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Animal Consciousness

The Interplay of Neural and Behavioural Evidence

Abstract: *We consider the relationship between neural and behavioural evidence for animal consciousness. We critically examine two recent studies: one neural and one behavioural. The first, on crows, finds different neural activity depending on whether a stimulus is reported as seen or unseen. However, to implicate this neural activity in consciousness, we must assume that a specific conditioned behaviour is a report of conscious experience. The second study, on macaques, records behaviours strikingly similar to patterns of conscious and unconscious perception in humans. However, confounds are only ruled out in human subjects, presupposing substantial neural similarity between humans and macaques. Taken together, the two studies reveal a sense in which neural and behavioural research rely on each other. Looking ahead, these two types of evidence could prove to be either mutually reinforcing or mutually undermining. The science of animal consciousness needs both neural and behavioural evidence, ideally obtained as part of a single coordinated programme.*

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1. Introduction

Consciousness raises some of the greatest challenges in science. Where are its neural circuits? What is its adaptive function? When did it evolve? Which animals are conscious? Many biologists set these questions aside as too difficult to answer. The questions are all the more daunting when we focus on phenomenal consciousness: subjective, qualitative experience. There is something it feels like to experience colours, sounds, odours, pleasures, pains, and so on, but nothing it feels like to be in dreamless sleep (Nagel, 1974; Schwitzgebel, 2016). This 'something it feels like' (or 'something it's like') is the property we want to understand.

Difficult as these questions are, the last few decades have provided some grounds for optimism about their tractability. A science of consciousness has emerged, which employs various methods to probe the neural and cognitive signatures of conscious experience. While substantial disagreement remains, consciousness scientists increasingly target the mechanisms underlying phenomenal consciousness, not just 'consciousness' in some other, more overtly functional sense of the word (such as 'access consciousness'; Block, 1995). So far, though, consciousness science has focused on humans, albeit with a substantial amount of work on non-human primates (e.g. Cowey and Stoerig, 1995; Moore *et al.*, 1995; Supèr, Spekreijse and Lamme, 2001). This raises the tantalizing prospect of using similar techniques to study consciousness in a much wider range of animals. But which techniques should we use, and how should we adapt them for non-human animals?

Our overarching question, posed by the editors of this special issue, is: *what is stronger evidence of consciousness in animals: behaviour or neural mechanisms?* This question does not imply that behavioural and neural evidence are opposed, or that we must choose between them. Both can be pursued in parallel and complement each other. For example, when faced with the issue of whether octopuses have conscious experiences, a case based on both behavioural evidence (e.g. conditioned place preference behaviour; Crook, 2021) and neural evidence (e.g. an unusually large vertical lobe, linked to learning and memory; Shomrat *et al.*, 2015) is clearly stronger than a case based on just one type of evidence. Various authors have, therefore, recommended criteria for animal sentience that include both behavioural and neural indicators (e.g. Birch *et al.*, 2021; Smith and Boyd, 1991; Sneddon *et al.*, 2014).

Even so, one can ask about the relationship between behavioural and neural evidence of consciousness (Boly *et al.*, 2013; Edelman and Seth, 2009; Paul *et al.*, 2020; Seth *et al.*, 2008). How do the two types of evidence interact? Is one intrinsically a higher-quality form of evidence than the other? Are they separate pieces of the puzzle, or interdependent in certain ways? Does one have precedence? To explore these questions, we will critically analyse two recent experimental studies. One appears to provide mainly neurofunctional evidence, but relies on assumptions about which behaviours are consciousness-linked. The second apparently provides mainly behavioural evidence, but assumes substantial neurofunctional similarity between the study species and humans. Together, these examples suggest ways that neural and behavioural research might be mutually reinforcing or mutually undermining. This leads us to propose a coordinated science of animal consciousness, where neural and behavioural researchers rigorously and systematically probe each other's assumptions.

2. Neural Evidence

There is a long history of attempting to dissociate conscious and unconscious processing in primates through neurological interventions. A landmark is the work by Cowey and Stoerig (1995) on blindsight in monkeys. In cases of blindsight, humans with lesions to the primary visual cortex (V1) report blindness in a particular region of the visual field — but can still use information presented in that region to perform at above-chance levels in forced-choice tasks. Cowey and Stoerig observed a similar dissociation between performance in two tasks in macaques with lesions to V1 (*ibid.*). One task required animals to condition their responses on the location of a stimulus (a forced-choice task), while the other required them to condition their responses on whether a stimulus was there at all (a yes-no task). Yoshida & Isa (2015) recently demonstrated a similar dissociation using more rigorous methods.

This may seem like compelling evidence of consciousness in monkeys. But there is a problem (Heyes, 2008; Shea and Heyes, 2010; Hampton, 2021). A sceptic will not grant the background assumption that the broadly 'report-like' behaviour in the yes-no task, where the macaques were tasked with discriminating between the presence of any visual stimulus and a blank screen, was reporting the *conscious* perception of a stimulus, rather than being just another behaviour guided by unconscious information. So Cowey and Stoerig's evidence will not convince a sceptic. It is more directly relevant to a different question: does conscious visual processing in monkeys — *presupposing that it exists* — depend on the same brain regions as conscious visual processing in humans?

It is important to note here that serious critics (such as Heyes) are not motivated by a belief that monkeys or other animals are *not* conscious. Their motivation is a concern about the quality of the evidence cited in support of ascriptions of consciousness. These concerns need to be taken seriously, even though (like Heyes)[2] we are already strongly inclined to ascribe consciousness to monkeys, and indeed to all mammals and birds.

Later in this section, we will discuss an innovative attempt to discover neural evidence of consciousness in corvids (Nieder, Wagener and Rinnert, 2020). We will consider how some of the criticisms of Cowey and Stoerig's work might extend to this study. First, however, we must introduce the human consciousness research it relies on — and the limitations of that research.

2.1. The search for neural correlates of consciousness in humans

In human consciousness science, a prominent approach is to compare brain activity associated with conscious and unconscious states (Lamme, 2006; Dehaene and Changeux, 2011). Activity that systematically co-occurs with conscious processing is described as a 'neural/neuronal correlate of consciousness' or NCC (Crick and Koch, 1990; Koch *et al.*, 2016; Rees, Kreiman and Koch, 2002). For example, NCC researchers may compare the neural signatures of awake versus anaesthetized people (Alkire and Miller 2005), dreaming versus dreamless sleep (Fazekas and Nemeth, 2018; Siclari *et al.*, 2017), and conscious versus unconscious perception (Kreiman, Fried and Koch, 2002).

The term 'correlate' is intended to be neutral about the metaphysical relationship between neural activity and conscious experience. The hope is that consciousness science can advance without metaphysical consensus. In fact, the term is potentially misleading, because

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[2] 'I assume on non-scientific grounds that many animals experience phenomenally conscious states — that they are not "beast machines" — and I find it plausible that, at some time in the future, the presence and character of these states will be discoverable by scientific methods' (Heyes, 2008, pp. 271–2).

correlation is a promiscuous relation: remote causes and effects of a variable often correlate with it, but we are not looking for the remote causes or effects of consciousness. If an experimenter controls the stimuli entering your brain, their brain's neural activity will correlate with your experiences, but that neural activity is a remote cause of your experience, not its basis. We really care about the *neural basis* of consciousness: neural activity that is intimately linked to consciousness and that in some sense *suffices* for it. We will use the term 'NCC' with the caveat that the neural activity of interest is not just a correlate: it is the neural basis of consciousness (Seth, 2009).

In the search for NCCs, human consciousness science has typically relied on subjects *voluntarily self-reporting* their conscious experiences. These reports may be verbal ('I saw…') or another voluntary motor response, like pressing a button when the stimulus is consciously seen (Kreiman, Fried and Koch, 2002). Self-reporting presents a notorious challenge: separating the neural basis of *consciousness* from the neural basis of *report*. To identify an NCC, we would have to be confident that *only* conscious experience systematically changes between conscious and non-conscious conditions (Crick and Koch, 1990). But if we rely on reports to identify the conscious condition, something else will also vary: the report will be systematically different in the conscious condition (Pitts, Metzler and Hillyard, 2014; Tsuchiya *et al.*, 2015). If different cognitive mechanisms are involved in reporting stimulus presence or absence, this would create a potential confound (but see Michel and Morales, 2020).

The self-report issue underpins ongoing debate over where consciousness arises in the human brain. One camp proposes the frontoparietal cortex, a network that unifies various input (e.g. sensory) and output systems (e.g. behaviour). Evidence comes from contrastive NCC studies linking frontoparietal activation to wakeful states and conscious information processing (Baars, 2005; Dehaene *et al.*, 2001). This view is associated with the global workspace theory of consciousness, which links conscious experience to a global broadcast mechanism. The proposed mechanism integrates representations from perceptual, affective, and memory systems, and broadcasts the integrated content back to both the input systems and various consumer systems, including decision-making, planning, and report mechanisms (Dehaene and Changeux, 2011, p. 209).

A second camp attributes this consciousness-linked frontoparietal activity to downstream metacognitive processes, such as introspection and report. They nominate a posterior cortical 'hot zone' as the true

NCC (Boly *et al.*, 2017; Koch *et al.*, 2016). This view is associated with rivals to global workspace theory, such as the integrated information theory (Tononi and Koch, 2015) and the recurrent processing theory (Lamme, 2006; Lamme, this issue). The dispute highlights the challenge that confounding cognitive processes pose to the NCC approach.

To reduce reliance on self-reports, no-report paradigms have been developed (Tsuchiya *et al.*, 2015; Pitts, Lutsyshyna and Hillyard, 2018). These use other behavioural and physiological correlates of consciousness. For example, Frässle *et al.* (2014) compared neural activity when humans either reported or did not report their experience. The study employed binocular rivalry, where individuals are simultaneously shown different stimuli in each eye. Humans perceive both stimuli but report seeing them alternate (Tong, Meng and Blake, 2006). Frässle *et al.* asked participants to report when the stimulus alternated, but also recorded no-report indicators of stimulus alternations (eye movements and pupil size). The subjective reports tightly correlated with the no-report measures. However, frontal activation differed between the report and no-report conditions, so this frontal activity was interpreted as a neural correlate of report, rather than a true NCC. No-report paradigms using eye movements have also been tested on animals (e.g. cats: Fries *et al.*, 1997; macaques: Kapoor *et al.*, 2020). The approach, as carried out in humans, does not avoid report entirely, because report is used to find and validate the no-report indicator. But report is intended to be a ladder we kick away: the validated no-report indicator can be used without report.

However, no-report paradigms face the challenge of disentangling the neural basis of consciousness from the neural basis of *preconscious* processing (Phillips, 2018). As an analogy, the speed of a falling barometer reading correlates with the intensity of an approaching storm, but the falling barometer reading is just a precursor to the storm, not the storm itself. In a similar vein, eye movements and pupil size may correlate with the content of representations in occipital visual areas, so, when those representations go on to be consciously perceived, these variables would correlate with the contents of conscious experience as well. Nonetheless, the representations might only be consciously perceived when they are globally broadcast. It begs the question against a global workspace theorist to assume that, by finding a good, no-report indicator of the contents of occipital visual areas, we have found the neural basis of consciousness. Maybe we have just found a good barometer.

We can distinguish two broad categories of potential confound, which correlate with consciousness without forming part of its basis: (i) cognitive, sensory, or perceptual processes that precede conscious experience, and (ii) cognitive and behavioural processes that follow and draw upon conscious experience. Following Aru *et al.* (2012), we call the former *NCC precursors* and the latter *NCC consequences*. NCC precursors may facilitate conscious processing without sufficing for it. An especially challenging NCC precursor to disentangle from consciousness (if it is distinct at all) is *attention*, the selective allocation of perceptual and cognitive resources to a particular stimulus (Chun, Golomb and Turk-Browne, 2011; Crump, Arnott and Bethell, 2018). In masking tasks, for instance, different attention levels may explain why some stimuli are seen and not others, confounding NCCs with the neural basis of attention (Lepauvre and Melloni, 2021; Nani *et al.*, 2019). Meanwhile, many theories posit that consciousness facilitates further cognitive functions, and the neural basis of these functions may be confounded with NCCs. In addition to report, other examples include task monitoring, working memory, and introspection (Aru *et al.*, 2012; Overgaard, 2004; Soto and Silvanto, 2014; Tsuchiya *et al.*, 2015). Even no-report paradigms may involve some metacognitive confounds, in addition to possible pre-conscious confounds (Overgaard and Fazekas, 2016).

2.2. Neural correlates of consciousness in crows?

With all this methodological controversy in the background, let us turn to corvids. Nieder, Wagener and Rinnert (2020) trained two carrion crows (*Corvus corone*) on a delayed stimulus detection task (Figure 1). In 50% of trials, a grey square flashed onscreen (stimulus present). In the other 50%, the screen stayed blank (stimulus absent). A 2.5-second delay followed, and then birds were shown a rule cue: either a red or blue square.

When the red square appeared, the correct (rewarded) motor response was to move if the stimulus had been present ('go'), but remain stationary if the stimulus had been absent ('no-go'). When the blue square appeared, the correct motor response was no-go if the stimulus had been present, but go if the stimulus had been absent. Birds did not know in advance whether the red or blue square would appear. In effect, the goal of the training was to teach the crows two conditional rules:

If you see the grey square, go only on the red cue.
If you do not see the grey square, go only on the blue cue.

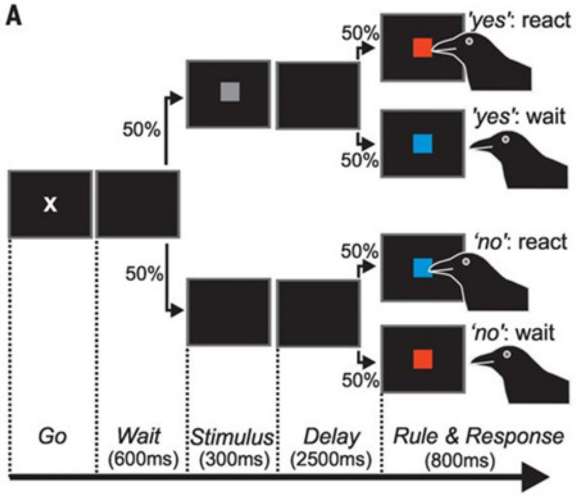

Figure 1. From Nieder, Wagener and Rinnert (2020) (reprinted with permission from AAAS).

This conditional responding plays, for Nieder *et al.*, the role that reports play in human NCC research. The birds were trained in conditions where the grey square was either absent or clearly visible. When the stimulus was high intensity and clearly visible, the crows learned to implement the rules with almost 100% accuracy (see Figures 1B and 1C in Nieder, Wagener and Rinnert, 2020). The researchers then reduced the visibility of the grey squares, to a point where the 'go on red' response was only observed about 50% of the time. This was taken as evidence that the grey square was only being *consciously perceived* about 50% of the time. In other words, the 'go on red' or 'no-go on blue' responses were interpreted as a *non-verbal report* of conscious perception of a grey square, whilst the 'no-go on red' and 'go on blue' responses were interpreted as a non-verbal report of the animal consciously perceiving no grey square.

To identify potential NCCs during the task, Nieder *et al.* recorded the activity of 480 neurons in the nidopallium caudolaterale, a functional analogue of the mammalian prefrontal cortex (Güntürkün, 2005). They compared neural firing for grey square stimuli of different intensities around the perceptual threshold, as well as between trials that led to 'go on red' and 'go on blue' responses. One population of neurons fired at the same rate for near-threshold stimuli of the same intensity, regardless of the crows' subsequent reports. This population was interpreted as registering stimulus intensity. A second neuron population fired at different rates for stimuli of the same intensity, *but correlated with the subsequent 'reporting' behaviour*. This population was interpreted as an NCC.

The conditional rule was important here. If crows always reported stimulus presence with either a go or no-go response, the different neural activity between reporting conditions (Nieder *et al.*'s proposed NCCs) could have been the basis of the upcoming motor response — not conscious perception of the stimulus. However, in the 2.5-second delay before the rule cue appeared, crows did not know whether the cued behaviour would be a go or no-go response. This depended on whether the rule cue was a red or blue square. Nieder *et al.*, therefore, claimed that the differential neural firing during the delay period could only be attributed to consciousness. They therefore concluded that the recorded activity is an 'empirical marker of avian consciousness' that 'excludes the proposition that only primates or other mammals possessing a layered cerebral cortex are endowed with sensory consciousness'.[3]

2.3. The challenge from unconscious vision

Let us now consider what a critic (in the style of Heyes, 2008) would say about this experiment. We think they would reply that, while the activity recorded in the nidopallium caudolaterale is evidence of processing that mediates between sensory and motor processes, it need not correspond to conscious perception. This is because there are various cognitive processes (such as task monitoring, inference,

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[3] As an aside, it is interesting to compare these results to those of an experiment on macaques by Supèr, Spekreijse and Lamme (2001). Supèr *et al.* trained monkeys to either report seeing (by making a saccadic eye movement) or not seeing a stimulus (by maintaining fixation), while recording neural activity in V1. They found that modulation of neural activity was strongly predictive of subsequent reporting behaviour (and not just stimulus-driven) when the stimulus was highly salient, yet uncorrelated with reporting behaviour when the stimulus was just perceptible. They concluded that the modulated activity 'seems to reflect some internal representation of the stimulus that may function as an intermediate between strictly sensory and decision-making processes'. A striking difference is that Supèr *et al.* found this 'intermediate' in V1, whereas Nieder *et al.* found their intermediate in an area linked to higher cognitive processing.

attention, working memory, planning, and intention formation) that mediate between sensory and motor processes, and that may be dissociable from conscious perception. For example, the differential neural activity could correspond to the crows registering a stimulus as unexpected, or as requiring a change to a default behavioural response.

Moreover, our critic would ask: were the crows' head movements really reports of conscious experience? The underlying assumption seems to be that such a sophisticated learned behaviour could not be achieved without conscious perception of the grey square. There is some plausibility to this, especially given the 2.5-second time delay between the grey square and the coloured cue. In humans, temporal integration over this sort of timescale, as required by trace conditioning paradigms, has only been observed when the stimuli are consciously perceived (Clark and Squire, 1998; 1999; Mudrik. Faivre and Koch, 2014; Yang *et al.*, 2017).

However, we can challenge the link between crows' head movements and consciousness. A particular issue is unconscious vision-for-action. Human subjects respond in sophisticated ways to masked primes: stimuli they do not consciously see (Ansorge, Kunde and Kiefer, 2014; Eimer and Schlaghecken, 2003). For example, masked stop signals inhibit motor actions (van Gaal *et al.*, 2009), a reaction similar to the crows' no-go responses, albeit in a simpler learning task. If unconsciously-perceived stimuli can prime response inhibition in humans, why not in crows? A critic may therefore object: *have we found the neural basis of consciousness in these crows, or the neural basis of unconscious vision-for-action?*

Can we overcome this objection? In their review of masked priming and its effects on executive function, Ansorge, Kunde and Kiefer (2014) concluded that a fundamental difference between primed and unprimed responses is *flexibility*. Masked primes influence a limited range of pre-set functions, such as no-go responses (e.g. van Gaal *et al.*, 2009) and simple reports (e.g. Pfister *et al.*, 2012). Ansorge *et al.* suggested that conscious processing enables people to formulate new plans and execute novel responses. Conscious cognition, therefore, has far more potential outcomes than unconscious cognition. The link between consciousness and flexible/novel behaviour has been emphasized by, among others, defenders of the global workspace theory (Dehaene, 2014), by Ginsburg, Jablonka, and collaborators in their work on unlimited associative learning (Bronfman, Ginsburg and Jablonka, 2016; Ginsburg and Jablonka, 2019; Birch, Ginsburg and

Jablonka, 2020), by Shea and Heyes (2010), and by Griffin (1976; 2013). It seems that humans are excellent subjects for consciousness research not specifically because they have language (though this clearly helps), but because they can easily perform *flexible, novel, untrained report behaviours*.

Applied to animals, these unconscious vision-for-action findings make operant behaviours unconvincing self-reports of conscious vision. We should instead record novel and flexible behavioural responses. Although corvids can display such behaviours (Bird and Emery, 2009; Emery and Clayton, 2004), they do not precisely track the perceived stimulus like a report would. The two crows in the Nieder *et al.* study underwent an eye-watering number of training trials (26,000 and 41,000, respectively; Nieder, personal communication). This raises the question of whether the behaviour is a genuine report of conscious perception or a trained response to an unconscious prime.

What might resolve this issue? One way forward could be to investigate the speed and flexibility of processing. Because unconscious responses only use a small set of pre-prepared options, they can be faster than conscious deliberation (Ansorge, Kunde and Kiefer, 2014). Humans subsequently trade-off the flexibility of conscious processing against its longer duration. Distinct fast and slow response systems might, therefore, indicate distinct unconscious and conscious processing in animals. We would expect the fast (unconscious) system to produce a limited range of simple responses (as in Nieder, Wagener and Rinnert, 2020), whilst a putative slow (conscious) system would generate diverse flexible behaviours.

Another characteristic of conscious perception is *integration* (Baars, 2005; Dehaene and Changeux, 2011; Lamme, 2006; Tononi and Koch, 2015). Humans consciously see an object's visual features, such as colour, shape, and texture, as one unified whole. Unconscious vision can process such features individually, but struggles to combine them (Tapia, Breitmeyer and Shooner, 2010). As such, evidence of conscious vision in animals would be more convincing if the learned rules required integrating multiple visual features, rather than just one feature (in Nieder, Wagener and Rinnert, 2020: colour).

In humans, integration across sensory modalities is also linked to conscious perception (Deroy *et al.*, 2016; Palmer and Ramsey, 2012; but see Arzi *et al.*, 2012; Faivre *et al.*, 2014; Scott *et al.*, 2018). Perhaps, then, we could train animals to report the stimulus presence using one sensory modality, with testing on the same stimuli in a different modality. For example, Solvi, Al-Khudhairy and Chittka (2020) rewarded bumblebees (*Bombus terrestris*) for approaching either a sphere or a cube, which the bees could see but not touch. When the lights were switched off, forcing the bees to rely on touch, they spent more time on the rewarded shape. A similar cross-modal paradigm, which required perceptual reports in an unexpected sensory modality, would represent the kind of flexible, novel reporting behaviour linked to conscious vision in humans. In general, the more integration of various kinds necessary to implement the 'reporting rule', the more plausible conscious perception of the stimulus becomes. Most convincing would be integration across time, across features, *and* across modalities.

But suppose we trained birds to report their experiences in integrative, flexible ways. At this point, what would recording neurons in the nidopallium caudolaterale add to the case for consciousness? It may tell us about the neural basis of consciousness in crows, but the basic case that crows are consciously perceiving the stimuli would be fundamentally behavioural. It would come from aspects of the report-like behaviour (i.e. that it involves integration across time and across visual features), plus an assumption that conscious vision facilitates these integrative functions in birds, as in humans (Birch, 2020). Finding that a specific brain region implements these functions would neither weaken nor strengthen this case. Moreover, we would still not have disentangled the proposed NCCs from NCC precursors and NCC consequences.

The upshot is that there is no 'neural shortcut' to evidence of conscious perception in animals. Understanding the relationship between conscious experience and behaviour, to identify behavioural markers of consciousness, is an indispensable step (see also Niv, 2021).

3. Behavioural Evidence

Many behaviours have been claimed to be good indicators of consciousness. Two examples are mirror self-recognition (Gallup, 1970; Heschl and Burkart, 2006; Kohda *et al.*, 2019) and motivational trade-offs (Appel and Elwood, 2009; Dunlop, Millsop and Laming, 2006; Elwood and Appel, 2009). However, sceptics often reply that, without evidence that *only* conscious processing could produce such behaviours, these indicators are not very convincing (e.g. Heyes, 2008; Irvine, 2020; Dawkins, 2021). Moreover, lists of behavioural criteria have usually been *post hoc* collations of disparate evidence, rather than frameworks for an integrated research programme. How might we find and validate behavioural indicators of consciousness? For one answer, let us turn to a recent study that attempts to dissociate unconscious and conscious perception in macaques (Ben-Haim *et al.*, 2021).

3.1. Separating conscious and unconscious perception in humans

Conscious and unconscious perception differ. When you watch a movie, you consciously see the scenes, settings, and characters. These elements are perceived *supraliminally* (i.e. consciously). But, if one frame of something else is discreetly slipped in, it may register *subliminally* (i.e. unconsciously). Human consciousness researchers have long exploited this difference to study the distinctive neural and cognitive signatures of conscious (as opposed to unconscious) processing.

One way to disentangle conscious from unconscious processing in humans involves crossover double dissociation paradigms, which aim to behaviourally dissociate different cognitive mechanisms (Debner and Jacoby, 1994; Dehaene, 2014; Merikle, Joordans and Stolz, 1995). So, to dissociate conscious from unconscious perception, we might use stimuli that elicit opposite behavioural responses depending on whether they are supraliminal or subliminal. For example, subjects might be shown a reference word (e.g. 'SPICE') either supraliminally or subliminally. They must then complete a word stem (e.g. 'SPI…') *without* using the reference word. When the reference is supraliminal, subjects tend to correctly give a different word (e.g. 'SPIKE'). When the reference is subliminal, subjects tend to incorrectly give the reference word. Although that example involves language, the general idea does not require it. As such, if we could find analogous double dissociation in other species, we could study the signatures of conscious processing in those species too.

3.2. Conscious and unconscious perception in macaques?

Ben-Haim *et al.* (2021) tested a crossover double dissociation paradigm on four rhesus macaques (*Macaca mulatta*), which were compared with 145 adult humans (Figure 2). The paradigm was a spatial cueing task, where subjects must locate a target stimulus displayed at one of two locations on a screen (Herreros, Lambert and Chica, 2017; Posner, 1980). Preceding the target was a predictive cue that appeared at the *opposite* location to the target. Such cues are called 'incongruent'. These incongruent cues were presented either supraliminally (for 250 ms) or subliminally (for 17 or 33 ms).

The authors hypothesized that conscious perception would *facilitate learning*, with subjects shown supraliminal cues learning the incongruent rule and locating the target faster than at chance level. Conversely, they hypothesized that stimuli perceived non-consciously would attract attention *without facilitating learning*, impairing task performance. The authors thus predicted slower responses than at chance level for the subliminal cues. Such findings would show a form of double dissociation: conscious processing improving performance by facilitating learning and non-conscious processing impairing performance by drawing attention.[4]

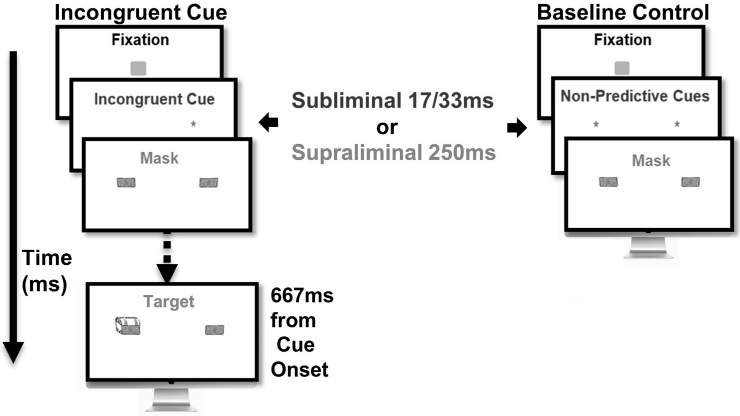

Figure 2. From Ben-Haim *et al.* (2021) (reprinted with permission from *PNAS*).

As predicted, both humans and macaques located the target faster following supraliminal cues than subliminal cues. When presented supraliminally, the incongruent cues also generated faster reaction times than non-predictive cues, whereas subliminal incongruent cues generated slower reaction times than subliminal non-predictive cues. Human subjects reported not having seen the subliminal cues,

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[4] Hampton (2021) finds this an inappropriate use of the term 'double dissociation', arguing that there must be two separate tasks for a true double dissociation, not just two effects on the same task in opposite directions. We will continue to say 'double dissociation' while acknowledging that the term may sometimes be defined more narrowly.

confirming that they were processed non-consciously. Conscious and non-conscious processing, therefore, generated opposite response patterns in this spatial-cueing task: supraliminal cues facilitated performance; subliminal cues impaired performance. This double dissociation was strikingly similar in macaques and humans.

Like Nieder *et al.*, Ben-Haim *et al.* make some bold claims about the quality of evidence of conscious visual perception (or, in their terms, awareness) provided by their study. They write that 'it was long considered impossible to untangle whether animals are aware or just conditionally or nonconsciously behaving. Here, we developed an empirical approach to address this question', and 'these results show that our species is not unique in terms of awareness to the environment or visual stimuli around us' (Ben-Haim *et al.*, 2021). While (as already noted) monkeys are not generally considered a controversial candidate for consciousness, the hope must be that the same methodological strategy can be extended to a wider range of animals, including more controversial candidates such as fish and invertebrates. So, let us again consider how a Heyes-style critic might respond.

3.3. The confound of signal strength

Supraliminal cues are stronger signals, so potentially easier to learn, than subliminal cues. As such, stronger signals — not conscious perception — may explain why supraliminal cues improve learning performance. The possible confounding effect of signal strength is a persistent issue in consciousness science (Lau, 2011).

Ben-Haim and colleagues sought to address the signal strength confound using two strategies. First, they informed some human subjects about the subliminal cues part way through the forced-choice experiment. Many subjects subsequently reported seeing the cues and performed nearly as well as in the supraliminal condition. Informing subjects did not increase signal strength, but nonetheless improved performance. This suggests that cue awareness, rather than signal strength, explains the opposite results for supraliminal and subliminal cues.

Second, in a further variation, human subjects were told at the outset that incongruent cues predicted the target's location, eliminating the need for learning. The response pattern persisted: subjects performed above chance when they reported seeing the cue and below chance when they reported not seeing the cue.

A critic may object: this indicates that signal strength did not underpin the dissociation *in humans*, but does not rule it out *in macaques*. Implicitly, Ben-Haim *et al.* invoke an argument from analogy. They assume that, given the similarities between humans and macaques, an alternative explanation which is implausible for humans is also implausible for macaques.

That argument from analogy is persuasive, but only against a background of substantial neurobiological similarity between humans and macaques — a background that makes consciousness in macaques extremely plausible to begin with. Even in other mammals, such as rats, masked stimuli do not reliably induce human-like response patterns (Dell, Arabzadeh and Price, 2018; 2019). As such, once we look beyond primates, addressing confounds in humans and relying on the argument from analogy is not a widely applicable approach. Evidence for conscious perception in more controversial candidates — such as bees, crabs, or octopuses — must avoid such a leap. In the case of these invertebrates, our imagined critic would argue that ruling out an alternative explanation based on signal strength *in humans* does not rule it out *in invertebrates* (or even in non-primate mammals).

3.4. Systematic facilitation as a solution to the signal strength problem

Does the signal strength problem have a more general solution? To avoid arguments from analogy, this is an urgent question for animal consciousness research. Here is one proposal: by varying stimulus duration (or contrast) continuously, we could use the double dissociation paradigm to identify a putative subliminal/supraliminal threshold — usually called a 'subjective threshold' — in our target species.

Suppose we identified a putative subjective threshold at around 50 ms, marked by a step change in task performance. We could then ask: do we find this *same* putative subjective threshold across a *range of tasks*? As discussed earlier, various cognitive abilities, especially forms of learning and integration, have been linked to consciousness (Ginsburg and Jablonka, 2019; Paul *et al.*, 2020). Trace conditioning apparently requires conscious awareness of the stimuli (Clark and Squire, 1998; 1999); cross-modal influence may need conscious perception of the influencing modality (Palmer and Ramsey, 2012); and reversal learning is at least faster for unmasked than masked stimuli (Travers, Frith and Shea, 2018). These diverse cognitive abilities might provide a natural cluster of markers of consciousness (Birch, 2020; Shea, 2012).

Finding the same threshold effect across many abilities, not just spatial cuing, would reveal a distinctive kind of processing. This processing would *systematically* facilitate the same range of abilities that conscious processing facilitates in humans (Birch, 2020). Our imagined critic would have to claim that signal strength alone produces the same threshold effect across various tasks — with ever less plausibility as the number and diversity of tasks increases.

Demonstrating a subjective threshold would be strong evidence for distinct conscious and unconscious perception in the target animal. It would be convincing even without a background of substantial neurobiological similarity — even, that is, for bees, crabs, or octopuses. So a priority for animal consciousness research is exploring whether above-threshold presentation of stimuli systematically facilitates diverse consciousness-linked abilities.

A downside to the 'systematic facilitation' approach is its demands on both animal and experimenter. A battery of diverse abilities must be studied in the target animal; paradigms identifying a subjective threshold (e.g. a form of masking) must be found and calibrated to the species' visual system; and, for each ability, its relation to the subjective threshold must be investigated. This is a daunting empirical challenge.

Rigorous evidence does not come cheap, and no one said animal consciousness research is easy. But we might worry about species without a wide enough cognitive repertoire for this approach. Perhaps it will work for octopuses or bees, but what about snails, earthworms, or sea slugs? The systematic facilitation approach can only deliver serious evidence of consciousness in species with the requisite cognitive sophistication (*cf.* Schwitzgebel, 2020, on snails). We do not know whether consciousness itself is limited to such taxa, or just our proposed cluster of cognitive markers.

4. Reflections

Our focal studies focused on corvids and macaques, which most researchers already regard as conscious (Low *et al.*, 2012), but we would have real difficulties using similar findings to make a case for consciousness in more controversial cases. The Nieder, Wagener and Rinnert (2020) corvid study's primarily neural approach arguably assumes too much about the link between conscious perception and behaviour. It relies on a certain learned behaviour (a controlled head movement) serving as a report of conscious perception. A sceptic about avian consciousness will ask for independent evidence linking the learned behaviour to consciousness. They will readily accept that some neural activity correlates with the putative report behaviour (after all, something must cause it), but they will doubt whether that activity underpins conscious experience.

Meanwhile, the Ben-Haim *et al.* (2021) primate study takes a primarily behavioural approach, but presupposes similar neural mechanisms in non-humans and humans. Otherwise, evidence against alternative explanations in humans would not cast doubt on alternative explanations in primates. This assumption is more reasonable for primates than for relatively distant taxa. Unfortunately for the Ben-Haim *et al.* approach, most current controversy about animal consciousness concerns the latter (e.g. invertebrates: Barron and Klein, 2016; Birch, 2020; Feinberg and Mallatt, 2016; Key, Arlinghaus and Browman, 2016; Mason, 2011; Mikhalevich and Powell, 2020).

Comparing these two studies is revealing about the interplay of neural and behavioural evidence in animal consciousness science. We can imagine a bright future where Nieder *et al.*-style neural programmes and Ben-Haim *et al.*-style behavioural programmes *complement* each other, supporting one another's assumptions and inferences. Careful behavioural work could reveal report-like behaviours that genuinely require supraliminal stimuli — behaviours not simply reliant on strong signals, but on a genuinely distinctive kind of processing that operates only on supraliminal stimuli. We have not yet reached this stage, except perhaps with primates. But, when we have, we could ask: what is the report-like behaviour's neural basis, and how does it compare to the neural basis of report in humans?

We would still need to disentangle the neural basis of consciousness from the neural basis of post-conscious cognitive processing, including report. However, evidence from non-mammalian animals might help with this general problem. If we achieve a detailed picture of the neural basis of reportable awareness in humans and in corvids (and even, perhaps, in fish, octopods, insects…), we can compare the two pictures, and evaluate hypotheses about which neural mechanisms are robustly necessary or sufficient for reportable awareness across species. We might, for example, find that some animal lineages have achieved reportable awareness of stimuli without any mechanism for global broadcasting — evidence against a global workspace theory of consciousness. Or some form of global broadcasting may always be present, and always underpin the distinctive kind of processing associated with supraliminal stimuli — evidence supporting a global workspace theory of consciousness. The animal evidence would help us confirm and falsify our general theories, and those theories could, in turn, guide the search for new indicators.

We can also envisage a darker future where neural and behavioural programmes *undermine* each other, refuting one other's assumptions and inferences. For example, a Nieder *et al.*-style 'animal NCC' programme could, for a long time, assume that a specific behaviour is a report of conscious perception, only to be confronted with compelling evidence that subliminal stimuli can elicit this behaviour. That would be unfortunate. Behavioural evidence can show initially impressive neurological studies to be less insightful than they appear.

Neural research could also undercut behavioural evidence. Imagine a masking protocol that, in a non-human species, dissociates subliminal and supraliminal stimuli across many tasks. This would seem like strong evidence for conscious perception. But would it still be such strong evidence if the neural mechanisms turned out to be profoundly different from the mechanisms in mammals?

Suppose that supraliminal stimulus processing involved recurrent processing in humans but wholly feedforward processing in non-humans (on the difference, see Lamme, 2006). Would we have discovered *conscious perception without recurrent processing*, or dissociated two kinds of processing which, though analogous to conscious and unconscious processing in humans, are *both wholly unconscious*? This debate would be difficult to resolve but not necessarily impossible, since the overall evidential picture might favour one of the two hypotheses. Nonetheless, neural evidence can undercut and complicate apparently compelling inferences from behaviour.

The lesson here is that neural and behavioural research should not proceed in isolation. Nieder *et al.*'s neural study relied on learnt behaviours, whilst Ben-Haim *et al.*'s behavioural study relied on neural similarity. Both assumptions may be valid. But neither assumption was independently validated, casting doubt on each study's case for consciousness. This also applies to consciousness science more broadly. Instead of the status quo — compiling *post hoc* lists of disparate indicators — we propose a more coordinated research programme, where neural and behavioural researchers directly test each other's assumptions. Such a collaboration may be impractical within individual studies — and Nieder *et al.* and Ben-Haim *et al.* made important contributions regardless — but should be an aim of the field as a whole. A coordinated, interdependent, neural-behavioural case for animal consciousness will be stronger than either case standing alone, or both standing separately.

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References

Alkire, M.T. & Miller, J. (2005) General anesthesia and the neural correlates of consciousness, *Progress in Brain Research*, **150**, pp. 229–597.

Ansorge, U., Kunde, W. & Kiefer, M. (2014) Unconscious vision and executive control: How unconscious processing and conscious action control interact, *Consciousness and Cognition*, **27**, pp. 268–287.

Appel, M. & Elwood, R.W. (2009) Motivational trade-offs and potential pain experience in hermit crabs, *Applied Animal Behaviour Science*, **119** (1–2), pp. 120–124.

Aru, J., Bachmann, T., Singer, W. & Melloni, L. (2012) Distilling the neural correlates of consciousness, *Neuroscience & Biobehavioral Reviews*, **36** (2), pp. 737–746.

Arzi, A., Shedlesky, L., Ben-Shaul, M., Nasser, K., Oksenberg, A., Hairston, I.S. & Sobel, N. (2012) Humans can learn new information during sleep, *Nature Neuroscience*, **15** (10), pp. 1460–1465.

Baars, B.J. (2005) Global workspace theory of consciousness: Toward a cognitive neuroscience of human experience, *Progress in Brain Research*, **150**, pp. 45–53.

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

Ben-Haim, M.S., Dal Monte, O., Fagan, N.A., Dunham, Y., Hassin, R.R., Chang, S.W. & Santos, L.R. (2021) Disentangling perceptual awareness from non-conscious processing in rhesus monkeys (Macaca mulatta), *Proceedings of the National Academy of Sciences*, **118** (15). doi: 10.1073/pnas.2017543118

Birch, J. (2020) The search for invertebrate consciousness, *Noûs*, advance of print. doi: 10.1111/nous.12351

Birch, J., Burn, C., Schnell, A., Browning, H. & Crump, A. (2021) *Review of the Evidence of Sentience in Cephalopod Molluscs and Decapod Crustaceans*, Department for Environment, Food & Rural Affairs (Defra).

Birch, J., Ginsburg, S. & Jablonka, E. (2020) Unlimited associative learning and the origins of consciousness: A primer and some predictions, *Biology & Philosophy*, **35** (6), pp. 1–23.

Bird, C.D. & Emery, N.J. (2009) Insightful problem solving and creative tool modification by captive nontool-using rooks, *Proceedings of the National Academy of Sciences*, **106** (25), pp. 10370–10375.

Block, N. (1995) On a confusion about a function of consciousness, *Behavioral and Brain Sciences*, **18** (2), pp. 227–247.

Boly, M., Seth, A.K., Wilke, M., Ingmundson, P., Baars, B., Laureys, S., Edelman, D.B. & Tsuchiya, N. (2013) Consciousness in humans and non-human animals: Recent advances and future directions, *Frontiers in Psychology*, **4**, art. 625. doi: 10.3389/fpsyg.2013.00625

Boly, M., Massimini, M., Tsuchiya, N., Postle, B.R., Koch, C. & Tononi, G. (2017) Are the neural correlates of consciousness in the front or in the back of the cerebral cortex? Clinical and neuroimaging evidence, *Journal of Neuroscience*, **37** (40), pp. 9603–9613.

Bronfman, Z.Z., Ginsburg, S. & Jablonka, E. (2016) The transition to minimal consciousness through the evolution of associative learning, *Frontiers in Psychology*, **7**, art. 1954.

Chun, M.M., Golomb, J.D. & Turk-Browne, N.B. (2011) A taxonomy of external and internal attention, *Annual Review of Psychology*, **62**, pp. 73–101.

Clark, R.E. & Squire, L.R. (1998) Classical conditioning and brain systems: The role of awareness, *Science*, **280** (5360), pp. 77–81.

Clark, R.E. & Squire, L.R. (1999) Human eyeblink classical conditioning: Effects of manipulating awareness of the stimulus contingencies, *Psychological Science*, **10**, pp. 14–18.

Cowey, A. & Stoerig, P. (1995) Blindsight in monkeys, *Nature*, **373** (6511), pp. 247–249.

Crick, F. & Koch, C. (1990) Towards a neurobiological theory of consciousness, *Seminars in the Neurosciences*, **2**, pp. 263–275.

Crook, R.J. (2021) Behavioral and neurophysiological evidence suggests affective pain experience in octopus, *Iscience*, **24** (3), 102229.

Crump, A., Arnott, G. & Bethell, E.J. (2018) Affect-driven attention biases as animal welfare indicators: Review and methods, *Animals*, **8** (8), art. 136.

Dawkins, M.S. (2021) *The Science of Animal Welfare: Understanding What Animals Want*, New York: Oxford University Press

Debner, J.A. & Jacoby, L.L. (1994) Unconscious perception: Attention, awareness, and control, *Journal of Experimental Psychology: Learning, Memory, and Cognition*, **20** (2), art. 304.

Dehaene, S. (2014) *Consciousness and the Brain: Deciphering How the Brain Codes Our Thoughts*, New York: Penguin.

Dehaene, S., Naccache, L., Cohen, L., Le Bihan, D., Mangin, J.F., Poline, J.B. & Rivière, D. (2001) Cerebral mechanisms of word masking and unconscious repetition priming, *Nature Neuroscience*, **4** (7), pp. 752–758.

Dehaene, S. & Changeux, J.-P. (2011) Experimental and theoretical approaches to conscious processing, *Neuron*, **70** (2), pp. 200–227.

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.

Dell, K.L., Arabzadeh, E. & Price, N.S. (2019) Differences in perceptual masking between humans and rats, *Brain and Behavior*, **9** (9), e01368.

Deroy, O., Faivre, N., Lunghi, C., Spence, C., Aller, M. & Noppeney, U. (2016) The complex interplay between multisensory integration and perceptual awareness, *Multisensory Research*, **29** (6–7), pp. 585–606.

Dunlop, R., Millsopp, S. & Laming, P. (2006) Avoidance learning in goldfish (Carassius auratus) and trout (Oncorhynchus mykiss) and implications for pain perception, *Applied Animal Behaviour Science*, **97** (2–4), pp. 255–271.

Edelman, D.B. & Seth, A.K. (2009) Animal consciousness: A synthetic approach, *Trends in Neurosciences*, **32** (9), pp. 476–484.

Eimer, M. & Schlaghecken, F. (2003) Response facilitation and inhibition in subliminal priming, *Biological Psychology*, **64** (1–2), pp. 7–26.

Elwood, R.W. & Appel, M. (2009) Pain experience in hermit crabs?, *Animal Behaviour*, **77** (5), pp. 1243–1246.

Emery, N.J. & Clayton, N.S. (2004) The mentality of crows: Convergent evolution of intelligence in corvids and apes, *Science*, **306** (5703), pp. 1903–1907.

Faivre, N., Mudrik, L., Schwartz, N. & Koch, C. (2014) Multisensory integration in complete unawareness: Evidence from audiovisual congruency priming, *Psychological Science*, **25** (11), pp. 2006–2016.

Fazekas, P. & Nemeth, G. (2018) Dream experiences and the neural correlates of perceptual consciousness and cognitive access, *Philosophical Transactions of the Royal Society B: Biological Sciences*, **373** (1755), 20170356.

Feinberg, T.E. & Mallatt, J.M. (2016) *The Ancient Origins of Consciousness: How the Brain Created Experience*, Cambridge, MA: MIT Press.

Frässle, S., Sommer, J., Jansen, A., Naber, M. & Einhäuser, W. (2014) Binocular rivalry: Frontal activity relates to introspection and action but not to perception, *Journal of Neuroscience*, **34** (5), pp. 1738–1747.

Fries, P., Roelfsema, P.R., Engel, A.K., König, P. & Singer, W. (1997) Synchronization of oscillatory responses in visual cortex correlates with perception in interocular rivalry, *Proceedings of the National Academy of Sciences*, **94** (23), pp. 12699–12704.

Gallup, G.G. (1970) Chimpanzees: Self-recognition, *Science*, **167** (3914), pp. 86–87.

Ginsburg, S. & Jablonka, E. (2019) *The Evolution of the Sensitive Soul: Learning and the Origins of Consciousness*, Cambridge, MA: MIT Press.

Griffin, D.R. (1976) *The Question of Animal Awareness: Evolutionary Continuity of Mental Experience*, New York: Rockefeller University Press.

Griffin, D.R. (2013) *Animal Minds: Beyond Cognition to Consciousness*, Chicago, IL: University of Chicago Press.

Güntürkün, O. (2005) The avian 'prefrontal cortex'and cognition, *Current Opinion in Neurobiology*, **15** (6), pp. 686–693.

Hampton, R.R. (2021) Animal consciousness: Should a new behavioral correlate in monkeys persuade agnostics?, *Current Biology*, **31** (12), R801–R803.

Herreros, L., Lambert, A.J. & Chica, A.B. (2017) Orienting of attention with and without cue awareness, *Neuropsychologia*, **99**, pp. 165–171.

Heschl, A. & Burkart, J. (2006) A new mark test for mirror self-recognition in non-human primates, *Primates*, **47** (3), pp. 187–198.

Heyes, C.M. (2008) Beast machines? Questions of animal consciousness, in Davies, M. & Weiskrantz, L. (eds.) *Frontiers of Consciousness*, Oxford: Oxford University Press.

Irvine, E. (2020) Developing valid behavioral indicators of animal pain, *Philosophical Topics*, **48** (1), pp. 129–153.

Kapoor, V., Dwarakanath, A., Safavi, S., Werner, J., Besserve, M., Panagiotaropoulos, T.I. & Logothetis, N.K. (2020) Decoding the contents of consciousness from prefrontal ensembles, *BioRxiv*, [Online], https://www.biorxiv.org/content/10.1101/2020.01.28.921841.full.pdf.

Key, B., Arlinghaus, R. & Browman, H.I. (2016) Insects cannot tell us anything about subjective experience or the origin of consciousness, *Proceedings of the National Academy of Sciences*, **113** (27), E3813–E3813.

Koch, C., Massimini, M., Boly, M. & Tononi, G. (2016) Neural correlates of consciousness: Progress and problems, *Nature Reviews Neuroscience*, **17** (5), pp. 307–321.

Kohda, M., Hotta, T., Takeyama, T., Awata, S., Tanaka, H., Asai, J.Y. & Jordan, A.L. (2019) If a fish can pass the mark test, what are the implications for consciousness and self-awareness testing in animals?, *PLoS Biology*, **17** (2), e3000021.

Kreiman, G., Fried, I. & Koch, C. (2002) Single-neuron correlates of subjective vision in the human medial temporal lobe, *Proceedings of the National Academy of Sciences*, **99** (12), pp. 8378–8383.

Lamme, V.A.F. (2006) Towards a true neural stance on consciousness, *Trends in Cognitive Sciences*, **10** (11), pp. 494–501.

Lamme, V.A.F. (this issue) Behavioural and neural evidence for conscious sensation in animals: An inescapable avenue towards biopsychism?, *Journal of Consciousness Studies*, **29** (3–4).

Lau, H. (2011) Theoretical motivations for investigating the neural correlates of consciousness, *Wiley Interdisciplinary Reviews: Cognitive Science*, **2** (1), pp. 1–7.

Lepauvre, A. & Melloni, L. (2021) The search for the neural correlate of consciousness: Progress and challenges, *Philosophy and the Mind Sciences*, **2**, pp. 1–28.

Low, P., Panksepp, J., Reiss, D., Edelman, D., Van Swinderen, B. & Koch, C. (2012, July) The Cambridge declaration on consciousness, *Francis Crick Memorial Conference*, Cambridge, England, pp. 1–2.

Mason, G.J. (2011) Invertebrate welfare: Where is the real evidence for conscious affective states?, *Trends in Ecology and Evolution*, **26** (5), pp. 212–213.

Merikle, P.M., Joordens, S. & Stolz, J.A. (1995) Measuring the relative magnitude of unconscious influences, *Consciousness and Cognition*, **4** (4), pp. 422–439.

Michel, M. & Morales, J. (2020) Minority reports: Consciousness and the prefrontal cortex, *Mind & Language*, **35** (4), pp. 493–513.

Mikhalevich, I. & Powell, R. (2020) Minds without spines: Evolutionarily inclusive animal ethics, *Animal Sentience*, **29** (1), pp. 1–25.

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*, **92** (18), pp. 8215–8218.

Mudrik, L., Faivre, N. & Koch, C. (2014) Information integration without awareness, *Trends in Cognitive Sciences*, **18** (9), pp. 488–496.

Nagel, T. (1974) What is it like to be a bat?, *Readings in Philosophy of Psychology*, **1**, pp. 159–168.

Nani, A., Manuello, J., Mancuso, L., Liloia, D., Costa, T. & Cauda, F. (2019) The neural correlates of consciousness and attention: Two sister processes of the brain, *Frontiers in Neuroscience*, **13**, art. 1169.

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

Niv, Y. (2021) The primacy of behavioral research for understanding the brain, *Behavioral Neuroscience*, **135** (5), pp. 601–609.

Overgaard, M. (2004) Confounding factors in contrastive analysis, *Synthese*, **141** (2), pp. 217–231.

Overgaard, M. & Fazekas, P. (2016) Can no-report paradigms extract true correlates of consciousness?, *Trends in Cognitive Sciences*, **20**, pp. 241–242.

Palmer, T.D. & Ramsey, A.K. (2012) The function of consciousness in multisensory integration, *Cognition*, **125** (3), pp. 353–364.

Paul, E.S., Sher, S., Tamietto, M., Winkielman, P. & Mendl, M.T. (2020) Towards a comparative science of emotion: Affect and consciousness in humans and animals, *Neuroscience & Biobehavioral Reviews*, **108**, pp. 749–770.

Pfister, R., Pohl, C., Kiesel, A. & Kunde, W. (2012) Your unconscious knows your name, *PLoS ONE*, **7** (3), e32402.

Phillips, I. (2018) The methodological puzzle of phenomenal consciousness, *Philosophical Transactions of the Royal Society B: Biological Sciences*, **373** (1755), 20170347.

Pitts, M.A., Metzler, S. & Hillyard, S.A. (2014) Isolating neural correlates of conscious perception from neural correlates of reporting ‘ne’s perception, *Frontiers in Psychology*, **5**, art. 1078.

Pitts, M.A., Lutsyshyna, L.A. & Hillyard, S.A. (2018) The relationship between attention and consciousness: An expanded taxonomy and implications for ‘no-report’ paradigms, *Philosophical Transactions of the Royal Society B: Biological Sciences*, **373** (1755), 20170348.

Posner, M.I. (1980) Orienting of attention, *Quarterly Journal of Experimental Psychology*, **32** (1), pp. 3–25.

Rees, G., Kreiman, G. & Koch, C. (2002) Neural correlates of consciousness in humans, *Nature Reviews Neuroscience*, **3** (4), pp. 261–270.

Schwitzgebel, E. (2016) Phenomenal consciousness, defined and defended as innocently as I can manage, *Journal of Consciousness Studies*, **23** (11–12), pp. 224–235.

Schwitzgebel, E. (2020) Is there something it’s like to be a garden snail?, in preparation, [Online], http://www.faculty.ucr.edu/~eschwitz/SchwitzAbs/Snails.htm [accessed 1 September 2021].

Scott, R.B., Samaha, J., Chrisley, R. & Dienes, Z. (2018) Prevailing theories of consciousness are challenged by novel cross-modal associations acquired between subliminal stimuli, *Cognition*, **175**, pp. 169–185.

Seth, A.K. (2009) Explanatory correlates of consciousness: Theoretical and computational challenges, *Cognitive Computation*, **1** (1), pp. 50–63.

Seth, A.K., Dienes, Z., Cleeremans, A., Overgaard, M. & Pessoa, L. (2008) Measuring consciousness: Relating behavioural and neurophysiological approaches, *Trends in Cognitive Sciences*, **12** (8), pp. 314–321.

Shea, N. (2012) Methodological encounters with the phenomenal kind, *Philosophy and Phenomenological Research*, **84** (2), art. 307.

Shea, N. & Heyes, C. (2010) Metamemory as evidence of animal consciousness: The type that does the trick, *Biology & Philosophy*, **25** (1), pp. 95–110.

Shomrat, T., Turchetti-Maia, A.L., Stern-Mentch, N., Basil, J.A. & Hochner, B. (2015) The vertical lobe of cephalopods: An attractive brain structure for understanding the evolution of advanced learning and memory systems, *Journal of Comparative Physiology A*, **201** (9), pp. 947–956.

Siclari, F., Baird, B., Perogamvros, L., Bernardi, G., LaRocque, J.J., Riedner, B., Boly, M., Postle, B.R. & Tononi, G. (2017) The neural correlates of dreaming, *Nature Neuroscience*, **20** (6), pp. 872–878.

Smith, J.A. & Boyd, K.M. (eds.) (1991) *Lives in the Balance: The Ethics of Using Animals in Biomedical Research*, Oxford: Oxford University Press.

Sneddon, L.U., Elwood, R.W., Adamo, S.A. & Leach, M.C. (2014) Defining and assessing animal pain, *Animal Behaviour*, **97**, pp. 201–212.

Solvi, C., Al-Khudhairy, S.G. & Chittka, L. (2020) Bumble bees display cross-modal object recognition between visual and tactile senses, *Science*, **367** (6480), pp. 910–912.

Soto, D. & Silvanto, J. (2014) Reappraising the relationship between working memory and conscious awareness, *Trends in Cognitive Sciences*, **18** (10), pp. 520–525.

Supèr, H., Spekreijse, H. & Lamme, V.A. (2001) Two distinct modes of sensory processing observed in monkey primary visual cortex (V1), *Nature Neuroscience*, **4** (3), pp. 304–310.

Tapia, E., Breitmeyer, B.G. & Shooner, C.R. (2010) Role of task-directed attention in nonconscious and conscious response priming by form and color, *Journal of Experimental Psychology: Human Perception and Performance*, **36** (1), art. 74.

Tong, F., Meng, M. & Blake, R. (2006) Neural bases of binocular rivalry, *Trends in Cognitive Sciences*, **10** (11), pp. 502–511.

Tononi, G. & Koch, C. (2015) Consciousness: Here, there and everywhere?, *Philosophical Transactions of the Royal Society B: Biological Sciences*, **370** (1668), 20140167.

Travers, E., Frith, C.D. & Shea, N. (2018) Learning rapidly about the relevance of visual cues requires conscious awareness, *Quarterly Journal of Experimental Psychology*, **71** (8), pp. 1698–1713.

Tsuchiya, N., Wilke, M., Frässle, S. & Lamme, V.A. (2015) No-report paradigms: Extracting the true neural correlates of consciousness, *Trends in Cognitive Sciences*, **19** (12), pp. 757–770.

van Gaal, S., Ridderinkhof, K.R., van den Wildenberg, W.P. & Lamme, V.A. (2009) Dissociating consciousness from inhibitory control: Evidence for unconsciously triggered response inhibition in the stop-signal task, *Journal of Experimental Psychology: Human Perception and Performance*, **35** (4), art. 1129.

Yang, Y.H., Tien, Y.H., Yang, P.L. & Yeh, S.L. (2017) Role of consciousness in temporal integration of semantic information, *Cognitive, Affective, & Behavioral Neuroscience*, **17** (5), pp. 954–972.

Yoshida, M. & Isa, T. (2015) Signal detection analysis of blindsight in monkeys, *Scientific Reports*, **5** (1), pp. 1–11.