

doi: 10.1093/nc/niz020 Research article

# Awareness as inference in a higher-order state space

# Stephen M. Fleming\*

Wellcome Centre for Human Neuroimaging, Institute of Neurology, 12 Queen Square, London WC1N 3AR, UK

\*Correspondence address. Wellcome Centre for Human Neuroimaging, University College London, 12 Queen Square, London WC1N 3AR, UK. Tel: +44 (0)20 344 84349; E-mail: stephen.fleming@ucl.ac.uk

#### **Abstract**

Humans have the ability to report the contents of their subjective experience—we can say to each other, 'I am aware of X'. The decision processes that support these reports about mental contents remain poorly understood. In this article, I propose a computational framework that characterizes awareness reports as metacognitive decisions (inference) about a generative model of perceptual content. This account is motivated from the perspective of how flexible hierarchical state spaces are built during learning and decision-making. Internal states supporting awareness reports, unlike those covarying with perceptual contents, are simple and abstract, varying along a 1D continuum from absent to present. A critical feature of this architecture is that it is both higher-order and asymmetric: a vast number of perceptual states is nested under 'present', but a much smaller number of possible states nested under 'absent'. Via simulations, I show that this asymmetry provides a natural account of observations of 'global ignition' in brain imaging studies of awareness reports.

Keywords: theories and models; computational modeling; consciousness; metacognition

#### Introduction

Humans have the ability to report the contents of their subjective experience—we can say to each other, 'I am aware of X'. Such reports, unlike many other aspects of behaviour, are intended to convey information about experience (Frith et al. 1999). This property of awareness reports makes them central to a science of consciousness, which has focused on measuring and quantifying differences in awareness while holding other aspects of stimuli and behavioural performance constant (Bernard 1993; Dehaene and Changeux 2011). In this article, I propose a computational framework that characterizes awareness reports as metacognitive decisions (inference) about a generative model of perceptual content. This higher-order state space (HOSS) framework builds on Bayesian approaches to perception that invoke hierarchical probabilistic inference as a route towards efficiently modelling the external world (von Helmholtz 1860; Kersten et al. 2004; Friston 2005; Hohwy 2013).

The outline of the article is as follows. I start by describing the psychological processes hypothesized to support awareness reports with reference to experimental paradigms commonly used to study conscious awareness. Second, I outline the central hypothesis, that awareness is a higher-order state in a generative model of perceptual contents. Third, I model a simple perceptual decision to explicate aspects of the framework, and distinguish it from other, related approaches such as signal detection theory (SDT; Green and Swets 1966; King and Dehaene 2014). Finally, I highlight empirical predictions that flow from the model, and how it relates to existing theories of consciousness such as global workspace and higher-order theories.

#### **Psychological Basis of Awareness Reports**

Several authors have proposed that the psychological basis of a (visual) awareness report is an internal decision about the visibility of perceptual contents (Ramsøy and Overgaard 2004; Sergent and Dehaene 2004; King and Dehaene 2014). (The same computational considerations likely hold for awareness of other sensory modalities—a focus on visibility here reflects a historical bias towards vision in studies of conscious awareness.) This implies that internal states supporting awareness reports,

unlike those covarying with perceptual contents themselves, are both simple and abstract—simple because they vary along a 1D continuum from unaware to aware, and abstract because they do not encode the perceptual state itself, only its presence or absence. Note that a better terminology for 'unaware' is really 'absent', 'unseen' or 'noise', as participants remain aware of seeing nothing on trials on which they report 'unaware'. Awareness reports also refer to different subsets of perceptual content: for instance, subjects may be asked 'did you see the word?', 'did you see the number?' or 'did you see anything at all?'. These two features imply that awareness reports are metacognitive decisions about a rich perceptual generative model. I will make this hypothesis more concrete in the next section.

A range of experimental paradigms have been developed to introduce variability in awareness reports while keeping other aspects of stimuli and behaviour fixed (see Kim and Blake 2005 for a review). For example, using backward masking, Dehaene et al. (2001) found that they could make words invisible while showing (via priming effects and brain imaging) that they were processed up to a semantic level. When subjects reported consciously seeing the words, whole-brain fMRI showed elevated activations in the parietal and prefrontal cortex, which have become known as 'global ignition' responses due to their nonlinear response profile in relation to stimulation strength (Del Cul et al. 2007; Dehaene and Changeux 2011). Since these classic studies, alternative explanations of frontoparietal ignition have been put forward, including that it is involved in the act of reporting, but not conscious awareness, or that it reflects greater performance capacity on conscious trials (Lau and Passingham 2006; Aru et al. 2012). These debates are ongoing (see Tsuchiya et al. 2015; Michel and Morales 2019, for recent arguments from both sides).

#### **Hypothesis**

In common with other predictive processing approaches, we assume that the brain is engaged in building a hierarchical, probabilistic generative model of the world, one in which inference and learning proceed using (approximations of) Bayes' rule. One algorithmic implementation of Bayesian generative models is predictive coding, whereby perceptual causes encoded at higher levels of the system generate predictions about incoming sensory data (Friston 2005; Hohwy 2013). Figure 1A presents an outline of this scheme, in which two perceptual causes (apple or orange) generate predictions that 'compete' to explain the incoming sensory data, while lower layers in turn signal the error in the current prediction. Via a prediction error minimization scheme, over time the best explanation of the sensory data is 'selected' at higher levels of the system.

The novel aspect of the current framework is its focus on incorporating awareness into the perceptual generative model—explaining how decisions to respond 'I am aware of X' or 'I am unaware of X' get made. (Note that here I am focusing on reportable states of awareness, and leaving aside the issue of whether non-reportable contents may be conscious (Block 1995, 2011). By adopting this stance, we can frame a clear question that is answerable by cognitive science: what are the computational processes involved in producing awareness reports? (Dennett 1993; Graziano 2013).)

The central hypothesis is:

Awareness is a higher-order state in a generative model of perceptual contents.

Awareness reports are governed by a second-order (metacognitive) inference about the state of a first-order (perceptual) generative model (Fleming and Daw 2017). One way of implementing this second-order inference is by adding an additional hierarchical state above the perceptual generative model, which I refer to as an 'awareness state' (Fig. 1B). Paralleling the psychological simplicity of awareness reports, the awareness state is also simple, and signals a probability of whether there is perceptual content in the lower layers (corresponding to reports of 'present' or 'absent'). It is also part of the generative model, such that if the model is run forward, states of presence (vs. absence) lead to the top-down generation of perceptual states in lower layers.

As we reviewed above, a central property of awareness states is that they are abstract—we can flexibly interrogate awareness of not only apples or oranges, but also many other aspects of perceptual experience. In the language of probabilistic generative models, this implies awareness states are factorized with respect to lowerorder perceptual causes. This notion of factorization is depicted in Fig. 1C for the case of awareness of different shapes (a circle or square). Rather than maintaining separate states for aware-ofcircle, aware-of-square, unaware-of-circle and unaware-of-square, this space can be factorized into two states, one for circle/square, and another for aware/unaware. However, this factorization is asymmetric (Fig. 1D). In the absence of awareness, there is (by definition) an absence of perceptual content, such that being unaware of a circle is similar to being unaware of a square. In contrast, a large number of potential perceptual states is nested under the awareness state of 'presence'. This imposes an asymmetry in the model architecture which we will leverage in the next section when seeking to account for global ignition responses.

#### Model

The model can be described formally in terms of a probabilistic graphical model (Pearl, 1988), where nodes correspond to unknown variables and the graph structure is used to indicate dependencies between variables. These graphs provide a concise description of how sensory data are generated (Fig. 2A).

W is a  $1 \times N$  vector that encodes the relative probabilities of each of N discrete perceptual states. A is a scalar awareness state encoding the probability of a perceptual state W being 'present'  $(w_1 \dots w_N)$  or 'absent'  $(w_0)$ . Each 'perceptual' state W here is discrete, but in practice this state space is likely to be multidimensional and also hierarchically organized. By expanding the graphical model to enumerate each discrete state (Fig. 2B), it is straightforward to see how this architecture imposes an asymmetry on the perceptual state space: awareness  $(a_1)$  entails the possibility of perceptual content ( $w_1 \dots w_N$ ), whereas unawareness leads to the absence of content  $(w_0)$ . To simulate multivariate sensory data (X), W in turn determines the value of  $\mu$ , which is a M × N matrix defining the location (mean) of a multivariate Gaussian in a feature space of dimensionality M.  $\Sigma$  is a  $M\times M$  covariance matrix which in the current simulations is fixed and independent of A and W.

When answering the query, 'Present or absent?', we compute the posterior P(A|X=x), marginalizing over perceptual states W:

$$\begin{split} P(A|X=x) & \propto \sum_{W} P(A)P(W|A)P(X=x|W) \\ & \propto P(A)\sum_{W} P(W|A)P(X=x|W) \end{split} \tag{1}$$

where the likelihood of X given W is:

$$P(X = x|W) \sim N(\mu_W, \Sigma)$$
 (2)

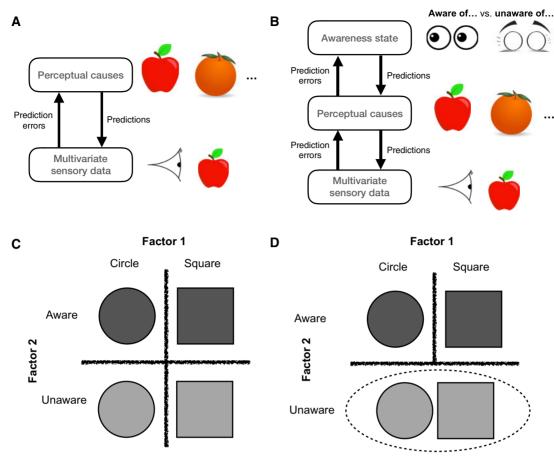


Figure 1. (A) Schematic of standard predictive coding architectures in which hypotheses about perceptual causes (predictions) are updated in response to prediction errors generated by incoming sensory data. (B) Extension of the predictive coding architecture in (A) to accommodate a higher-order awareness state. (C) Factorization of awareness and perceptual content. (D) Illustration of the asymmetry that ensues from factorizing an awareness state; being unaware of a circle is a similar state to being unaware of a square.

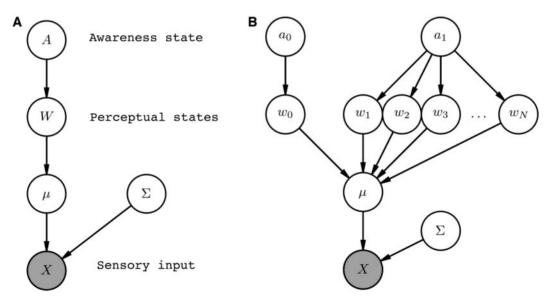


Figure 2. (A) Probabilistic graphical model of awareness reports. Nodes represent random variables and the graph structure is used to indicate dependencies as indicated by directed arrows. The shaded node indicates that this variable is observed by the system as sensory input. (B) Expanded version of the graphical model from panel (A) that makes explicit the asymmetry in the state space. Figures created using the Daft package in Python.

As in standard models of perceptual decision-making such as SDT, inference on contents W is also straightforward:

$$P(W|X=x) \propto \sum_{A} P(A)P(W|A)P(X=x|W) \tag{3} \label{eq:3}$$

#### Simulations

To simulate the model, I build on previous work using a 2D feature space to capture important features of multidimensional perceptual categorization (King and Dehaene 2014). Each axis represents the strength of activation of one of two possible stimulus features, such as leftward or rightward tilted grating orientations (see Fig. 3). The origin represents low activation on both features, consistent with no stimulus (or noise) being presented. As in the more general case described in the previous section, each stimulus category generates samples from a multivariate Gaussian whose mean is dominated by one or other feature. Thus, if I receive a sample of X = [20], I can be confident that I was shown a left-tilted stimulus; if I receive a sample X = [02], I can be confident in seeing a right-tilted stimulus.

King and Dehaene (2014) showed that by placing different types of decision criteria onto this space, multiple empirical relationships between discrimination performance, confidence and visibility could be simulated. In their model, visibility was modelled as the distance from the origin, and stimulus awareness reflected a first-order perceptual categorization in which 'absent' was one of several potential stimulus classes (Fig. 3A).

Our model builds closely on theirs and inherits the benefits of being able to accommodate dissociations between forcedchoice responding and awareness reports. However, it differs in proposing that awareness is not inherent to perceptual categorization; instead, perceptual categorization is nested under a generative model of awareness (Fig. 3B). In other words, unlike in SDT, deciding that a stimulus is 'absent' in the HOSS model is governed by a more abstract state than deciding a stimulus is tilted to the left or right. We will see that this seemingly minor change in architecture leads to important consequences for the relationship between awareness and global ignition.

To explore the properties of the model, I simulate inference at different levels of the hierarchy for the two-class stimulus discrimination problem described in Fig. 3B. I first simulate, for a variety of 2D inputs (X's), the probability of saying 'aware' or 'seen' ( $P(A = a_1|X = x)$ ). Figure 4A shows that this probability rises in a graded manner from the lower left corner of the graph (low activation of any feature) to the upper right (high activation of both features). In contrast, confidence in making a discrimination response (e.g. rightward vs. leftward) increases away from the major diagonal (Fig. 4B), as the model becomes sure that the sample was generated by either a leftward or rightward tilted stimulus. As in King and Dehaene (2014), these changes in discrimination confidence also occur in the absence of reporting

I next simulate a proxy for prediction error at each layer in the model—in other words, how much belief change was induced by the sensory sample. I use the Kullback-Leibler (K-L)

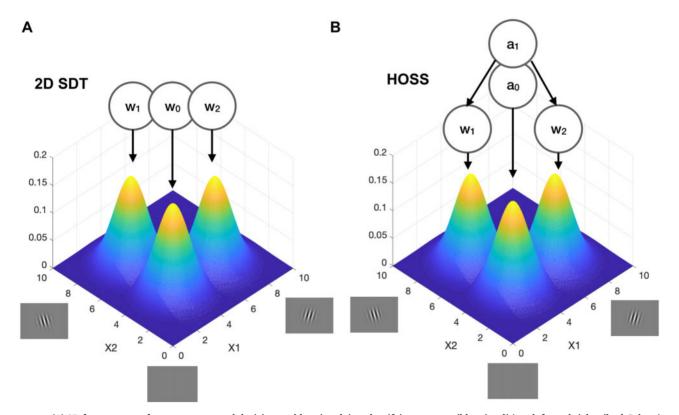


Figure 3. (A) 2D feature space for a toy perceptual decision problem involving classifying two possible stimuli (e.g. left- and right-tilted Gabors). Each Gaussian indicates the likelihood of observing a pair of features (e.g. orientation) given each stimulus class (where  $\mu = [3.57]$ , [7.3.5] or [3.53.5] and Σ is the identity matrix). The right-tilted stimuli occupy the right-hand side of the grid; left-tilted stimuli occupy the left-hand side of the grid. The absence of stimulation is represented by a distribution in which activation of each feature is low towards the origin. In 2D SDT, there are three stimulus classes organized in a flat (non-hierarchical) structure. (B) The same 2D feature space from (A), modified to make explicit the hierarchical aspect of the HOSS model. A higher-order awareness state ( $a_1$ ) nests perceptual states  $w_1$  and  $w_2$ .

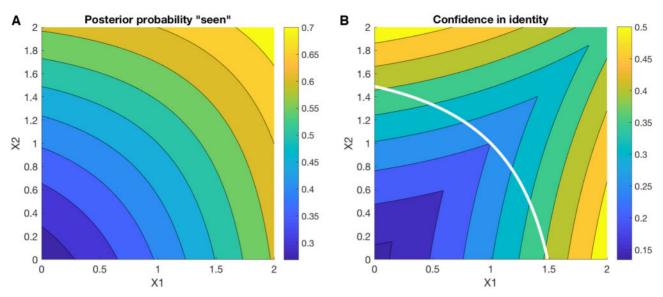


Figure 4. Simulations of inference on (A) awareness state A and (B) perceptual states W, as a function of sensory input X (where  $\mu =$ [0.51.5], [1.50.5] or [0.50.5] and  $\Sigma$  is the identity matrix). In panel (A), the posterior probability of a report of 'presence' rises from the lower left to the upper right of the grid. In panel (B), confidence in stimulus identify (e.g. left- or right-tilted Gabor) increases towards the corners of the grid. Overlaid in white is the 0.5 contour from panel (A) showing that graded changes in confidence in identity still occur on trials that have a high likelihood of being classed as 'unseen' by the model. Confidence in identity was computed as  $\max[P(w_1|X=x), P(w_2|X=x)]$ .

divergence as a compact summary of how far the posterior probability distribution at each level in the network differs from the prior. Flat priors were used for both the A and W levels. The K-L divergence is a measure of Bayesian surprise, which under predictive coding accounts is linked to neural activation at each level in a hierarchical network (Friston 2005; Summerfield and de Lange 2014). For instance, if the model starts out with a strong prior that it will see gratings of either orientation, but a grating is omitted, this constitutes a large prediction error (an unexpected absence). Thus, computing K-L divergence provides a rough proxy for the amount of 'activation' we would expect as a function of different types of decision.

At the level of perceptual states W, there is substantial asymmetry in the K-L divergence expected when the model says 'seen' vs. 'unseen' (Fig. 5A). This is due to the large belief updates invoked in the perceptual layer W by samples that deviate from the origin. In contrast, when we compute K-L divergence for the awareness state (Fig. 5B), the level of prediction error is symmetric across seen and unseen decisions. This is because at this level inference on presence and absence is symmetric. When simulating these belief updates over a range of precisions to mimic increasing stimulus-onset asynchrony in a typical backward-masking experiment, we see that the asymmetry in K-L divergence of the W states increases with stimulus-onset asynchrony (SOA), producing an ignition-like pattern when the stimulus is 'seen' (Fig. 5C).

#### **Empirical Predictions**

The model is currently situated at a computational level and remains agnostic about temporal dynamics and neural implementation. (For recent work translating probabilistic graphical models into models of neuronal message passing see George et al. (2017) and Friston et al. (2017).). Here, I instead focus on coarser-scale predictions about the neural correlates of awareness reports in typical consciousness experiments.

First, as hinted above, an asymmetric state space for presence and absence suggests there will be greater summed prediction error in the entire network on presence decisions (as summarized by K-L divergence at each node of W). This may be a computational correlate of the global ignition responses often found to track awareness reports (Del Cul et al. 2007; Dehaene and Changeux 2011).

Second, the model predicts that awareness reports (but not discrimination performance, which relies on lower-order inference on W) will depend on higher-order states. These may be instantiated in neural populations in prefrontal and parietal cortex (Lau and Rosenthal 2011). Thus, it may be possible to silence or otherwise inactivate the neural substrates of an awareness state without affecting performance—a type of blindsight (Weiskrantz 1999; Del Cul et al. 2009). However, to the extent that this network is flexible in its functional contribution to higher cognition, showing both 'multiple demand' characteristics (Duncan 2010) and mixed selectivity (Mante et al. 2013), we should also not be surprised by null results, given that single lesions may belie redundancy in its contribution to awareness (Michel and Morales 2019).

Third, for the uppermost awareness state, we expect symmetry-decisions in favour of both presence and absence will lead to belief updates of similar magnitude. There has been limited focus on examining decisions about stimulus absence (as these decisions are often used as a baseline or control condition in studies of perceptual awareness). However, existing data are compatible with symmetric encoding of presence and absence at the upper level of the visual hierarchy, in primate lateral prefrontal cortex (LPFC; Panagiotaropoulos et al. 2012). Merten and Nieder (2012) trained monkeys to report the presence or absence of a variety of low-contrast shapes presented near to visual threshold. Neural activity tracking the decision (present or absent) was decorrelated from that involved in planning a motor response by use of a post-stimulus cue that varied from trial to trial. Distinct neural populations tracked the decision to report 'seen' vs. 'unseen'. Importantly the magnitude of activation of

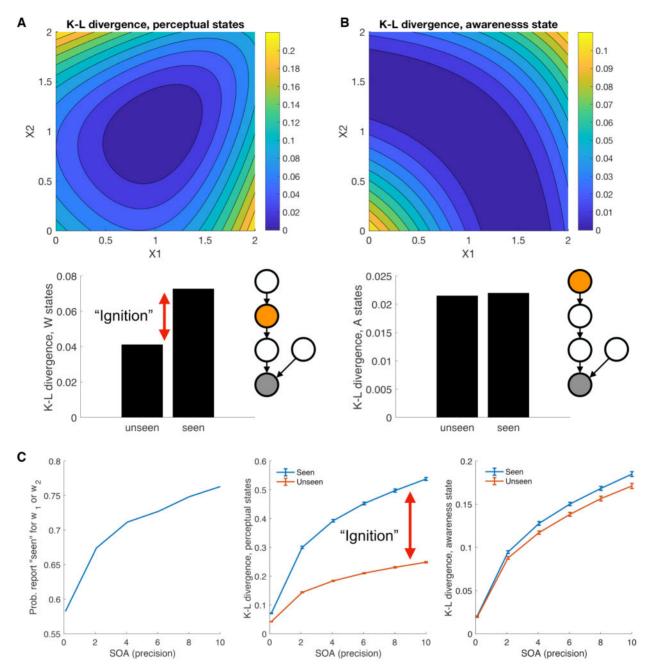


Figure 5. (A, B) K-L divergence for (A) perceptual states W and (B) awareness state A as a function of sensory input X. K-L divergence quantifies the change from prior to posterior after seeing the stimulus X and provides a metric for the magnitude of belief update at different levels of the network. The lower panels show the averaged K-L divergence for both W and A as a function of whether the model reports presence  $(P(A = a_1|X = x) > 0.5)$  or absence. The network nodes correspond to those in Fig. 2A and the orange node indicates the node for which the K-L divergence is calculated. (C) Behaviour of the network in a simulated masking experiment at various levels of SOA (modelled as increasing sensory precision) in which sensory evidence was sampled from the three stimulus classes shown in Fig. 3B. The left-hand panel shows that the model is more likely to report 'seen' as SOA increases. The middle panel shows the K-L divergence at the level of perceptual states W as a function of whether the model reports presence  $(P(A = a_1|X = x) > 0.5)$  or absence. The expected K-L divergence is asymmetric, with a bigger average belief update following 'seen' decisions (a computational correlate of global ignition). The right-hand panel shows the average K-L divergence of awareness state A as a function of whether the model reports presence  $(P(A = a_1|X = x) > 0.5)$  or absence. At this level the expected K-L divergence is relatively symmetric for 'seen' and 'unseen' decisions.

these populations was similar in timing and strength, suggesting a symmetric encoding of awareness in LPFC. Using fMRI, Christensen et al. (2006) also observed symmetric activation for judgments of presence and absence (compared to an

intermediate visibility rating) in anterior prefrontal cortex, whereas a global ignition response was seen for presence (compared to absence) in a widespread frontoparietal/striatal network.

More broadly, the current framework suggests that focusing on inference about absence will be particularly fruitful for understanding the neural and computational basis of conscious awareness (Merten and Nieder 2012; Farennikova 2013; Merten and Nieder 2013).

## **Role of Precision Estimation in Resolving Awareness States**

The current simulations assume that the noise of sensory input is fixed, but in reality this parameter would also need to be estimated. A range of disambiguating cues are likely to prove important in such an estimation scheme and thereby affect an inference on awareness. For instance, beliefs about the state of attention or other properties of the sensory system provide global, low-dimensional cues as to the state of awareness (Lau 2008; Graziano 2013). Computationally these cues may be implemented as beliefs about precision (priors on  $\Sigma$  in the model in Fig. 2A), where precision refers to the inverse of the noise (variability) we expect from a particular sensory channel.

Another source of information about sensory precision is proprioceptive and interoceptive input about bodily states. Consider the following thought experiment in which we set up two conditions in a dark room, one in which the subject has their eyes open and one in which they have their eyes closed. Now imagine that we have arranged for neural activity in early visual areas to be identical in the two cases (the X's are the same), and that in both cases the subject is told (for instance via an auditory cue) that there might have been a faint flash of light. Despite the visual activity being identical, the subject can be sure that they didn't see anything when their eyes were closed compared to when they were open. In other words, proprioception provides disambiguating information as to the current state of awareness-when the eyes are open we expect to have higher precision input than when the eyes are closed.

One straightforward way of introducing this relationship is to allow precision itself to depend on awareness (a connection between A and  $\Sigma$  in Fig. 2A). Such a modification implies that an awareness state may be 2D, encoding the distinction between whether something has the potential to be seen (high vs. low expected precision or eyes open vs. eyes closed) as well as whether something is seen (present vs. absent; Metzinger 2014; Limanowski and Friston 2018). This aspect of the HOSS model is also in keeping with Graziano's attention schema model of consciousness, in which awareness is equated to a model of attention (Graziano, 2013). However, in contrast to the attention schema approach, in HOSS a model of attention provides a critical input into resolving ambiguity about whether we are aware or not (by affecting beliefs about precision), rather than determining awareness itself.

# Relationship to Other Theories of Consciousness

The goal of the higher-order state-space (HOSS) approach outlined here is modest-to delineate computations supporting metacognitive reports about awareness. This is a useful place to start given that report (or the potential for report) is the jumping-off point for a scientific study of consciousness.

A stronger reading of the model is that conscious awareness and metacognitive reports depend on shared mechanisms in the human brain (Shaver et al. 2008; Brown et al. 2019). This stronger version shares similarities with higher-order theories of consciousness, particularly Lau's proposal that consciousness involves 'signal detection on the mind' (Lau 2008; Hohwy 2015). Notably, a process of hierarchical inference may take place via passive message-passing without any strategic, cognitive access to this information e.g. in working memory (Carruthers 2017), making it compatible with higher-order representational accounts of phenomenal consciousness (Brown

However, while inference on higher-order states is, on this view, necessary for awareness, it may not be sufficient. In HOSS, the higher-order awareness state is simple and lowdimensional. Lower-order states clearly make a contribution to perceptual experience under this arrangement—a variant of the 'joint determination' view advocated by Lau and Brown (2019). However, it seems an empirical question as to the relative granularity of higher-order and first-order representations, and a range of intermediate views are plausible. The more important point is that the state space is factorized to allow two separate causes of the sensory data—what it is, and whether I have seen it. In other words, becoming aware of a red, tilted object may depend on learning an abstract, factorized state of presence/absence that is not bound up with the states of being red or tilted. This is likely to be computationally demanding in a rich, multidimensional state space (as it requires marginalizing over W) and may be rare in most cognitive systems.

HOSS also provides a new perspective on global workspace (GWS) architectures. GWS proposes that consciousness occurs when information is 'globally broadcast' throughout the brain. As a result of global broadcast, cognitive and linguistic machinery have access to information about a particular stimulus or subpersonal mental state (Dehaene et al. 1998). HOSS retains the 'global' aspect of GWS, in that an awareness state is hierarchically higher with respect to the range of possible perceptual states, and therefore has a wide conceptual purview. However, HOSS recasts ignition-like activations as asymmetric inference about stimulus presence rather than a consequence of stimulus content being 'broadcast'. Such a move potentially resolves the conundrum of how global broadcast directly accounts for systems claiming to be conscious of a stimulus without positing additional machinery. Global access to the workspace allows the system to say 'there is an X', but not endow it with the capacity to report awareness of X. This point is made concisely by Graziano (Graziano 2016):

Consider asking 'Are you aware of the apple?' The search engine searches the internal model and finds no answer. It finds information about an apple, but no information about what 'awareness' is, or whether it has any of it... It cannot answer the question. It does not compute in this domain.

In other words, it is difficult to see how such a system can be actively aware of the absence of stimulation when global broadcast is constitutive of awareness. The state space approach outlined here is designed explicitly to compute in this domain, and therefore does not suffer from the same problem. Another critical difference between GWS and HOSS is that HOSS predicts prefrontal involvement for active decisions about stimulus absence, whereas GWS predicts that PFC remains quiescent on such trials due to a failure of the stimulus to gain access to the

Finally, to the extent that abstract awareness states need to be learnt or constructed, creating this level may require a protracted period of development. Such development would begin with creating a perceptual generative model (W) before a more

general property (awareness) could be abstracted from these perceptual states. This is consistent with Cleeremans' 'radical plasticity thesis' in which consciousness is underpinned by learning abstract representations of both ourselves and the world (Cleeremans 2011).

#### **Research Questions**

I close with questions for future research motivated by the current computational sketch:

- 1. How are awareness states represented in neural activity? Are presence and absence encoded symmetrically?
- 2. Is a (neural) representation of awareness factorized with respect to other aspects of perceptual content?
- 3. How are awareness states learned?

#### Data availability

Model and simulation code can be accessed at https://github. com/smfleming/HOSS.

### **Acknowledgements**

I am grateful to the Metacognition and Theoretical Neurobiology groups at the Wellcome Centre for Human Neuroimaging and members of the University of London Institute of Philosophy for helpful discussions. I thank Matan Mazor, Oliver Hulme, Chris Frith, Nicholas Shea, Karl Friston and two anonymous reviewers for comments on previous drafts of this manuscript. This work was supported by a Wellcome/Royal Society Sir Henry Dale Fellowship (206648/Z/17/Z).

#### References

- Aru J, Bachmann T, Singer W, et al. Distilling the neural correlates of consciousness. Neurosci Biobehav Rev 2012;36:737-46.
- Baars BJ. A Cognitive Theory of Consciousness. Cambridge, UK: Cambridge University Press, 1993.
- Block N. On a confusion about a function of consciousness. Brain Behav Sci 1995;18:227-47.
- Block N. Perceptual consciousness overflows cognitive access. Trends Cogn Sci 2011;15:567–75.
- Brown R. The HOROR theory of phenomenal consciousness. Philos Stud 2015;172:1783-94.
- Brown R, Lau H, Le Doux J. The Misunderstood Higher-Order Approach to Consciousness. preprint, PsyArXiv, 2019.
- Carruthers P. Block's overflow argument. Pac Philos Q 2017;98:
- Christensen MS, Ramsøy TZ, Lund TE, et al. An fmri study of the neural correlates of graded visual perception. Neuroimage 2006; **31**:1711-25.
- Cleeremans A. The radical plasticity thesis: how the brain learns to be conscious. Front Psychol 2011;2:1-12.
- Dehaene S, Changeux J-P. Experimental and theoretical approaches to conscious processing. Neuron 2011;70:200-27.
- Dehaene S, Kerszberg M, Changeux JP. A neuronal model of a global workspace in effortful cognitive tasks. Proc Natl Acad Sci USA 1998;95:14529-34.
- Dehaene S, Naccache L, Cohen L, et al. Cerebral mechanisms of word masking and unconscious repetition priming. Nat Neurosci 2001;4:752.

- Del Cul A, Baillet S, Dehaene S. Brain dynamics underlying the nonlinear threshold for access to consciousness. PLoS Biol 2007:5:e260.
- Del Cul A. Dehaene S. Reves P. et al. Causal role of prefrontal cortex in the threshold for access to consciousness. Brain 2009: 132:2531-40.
- Dennett DC. Consciousness Explained. Penguin UK, 1993.
- Green DM, Swets JA. Signal Detection Theory and Psychophysics. New York: Wiley, 1966.
- Duncan J. The multiple-demand (MD) system of the primate brain: mental programs for intelligent behaviour. Trends Cogn Sci 2010:14:172-9.
- Farennikova A. Seeing Absence. Philosophical Studies 2013;166: 429-54.
- Fleming SM, Daw ND. Self-evaluation of decision-making: a general Bayesian framework for metacognitive computation. Psychol Rev 2017;124:91-114.
- Friston K. A theory of cortical responses. Philos Trans R Soc Lond B Biol Sci 2005;360:815-36.
- Friston KJ, Parr T, de Vries B. The graphical brain: Belief propagation and active inference. Netw Neurosci 2017;1:381-414.
- Frith C, Perry R, Lumer E. The neural correlates of conscious experience: an experimental framework. Trends Cogn Sci 1999;3:
- George D, Lehrach W, Kansky K, et al. A generative vision model that trains with high data efficiency and breaks text-based CAPTCHAs. Science 2017;358.
- Graziano MSA. Consciousness engineered. J Conscious Stud 2016; 23:98-115
- Graziano MSA. Consciousness and the Social Brain. Oxford University Press, 2013.
- Hohwy J. Prediction error minimization, mental and developmental disorder, and statistical theories of consciousness. In: Gennaro RJ (ed.), Disturbed Consciousness: New Essays on Psychopathology and Theories of Consciousness. Cambridge, MA: MIT Press, 2015, 293-324.
- Hohwy J. The Predictive Mind. Oxford University Press, 2013.
- Kanai R, Walsh V, Tseng C. Subjective discriminability of invisibility: a framework for distinguishing perceptual and attentional failures of awareness. Conscious Cogn 2010;19:1045-57.
- Kersten D, Mamassian P, Yuille A. Object perception as Bayesian inference. Annu Rev Psychol 2004;55:271-304.
- Kim C-Y, Blake R. Psychophysical magic: rendering the visible 'invisible'. Trends Cogn Sci 2005;9:381-8.
- King J-R, Dehaene S. A model of subjective report and objective discrimination as categorical decisions in a vast representational space. Philos Trans R Soc Lond B Biol Sci 2014;369: 20130204.
- Lau H, Brown R. The emperor's new phenomenology? The empirical case for conscious experience without first-order representations. In: Pautz A and Stoljar D (eds), Blockheads! Essays on Ned Block's Philosophy of Mind and Consciousness. Cambridge, MA: MIT Press, 2019.
- Lau H, Rosenthal D. Empirical support for higher-order theories of conscious awareness. Trends Cogn Sci 2011;15:365-73.
- Lau HC, Passingham RE. Relative blindsight in normal observers and the neural correlate of visual consciousness. Proc Natl Acad Sci USA 2006;103:18763-8.
- Lau HC. A higher order Bayesian decision theory of consciousness. Progr Brain Res 2008;168:35-48.
- Limanowski J, Friston K. 'Seeing the dark': grounding phenomenal transparency and opacity in precision estimation for active inference. Front Psychol 2018;9.

- Mante V, Sussillo D, Shenoy KV, et al. Context-dependent computation by recurrent dynamics in prefrontal cortex. *Nature* 2013:503:78.
- Martin J-R, Dokic J. Seeing absence or absence of seeing? Thought J Philos 2013;2:117–25.
- Merten K, Nieder A. Active encoding of decisions about stimulus absence in primate prefrontal cortex neurons. *Proc Natl Acad Sci USA* 2012;**109**:6289–94.
- Merten K, Nieder A. Comparison of abstract decision encoding in the monkey prefrontal cortex, the presupplementary, and cingulate motor areas. *J Neurophysiol* 2013;**110**:19–32.
- Metzinger T. How does the brain encode epistemic reliability? Perceptual presence, phenomenal transparency, and counterfactual richness. Cogn Neurosci 2014;5:122–4.
- Michel M, Morales M. Minority reports: consciousness and the prefrontal cortex. Mind Lang 2019.
- Panagiotaropoulos TI, Deco G, Kapoor V, et al. Neuronal discharges and gamma oscillations explicitly reflect visual consciousness in the lateral prefrontal cortex. Neuron 2012;74: 924–35.

- Pearl J. Probabilistic Reasoning in Intelligent Systems: Networks of Plausible Inference. Burlington, MA: Morgan Kaufmann Publishers, 1988.
- Ramsøy TZ, Overgaard M. Introspection and subliminal perception. Phenomenol Cogn Sci 2004;3:1–23.
- Sergent C, Dehaene S. Is consciousness a gradual phenomenon? Evidence for an all-or-none bifurcation during the attentional blink. Psychol Sci 2004;15:720–8.
- Shaver E, Maniscalco B, Lau HC. Awareness as confidence. Anthropol Philos 2008;9:58–65.
- Summerfield C, de Lange FP. Expectation in perceptual decision making: neural and computational mechanisms. Nat Rev Neurosci 2014;15:745–56.
- Tsuchiya N, Wilke M, Frässle S, et al. No-report paradigms: extracting the true neural correlates of consciousness. *Trends Cogn Sci* 2015;19:757–70.
- von Helmholtz H. Treatise on Physiological Optics 1860.
- Weiskrantz L. Consciousness Lost and Found: A Neuropsychological Exploration. Oxford: OUP, 1999.