Consciousness as Inference in Time

A Commentary on Victor Lamme

Lucia Melloni

Unraveling the neural correlates of conscious remains one of the great challenges of our time. Victor Lamme proposes that neural integration through feedback loops is what differentiates conscious from unconscious processing. Here, I review his hypothesis, focusing on the spatial scale of integration as well as the possible neural mechanisms involved. I go on to show that any theory of the neural correlates of consciousness is incomplete if it cannot account for how prior knowledge shapes perception and how this form of integration occurs. Finally, I propose that integration across moments in time is a crucial but hitherto neglected aspect of conscious perception, which creates the "flow" of conscious experience.

Commentator

Lucia Melloni
lucia.melloni@brain.mpg.de

Max Planck Institute for Brain Research
Frankfurt a. M., Germany

Target Author

Victor Lamme
victorlamme@gmail.com

Universiteit van Amsterdam
Amsterdam, Netherlands,

Editors

Thomas Metzinger
metzinger@uni-mainz.de

Johannes Gutenberg-Universität
Mainz, Germany

Jennifer M. Windt
jennifer.windt@monash.edu

Monash University
Melbourne, Australia

1 Qualia 2.1: Integration is key but is it all?

Why do we see the way we *see*? How is our perception different from the way a photograph is acquired on the sensor chip of a digital camera? It seems obvious that we do not see an image made of individual pixels but an integrated, smooth, colourful, and vivid image. What is the neural substrate of this marvellous capacity that makes us feel and experience the way we do? These are the central questions that Victor Lamme sets out to address in his paper *The Crack of Dawn: Perceptual Functions and Neural Mechanisms that Mark the Transition from Unconscious Processing to Conscious Vision.*

This is by no means an easy task, even when one stays away from the difficult problem of qualia or "what it is like to be" (Nagel 1974). The question of how awareness arises has preoccupied philosophers and scientists for centuries, and while significant progress has been made in recent decades we are still far from reaching a conclusion (Dehaene 2014; Koch 2004). One thing is clear however: success in understanding the neural machinery that instantiates consciousness rests on identifying the fundamental features that characterise a state as conscious and that distinguish it from unconscious states.

A remarkable discovery of the past century is that a significant portion of all mental operations, including fairly complex ones such as decision-making and perceptual categorisation, can be carried out unconsciously. Take the case of language: while it seems effortless to understand the words that you are currently reading, you do not have conscious access to the syntactic processes that ultimately allow you to grasp the relations between the elements of this sentence and thus its meaning. These complex mental operations occur "behind the scene" of consciousness. Given that so many intricate processes can operate unconsciously, one cannot but wonder what consciousness is good for. Which mental processes *require* consciousness, if any? And if so, what really distinguishes conscious from unconscious cognition? Victor Lamme offers a stimulating and comprehensive review of processes in vision that can be performed outside the realm of awareness. The list is long and may be surprising (also see Kouider & Dehaene 2007), ranging from detection of simple (e.g., oriented lines) and complex features (e.g., faces; Almeida et al. 2013; de Gardelle et al. 2011; Del Zotto et al. 2013), to mathematical operations such as abstract comparisons between quantities (Greenwald et al. 2003), to triggering of motor plans (Dehaene et al. 1998), and even error-related responses to stimuli that fully escape our consciousness (Cohen et al. 2009).

What do we need consciousness for, then? Lamme proposes that consciousness is required when all sources of information need to be integrated. For instance, when we see a face, we can not only *detect* that is a face, a process that can be performed unconsciously, but also *identify* it as that of our friend Billy, whom we have not seen in ten years and that we *remember* warmheartedly from our childhood. Consciousness brings this *unified* moment in which all comes together: previous experiences are retrieved from memory (e.g., do we have reason to like Billy?) and unified with the context of the current experience (e.g., where are we now?), but also intertwined with predictions for future actions (e.g., would we like to engage in a conversation?). Thus, in one single moment, past,

present and future come together and form a unified conscious experience. Many scientists nowadays agree that conscious experience provides an abstract summary of all available sources of information, from which many features are filtered out and reinterpreted in a format that is most useful for further actions, thoughts, deliberations, and chain operations that cannot be processed by non-conscious processors (Lamme this collection; Baars 2002; Dehaene 2014; Melloni & Singer 2010). Hence, what reaches our perception is a highly processed, "interpreted" version of the world. One key intuition is that the unification and "interpretation" of the experience that reaches our consciousness is achieved through the activation of myriads of neurons that signal individual features, but that it is by virtue of *integrating* their information through dynamic interactions (for example via synchronous coordination of their activity or via feedback processes) that a coherent experience across senses, space, and time comes about.

An important caveat is that integration of information *per se* is unlikely to distinguish conscious from unconscious processing as integration of many features can also proceed unconsciously (Dehaene et al. 1998; Gaillard et al. 2009; Lin & He 2009; Melloni et al. 2007; Melloni & Rodriguez 2007; Mudrik et al. 2014). In fact, integration through convergence is a key principle of the wiring of the brain, which explains the mere existence of feature-selective neurons that respond to motion, shape, or complex stimuli such as faces, and that process information in an unconscious manner. If it is not integration *per se*, then what kind of integration are we talking about?[1] We and others (Melloni & Singer 2010; Thompson & Varela 2001;

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1 Giulio Tononi (2004; Tononi & Koch 2008) argues that not only integration but also differentiation/segregation (e.g., distinguishing a particular state from all possible other states) is characteristic of conscious states. However, even when both conditions are met, say integration through convergence is observed in FFA and differentiated from other states, e.g., there is no activation in PPA, an area selective to processing places, and thus there is no guarantee that this would constitute a conscious state. In fact, experimental evidence suggests that such feature-selective processing can indeed proceed unconsciously, for example in the case of face processing under conditions of masking (de Gardelle et al. 2011), continuous flash suppression (Almeida et al. 2013), and in blindsight patients (Del Zotto et al. 2013).

Varela et al. 2001) have previously argued for a distinction between *local* and *global* integration, and proposed that the spatial scale of integration differentiates between unconscious and conscious states: unconscious processing is observed when local integration occurs within the divergent-convergent feedforward architecture; conscious processing however requires long-range integration through neural synchronization, which integrates information across the various levels of the cortical processing hierarchy.

Indeed, in recent years, a wealth of experimental studies (Aru et al. 2012; Gaillard et al. 2009; Hipp et al. 2011; Melloni et al. 2007; Melloni & Rodriguez 2007) have provided support to the idea that long-range integration through synchronous coupling is a mechanism for conscious perception, and that the spatial scale of synchronisation strongly correlates with the perceptual outcome. For example, we have shown that masked words are only consciously perceived when accompanied by a burst of long-distance synchronization in the gamma band, while unconscious processing, even up to a semantic level, elicits only local gamma oscillations (Melloni et al. 2007; Melloni & Rodriguez 2007). Although controversy still persists as to whether long-range integration necessitates the involvement of particular brain areas (Dehaene 2014; Edelman & Tononi 2000) or not (Lamme this collection; Melloni & Singer 2010), it is reassuring to witness some convergence on the results that have even led to clinical applications (e.g., coma classification, King et al. 2013). In his most recent work, Victor Lamme now also assigns a central role to the spatial scale of the integration for consciousness, joining an ever-increasing number of researchers proposing long-range integration as key to consciousness (Dehaene & Changeux 2011; Edelman & Tononi 2000; Melloni & Singer 2010; Thompson & Varela 2001). An interesting point of divergence from other theories is that while Lamme assigns a particular role to feedback and horizontal connections in the integration of information for consciousness, other theories, including our own, hypothesise that it is the synchronisation of neural populations that glues all experiences into one, thereby instantiating con-

sciousness. As empirical data and theoretical considerations continue to accumulate, we expect that this and other pressing challenges such as identifying how far is "long" in the brain, or whether "long" involves the activation of specific neural cell populations, specific areas, and/or a specified number of nodes will become addressable.

However, imagine those questions have been addressed and we know that integration on a particular spatial scale is key to consciousness; would we have understood what consciousness is or how it comes about? Here I propose that we would not, as any theory that does not account for two fundamental, hitherto neglected aspects of conscious experience will fall short of explaining consciousness. In particular, our experience is never an island in isolation, but instead is shaped by previous knowledge, by priors that stem from the preceding context or from our history of learning. These priors determine our perception; and thus understanding how they become integrated is paramount to explaining consciousness. However, an even more pressing problem is that conscious experience unfolds over time, whereby the recent past moulds the current moment, which in turn creates predictions for moments to come, i.e., the future. How all those temporal processes intertwine and define our experience (the flow of consciousness) is something that most research has neglected. In the following sections I will review current research that we and others have undertaken with the purpose of raising awareness of these overlooked integrative properties of conscious experience and the challenges that they entail for the study of consciousness.

2 Consciousness as an inferential process and the consequences for the neural mechanism of conscious perception

One central and characteristic feature of conscious perception is its constructive nature. In contrast to unconscious cognition, which is directly driven by sensory stimulation, the images that reach consciousness often bear little resemblance to reality. Indeed, percepts in our

mind can be understood as useful distortions of reality in which only specific parts of the physical input are represented while being enriched with a model of the world that has been learned and that provides context to the current moment. In the words of Heinz von Foerster (1984), "the world, as we perceive it, is our own invention". To provide a striking example of this, consider the image on the right (Figure 1) and try to figure out what it shows. Most people at first see a collection of black and white blobs, much like the input that strikes our retina—a raw, uninterpreted signal. Now, rotate the page upside down. Voila! You will clearly see a face (do you recognize whose face it is?). Remarkably, you can turn the page back and you will continue seeing the face. Once you have recognized the image, the visual system has created a *prior*, an expectation that enriches perception. This example is not mere curiosity. Most of our behaviour and perceptions are based on predictions: we do not wait for visual input to impinge our eyes, we *actively* look for it. We cannot, however, initiate a rational search for an object without making *predictions* about "what" it is, "where" it is likely to be, and even "when" it is likely to be there. The brain's ability to make predictions and to mould its data gathering accordingly is thus essential for its ability to evaluate options, make life-critical decisions, and generate adaptive behaviour.

While the constructive nature of perception is undeniable and may even appear as one of its defining features, surprisingly little research has been carried out to understand how previous experience interacts with consciousness. Most importantly, the scientific community has not embraced an understanding of consciousness in the context of a flow of experience in which every moment is integrated with past moments and interfaced with expectations about what will happen in the future (but see Varela 1999). A possible reason for neglecting the contribution of previous experience is that this integration of past with present moments has been understood as a process of "unconscious inference" (following von Helmholtz 1866/1962), or, in Victor Lamme's words, in the context of the "automaticity of the many ex-

pectation effects." However, this inferential process is carried out in the backstage of consciousness, and it is only the result that we consciously experience. This bears resemblance to syntactic analysis, which is also carried out automatically and unconsciously, but is paramount to conscious access to meaning. Without unconscious syntactic analysis we would not be able to "consciously" understand text; nor is its automatic activation under our control. In the same vein, our conscious perception would be totally different if prior knowledge did not help us enrich or even construct our experience, endowing it with meaning. In fact, it has been proposed that alterations in perception, i.e., the defragmented sensory experience observed in schizophrenics and autistic people can be the result of a deficit in this inferential process (Jardri & Deneve 2013; Pellicano & Burr 2012), underscoring the fundamental role that perceptual inference plays in conscious perception.

One promising framework within which the influence of previous experience through unconscious inference can be understood is the Bayesian framework. When applied to perception, each mathematically-formulated ingredient of this framework can be assigned a perceptual counterpart, with previous experience referring to the prior, the current moment referring to the likelihood, unconscious inference referring to Bayes rule (which combines the prior with the likelihood in an optimal way), and the result—our perception—referring to (the peak of) the posterior distribution. This idea has recently proven to be a powerful tool for understanding perception not only in terms of modelling behaviour, but also as a theoretical framework for understanding how perception arises in the brain. A prominent implementation of the latter is Predictive Coding (Friston 2010). This theory postulates that the brain builds models (priors) of the world based on previous experience, which are used to explain the current inputs. This occurs iteratively *across all levels in the cortical hierarchy* with the goal of minimising predictions errors, i.e., the difference between what is expected and the incoming sensory input, which are energetically costly. This minimization process can either be achieved by chan-

ging the way the system samples its environment, or by changing its models. Relevant for this discussion is the idea that perceptual inference, in the Predictive Coding framework, implies that all levels in the hierarchy reach an agreement, i.e., minimise all prediction errors, much like the idea of a unified/integrative moment as proposed by Victor Lamme and others (Dehaene 2014; Edelman & Tononi 2000; Melloni & Singer 2010). While Predictive Coding by itself is currently agnostic as to whether such unified agreement represents a conscious state, the central tenet that integration across all levels is what the system strives for still holds. This allows for the formulation of interesting, testable predictions about the Neural Correlates of Consciousness (NCC).

In recent years research in my lab has focused on understanding how previous experience enriches perception, how expectations alter the NCC, and how this can be understood within the Predictive Coding framework. The central idea that motivated these studies was to test whether or not the NCC are context independent, i.e., impervious to the influence of expectations, as many theories implicitly postulate. To test this hypothesis we presented subjects with illusory letters, that is letters whose borders where not explicitly defined but instead required the activation of figure–ground segregation cues. We reasoned that providing subjects with a prior, i.e., knowing which letter would be presented next, would facilitate the figure–ground segregation process, making an initially invisible letter clearly visible. In line with our expectations, we observed that the threshold of conscious perception is not fixed but instead changes depending on the availability of previous knowledge: subjects are able to perceive a stimulus on the basis of minimal sensory information when they have a clear expectation. We were able to confirm this result in a series of different paradigms in which expectations could be generated online from recent experience as in the example of the letter given above (Melloni et al. 2011; Schwiedrzik et al. 2014), drawn from memory based on prior exposure to clearly visible natural images (Aru et al. 2012), stem from a life-long history of association between letters

and colour as in grapheme-colour synaesthesia (van Leeuwen et al. 2013), or result from systematic training as in perceptual learning (Schwiedrzik et al. 2009, 2011). These studies allowed us to test not only whether the behavioural threshold of conscious perception is fixed, but also how previous knowledge would affect the neural "construction" of conscious percepts.

Figure 1: Can you recognize what this is? If not, rotate the image. Note that once you turn it back around the object is now clear.

A first hypothesis we derived from the Predictive Coding framework was that the presence of strong priors should have an effect of how quickly content reaches awareness. If conscious perception is the result of a process that iterates until information is consistent between the different levels of the hierarchy (Di Lollo et al. 2000), i.e., until all prediction errors are minimised, then having a better model of the input based on prior knowledge may speed up this process. Indeed and contrary to the com-
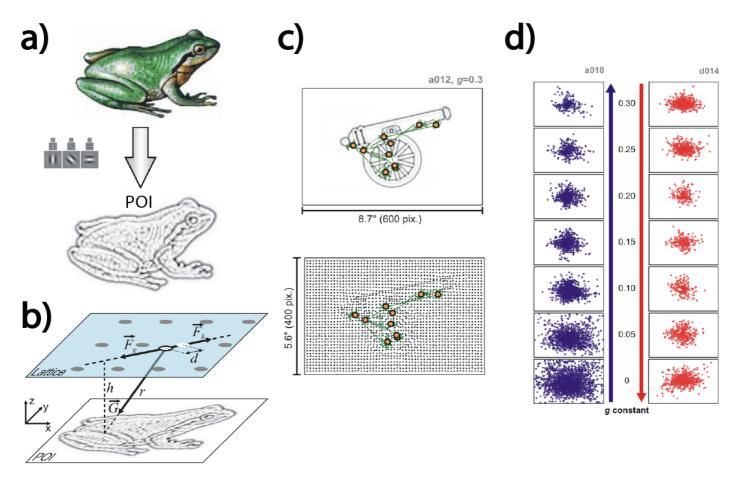
Figure 2: (a) Original images are filtered through a series of gabor wavelets, which allows the estimation of the points of maximal local information (Points of Maximal Information, POI) in the source image. (b) Dots of an elastic lattice are created by mapping the POI in the projection plane, and attracting them by the projection F0 of a gravitational force G. (c) Pattern of saccades/fixations when subjects recognise a stimulus and its underlying POI map. (d) Pattern of fixations for stimuli of different degradation levels from high degradation (0) to low degradation (0.30). Dots in blue correspond to fixations when subjects do not have an expectation of the stimuli, dots in red correspond to patterns of fixation observed in the presence of expectations. Note that in the presence of expectations, the distribution of fixations are much less scattered. From Moca et al. (2011).

mon belief that information processing in the brain has a fixed latency, we observed that the NCC shifts in time when a prior is available. While the electrophysiological difference between seen and unseen letters occurred around 300ms when it exclusively depended on sensory evidence, it occurred as early as 200ms when priors were available (Melloni et al. 2011). Thus, priors sped up information processing by 100ms. These results have important implications for the search for the NCC as they show that conscious processing is not bound to a particular time, but can flexibly adjust its timing depending on the task at hand, the readiness of the system, or the presence of expectations.

They also pose a challenge to theories that postulate that the NCC always occur late, as proposed by Victor Lamme (this collection) or Stanislas Dehaene (2014).

A second prediction that follows from the principle of minimising prediction errors is that in the presence of priors, activity in lower areas can be "explained away" by priors in higher brain areas (Murray et al. 2004); this entails that when inputs can be fully predicted based on previous experience, they do not elicit prediction errors. To test this hypothesis, we took the same study to the MEG and performed source localisation. Here, we found that priors sparsify the networks involved in processing the

stimulus, such that when a prior is present only the brain areas that are most diagnostic to the stimulus features are activated (Mayer et al. in preparation). All alternative interpretations of the stimulus are thus "explained away". Thus, consciousness and its neural correlates appear as mobile targets, which adjust their locus in the presence of expectations. This poses a further challenge to the search for the NCC, as not only the timing, but also the location of neural activation does not appear as a diagnostic feature for the NCC.

Finally, Predictive Coding also suggests that priors may be used to change the way information is sampled, as the models derived from previous experience can be used to optimise the search for the most relevant information (Friston et al. 2012). Only rarely do we keep our gaze still and wait for the world to bring novel information; instead, we scan images through rhythmic patterns of eye movements accompanied by fixations. This active sensing view implies that perception is not a passive phenomenon in which the system waits for information to hit the sensory transducers, but instead an active process that seeks information through exploratory routines (Melloni et al. 2009; Schroeder et al. 2010). To test whether and how priors affect the sampling of information we developed stimuli for which we could quantify the local information content at each point (Figure 2) and determined the efficiency of information extraction based on eye movements in the presence or absence of expectations. Figure 2 shows that when subjects have prior knowledge of the object they are trying to perceive, they can immediately orient their eyes to areas of most diagnostic information for the perception of an object. At the same time, the sampling of information becomes sparser, concentrating eye movements to maximally informative areas (Moca et al. 2011). This implies that priors direct our exploratory motor routines, thus optimising perception.

Overall, these studies show that previous experience enriches the contents of consciousness and fundamentally changes the way information is processed in our brain, enhancing speed and efficiency. This raises questions for

theories that propose a fixed latency or neural locus for conscious access, but also complicates the quest for the NCC, as they turn out to differ in time and location depending on the precision and accuracy of expectations. Although current formulations of Predictive Coding do not make specific predictions about consciousness, this framework may nevertheless prove to be an important starting point in trying to understand these effects. In fact, more explicit theoretical links between Predictive Coding and consciousness are now being worked out (e.g., Clark 2013; Hohwy 2013; Seth et al. 2011)— after all, Predictive Coding has been framed as a unifying theory of the brain (Friston 2010), which would fall short if consciousness was left unexplained.

3 The neglected dimension of consciousness: Time and the flow of consciousness

But is that all? One dimension of our experience that is often neglected is time. Of course, time is an implicit component of previous experience, however, it may also be revealing to consider time by itself. In fact, living organisms seldom encounter a static image in isolation, but are instead confronted with a flow of temporally-correlated sensory inputs (Schwartz et al. 2007). Imagine for instance a tennis match, and picture the tennis ball flying over the field. If queried, you could easily estimate where the ball is, but also where it was a second ago and where it will be in a few milliseconds. Event-objects of the conscious mind[2] thus per definition unfold in time and we also act in time: we make use of current and previous input to figure out the most appropriate response predicting their consequences. There is thus a continuum of interdependencies along the time dimension whereby every past moment is *integrated* with the present and projected into the future, giving rise to the flow of consciousness. The same way

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2 We are usually conscious of objects, and become so by virtue of their being differentiated from the background, but also because their internal features are linked or bound in some way. Objects and their internal features do not need to be static entities but can have temporal dynamics, i.e., they develop or change in time. In this case, they become events (and thus event-objects of the conscious mind).

we have been thinking about the integration of multiple source of information *within* a given moment of time, such as multiple features of a single object, there is thus integration *across* time. A case in point is strikingly vivid perceptual aftereffects, such as the waterfall illusion, where viewing motion in one direction for several seconds causes a subsequently presented static image to move in the opposite direction (Purkinje 1820). Such effects are not limited to basic perceptual features such as motion direction, colour, or orientation, but also affect high-level percepts such as the perceived gender of faces (Webster et al. 2004), numerosity (Burr & Ross 2008), or gaze direction (Jenkins et al. 2006); and they are not limited to fleeting illusions that vanish almost instantaneously, but may persist for days or even weeks (Jones & Holding 1975). This indicates that our current experience is embedded into a continuous flow of previous experience at multiple time scales, ranging from lifelong experience with our environment to short-term, moment-by-moment effects that arise from our most recent encounters, even if just milliseconds ago.

The past thus leaves traces (predictions) that determine the current contents of consciousness. This has the consequence that the contents of consciousness represent an aggregate of imprints from the past and the present moment that jointly promote a sense of *stability over time*. However, through which mechanism these interdependencies affect our perception is currently unclear. Experimentally, the multiple time-scales of previous experience are particularly evident when subjects are confronted with sequences of multistable stimuli such as the Necker cube.[3] Because the sensory information these stimuli provide by themselves is insufficient to determine perception, they are particularly susceptible to the effects of previous experience. Under these conditions, one can observe two different effects that temporal dependencies entail: on the one hand, an *attractive* effect, which increases the likelihood of continuing to perceive the same stimulus, and on the other hand a *repulsive* effect, which increases the like-

lihood of perceiving something different. The former is often referred to as hysteresis, priming, stabilisation, or perceptual memory, while the latter is commonly known as perceptual adaptation.

Recently, Chopin & Mamassian (2012) studied the temporal dynamics of these serial dependencies, addressing the question of which part of the perceptual history the system retains and how remote and recent experiences differentially determine perception. They observed a remarkable dissociation between long stretches of time that occurred in the remote past (in their case several minutes) and short stretches of time that had just recently occurred (a few seconds ago): while the former had a positive correlation with perception, and thus ensured stability over time (hysteresis), the latter had a negative correlation to perception, that is, it promoted alternative interpretations (adaptation). These two timescales indicate that previous experience can act along at least two separate timescales and hence, that there may be several mechanisms at work. Using functional magnetic resonance imaging, we set out to further elucidate how these effects are implemented in the brain, how the brain entertains these two opposing processes without mutual interference, and what determines their direction (Schwiedrzik et al. 2014). Presenting multistable visual stimuli sequentially, we found that although affecting our perception concurrently, hysteresis and adaptation map into distinct cortical networks: a widespread network of higher-order visual and fronto-parietal areas was involved in hysteresis, while adaptation was confined to early visual areas (areas V2/V3). Importantly, hysteresis and adaptation bear a differential relation with whether or not the stimuli were consciously perceived: while adaptation was present even if the adapting interpretation was not consciously perceived (in agreement with previous reports, e.g., Hock et al. 1996), hysteresis depended on what was previously consciously perceived. Hence, conscious experiences in the past affected the present experience, preserving continuity in time, while unconscious processing had the opposite effect, bringing change and novelty to perception.

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3 But they are by no means limited to ambiguous stimuli (Fischer & Whitney 2014; Treisman 1984).

This brings us back to the question of neural integration, indicating that even in the case of *integration over time,* the spatial scale at which neuronal processing occurs determines whether content enters awareness or not: in the case of hysteresis, a conscious moment is integrated in time with another conscious moment, which involves a widespread cortical network, while in the case of adaptation, prior information is only integrated within a local module, which happens irrespective of whether this prior information is consciously experienced or not, similar to Lamme's "base grouping". This interpretation fits with results that have been obtained in the auditory domain in which short temporal regularities can be detected unconsciously eliciting a locally generated event-related potential (ERP), termed mismatch negativity (MMN), while detection of long-term regularities depends on conscious perception, which elicits an electrophysiological response known as P300 from a widespread network of brain areas (Bekinschtein et al. 2009; Faugeras et al. 2011).

Together, I propose that these results mesh well with the idea that one of the functions of consciousness is to interpret the world in *long timescales*, bringing together the *now* with the past beyond the simple and automatic input-output relations rooted in unconscious processors, thus allowing for the extraction of more complex and abstract regularities. Brain areas with longer time constants such as the prefrontal cortex (Fuster 1973) would extract the world's statistics from the remote past, creating a model of the world that keeps a stable picture. In contrast, early sensory areas with short time constants act on shorter timescales, sampling the world for alternative interpretations, thus allowing the system to stay tuned to deviations from the long-term statistics (Clifford 2012; Snyder et al. under review).[4]

While previous studies and established experimental paradigms have mostly focused on the "nowness" of conscious perception, it ap-

pears that much remains to be learned about consciousness and its fundamental phenomenological characteristics such as its flow and our sense of stability over time. In fact, considering that much of what we currently know about the NCC stems from "static" paradigms, and by those I mean paradigms that do not take the temporal context in which the stimuli unravel into account and thus only inform us about what has "changed" in consciousness, we in fact only have access to the neural processes related to the *update* of contents in consciousness, while the mechanisms at play in the *maintenance* or continuity of our experience remain obscure (but see Kleinschmidt et al. 2002). The *present* might be known, but the *flow* is still a mystery!

Thus I propose that a full account of consciousness requires a reappraisal of our object of study in which we incorporate the temporal flow of consciousness as another fundamental property that needs to be explained. This calls for a dynamic view in which a train of conscious states (the flow) would be captured as successions of neuronal meta-assemblies, each with a particular relaxation time, followed by phase transitions, which determine the time of emergence, dominance, and dissolution of a state that leads to another perceptual cycle (Melloni & Singer 2010; Varela 1999). In this framework, the rate-limiting factor for the formation of a new meta-assembly would correspond to the time needed to establish stable phase relations; while the different time constants promoting stability vs. change may be implemented by different oscillatory frequency bands, in addition to the intrinsic time window of integration of a given area (Chaudhuri et al. 2014).

In summary, much remains to be discovered about consciousness and its neural correlates, but significant progress has already been made since the seminal paper by Crick & Koch (1990) that got the field going about twenty-five years ago. Victor Lamme's experimental work and theoretical proposals on the role of feedback connections and reentrant activity in conscious perception have been central to bringing us closer to an understanding of the neural processes that allow us to "see". His paper in this volume contains an erudite review

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4 Similarly, higher areas have larger receptive fields than lower areas, allowing integration over larger regions of space, and are often more broadly tuned (i.e., allow for more variability in the stimulus, e.g., different views of the same object). This resonates well with psychophysical evidence that hysteresis is spatially less specific and more broadly tuned than adaptation (Gepshtein & Kubovy 2005; Knapen et al. 2009).

of the present knowledge against a background of thought provoking hypotheses, e.g., that the function of consciousness is to solve difficult perceptual problems. In Lamme's view, consciousness is there to create, while unconscious processes are there to utilise. In close analogy to any creative process, consciousness in Lamme's framework is slow and takes time and resources to develop. In a way, his proposal is that it is all about distance, or time. This is a powerful intuition, and an idea worth exploring, yet its contribution does not end there—more than that, it serves as a reminder of a central characteristic of consciousness that is not yet fully explored, namely that conscious experience unfolds at a characteristic spatio-temporal scale, and that it is this flow in space/time that brings the strong sense of experiential stability and continuity. The interwoven temporal scales of the flow of consciousness that bring about the "unity of experience" remain the next challenge, and maybe the one that will finally unlock the mystery of consciousness.

3.1 Acknowledgements

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