Separating conscious and unconscious perception in animals

Andrew Crump[1] and Jonathan Birch[1]

[1] Centre for Philosophy of Natural and Social Science, London School of Economics and Political Science, Houghton Street, London, WC2A 2AE, UK.

Summary: *In a new study, Ben-Haim et al. use subliminal stimuli to separate conscious and unconscious perception in macaques. A programme of this type, using a range of cognitive tasks, is a promising way to look for conscious perception in more controversial cases.*

The search for animal consciousness

Conscious experience raises some of the thorniest problems in science. Where in the brain are its neural circuits? What is its adaptive function? When did it evolve? Which animals are conscious and which are not? Many biologists set these questions aside as too difficult to answer. However, the last few decades have seen the advent of a science of human consciousness that employs a battery of methods to probe the neural and cognitive signatures of conscious experience. This raises the tantalizing prospect of drawing on techniques from consciousness science to gain insight into consciousness in other animals.

Where should we start? A tempting proposition is that we should look for *neuronal correlates* of consciousness (or "NCCs") in other animals, just as consciousness researchers have looked for human NCCs. This, however, is fraught with difficulty. The search for the human NCCs has not yet generated any consensus. Even if there were a consensus, we would not know what alternative implementations may be possible, and it would be hasty to assume that the human way of implementing consciousness is the only way.

An alternative approach is to look for cognitive and behavioural abilities linked to consciousness, such as certain forms of metacognition and associative learning (Birch 2020). However, pitfalls lurk here too. We know from the human case that high-level functions can occur unconsciously (Hassin 2013). Humans, for instance, may "drift off" while driving, executing the skill without any conscious control. So which behaviours and cognitive functions really involve consciousness?

The double-dissociation approach

In humans, there is a difference between conscious and unconscious perception. When you watch a movie, you consciously see the characters. But, if a single frame of something else is discreetly slipped in, it may register *subliminally*. Researchers in consciousness science have long exploited this difference to study the distinctive neural and cognitive signatures of conscious (as opposed to unconscious) processing. If we could find an analogous difference in other species, we could study the signatures of conscious processing in those species too.

A recent study by Ben-Haim et al. (2021) attempts exactly this. One way to disentangle conscious from unconscious processing in humans involves crossover double dissociation paradigms (Dehaene 2014). These tasks present pairs of consciously visible (*supraliminal*) and subliminal stimuli that elicit opposite behavioural responses. 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. Ben-Haim et al. (2021) tested a crossover double dissociation paradigm on four rhesus macaques (*Macaca mulatta*), which were compared with 145 adult humans. The paradigm was a spatial cueing task, where subjects must locate a target stimulus displayed at one of two locations on a screen. Preceding the target was a predictive cue that appeared at the *opposite* location to the target. Such a cue is called an "incongruent" cue. These incongruent cues were presented either supraliminally (for 250 ms) or subliminally (for 17 or 33 ms).

The authors hypothesised 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 nonconsciously 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 "double dissociation": conscious processing improving performance and nonconscious processing impairing performance.

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

The confounding influence of signal strength

Supraliminal cues are stronger signals, and thus potentially easier to learn about, than subliminal cues. In other words, improved learning performance may have nothing to do with stimuli being consciously perceived and may simply be explained by the stimuli being stronger to begin with. The possible confounding effect of signal strength is a persistent issue in consciousness science (Lau 2011).

Ben-Haim et al. addressed this using two strategies. First, they informed some human subjects about the subliminal cues partway 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 informed from the outset that incongruent cues predicted the target's location, so that no learning was needed. The response pattern persisted: subjects still performed above chance when they reported seeing the cue and below chance when they reported not seeing the cue.

A critic may object: this is evidence that the dissociation was not due to signal strength alone *in humans*, but it does not rule out this alternative explanation *in macaques*. Implicitly, Ben-Haim et al. bridge this gap with an argument from analogy. They assume that, given the close 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 the attribution of consciousness to macaques extremely plausible to begin with. A case for conscious perception in a more controversial candidate—such as bees, crabs, or octopuses—would have to avoid such a move. In the case of bees, our imagined critic would argue that ruling out an alternative explanation based on signal strength *in humans* does not rule it out *in bees*.

Looking for systematic facilitation

Does the signal strength problem have a more widely applicable solution? We see this as 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 found evidence of a putative subjective threshold at around 50ms, 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?* In particular, do we find this threshold effect not just in spatial cuing but also in other abilities linked to conscious perception in humans, such as metacognition, trace conditioning, cross-modal learning, reversal learning, and the interpretation of three-dimensional scenes?

Finding the same threshold effect across many abilities would be compelling evidence that a distinctive kind of processing *systematically* facilitates the same range of abilities that conscious processing facilitates in humans. Our imagined critic would have to resort to the idea that increasing signal strength could still produce the same threshold effect across a range of tasks for some other reason—an idea that becomes ever more unlikely as the number and diversity of tasks increases.

Evidence for a subjective threshold would be convincing evidence for a distinction between conscious and unconscious perception in the target animal. We think 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.

Funding
This research is part of a project that has received funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme, Grant Number 851145.

References

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 nonconscious processing in rhesus monkeys (Macaca mulatta). *Proceedings of the National Academy of Sciences, 118*(15), e2017543118. https://doi.org/10.1073/pnas.2017543118

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

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

Hassin, R. R. (2013). Yes it can: On the functional abilities of the human unconscious. *Perspectives on Psychological Science, 8*(2), 195-207. https://doi.org/10.1177/1745691612460684

Lau, H. (2011). Theoretical motivations for investigating the neural correlates of consciousness. *WIREs Cognitive Science*, *2(1)*, 1-7. https://doi.org/10.1002/wcs.93