Neuropsychologia 51 (2013) 1050–1060

Contents lists available at SciVerse ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Anchoring visual subjective experience in a neural model: The coarse vividness hypothesis

Florence Campana, Catherine Tallon-Baudry *

Cognitive Neuroscience Laboratory INSERM-ENS U960, Ecole Normale Supérieure, Paris, France

ARTICLE INFO

Article history:
Received 16 November 2012
Received in revised form
18 February 2013
Accepted 27 February 2013
Available online 13 March 2013

Keywords:
Perceptual consciousness
Subjective experience
Visual system
Scene categorization
Sperling experiment
Change blindness

ABSTRACT

Subjective experience often accompanies perception and cognition. This elusive feeling is difficult to characterize, both theoretically and experimentally. Perceptual subjective experience is at the heart of a theoretical debate in consciousness research: does it correspond to a genuine psychological and biological process independent from cognitive abilities, or is it a cognitive illusion, a post-hoc construct, implying that perceptual consciousness can be reduced to a sum of cognitive functions? We reconsider this debate in the light of known properties of the visual system, derived from studies on visual object and scene recognition but not specifically targeting consciousness issues. We propose here that initial visual subjective experience is characterized by two key properties, coarseness and vividness: initial subjective experience is integrated, meaningful, but does not contain detailed information. Subjective experience is likely to arise first in high-level visual areas, in which information is encoded in a coarse and integrated manner. We propose that initial subjective experience is related to the concept of "vision at a glance", thought to result from a fast, implicit feed-forward sweep of activity in the visual system progressing from low-level areas to high-level areas (Hochstein and Ahissar (2002) *Neuron*, *36*, 791–804). The details needed to overtly guide behavior would be retrieved in a secondary processing step of "vision with scrutiny", proceeding in a feed-back manner, from high-level to low-level areas. This secondary and optional descending process could thus later enrich conscious visual percepts with details. Our hypothesis provides parsimonious explanations for two intriguing findings: the double dissociation between attention and consciousness, and the mismatch between objective measures and subjective reports, that is sometimes used to argue that subjective experience is an illusion. We argue here that because visual subjective experience is initially coarse, it should not be probed by asking subjects to specify details. The coarse vividness hypothesis therefore offers a framework that accounts for the existence of an initial genuine subjective experience, defined by its coarseness and vividness, optionally followed by more refined and detailed processing that could underlie finer perceptual and cognitive abilities.

1. Introduction

Perceptual subjective experience refers to the way the world appears to us via our senses. It is an intuitive notion, fundamentally constitutive of our human nature. We all share the intuition that a robot, however smart, is lacking any feeling associated with the complex operations that it can execute: a robot is not human, therefore it lacks subjective experience. Subjective experience nevertheless remains an elusive notion, difficult to frame in a scientific theory, since it is essentially a private experience, that is not easily accessible to the experimenter. Nagel (1974) famously illustrated this idea by pointing out that even if we were an expert about the machinery of a bat, we could not imagine what it is like to be a bat, what it feels like to be a bat, or more generally what it feels like to be anyone else. Here, we concentrate on subjective visual experience, the sensation that sometimes accompany neural visual processing (Kanai & Tsuchiya, 2012).

In the last 20 years, the search for the neural correlates of consciousness has been very active. Leaving aside concepts and theories, most studies on visual consciousness adopted a pragmatic approach (Crick & Koch, 1990), and contrasted neural responses to stimuli that were consciously perceived vs. stimuli that remained unnoticed. But what does such a contrast tell us about visual consciousness? Does it pertain to information processing that could take place in a robot, or does it pertain to the neural basis of subjective experience? Since these questions were most often not explicitly addressed, subjective visual experience remains an underspecified issue in cognitive neuroscience. On the

* Corresponding author. Tel.: +33 144 32 27 93; fax: +33 144 32 26 42.
E-mail address: catherine.tallon-baudry@ens.fr (C. Tallon-Baudry).

0028-3932/$ - see front matter © 2013 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.neuropsychologia.2013.02.021

other hand, the nature of subjective perceptual experience is hotly debated from a theoretical point of view. Some philosophers argue that subjective experience is a cognitive illusion (Dennett, 1991; O'Regan & Noe, 2001), a post-hoc cognitive reconstruction rather than an immediate experience (Cohen & Dennett, 2011; Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006), whereas others emphasize that subjective experience is central to consciousness and is distinct from cognitive abilities (Block, 2007). At the other end of the spectrum, many visual scientists do actually study consciousness without mentioning it, since any study on explicit visual perception pertains to visual consciousness.

In this paper, we review neural and behavioral studies on visual recognition, whether or not addressing directly and explicitly the issue of subjective experience, and show how the architecture of the visual system constrains conscious perception. In the light of those constraints, we propose that the distinctive feature of initial subjective experience is coarse vividness: initial subjective experience is rich, integrated and meaningful, but does not contain much details. We provide a physiologically plausible model that accounts for this property and that articulates the quality of subjective experience with neural information processing. We then show how two intensely debated issues in consciousness research, namely the interpretation of change blindness studies and of the Sperling experiment, and the dissociation between attention and consciousness, can be parsimoniously interpreted in the framework of the coarse vividness hypothesis.

2. The disputed status of subjective experience

Subjective experience is at the heart of a vivid theoretical debate questioning the possibility that conscious experience exists independently of cognitive functions. Some argue that consciousness is reducible to cognitive functions (Cohen & Dennett, 2011; Kouider, de Gardelle, Sackur, & Dupoux, 2010). In this functionalist approach, consciousness is mainly considered as a combination of high-level cognitive functions, and, in this view, subjective experience is either absent or thought to arise somehow from the interactions between those high-level cognitive functions. In the original formulation of the global workspace theory, Baars wrote that "Consciousness seems to be the publicity organ of the brain. It is a facility for accessing, disseminating and exchanging information, and for exercising global coordination and control" and defined conscious experience as "the spotlight of attention shining on the stage of working memory" (Baars, 1997). Dehaene and Naccache (2001) further proposed that "this global availability of information [...] is what we subjectively experience as a conscious state". Alternatively, subjective experience could be distinct from the cognitive functions often associated with consciousness (Block, 2007; Lamme, 2006; Tallon-Baudry, 2012). If this were the case, then we are back to the "hard problem" (Chalmers, 1995): "The hard problem is hard precisely because it is not a problem about the performance of functions. The problem persists even when all the performance of all the relevant functions is explained". In other words, how can we account for the fact that we are *experiencing* those items we attend to, we exert control upon, we remember? What is the nature of this subjective experience? Could it be distinct from cognitive functions?

2.1. The difficulty of studying subjective experience

Subjective experience is a private experience, that is not easily accessible to the experimenter. Psychologists operationalized measures of subjective experience in detection tasks. Typically, in such experiments, a weak stimulus is presented or not, and subjects have to report whether they saw a stimulus or not. Detection is subjective and private: what matters is the experience of the subject, independently of the physical presence or absence of the stimulus. The experimenter cannot objectively verify the veracity of subjects' reports—a subject could be systematically lying for instance. Besides, even if subjects try to report faithfully their experience, the final outcome depends on subjects' willingness to report faint impressions. Signal detection theory (Ratcliff, 1978; Swets, Tanner, & Birdsall, 1961) was introduced as an influential tool to map subjects' reports onto the physical stimulus space by computing two hidden variables, perceptual sensitivity, or objective ability at discriminating between stimulus absent and stimulus present trials, and criterion, or willingness to report faint signals as "seen". The notion of subjective experience was excluded from the interpretation framework. Analyzing detection task data in the signal detection theory framework further revealed that subjects' criterion could be highly variable, both within and between subjects: some subjects may be prone to reporting seeing a stimulus in the presence of weak evidence, while others are more conservative and only report stimulus presence when their sensory experience was extremely vivid. Between-subject differences in criterion, as well as potential within-subject fluctuations of criterion over time, were considered as a source of noise in the data. To minimize this source of variability, more objective tasks were developed. For instance, subjects were asked in which time interval a stimulus was presented (Foley & Legge, 1981; Gorea, 1986; Thomas, 1985; Watson & Robson, 1981). More radically, discrimination tasks, in which subjects are no longer asked about their own experience, were introduced: subjects were asked about a physical feature of the stimulus, such as "was it tilted left or right?", or "was it a face or a house?". Such tasks are considered as objective, in the sense that the experimenter can tell whether the subject's answer is correct or not. Those tasks are also often unbiased by criterion issues, since there is no reason why a subject would be more willing to respond "tilted left" more often than "tilted right". The evolution of psychophysics toward objective tasks illustrates well the difficulties that are inherent to the study of private subjective experience. Behavioral methods tailored to study subjective experience are currently being developed (Overgaard, Nielsen, & Fuglsang-Frederiksen, 2004; Sandberg, Timmermans, Overgaard, & Cleeremans, 2010; Seth, Dienes, Cleeremans, Overgaard, & Pessoa, 2008), but have not yet been extensively used in neuroimaging studies.

As a consequence of the inherent difficulty to study subjective experience, neuroimaging studies of consciousness display a full panel of attitudes toward subjective measures. Some studies relied solely on subjective measures, despite potential caveats related to criterion (Ress & Heeger, 2003; Tse, Martinez-Conde, Schlegel, & Macknik, 2005). Others authors were more cautious, and assessed the validity of subjective measures by checking that objective performance was above chance when subjects reported seeing the stimulus, and at chance (Liu, Paradis, Yahia-Cherif, & Tallon-Baudry, 2012; Wyart, Dehaene, & Tallon-Baudry, 2012; Wyart & Tallon-Baudry, 2008) or close to chance (Del Cul, Baillet, & Dehaene, 2007), when subjects reported not seeing the stimulus. The rationale here is that consciously seeing should be accompanied by a marked improvement of perceptual abilities such as discrimination or identification. At the other end of the spectrum, a number of studies relied on objective performance only (Boehler, Schoenfeld, Heinze, & Hopf, 2008; Koivisto, Revonsuo, & Lehtonen, 2006; Schurger, Pereira, Treisman, & Cohen, 2010; Schwarzkopf & Rees, 2011). These examples illustrate the commonly held assumption that subjective experience and the behavior reflected by objective performance are tightly related, and therefore share common underlying neural processes. This assumption has proved useful, because it implies that subjective experience can be studied using the classical tools developed to measure objective perception and cognition. However, the heart of the debate is whether or not subjective experience can be reduced to a sum of objective cognitive processes. If the link between subjective experience and objective measures is assumed, it cannot be experimentally tested. This point is all the more important that when subjective and objective measures are considered separately, some degree of behavioral or neural uncoupling can be observed, as detailed below.

2.2. Subjective experience may be distinct from information processing abilities

First evidence for a distinction between subjective awareness and information processing abilities came from a particular form of blindsight, called type 2 blindsight. Those patients have a lesion of early visual cortex that prevents them from seeing. Surprisingly, they display blindsight abilities: despite having no conscious visual experience, they can perform better than chance when discriminating stimuli presented in their blind field. Type 2 blindsight patients develop in addition an atypical form of awareness, a "feeling that something happened" in their blind field (Sahraie, Hibbard, Trevethan, Ritchie, & Weiskrantz, 2010; Weiskrantz, Barbur, & Sahraie, 1995). A type-2 blindsight patient can therefore objectively discriminate a stimulus better than chance, and perform equally well whether or not the stimulus was accompanied by a subjective feeling (Schurger, Cowey, & Tallon-Baudry, 2006). Interestingly, gamma-band oscillations were found to correlate with subjective reports of this unusual form of awareness, independently from the accuracy of orientation discrimination. Those experiments strongly suggest that subjective experience and discrimination abilities may be uncoupled—at least in those patients.

There is growing experimental evidence for a behavioral dissociation between subjective reports and objective performance in normal subjects. Using metaconstrast masking, Lau and Passingham (2006) showed in eight subjects that the subjective experience of a figure and objective shape identification can be dissociated by varying target-mask SOAs. The U-shaped curve of metacontrast masking enabled the authors to identify two distinct SOAs at which objective accuracies were similar, whereas subjects reported seeing the stimulus more often at the longest of these SOAs. This result suggests that experiencing the presence of a figure is distinct from the ability to determine its shape. In line with this idea, subjective detection and objective discrimination were found to be sometimes uncoupled, at least in some subjects (Barlasov-Ioffe & Hochstein, 2008). A TMS study also revealed a dissociation between objective performance and subjective experience (Overgaard et al., 2004): objective performance remained high and unaffected while subjective experience was rated as less vivid. Another indication that objective performance and subjective reports may be uncoupled comes from attention studies (Hsu, George, Wyart, & Tallon-Baudry, 2011). While both voluntary and involuntary attention increased stimulus subjective detection to a similar extent, they impacted objective orientation discrimination differently: in the objective task, voluntary attention shortened reaction times in "seen" trials, while involuntary attention shortened reaction times in "unseen" trials. Similarly, attention can affect objective orientation discrimination and subjective confidence judgment differently (Wilimzig, Tsuchiya, Fahle, & Koch, 2008). By showing a differential effect of attention on subjective reports and objective performance, these studies suggest that subjective experience and objective performance may be distinct mechanisms. Following the same logic, perceptual learning differentially affects objective performance and subjective visibility ratings (Schwiedrzik, Singer, & Melloni, 2011): after practice, when learnt stimuli were moved to a new location, objective performance dropped, while subjective visibility remained improved by learning. This suggests that subjective experience and objective performance may arise from areas with different spatial resolutions.

The neural correlates of subjective experience and objective performance could also be partly dissociated (Hesselmann, Hebart, & Malach, 2011). fMRI correlates of subjective visibility were found in the ventral visual pathway, and, to some extent, inferior parietal sulcus. Correlates of objective accuracy at localizing unseen target were more difficult to extract but were mostly found in early visual areas. These results indicate that objective performance and subjective experience may arise from distinct anatomical substrates.

The studies reviewed above reveal that uncoupling between subjective experience and objective performance is not confined to blindsight patients, but can be observed in a variety of paradigms in normal participants. The commonly held assumption that subjective experience and objective performance co-vary should therefore be reconsidered. It follows that those studies that relied on objective performance to search for the neural mechanisms of consciousness have to be re-evaluated. From a more theoretical point of view, if cognitive functions and subjective experience are distinct processes, they should exhibit distinct properties. What is the distinctive signature of subjective experience? We will develop below the idea that coarseness and vividness are key and distinctive characteristics of initial subjective experience, that objective measures may be unable to capture.

3. The coarse vividness hypothesis

3.1. Specifying the richness of subjective experience

Our spontaneous experience of the visual environment is a rich one. Although this richness has not been measured by the conventional tools of experimental psychology, both subjects' spontaneous reports and our own everyday experience point to vivid contents of consciousness. As nicely expressed by Biederman (1972), "if we glance at the world, our subjective impression is of clear and almost instantaneous perception and comprehension of what we are looking at". The clarity and richness of subjective experience could logically stem from rich, detailed internal representations of the external world. However, experimental data indicate a mismatch between the richness of subjective experience and the richness of internal representations. A well-known example of mismatch comes from change blindness studies. In those studies (Rensink, 2002; Simons & Levin, 1997), two images of the same visual scene differing by one item are presented in rapid succession. Although the change can be massive, it often remains unnoticed. In other words, subjects have the feeling they see the entire visual scene – a rich subjective experience – but they are unable to report accurately the details of the visual scene. The experienced richness of subjective experience could therefore be an illusion (O'Regan & Noe, 2001), a post-hoc cognitive reconstruction rather than an immediate percept (Cohen & Dennett, 2011; Dehaene et al., 2006). We suggest however that an alternative explanation exists: the discrepancy between the richness of subjective experience and poor objective performance could arise from a misunderstanding about the word "richness".

The concept of richness is central: if subjects claim to have a rich subjective experience, but cannot back up this claim in objective tasks, then the existence of subjective experience should be questioned. But what is really meant by "rich"? It turns out that the crucial concept of richness is underspecified in the current literature on subjective experience (Irvine, 2011). A rich experience is, often implicitly, considered to necessarily contain a lot of details. This assumption is at the core of the reasoning leading to the conclusion that subjective experience is an illusion, as described above. We would like here to consider the possibility that "rich" does not necessarily mean "detailed". If this were true, then the reasoning leading to conclude on the illusory nature of subjective experience could be intrinsically flawed. We now examine the idea of "richness": what would it mean to have a rich experience without detailed contents? Where could richness come from, if not from detailed internal representations?

Let us first consider some examples. Imagine a painting by Hieronymus Bosch. Now imagine a painting by Pieter Brueghel. You probably had in both cases a vivid feeling. Although those painters both produced highly detailed and crowded scenes, it is extremely difficult to be specific about those details, further than maybe indoor scene crowded with fantastical animals vs. outdoor scenes: subjective experience seems rather coarse. Subjective experience nevertheless appears quite vivid. The subjective feelings elicited by imagining those two paintings are clearly distinct. The distinction between Bosch's and Brueghel's paintings in memory does not come from specific details. Rather, subjective experience seems to be colored by the specific artistic style of each painter. Note that this analogy calls onto memory and mental imagery, while our proposal deals with visual perception. Another example dealing more directly with perceptual consciousness is weather prediction: if you have a look through the window, you are probably able to predict whether a thunderstorm is coming or not, although unable to describe the precise shape of the cumulonimbus that led you to formulate this prediction. The overall aspect of clouds in the sky can lead you to a vivid percept, meaningful since it can lead to a prediction, but devoid of any specific details.

We propose that the richness of subjective experience corresponds to two central traits: vividness and coarseness. Subjective experience is vivid, in the sense that it is strong and distinctive, as when looking at a Bosch vs. Brueghel's paintings. The richness of subjective experience also seems to stem from the global meaning one assigns to a visual scene, rather than the amount of local details, as when predicting an upcoming thunderstorm. Subjective experience is coarse, in the sense that it has no detailed content—you can experience the difference between two artistic styles without providing specific details supporting the distinction. This coarseness could account for the difficulty we have to verbalize subjective experience, to communicate perceptual sensations. Words typically describe well-defined items and entities, and may therefore be poorly suited to describe a coarse, overall feeling such as a specific artistic style as in the Bosch vs. Brueghel example. The description of introspective reports made in the late nineteenth century also emphasizes both vividness and coarseness, by suggesting the existence of "vague and elusive processes, which carry as if in a nutshell the entire meaning of a situation" (quotation from Titchener reported in Hurlburt and Heavey (2001)). It is worth underlining here that the coarseness and vividness of subjective experience parallel the integration and differentiation that are thought to be fundamental properties of consciousness (Tononi & Edelman, 1998). We will now present a physiologically plausible model that could account for initially coarse and vivid conscious percepts.

3.2. *A physiologically plausible model for the coarse vividness hypothesis*

Ten years ago, Hochstein and Ahissar (2002) proposed an influential physiological model of visual processing, derived from studies on perceptual learning, but supported by animal electrophysiological recordings (Buffalo, Fries, Landman, Liang, & Desimone, 2010; Lamme, RodriguezRodriguez, & Spekreijse, 1999; Poort et al., 2012) and human behavioral (Grill-Spector & Kanwisher, 2005; Torralba, Oliva, Castelhano, & Henderson, 2006) or neuroimaging (Goffaux et al., 2011; Lamme, 2010) studies. In this model (Fig. 1A), visual features are analyzed in early visual areas and are rapidly integrated at further stages of the visual hierarchy. This first step is achieved rapidly, automatically, enabling "vision at a glance". This fast initial wave of processing is also referred to in the literature as the "feed-forward sweep" (Lamme & Roelfsema, 2000) and would be implicit. The retrieval of more detailed information, or "vision with scrutiny", would then depend on a later descending wave progressing in a reverse order in the visual hierarchy, from top to bottom in an optional zooming-in mode. Detailed information would then be progressively added to visual content in a secondary-step. The word "consciousness" was used with caution by the authors, but this model clearly assumes that conscious visual perception would initially take place at high-level visual areas, at the top of the feed-forward sweep, and could then proceed back to low-level areas.

We propose here to specify Hochstein and Ahissar (2002) model regarding visual consciousness (Fig. 1B and C). Our proposal is that subjective experience would initially correspond to the first activation of high-level visual areas, once the feed-forward sweep is completed (Fig. 1B). This subjective experience is vivid and meaningful in the sense that it corresponds to processed and integrated information. It is also coarse because it takes place in regions that do not explicitly encode details—quite on the contrary, high-level visual areas are typically invariant to object size or viewing angle. Our proposal would therefore account for the possibility of a rich subjective experience without a detailed content. The details necessary to perform most objective tasks would require further optional descending, backward processing, along the feed-back sweep of "vision with scrutiny". In this view, two types of rich representations can be formed (Fig. 1C). The first one corresponds to an overall appraisal of the gist of the scene, to grasp the general meaning of the scene (Fig. 1C, left). Another type of rich representation focuses on specific details, depending on behavioral goals (Fig. 1C, right). In other words, our proposal is that if a conscious percept is formed, it initially takes place in high-order visual areas. Its initial content is therefore integrated and coarse. This first step can be followed by a secondary and optional descending process that enriches the conscious percept with details, according to behavioral goals. In this view, conscious contents can develop over time along a continuum, from coarse and vivid to detailed and accurate.

3.3. *Relationship with other models*

Before discussing arguments in favor of this proposal, it is worth underlining that our proposal differs from other neural models of consciousness emphasizing the importance of recurrent processing and feed-back connections (Dehaene, Sergent, & Changeux, 2003; Lamme, 2006). In those models, feed-back processes, either within the ventral pathway (Lamme, 2006) or encompassing fronto-parietal regions (Dehaene et al., 2003), trigger conscious experience. In the current proposal, a necessary condition for the emergence of subjective experience would be the activation of high-level visual areas, not recurrent processing connecting distant areas. Feed-back would only be necessary to retrieve finer-grained information pertaining to this initial coarse representation, via an optional zooming-in mechanism. In our view, conscious access to information encoded in low-level visual areas would therefore be dependent on the completion of mechanisms taking place at higher stages. This is different from the partial awareness view, in which "lower and higher levels are

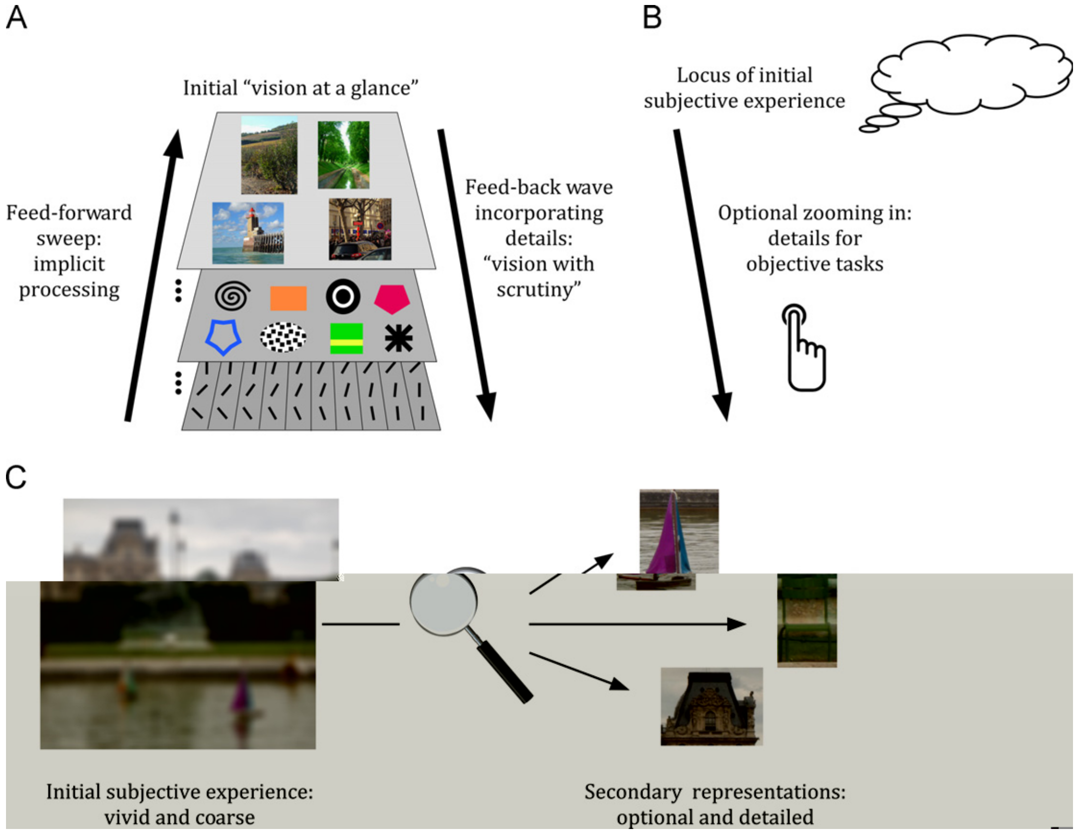

Fig. 1. The coarse vividness hypothesis. (A) The Hochstein & Ahissar model, redrawn from Hochstein and Ahissar (2002). In this model, vision proceeds in two steps: a fast feed-forward sweep, from low to high-level visual areas, would integrate local information to build an overall description of the scene, enabling "vision at a glance". This initial step would be followed by a descending process, with information flowing backwards from high to low-level visual areas. This second step of "vision with scrutiny" would incorporate details in explicit vision. (B) Specifying subjective experience. We propose that conscious vision operates from top to bottom, with a coarse initial subjective experience taking place at the highest level of the hierarchy, in areas with large receptive fields responding to overall shapes, objects or scenes. As a result, initial subjective experience would be intrinsically coarse, but would correspond to meaningful categories. When required by behavioral goals or specific task instructions, conscious details would be later added to this initial coarse percept. (C) Two different types of "richness". Initial subjective experience would be akin to a low-frequency content picture, with enough information to grasp the overall meaning—here an outdoor scene, in a city. A second step of processing would be necessary to retrieve and focus on those details that guide behavior. Depending on one's goal, one may focus on the chair, on an architectural detail in the background, or on the toy boat in the foreground.

accessed independently" (Kouider et al., 2010). Note that we do not specify here which mechanisms give rise to consciousness, rather, we specify that if consciousness occurs, its contents initially fit with the level of description encountered in high-level areas, and then with the more detailed level found in lower-level areas.

At a more conceptual level, our proposal also differs from existing theories. There are currently two main and opposing philosophical theories of conscious perceptual experience. In the functionalist view, visual consciousness is considered as a single entity, defined by any percept subjects can report (Cohen, van Gaal, Ridderinkhof, & Lamme, 2009). This view has been criticized because it does not capture the subjective aspects of visual experience (Lamme, 2010; Lau, 2008). The alternative proposal offers a dual account of consciousness: a cognitive component, necessary to report the contents of consciousness, and a phenomenal component, underlying the "what-is-it-likeness" of conscious experiences, that can occur in the absence of the cognitive component (Block, 2007). This dual account of consciousness infers the existence of subjective experiences that cannot be reported, and therefore has been criticized because it cannot be tested experimentally (Cohen & Dennett, 2011; Kouider et al., 2010). In our proposal, perceptual subjective experience is organized along a continuum and evolves over time: subjective experience is initially coarse, and hence difficult to report, but nevertheless a vivid and meaningful experience. It can later on be further enriched with more detailed information, selected according to behavioral goals. Our proposal therefore accounts for both the existence of subjective experiences difficult to verbalize, at the initial stage of conscious percepts, and the existence of goal-oriented, accurate and detailed conscious percepts that are more easily reported, after the secondary descending process.

4. Experimental evidence supporting the coarse vividness hypothesis

4.1. Existence of integrated percepts without details

The coarse vividness hypothesis requires the existence of integrated, meaningful percepts that are nevertheless devoid of specific details. This stands in contrast with our intuition that the contents of our visual perception are detailed. However, as pointed out by the Gestalt theory, the very existence of visual illusions indicates that perception is a construction that produces integrated and meaningful entities. Because we all spontaneously perceive those visual illusions, this idea seems rather intuitive. However some experimental settings push this idea further: we not only perceive integrated information, but we may actually not be able to retrieve the local, detailed information that led to build those percepts. Indeed, subjects can report an integrated property of an array of stimuli without accurately perceiving separately each stimulus. Subjects can estimate the mean orientation (Parkes, Lund, Angelucci, Solomon, & Morgan, 2001) or size (Ariely, 2001) across an array of visual items, without being able to report accurately the orientation or size of each item. Similarly, subjects are able to evaluate the mean emotion of an array of four faces, despite being at chance level to identify the faces constituting the array (Haberman & Whitney, 2009). Taken together, those results suggest that once local elements are combined into an integrated percept, detailed information about those local elements may not easily be retrieved consciously. Spontaneous experience indeed seems to be dominated by integrated and meaningful entities, as shown in an elegant rivalry experiment (Kovacs, Papathomas, Yang, & Feher, 1996). Two distinct non-coherent images, that would elicit a coherent percept if fused, were presented separately to the two eyes. Subjects reported most often a coherent percept, implying that integration into a coherent percept overrides the process of selection of information of one eye for dominance. This experiment nicely illustrates the way our brain integrates information to build meaningful representations, and further shows that spontaneous subjective reports preferentially correspond to those integrated representations.

Last, the idea that the presence of a percept does not imply a detailed content is also supported by neural evidence. In a change blindness experiment, subjects indicated both whether they experienced a change and whether they could specify the identity of the object that changed. The neural correlate of change awareness was identical whether or not subjects could specify which object changed (Busch, Frund, & Herrmann, 2010), suggesting that the experience that "something changed" was independent from knowing more specifically which object changed.

4.2. Initial is integrated without details, more time is needed to retrieve details

In the coarse vividness framework, visual experience is initially dominated by an overall grasp of the scene, with details being progressively isolated with further processing along the descending pathway. A number of experimental data, not necessarily formulated in the framework of consciousness studies, are in agreement with the prediction that the global structure, or "gist" of an image comes first, with explicit perception proceeding from integrated to detailed contents.

The most famous example that one "perceives the forest before trees" comes from the pioneering work of Navon (1977). Navon (1977) presented subjects with hierarchical stimuli, made of small letters (Hs for instance), spatially arranged so as to define a larger letter that could be congruent (a large H) or incongruent (a large S for instance). Subjects were slower when they had to report the identity of the small letter, as compared with the large letter, suggesting that an additional processing step is needed to report local information. This result, although it has since been criticized (Kimchi, 1992), is in line with the existence of the descending pathway of "vision with scrutiny" (Hochstein & Ahissar, 2002).

Behavioral studies on scene categorization offer striking examples of visual percepts that are initially coarse, but that get more elaborate and precise when processing time is prolonged. Oliva and Torralba (2006) created hybrid images containing the overall spatial layout of one visual scene, and the detailed information of another one. When presented with hybrid images rapidly followed by a mask, subjects extracted the meaning of the scene according to the overall spatial layout, rather than according to the fine details encoded in the spatial high-frequency domain. However, when the presentation time of masked hybrid images was prolonged, subjects extracted the meaning of the hybrid scene based on image details, suggesting that additional time is required to move from low- to high-resolution explicit vision. Similarly, when subjects were briefly presented with natural scenes, they could accurately discriminate between two general categories, such as animal vs. non-animal, with very short reaction times (Thorpe, Fize, & Marlot, 1996). However subjects were slower to discriminate (Grill-Spector & Kanwisher, 2005; Mace, Joubert, Nespoulous, & Fabre-Thorpe, 2009), or impaired at discriminating (Evans & Treisman, 2005), between more refined categories, such as bird or non-bird or dog vs. non-dog. Besides, fast scene categorization is not impaired when images are turned upside-down (Evans & Treisman, 2005). Altogether, these findings suggest that the information used for fast categorization consists of unbound features and rely on natural image statistics, but is not necessarily segmented into well-defined entities (Evans & Treisman, 2005; Oliva & Torralba, 2006). This suggests that initial percepts are coarse, in the sense that they do not refer to fully segmented scenes. To summarize, results on image categorization are in keeping with the idea that conscious vision proceeds from coarse representations, sufficient to identify the gist of a visual scene, to detailed information necessary to discriminate between more refined categories.

4.3. Neural evidence for an initial coarse experience in high-level visual areas

When and were are coarse representations established? Studies on visual scene categorization highlight the role of the feed-forward sweep. In a rapid visual categorization task, EEG responses distinguish between scene categories within 100–150 ms after the appearance of the visual scene (Thorpe et al., 1996), in the ventral visual pathway (Liu, Agam, Madsen, & Kreiman, 2009). Those latencies are compatible with the first activations of neurons in the infero-temporal pathway (Baylis & Rolls, 1987; Lamme & Roelfsema, 2000; Rolls, Aggelopoulos, & Zheng, 2003; Schmolesky et al., 1998), where representations are coarse due to large receptive field size and invariance properties (Logothetis & Sheinberg, 1996; Tanaka, 1996). The coarse representations required for rapid categorization could thus correspond to the activation of ventral regions by the feed-forward sweep. This interpretation is strengthened by the fact that a purely feed-forward model of visual processing, from V1 to IT, can fit human performance extremely well in rapid categorization tasks (Serre, Oliva, & Poggio, 2007).

In humans, lateral occipital regions seem to play a specific role in visual object processing, and could constitute a plausible locus for coarse object representations: those regions are activated in response to objects, but not to their scrambled counterparts (Grill-Spector, Kourtzi, & Kanwisher, 2001; Grill-Spector, Kushnir, Edelman, Itzchak, & Malach, 1998). Interestingly, a number of neuroimaging studies on visual consciousness find correlates of detection in those regions (Hesselmann et al., 2011; Liu et al., 2012; Tong, Nakayama, Vaughan, & Kanwisher, 1998; Tse et al., 2005; Tsubomi et al., 2012; Wyart & Tallon-Baudry, 2009). Importantly in some of those studies, activations of frontal and parietal regions were observed, but were not related to stimulus visibility (Liu et al., 2012; Tsubomi et al., 2012). Those results are compatible with the notion that subjective experience takes place in lateral occipital regions, with activations in frontal and parietal regions taking place either as a consequence of consciousness (Knapen, Brascamp, Pearson, van Ee, & Blake, 2011), or independently from consciousness (Cohen et al., 2009; Hester, Foxe, Molholm, Shpaner, & Garavan, 2005; Lau & Passingham, 2007; Sumner et al., 2007; van Gaal, Ridderinkhof, Fahrenfort, Scholte, & Lamme, 2008).

Correlates of consciousness have also been found in lower-level visual areas (Ress & Heeger, 2003; Tong, 2003). However, those correlates could appear at a late stage of processing, and therefore reflect a secondary activation, fed-back from higher visual areas. In humans, correlates of visibility in V1 are not observed during the initial activation of this area, but about 50 ms later (Boehler et al., 2008). In monkeys (Super, Spekreijse, & Lamme, 2001), a neural correlate of visibility has been observed in V1: neurons respond differently for figure and ground, but only when the animal detects the figure. Because this correlate of visibility appears at long latencies, it is considered to be due to feed-back. TMS studies disrupting processing in low vs. high-level visual areas reveal that V1/V2 appear necessary to perception both at the beginning and the end of visual processing, with higher visual areas being necessary in an intermediate time window (Koivisto, Railo, Revonsuo, Vanni, & Salminen-Vaparanta, 2011; Pascual-Leone & Walsh, 2001; Silvanto, Lavie, & Walsh, 2005; Wokke, Vandenbroucke, Scholte, & Lamme, 2013). Those results are compatible with the double wave of Hochstein and Ahissar (2002) model. The original interpretation of those studies emphasized the role of feed-back from high to low-level areas in the emergence of conscious percepts. However it should be noted that the task and stimuli used may have promoted the use of detailed information, and therefore the need of feed-back processing. In one experiment (Silvanto et al., 2005), subjects had to report motion across very short distances, a process that may have recruited the small receptive fields of V1. In another experiment (Koivisto et al., 2011), subjects had to categorize natural scenes, but did so with slow reaction times, in the order of 500 ms as opposed to other studies on ultra-rapid categorization, in which reaction times could be as short as 200 ms (Thorpe et al., 1996): subjects had time to focus on details retrieved along the descending pathway to categorize the scene.

To conclude, a number of behavioral and neural arguments point for the existence of initially coarse representations in high-level visual areas, later enriched with details. Coarseness derives from two properties of high-level visual areas: the large receptive field size, that imposes a rough spatial grain, and the presumed unsegmented nature of initial visual representations in those regions. It may appear counterintuitive to suggest that conscious contents are initially unsegmented. However, there is growing evidence that binding and segmentation can take place unconsciously, in anesthetized animals (Gray, König, Engel, & Singer, 1989) as well as in humans (Norman, Heywood, & Kentridge, in press; Tarokh, 2009). Besides, the idea that initial contents of consciousness are not segmented into well-defined entities can be related to the difficulty we have to verbally describe those initial contents.

5. Explanatory power of the coarse vividness hypothesis

In the framework of the coarse vividness hypothesis, two intensely debated issues in consciousness research, namely the interpretation of change blindness studies and of the Sperling experiment on the one hand, and the dissociation between attention and consciousness on the other hand, can be parsimoniously re-interpreted.

5.1. Initial subjective experience should be probed at an integrated level

As developed above, a rich experience has often been considered to necessarily contain a lot of details. Based on this idea, some argue that the existence of subjective experience should be questioned, because subjects cannot always report details in experimental situations where they claim seeing everything. We argue here that the logic of the argument could be intrinsically flawed: if one admits that initial subjective experience is vivid but coarse, then, by definition, it does not contain details. Probing initial subjective experience by asking about scene details is therefore fraught with a conceptual error: initial subjective experience by nature is not detailed. We illustrate this reasoning by reconsidering two series of experiments.

The results of the Sperling experiment (Sperling, 1960) were initially considered to support the idea of rich internal representations. In this paradigm, participants typically briefly view an array of 4×3 letters and are asked to report as many items as possible. They can usually report accurately 3 to 4 letters, corresponding to the classical capacity limit of short term memory, although subjects have the feeling of seeing more. In another condition, an auditory cue is delivered after array disappearance. The tone of the auditory cue indicates the subject which line of the array should be reported. Subjects can accurately report the cued line of 4 letters, wherever the cue is located. Sperling concluded that the information about each letter of the whole array was therefore present in the system, and stored in what he called the iconic memory buffer, with a much larger capacity than the short term memory buffer. The philosopher Ned Block (2007) proposed that the richness of subjective experience arises from the content of the iconic memory buffer—even if due to the limits of short term memory, only 3 to 4 items can be described. In this sense, subjective experience has a higher capacity than the system that enables subjects to report letters. However, this interpretation has been questioned in a follow-up study (de Gardelle, Sackur, & Kouider, 2009). The authors modified the Sperling paradigm and introduced unexpected pseudo-letters in the array. Participants tended to report the real letter corresponding to the pseudo-letter, thereby questioning the accuracy of subjects' visual experience. This would indicate that the richness of subjective experience is an illusion.

We propose to reconsider the interpretation of the Sperling experiment in the framework of the coarse vividness hypothesis: subjective experience may not have been probed at an appropriate level, because asking about letter identity typically taps onto detailed representations. In the framework of the coarse vividness hypothesis, the rich experience spontaneously reported by subjects would not be composed of a series of fully resolved items, because presentation times were brief; rather, subjects may experience an array, i.e., unspecified objects having specific spatial relationships. Because this array is not an ecological stimulus, it has no global meaning. The overall percept, the "forest", or the "gist" of the scene, is all the more difficult to describe verbally.

The change blindness paradigm was also considered to point toward an illusory richness of subjective experience. In those studies (Rensink, 2002; Simons & Levin, 1997), subjects miss massive change in natural images when the change appears between two successive rapid presentations despite claiming to experience the whole image. For instance, subjects may not notice that a building in a city landscape is displaced, or that the engine of an airplane is removed. Following the same logic as in the Sperling experiment, it has been argued that the richness of experience spontaneously reported is illusory (O'Regan & Noe, 2001). We propose a different interpretation: subjects correctly identify the overall nature of the visual scene—whether it is a cityscape or a landscape, whether it is a street view or an airport. In this sense, subjective experience is rich and accurate. But it is also coarse: details, such as the exact location of a building, or the presence of an engine, are not part of this initial percept. Since images are displayed in rapid succession, the secondary descending process cannot take place. In line with this interpretation, subjects detect changes that affect the gist of the visual scene more readily than changes that leave the overall category of the image intact (Sampanes, Tseng, & Bridgeman, 2008). Those results are compatible with the idea that subjects' initial subjective experience corresponds to the gist of the visual scene, without any specific detail on the components of the scene. When a change occurs but leaves the gist intact, initial subjective experience is not altered, and the change remains unnoticed, even if the changed item is large.

5.2. Revisiting the links between attention and consciousness

There is an ongoing debate on the links between attention and consciousness, some considering that attention is a necessary prerequisite for consciousness (Cohen, Cavanagh, Chun, & Nakayama, 2012; Dehaene et al., 2006; Posner, 1994, 2012), others arguing that attention and consciousness are entirely distinct processes (Koch & Tsuchiya, 2007; Lamme, 2003; Tallon-Baudry, 2012). We refer the reader to those papers for a full discussion of the links between attention and consciousness, and concentrate here on a selection of experimental facts particularly relevant to the coarse vividness hypothesis.

There is mounting evidence for a dissociation between attention and consciousness, both at the neural (Koivisto et al., 2006; Schurger, Cowey, Cohen, Treisman, & Tallon-Baudry, 2008; Tsubomi et al., 2012; Wyart et al., 2012; Wyart & Tallon-Baudry, 2008) (but see (Koivisto, Kainulainen, & Revonsuo, 2009) for a different conclusion) and the behavioral level (Hsu et al., 2011; Kentridge, Heywood, & Weiskrantz, 1999; Kentridge, Nijboer, & Heywood, 2008; Norman et al., in press; van Boxtel, Tsuchiya, & Koch, 2010). Results from our group (Wyart & Tallon-Baudry, 2008) show that when subjects orient their attention toward a given location according to a central predictive arrow, they detect stimuli more often on the attended side, suggesting that attention facilitates consciousness, in agreement with the behavioral literature. However neural data tell another story: in retinotopic areas, attended stimuli, seen or unseen, give rise to enhanced high-frequency gamma-band oscillations. Conversely in lateral occipital regions (Wyart & Tallon-Baudry, 2009), seen stimuli give rise to larger mid-frequency gamma-band oscillations, independently from the attentional status of the stimulus. This double dissociation between the neural correlates of attention and awareness could be qualitatively reproduced in type 2 blindsight patient GY, at identical levels of performance in seen and unseen trials (Schurger et al., 2008). A similar double dissociation between the neural correlates of visual consciousness and spatial attention could be observed also in evoked responses using masked stimuli (Wyart et al., 2012). Last, a double dissociation of the fMRI correlates of attention and stimulus visibility was obtained, with visibility associated with the right lateral occipital region and attention with the inferior frontal gyrus and intraparietal sulcus (Tsubomi et al., 2012).

The idea that attention and consciousness are distinct appears at first rather counterintuitive: attention is considered to be a function that enables us to see better. But at which level does attention operates? Does attention allow to "see better" the details of the visual scene, once subjective experience has been formed? Or does attention foster the formation of the initial, global percept that can give rise to subjective experience?

Attention could, in principle, act in three distinct ways: it could selectively amplify signals in the ascending, feed-forward sweep, it could selectively amplify signals along the descending, feed-back pathway, or it could affect decisional processes, in particular the bias of a subject to report an experience, independently from the strength of sensory input (Chanes, Quentin, Tallon-Baudry, & Valero-Cabré, 2013; Wyart & Tallon-Baudry, 2009). To determine whether or not attention directly affects subjective experience, the critical question is therefore whether attention first affects initial responses in primary visual cortex, with attentional modulations begin propagated to the whole feed-forward sweep, or whether attention first targets the highest level of the visual hierarchy, and is then fed-back along the descending pathway.

There is now solid evidence from monkey electrophysiology that attention can proceed in a backward manner, from high-level visual areas down to V1 (Buffalo et al., 2010; Luck, Chelazzi, Hillyard, & Desimone, 1997; Mehta, Ulbert, & Schroeder, 2000). Recordings in areas V1, V2 and V4 of monkeys performing a detection task at the attended location revealed that attentional modulations appear first in area V4, then in V2 and finally in V1 (Buffalo et al., 2010). Those results are compatible with the idea that coarse information in V4 is selected, and the finer details encoded in V1 are being selectively amplified by attention only at a later stage. Conversely, attention does not seem to operate in the feed-forward sweep of visual processing since attention does not alter the initial wave of neural activity, neither in monkey area V4 (Lee, Williford, & Maunsell, 2007), nor in area V1 (Roelfsema, Lamme, & Spekreijse, 1998; Vidyasagar, 1998). Those results in monkeys are in line with numerous converging evidence in humans, showing that the first attentional modulations take place around 100 ms in extra-striate visual cortex (Luck, Woodman, & Vogel, 2000). The attentional modulation commonly observed in V1 in fMRI data corresponds to late attentional effects fed-back from higher visual areas (Di Russo, Martinez, & Hillyard, 2003; Martinez et al., 1999; Noesselt et al., 2002).

This overview of the literature unambiguously points toward an impact of attention on visual processing in the descending pathway, during the optional focusing on details of the visual scene. It should be noted however that a small number of recent studies suggested that attention could modulate the earliest responses in V1, at the beginning of the feed-forward sweep (Fu et al., 2009; Kelly, Gomez-Ramirez, & Foxe, 2008; Poghosyan & Ioannides, 2008; Zhang, Zhaoping, Zhou, & Fang, 2012), although a number of methodological considerations still remain to be addressed (Acunzo, Mackenzie, & van Rossum, 2012). Second, attention corresponds to such a broad concept and can be operationalized in so many different ways that a simple picture is unlikely to capture its complexity, and different forms of attention and/or expectancy may impact visual processing at different processing steps. Still, in the case of endogenous, voluntary spatial attention that has been so far been mostly studied, a large body of electrophysiological data point toward attentional influences along the descending pathway.

Bearing in mind that attention may mostly affect feed-back processing, it becomes easier to understand why double dissociations between attention and consciousness could repeatedly be observed in neural data. In this framework, conscious report would mainly depend on neural activity at the top of the feed-forward wave, potentially located in lateral occipital regions for simple visual stimuli (Hesselmann et al., 2011; Liu et al., 2012; Tsubomi et al., 2012; Wyart & Tallon-Baudry, 2009), independently from attentional amplification taking place in the descending pathway. Conversely, attention could affect the descending, feed-back wave, independently from the specific consciousness-related process taking place in lateral occipital regions. The accumulation of those two types of activities in a single decisional process would lead subjects to report the presence of a stimulus more often on the attended side (Tallon-Baudry, 2012; Wyart & Tallon-Baudry, 2008).

A descending influence of attention on visual processes can also account for some intriguing behavioral findings. First, some visual processes seem to be rather immune to attention. In particular, the coarse processing of a visual scene can be performed in the periphery, while subjects perform a central attentionally demanding task (Li, VanRullen, Koch, & Perona, 2002). In other words, attention is not necessary to coarsely extract information from a visual scene, a process that would take place in the ascending, automatic feed-forward sweep. Second, the type of attentional strategy used by subjects can depend on stimulus visibility (Hsu et al., 2011): in response to the same attentional cue, seeing or not the stimulus determined the type of attentional process (voluntary or involuntary) that was applied. This intriguing result can be readily interpreted if one admits that seeing consciously the stimulus or not can affect subsequent processing in the descending pathway, where attention operates. Last, it was recently shown that an attentional cue presented several hundred milliseconds after stimulus disappearance can foster the conscious perception of a stimulus that would otherwise have remained unreported (Sergent et al., 2013). Here, attention cannot impact stimulus detection by amplifying initial responses to the stimulus, since the attentional cue is presented long after the feed-forward sweep is completed. It must therefore impact a later processing stage—either the descending pathway or a secondary feed-forward/feed-back cycle.

To summarize, electrophysiological studies of spatial attention reveal that attention proceeds in backward manner, along the descending pathway of the reverse hierarchy. If, as we propose, subjective experience takes place initially in high-level visual areas, it may be independent from spatial attention. This would explain why double dissociations between neural correlates of attention and visual consciousness can be observed, why fast scene categorization can be independent from attention, and why stimulus visibility may influence the type of attention deployed. This interpretation does not preclude that attention influences subjective reports: the final report of the subject may be based not only on initial subjective experience, but also on the more refined information extracted from the descending process, that is sensitive to attention.

6. Conclusions

We relate here a classical model of visual processing backed up by numerous experimental findings in vision research with experimental results and ongoing theoretical controversies in consciousness. The articulation between consciousness studies and the physiology of the visual system appears to be centered on the core concept of "richness of representations".

We propose that the defining property of initial subjective experience is coarse vividness. The richness of initial subjective experience stems from the overall color, from the rough interpretation conveyed by rapid feed-forward visual processing, akin to the gist of a visual scene. In this view, subjective experience is likely to arise in high-level visual areas, where integrated and coarse representations are encoded, and whose initial activation would correspond to the starting point of conscious vision. Details of the visual scene would be incorporated to conscious perception at a later stage, proceeding from high- to low-level visual areas. In most natural and experimental situations, this later descending process is likely to take place because some details are relevant for goal-oriented behavior. However, when there are no cognitive constraints, as when appreciating an abstract painting for instance, subjective experience can linger at the integrated and coarse level.

We argue that the debate on the nature and existence of subjective experience is biased by experimental arguments that may not appropriately target subjective experience: the existence of a coarsely defined subjective feeling cannot be probed by measuring objective behavioral responses to specific details. It follows that the arguments used to deny the existence of subjective experience should be reconsidered, and new neuroimaging studies targeting specifically initial subjective experience should be developed. In the coarse vividness hypothesis, subjective experience is a genuine phenomenon, that can be accounted for in a realistic neural framework. The novelty of our approach is to propose that subjective experience develops over time, along a continuum: it initially consists of a coarse and vivid experience, followed by an optional addition of specific details. In this view, detailed and accurate representations are not a hallmark of visual consciousness, and therefore, good performance on details cannot be taken as a behavioral signature of visual consciousness. This proposal reconciles two opposite views on perceptual consciousness: one that focuses mostly on the phenomenal component – that would correspond in our proposal to the initial coarse subjective experience – and a mostly functionalist view of conscious experience – that would correspond in our proposal to the secondary detailed representation.

Acknowledgements

This work was supported by a grant "NonExCo" from Agence Nationale de la Recherche (ANR-BLAN-12-BSH2-0002-01). We thank the reviewers for their insightful and constructive comments.

References

Acunzo, D. J., Mackenzie, G., & van Rossum, M. C. (2012). Systematic biases in early ERP and ERF components as a result of high-pass filtering. *Journal of Neuroscience Methods*, *209*, 212–218.

Ariely, D. (2001). Seeing sets: representation by statistical properties. *Psychological Science*, *12*, 157–162.

Baars, B. J. (1997). In the theatre of consciousness: global workspace theory, a rigorous scientific theory of consciousness. *Journal of Consciousness Studies*, *4*, 292–309.

Barlasov-Ioffe, A., & Hochstein, S. (2008). Perceiving illusory contours: figure detection and shape discrimination. *Journal of Vision*, *8*(14), 11–15.

Baylis, G. C., & Rolls, E. T. (1987). Responses of neurons in the inferior temporal cortex in short term and serial recognition memory tasks. *Experimental Brain Research*, *65*, 614–622.

Biederman, I. (1972). Perceiving real-world scenes. *Science*, *177*, 77–80.

Block, N. (2007). Consciousness, accessibility, and the mesh between psychology and neuroscience. *Behavioral and Brain Sciences*, *30*, 481–499 discussion 499–548.

Boehler, C. N., Schoenfeld, M. A., Heinze, H. J., & Hopf, J. M. (2008). Rapid recurrent processing gates awareness in primary visual cortex. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 8742–8747.

van Boxtel, J. J., Tsuchiya, N., & Koch, C. (2010). Opposing effects of attention and consciousness on afterimages. *Proceedings of the National Academy of Sciences of the United States of America*, *107*, 8883–8888.

Buffalo, E. A., Fries, P., Landman, R., Liang, H., & Desimone, R.. (2010). A backward progression of attentional effects in the ventral stream. *Proceedings of the National Academy of Sciences of the United States of America*, *107*, 361–365.

Busch, N. A., Frund, I., & Herrmann, C. S. (2010). Electrophysiological evidence for different types of change detection and change blindness. *Journal of Cognitive Neuroscience*, *22*, 1852–1869.

Chalmers, D. J. (1995). Facing up to the problem of consciousness. *Journal of Consciousness Studies*, *2*, 200–219.

Chanes, L., Quentin, R., Tallon-Baudry, C., & Valero-Cabré, A. (2013). Causal frequency-specific contributions of frontal spatiotemporal patterns induced by non-invasive neurostimulation to human visual performance. *Journal of Neuroscience, 33*, 5000–5005.

Cohen, M. A., & Dennett, D. C. (2011). Consciousness cannot be separated from function. *Trends in Cognitive Sciences*, *15*, 358–364.

Cohen, M. A., Cavanagh, P., Chun, M. M., & Nakayama, K. (2012). The attentional requirements of consciousness. *Trends in Cognitive Sciences*, *16*, 411–417.

Cohen, M. X., van Gaal, S., Ridderinkhof, K. R., & Lamme, V. A. (2009). Unconscious errors enhance prefrontal-occipital oscillatory synchrony. *Frontiers in Human Neuroscience*, *3*, 54.

Crick, F., & Koch, C. (1990). Towards a neurobiological theory of consciousness. *Seminars in the Neurosciences*, *2*, 263–275.

Dehaene, S., & Naccache, L. (2001). Towards a cognitive neuroscience of consciousness: basic evidence and a workspace framework. *Cognition*, *79*, 1–37.

Dehaene, S., Sergent, C., & Changeux, J. P. (2003). A neuronal network model linking subjective reports and objective physiological data during conscious perception. *Proceedings of the National Academy of Sciences of the United States of America*, *100*, 8520–8525.

Dehaene, S., Changeux, J. P., Naccache, L., Sackur, J., & Sergent, C. (2006). Conscious, preconscious, and subliminal processing: a testable taxonomy. *Trends in Cognitive Sciences*, *10*, 204–211.

Del Cul, A., Baillet, S., & Dehaene, S. (2007). Brain dynamics underlying the nonlinear threshold for access to consciousness. *PLoS Biology*, *5*, e260.

Dennett, D. C. (1991). *Consciousness explained*. Boston, MA: Little, Brown & Co.

Di Russo, F., Martinez, A., & Hillyard, S. A. (2003). Source analysis of event-related cortical activity during visuo-spatial attention. *Cerebral Cortex*, *13*, 486–499.

Evans, K., & Treisman, A. (2005). Perception of objects in natural scenes: is it really attention free? *Journal of Experimental Psychology: Human Perception and Performance*, *31*, 1476–1492.

Foley, J. M., & Legge, G. E. (1981). Contrast detection and near-threshold discrimination in human vision. *Vision Research*, *21*, 1041–1053.

Fu, S., Huang, Y., Luo, Y., Wang, Y., Fedota, J., Greenwood, P. M., et al. (2009). Perceptual load interacts with involuntary attention at early processing stages: event-related potential studies. *NeuroImage*, *48*, 191–199.

van Gaal, S., Ridderinkhof, K. R., Fahrenfort, J. J., Scholte, H. S., & Lamme, V. A. (2008). Frontal cortex mediates unconsciously triggered inhibitory control. *Proceedings of the National Academy of Sciences of the United States of America*, *28*, 8053–8062.

Goffaux, V., Peters, J., Haubrechts, J., Schiltz, C., Jansma, B., & Goebel, R. (2011). From coarse to fine? Spatial and temporal dynamics of cortical face processing. *Cerebral Cortex*, *21*, 467–476.

Gorea, A. (1986). Temporal integration characteristics in spatial frequency identification. *Vision Research*, *26*, 511–515.

Gray, C. M., König, P., Engel, A. K., & Singer, W. (1989). Oscillatory responses in cat visual cortex exhibit inter-columnar synchronization which reflects global stimulus properties. *Nature*, *338*, 334–337.

Grill-Spector, K., & Kanwisher, N. (2005). Visual recognition: as soon as you know it is there, you know what it is. *Psychological Science*, *16*, 152–160.

Grill-Spector, K., Kushnir, T., Edelman, S., Itzchak, Y., & Malach, R. (1998). Cue-invariant activation in object-related areas of the human occipital lobe. *Neuron*, *21*, 191–202.

Grill-Spector, K., Kourtzi, Z., & Kanwisher, N. (2001). The lateral occipital complex and its role in object recognition. *Vision Research*, *41*, 1409–1422.

Haberman, J., & Whitney, D. (2009). Seeing the mean: ensemble coding for sets of faces. *Journal of Experimental Psychology: Human Perception and Performance*, *35*, 718–734.

Hesselmann, G., Hebart, M., & Malach, R. (2011). Differential BOLD activity associated with subjective and objective reports during ‘‘blindsight’’ in normal observers. *Journal of Neuroscience*, *31*, 12936–12944.

Hester, R., Foxe, J. J., Molholm, S., Shpaner, M., & Garavan, H. (2005). Neural mechanisms involved in error processing: a comparison of errors made with and without awareness. *NeuroImage*, *27*, 602–608.

Hochstein, S., & Ahissar, M. (2002). View from the top: hierarchies and reverse hierarchies in the visual system. *Neuron*, *36*, 791–804.

Hsu, S. M., George, N., Wyart, V., & Tallon-Baudry, C. (2011). Voluntary and involuntary spatial attentions interact differently with awareness. *Neuropsychologia*, *49*, 2465–2474.

Hurlburt, R. T., & Heavey, C. L. (2001). Telling what we know: describing inner experience. *Trends in Cognitive Sciences*, *5*, 400–403.

Irvine, E. (2011). Rich experience and sensory memory. *Philosophical Psychology*, *24*, 159–176.

Kanai, R., & Tsuchiya, N. (2012). Qualia. *Current Biology*, *22*, R392–R396.

Kelly, S. P., Gomez-Ramirez, M., & Foxe, J. J. (2008). Spatial attention modulates initial afferent activity in human primary visual cortex. *Cerebral Cortex*, *18*, 2629–2636.

Kentridge, R. W., Heywood, C. A., & Weiskrantz, L. (1999). Attention without awareness in blindsight. *Proceedings of the Royal Society London B: Biological Sciences*, *266*, 1805–1811.

Kentridge, R. W., Nijboer, T. C., & Heywood, C. A. (2008). Attended but unseen: visual attention is not sufficient for visual awareness. *Neuropsychologia*, *46*, 864–869.

Kimchi, R. (1992). Primacy of wholistic processing and global/local paradigm: a critical review. *Psychological Bulletin*, *112*, 24–38.

Knapen, T., Brascamp, J., Pearson, J., van Ee, R., & Blake, R. (2011). The role of frontal and parietal brain areas in bistable perception. *Journal of Neuroscience*, *31*, 10293–10301.

Koch, C., & Tsuchiya, N. (2007). Attention and consciousness: two distinct brain processes. *Trends in Cognitive Sciences*, *11*, 16–22.

Koivisto, M., Revonsuo, A., & Lehtonen, M. (2006). Independence of visual awareness from the scope of attention: an electrophysiological study. *Cerebal Cortex*, *16*, 415–424.

Koivisto, M., Kainulainen, P., & Revonsuo, A. (2009). The relationship between awareness and attention: evidence from ERP responses. *Neuropsychologia*, *47*, 2891–2899.

Koivisto, M., Railo, H., Revonsuo, A., Vanni, S., & Salminen-Vaparanta, N. (2011). Recurrent processing in V1/V2 contributes to categorization of natural scenes. *Journal of Neuroscience*, *31*, 2488–2492.

Kouider, S., de Gardelle, V., Sackur, J., & Dupoux, E. (2010). How rich is consciousness? The partial awareness hypothesis. *Trends in Cognitive Sciences*, *14*, 301–307.

Kovacs, I., Papathomas, T. V., Yang, M., & Feher, A. (1996). When the brain changes its mind: interocular grouping during binocular rivalry. *Proceedings of the National Academy of Sciences of the United States of America*, *93*, 15508–15511.

Lamme, V. A. (2003). Why visual attention and awareness are different. *Trends in Cognitive Sciences*, *7*, 12–18.

Lamme, V. A. (2006). Towards a true neural stance on consciousness. *Trends in Cognitive Sciences*, *10*, 494–501.

Lamme, V. A. (2010). How neuroscience will change our view on consciousness. *Cognitive Neuroscience*, *1*, 204–220.

Lamme, V. A., & Roelfsema, P. R. (2000). The distinct modes of vision offered by feedforward and recurrent processing. *Trends in Neurosciences*, *23*, 571–579.

Lamme, V. A., RodriguezRodriguez, V., & Spekreijse, H. (1999). Separate processing dynamics for texture elements, boundaries and surfaces in primary visual cortex of the macaque monkey. *Cerebral Cortex*, *9*, 406–413.

Lau, H. C. (2008). Are we studying consciousness yet. *Frontiers of Consciousness: Chichele Lectures*, 245–258.

Lau, H. C., & Passingham, R. E. (2006). Relative blindsight in normal observers and the neural correlate of visual consciousness. *Proceedings of the National Academy of Sciences of the United States of America*, *103*, 18763–18768.

Lau, H. C., & Passingham, R. E. (2007). Unconscious activation of the cognitive control system in the human prefrontal cortex. *Journal of Neuroscience*, *27*, 5805–5811.

Lee, J., Williford, T., & Maunsell, J. H. (2007). Spatial attention and the latency of neuronal responses in macaque area V4. *Journal of Neuroscience*, *27*, 9632–9637.

Li, F. F., VanRullen, R., Koch, C., & Perona, P. (2002). Rapid natural scene categorization in the near absence of attention. *Proceedings of the National Academy of Sciences of the United States of America*, *99*, 9596–9601.

Liu, H., Agam, Y., Madsen, J. R., & Kreiman, G. (2009). Timing, timing, timing: fast decoding of object information from intracranial field potentials in human visual cortex. *Neuron*, *62*, 281–290.

Liu, Y., Paradis, A. L., Yahia-Cherif, L., & Tallon-Baudry, C. (2012). Activity in the lateral occipital cortex between 200 and 300 ms distinguishes between physically identical seen and unseen stimuli. *Frontiers in Human Neuroscience*, *6*, 211.

Logothetis, N. K., & Sheinberg, D. L. (1996). Visual object recognition. *Annual Review of Neuroscience*, *19*, 577–621.

Luck, S. J., Chelazzi, L., Hillyard, S. A., & Desimone, R. (1997). Neural mechanisms of spatial selective attention in areas V1, V2, and V4 of macaque visual cortex. *Journal of Neurophysiology*, *77*, 24–42.

Luck, S. J., Woodman, G. F., & Vogel, E. K. (2000). Event-related potential studies of attention. *Trends in Cognitive Sciences*, *4*, 432–440.

Mace, M. J., Joubert, O. R., Nespoulous, J. L., & Fabre-Thorpe, M. (2009). The time-course of visual categorizations: you spot the animal faster than the bird. *PLoS One*, *4*, e5927.

Martinez, A., AnlloVento, L., Sereno, M. I., Frank, L. R., Buxton, R. B., Dubowitz, D J, et al. (1999). Involvement of striate and extrastriate visual cortical areas in spatial attention. *Nature Neuroscience*, *2*, 364–369.

Mehta, S. D., Ulbert, I., & Schroeder, C. E. (2000). Intermodal selective attention in monkeys. I: Distribution and timing of effects across visual areas. *Cerebral Cortex*, *10*, 343–358.

Nagel, T. (1974). What is it like to be a bat? *The Philosophical Review*, *83*, 435–450.

Navon, D. (1977). Forest before trees: the precedence of global features in visual perception. *Cognitive Psychology*, *9*, 353–383.

Noesselt, T., Hillyard, S. A., Woldorff, M. G., Schoenfeld, A., Hagner, T., Jancke, L, et al. (2002). Delayed striate cortical activation during spatial attention. *Neuron*, *35*, 575–587.

Norman, L., Heywood, C., & Kentridge, R. (in press). *Object-based attention without awareness*.

Oliva, A., & Torralba, A. (2006). Building the gist of a scene: the roles of global image features in recognition. *Progress in Brain Research*, *155*, 23–36.

Overgaard, M., Nielsen, J. F., & Fuglsang-Frederiksen, A. (2004). A TMS study of the ventral projections from V1 with implications for the finding of neural correlates of consciousness. *Brain and Cognition*, *54*, 58–64.

O'Regan, J. K., & Noe, A. (2001). A sensorimotor account of vision and visual consciousness. *Behavioral and Brain Sciences*, *24*, 939–973 discussion 973-1031.

Parkes, L., Lund, J., Angelucci, A., Solomon, J. A., & Morgan, M. (2001). Compulsory averaging of crowded orientation signals in human vision. *Nature Neuroscience*, *4*, 739–744.

Pascual-Leone, A., & Walsh, V. (2001). Fast backprojections from the motion to the primary visual area necessary for visual awareness. *Science*, *292*, 510–512.

Poghosyan, V., & Ioannides, A. A. (2008). Attention modulates earliest responses in the primary auditory and visual cortices. *Neuron*, *58*, 802–813.

Poort, J., Raudies, F., Wannig, A., Lamme, V. A., Neumann, H., & Roelfsema, P. R. (2012). The role of attention in figure-ground segregation in areas V1 and V4 of the visual cortex. *Neuron*, *75*, 143–156.

Posner, M. I. (1994). Attention: the mechanisms of consciousness. *Proceedings of the National Academy of Sciences of the United States of America*, *91*, 7398–7403.

Posner, M. I. (2012). Attentional networks and consciousness. *Frontiers in Psychology*, *3*, 64.

Ratcliff, R. (1978). A theory of memory retrieval. *Psychological Review*, *85*, 59–108.

Rensink, R. A. (2002). Change detection. *Annual Review of Psychology*, *53*, 245–277.

Ress, D., & Heeger, D. J. (2003). Neuronal correlates of perception in early visual cortex. *Nature Neuroscience*, *6*, 414–420.

Roelfsema, P. R., Lamme, V. A. F., & Spekreijse, H. (1998). Object-based attention in the primary visual cortex of the macaque monkey. *Nature*, *395*, 376–381.

Rolls, E. T., Aggelopoulos, N. C., & Zheng, F. (2003). The receptive fields of inferior temporal cortex neurons in natural scenes. *Journal of Neuroscience*, *23*, 339–348.

Sahraie, A., Hibbard, P. B., Trevethan, C. T., Ritchie, K. L., & Weiskrantz, L. (2010). Consciousness of the first order in blindsight. *Proceedings of the National Academy of Sciences of the United States of America*, *107*, 21217–21222.

Sampanes, A. C., Tseng, P., & Bridgeman, B. (2008). The role of gist in scene recognition. *Vision Research*, *48*, 2275–2283.

Sandberg, K., Timmermans, B., Overgaard, M., & Cleeremans, A. (2010). Measuring consciousness: is one measure better than the other? *Consciousness and Cognition*, *19*, 1069–1078.

Schmolesky, M. T., Wang, Y. C., Hanes, D. P., Thompson, K. G., Leutgeb, S., Schall, J. D., et al. (1998). Signal timing across the macaque visual system. *Journal of Neurophysiology*, *79*, 3272–3278.

Schurger, A., Cowey, A., & Tallon-Baudry, C. (2006). Induced gamma-band oscillations correlate with awareness in hemianopic patient GY. *Neuropsychologia*, *44*, 1796–1803.

Schurger, A., Cowey, A., Cohen, J. D., Treisman, A., & Tallon-Baudry, C. (2008). Distinct and independent correlates of attention and awareness in a hemianopic patient. *Neuropsychologia*, *46*, 2189–2197.

Schurger, A., Pereira, F., Treisman, A., & Cohen, J. D. (2010). Reproducibility distinguishes conscious from nonconscious neural representations. *Science*, *327*, 97–99.

Schwarzkopf, D. S., & Rees, G. (2011). Interpreting local visual features as a global shape requires awareness. *Proceedings of the Royal Society London B: Biological Sciences*, *278*, 2207–2215.

Schwiedrzik, C. M., Singer, W., & Melloni, L. (2011). Subjective and objective learning effects dissociate in space and in time. *Proceedings of the National Academy of Sciences of the United States of America*, *108*, 4506–4511.

Sergent, C., Wyart, V., Babo-Rebelo, M., Cohen, L., Naccache, L., & Tallon-Baudry, C. (2013). Cueing attention after the stimulus is gone can retrospectively trigger conscious perception. *Current Biology*, *23*, 150–155.

Serre, T., Oliva, A., & Poggio, T. (2007). A feedforward architecture accounts for rapid categorization. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 6424–6429.

Seth, A. K., Dienes, Z., Cleeremans, A., Overgaard, M., & Pessoa, L. (2008). Measuring consciousness: relating behavioural and neurophysiological approaches. *Trends in Cognitive Sciences*, *12*, 314–321.

Silvanto, J., Lavie, N., & Walsh, V. (2005). Double dissociation of V1 and V5/MT activity in visual awareness. *Cerebral Cortex*, *15*, 1736–1741.

Simons, D. J., & Levin, D. T. (1997). Change blindness. *Trends in Cognitive Sciences*, *1*, 261–267.

Sperling, G. (1960). The information available in brief visual presentations. *Psychological Monographs: General and Applied*, *74*, 1–30.

Sumner, P., Nachev, P., Morris, P., Peters, A. M., Jackson, S. R., Kennard, C., et al. (2007). Human medial frontal cortex mediates unconscious inhibition of voluntary action. *Neuron*, *54*, 697–711.

Super, H., Spekreijse, H., & Lamme, V. A. F. (2001). Two distinct modes of sensory processing observed in monkey primary visual cortex (V1). *Nature Neuroscience*, *4*, 304–310.

Swets, J., Tanner, W. P., Jr., & Birdsall, T. G. (1961). Decision processes in perception. *Psychological Review*, *68*, 301–340.

Tallon-Baudry, C. (2012). On the neural mechanisms subserving consciousness and attention. *Frontiers in Psychology*, *2*, 397.

Tanaka, K. (1996). Inferotemporal cortex and object vision. *Annual Review of Neuroscience*, *19*, 109–139.

Tarokh, L. (2009). *EEG oscillations induced by contour closure in a noisy visual field*, *196*, 55–62.

Thomas, J. P. (1985). Effect of static-noise and grating masks on detection and identification of grating targets. *Journal of the Optical Society of America A*, *2*, 1586–1592.

Thorpe, S., Fize, D., & Marlot, C. (1996). Speed of visual processing in the human visual system. *Nature*, *381*, 520–522.

Tong, F. (2003). Primary visual cortex and visual awareness. *Nature Reviews Neuroscience*, *4*, 219–229.

Tong, F., Nakayama, K., Vaughan, J. T., & Kanwisher, N. (1998). Binocular rivalry and visual awareness in human extrastriate cortex. *Neuron*, *21*, 753–759.

Tononi, G., & Edelman, G. E. (1998). Consciousness and complexity. *Science*, *282*, 1846–1851.

Torralba, A., Oliva, A., Castelhano, M. S., & Henderson, J. M. (2006). Contextual guidance of eye movements and attention in real-world scenes: the role of global features on object search. *Psychological Review*, *113*, 766–786.

Tse, P. U., Martinez-Conde, S., Schlegel, A. A., & Macknik, S. L. (2005). Visibility, visual awareness, and visual masking of simple unattended targets are confined to areas in the occipital cortex beyond human V1/V2. *Proceedings of the National Academy of Sciences of the United States of America*, *102*, 17178–17183.

Tsubomi, H., Ikeda, T., Hanakawa, T., Hirose, N., Fukuyama, H., & Osaka, N. (2012). Dissociable neural activations of conscious visibility and attention. *Journal of Cognitive Neuroscience*, *24*, 496–506.

Vidyasagar, T. R. (1998). Gating of neuronal responses in macaque primary visual cortex by an attentional spotlight. *NeuroReport*, *9*, 1947–1952.

Watson, A. B., & Robson, J. G. (1981). Discrimination at threshold: labelled detectors in human vision. *Vision Research*, *21*, 1115–1122.

Weiskrantz, L., Barbur, J. L., & Sahraie, A. (1995). Parameters affecting conscious versus unconscious visual discrimination with damage to the visual cortex (V1). *Proceedings of the National Academy of Sciences of the United States of America*, *92*, 6122–6126.

Wilimzig, C., Tsuchiya, N., Fahle, M., & Koch, C. (2008). Spatial attention increases performance but not subjective confidence in a discrimination task. *Journal of Vision*, *8*, 1–10.

Wokke, M. E., Vandenbroucke, A. R. E., Scholte, H. S., & Lamme, V. A. (2013). Confuse your illusion: feedback to early visual cortex contributes to perceptual completion. *Psychological Science*, *24*, 63–71.

Wyart, V., & Tallon-Baudry, C. (2008). A neural dissociation between visual awareness and spatial attention. *Journal of Neuroscience*, *28*, 2667–2679.

Wyart, V., & Tallon-Baudry, C. (2009). How ongoing fluctuations in human visual cortex predict perceptual awareness: baseline shift versus decision bias. *Journal of Neuroscience*, *29*, 8715–8725.

Wyart, V., Dehaene, S., & Tallon-Baudry, C. (2012). Early dissociation between neural signatures of endogenous spatial attention and perceptual awareness during visual masking. *Frontiers in Human Neuroscience*, 6.

Zhang, X., Zhaoping, L., Zhou, T., & Fang, F. (2012). Neural activities in V1 create a bottom-up saliency map. *Neuron*, *73*, 183–192.

de Gardelle, V., Sackur, J., & Kouider, S. (2009). Perceptual illusions in brief visual presentations. *Consciousness and Cognition*, *18*, 569–577.