Perceptual awareness and its neural basis: bridging experimental and theoretical paradigms

Antonino Raffone1, Narayanan Srinivasan2 and Cees van Leeuwen3

1Department of Psychology, ‘Sapienza’ University of Rome, Rome, Italy
2Centre of Behavioural and Cognitive Sciences, University of Allahabad, Allahabad, India
3Laboratory for Perceptual Dynamics, KU Leuven, Leuven, Belgium

Understanding consciousness is a major scientific challenge of our times, and perceptual awareness is an integral part of that challenge. This Theme Issue aims to provide a timely focus on crucial insights from leading scientists on perceptual awareness and its neural basis. The issue refers to key research questions and findings in perceptual awareness research and aims to be a catalyst for further research, by bringing together the state-of-the-art. It shows how bridges are being built between empirical and theoretical research and proposes new directions for the study of multisensory awareness and the role of the states of the body therein. In this introduction, we highlight crucial problems that have characterized the development of the study of perceptual awareness. We then provide an overview of major experimental and theoretical paradigms related to perceptual awareness and its neural basis. Finally, we present an overview of the Theme Issue, with reference to the contributed articles and their relationships.

1. Study of perceptual awareness and related functions in cognitive psychology

Researchers in cognitive psychology in the 1970s mostly addressed consciousness in terms of attentional, as opposed to automatic, processing [1–5]. The former, sometimes called ‘conscious attention’ [2], could be characterized as a slow, serial process, with a limited capacity but flexible, as opposed to fast, parallel and high-capacity but rigid automatic processes. Such dichotomies have shaped but also limited our thinking of consciousness as a legitimate subject of study in its own right. It thus seems that, despite the persistent interest in conscious processing, a major change in scientific perspective was needed to enable the established experimental methods and constructs to be assimilated within the developing field of scientific investigation of consciousness and its neural correlates, and perceptual awareness in particular. This change in perspective has only happened in the past few decades.

Whilst cognitive psychology framed consciousness in relation to attention and in opposition to automaticity, perceptual awareness studies were similarly focused on a dichotomy: that of detectable versus subliminal stimuli. A frequently used technique was visual masking, the reduction (or elimination) of visibility of a briefly presented (50 ms or less) stimulus (‘target’) by the presentation of a second brief stimulus (‘mask’). Masking was introduced near the end of the nineteenth and beginning of the twentieth century [6,7], and has been extensively studied since then [8]. The method has contributed to understanding the time course of processing visual stimuli and attributes, especially in relation to iconic memory [9]. The notion of iconic memory was soon assimilated in influential cognitive models [10]. In the 1980s, Anthony Marcel [11,12] used masking in his systematic investigations on subliminal perception. However, Holender [13] argued that the notion of subliminal processing is misleading; in his view, identification in masking conditions should, one way or another, involve consciousness.
Over the past few decades, the results of masking studies have evolved to study visual awareness and its neural basis in their own right (e.g. [11,14–16]; see also [17]). Iconic memory has explicitly been associated with (phenomenal) consciousness in relatively recent theoretical developments [18–21]. Finally, masking has recently been used to gain insights into the speed of consolidation in visual working memory [22,23], a phenomenon related to both attentional and conscious processing [24,25].

Another phenomenon of particular relevance for understanding visual awareness is perceptual switching [26]. Perceptual switching has been studied using multistable stimuli, and in particular bistable figures and binocular rivalry. In binocular rivalry [27], dissimilar monocular stimuli presented to corresponding locations of the two retinas result in competition for perceptual dominance and alternations in perceptual awareness of the competing stimuli over time. Although binocular rivalry has systematically been studied from the nineteenth century and investigated extensively through the twentieth century [28], only in the past few decades has the phenomenon been investigated systematically in relation to theories of perceptual awareness and its neural correlates [28]; see also [29–32].

Another important paradigm that has impacted on the study of perceptual awareness and related attentional functions is the attentional blink phenomenon [33]. The attentional blink occurs when two targets have to be detected with rapid serial visual presentation (see also [25]). The second target is often not detected when presented within a few hundred milliseconds after the first one. Whereas this phenomenon has initially been treated in terms of attentional limitations, later studies have emphasized the role of control operations distinct from attention [34–36]. Another example is inattentional blindness. This phenomenon occurs when an unattended but salient stimulus is not detected owing to the engagement in processing another stimulus [37]. Initially, also this topic was exclusively studied under the veil of attention. However, the inattentional blindness paradigm in particular is suitable for differentiating between attention and certain aspects of consciousness addressed in this Theme Issue [25,38]. Finally, the third phenomenon casting new light on the relation of attentional and conscious processes is repetition blindness, i.e. the failure to recognize the second happening of a visual display observed in rapid serial visual presentation [39].

In addition to focusing on accurate conscious perception, efforts have been made to investigate whether attention alters perceptual appearance [38,40]. Cued stimuli are perceived to be of higher contrast than uncued stimuli [40]. Appearance based on higher order perceptual features also has been shown to be influenced by attention [41]. Differences in attentional scope [42] and attentional load [38] also influence perceptual awareness. While attention does seem to influence awareness, recent debates have also focused on whether attention is necessary or sufficient for perceptual awareness [43].

Besides attention, a range of cognitive functions and processes are linked to perceptual awareness and conscious access to selected perceptual contents. It is generally acknowledged that when a stimulus is consciously accessible, it is possible to readily perform a variety of higher level cognitive operations related to it, including explicit memorization, reasoning, planning, evaluation of alternatives, decision-making, voluntary control of attention and verbal report [18,44,45]. Perceptual awareness has also been related to working memory [20], the cognitive system for short-term maintenance and manipulation of task-relevant information [46]. Finally, perceptual awareness has been modelled based on decision theoretic assumptions [47] and evidence accumulation processes [48].

2. Understanding the neural basis of perceptual awareness

The call to understand the neural mechanisms of conscious experience is old [49] but it has gained momentum in the past three decades. Bernard Baars’ influential global workspace theory (GWT; [44,50,51]) has played a pivotal role in the development of the neuroscientific study of consciousness. GWT is a functional theory (see also [25]). In particular, it has proposed a compelling characterization of conscious processes as related to crucial cognitive functions, such as attention and working memory, and their neural correlates. An important aspect of GWT is the notion of conscious access, related to global workspace (GW) representation and processing, to contents represented at an unconscious level in widespread modules in the brain. Complementarily, the GW broadcasts accessed information globally across the brain regions and is instrumental in establishing cognitive control, for example the focus of attention.

The notion of conscious access and related GW processing was endorsed by the philosopher Ned Block [18,19], who proposed the influential distinction between phenomenal consciousness and access consciousness. According to Block, phenomenally conscious content is what differs between experiences such as of red and green, whereas access conscious content is content information that is broadcast in the GW (see, however, [52] for a different view). This proposal has had impact on debates about perceptual awareness and its neural basis [15,20,21].

Toward the end of the 1990s, Stanislas Dehaene et al. [45] proposed the global neuronal workspace (GNW) model, which characterized the GW in terms of plausible brain systems and processes, in the light of joint psychophysical, neuroimaging and computational modelling investigations (see [53] for a review; see also [17,25,47]). The GNW model has also led to the proposal of a taxonomy with unconscious, preconscious and conscious levels of representation [15] in which the preconscious level provides an alternative to the notion of phenomenal consciousness proposed by Block. In the past few years, the GNW model has inspired a new trend of theoretical developments in which series of discrete conscious processes, involving GW transitions, are considered as related to mental programmes controlling multiple steps or routines in cognitive tasks ([48,54–56], about the role of discreteness in perceptual processing). The GNW [34,47,57] model has led to the emphasis on the ‘all-or-none’ character of conscious representations, whereas other approaches ([58]; see also [52]) suggest a graded account. Such positions might, however, be reconciled [25,59].

The GW notion advanced in GWT, GNW, involves the notion of a global-scale neural assembly (neuronal coalition). In particular, according to the GNW model, massive recurrent interactions in the brain, involving prefronto-parietal areas, are needed to enable conscious representations in the GW, in terms of a winner-take-all dynamics between assemblies representing different mental contents. Related to the GNW approach, Maia & Cleeremans [60] argued that a strong and sustained neuronal firing at the global assembly level makes it more
likely that the representation encoded by a given assembly will reach the conscious level of representation.

As an important milestone, Crick & Koch [61] oriented research towards the neural correlates of consciousness (NCC), meant as the minimal set of neuronal events and mechanisms sufficient for a specific conscious percept (see also [29]). Several methodologies have been used to identify the NCC [62]. An example of an attempt to identify NCC comes from the study by Steinberg & Logothetis [63] who used the phenomenon of binocular rivalry and significant correlation between neuronal activity and the conscious percept in infero-temporal cortex but not V1. Conscious perception also has been investigated in the context of different sub-systems in vision ([64]; see also [14]). In terms of visual pathways, Milner & Goodale [64] have argued that the ventral stream is for conscious perception and dorsal stream is for actions (see, however, [14]).

Lesion studies in patients have also led to important insights about the neural basis of perceptual awareness, in particular, the studies on neglect and extinction, characterized by deficits in perceiving contralesional stimuli, conducted by Driver & Vuilleumier [65]. Studies on blindsight [66], the clinical condition in which a patient responds to visual stimuli without consciously perceiving them, have led to important insights on perceptual awareness (see also [52]).

The time course of conscious perception has been studied using event-related potential (ERP) components associated with awareness. For example, Railo et al. [67] argue that the visual awareness negativity component that occurs around 200 ms after stimulus presentation might be associated with conscious perception, and late positivity that occurs around 300–400 ms after stimulus presentation might be associated with conscious access (see also [25]). Another compelling example of study on ERP components related to both unconscious and conscious language-related visual processing is provided by the work of van Gaal et al. [17]. Also, functional magnetic resonance imaging studies have contributed to shed light on the neural basis of perceptual awareness, such as those concerning visual masking (see [15] for a review), perceptual rivalry [68] and attentional blink [69].

In the past three decades, temporal correlations, spike synchronization and neural oscillations have been proposed to play a critical role in binding [70–73] and have inspired several models of perceptual processes, such as those about perceptual grouping [74] and feature binding [75], which involved dynamic neural assemblies within and between areas of the visual system. Their relevance for perceptual awareness, in terms of synchronous cortical assemblies, was emphasized in the following years [76]. Spike synchronization in visual cortex was also proposed to account for binocular rivalry [77]. More recently, oscillatory spike synchronization has been studied for its roles in visual attention [78] and in communication between brain areas [79], thus with relevance for conscious access processes. Nikolaev et al. [80] showed that the amount of information to be communicated between brain areas is directly proportional to the duration of an interval of synchronized activity, the coherence interval [81]. Other approaches emphasize slower oscillations in the brain [56]. Recent studies [82] also highlight the importance of travelling waves of synchronous activity for communication between brain areas, and thus appear to support the view that the GW is a functional rather than an anatomical concept.

Synchronization-based processes are also crucial, for example, in Francisco Varela’s approach [83,84] to the emergence of consciousness in brain dynamics, with a special emphasis on (global) resonant assemblies and transient brain patterns of oscillatory synchronization and desynchronization. The approach of Varela and collaborators has stressed coherent oscillatory patterns in the thalamo-cortical system in the gamma range (see also [32,55,85]). This view has been supported by the compelling findings of electroencephalographic patterns related to subjective awareness of visual stimuli [84]. Varela [86] (see also [87]) has also introduced the neuro-phenomenological approach, in which quantitative measures of neural activity are combined on a momentary basis with first-person data about the subject’s experience. Participants’ reports can thus be useful in identifying variability in brain activity from moment to moment, which might guide the detection and interpretation of neural processes correlated to different aspects of conscious experience.

Another influential theoretical approach to the neural processes underlying consciousness has been proposed by Tononi & Edelman [88], in terms of the dynamic core model of consciousness. This model is based on re-entrant signalling in the brain and neural complexity, as related to the interplay of integration and differentiation of coherent as well as constantly changing large-scale neural activity patterns. The role of recurrent cortical processing for the emergence of conscious percepts has also been stressed by Lamme & Roelfsema [89], in contrast to feel-forward processing (‘sweep’) related to unconscious vision (see also [14]). In contrast to the GW model, these authors suggested that virtually any recurrent loop, even locally within visual cortex, might suffice to cause conscious-level processing. Related to this view, Lamme [20,21] proposed that recurrent processing can be related to both phenomenal and access consciousness [18,19], which would be, however, characterized by a differential involvement of selective attention and response selection mechanisms.

Finally, the study of the cortical basis of perceptual awareness appears to be characterized by the contrast between hierarchical models proposing that only higher level extrastriate areas are directly involved in visual awareness [90], and interaction models [91] proposing that V1 participates directly in visual awareness by recurrent interactions with extrastriate areas. However, these apparently contrasting views might be reconciled in frameworks emphasizing different levels of representation and multiple stages of processing [25].

3. This Theme Issue at a glance

This Theme Issue considers in depth several facets of cognition linked to perceptual awareness. Two crucial and complementary aspects of awareness research are given by the understanding of the constraints leading to conscious contents, and the understanding of the different properties and mechanisms of conscious and unconscious processing (for this aspect, see in particular [14,17]). Both these aspects are considered in depth, together with relevant foundational (see in particular [52]) and methodological (see in particular [92]) problems. Insights with patient studies are also considered and bridged with evidence from psychophysical experiments [32]. Other contributions integrate psychophysical, neurophysiological and neuroanatomical evidence with views stemming from computational models [14,25], and also with relevant philosophical implications [14].
In addition to a number of articles on visual awareness, articles in this Theme Issue cover auditory perception [56], multisensory perception [92] and the role of bodily signals for perceptual awareness [93].

Several contributions in the Theme Issue emphasize multiple levels of representation [25,52,59] and attempt to reconcile apparently contradictory findings about key aspects of the addressed problem. The Theme Issue includes efforts beyond apparently conflicting theoretical positions, with special reference to dichotomous versus graded accounts of conscious representation [59] and about different theories of attention [25,38]. Moreover, it integrates empirical findings and theoretical perspectives about several aspects of perceptual awareness.

Several of the contributed articles report new experimental findings supporting theoretical claims, hypotheses and predictions [17,38,47,56,59]. Others emphasize review and theoretical aspects; however, they are systematically and critically related to relevant empirical findings with different experimental paradigms. One of the contributions, by King & Dehaene [47], presents a compelling computational model of subjective report and objective discrimination based on decision theoretic assumptions and provides a successful experimental test of one of its main predictions.

Overall, the Theme Issue highlights the importance of an interdisciplinary and methodologically integrated approach to the study of consciousness and perceptual awareness in particular, with the balanced integration of psychological experiments and theories/models, neuropsychological, clinical studies and philosophical analysis. It comprises contributions focused on advances about more ‘classical’ aspects of perceptual awareness, such as visual masking [14], binocular rivalry [29,32], the roles of attention [25,38] and conscious access, such as inattentional blindness and attentional blink [25], and others stressing new interesting directions to explore, such as the cyclic (discrete) nature of perception in vision versus audition [56], multisensory awareness [92] and the role of internal body representations for enabling subjectivity in perceptual experiences [93]. Visual search findings and theories are also considered [29].

Fast and slow brain oscillations and processing steps as related to perceptual awareness, attentional and conscious processes are considered across several articles in the Theme Issue [25,32,56]. Some of the contributed articles with a neuroscience focus emphasize (visual) cortical systems (pathways), with a revised functional perspective [14], whereas others, with a neurodynamic emphasis [25,32], also refer to interactions between visual cortex and the thalamus, with special reference to the pulvinar, a collection of higher order associative thalamic nuclei, of which the functional importance for perceptual awareness and attention is increasingly recognized.

Articles in the Theme Issue also present pronounced critical stances, for example in Blake et al. [29] about the implications of binocular rivalry research for understanding the NCC. Critical stances, with special reference to methodological issues and their limitations in addressing multisensory constraints of awareness, are also emphasized in the article of Deroy et al. [92].

Understanding perceptual awareness and its neural basis is a major challenge for current research in psychology, cognitive science and neuroscience; meeting the challenge will have crucial philosophical implications and impact research on perception, attention, working memory and decision, among others. Each of these is a major area of cross-disciplinary research. Given all this, the present Theme Issue is expected to be of interest to a broad audience of scientists and philosophers. While providing timely and original insights to key problems on the addressed theme, it suggests further avenues into this fascinating field of research.

Acknowledgements. We thank Helen Eaton, Commissioning Editor of the journal, for her crucial support and advice in our guest editor work for this Theme Issue. We also thank the authors who have contributed to this Theme Issue and all the referees for their important remarks, comments and suggestions.

Funding statement. C.v.L. is aided by an Odysseus grant from the Flemish Organization for Science (FWO).

References

7. Sherrington CS. 1897 On the reciprocal action in the retina as studied by means of some rotating discs. J. Physiol. 21, 33–54.
14. Breitmeyer BG. 2014 Contributions of magnocellular and parvocellular channels to conscious and non-conscious vision. Phil. Trans. R.


63. Steinberg DL, Logothetis NK. 1997 The role of
     temporal cortical areas in perceptual organization.
     1073/pnas.94.7.3408)
64. Milner AD, Goodale MA. 1995 The visual brain in
65. Driver J, Vuilleumier PO. 2001 Perceptual awareness
     The visual brain in

66. Weiskrantz L. 1986 Blindsight: a case study and
67. Railo H, Koivisto M, Revonsuo A. 2011 Tracking the
     processes behind conscious perception: a review of
     event-related potential correlates of visual
68. Tong F, Meng M, Blake R. 2006 Neural bases of
69. Marois R, Chun MM, Gore JC. 2000 Neural correlates
     vistas on integration in the nervous system. Trends Neurosci. 15, 218 – 226. (doi:10.1016/0166-
     2236(92)00039-B)
71. Von der Malsburg C. 1981 The correlation theory of
     brain function. Göttingen, Germany: Max-Plank-Institute for Biophysical Chemistry.
72. Eckhorn R, Bauer R, Jordan W, Brosch M, Kruse W,
     Munk M, Reitboeck HJ. 1988 Coherent oscillations: a
     BF00202899)
73. Gray CM, Konig P, Engel AK, Singer W. 1989
     Oscillatory responses in cat visual cortex exhibit
     inter-columnar synchronization which reflects global
     stimulus properties. Nature 338, 334 – 337. (doi:10.1038/338334a0)
     perceptual grouping and figure-ground segregation
     by means of active reentrant circuits. Proc. Natl
     Acad. Sci. USA 88, 129 – 133. (doi:10.1073/pnas.88.1.129)
75. Tononi G, Sporns O, Edelman GM. 1992 Reentry and
     the problem of integrating multiple cortical areas:
     simulation of dynamic integration in the visual
76. Engel AK, Singer W. 2001 Temporal binding and the
     Sci. 5, 16 – 25. (doi:10.1016/S1364-6613(00)
     01568-0)
77. Lumer ED. 1998 A neural model of binocular
     integration and rivalry based on the coordination
     of action-potential timing in primary visual
78. Womelsdorf T, Fries P. 2007 The role of neuronal
     synchronization in selective attention. Curr. Opin.
79. Fries P. 2005 A mechanism for cognitive dynamics:
     neuronal communication through neuronal
     2236(05)00131-8)
80. Nikolaev AR, Gepshtein S, Gong P, van Leeuwen C.
     2010 Duration of coherence intervals in electrical
     brain activity in perceptual organization. Cereb.
81. van Leeuwen C, Gong P, Nikolaev AR. 2002
     Coherence intervals in the brain and their role in
     inner psychophysics. In Fechner day 2002 (eds
     JA Da Silva, EH Matsushima, MR Ribeiro-Filho), pp. 151 – 155. Ribeirao Preto, Brazil: ISP.
82. Alexander DM et al. 2013 Traveling waves and trial
     averaging; the nature of single-trial and averaged
     brain responses in large-scale cortical signals.
     neuroimage.2013.01.016)
83. Varela F. 1995 Resonant cell assemblies: a new
     approach to cognitive functioning and neuronal
85. Tononi G, Edelman GM. 1998 Consciousness and
     1126/science.282.5395.1846)
86. Lamme WA, Roelfsema PR. 2000 The distinct
     modes of vision offered by feedforward and
     recurrent processing. Trends Neurosci. 23, 571 – 579. (doi:10.1016/S0166-
     2236(00)00165-7)
87. Crick FC, Koch C. 1995 Are we aware of neural
     activity in primary visual cortex? Nature 375,
     121 – 123. (doi:10.1038/375121a0)
88. Tong F. 2003 Primary visual cortex and visual
     1038/nn1055)
89. Derry O, Chen Y-C, Spence C. 2014 Multisensory
     constraints on awareness. Phil. Trans. R. Soc. B
90. Park H-D, Tallon-Baudry C. 2014 The neural
     subjective frame: from bodily signals to perceptual