



Paul, E. S., & Mendl, M. T. (2016). If insects have phenomenal consciousness, could they suffer? *Animal Sentience*, 1(9), [128].

Publisher's PDF, also known as Version of record

License (if available):
CC BY-NC

[Link to publication record in Explore Bristol Research](#)
PDF-document

This is the final published version of the article (version of record). It first appeared online via The Humane Society of the USA at <http://animalstudiesrepository.org/animsent/vol1/iss9/16/>. Please refer to any applicable terms of use of the publisher.

University of Bristol - Explore Bristol Research

General rights

This document is made available in accordance with publisher policies. Please cite only the published version using the reference above. Full terms of use are available:
<http://www.bristol.ac.uk/pure/about/ebr-terms.html>

If insects have phenomenal consciousness, could they suffer?

Commentary on [Klein & Barron](#) on *Insect Experience*

Elizabeth S. Paul & Michael T. Mendl

Centre for Behavioural Biology, School of Veterinary Science
University of Bristol

Abstract: Klein & Barron's (K & B's) suggestion that insects have the capacity for phenomenal consciousness is a refreshing and challenging departure from the cautious and agnostic stance that is taken by many researchers when considering this possibility. It is impossible to falsify the sceptic's view that neural and behavioural parallels between humans and insects need not imply either similar conscious experience or even any phenomenal consciousness in insects at all. But if K & B are right, it is important to consider the possible *contents* of insect consciousness. Here we discuss whether affective consciousness, with its implications for potential suffering, might also be part of the simulated perceptual conscious world that K & B propose.

[Elizabeth S. Paul](#), Senior Research Fellow, University of Bristol, comparative psychologist, studies "emotion" and "mood" in human and non-human animals, reward processing in reinforcement learning, how emotions and moods influence decision-making, and empathy and individual variation in anthropomorphic thinking.



<http://www.bristol.ac.uk/vetscience/people/38480/>

[Michael T. Mendl](#), Professor of Animal Behavior and Welfare, University of Bristol, studies how attention, memory and decision-making influence and are influenced by affective state. In humans, affect-induced modulation of decision-making leads to "cognitive bias." Can it be observed in animals and used as a novel indicator of animal affect (emotion) and welfare?



<http://www.bristol.ac.uk/vetscience/people/michael-t-mendl/>

Klein & Barron (2016; henceforth K & B) follow Merker's (2007) suggestion that dynamic integration of sensory information about the environment and the organism's place in it, together with information about the organism's current homeostatic requirements, generates a neural model that provides a "unique, unified perspective on the world" (K & B, p. 3) and produces consciousness. Merker argues that the vertebrate (human) midbrain is necessary and sufficient for consciousness, and that it embodies the neural simulation described above, integrating information from different decision-making domains — motivation, target (goal) selection, and action selection via a common-currency "conscious mode of function" (Merker, p. 71). K & B contend that the functional architecture of the insect brain has many parallels with that of the vertebrate midbrain and is thus capable of the same neural modelling, and hence of conscious experience.

But is consciousness a necessary corollary of neural computations of this sort -- and does evidence of a similar functional architecture in human and insect brains inevitably imply a similar capacity for conscious experience? Even in humans, “blindsight” patients who are unable to report consciously seeing anything in their impaired visual field can exhibit precise real-time visually guided action and target selection (e.g., fine-tuning grasp to target size; avoiding obstacles). Interestingly, when a short delay is introduced between visual access to the task and task performance, these patients fail to fine-tune their movements or avoid obstacles; hence under these circumstances conscious experience is required (Striemer et al., 2009; Whitwell et al., 2011). Although damage to cortical pathways is involved in these phenomena, and there is debate as to whether blindsight patients truly lack phenomenal awareness in their impaired visual field (e.g., Merker), these findings raise the possibility that insects show neural coordination of motivation, target selection and action in the absence of conscious experience, at least in real-time. This possibility could be countered by good performance in tasks where there is a delay between target selection and action or goal acquisition. Sophisticated detour behaviour by jumping spiders hunting prey (Tarsitano & Jackson, 1997) may provide one such example.

Notwithstanding these arguments, we find K & B’s proposal engaging and persuasive. We will now consider the potential contents of insect consciousness, should K & B turn out to be right. Although they avoid detailed consideration of this issue, K & B’s approach, like Merker’s, emphasises a perceptual, visual perspective. Merker (p. 72) speculates that “in its primitive beginnings, the ‘world’ of the proposed neural reality simulator presumably amounted to no more than a two-dimensional screen-like map of spatial directions on which potential targets might appear as mere loci of motion in an otherwise featureless noise field, defined more by their displacement than by any object features.” Such imaginings of the contents of subjective experience appear to sit well with K & B’s arguments for insect consciousness. Although predominantly visual, the same principles could conceivably be applied to a simulated world dominated by olfactory or auditory inputs.

Within this simulated world, K & B (p. 5) note that “The motivational and physiological states of the organism prioritize target and action selection.” Goal prioritization and decision-making involve reward and punishment valuation mechanisms, adding an affective dimension to the simulation and, potentially, to the contents of consciousness. A primarily perceptually based consciousness could incorporate valuation of targets in a purely visual way by representing important goals as larger or more intense visual signals in the simulated world. Alternatively, affective consciousness – positively or negatively valenced feelings induced by fitness-enhancing or threatening stimuli – may have preceded perceptual experience as a common currency for evaluating different courses of action across functionally distinct domains (Cabanac, 1992; Mendl et al., 2010). Or both perceptual and affective consciousness may have emerged simultaneously as components of the simulated world.

If either of the latter two scenarios applies in insects, the capacity for consciousness suggested by K & B would include subjective experience of affect (e.g., emotions), thus raising the possibility that insects can suffer, something that researchers and non-scientists think unlikely (Paul, 1995). The implications would therefore be significant, particularly ethically: At present insects are given no legal protection at all from harm. What is the

evidence that affective consciousness may be part of the simulated world proposed by K & B?

Darwin (2009/1872, p. 347) attributed human-like emotions to insects: “Even insects express anger, terror, jealousy and love, by their stridulation.” For him, the functional and behavioural similarities between human and animal behaviour in emotive situations (e.g., in response to the arrival of a reward or a punisher) implied similarly subjective emotional experiences. Insects certainly show behavioural responses that resemble the fundamental features of emotions. Anderson & Adolphs (2014) call these “emotion primitives,” listing elements such as valence, scalability, and persistence as being critical for assigning emotion-like states to non-human animals. Fruit flies (*Drosophila melanogaster*), for example, show freezing and avoidance of a repeated looming shadow that becomes more intense with repeated exposure, and persists across time even after the shadow is removed. Gibson et al. (2015) argue that this reflects an emotion-like “internal defensive state” (p. 1401).

Perhaps more compelling than immediate responses to stimuli is evidence that animals have background affective states, or “moods,” that function to moderate responses to events and guide decision-making, particularly under ambiguity. We (Mendl et al., 2010) hypothesize that an animal’s past experiences of reward and punishment across a range of functional domains (e.g., foraging, predator avoidance, intra-specific competition) determine its current mood state. Assuming a correlation between past experience and future probability of rewards and punishers, individuals can then make use of their mood state to “best guess” whether a novel or ambiguous stimulus is likely to be good or bad news; a negative mood should lead to enhanced expectation of punishment and/or decreased expectation of reward, resulting in cautious or “pessimistically” biased judgements of ambiguity (see also Nettle & Bateson, 2012). Honeybees, like a wide range of vertebrate species (Harding et al., 2004; Mendl et al., 2009; Gygas, 2014; Roelofs et al., 2016), show such affect-induced judgement biases (Bateson et al., 2011). Humans appear to make such judgements by reflecting on their subjective feelings, using the “how do I feel about it?” heuristic (Schwartz & Clore, 1983; Paul et al., 2005). This raises the possibility that affective consciousness plays a role in biasing judgements in insects and other invertebrates too.

Although these examples are suggestive of affect-like states in insects, they do not provide conclusive evidence of conscious affective experience. Even in humans, there is no one-to-one correspondence between reported emotional feelings and the behavioural and physiological components of emotional states. For example, Winkielman et al. (2005) found that participants viewing emotionally salient images showed behaviour indicative of an altered affective state (enhanced “liking” of a sweet drink, expressed through willingness to drink more and pay more for it) despite the absence of any change in subjectively experienced pleasure when consuming the drink. In terms of affect-induced judgement biases, it is possible to conceive a neural mechanism that reflects cumulative experience of reward and punishment and interfaces with action selection processes without needing to invoke conscious experience (Mendl et al., 2011). A candidate is changes in tonic firing of PPL and PAM dopaminergic neurones that code the valence of sensory input and moderate the balance of approach and avoidance tendencies in *D. melanogaster* (Aso et al., 2014). As Anderson & Adolphs (2014) note, descriptions of (and inferences from) behavioural observations should be separated from conclusions about subjective experience: “animals,

like humans, have central emotion states even if they are not consciously aware of them” (p. 190). In other words, neurophysiological and behavioural evidence of (operationally defined) affect-like states in non-human animals need not imply that such states are felt (sentient).

K & B’s challenging proposal urges us to think more deeply about the possibility that insects have the capacity for consciousness. If they are right, the obvious next question concerns the contents of insect subjective experience and, from an ethical standpoint, whether there is an affective component. A number of approaches can build on K & B’s arguments to start investigating the possible existence of insect affect and address the inevitable question that will arise about whether the operationally identified affect-like processes are actually being felt.

Acknowledgements

E.S.P. was supported by grants from the UK National Centre for the Replacement, Refinement & Reduction of Animals in Research (NC3Rs) research council (grant K/00008X/1 to M.T.M.), and the UK Biotechnology and Biological Sciences Research Council (BBSRC) (grant BB/K00042X/1 to C.J. Nicol).

References

- Anderson, D.J. & Adolphs, R. (2014). A framework for studying emotions across species. *Cell*, 157, 187-200.
- Aso, Y., Sitaraman, D., Ichinose, T., Kaun, K.R., Vogt, K., Belliard-Guérin, G., Plaçais, P-Y., Robie, A.A., Yamagata, N., Schnaitmann, C., Rowell, W.J., Johnston, R.M., Ngo, T-T.B., Chen, N., Korff, W., Nitabach, M.N., Heberlein, U., Preat, T., Branson, K.M., Tanimoto, H. & Rubin, G.M. (2014). Mushroom body output neurons encode valence and guide memory-based action selection in *Drosophila*. *eLIFE*, 2014;3:e04580
- Bateson, M., Desire, S., Gartside, S.E. & Wright, G.A. (2011). Agitated honeybees exhibit pessimistic cognitive biases. *Current Biology*, 21, 1070-1073.
- Cabanac, M. (1992). Pleasure - the common currency. *Journal of Theoretical Biology*, 155, 173–200.
- Darwin C. (2009/1872). *The Expression of the Emotions in Man and Animals*. London: Harper Perennial.
- Gibson, W.T., Gonzalez, C.R., Fernandez, C., Ramasamy, L., Tabachnik, T., Du, R.R., Felsen, P.D., Maire, M.R., Perona, P. & Anderson, D.J. (2015). Behavioral responses to a repetitive visual threat stimulus express a persistent state of defensive arousal in *Drosophila*. *Current Biology*, 25, 1401-1425.
- Gygax, L. (2014). The A to Z of statistics for testing cognitive judgement bias. *Animal Behaviour*, 95, 59-69.
- Harding, E.J., Paul, E.S. & Mendl, M. (2004). Cognitive bias and affective state. *Nature*, 427, 312.
- Klein, C., & Barron, A. B. (2016). [Insects have the capacity for subjective experience](#). *Animal Sentience* 2016.100.
- Mendl, M., Burman, O.H.P. & Paul, E.S. (2010). An integrative and functional framework for the study of animal emotion and mood. *Proceedings of the Royal Society B – Biological Sciences*, 277, 2895-2904.

- Mendl, M., Burman, O.H.P., Parker, R.M.A. & Paul, E.S. (2009). Cognitive bias as an indicator of animal emotion and welfare: emerging evidence and underlying mechanisms. *Applied Animal Behaviour Science*, *118*, 161-181.
- Mendl, M., Paul, E.S. & Chittka, L. (2011). Animal behaviour: emotion in invertebrates? *Current Biology*, *21*(12), R463-465.
- Merker, B. (2007). Consciousness without a cerebral cortex: a challenge for neuroscience and medicine. *Behavioral and Brain Sciences*, *30*, 63-134.
- Nettle, D. & Bateson, M. (2013). The evolutionary origins of mood and its disorders. *Current Biology*, *22*, R712-721.
- Paul, E.S. (1995). Us and them: scientists' and animal rights campaigners' views of the animal experimentation debate. *Society & Animals*, *3*, 1-21.
- Paul, E.S., Harding, E.J. & Mendl, M. (2005). Measuring emotional processes in animals: the utility of a cognitive approach. *Neuroscience and Biobehavioral Reviews*, *29*, 469-491.
- Roelofs, S., Boleij, H., Nordquist, R.E. & van der Staay, F.J. (2016). Making decisions under ambiguity: judgment bias tasks for assessing emotional state in animals. *Frontiers in Behavioral Neuroscience*, *10*, article 119.
- Schwarz, N. & Clore, G.L. (1983). Mood, misattribution, and judgements of well-being – informative and directive functions of affective states. *Journal of Personality and Social Psychology*, *45*, 513-523.
- Striemer, C.L., Chapman, C.S. & Goodale, M.A. (2009). "Real-time" obstacle avoidance in the absence of primary visual cortex. *Proceedings of the National Academy of Science of the United States of America*, *106*, 15996-16001.
- Tarsitano, M.S. & Jackson, R.R. (1997). Araneophagic jumping spiders discriminate between detour routes that do and do not lead to prey. *Animal Behaviour*, *53*, 257-266.
- Whitwell, R.L., Striemer, C.L., Nicolle, D.A. & Goodale, M.A. (2011). Grasping the non-conscious: preserved grip scaling to unseen objects for immediate but not delayed grasping following a unilateral lesion to primary visual cortex. *Vision Research*, *51*, 908-924.
- Winkielman, P., Berridge, K.C. & Wilbarger, J.L. (2005). Unconscious affective reactions to masked happy versus angry faces influence consumption behaviour and judgements of value. *Personality and Social Psychology Bulletin*, *31*, 121-135.