12.006

Bridgeman, B. (1980) Temporal response characteristics of cells in monkey striate cortex measured with metacontrast masking and brightness discrimination, *Brain Research*, **196** (2), pp. 347–364. doi: 10.1016/0006-8993(80)90400-x

Bridi, J.C., Ludlow, Z.N., Kottler, B., Hartmann, B., Vanden Broeck, L., Dearlove, J., Göker, M., Strausfeld, N.J., Callaerts, P. & Hirth, F. (2020) Ancestral regulatory mechanisms specify conserved midbrain circuitry in arthropods and vertebrates, *Proceedings of the National Academy of Sciences USA*, **117** (32), pp. 19544–19555. doi: 10.1073/pnas.1918797117

Carter, O., van Swinderen, B., Leopold, D.A., Collin, S.P. & Maier, A. (2020) Perceptual rivalry across animal species, *Journal of Comparative Neurology*, **528** (17), pp. 3123–3133. doi: 10.1002/cne.24939

Chalmers, D.J. (1995) Facing up to the problem of consciousness, *Journal of Consciousness Studies*, **2** (3), pp. 200–219.

Cirelli, C. & Tononi, G. (2017) The sleeping brain, *Cerebrum Dana Forum Brain Science*, [Online], https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5501041/ [4 May 2018].

Cohen, D., van Swinderen, B. & Tsuchiya, N. (2018) Isoflurane impairs low frequency feedback but leaves high frequency feedforward connectivity intact in the fly brain, *eneuro*, **2018**. doi: 10.1523/eneuro.0329-17.2018

Cook, N.D., Carvalho, G.B. & Damasio, A. (2014) From membrane excitability to metazoan psychology, *Trends in Neurosciences*, **37** (12), pp. 698–705. doi: 10.1016/j.tins.2014.07.011

Cowey, A. & Stoerig, P. (1995) Blindsight in monkeys, *Nature*, **373** (6511), pp. 247–249. doi: 10.1038/373247a0

Dell, K.L., Arabzadeh, E. & Price, N.S.C. (2018) Human-like perceptual masking is difficult to observe in rats performing an orientation discrimination task, *PLoS ONE*, **13** (11), e0207179. doi: 10.1371/journal.pone.0207179

Dell, K.L., Arabzadeh, E. & Price, N.S.C. (2019) Differences in perceptual masking between humans and rats, *Brain & Behavior*, **9** (9), e01368. doi: 10.1002/brb3.1368

Donner, T.H., Sagi, D., Bonneh, Y.S. & Heeger, D.J. (2008) Opposite neural signatures of motion-induced blindness in human dorsal and ventral visual cortex, *Journal of Neuroscience*, **28** (41), pp. 10298–10310. doi: 10.1523/JNEUROSCI.2371-08.2008

Edelman, D.B. & Seth, A.K. (2009) Animal consciousness: A synthetic approach, *Trends in Neurosciences*, **32**, pp. 476–484. doi: 10.1016/j.tins.2009.05.008

Fahrenfort, J.J., Scholte, H.S. & Lamme, V.A.F. (2007) Masking disrupts reentrant processing in human visual cortex, *Journal of Cognitive Neuroscience*, **19**, pp. 1488–1497. doi: 10.1162/jocn.2007.19.9.1488

Fammartino, A., Verdaguer, B., Fournier, J., Tamietti, G., Carbonne, F., Esquerré-Tugayé, M.-T. & Cardinale, F. (2010) Coordinated transcriptional regulation of the divinyl ether biosynthetic genes in tobacco by signal molecules related to defense, *Plant Physiology & Biochemistry*, **48** (4), pp. 225–231. doi: 10.1016/j.plaphy.2010.01.012

Fitch, W.T. (2020) Animal cognition and the evolution of human language: Why we cannot focus solely on communication, *Philosophical Transactions of the Royal Society B: Biological Sciences*, **375** (1789), 20190046. doi: 10.1098/rstb.2019.0046

Flohr, H., Glade, U. & Motzko, D. (1998) The role of the NMDA synapse in general anesthesia, *Toxicology Letters*, **100–101**, pp. 23–29.

Fulda, F.C. (2020) Biopsychism: Life between computation and cognition, *Interdisciplinary Science Reviews*, **45** (3), pp. 315–330. doi: 10.1080/03080188.2020.1794381.

Gallup Jr., G.G. & Anderson, J.R. (2020) Self-recognition in animals: Where do we stand 50 years later? Lessons from cleaner wrasse and other species, *Psychology of Consciousness: Theory, Research & Practice*, **7** (1), pp. 46–58. doi: 10.1037/cns0000206

Havlík, M., Kozáková, E. & Horáček, J. (2017) Why and how: The future of the central questions of consciousness, *Frontiers in Psychology*, **8**, art. 1797. doi: 10.3389/fpsyg.2017.01797

Helfrich-Förster, C. (2018) Sleep in insects, *Annual Review of Entomology*, **63** (1), pp. 69–86. doi: 10.1146/annurev-ento-020117-043201

Hervais-Adelman, A., Legrand, L.B., Zhan, M., Tamietto, M., de Gelder, B. & Pegna, A.J. (2015) Looming sensitive cortical regions without V1 input: Evidence from a patient with bilateral cortical blindness, *Frontiers in Integrative Neuroscience*, **9**, art. 51. doi: 10.3389/fnint.2015.00051

Kelly, M.L., Collin, S.P., Hemmi, J.M. & Lesku, J.A. (2019) Evidence for sleep in sharks and rays: Behavioural, physiological, and evolutionary considerations, *Brain, Behavior & Evolution*, **94** (1–4), pp. 37–50. doi: 10.1159/000504123

Kim, C.Y. & Blake, R. (2005) Psychophysical magic: Rendering the visible 'invisible', *Trends in Cognitive Sciences*, **9**, pp. 381–388. doi: 10.1016/j.tics. 2005.06.012

Kinoshita, M., Kato, R., Isa, K., Kobayashi, K., Kobayashi, K., Onoe, H. & Isa, T. (2019) Dissecting the circuit for blindsight to reveal the critical role of pulvinar and superior colliculus, *Nature Communications*, **10** (1), art. 135. doi: 10.1038/ s41467-018-08058-0

Klink, P.C., Self, M.W., Lamme, V.A., Roelfsema, P.R. & Miller, S.M. (2015) Theories and methods in the scientific study of consciousness, *The Constitution of Phenomenal Consciousness: Toward a Science and Theory*, **92**.

Ko, Y. & Lau, H. (2012) A detection theoretic explanation of blindsight suggests a link between conscious perception and metacognition, *Philosophical Transactions of the Royal Society B: Biological Sciences*, **367** (1594), pp. 1401–1411. doi: 10.1098/rstb.2011.0380

Koch, C., Massimini, M., Boly, M. & Tononi, G. (2016) Neural correlates of consciousness: Progress and problems, *Nature Reviews Neuroscience*, **17** (5), art. 5. doi: 10.1038/nrn.2016.22

Kotsovolis, G. & Komninos, G. (2009) Awareness during anesthesia: How sure can we be that the patient is sleeping indeed?, *Hippokratia*, **13** (2), pp. 83–89.

Kovács, G., Vogels, R. & Orban, G.A. (1995) Cortical correlate of pattern backward masking., *Proceedings of the National Academy of Sciences USA*, **92** (12), pp. 5587–5591.

Lamme, V.A.F. (1995) The neurophysiology of figure-ground segregation in primary visual cortex, *Journal of Neuroscience*, **15**, pp. 1605–1615.

Lamme, V.A.F. (2006) Towards a true neural stance on consciousness, *Trends in Cognitive Sciences*, **10**, pp. 494–501. doi: 10.1016/j.tics.2006.09.001

Lamme, V.A.F. (2010) How neuroscience will change our view on consciousness, *Cognitive Neuroscience*, **1**, pp. 204–220. doi: 10.1080/17588921003731586

Lamme, V.A.F. (2018) Challenges for theories of consciousness: Seeing or knowing, the missing ingredient and how to deal with panpsychism, *Philosophical Transactions of the Royal Society B: Biological Sciences*, **373**, art. 1755. doi: 10.1098/rstb.2017.0344

Lamme, V.A.F. (2020) Visual functions generating conscious seeing, *Frontiers in Psychology*, **11**, art. 83. doi: 10.3389/fpsyg.2020.00083

Lamme, V.A.F., Supèr, H. & Spekreijse, H. (1998) Feedforward, horizontal, and feedback processing in the visual cortex, *Current Opinion in Neurobiology*, **8**, pp. 529–535.

Lamme, V.A.F., Zipser, K. & Spekreijse, H. (1998) Figure-ground activity in primary visual cortex is suppressed by anesthesia, *Proceedings of the National Academy of Sciences USA*, **95**, pp. 3263–3268.

Lamme, V.A.F. & Roelfsema, P.R. (2000) The distinct modes of vision offered by feedforward and recurrent processing, *Trends in Neurosciences*, **23**, pp. 571–579.

Lamme, V.A.F., Zipser, K. & Spekreijse, H. (2001) Masking interrupts figure-ground signals in V1, *Journal of Vision*, **1**, p. 32.

Laureys, S. (2005) The neural correlate of (un)awareness: Lessons from the vegetative state, *Trends in Cognitive Sciences*, **9** (12), art. 12. doi: 10.1016/j.tics.2005.10.010.

Leopold, D.A., Maier, A. & Logothetis, N.K. (2003) Measuring subjective visual perception in the nonhuman primate, in Jack, A. & Roepstorff (eds.) *Trusting the Subject?*, vol. 1, pp. 115–130, Exeter: Imprint Academic.

Leung, A., Cohen, D., van Swinderen, B. & Tsuchiya, N. (2021) Integrated information structure collapses with anesthetic loss of conscious arousal in Drosophila melanogaster, *PLoS Computational Biology*, **17** (2), e1008722. doi: 10.1371/journal.pcbi.1008722

Leung, L.C., Wang, G.X., Madelaine, R., Skariah, G., Kawakami, K., Deisseroth, K., Urban, A.E. & Mourrain P. (2019) Neural signatures of sleep in zebrafish, *Nature*, **571** (7764), pp. 198–204. doi: 10.1038/s41586-019-1336-7

Logothetis, N.K. (1998) Single units and conscious vision., *Philosophical Transactions of the Royal Society B: Biological Sciences*, **353** (1377), pp. 1801–1818.

Loreto, F., Barta, C., Brilli, F. & Nogues, I. (2006) On the induction of volatile organic compound emissions by plants as consequence of wounding or fluctuations of light and temperature, *Plant, Cell & Environment*, **29** (9), pp. 1820–1828. doi: 10.1111/j.1365-3040.2006.01561.x

Maksimov, M., Vaht, M., Harro, J. & Bachmann, T. (2013) Can common functional gene variants affect visual discrimination in metacontrast masking?, *PLoS ONE*, **8** (1), e55287. doi: 10.1371/journal.pone.0055287

Michalareas, G., Vezoli, J., van Pelt, S., Schoffelen, J.-M., Kennedy, H. & Fries, P. (2016) Alpha-beta and gamma rhythms subserve feedback and feedforward influences among human visual cortical areas, *Neuron*, **89** (2), pp. 384–397. doi: 10.1016/j.neuron.2015.12.018

Michel, M. & Lau, H. (2021) Is blindsight possible under signal detection theory? Comment on Phillips (2021), *Psychological Review*, **128** (3), pp. 585–591. doi: 10.1037/rev0000266

Moore, T., Rodman, H.R. Repp, A.B. & Gross, C.G. (1995) Localization of visual stimuli after striate cortex damage in monkeys: Parallels with human blindsight, *Proceedings of the National Academy of Sciences USA*, **92**, pp. 8215–8218.

Nieder, A., Wagener, L. & Rinnert, P. (2020) A neural correlate of sensory consciousness in a corvid bird, *Science*, **369** (6511), pp. 1626–1629. doi: 10.1126/science.abb1447

Nitz, D.A., van Swinderen, B., Tononi, G. & Greenspan, R.J. (2002) Electrophysiological correlates of rest and activity in Drosophila melanogaster, *Current Biology*, **12** (22), pp. 1934–1940. doi: 10.1016/S0960-9822(02)01300-3

Northoff, G. & Lamme, V.A.F. (2020) Neural signs and mechanisms of consciousness: Is there a potential convergence of theories of consciousness in sight?, *Neuroscience & Biobehavioral Reviews*, **118**, pp. 568–587. doi: 10.1016/j.neubiorev.2020.07.019

Nunn, J.F., Sturrock, J.E., Wills, E.J., Richmond, J.E. & McPherson, C.K. (1974) The effect of inhalational anaesthetics on the swimming velocity of Tetrahymena pyriformis, *Journal of Cell Science*, **15** (3), pp. 537–554.

Oudiette, D., Leu, S., Pottier, M., Buzare, M.-A., Brion, A. & Arnulf, I. (2009) Dreamlike mentations during sleepwalking and sleep terrors in adults, *Sleep*, **32** (12), pp. 1621–1627.

Penn, D.C. & Povinelli, D.J. (2007) On the lack of evidence that non-human animals possess anything remotely resembling a 'theory of mind', *Philosophical Transactions of the Royal Society B: Biological Sciences*, **362** (1480), pp. 731–744. doi: 10.1098/rstb.2006.2023

Pennartz, C.M.A., Farisco, M. & Evers, K. (2019) Indicators and criteria of consciousness in animals and intelligent machines: An inside-out approach, *Frontiers in Systems Neuroscience*, **13**, art. 25. doi: 10.3389/fnsys.2019.00025

Perry, C.J. & Barron, A.B. (2013) Honey bees selectively avoid difficult choices, *Proceedings of the National Academy of Sciences*, **110** (47), pp. 19155–19159. doi: 10.1073/pnas.1314571110

Petruno, S.K., Clark, R.E. & Reinagel, P. (2013) Evidence that primary visual cortex is required for image, orientation, and motion discrimination by rats, *PLoS ONE*, **8** (2), e56543. doi: 10.1371/journal.pone.0056543

Phillips, I. (2021) Bias and blindsight: A reply to Michel and Lau (2021), *Psychological Review*, **128** (3), pp. 592–595. doi: 10.1037/rev0000277

Rattenborg, N.C., de la Iglesia, H.O., Kempenaers, B., Lesku, J.A., Meerlo, P. & Scriba, M.F. (2017) Sleep research goes wild: New methods and approaches to investigate the ecology, evolution and functions of sleep, *Philosophical Transactions of the Roysal Society B: Biological Sciences*, **372** (1734), 20160251. doi: 10.1098/rstb.2016.0251

Reber, A.S. (2018) *The First Minds: Caterpillars, Karyotes, and Consciousness*, New York: Oxford University Press. doi: 10.1093/oso/9780190854157.001.0001

Robichaud, L. & Stelmach, L.B. (2003) Inducing blindsight in normal observers, *Psychonomic Bulletin & Review*, **10**, pp. 206–209.

Rolls, E.T. & Tovee, M.J. (1994) Processing speed in the cerebral cortex and the neurophysiology of visual masking, *Proceedings of the Royal Society B: Biological Sciences*, **257**, pp. 9–15. doi: 10.1098/rspb.1994.0087

Rosanova, M., Gosseries, O., Casarotto, S., Boly, M., Casali, A.G., Bruno, M.-A., Mariotti, M., Boveroux, P., Tononi, G., Laureys, S. & Massimini, M. (2012) Recovery of cortical effective connectivity and recovery of consciousness in vegetative patients, *Brain*, **135** (4), art. 4. doi: 10.1093/brain/awr340

Sarasso, S., Boly, M., Napolitani, M., Gosseries, O., Charland-Verville, V., Casarotto, S., Rosanova, M., Girardi Casali, A., Brichant, J.-F., Boveroux, P., Rex, S., Tononi, G., Laureys, S. & Massimini, M. (2015) Consciousness and complexity during unresponsiveness induced by propofol, xenon, and ketamine, *Current Biology*, **25** (23), art. 23. doi: 10.1016/j.cub.2015.10.014

Self, M.W., Kooijmans, R.N., Supèr, H., Lamme, V.A.F. & Roelfsema, P.R. (2012) Different glutamate receptors convey feedforward and recurrent processing in macaque V1, *Proceedings of the National Academy of Sciences USA*, **109**, pp. 11031–11036. doi: 10.1073/pnas.1119527109

SelfAwarePatterns (2020) The issues with biopsychism, *SelfAwarePatterns*, [Online] https://selfawarepatterns.com/2020/05/16/the-issues-with-biopsychism/ [accessed 26 November 2021].

Stein, T., Kaiser, D., Fahrenfort, J.J. & van Gaal, S. (2020) Processing of subjectively and objectively invisible stimuli in human visual cortex, *bioRxiv*. doi: 10.1101/2020.11.11.376681

Stoerig, P. (1997) Blindsight in man and monkey, *Brain*, **120** (3), pp. 535–559. doi: 10.1093/brain/120.3.535

Supèr, H., Spekreijse, H. & Lamme, V.A.F. (2001) Two distinct modes of sensory processing observed in monkey primary visual cortex (V1), *Nature Neuroscience*, **4** (3), art. 3. doi: 10.1038/85170

Supèr, H., van der Togt, C., Spekreijse, H. & Lamme, V.A.F. (2003) Internal state of monkey primary visual cortex (V1) predicts figure-ground perception, *Journal of Neuroscience*, **23**, pp. 3407–3414.

Tong, F., Meng, M. & Blake, R. (2006) Neural bases of binocular rivalry, *Trends in Cognitive Science*, **10** (11), pp. 502–511. doi: 10.1016/j.tics.2006.09.003

Tononi, G. & Massimini, M. (2008) Why does consciousness fade in early sleep?, *Annals of the National Academy of Sciences*, **1129**, pp. 330–334. doi: 10.1196/annals.1417.024

Tononi, G. & Cirelli, C. (2014) Sleep and the price of plasticity: From synaptic and cellular homeostasis to memory consolidation and integration, *Neuron*, **81** (1), pp. 12–34. doi: 10.1016/j.neuron.2013.12.025

Tudor, M., Tudor, L. & Tudor, K.I. (2005) Hans Berger (1873–1941) — the history of electroencephalography, *Acta medica Croatica: casopis Hravatske akademije medicinskih znanosti*, **59** (4), pp. 307–313.

van Kerkoerle, T., Self, M.W., Dagnino, B., Gariel-Mathis, M.-A., Poort, J., van der Togt, C. & Roelfsema, P.R. (2014) Alpha and gamma oscillations characterize feedback and feedforward processing in monkey visual cortex, *Proceedings of the National Academy of Sciences USA*, **111** (40), pp. 14332–14341. doi: 10.1073/pnas.1402773111

Vinauger, C., Lahondère, C., Wolff, G.H., Locke, L.T., Liaw, J.E., Parrish, J.Z., Akbari, O.S., Dickinson, M.H. & Riffell, J.A. (2018) Modulation of host learning in Aedes aegypti mosquitoes, *Current Biology*, **28** (3), pp. 333–344. doi: 10.1016/j.cub.2017.12.015

Weiskrantz, L. (1996) Blindsight revisited, *Current Opinion in Neurobiology*, **6**, pp. 215–220.

Weiskrantz, L. (2004) Roots of blindsight, *Progress in Brain Research*, **144**, pp. 229–241. doi: 10.1016/s0079-6123(03)14416-0

White, D.C. & Dundas, C.R. (1969) The effect of anaesthetic agents on the emission of light by luminous bacteria, *British Journal of Anaesthesia*, **41** (2), p. 194.

Wudick, M.M., Michard, E., Oliveira Nunes, C. & Feijó, J.A. (2018) Comparing plant and animal glutamate receptors: Common traits but different fates?, *Journal of Experimental Botany*, **69** (17), pp. 4151–4163. doi: 10.1093/jxb/ery153

Wynne, C.D.L. (2004) The perils of anthropomorphism, *Nature*, **428** (6983), pp. 606–606. doi: 10.1038/428606a

Yokawa, K., Kagenishi, T., Pavlovič, A., Gall, S., Weiland, M., Mancuso, S. & Baluška, F. (2018) Anaesthetics stop diverse plant organ movements, affect endocytic vesicle recycling and ROS homeostasis, and block action potentials in Venus flytraps, *Annals of Botany*, **122** (5), pp. 747–756. doi: 10.1093/aob/mcx155

Yokawa, K., Kagenishi, T. & Baluška, F. (2019) Anesthetics, anesthesia, and plants, *Trends in Plant Sciences*, **24** (1), pp. 12–14. doi: 10.1016/j.tplants.2018.10.006.

Yoshida, M. & Isa, T. (2015) Signal detection analysis of blindsight in monkeys, *Scientific Reports*, **5** (1), 10755. doi: 10.1038/srep10755

Zalucki, O. & van Swinderen, B. (2016) What is unconsciousness in a fly or a worm? A review of general anesthesia in different animal models, *Consciousness & Cognition*, **44**, pp. 72–88. doi: 10.1016/j.concog.2016.06.017

Zhan, Y., Alonso San Alberto, D., Rusch, C., Riffell, J.A. & Montell, C. (2021) Elimination of vision-guided target attraction in Aedes aegypti using CRISPR, *Current Biology*, July 2021. doi: 10.1016/j.cub.2021.07.003

Zipser, K., Lamme, V.A.F. & Schiller, P.H. (1996) Contextual modulation in primary visual cortex, *Journal of Neuroscience*, **16**, pp. 7376–7389.

Zou, J., He, S. & Zhang, P. (2016) Binocular rivalry from invisible patterns, *Proceedings of the National Academy of Sciences*, **113** (30), pp. 8408–8413. doi: 10.1073/pnas.1604816113