Consciousness and Cognition 80 (2020) 102917

Contents lists available at ScienceDirect

Consciousness and Cognition

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

ERP and MEG correlates of visual consciousness: The second decade[☆]

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ARTICLE INFO

Keywords:
Neural correlates of consciousness
Event-related potentials
Event-related fields
Visual awareness negativity
Late positivity
Global Neuronal Workspace theory
Recurrent processing theory

ABSTRACT

The first decade of event-related potential (ERP) research had established that the most consistent correlates of the onset of visual consciousness are the early visual awareness negativity (VAN), a posterior negative component in the N2 time range, and the late positivity (LP), an anterior positive component in the P3 time range. Two earlier extensive reviews ten years ago had concluded that VAN is the earliest and most reliable correlate of visual phenomenal consciousness, whereas LP probably reflects later processes associated with reflective/access consciousness. This article provides an update to those earlier reviews. ERP and MEG studies that have appeared since 2010 and directly compared ERPs between aware and unaware conditions are reviewed, and important new developments in the field are discussed. The result corroborates VAN as the earliest and most consistent signature of visual phenomenal consciousness, and casts further doubt on LP as an ERP correlate of phenomenal consciousness.

1. Introduction

In the 21st century, consciousness remains one of the most exciting and, at the same time, most elusive topics in science. Ever since consciousness became a respectable topic in the late 1980s (Baars, 1988), the dominating approach has been the search for the "neural correlates of consciousness" (NCCs), that is (roughly), the set of neural populations and activities in the brain that are minimally sufficient for bringing about consciousness.

The scope of this article is restricted to electro- and magnetophysiological correlates of *visual* consciousness. Visual consciousness (or, synonymously, visual awareness), is the most prominent "model system" for the empirical study of consciousness, mostly because the visual system is one of the best-studied parts of the central nervous system, and because "the visual input is often highly structured yet easy to control" (Crick & Koch, 1998, p. 97; see also Crick & Koch, 1990; Revonsuo, 2006, p. 74). The standard technique is to present a participant with a visual stimulus and then have her report whether or not she has consciously perceived it. In the past decades, a number of ingenious methods have been developed which allow the researcher to establish a "minimal contrast" (Dehaene, 2014, p. 26) between "seen" (in the sense of "consciously perceived") and "unseen" stimuli. The general strategy for producing "seen" and "unseen" conditions is to vary the presented physical stimulus as minimally as possible—ideally, to keep it physically constant near the threshold of awareness—while generating differences only in subjective awareness of the stimulus. For example, in *backward masking*, a different, often nonsensical, stimulus is presented shortly after the target stimulus (Bachmann &

☆ This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.
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https://doi.org/10.1016/j.concog.2020.102917
Received 28 November 2019; Received in revised form 14 February 2020; Accepted 7 March 2020

Francis, 2013). If applied at the right time, this has the effect of decreasing the visibility of the target or rendering it invisible to the participant (for an overview over different kinds of masking, see Bachmann and Francis, 2013, p. 4). Transcranial magnetic stimulation (TMS) can, in effect, also be used as a masking technique (for review, see de Graaf, Koivisto, Jacobs, & Sack, 2014). Alternatively, the stimulus can be presented in *low contrast* so that it is seen in about half of the trials and unseen in the other half (for review of these and other common methods of achieving minimal contrasts, see Dehaene & Changeux, 2011, p. 201).

Using these methods in combination with brain imaging and other measures of brain function, the NCCs can be investigated. The underlying reasoning is that the physical similarity (or, ideally, identity) of the stimuli in seen and unseen trials should minimize (or even eliminate) the differences in preconscious sensory processes and leave only the difference between conscious and nonconscious processing for brain imaging to detect. Combining the strengths of methods such as functional magnetic resonance imaging (fMRI) and electroencephalographic (EEG) event-related potentials (ERP), and integrating constraints from anatomical, neuropsychological, computational, and other investigations, it is possible to theorize about the NCCs, and this has led to a burgeoning empirical literature.

One old but still ongoing empirical controversy in this field concerns the proper electrophysiological signature of the onset of consciousness. Some groups of researchers suggest that an ERP component called the P3, which occurs relatively late (about 300 ms after stimulus onset) embodies this signature (e.g., Dehaene, 2014; Del Cul, Baillet, & Dehaene, 2007; Lamy, Salti, & Bar-Haim, 2008; Salti, Bar-Haim, & Lamy, 2012), while other groups have found earlier signatures, the most consistently observed of which is called "visual awareness negativity" (or VAN for short), arising already after about 200 ms (Koivisto & Revonsuo, 2010). The VAN and P3 will be described in detail below, in Sections 2.3.1 and 2.3.2.

This article focuses on the "early" vs. "late" controversy. Section 2 introduces some important conceptual distinctions and the most relevant background theories, and presents the controversy in more detail. Section 3 provides a comprehensive review of ERP and magnetoencephalography (MEG) studies on visual awareness of the past decade. A number of subsections highlight important empirical, methodological, and conceptual developments that currently shape the field. Section 4 summarizes the results of the previous sections and relates them to the conceptual and theoretical questions outlined in Section 2.

2. Preliminaries: concepts, theories, and the "early" vs. "late" debate

2.1. Concepts of consciousness

Any science of consciousness should be as clear as possible about what it is talking about, since "[o]ur philosophical commitments tend to guide the empirical science we make" (Revonsuo, 2006, p. 138)—even if they remain implicit. One of the most central and momentous distinctions is that between *phenomenal consciousness* and *access consciousness*, first introduced by Block (1995). "Phenomenal consciousness" refers to subjective experience, the "what-it-is-like"-ness (Nagel, 1974) of our every sensation and thought. Owing to its private nature (everyone experiences it, but no one can directly know anything about *others'* experience), phenomenal consciousness seems at the same time indubitable and difficult to tract scientifically. The standard way to establish its presence in experimental contexts is to rely on subjects' reports on whether and what they have experienced, but recently, so-called no-report paradigms (see Section 3.2.4) have been explored as well (Tsuchiya, Wilke, Frässle, & Lamme, 2015). "Access consciousness", or "reflective consciousness", as some authors—including us—prefer to call it (Koivisto & Revonsuo, 2010; Railo, Koivisto, & Revonsuo, 2011; Revonsuo, 2006), does not refer to subjective experience at all, but rather to a system's central access to information, which then "can be used to control reasoning and behavior" (Block, 1995, p. 229). It is defined by Block as a purely cognitive, information-processing notion, and as such it is arguably possible even in systems that lack all phenomenal consciousness. However, some empirical scientists equate these two notions of consciousness and identify consciousness with global access to information (see Section 2.2). This article is primarily concerned with the subjective aspect of experience, and hence with *phenomenal* consciousness—even if it should eventually turn out to be identical with reflective/access consciousness.

Another important distinction is that between the *state* (or *level*) of consciousness and the *contents* of consciousness (e.g. Hohwy, 2009; Koch, Massimini, Boly, & Tononi, 2016a). On the one hand, there is a difference between various states of consciousness (such as coma, the vegetative state, and the fully conscious wakeful state) that can be arranged on a continuum of different levels of awareness (e.g. Di Perri et al., 2014; Laureys, 2005). On the other hand, there are differences between the contents of consciousness *within* each state that can count as at least minimally conscious. Normally, our ever-changing subjective visual experience features a multitude of different qualities, objects, and scenes—i.e., of different contents. The search for NCCs can focus on either of these two aspects of consciousness; accordingly, Koch et al. (2016a, p. 308) distinguish between the "full NCC" and the "content-specific NCC". Of course, the two aspects are interrelated: for example, a minimally conscious patient presumably enjoys only a greatly reduced form of subjective experience. This entanglement raises some methodological issues, the implications of which have recently been discussed by a number of authors (Aru, Bachmann, Singer, & Melloni, 2012; Bachmann & Hudetz, 2014; Hohwy, 2009). However, since the majority of studies pertaining to the "early" vs. "late" debate have focused on the contents of consciousness and consequently on the content-specific NCCs, and have experimented only with healthy, awake, fully conscious subjects, we ignore these complications here and focus exclusively on the contents of visual consciousness, assuming a "normal" state of alert, conscious wakefulness.

Even with this restriction in place, the concept of NCCs raises some issues worthy of consideration. Presumably, conscious processing has both *prerequisites* and *consequences* (Aru et al., 2012; de Graaf, Hsieh, & Sack, 2012), that is, there are processes that regularly, or even necessarily, precede conscious perception, and others that follow it. Now if the task is to isolate the NCC proper, rather than the correlates of these various processes, it is absolutely crucial to control for such confounds. A prime example of a confounding process are the varieties of attention (Koch & Tsuchiya, 2007, 2012); another one are the processes associated with subjects' reports about their awareness (or lack thereof). These and other confounds will be discussed in Section 3 below.

A final clarification is in place: most of the research on the content-specific NCC, and in particular electrophysiological research, tries to find the correlates of the *onset* of consciousness, that is, the moment when a given content first becomes conscious. This is hardly ever made explicit; a rare exception is the study by Andersen, Pedersen, Sandberg, and Overgaard (2016), who distinguish the "becoming conscious" of a stimulus from its "remaining conscious", and clearly state that they are interested in the former. Of course, a precise moment in time when a stimulus suddenly becomes conscious is an—albeit useful—abstraction, and there is also an important tradition studying the "microgenesis" of consciousness (Bachmann, 2000; see also Salti, Harel, & Marti, 2019, for a recent perspective on this matter). This is not unrelated to the question of different degrees of consciousness, which will be discussed in detail in Section 3.2.7.

2.2. Relevant empirical theories of consciousness

The two most relevant empirical theories in the context of the "early" vs. "late" debate are the "Global Neuronal Workspace" theory (Dehaene, 2014; Dehaene & Changeux, 2011; Dehaene, Kerszberg, & Changeux, 1998; Dehaene & Naccache, 2001) and the "Recurrent Processing" theory (Lamme, 2000, 2006, 2010a; Lamme & Roelfsema, 2000). This is because they are the empirical theories that make the most detailed predictions as to *when* consciousness should arise in the brain. Both are briefly introduced in the following two subsections. There are, of course other theories of consciousness, such as "microconsciousness" theory (Zeki & Bartels, 1999), "higher-order thought" (HOT) theories (Gennaro, 2018; Lau & Rosenthal, 2011), and the "information integration" theory (IIT) of consciousness (Tononi, 2004). In our view, however, these theories are more difficult to evaluate in terms of the "early" vs. "late" debate, and therefore we chose to ignore them for the purposes of this review.

2.2.1. The Global Neuronal Workspace Theory

The Global Neuronal Workspace theory (GNWT) is a neuroscientifically updated version of the older, purely cognitive "Global Workspace theory" (Baars, 1988). According to GNWT, consciousness arises when the outputs of multiple specialized neuro-cognitive processes gain access to a dedicated "workspace" system that distributes them so that they become globally available to the organism; indeed, "[a]ccording to this theory, consciousness is just brain-wide information sharing" (Dehaene, 2014, p. 165). This "broadcasting", and hence consciousness, is required by a number of higher cognitive processes, such as "durable and explicit information maintenance, novel combinations of operations, and intentional behavior" (Dehaene & Naccache, 2001, p. 9). Anatomically, the workspace system is thought to consist of long-distance connections distributed throughout and across prefrontal and parietal brain regions, predominantly arising from pyramidal neurons in cortical layers II and III, and additionally involving "the nonspecific thalamic nuclei, the basal ganglia, and some cortical nodes" (Dehaene & Changeux, 2011, p. 214). Crucially, in order to get access to the workspace system, inputs must cross a threshold for "ignition", and this requires that they be selected by attention. According to GNWT, attention is thus "a necessary prerequisite for conscious perception" (Dehaene & Naccache, 2001, p. 8). It follows that the onset of consciousness cannot occur prior to the operations of attentional processes, and not before large-scale activation of the fronto-parietal workspace regions has occurred. This suggests the prediction that the earliest physiological correlates of consciousness should have a relatively large latency relative to stimulus onset—and indeed, the proponents of GNWT tend to regard the P3b component, which begins approximately 300–500 ms post stimulus, as the earliest ERP signature of consciousness (e.g., Dehaene, 2014; Dehaene & Changeux, 2011). In the "early" vs. "late" debate, GNWT is thus clearly on the "late" side. Another important prediction the theory makes is that the sudden "ignition" that occurs beyond threshold should manifest itself in a non-linear increase of the ERP signature of consciousness, an "all-or-none" pattern which has indeed been found by a number of studies (Del Cul et al., 2007; Sergent, Baillet, & Dehaene, 2005; Sergent & Dehaene, 2004).

2.2.2. The Recurrent Processing theory

The Recurrent Processing theory (RPT) was developed mainly by Victor Lamme (Lamme, 2000, 2006, 2010a; Lamme & Roelfsema, 2000). Its main tenet is that purely feedforward activity in the brain is not sufficient for consciousness, but that feedback activity, or "recurrent processing" from "higher" to "lower" areas in the brain is necessary for awareness to occur. When a stimulus is presented to the visual system, it causes activation that spreads from the retina via the lateral geniculate nucleus of the thalamus to the primary visual cortex (V1), and from there to other cortical visual and motor areas, up to the most prefrontal areas. This forward spread of activation throughout the brain is completed within 100–150 ms after stimulus presentation, and is called the "fast feedforward sweep" (FFS) by Lamme. Already the FFS "enables a rapid extraction of complex and meaningful features from the visual scene, and lays down potential motor responses to act on the incoming information" (Lamme, 2006, p. 497). However, as soon as the feedforward activity reaches a given area, activation also spreads back to lower areas via feedback connections; and according to RPT, it is only during this recurrent processing that visual awareness of the stimulus can arise. Indeed, Lamme (2006, p. 499, italics in original) states that "[w]e could even *define* consciousness as recurrent processing." In the latest formulation of his theory, Lamme distinguishes four stages of visual neural processing (Lamme, 2010a). Both the FFS and recurrent processing are subdivided into "superficial" and "deep" (or "widespread") stages. This subdivision is intended to capture the dimension of attention: only attended stimuli reach the "deep" stages of either feedforward or recurrent processing and make it to the higher levels of the visual hierarchy, while both unattended and attended stimuli reach awareness, provided that there is recurrent processing, be it superficial or deep. In other words, the dimension of attention is orthogonal to that of awareness, and both attention and awareness can occur independently of each other. Thus, unlike in GNWT, attention is *not* a necessary prerequisite for awareness in RPT. And since recurrent processing does not have to wait until the FFS is completed, but begins as soon as the latter has reached the first areas that feature feedback connections, RPT predicts an "early" onset of consciousness, and situates itself accordingly in the "early" vs. "late" debate.

2.3. The "early" vs. "late" debate in the context of the science of consciousness

As the preceding discussion indicates, the "early" vs. "late" debate does not occur in a vacuum. The question of timing is systematically related to that of location. While neither theory strictly localizes consciousness in any particular area of the brain, GNWT stresses the crucial importance of frontally and parietally located areas in the process of "broadcasting", while according to RPT, consciousness arises already with the occurrence of relatively local, occipito-temporal recurrent processing. Moreover, while not devoid of intrinsic interest, the answers to the "where" and "when" questions are ultimately instrumental in determining the answers to the far more interesting and vexing "hard" questions (Chalmers, 2007) of why and how consciousness arises in and from the brain. Note that RPT does not address these questions (it does not tell us why and how consciousness should arise from recurrent processing), and that GNWT answers them only at the price of identifying phenomenal consciousness with certain cognitive operations that seem to have no necessary connection to it. Nevertheless, if these problems are to find an answer at all, the search for the NCC, if successful, will probably make an important contribution to it. The rest of this section introduces the opposing positions and the ERP correlates at stake in some more detail. It should also be noted from the outset that the neat mapping of the "early" position on RPT and the "late" position on GNWT, while roughly true and certainly tempting, is really a simplification. In Section 4, their relationship is discussed in a more nuanced way.

The "early" vs. "late" controversy has largely focused on two candidates for ERP correlates of visual consciousness: the visual awareness negativity in the N2 time range, and the P3, to be introduced in the upcoming sections. It should be noted, however, that some researchers used to defend a third, "very early", position in the debate. A fraction of the ERP studies reviewed by Koivisto and Revonsuo (2010) had identified an enhanced P1 component around 100 ms as correlated with awareness. However, many studies have failed to find awareness-related P1, and those that did were usually open to attention and arousal confounds (Railo et al., 2011). By now, even the Estonian researcher Talis Bachmann and his research group, who used to be the most outspoken proponents of the "very early" view (Aru & Bachmann, 2009; Bachmann, 2009), have abandoned that position (Rutiku, Aru, & Bachmann, 2016; Rutiku & Bachmann, 2017; Rutiku, Martin, Bachmann, & Aru, 2015), and now hold "that such early responses do not seem to be markers of direct conscious perception of near-threshold stimuli" (Rutiku et al., 2016). It seems, then, that the case on the "very early" position in the debate is closed with a negative answer.

2.3.1. The "early" component: visual awareness negativity

Early on, the research group of Mika Koivisto and Antti Revonsuo had, over the course of several experiments, consistently identified a negative deflection around 200 ms after stimulus onset in the ERPs for conditions in which the subjects were aware of the presented stimuli, when compared to the ERPs for conditions in which they were not. This ERP difference can elegantly be visualized in a so-called difference wave (the waveform that results when the ERP elicited in the "aware" condition is subtracted from the ERP in the "unaware" condition; see Fig. 1), and has been termed the "visual awareness negativity" (or VAN) (Koivisto & Revonsuo, 2003; Ojanen, Revonsuo, & Sams, 2003; Wilenius-Emet, Revonsuo, & Ojanen, 2004). The VAN is typically observed over posterior scalp electrode sites, in particular occipital and posterior temporal ones (see Fig. 2), and its amplitude is considerably stronger over the hemisphere contralateral to the side of the visual field where the stimulus is presented (Eklund & Wiens, 2018; Koivisto & Grassini, 2016). There are relatively few attempts to localize the cortical generators of the VAN; no doubt this is partly because EEG is notoriously ill-suited for localizing the origins of the waveforms it detects. MEG permits slightly more reliable source reconstructions. An early MEG study identified awareness-related activity in the right lateral occipital cortex, indicating that VAN may be generated along the ventral visual stream (Vanni, Revonsuo, Saarinen, & Hari, 1996); consistent with this result, a newer MEG study found

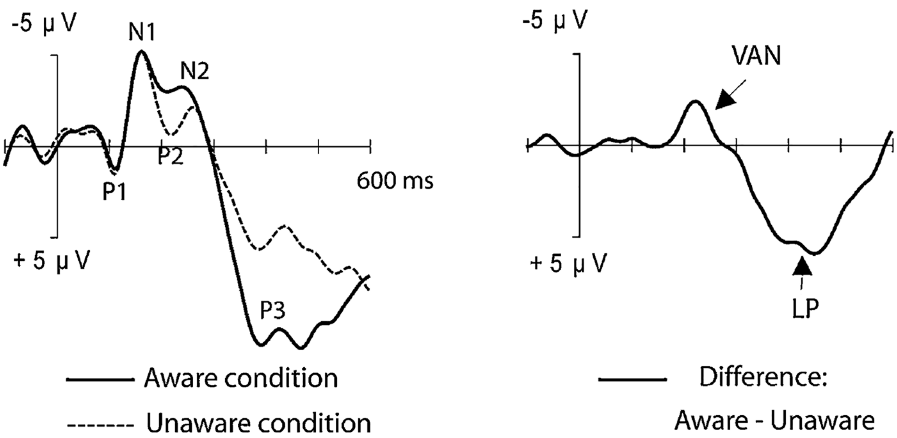

Fig. 1. Left: the typical time course of ERPs over occipital sites in response to a visual stimulus; right: the difference wave resulting from subtraction of the unaware from the aware condition. Reprinted from Neuroscience and Biobehavioral Reviews 34, Koivisto & Revonsuo, Event-related potential correlates of visual awareness, p. 923, 2010, with permission from Elsevier.

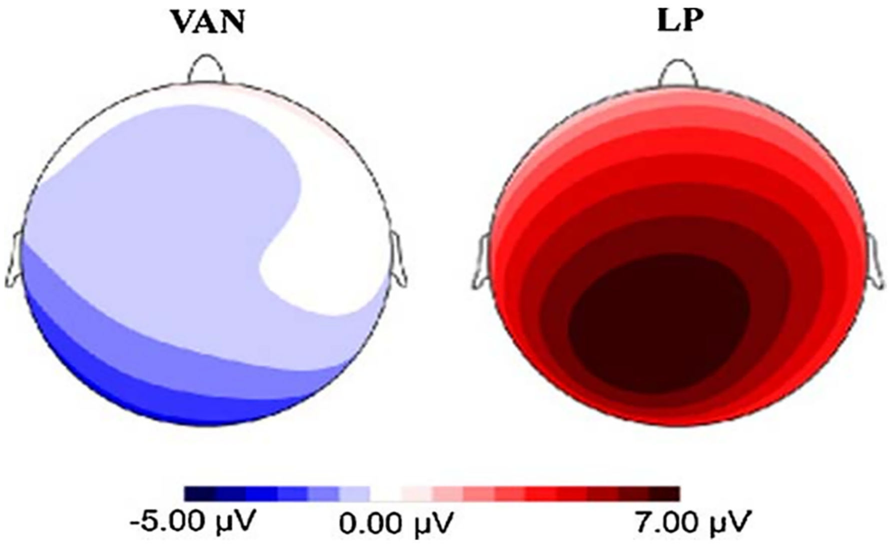

Fig. 2. Typical scalp distribution of the VAN and LP components. Reprinted from Neuroscience and Biobehavioral Reviews 34, Koivisto & Revonsuo, Event-related potential correlates of visual awareness, p. 928, 2010, with permission from Elsevier.

posterior activity between 190 and 350 ms "bilaterally on the lateral convexity of the occipito-temporal region, in the Lateral Occipital (LO) complex, as well as in the right posterior infero-temporal region" (Liu, Paradis, Yahia-Cherif, & Tallon-Baudry, 2012). Similarly, in a source reconstruction on the data of an ERP experiment on awareness (Koivisto, Kainulainen, & Revonsuo, 2009) with low resolution electromagnetic tomography (LORETA), Koivisto and Revonsuo found "that contralateral occipital and temporal lobes were sensitive to the manipulation of awareness" (Koivisto & Revonsuo, 2010, p. 931); and another group, using local autoregressive averaging (LAURA), again identified the lateral-occipital complex in the ventral stream as the source of VAN (Pitts, Martínez, & Hillyard, 2011). The converging evidence from different source localization techniques, performed over data from a variety of experiments using different paradigms, permits a relatively confident judgment as to the occipito-temporal origin of the VAN.

Regarding the timing of VAN, the 200 ms are a rough value; more precisely, the *onset* of VAN (i.e., the earliest time point when the ERP of the "aware" condition becomes different from that of the "unaware" condition) often begins already after 100 ms, while its *peak latency* usually lies between 200 and 250 ms post-stimulus, in the N1-N2 latency range. Under some conditions, considerably later VAN onset and peak latencies have also been observed (Koivisto & Revonsuo, 2010); this often happens in studies using low-contrast stimuli (Wilenius & Revonsuo, 2007) and, more generally, low stimulus visibility (Railo & Koivisto, 2009b). In many studies by other research groups, the VAN has been called "N2", because it occurs during the second large negative deflection visible in the ERP. Several other ERP components regularly occur in the N1-N2 time range under certain conditions, such as the face-related N170, the attention-related N2pc and selection negativity (SN), and the reversal negativity (RN), which is associated with perceptual reversals during bistable perception (Koivisto & Revonsuo, 2010). The term "visual awareness negativity" is intended to refer to only the part of the N2 that is specifically related to visual awareness. Evidently, it is of great importance to experimentally isolate the VAN from all the other N2 components, and thereby to confirm that it is not a prerequisite of consciousness, or some regularly co-occurring process. For a while, Pitts and colleagues in the USA preferred to refer to the "N2", because they felt that this isolation had not yet been achieved to a sufficient degree (Pitts et al., 2011; Pitts, Padwal, Fennelly, Martínez, & Hillyard, 2014); however, in spite of persisting doubts, by now they have adopted the term "VAN" (Pitts, Metzler, & Hillyard, 2014; Shafto & Pitts, 2015). Notably, early research on "perceptual closure", the process of object identification based on incomplete information, had revealed a component strikingly similar to the VAN in just about every respect (except that it was not lateralized, which is not surprising given that the stimuli were always presented in the center of the visual field), which the authors termed "closure-related negativity", or N_{CL} (Doniger et al., 2000, 2001; Sehatpour, Molholm, Javitt, & Foxe, 2006). These studies used ERP contrasts of complete objects with objects that were scrambled to various degrees, very similar to some of the studies mentioned above (Ojanen et al., 2003; Vanni et al., 1996; Wilenius-Emet et al., 2004). The N_{CL} amplitude was greatest when objects were identified, but "it was also modulated at levels of object fragmentation preceding explicit identification. As such, it was clearly related to object processing rather than identification itself" (Sehatpour et al., 2006, p. 614). Thus, it seems no stretch to state that in all likelihood, the VAN and the N_{CL} are overlapping to a large degree, or perhaps even identical.

2.3.2. The "late" component: P3/LP

The second candidate for an awareness-related ERP component is the P3 (i.e., the third positive peak clearly visible in the ERP), often also called the "P300" (because it peaks around 300 ms after stimulus onset). More precisely, the candidate is the *difference* in P3 amplitude between aware and unaware conditions (the amplitude is typically greater in aware conditions), often called the "late positivity" (or LP; see Fig. 1). Like the N2, the P3 in fact denotes a whole family of components occurring in the same time range, each of which occurs under specific conditions (and fails to occur under others). Although the P3 was discovered already more than

50 years ago, both its cerebral origins and the function or functions it reflects have not been clearly determined. It has become clear, however, that the P3 reflects several different cognitive processes, and therefore in all likelihood has multiple cerebral sources (Picton, 1992; Polich, 2007). A clear distinction can be made between a P3a component with a frontal scalp distribution, peaking around 250 ms after stimulus onset, and more posterior P3b component which peaks around 350 ms (Picton, 1992). A LORETA study localized the P3a generators "in cingulate, frontal and right parietal areas", and the P3b generators in "bilateral frontal, parietal, limbic, cingulate and temporo-occipital regions" (Volpe et al., 2007, p. 220). Hippocampal sites also seem to be involved (Ludowig, Bien, Elger, & Rosburg, 2010; but see Verleger, Jaśkowski, & Wascher, 2005, p. 166). As the amplitude of the P3 varies with stimulus probability, it has been associated with context-updating in working memory (Donchin, 1981), and also, already before consciousness attained scientific reputability around 1990, to the transfer of information to "'controlled' ('conscious' or 'aware') processing" (Picton, 1984, p. 174). Today, the P3a component is commonly associated with bottom-up, stimulus-driven attention mechanisms (Polich, 2007) that can occur both consciously and nonconsciously (Dehaene & Changeux, 2011), while the P3b is related to "the effortful processing of task-relevant events" (Volpe et al., 2007), and to the memory processing of such events (Polich, 2007). Another theory views the P3b as reflecting a kind of monitoring process mediating between stimulus perception and response initiation (Verleger et al., 2005), and reflecting so-called "S–R links" between stimulus and response that become temporarily fixed through task instruction or practice (e.g., Verleger, 2020). A recent review compared nine candidate generator processes in light of the available evidence and came to the conclusion that context-updating and S–R link (re-)activation are still among the most promising, while conscious processing fared the worst out of all nine hypotheses (Verleger, 2020); however, proponents of the "late" camp still view the P3b as strongly correlated with subjective awareness, and as a reliable signature of consciousness (Dehaene, 2014; Dehaene & Changeux, 2011; Del Cul et al., 2007; Naccache, Marti, Sitt, Trübutschek, & Berkovitch, 2016; Sergent et al., 2005; Sergent & Naccache, 2012).

It should be noted that the proponents of the "early" view usually also report an enhanced P3 (i.e., an LP) in addition to the VAN (Koivisto & Revonsuo, 2010), so the issue is not whether or not it occurs, but whether it is correlated specifically with consciousness as opposed to certain post-perceptual processes, such as decision-making, or report-related processes. We view these latter processes as aspects of reflective/access consciousness, and propose to regard the VAN as the correlate of *phenomenal* consciousness, and the LP as the correlate of *reflective/access* consciousness. In other words, in our view, there are two separate but consecutive ERP correlates of visual awareness, and VAN is the earlier of the two. In light of the recent debate about the prerequisites and consequences of consciousness (see Section 2.1 above), the issue may be reframed, so that the question with respect to the LP (specifically, the P3b) becomes whether it reflects a *proper* NCC or a regular *consequence* of consciousness. Conversely, the "late" proponents have not always detected VAN (Lamy et al., 2008; Salti et al., 2012), leaving the possibility that VAN reflects some non-necessary *prerequisite* of awareness rather than awareness itself. In the next section, the relevant ERP evidence pertaining to these questions will be thoroughly examined.

3. Electrophysiological evidence for "early" and "late": a review of ERP studies

In the past two decades, a large body of ERP studies on the question of the timing of consciousness has accumulated. In 2010, a review summarized the findings that had appeared until then, reporting for each study whether they had found NCCs in the "very early" (enhanced positivity around 100 ms after stimulus onset), the "early" (enhanced negativity around 200 ms), and the "late" (enhanced positivity around 400 ms) time range (Koivisto & Revonsuo, 2010). Another review in 2011 repeated these results and highlighted the relative independence of the early negativity from attentional processes (Railo et al., 2011). In the following two sections, we will first summarize the results and open questions of those reviews, and then provide an update by examining relevant ERP studies that have appeared since 2010. Since the "very early" view is not at issue anymore, this update will focus exclusively on the remaining "early" and "late" time ranges. Like in the earlier review, other electrophysiological measures besides ERPs, like time-frequency analyses, will not be taken into account.

3.1. Results of the reviews by Koivisto and Revonsuo (2010) and Railo et al. (2011)

The review by Koivisto and Revonsuo (2010) included ERP studies from 1999 onward that compared the ERPs of aware and unaware conditions across a variety of paradigms, namely "different forms of masking, contrast level, attentional blink, change blindness, and bistable perception" (Koivisto & Revonsuo, 2010, p. 923). Of 39 reviewed studies, 13 reported enhanced very early negativity in the P1 range, 32 reported enhanced negativity in the N1-N2 range (VAN), and 36 reported enhanced late positivity (LP, or enhanced P3) in at least one aware-unaware comparison condition. However, only 29 studies reported P3 for *all* aware conditions, while 30 studies reported VAN for all aware conditions (not counting the studies reporting "attenuated" findings in one or more conditions). Going by the sheer numbers, VAN and LP thus seemed about equally reliable as NCCs; however, further analysis of the individual studies was clearly in favor of VAN as the more reliable NCC. Apart from an experiment on bistable perception that was not further discussed in the review, the only study that reported lack of VAN in one of its aware conditions was an experiment that attempted to disentangle awareness from spatial attention, and found that awareness of a stimulus seems to depend on the presence of spatial attention to the region in which the stimulus occurs (Koivisto et al., 2009). The seven studies that failed to find LP for one or more of the aware conditions were all from a series of experiments by Koivisto and colleagues that controlled for various aspects of attention, and some other possible confounds. As reviewed in Railo et al. (2011), while VAN was found across the board, Koivisto, Revonsuo, and Salminen (2005) found only attenuated LP when controlling for object-based attention; Koivisto, Revonsuo, and Lehtonen (2006) found no LP in the local attention condition when controlling for the scope (local/global) of attention; Koivisto et al.

(2008) found only attenuated LP for low-contrast stimuli when they used random stimulus onsets; Koivisto and Revonsuo (2007) and Koivisto et al. (2009) found no LP for either target or non-target stimuli that were not spatially attended; and Koivisto and Revonsuo (2008b) found no LP when controlling for selective feature-based attention. All but one of these experiments used masking paradigms (one used low-contrast stimuli instead). In a combined attentional blink/repetition blindness experiment, Koivisto and Revonsuo (2008a) found no P3 difference between recognized (aware) and unrecognized (unaware) targets when the stimulus was repeated. Moreover, in some of the studies that reported LP but no VAN, the explanation is that the authors simply did not bother to look in the N2 time range, while others failed to differentiate between the correct localization of a stimulus and awareness of it (in particular, Babiloni, Vecchio, Miriello, Romani, & Rossini, 2006; Lamy et al., 2008). Since the VAN is a relatively small deflection compared to the large P3, a lack of statistical sensitivity may be another reason for these null findings (Koivisto & Revonsuo, 2010, p. 927).

Overall, the 2010 and 2011 reviews point towards the VAN as the earliest reliable ERP correlate of consciousness. Besides the mentioned paradigms, VAN was also found in studies using low-contrast stimuli (e.g., Ojanen et al., 2003; Pins & ffytche, 2003), even when controlling for physical stimulus differences (Wilenius & Revonsuo, 2007); in studies of change blindness (e.g., Koivisto & Revonsuo, 2003, 2005); in metacontrast masking (Railo & Koivisto, 2009b) and in studies of bistable perception (e.g., Kaernbach, Schröger, Jacobsen, & Roeber, 1999). Indeed, even two of the most important studies carried out by the "late" camp found VAN (Del Cul et al., 2007; Sergent et al., 2005), but they concluded that it cannot reflect consciousness because, unlike the P3, it did not follow the characteristic non-linear all-or-none pattern in activation increase that GNWT predicts for stimuli that make it beyond the threshold for "global ignition" (see Section 2.2.1 above). Of course, this reasoning presupposes what it purports to show, namely, the truth of GNWT, or at least, of one of its central predictions (Koivisto & Revonsuo, 2010). Furthermore, the results of Del Cul et al. (2007), who used a quasi-continuous variation of stimulus onset asynchrony (SOA), were probably afflicted by floor and ceiling effects (Railo & Koivisto, 2009b, p. 795; Railo et al., 2011, p. 979), while those of Sergent et al. (2005) "might have artificially dichotomized the visibility ratings" (Railo & Koivisto, 2009b, p. 795).

As mentioned, a number of confounds have been addressed in the literature on VAN and P3/LP as correlates of visual awareness until 2010. Besides controls for physical stimulus differences and the effects of masks in various ways (Del Cul et al., 2007; Koivisto et al., 2009; Koivisto & Revonsuo, 2008b; Railo & Koivisto, 2009a, 2009b; Wilenius & Revonsuo, 2007; Wilenius-Emet et al., 2004), the series of experiments on attentional confounds of VAN is particularly noteworthy. VAN has been successfully dissociated from the SN component associated with feature- and object-based attention, and it has been shown that VAN is independent from the scope of attention, while the allocation of spatial attention to the stimulus region seems necessary for VAN to occur (see also Koivisto et al., 2009, for a review). Moreover, there are some grounds for assuming that VAN is distinct from the attention-related N2pc (Koivisto & Revonsuo, 2010, pp. 926–927).

3.2. An update on the 2010 and 2011 reviews

This new review uses the same inclusion criteria for studies as did the one by Koivisto and Revonsuo (2010): ERP studies that have appeared since 2010 and directly compared target-locked ERPs of aware and unaware conditions are included. Table 1 lists all reviewed studies, sorted by the type of manipulation used, and reports their findings in the N2 range (around 200 ms after stimulus onset) and the P3 range (around 400 ms). A "yes" entry means that activity in the respective time range was found and reported; a "no" entry means that no activity in the respective time range was found and reported; and no entry (an empty field) means that the respective time range was not investigated, and/or no results for that time range were reported. "Attenuated" means that the VAN or LP amplitude varied in one or more conditions, indicating an experimentally induced decrease in the amplitude of the respective component in one of the aware conditions. Special cases that are difficult to fit into this framework are marked with one or more asterisks (*), and more information about them is provided in the legend of Table 1. In total, 30 studies were reviewed, of which 20 found VAN and 13 found LP in all tested aware conditions (again, not counting the studies reporting "attenuated" findings). This result corroborates the one reached by Koivisto and Revonsuo (2010) and Railo et al. (2011) that VAN is a more reliable ERP correlate of visual awareness than LP. At the same time, the informativeness of these numbers, and of Table 1, is limited, as they conceal important new questions that have emerged in ERP research on visual consciousness, and new approaches that have been explored to tackle them. Consequently, Table 1 glosses over important differences between the studies. Below, these are discussed in detail, and the new developments will be described. Furthermore, a number of MEG studies highly relevant to the "early" vs. "late" debate have been carried out over the past ten years. They are listed in a separate Table 2, and are likewise reviewed below (in Section 3.3).

3.2.1. Objective task-performance as a potential confound

The study by Lamy et al. (2008) had drawn attention to an important confound that may have distorted earlier results: previous studies had failed to control for objective task-performance, and not taken into account the factor of whether participants performed a given task correctly or not. In effect, mixing up "unaware-correct" and "unaware-incorrect" trials in the analysis can lead to drastically varying baselines of the unaware condition, which influences the magnitude and possibly also the scalp distribution of the difference between "unaware" and "aware" conditions. Potentially, this can dramatically distort the results, leading to false positive and/or false null findings in different experiments. Lamy et al. (2008) controlled for this confound by comparing only ERPs for "aware-correct" and "unaware-correct" trials, while discarding, for the purposes of this comparison, all trials on which subjects had performed incorrectly. Since they found LP but no VAN for the "aware" condition when comparing ERPs in this way, they concluded that previous VAN findings were probably due to the failure to control for task-performance. In a follow-up study, Salti et al. (2012) reproduced this result (LP but no VAN), while simultaneously controlling for the level of confidence of the subjects' awareness report.

Table 1
Results of the Review of ERP Studies for VAN (N2 range) and LP (P3 range).

Manipulation	Study	Enhanced early negativity (N2 range)	Enhanced late positivity (P3 range)
Contrast	Chica et al. (2010)		Yes
	Eklund and Wiens (2018)	Yes/Yes	Yes/Yes
	Koivisto et al. (2016)	Yes/Yes	Yes/Attenuated
	Koivisto and Grassini (2016)	Yes	Yes
	Koivisto et al. (2017)	Yes/No	Yes/Yes
	Koivisto et al. (2018)	Yes/Yes/Yes	Yes/Yes/Attenuated
	Melloni et al. (2011)	Yes/Yes	Yes/No
	Rutiku et al. (2016)	Yes/No*	Yes/Yes*
	Tagliabue et al. (2016)	Yes**	Yes**
	Ye and Lyu (2019)	Yes/Yes	Yes/Attenuated
	Ye et al. (2019)	Yes/Yes	Yes/Attenuated
Masking	Babiloni et al. (2016)	No/No/Yes	Attenuated/No/No
	Davoodi et al. (2015)	No/No	Yes/Attenuated
	Del Zotto and Pegna (2015)	Yes/Yes	Yes/Attenuated
	Derda et al. (2019)	Yes**	No**
	Fu et al. (2017)	Yes**	Yes**
	Jimenez et al. (2018)	Yes**	Yes**
	Pitts, Metzler, et al. (2014)	Yes/Yes	Yes/No
	Railo et al. (2015)	Yes	Yes
	Rutiku et al. (2015)	Yes/Yes	Yes/Yes
	Salti et al. (2012)	No	Yes
Inattentional Blindness	Pitts et al. (2011)	Yes/Yes	Yes/No
	Schelonka et al. (2017)	Yes/Yes	Yes/No
	Shafto and Pitts (2015)	Yes/Yes	Yes/No
	Harris et al. (forthcoming)	Yes	
Attentional Blink	Batterink et al. (2012)	No/No	No/Yes
	Weller et al. (2019)		
Change Blindness	Scrivener et al. (2019)	No/No	Yes/Yes
Other	Boncompte and Cosmelli (2018)	No	Yes
	Pitts, Padwal, et al. (2014)	Yes/Yes/Yes/Yes	Yes/No/Yes/Attenuated

Note. For each study, we report which of the two relevant ERP correlates (VAN and LP) have been found. In the case of two or more entries, the studies have employed more than one experimental condition. *) The study by Rutiku et al. (2016) used over 70 different stimuli, and carried out 100 contrastive analyses in total, of which 81 found VAN, and 100 found LP. **) The studies by Derda et al. (2019) Fu et al. (2017), Jimenez et al. (2018), and Tagliabue et al. (2016) have compared different Perceptual Awareness Scale (PAS) contrasts (see Section 3.2.7); the amplitudes of the components they found mostly varied with PAS rating (either gradually or dichotomously). In the study by Derda et al. (2019), LP did not discriminate between seen and unseen trials in their "low level of processing" condition (see Section 3.2.7).

However, both studies also failed to detect any difference in ERPs between "unaware-incorrect" and "unaware-correct" conditions in the VAN time window.

This challenge has been taken up by at least two studies. Koivisto and Grassini (2016) suspected that the reason for the null findings of Lamy et al. (2008) and Salti et al. (2012) was a lack of sensitivity for the comparatively small VAN component. To make their study more sensitive, they used a larger stimulus, low-contrast Gabor patches instead of masking (in order to eliminate any possible noise introduced by the masks), and they controlled for lateralization. Because the VAN is hypothesized to reflect local recurrent processing in visual cortex, it is assumed to emerge in the hemisphere contralateral to the visual field in which the stimulus occurs. With these modifications in place, Koivisto and Grassini (2016) found both VAN and LP for the "aware" condition while controlling for task performance. A signal detection analysis revealed that LP was reduced when subjects adopted a conservative response criterion in the forced-choice localization task that the experiment employed, suggesting that the P3 is associated with post-perceptual processes such as "participants' *meta*-cognitive evaluations concerning their awareness" (Koivisto & Grassini, 2016, p. 242) rather than with awareness *per se*. A preregistered further study tried to determine which of the three modifications in this experiment had been the one that was successful in increasing the sensitivity sufficiently for VAN to be detected. Eklund and Wiens (2018) closely followed Koivisto and Grassini (2016), but used two different Gabor patch sizes. They found VAN and LP for aware trials, and no evidence for an effect of stimulus size. Presumably, then—apart from the already mentioned possibility of a lack of sensitivity—either unwanted mask effects or the lack of control for lateralization were responsible for the VAN null findings in the studies of Lamy, Salti, and colleagues. These possibilities could be investigated with new experiments, and perhaps via reanalysis of their data with hemisphere as an additional factor.

3.2.2. A new contrastive ERP paradigm: inattentional blindness

An interesting novelty relative to the 2010 review is the adaptation of the inattentional blindness paradigm for use in ERP studies by Michael Pitts and colleagues (note that the studies reviewed in this section are also discussed in another recent review, Hutchinson, 2019, that arrives at conclusions very similar to the ones drawn here). In inattentional blindness, subjects can miss even

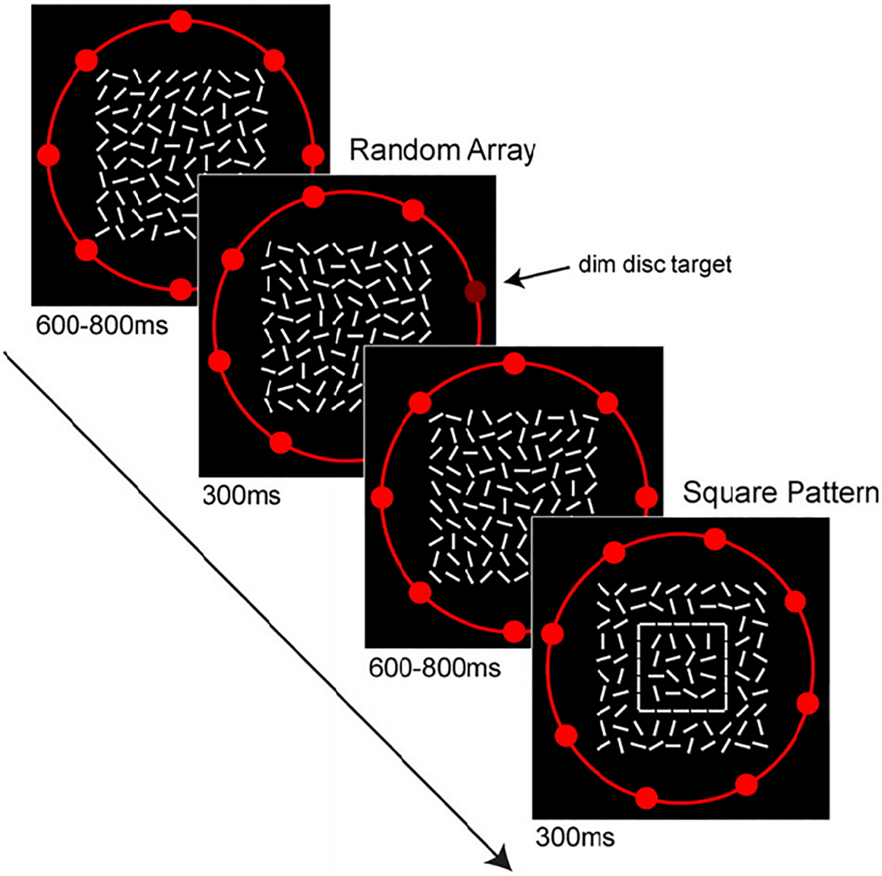

Fig. 3. Example of the stimuli used in the first published inattentional blindness study by Pitts and colleagues. Besides frequently presented square patterns and random arrays, there were also rarely presented diamond (45° tilted square) patterns. Reprinted from NeuroImage 101, Pitts, Padwal, et al., Gamma band activity and the P3 reflect post-perceptual processes, not visual awareness, p. 338, 2014, with permission from Elsevier.

quite salient stimuli right in the middle of their visual field, if their attention is focused on a distracter task (Mack & Rock, 1998). In a classical experiment, subjects failed to detect even a man dressed up as a gorilla walking into the scene and pounding his chest, when they were distracted with counting the passes of a handball team (Simons & Chabris, 1999). The problem with inattentional blindness as a paradigm in ERP research is that for ERP analyses, many trials have to be averaged in order to distill a visible, statistically significant effect. However, in inattentional blindness, once a subject has become aware of the “hidden” stimulus, she will notice it in the future. Requiring her to report on her awareness of a hidden stimulus will inevitably induce her to look out for such stimuli in all further trials. Pitts et al. (2011) got around this problem by requiring reports not after each single trial, but only after an entire block (see Fig. 4; note that this Figure is from Pitts, Padwal, et al., 2014, who analyzed the raw data from Pitts et al., 2011). During a first phase, they presented a grid of line segments, which could either be randomly configured or produce patterns (frequently, squares, and rarely, diamonds). The grid was surrounded by a ring of red discs, one of which appeared fainter than the others (see Fig. 3). The subjects’ primary task was to detect which of the discs was faint on each trial, and this was supposed to keep their attention away from the grid shapes that would occur on some of the trials. After the first phase, subjects were first asked whether they saw any patterns, and then they were presented with example patterns (including squares and diamonds) and asked to rate their confidence in having seen each of them. About half of the subjects were oblivious to any patterns presented. The same procedure was then repeated, followed by the same questions, and this time, all subjects reported that they had seen the squares. In a third phase, subjects were asked to ignore the ring of red discs and focus on the grid in order to detect the—rare—diamond patterns, which they easily accomplished. Pitts and colleagues then compared the ERPs of phase-one trials of subjects who were “inattentionally blind” according to the questions after the first phase with the ERPs of phase-two trials, thereby obtaining an aware/unaware contrast. They also compared the ERPs of subjects who had been aware of the squares during phase one with the ERPs of those who had not, producing another aware/unaware contrast. Finally, they compared the ERPs for squares versus random patterns within phase three, when the squares were task-relevant (as they had to be discriminated from the target diamonds). They found a negative component that strongly resembled the VAN (except for a somewhat late timing) for aware conditions, irrespective of task-relevance, as well as an SN component that was present only in phase three, thereby confirming the dissociation of SN and VAN reported by Koivisto et al. (2009). The most outstanding finding in the context of the “early” vs. “late” debate, however, was that LP occurred only when the

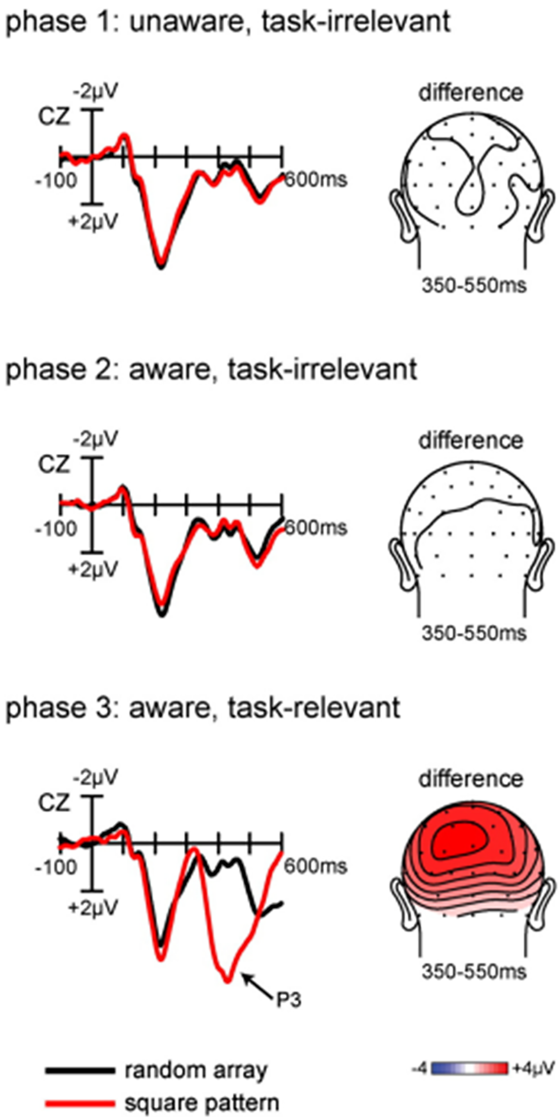

Fig. 4. The three phases of the inattentional blindness paradigm by Pitts and colleagues. P3 occurs only in phase 3, when the hidden target is task-relevant. Reprinted from NeuroImage 101, Pitts, Padwal, et al., Gamma band activity and the P3 reflect post-perceptual processes, not visual awareness, p. 340, 2014, with permission from Elsevier.

stimulus was both aware and task-relevant (see Fig. 4). This strongly suggests that the LP component reflects postperceptual processing of task-relevant stimuli (i.e., reflective or access consciousness) rather than conscious awareness (i.e., the onset of phenomenal consciousness of the stimulus) as such.

Shafto and Pitts (2015) modified this paradigm by using a grid of line segments that would align to form female faces in some trials (some with missing features), on which they superimposed concentric rings with moving green dots, some of which sometimes brightened up for a short time. The distracter (i.e., primary) task consisted in detecting when these changes in brightness happened; by superimposing the distracter stimuli on the "hidden" stimuli of interest (i.e., the faces), Shafto and Pitts controlled for spatial attention. The procedure closely followed that of the previous experiment, with phase one and two followed by questions analogous to those of Pitts et al. (2011). In phase three, subjects were required to detect the faces with missing features. ERPs were then compared as in Pitts et al. (2011). Apart from a face-specific N170 component during aware conditions, Shafto and Pitts again found VAN to correlate with awareness irrespective of task-relevance, while SN and P3b appeared only in phase three, when the faces became task-relevant.

Schelonka, Graulty, Canseco-Gonzalez, and Pitts (2017) carried out a further variation of the paradigm, this time focusing on orthographic and lexical processing. Using a similar grid of line segments and similar distracter tasks as Shafto and Pitts (2015), the "hidden" stimuli were word forms (either proper words or consonant strings). Once again, they found VAN to correlate with awareness and P3b to correlate with task-relevance.

Harris, Dux, and Mattingley (forthcoming) used yet another slight variation of the paradigm in order to investigate post-stimulus alpha power. They also carried out an ERP analysis, and found VAN. Already assuming that LP reflects post-perceptual processes, the authors did not investigate the P3 time range.

Inattentional blindness is a welcome addition to the established corpus of paradigms in experimental consciousness research. Its decisive advantage over other paradigms is that it permits the researcher to isolate awareness-related ERP activity from all post-perceptual processing, as there is no requirement to memorize, report, or otherwise act on, or immediately "access" aware stimuli during phases one and two. However, there are also some disadvantages, most of which have already been mentioned by Pitts, Padwal, et al. (2014): since awareness-reports can be obtained only after the presentation of entire blocks in order to maintain the inattentional blindness effect, it is impossible to know on which, and on how many, trials subjects were actually aware of the "hidden" stimuli. Subjects who were aware on many trials will thus be grouped together with subjects who were aware only on few trials, which will affect the ERPs obtained from this group; and it will presumably affect them differently in different experiments, because the "hidden" stimuli can be expected to differ in salience (e.g., rectangle shapes versus human faces), which is likely to have an influence on the number of trials that become aware especially during phase one. Pitts, Padwal, et al. (2014) tried to alleviate such concerns by having subjects estimate their number of aware trials. These subjective estimates correlated with VAN amplitude, and therefore are probably reliable to some degree. Another disadvantage is that counterbalancing of the blocks is not possible, since the order of phases is fixed. However, this is not a problem for the within-phase ERP comparisons, which are the most important ones in this paradigm. Finally, it is by definition impossible to manipulate attention and awareness independently in inattentional blindness paradigms, although this drawback is shared by many other paradigms (see Pitts, Padwal, et al., 2014, p. 348).

3.2.3. Task-relevance: an important confound in studies of awareness

The results by Pitts and colleagues on P3 and task-relevance are particularly important because the stimuli in the vast majority of previous studies were task-relevant, and consequently, their LP/P3 findings suffer from a potentially devastating confound (this concerns, for example, Del Cul et al., 2007; Lamy et al., 2008; Salti et al., 2012; Sergent et al., 2005; and most of the studies by Koivisto and colleagues). One exception is the study by Koivisto and Revonsuo (2008b), which featured a passive viewing condition without any task. In striking agreement with the results just discussed, they had found that LP was completely eliminated in this condition. Moreover, many of the earlier studies on the relationship between attention and awareness required the participants to attend to and report only target—and hence, task-relevant—stimuli and not to respond to non-target—and hence, task-irrelevant—stimuli (Koivisto et al., 2005, 2009; Koivisto & Revonsuo, 2007, 2008b). These studies showed VAN in response to both targets and non-targets, whereas LP was present for targets but eliminated or attenuated for task-irrelevant non-targets. This already showed the dependence of LP on task-relevance, even if the term was not used explicitly.

Pitts and colleagues reproduced and extended their findings in further studies. Pitts, Padwal, et al. (2014) abandoned the ring of discs and presented patches of colored line segments in the same grid region in which they presented horizontal and vertical rectangle shapes, thereby controlling for spatial attention and competition between objects. This study focused on task-relevance in aware trials, so there was no need to induce inattentional blindness. Instead, subjects were shown both types of stimuli in advance, and then simply required to respond to either the color patches or the rectangle shapes. ERPs were then compared for rectangle shapes vs. random stimuli, both when they were relevant and when they were irrelevant. As they had predicted, Pitts et al. found LP for the shapes only when they were task-relevant. In another experiment reported in the same study, they manipulated the *degree* of task-relevance, operationalized as the degree of similarity between the target and other stimuli. They found that LP amplitude correlated positively with the degree of task-relevance, and that LP was again only present for stimuli that had at least some degree of task-relevance.

A drawback of this study and the inattentional blindness studies is that they did not feature a task-relevant but unaware condition, which would be required for a complete double dissociation of awareness and task-relevance. Pitts, Metzler, et al. (2014) realized a 2×2 design in a backward masking paradigm with two SOAs, one of which was sufficiently short (16 ms) to ensure that the target became unaware, and the other one of which (300 ms) guaranteed that the mask did not interfere with stimulus visibility. They used variations of stimuli from their earlier experiments: a grid of line segments, which aligned to form square or diamond shapes on some trials, and either three or four patches of colored line segments on others. The task on each block was to detect either the patches with three lines colored or the diamond stimuli, and report them via button pressure. The twist here was that all target stimuli were discarded for the analysis (thereby removing any motor preparation and execution confounds), and only the ERPs of the non-target stimuli used for comparisons. In each task, the non-target of the same category (in the diamond-detection task: the square) was deemed task-relevant, and the stimuli of the other category task-irrelevant. In combination with masking, this yielded four conditions, among them the sought-after "unaware/task-relevant" condition. The ERP analysis revealed VAN to be "consistently associated with perceptual awareness; in contrast, "the P3b was present in some of the unaware, task-relevant conditions, and absent in some of the aware, task-irrelevant conditions" (Pitts, Metzler, et al., 2014, p. 11). This is particularly interesting, because it goes beyond all the results reviewed here so far. The previous ERP studies by Pitts et al. had questioned the *necessity* of the process generating the P3b component for awareness by showing that awareness could occur without the P3b (namely, in task-irrelevant conditions). The finding that the P3b can also occur in *unaware* conditions seems to show that its presence is not *sufficient* for establishing awareness, either. Note, however, that the P3b finding may be due to a number of participants who occasionally reported seeing the target despite masking.

Silverstein, Snodgrass, Shevrin, and Kushwaha (2015) provided independent evidence for this insufficiency by employing a subliminal oddball paradigm. They presented rare and frequent words for extremely brief periods, followed by masks, to achieve complete stimulus invisibility, and asked subjects to closely attend to the subliminal stimuli (even though they protested that they could not see anything to focus attention on). Silverstein and colleagues employed a further condition including a detection task, and applied signal detection theory to ensure that subjects were unable to detect the subliminal stimuli above chance. What they found was that, just like in supraliminal oddball experiments, the rare stimuli elicited larger P3, followed by a sustained late slow wave, than the frequent stimuli—although all stimuli were unconscious and undetectable. However, note that the baselines for "frequent" and "rare" ERPs seem to be sloppily aligned, which potentially invalidates the significance of the P3 finding. A principal component analysis (PCA) identified separate P3a and P3b components, and thus verified that they had indeed found unconscious P3b.

3.2.4. No-report paradigms and other ways to winnow the NCC from its prerequisites and consequences

The results discussed in the previous sections underscore how vitally important it is to distinguish the NCCs from their prerequisites and consequences. Many of the results reviewed here depict the P3b as a prime example of an ERP component reflecting a post-perceptual process (or a number thereof) that has been systematically conflated with the proper NCC because of insufficient controls for task-related activity. A recent study by Koivisto, Ruohola, Vahtera, Lehmusvuo, and Intaite (2018) using low-contrast stimuli and a dual-task paradigm may serve as yet another example. Here the VAN was dissociated from the effects of working memory—another important potential confound stemming from an arguably post-perceptual process—under three different conditions; even the LP was modulated by working memory only under heavy executive load.

Another study by the same group showed that LP cannot possibly be causally implicated in generating consciousness, by demonstrating that the fastest conscious reports occurred earlier than the onset of that ERP component (Railo, Revonsuo, & Koivisto, 2015). Using TMS as a masking technique (applied either ipsi- or contralaterally to the visual field half in which the stimulus was presented, with only the contralateral perturbation resulting in a masking effect) enabled them to use clearly visible high-contrast stimuli and thereby to achieve extremely fast reaction times for the subjects' conscious reports, which were submitted in the form of a GO/NOGO task response. Analyzing grand average summary statistics as well as single trials, the authors were able to show that VAN preceded even the earliest conscious reports, while LP always overlapped with or occurred after them.

As a way of dealing specifically with report-related confounds (which may include all kinds of post-perceptual processes, such as working memory, response selection, motor preparations and executions, etc.), no-report paradigms have recently been discussed extensively (Koch et al., 2016a; Overgaard & Fazekas, 2016; Tsuchiya, Frässle, Wilke, & Lamme, 2016; Tsuchiya et al., 2015). Such paradigms may replace requirements of subjective awareness reports with objective measurements, e.g., eye movement or pupil dilation in response to perceptual shifts in binocular rivalry (Tsuchiya et al., 2015). Another way is the "inclusion of no-report control conditions" into classical report-based paradigms (Tsuchiya et al., 2016, p. 242). Just such a combination of report and no-report conditions has been realized in a recent ERP experiment (Koivisto, Salminen-Vaparanta, Grassini, & Revonsuo, 2016). The authors of this study presented low-contrast Gabor patches in a "go"/"no go" task and counterbalanced the response requirements: in one condition, subjects had to respond when they saw the stimulus and not respond when they saw nothing, whereas in another condition, they had to respond when they did *not* see the stimulus (and *not* respond when they did see it). This enabled the Koivisto and colleagues to compare the ERPs of four conditions: "aware-GO, aware-NOGO, unaware-GO, and unaware-NOGO" (Koivisto et al., 2016, p. 3). They found VAN to be present in all aware (and absent in all unaware) conditions, and no difference in VAN between the aware-GO and aware-NOGO conditions, suggesting that VAN was not changed by response requirements. In contrast, while LP was likewise present only in aware conditions, its amplitude was larger in the aware-GO than in the aware-NOGO condition. While it remains open why such a difference was not observable between the unaware GO and NOGO conditions, this result clearly suggests that P3 is at least in part caused by response-related processes occurring only after the stimulus has already become conscious.

The ERPs obtained in this experiment may still include some activity that is indirectly related to reports; for example, in principle even the VAN found here might still include activity related to perceptual decisions, or, during NOGO conditions, to response inhibition, that remained undetected, perhaps for a lack of sensitivity. Other paradigms may be even more powerful in isolating the NCC from its consequences. In fact, the inattentional blindness paradigm discussed in Section 3.2.2 is a particularly powerful instance of a no-report paradigm, that can arguably avoid "any and all post-NCC confounds", so that "a potential NCC can be fully dissociated from cognitive access and attention" (Tsuchiya et al., 2016, p. 243). It should also be noted that no-report paradigms have occasionally been employed already *avant la lettre*; an example is the passive viewing task employed by Koivisto and Revonsuo in an already mentioned experiment (Koivisto and Revonsuo, 2008b). One problem with passive viewing conditions, however, is that they might induce mind-wandering and suffer from a "lack of control over closely related processes such as attention and working memory" (Pitts, Lutsyshyna, & Hillyard, 2018, p. 8), which arguably renders them less than ideal for NCC research.

No-report paradigms are not without their own problems and limitations. Notably, while they can exclude certain confounds, and thereby help to narrow down the space of possible NCCs, they may still overestimate the NCC "by including certain pre-NCC activity" (Overgaard & Fazekas, 2016, p. 241). The most reasonable way to proceed is surely to combine no-report paradigms with conventional ones, to include no-report conditions in the latter, and to employ both kinds of paradigms across the whole range of available techniques for manipulating awareness and other parameters of interest (Tsuchiya et al., 2016).

3.2.5. The relationship between consciousness and attention

Another major potential confound in NCC research is attention, and the relationship between awareness and attention is a fundamental issue in the science of consciousness (Aru & Bachmann, 2013; Cohen, Cavanagh, Chun, & Nakayama, 2012a, 2012b; Koch & Tsuchiya, 2007, 2012; Lamme, 2003, 2004; Noah & Mangun, 2019; Tsuchiya, Block, & Koch, 2012; Tsuchiya & Koch, 2016; Van Boxtel & Tsuchiya, 2015; Van Boxtel, Tsuchiya, & Koch, 2010). As noted in Section 2.2.1, according to GNWT, attention is a necessary prerequisite for conscious access, and if this is true, it obviously affects the search for the NCCs. In particular, any claim about a putative NCC must be substantiated by showing that it is not, in fact, merely a correlate of a necessary prerequisite of consciousness, namely, attention.

The issue is complicated further by the fact that attention is no more unitary a concept than consciousness. A basic distinction separates exogenous, bottom-up attention from endogenous, top-down attention. The former is automatically attracted by salient (e.g., by particularly strong, and often, by evolutionarily relevant) stimuli, whereas the latter can be employed voluntarily, according to the task at hand. Both forms of attention can be feature- or object-based; they can be employed to global or to local features of an object or a scene; and also to particular spatial or temporal regions (see Eysenck & Keane, 2015, Chapter 5, for an overview). These varieties of attention constitute subsystems that can operate quite independently of each other (Cohen, Cavanagh, Chun, & Nakayama, 2012b; Tsuchiya & Koch, 2016), although it is not yet clear how (dis-)integrated their mechanisms are at the neural level. Since the mid-2000s, a number of researchers have begun to state and defend a double dissociation between top-down attention and visual awareness (Koch & Tsuchiya, 2007, 2012; Tsuchiya et al., 2012; Tsuchiya & Koch, 2016; Van Boxtel et al., 2010), while others insist that the dissociation runs only one way, and top-down attention remains necessary for awareness (Cohen et al., 2012a, 2012b; Noah & Mangun, 2019).

In the field of ERP research, the most pressing question is whether the ERP correlates of the various forms of attention can be separated from those of awareness. As noted in Section 3.1, a number of successful dissociations of the VAN from several attention-related components, such as the SN, had already been achieved prior to 2010 by Koivisto and colleagues (reviewed in Koivisto et al., 2009, and Railo et al., 2011). Since then, further ERP studies have been carried out.

While most work on the relationship of attention and awareness focuses on endogenous, top-down attention, Chica, Lasaponara, Lupiáñez, Doricchi, and Bartolomeo (2010) investigated how exogenous, bottom-up attention interacts with visual awareness. This is usually considered difficult, because manipulating the salience of a stimulus almost inevitably implies manipulating its physical properties, thereby introducing an unwanted confound (Van Boxtel et al., 2010). Chica and colleagues used low-contrast gratings with slightly different orientations as stimuli, while they presented peripheral salient, but uninformative cues in order to manipulate exogenous attention. They reasoned that "[i]f exogenous attention improved conscious perception, more targets should be consciously reported at the exogenously attended location" (Chica et al., 2010, p. 1206), which is what they found. In an analysis of ERPs locked to the appearance of the cue, they found a strong P100 component both for seen targets when the cue was valid, and for unseen targets when the cue was invalid. Chica et al. interpreted this component to reflect the capture of exogenous attention by the cue, and concluded that both the successful attraction of exogenous attention to the relevant location by a valid cue and the failure of a misleading cue to attract exogenous attention to the wrong location facilitate conscious perception. Comparing the target-locked ERPs of the aware and unaware conditions, they found an LP that had a slightly earlier onset latency for seen targets at invalid locations, which they interpreted as a sign of a re-orientation of exogenous attention from the invalid cue to the target. This study reported no VAN, and apparently the N2 time window has not been scrutinized by the authors. Accordingly, nothing can be learned from this study about possible effects of exogenous attention on the VAN. Studies explicitly inquiring about this relationship remain to be carried out.

Del Zotto and Pegna (2015) investigated "the interactions between non-spatial selective attention, awareness and emotion processing" (Del Zotto & Pegna, 2015, p. 1) in a backward masking paradigm, using faces with different emotional expressions as stimuli, and a categorization task supposed to engage selective attention. Their results reproduced the dissociation of VAN and SN found in earlier studies (Koivisto et al., 2009, 2005; Koivisto & Revonsuo, 2007, 2008b); moreover, P3 depended on selective attention in that it was larger for targets than for non-targets, irrespective of awareness, suggesting to the authors "that the P300 should rather be seen as a consequence of consciousness, related for example to post-perceptual processing, rather than to awareness *per se*" (Del Zotto & Pegna, 2015, p. 10).

Chen, Wang, Yu, and Liu (2017) investigated the relation of exogenous feature-based attention and awareness. Since their ERPs were cue- rather than target-locked, resulting in different baselines and component latencies, their results are not directly comparable to the other studies reviewed here, and therefore do not appear in Table 1. They are interesting nonetheless, as they suggest that exogenous attention can be dissociated from awareness just as well as endogenous attention. More studies are of course needed to corroborate this isolated finding.

Overall, the relationship between attention and consciousness is still perplexing, and the effects of different forms of attention on putative ERP correlates of visual awareness are, in large part, far from established. The results reviewed by Koivisto et al. (2009) are an important first foray into this territory, but they need to be replicated under different conditions, taking into account the possible confounds that have been discussed in the past ten years, and under review here: objective task-performance, task-relevance, expectations, etc. The exciting new results on exogenous attention and awareness should explicitly be investigated in their relationship to the VAN in future studies in order to corroborate or undermine, as the case may be, its status as a proper ERP correlate of visual awareness.

3.2.6. The role of expectations and prior beliefs

The recent decade of cognitive and computational neuroscience has seen an ever-increasing interest in the role of expectations in perception, and perception has frequently been treated as, fundamentally, a problem of (Bayesian) inference (Kersten & Yuille, 2014; Olshausen, 2014). Given the importance of the topic, it is surprising that, so far, only one ERP study (Melloni, Schwiedrzik, Müller, Rodriguez, & Singer, 2011) has investigated the effect of expectations on visual awareness in a way that fits the inclusion criteria of this review. To manipulate expectations, the authors presented stimuli (letters, numbers, or symbols) in a "ladder" procedure, repeating the same stimulus eleven times, with contrast (visibility) increasing step-wise over the first six trials (the "ascending" part of the sequence), and decreasing contrast over the remaining five (the "descending" part), as visualized in Fig. 5. Participants were to report their level of subjective visibility on a graded perceptual awareness scale. They became aware of the stimuli more often during

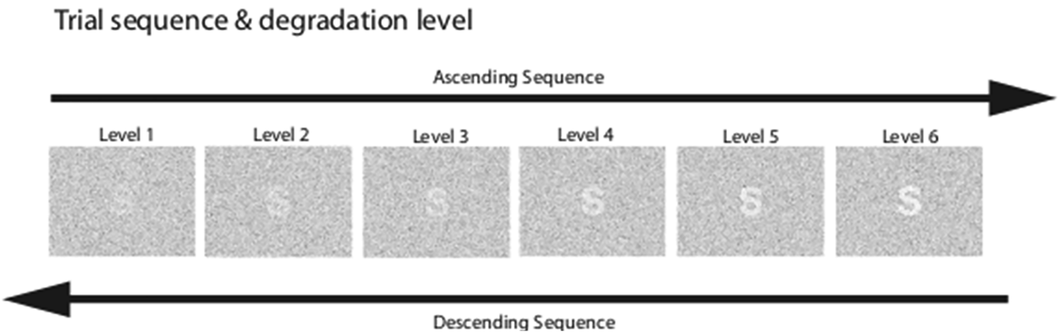

Fig. 5. Visualization of the stimulus sequence used by Melloni and colleagues. Stimulus contrast increased over six degradation levels, then decreased over the same six levels. Reprinted from The Journal of Neuroscience 31(4), Melloni et al., Expectations Change the Signature and Timing of Electrophysiological Correlates of Perceptual Awareness, p. 1387, 2011.

the descending part of the sequence, showing that conscious perception changed non-linearly with degradation level depending on the sequence (ascending vs. descending), an instance of an effect called "hysteresis" (Kleinschmidt, Büchel, Hutton, Friston, & Frackowiak, 2002). Plausibly, this effect was due to the presence of expectations in the subjects in the descending part, built up during the ascending part.

Melloni and colleagues found that the only ERP component that differentiated between seen and unseen trials in both the ascending and descending parts of the sequence was the P2, which was significantly reduced in amplitude in the seen trials (i.e., VAN). P2 amplitude was smaller (i.e., VAN amplitude larger) during the descending part, that is, in the presence of perceptual expectations, but only at low stimulus contrasts, suggesting "that P2 attenuation is mainly related to visibility rather than degradation or expectancy per se" (Melloni et al., 2011, p. 1391). The P3 component was higher in amplitude for seen than for unseen trials, but only in the ascending part of the sequence, suggesting that it is an ERP correlate of visual awareness "only in the absence of expectations" (Melloni et al., 2011, p. 1395). In a control experiment, in which different stimuli were used on each trial during a sequence in order to control for possible sequence effects, and in which, consequently, no stimulus-specific expectations could be built up by the brain, the P3 reflected "visibility more closely than P2" (Melloni et al., 2011, p. 1395) in that only the P3 curve showed a non-linear increase at visibility threshold (as in the studies of Del Cul et al., 2007; Sergent et al., 2005; and Sergent & Dehaene, 2004), whereas the P2 generally decreased (i.e., the VAN increased) linearly with stimulus visibility. However, as already noted above in Section 3.1, this reasoning presupposes that an ERP component reflects consciousness better if it increases non-linearly. The dubiousness of this assumption will be further discussed below in Section 3.2.7.

Overall, the authors interpret their results to show that the onset of awareness is neither "early" nor "late" *per se*, but that the latency of the electrophysiological NCC depends on the presence or absence of expectations in the perceiving subject. This interpretation is most interesting in the present context, as it is conceivable that some form of expectations was always present in earlier studies; at any rate, this factor has never been systematically controlled for. Pinto, van Gaal, de Lange, Lamme, and Seth (2015) have provided further behavioral evidence that the presence of expectations accelerates the onset of visual awareness both for detection and identification in a continuous flash suppression paradigm. Clearly, more electrophysiological studies addressing expectancy, and its interaction with other factors such as task-relevance and attention, are urgently called for.

Both Melloni et al. (2011) and Pinto et al. (2015) explicitly relate their studies to a particularly important inferential account of perception, namely "predictive coding", also—barring subtle differences—known as "prediction error minimization" (Hohwy, 2013, 2015) or "predictive processing" (Clark, 2013, 2016; Keller & Mrsic-Flogel, 2018), and intimately related to Karl Friston's "free-energy principle" (Friston, 2005, 2009). According to such accounts, the brain is fundamentally engaged in generating predictions about the expected sensory input, and optimizing its prior beliefs, which are implemented in a hierarchical generative model of the external world. Melloni et al. (2011, p. 1394) note the seemingly high compatibility of predictive coding and RPT: while the latter associates recurrent feedback activity with conscious awareness, the former identifies it with the predictions generated by the brain (see also Pennartz, Dora, Muckli, & Lorteije, 2019). If one assumes, as is done in leading formulations of predictive coding, that "perceptual content *is* the predictions of the currently best hypothesis about the world" (Hohwy, 2013, p. 48, italics in original), then one might even argue that predictive coding, by assigning a specific functional role to recurrent processing, goes some way toward explaining *why* recurrent processing should be accompanied by phenomenal consciousness (although, of course, it remains equally mysterious why phenomenal contents should be identical to neural predictions). However, predictive coding is probably also compatible with GNWT (e.g., Hohwy, 2013, chapter 10; Whyte, 2019). A thorough investigation of the exact relations between the various empirical theories of consciousness and the predictive coding scheme remains to be carried out, and is beyond the scope of this review. One of the topics that may look quite differently from a predictive coding perspective is the relationship between consciousness and attention, which latter is often associated with so-called "precision weighting" of prediction error units throughout the cortical hierarchy (e.g., Clark, 2013; Hohwy, 2013, chapter 3).

ERP research need not await these theoretical developments, however, as the study by Melloni et al. (2011) demonstrates. At some distance from research specifically related to conscious awareness, an electrophysiological literature looking for predictions in the brain is already developing (e.g., Bendixen, SanMiguel, & Schröger, 2012; Stefanics, Kremláček, & Czigler, 2014; Winkler & Czigler, 2012), and it will be most fruitful to make the connection to consciousness research and the literature reviewed here.

3.2.7. Awareness: graded, dichotomous, or both?

Yet another intensely debated topic in the science of consciousness is the nature of awareness as either graded or dichotomous. In line with GNWT's hypothesis that conscious access to a stimulus requires the neural activity induced by it to cross a threshold of "global ignition", the studies carried out by this camp generally found a non-linear increase in neural activation for stimuli that became conscious (Del Cul et al., 2007; Sergent et al., 2005; Sergent & Dehaene, 2004; see Section 2.2.1 above). These studies used a quasi-continuous scale to capture subjects' conscious reports, where visibility ratings fell on one of 21 contiguous positions, with only the extreme ends of the scale labeled as "nothing seen", and "maximal visibility", respectively. The distribution of the visibility scores turned out to be bimodal in these experiments, with almost all of the ratings falling on the extreme ends. From this result, the authors concluded that visual consciousness is an all-or-none phenomenon, just like GNWT predicts.

However, another group of researchers produced diverging evidence. Exploring different scales of visibility ratings, Ramsøy and Overgaard (2004) found that their subjects, when encouraged to rate visibility in whichever way seemed most convenient to them, all converged on a four-point scale with the categories "no experience", "brief glimpse", "almost clear image", and "absolutely clear image". The score on this "perceptual awareness scale" (PAS) co-varied linearly with both stimulus duration and probability of a correct answer in a variety of tasks, including shape and color discrimination (Ramsøy & Overgaard, 2004) and stimulus localization (Overgaard, Rote, Mouridsen, & Ramsøy, 2006; Ramsøy & Overgaard, 2004), across different report modalities. To the authors, this suggested that visual consciousness is a phenomenon that admits of different degrees, rather than being simply "present" or "absent".

The PAS, as well as modified versions of it, have been used in a number of ERP studies of visual consciousness, including some of the already mentioned ones (Eklund & Wiens, 2018; Koivisto & Grassini, 2016; Melloni et al., 2011). In these studies, the PAS has usually been artificially dichotomized (i.e., the lowest and the highest two response categories have been collapsed) for the purposes of analysis, mainly because of difficulties in obtaining enough responses in each category while keeping the stimulus physically constant.

One study explicitly set out to compare ERPs for all four PAS categories, using low-contrast stimuli at detection threshold (Tagliabue, Mazzi, Bagattini, & Savazzi, 2016). It found that both the VAN and LP amplitudes correlated linearly and positively with PAS ratings (see Fig. 6). Given that the P3, as evidenced by many of the studies reviewed here, is likely to reflect post-perceptual processes rather than consciousness as such, the authors suggest that the increase in LP amplitude might index "different levels of accumulation of sensory evidence", in line with Melloni et al. (2011), or "working memory update", in line with Polich (2007) (Tagliabue et al., 2016, p. 8).

Windey, Gevers, and Cleeremans (2013) observed that studies producing results that favor a graded view of consciousness have usually used simple stimuli (such as simple shapes and colors) and tasks (e.g., simple detection), while studies supporting a dichotomous notion of consciousness typically employed more complex stimuli (e.g., letters and words) and tasks (e.g., word identification and object categorization tasks). They suspected that what they call the "level of processing" affects the distribution of visibility ratings on PAS and similar scales. In a masking study, they gave their subjects both a low-level and a high-level task (color identification and numerical judgments, respectively), but used identical stimuli (colored numbers) in both tasks.

Visibility ratings were obtained using the PAS. The results confirmed their suspicion and led them to put forward a "levels of processing hypothesis": low-level stimuli and tasks exhibit "a graded relationship between stimulus duration and visibility" and yield

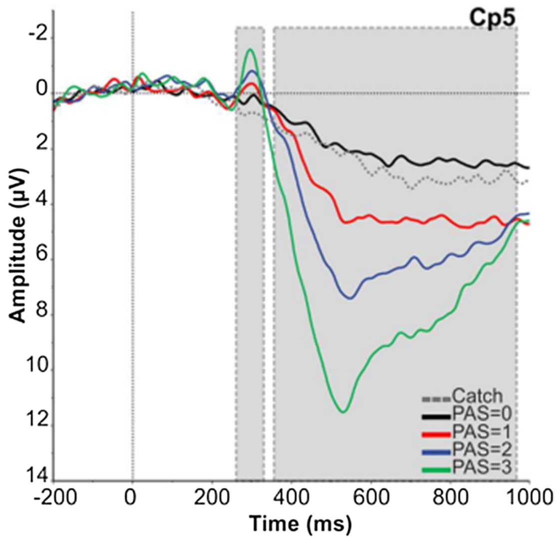

Fig. 6. Both VAN and LP amplitudes co-vary linearly with PAS score. Reprinted from Frontiers in Psychology 7, Tagliabue et al., Early Local Activity in Temporal Areas Reflects Graded Content of Visual Perception, p. 4, 2016.

a linear psychophysical curve when plotting these two parameters against each other, while high-level stimuli and tasks lead to non-linear curves and dichotomous visibility ratings (Windey et al., 2013, p. 404). The "levels of processing hypothesis" integrates the conflicting views in that, according to it, consciousness is neither exclusively graded nor exclusively dichotomous, but both, depending on the level of processing that a stimulus or task demands.

Building upon this insight, a number of researchers have realized that stimulus and task complexity have not been taken into account to a sufficient degree in ERP research on visual awareness, and attempted to remedy this situation. Koivisto, Grassini, Salminen-Vaparanta, and Revonsuo (2017) presented low-contrast stimuli, and used a modified PAS to define distinct thresholds for detection and identification, reasoning that the latter is a more complex task requiring a higher level of processing. The difference between the lowest two PAS ratings ("I did not see any stimulus" vs. "I saw something (but could not identify the stimulus)") defined the detection threshold, while the difference between the latter and the next-higher rating ("I saw the stimulus almost clearly (and could identify it)") defined the identification threshold. Expecting to find both VAN and LP in all aware trials (regardless in which of these two ways "awareness" was operationalized) when comparing ERPs according to these PAS contrasts, to their surprise, the authors found VAN to correlate only with detection, but not with identification, whereas LP correlated with both. More precisely, given that the stimuli had already been detected by the participants when they identified them, and hence the VAN associated with detection was already included in the baseline of the identification condition, the authors found no *additional* VAN to be associated with identification. Although this result does not directly speak to the "levels of processing hypothesis" in that it does not compare PAS distributions at different levels of processing (but instead uses different PAS contrasts to define such levels), it is clearly compatible with it, and pushing in the same direction in that it identifies different ERP correlates for awareness at different levels of processing.

Another study explored the "levels of processing hypothesis" more directly by investigating whether and how the amplitudes of VAN and LP were affected by different levels of processing (Jimenez, Grassini, Montoro, Luna, & Koivisto, 2018). Using backward masking and a low-level target detection task, as well as a high-level number/letter identification task, they found that VAN amplitude varied with PAS ratings in a graded manner only in the low-level task, whereas LP amplitude varied gradually with PAS ratings in both the low- and the high-level tasks. The fact that only VAN was affected by the level of processing suggested to the authors that the level of processing manipulation effects recurrent processing in the visual cortex, maybe modulated by attention. The result that LP varied gradually and never dichotomously is in conflict with the "levels of processing hypothesis"; Jimenez and colleagues propose the interpretation that their "high-level task" was in fact not high enough to produce dichotomous LP amplitude variation, as it involved stimulus identification, but, unlike, e.g., the study by Del Cul et al. (2007), no "higher cognitive and decision-making processes (such as comparison of meanings)" (Jimenez et al., 2018).

Fu et al. (2017) used complex natural scene stimuli in both color photograph and line-drawing versions in a scene categorization task and backward masking at different SOAs, and found that while the VAN amplitude increased variably with PAS ratings, "LP (or P3) amplitudes seemed to change non-linearly with subjective ratings" (Fu et al., 2017, p. 10). They interpret this along the lines of Koivisto and colleagues (see Section 2.3.2), and suggest that VAN reflects phenomenal consciousness, while LP reflects reflective/access consciousness. When taken together with the study by Tagliabue et al. (2016), the results directly contradict those of the study by Jimenez et al. (2018). In the latter, only the VAN was affected by the level of processing, whereas both Tagliabue et al.'s study (which used simple Gabor stimuli) and Fu et al.'s study (which used complex natural scene stimuli) found graded VAN, while the LP was apparently affected by the level of processing (graded for simple stimuli in Tagliabue et al.; dichotomous for complex stimuli in Fu et al.).

A recent study by Windey and colleagues arrived at similar results (Derda et al., 2019). The authors operationalized the "level of processing" differently from Jimenez et al. (2018). Instead of distinguishing a "detection" from an "identification" task, they presented their subjects with colored digits either smaller or greater than 5, and required either a "color judgment" (low level of processing; LL condition) or a "magnitude judgment" (high level of processing; HL condition). While the VAN amplitude correlated with PAS ratings in both the LL and HL conditions, the LP amplitude did so only in the HL condition; moreover, P3 could not even discriminate between seen and unseen trials in the LL condition. The result, which squarely contradicts the one arrived at by Jimenez and colleagues, shows that it is crucial to give a precise meaning to the phrase "level of processing" and operationalize it in comparable ways in order to avoid confusion.

It has rightly been noted that one has to be careful in specifying precisely which aspect or aspects of consciousness one takes to be graded or dichotomous (Windey & Cleeremans, 2015; Windey, Vermeiren, Atas, & Cleeremans, 2014). A graded notion of consciousness is often associated with RPT (e.g., Windey et al., 2013, p. 405), while GNWT is taken to be committed to a dichotomous concept of awareness. However, such a view is actually too simplistic. The proponents of GNWT have refined their notion of access and put forward the "partial awareness hypothesis" (Kouider, de Gardelle, Sackur, & Dupoux, 2010). According to this hypothesis, the *mechanisms* of consciousness operate in an all-or-none fashion, while what they provide access to is a hierarchy of representations of a given stimulus on different levels of coarser or finer detail. These levels can be accessed independently of each other (depending on signal strength and other factors, such as expectations), giving rise to a *phenomenology* of conscious access that is gradual rather than dichotomous. As for RPT, contrary to what, e.g., Timmermans, Windey, and Cleeremans (2010) read into Lamme's account, there does not seem to be an intrinsic connection between RPT and graded awareness; in fact, Lamme can be read as advocating something very close to the "partial awareness hypothesis": "The theory predicts that as soon as you have modules representing different aspects of a scene engage in recurrent interactions, you will have a core of conscious sensation linked to whatever is represented by these modules. Adding more modules—of a lower or higher level—makes the conscious sensation of a richer content, but not more or less conscious" (Lamme, 2010b, p. 235). If the outputs of these "modules" are understood as representations at different levels of detail, as described by Kouider et al. (2010), then the only obvious difference to the latter's "partial awareness hypothesis" lies in the

Table 2
Results of the Review of MEG Studies for VAN (N2 range) and LP (P3 range).

Manipulation	Study	Enhanced early negativity (N2 range)	Enhanced late positivity (P3 range)
Contrast	Liu et al. (2012)	Yes	No
Masking	Andersen et al. (2016)*	Yes/Yes/Yes*	No/No/No*
	Wyart et al. (2012)	?	?
Threshold duration	Sekar et al. (2013)	Yes/Yes	Yes/Attenuated
Bistable perception	Sandberg et al. (2013)	Yes	Attenuated
	Sandberg et al. (2014)	Yes	Attenuated

Note. For each study, we report which of the two relevant MEG correlates (the equivalents of the ERP components VAN and LP in terms of both temporal occurrence and scalp distribution) have been found. In the case of two or more entries, the studies have employed more than one experimental condition. *) The study by Andersen et al. (2016) used multivariate pattern analysis instead of classical analysis of ERP/ERF time ranges; note that therefore, strictly speaking, the study does not satisfy the inclusion criteria for this table. We include it nonetheless because the authors explicitly relate their results to the VAN and LP time ranges. ?) The MEG correlates found by Wyart et al. (2012) resembled VAN and LP, but their timing is too early to identify them with these components.

mechanisms taken to be responsible for conscious awareness—local recurrent processing vs. distributed global workspace activation.

Overall, it seems that more work needs to be done before the issue of graded vs. dichotomous awareness can be settled—both empirically, as the ERP results reviewed here do not speak unequivocally for either view (nor is it clear just how they should be interpreted with regard to the "levels of processing hypothesis"), and theoretically, as neither the exact relationships between the "levels of processing" and the "partial awareness" hypotheses, nor the relationships of both RPT and GNWT to either of them have been explicated in sufficient detail. The conflicting results of two MEG studies (Andersen et al., 2016; Sekar, Findley, Poeppel, & Llinás, 2013), to be reviewed in the next section, add to this ambiguity.

In sum, new developments in research on ERP correlates of visual consciousness abound and raise more questions than they answer. However, among the questions that they *do* answer is the one about the earliest and most reliable correlate: the VAN, or visual awareness negativity, is the most promising candidate for a genuine NCC, while the occurrence of the later LP is far more contingent on reflective, post-perceptual processes.

3.3. A review of recent MEG studies on the correlates of visual awareness

This section reviews seven MEG studies that have been carried out on the correlates of visual consciousness since 2010. The inclusion criteria are the same as above for the ERP studies. As can be ascertained from Table 2 below, the results are even more univocal than the ERP results: all but two of the studies found VAN in all aware conditions, and none of them found LP in all aware conditions. This further corroborates the main result of this review. The individual studies are briefly discussed below. Note that "VAN", "LP", and "P3" are primarily the names of ERP components, and that their event-related field (ERF) equivalents are usually given different names. Here, we use "VAN" and "LP" to refer to awareness-related amplitude differences of both ERP and ERF components.

The already mentioned study by Liu et al. (2012) used low-contrast colored gratings in two different orientations and an objective (two-alternative forced choice about stimulus orientation) as well as a subjective task (deciding whether a grating was present). They found VAN and localized it in the lateral-occipital complex (see also Section 2.3.1). Additionally, they found gamma-band oscillations associated with aware trials; as Pitts, Padwal, et al. (2014) have pointed out, however, these probably reflect post-perceptual processes rather than visual awareness. No frontal or parietal activity whatsoever was found to be related to awareness.

The study by Wyart, Dehaene, and Tallon-Baudry (2012) investigated the influence of endogenous spatial attention on conscious awareness. They found an early occipito-temporal correlate of conscious detection at 110–130 ms after target stimulus onset, as well as a later temporo-frontal one at 220–240 ms after target onset. Both were independent of endogenous spatial attention, which manifested itself in a separate component around 100 ms after target onset. The authors concluded that, *contra* Koivisto et al. (2009), visual awareness can be dissociated from endogenous spatial attention. However, whereas the latter had used bilateral stimuli in order to control for exogenous shifts of spatial attention toward stimuli in the "unattended" half of the visual field, Wyart et al. (2012)—like Koivisto and Revonsuo (2007)—failed to provide such control by using unilateral stimuli. The early correlate of awareness found by Wyart and colleagues was graded in the sense that it was modulated by both subjective awareness and physical stimulus presence (or absence), while the late correlate was "all-or-none" in that it was not influenced by the presence or absence of the stimulus. The correlates strongly resemble the VAN and LP except for their highly unusual, far too early timings; consequently, we have chosen to index them with question marks in the corresponding row in Table 2. In any case, the early correlate occurred too late to be identical to the "very early" P1 activity mentioned in Section 2.3 above, which typically occurs even earlier, around 100 ms after stimulus onset (Railo et al., 2011).

Sandberg and colleagues carried out two studies on bistable perception, the only ones in this review. Sandberg et al. (2013) studied face perception during intermittent binocular rivalry (using a face on one eye, and a grating on the other). Usually, in binocular rivalry subjects are continually presented with a different stimulus to each eye. In intermittent binocular rivalry, however, the presentation is interrupted by periods of blank displays of arbitrary duration, up to several seconds. This leads to a drastic reduction of the rate at which the subject's percept alternates, an effect called "stabilization" (Leopold, Wilke, Maier, & Logothetis, 2002). In the classical univariate analysis of event-related fields (ERFs), Sandberg and colleagues found the M170 (the magnetoencephalographic equivalent of the face-specific N170 ERP component) and the P2m (the equivalent of the P3 component in ERP) to correlate with conscious face perception. In an additional multivariate prediction analysis, they applied a machine learning algorithm to detect the time ranges in which the evoked responses were most predictive of conscious perception (in other words, they "decoded" conscious perception from brain activity). This analysis confirmed that activity in the N2 and early P3 time range best predicted conscious face perception, while activity after 300 ms post-stimulus was not predictive at all. Interestingly, these predictions were possible even across subjects, i.e., the time course of brain activity of one subject could successfully predict the onset of conscious face perception in other subjects. Source analysis revealed that fronto-parietal activation was far worse at predicting consciousness than posterior activation, contrary to the findings of Del Cul et al. (2007) and Sergent et al. (2005). The authors note the possibility that this was because these earlier studies compared awareness of a stimulus with no awareness at all, whereas binocular rivalry studies, by their nature, compare awareness of a stimulus with awareness of another stimulus. In a follow-up study, Sandberg et al. (2014) used the same stimuli to investigate the MEG correlates of conscious face perception, perceptual reversals, and stabilization. Regarding conscious perception, they reproduced the results of their previous study (M170 and P2m).

The remaining two studies to be reviewed here addressed the graded/dichotomous controversy. Sekar et al. (2013) presented numbers (0 to 9) at threshold contrast and obtained visibility ratings using a four-point scale that applied PAS-like rating categories to confidence rather than percept quality ratings. While they acknowledged the potentially important distinction between detection and identification, it made no difference in their ERF analysis: they found both a mid-latency and a late-latency component (i.e., VAN and LP) for aware trials, regardless of the degree of awareness according to the certainty rating. Although the mid-latency component increased gradually with certainty rating, this increase remained insignificant in pairwise comparisons, which the authors interpreted as evidence that consciousness is all-or-none rather than gradual. However, they note the possibility that their study was not sensitive enough to detect more graded nuances, the existence of which is, after all, suggested by the very fact that subjects used the full range of options when rating visibility. The late-latency component had a similar peak amplitude for lowest ("didn't see") and the next-higher ("couldn't identify") visibility rating condition and was thus less reliable as an NCC than the mid-latency component, in which this contrast was significant.

Andersen et al. (2016) used an identification task (diamond vs. square shapes) in combination with the PAS in a backward masking paradigm and applied multivariate pattern analysis to identify the time range and cortical location in which activity was most predictive of graded visual awareness. They compared all three possible conditions resulting from contrasts of contiguous PAS categories, i.e., "no experience"/"weak experience", "weak/almost clear experience", and "almost clear/clear experience". The results were overwhelmingly clear: occipital sources were the only ones to contain information capable of decoding all three PAS contrasts above chance, and "only the VAN time range was associated with a significant increase in classification accuracy" (Andersen et al., 2016, p. 2682). Frontal activity was utterly powerless to predict any but one of the PAS contrasts, as was any activity in the P3 time range.

One noteworthy development visible in recent MEG (and, sometimes, ERP) research is the predictive approach, i.e., the use of multivariate pattern analysis with the help of machine learning algorithms. One strength of this approach is its ability to detect distributed patterns of information that would be difficult to detect by conventional means of univariate analysis of summary statistics such as mean peak amplitudes or latencies (e.g., Sandberg et al., 2013, p. 977). In the study of Andersen et al. (2016), univariate analysis did not lead to statistically significant results, while the predictive approach revealed enhanced activity in the N1-N2 range. Another possible advantage follows from the reasoning that the activity most predictive of conscious awareness is also the activity most likely to reflect consciousness *per se*, as opposed to its prerequisites or consequences (Andersen et al., 2016, p. 2679). However, this reasoning is, of course, not valid for processes that precede (or follow) consciousness *necessarily*, or at least with great regularity.

The multivariate pattern approach can be driven even beyond mere comparison of "aware" with "unaware" trials; in fact, using so-called "mental state decoding", it is possible to decode the specific *contents* of consciousness from neural activity, and thus to arrive at what has been called the "core neural correlates of contents of consciousness (NCCCs)" (Haynes, 2015, p. 1). Applying this approach to EEG and MEG data, Salti et al. (2015) were able to decode the location of a line segment out of eight alternative locations for up to 800 ms both for "seen" and "unseen" trials, with a relative increase of activity in seen trials after 270 ms. The authors also performed a cursory analysis of ERP/ERF time ranges for "seen" vs. "unseen" trials, excluding all "incorrect" trials in order to control for task-performance (as in the studies discussed in Section 3.2.1 above). They found activity both in the N2 and P3 time ranges, albeit with rather untypical scalp distributions for both activation clusters; however, as this analysis was peripheral to the authors' main goals, we do not include its result in Table 2. The mental state decoding approach (Haynes, 2009, 2015; Haynes & Rees, 2006) certainly holds great promise in permitting us to identify content-specific brain activity, and potentially in distinguishing it from activity underlying visual awareness more generally, i.e., independently of specific contents. At the same time, this approach marks the point where it finally becomes impossible to evaluate research on the NCCs along the more conventional lines underlying the simple tabulation of time ranges on which this and earlier reviews relied. This only testifies to the immense diversity and flexibility of the methods available to the study of consciousness, which has not become one bit less exciting since the early days.

Overall, the MEG studies reviewed here confirm the view that VAN and the corresponding MEG correlate are the earliest and most reliable electro- and magnetophysiological correlates of visual consciousness. It seems, then, that the "early" vs. "late" debate is settled—at least as far as this question is concerned. The next section will evaluate the importance of this finding in the broader context of consciousness research.

4. Conclusion

The main empirical result of this review is that no ERP or MEG correlate is more closely related to visual awareness than the VAN. The occurrence and modulation of the LP is far more contingent on a variety of factors, such as task-relevance, expectations, and reports, making it more likely to reflect post-perceptual processes. Furthermore, the P3b can occur during unconscious processing, undermining the claims by proponents of GNWT that it is sufficient to demonstrate the presence of consciousness.

The theoretical implications of this result, however, are less straightforward. It is clear that the empirical evidence clashes with some of the most central predictions of GNWT: the P3b is no reliable marker of consciousness at all; frontal, allegedly workspace-associated activation does not seem necessary for a stimulus to become conscious; there is evidence that consciousness might be gradual rather than an all-or-none phenomenon; and the demonstrably most reliable ERP correlate of consciousness occurs much earlier than GNWT hypothesizes.

This picture appears even more substantiated if one looks beyond the "early" vs. "late" debate. Corresponding to the "early" vs "late" debate, there is a "front of the head" vs. "back of the head" debate (Boly et al., 2017; Koch et al., 2016a; Koch, Massimini, Boly, & Tononi, 2016b; Naber & Brascamp, 2015; Odegaard, Knight, & Lau, 2017; Safavi, Kapoor, Logothetis, & Panagiotaropoulos, 2014; Sandberg, Frässle, & Pitts, 2016), and it is becoming increasingly clear, not least due to the new no-report paradigms, that frontal activation is in fact not necessary for consciousness (Overgaard, 2017), and that awareness-related activation is located in a "posterior hot zone" instead (Koch et al., 2016a). The pioneers of the mental state decoding approach likewise report that their "experiments consistently fail to show any sensory information in the frontal cortex" (Haynes, 2015, p. 16). Evidently, this is in formidable congruence with the source localization results from the ERP and MEG studies reviewed here.

On the other hand, it is not inconceivable that GNWT can be rescued by modifying it sufficiently to accommodate its threatened predictions. As the "partial awareness hypothesis" (Kouider et al., 2010) testifies, GNWT is versatile enough to integrate findings that appear to be incompatible with it at first. Maybe it is possible, then, to drop the P3b as a central signature of consciousness, and fronto-parietal cortex as the central seat of workspace neurons, and still maintain some viable version of GNWT. However, it is doubtful whether this new theory would have enough in common with GNWT to be recognizable as a version of it. The "partial awareness hypothesis" might be a case in point here. On the one hand, it makes room for findings apparently contradicting GNWT's view that consciousness is dichotomous. On the other hand, it still seems committed to broadly distributed fronto-parietal activation even for degraded, lower-level representations to become consciously accessed—otherwise, the concept of a "global workspace" becomes almost empty. If local, posterior activation were sufficient for conscious access, there would remain no meaningful distinction (in terms of localization) between GNWT and other, "local" theories like RPT. It seems, then, that the star of GNWT is waning indeed.

However, this does not mean that the case for RPT has been made conclusively. Although it has a lot of evidence in its favor—not least from many of the studies reviewed here—, there are many ambiguities and unresolved issues, too. For example, it is not yet clear precisely how to interpret the findings that speak for the "levels of processing hypothesis" in the context of RPT. One possibility, favored by some authors, is that recurrent processing can occur in degrees and coincides with the onset of phenomenal consciousness, while the more dichotomous awareness ratings occurring at higher levels of (e.g., semantic) processing reflect the workings of reflective/access consciousness (Jimenez et al., 2018; Koivisto et al., 2017). Windey and colleagues themselves propose the "levels of processing hypothesis" as an integration of central elements of both RPT and GNWT, and thus as a first step toward a new theory that transcends both (Windey & Cleeremans, 2015; Windey et al., 2013, 2014).

For another thing, while the VAN is often taken to reflect recurrent processing, and does indeed correlate well with conscious awareness, even here there remains considerable uncertainty. Many authors are still cautious about addressing VAN as an NCC. In particular, Pitts and colleagues are always careful to point out that "it remains possible that the VAN reflects a particular type of attentional process that is necessary for awareness but not identical (in this case the label "visual awareness negativity" would be premature and potentially misleading)" (Schelonka et al., 2017, p. 68). In fact, they argue that VAN might reflect workspace access, and they still prefer theories that hold attention to be necessary for awareness, such as GNWT, to theories that do not, such as RPT. However, their claim that "[u]nfortunately, the VAN as currently understood cannot distinguish between existing theories of consciousness" (Schelonka et al., 2017, p. 69) seems exaggerated; as we argued above, GNWT would have to be modified almost beyond recognition in order to accommodate all its anomalies.

Finally, it is as yet unclear how to integrate the new theoretical developments with the existing theories. Notably, the predictive coding framework awaits its theoretical connection with both RPT and GNWT. On the empirical side, the role of expectations and its influence on ERP correlates of consciousness, in particular on the VAN, need to be investigated further. Before these steps are taken, it will be premature to pass the final judgment over GNWT and RPT. It is well possible that some new theory will at once integrate and transcend them.

Overall, this review confirms the VAN component as the earliest and most reliable marker of visual awareness, and at the same time it provides an overview of the current state of ERP and MEG research on visual consciousness. New paradigms have unearthed a number of complications, and in a way it seems that the "early" vs. "late" debate has been transformed rather than settled. For example, maybe, consciousness is sometimes early and sometimes late, depending on the presence or absence of expectations (Melloni et al., 2011). Maybe consciousness is early for detection, but late for identification (Koivisto et al., 2017). Or maybe a combination of many such factors influences the timing of the onset of consciousness; and perhaps mental state decoding will reveal subtle differences in timing for different conscious contents. Many are the developments, and there is no shortage of experimental work to be done. New questions abound, and old studies have to be reevaluated in the light of new findings and possible confounds. We hope that this review will help to facilitate new research and spawn new experiments.

CRediT authorship contribution statement

Jona Förster: Conceptualization, Writing - original draft, Writing - review & editing. **Mika Koivisto:** Writing - review & editing, Supervision. **Antti Revonsuo:** Conceptualization, Writing - review & editing, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank two anonymous reviewers for their constructive comments on an earlier version of the manuscript.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.concog.2020.102917.

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