Review

Distilling the neural correlates of consciousness

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ABSTRACT

Solving the problem of consciousness remains one of the biggest challenges in modern science. One key step towards understanding consciousness is to empirically narrow down neural processes associated with the subjective experience of a particular content. To unravel these neural correlates of consciousness (NCC) a common scientific strategy is to compare perceptual conditions in which consciousness of a particular content is present with those in which it is absent, and to determine differences in measures of brain activity (the so called "contrastive analysis"). However, this comparison appears not to reveal exclusively the NCC, as the NCC proper can be confounded with prerequisites for and consequences of conscious processing of the particular content. This implies that previous results cannot be unequivocally interpreted as reflecting the neural correlates of conscious experience. Here we review evidence supporting this conjecture and suggest experimental strategies to untangle the NCC from the prerequisites and consequences of conscious experience in order to further develop the otherwise valid and valuable contrastive methodology.

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1. Introduction

1.1. Contrastive analysis as the key methodological strategy in consciousness research

The problem of consciousness could be approached scientifically only after concrete research strategies were suggested and research problems were defined (Baars, 1989; Crick and Koch, 1990). Since then, an important research goal has been to find the minimal set of neural processes that are together sufficient for the conscious experience of a particular *content* – the neural correlates of consciousness (NCC). This purpose is complementary to the research tradition about general *states* of awareness (e.g., awake, NREM sleep, vegetative state) where consciousness and lack of consciousness are contrasted (Koch, 2004; Laureys and Tononi, 2010). In this paper we deal with the former aspect where NCC are studied in relation to the content of perception as opposed to treating consciousness as a state variable.

When investigating the neural correlates that underlie the content of our consciousness a common and widely accepted strategy has been to hold the stimulus conditions similar while conscious perception varies as the dependent measure – on some trials the subject perceives the target consciously, on other trials not. This experimental approach, known as the contrastive analysis (Baars, 1989), is implemented in various experimental paradigms (Bachmann et al., 2011; Kim and Blake, 2005) and combined with measures of neural activity has brought about important insights into the NCC (Dehaene and Changeux, 2011; Koivisto and Revonsuo, 2010; Rees, 2007; Tononi and Koch, 2008). The asserted advantage of the contrastive analysis is the following: by comparing conscious and non-conscious perception, the NCC can be unraveled without confounding it with unconscious processes involved in target perception that take place in both conditions. However, despite the apparently straightforward logic of this approach the results are inconclusive and contradictory. For instance, some studies report differences between conscious and non-conscious conditions starting already at stimulus onset or around 100 ms post-stimulus (Aru and Bachmann, 2009a,b; Melloni et al., 2007; Pins and Ffytche, 2003), others have only found differences in later phases (>300 ms) (Del Cul et al., 2007; Gaillard et al., 2009). These contradictory results can be understood when considering a severe methodological pitfall: the result of the contrast between trials with and without conscious perception of a target is not only the NCC proper but could also reflect processes that in a particular experiment paradigm, regularly and lawfully, precede and/or follow conscious perception without directly corresponding to the subjective experience (Bachmann, 2009; de Graaf et al., 2012; Melloni and Singer, 2010). These processes need to be distinguished and disentangled from each other before we can understand the crucial neural mechanisms underlying conscious experience. Fig. 1 illustrates the development of enthusiastic proposals as well as critical ideas in the science of consciousness. The recent criticism on the contrastive analysis is expected to pave the way for further positive developments and experimental paradigms that will eventually lead us closer to unraveling the neural processes directly associated with conscious experience.

2. The 3 NCCs

In what follows we recapitulate the two new types of NCCs proposed previously (Bachmann, 2009; de Graaf et al., 2012; Melloni and Singer, 2010): the prerequisites for and the consequences of conscious perception, in short NCC-pr and NCC-co, respectively. We also highlight arguments that support the existence of these processes confounding the search for the NCC. For the sake of clarity we start with the existing definition of the NCC.

## 2.1. NCC for processes directly corresponding to conscious experience

NCC is a neural process that directly corresponds to the phenomenal experience of the target. NCC is the "minimal set of neural events jointly sufficient for a specific conscious experience (given the appropriate enabling conditions)" (Koch, 2004). In other words, if we would stimulate or generate these neural events, a particular conscious experience would happen. Therefore, NCC is the process we need to study in order to understand how conscious experience of a particular content is related to the neuronal processes of the brain. Previously, it has been thought that the contrastive analysis, as commonly used, directly reveals the NCC (Fig. 2a). Recently, however it has been argued that the result of the contrast between trials with and without conscious perception can also be processes that precede or follow conscious perception (Fig. 2b).

2.2. Prerequisite processes carrying no actual conscious contents (NCC-pr)

These processes are different in the conditions ⟨target in consciousness⟩ vs. ⟨target not in consciousness⟩ and participate in determining in the particular experimental setup if the target appears in consciousness, but are not part of the NCC (Bachmann, 2009; de Graaf et al., 2012). There are many different processes that can act as NCC-prs. Hence, one particular NCC-pr need not be sufficient or even necessary for generating a conscious experience of the target, but some kind of NCC-pr might be necessary to bring about the very processes of NCC.

In a paradigm with transient stimulation an example of NCC-pr (Fig. 3a and b) is the stochastic fluctuations in the excitability of neurons. For long, it has been recognized that the ability to perceive a weak signal fluctuates over time – an effect that has been exploited by the contrastive method to create conscious vs. non-conscious conditions. However, only recently it was shown that fluctuations of ongoing brain activity, as indexed by the phase of pre-stimulus oscillations, systematically determine these behavioral dynamics (Busch et al., 2009; Mathewson et al., 2009; Monto et al., 2008). The phase of ongoing alpha (10 Hz) oscillations also determines the effectiveness with which a single TMS pulse elicited a phosphene: with a 15% increase in the likelihood of a perceptual outcome (phosphene) between opposite phases (Dugue et al., 2011). This effect was observed over an extended time period (~400 ms), showing that processes correlating with conscious perception of the target clearly precede the experience itself. As all this takes place in the pre-stimulus interval (being it either before stimulus presentation or TMS pulse application), where no conscious experience of the actual target could have emerged, it constitutes a NCC-pr. Other studies relating pre-stimulus activity to subjective reports show that NCC-pr can reflect spontaneous excitability as also indexed by oscillatory power (Ergenoglu et al., 2004; Linkenkaer-Hansen et al., 2004; Romei et al., 2008; van Dijk et al., 2008) and that the NCC-pr can be linked to attention (Thut et al., 2006; Worden et al., 2000; Wyart and Tallon-Baudry, 2009), decision bias (Wyart and Tallon-Baudry, 2009) and potentially other processes.

In the experimental paradigms with sustained epochs of perception (Fig. 3c), NCC-prs can manifest themselves in various ways. For example, for binocular rivalry it was proposed more than a century ago and shown recently (Alais et al., 2010) that adaptation leading to weakening of reciprocal inhibition determines the alternations between competing stimuli. More precisely, neurons coding for the dominant stimulus adapt over time, which in turn weakens the inhibition of the suppressed stimulus, increasing its neuronal responses and thus bringing that stimulus into consciousness. Importantly, (reciprocal) inhibition could be seen as NCC-pr,
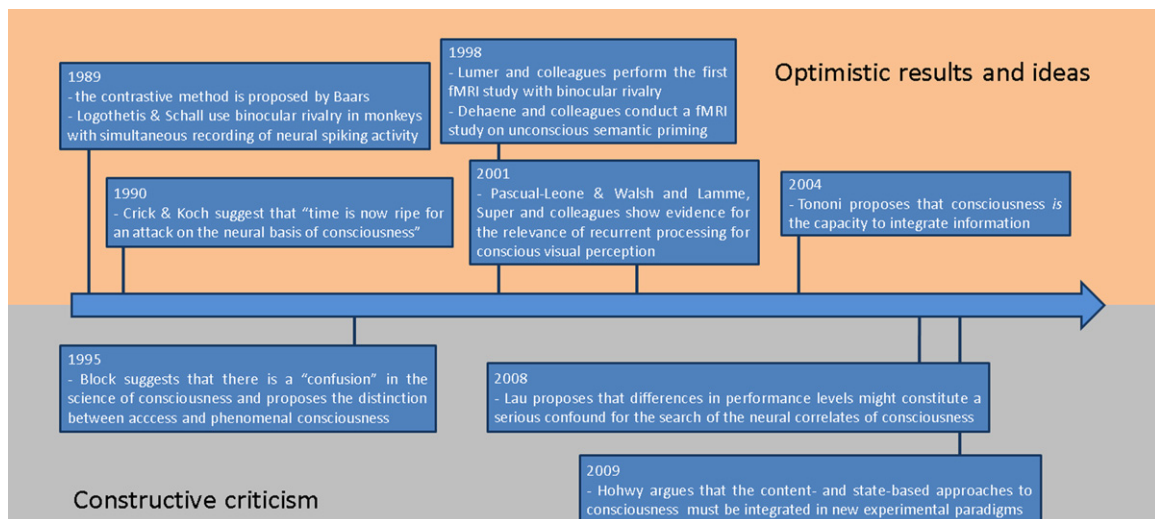
Fig. 1. A time-line of the major events in the science of consciousness. The time-line illustrates that fresh optimistic theoretical and empirical insights are always followed by critical evaluation of these ideas and results. Therefore, the recognition of the problem regarding the prerequisites for and consequences of NCC is a logical corollary of the popularity of the contrastive method in the science of consciousness. The acknowledgement of the problem should be followed by clever experiments trying to separate the prerequisites for and consequences of conscious perception from the processes that reflect NCC directly. (The selection of the events for the time-line was necessarily subjective and we apologize to all the co-researchers who feel that their work has been neglected.)

as it contributes to which target will be consciously perceived and is different between the two contrastive conditions (a particular target in consciousness vs. not in consciousness). However, it is not part of the neural processes sufficient for generating or maintaining conscious experience of that target.

### 2.3. Consequences following actual conscious experience (NCC-co)

These processes appear as after-effects when NCC is or just has been present, but are not a part of the minimally sufficient mechanisms of the conscious experience of the target. These processes are the consequences of conscious perception (de Graaf et al., 2012; Melloni and Singer, 2010). The existence of such processes is a logical consequence of assigning any function to conscious perception – if conscious perception enables certain processes that unconscious perception does not, these processes would inevitably appear in the contrast between trials with and without conscious perception, even if they are solely the consequences and not the direct correlates of consciousness. Importantly, most theories of consciousness do confer a function to consciousness in the chain of information processing (Seth, 2009), for instance sustained maintenance of information, access to long-term memory, novel combinations of operations, and intentional behavior.

For example, it is known that neurons in the medial temporal lobe (MTL) respond in all-or-none fashion, closely following the subjective report of the patient (Quiroga et al., 2008). The fidelity with which MTL neurons follow the subjective visibility of the stimuli is so high that conscious versus non-conscious trials can be distinguished solely based on the neurons' firing rate: either the neuron responds when the subject reports to have consciously recognized the picture, or stay completely silent when the image did not reach consciousness. However, damage to the MTL-system (or even its complete resection) does not affect moment-to-moment conscious perception (Crick and Koch, 1990; Postle, 2009), but only the formation of a memory trace. That is, subjects will continue to have subjective experience but will have no memory of it. Therefore, such all-or-none responses in MTL, even though closely following the subject's report, do not correspond to the NCC but are instead part of the NCC-co reflecting processes related to memory consolidation.

In addition, NCC-co processes can also reflect differences in performance. Usually, conditions in which subjects are conscious of the stimuli correlate with higher performance (for instance higher detectability or discriminability) than when subjects are not conscious of the stimuli. Thus, it has been claimed that a part of the brain activity observed using the contrast between conscious and non-conscious perception pertains to differences in performance instead of conscious experience (Lau, 2008). Direct evidence for this claim comes from a recent neuroimaging study (Lau and Passingham, 2006) reporting that when performance was equalized between conditions, so that only subjective experience varied, only dorsolateral prefrontal cortex distinguished conscious from unconscious conditions as opposed to the extensive fronto-parietal network typically reported in previous studies (Dehaene and Naccache, 2001). Recent studies in which performance was assessed alongside with subjective experience further confirm that these two processes can indeed dissociate in time, space and, importantly, in neural locus (Hesselmann et al., 2011; Lamy et al., 2009; Schwiedrzik et al., 2011). This highlights that performance and subjective experience are not interchangeable and that to investigate NCC proper, performance has to be controlled for.

2.4. The 3 NCCs: conclusions

Thus, despite the principal methodological importance of the contrastive analysis, the method, as commonly used, seems to lack the required specificity to unravel the neuronal processes exclusively related to the subjective experience. In fact, simply contrasting conscious to non-conscious conditions could also reflect processes preceding or following the NCC. The problem exists in all experimental paradigms currently used to investigate consciousness (Fig. 3), regardless of whether differences in conscious perception result from internal switches in brain states, such as in binocular rivalry, or from external manipulations of visibility, as for example achieved by varying the SOA in masking experiments. It is conceivable that the distinction between the 3 NCCs also applies to studies in which different states of consciousness are contrasted (e.g. deep sleep vs. waking or vegetative state vs. minimally conscious states), as these conditions do not exclusively differ in the consciousness state (which is the intended manipulation), but could also do so in their prerequisite processes and
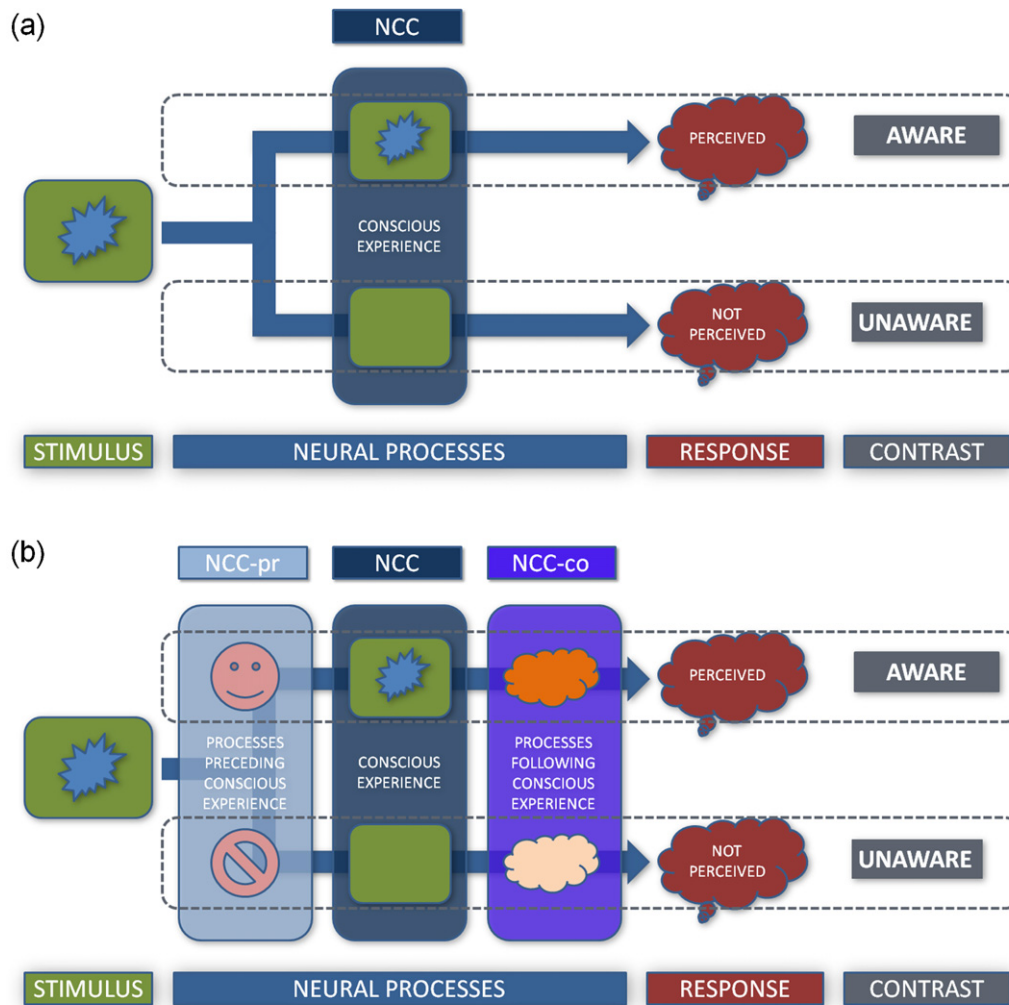
Fig. 2. Neural processes revealed by the contrastive analysis. In the contrastive analysis, a stimulus (here a blue "splash") is presented so that it sometimes appears in conscious experience and sometimes not. On each trial the subject gives a response indicating whether the stimulus was consciously perceived or not. Neural processes are sorted according to the subjective responses to "aware" and "unaware" conditions, which are compared to each other. What neural processes can be the outcome of this contrast? (a) The traditional view on contrastive analysis assumes that the only difference between these conditions is the subjective experience of the stimulus. Thus, the contrastive analysis appears suitable to reveal the neural correlates of subjective experience (NCC). (b) The proposed interpretation of contrastive analysis. According to this view the outcome of contrastive analysis consists besides the NCC of two other processes – NCC-pr and NCC-co. NCC-pr corresponds to unconscious processes that though related to conscious perception of a stimulus (e.g., attention that enhances weak information to cross the threshold of consciousness) appear before any subjective experience emerges. NCC-co represents the consequences of consciously perceiving the stimulus. Consequently, if this view is correct, the traditional contrastive analysis by itself cannot exclusively reveal the NCC because it confounds NCC with these other processes that do not directly correspond to the conscious experience of the stimulus.

especially in the consequences (in the conscious state people think, access long-term memory, have intentions etc.). It will be necessary to determine if and how much the 3 NCC problem applies to other areas of research where conscious experience is investigated (e.g. studies of conscious intentions, introspection, imagery, dreams, inner speech etc.).

This conjecture implies that previous results based on the contrast between trials with and without conscious perception of a particular content cannot be unequivocally interpreted as reflecting the NCC, as they could also represent other processes. Given that the majority of studies investigating consciousness have used such contrasts (Dehaene and Changeux, 2011; Koivisto and Revonsuo, 2010; Rees, 2007; Rees et al., 2002; Tononi and Koch, 2008) such reinterpretation might have a major impact on consciousness research and on current theories on the neural mechanisms of consciousness. As long as the NCC proper cannot be clearly dissociated from these other processes, we should be cautious when relating any experimental finding about neural processes correlating with conscious experience to the NCC. Therefore, if we want to proceed

in understanding consciousness, the NCC has to be experimentally distilled from the prerequisites for and the consequences of conscious perception. As mentioned above, the problem of 3 NCCs may also apply to other areas in the study of conscious experience besides the investigation of conscious perception. Here we focus on the latter as it constitutes the best studied aspect of conscious experience. However, it might prove fruitful to apply the concept of 3 NCCs also to these other aspects of conscious experience as alternative solutions to disentangle the 3 NCC conundrum might emerge from that research.

3. Distilling consciousness: disentangling the NCCs

There is probably no single experiment with today's research techniques that would yield a clear separation between NCC and NCC-pr or NCC and NCC-co. As discussed above, the contrast between trials with and without conscious perception of a particular content does not dissociate these processes. In what follows, we propose research strategies to separate the NCC from the
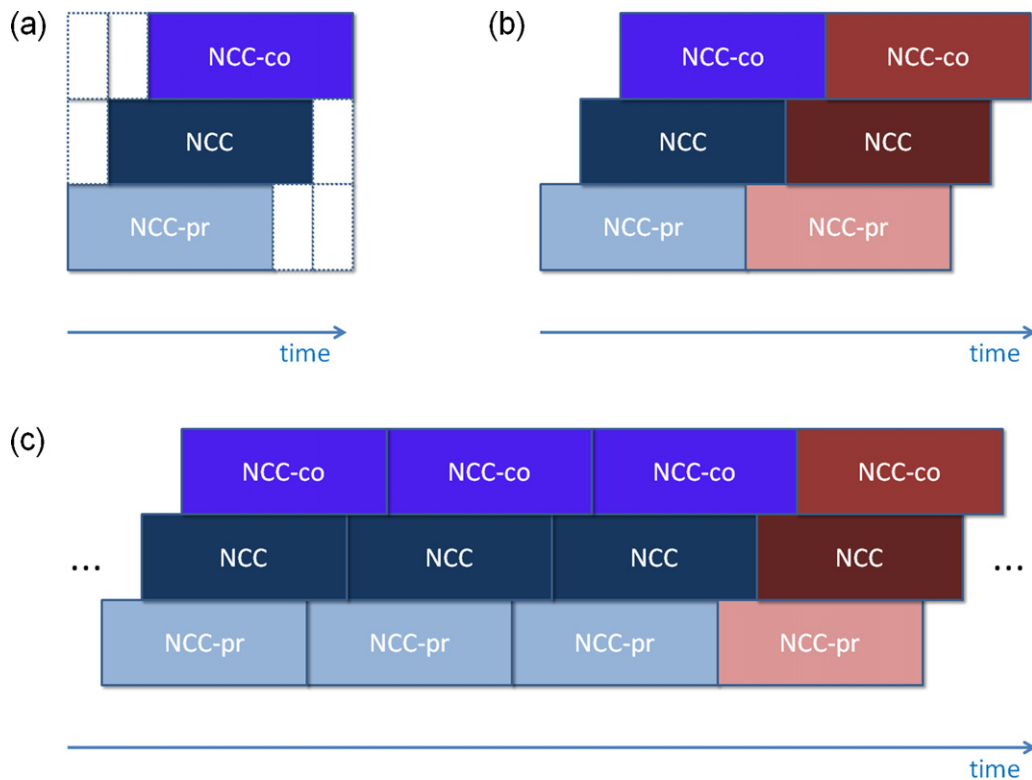
Fig. 3. Possible temporal relationships between NCC, NCC-pr and NCC-co in various experimental situations. (a) If a single transient stimulus is presented, NCC-pr, NCC and NCC-co are evoked. Areas with dotted outlines indicate that the temporal differences and overlap between the 3 NCCs is currently unknown. This scenario corresponds to experimental paradigms like threshold stimulation. (b) If two (or more) transient stimuli are presented sequentially, the different NCCs of these different stimuli can be overlapping in time. This scenario corresponds to experimental paradigms like masking or attentional blink. (c) In experimental situations with longer epochs of perception, each epoch can be understood as a succession of the transient events (as in a), where the NCC of time point t can overlap with NCC-co from time point $t-1$ and NCC-pr from time point $t+1$. This scenario corresponds to experimental paradigms like binocular rivalry or motion induced blindness. Similar ideas on the temporal overlap of the processes unfolding within pre-conscious and conscious stages of percept formation have been also proposed previously (Brown, 1988).

NCC-prs and NCC-cos (see also de Graaf et al., 2012; Melloni and Singer, 2010). Success in understanding the neuronal processes directly underlying conscious experience rests upon distinguishing and disentangling its confounds.

3.1. Disentangling NCC-pr from NCC

There is no question that processes differentiating conscious from non-conscious stimuli already before stimuli onset correspond to NCC-pr. Beyond that, difficulties begin. As NCC-pr can potentially appear after stimulus onset but also concurrently with NCC, there is no simple time criterion that separates NCC-pr from NCC. Furthermore, an interesting theoretical but also empirically challenging problem arises when considering that the NCC-pr do not only have to appear before the NCC but can also stay active during the NCC (Fig. 3). If NCC-pr is there only to "ignite" NCC by preceding it, the empirical study and measurement of NCC is tractable because later epochs of target experience in long-duration target stimuli are not confounded with NCC-pr. However, we currently lack the required knowledge about the NCC-prs to make any claims about their duration or temporal structure.

The most straightforward way to disentangle NCC-pr from NCC is to directly manipulate the NCC-pr processes, and compare the neural signatures that are common to all of them. We assume that different NCC-pr would elicit distinct neural activities, while neural process directly involved in consciousness would be invariantly present in all conditions. As an example, consider a "consciousness task" in which a stimulus under identical stimulation conditions (e.g., a masking experiment with invariant masks and SOAs) is sometimes consciously perceived and sometimes not. As discussed above, this approach would lead to the problem of 3 NCCs. However, now, in an additional step, in the same experimental setup with the same stimuli, we could vary potential NCC-prs such as for instance stimulus expectation, adaptation, working memory or allocation of attention independently. Specifically, in one condition stimuli could be brought to consciousness through expectation (Melloni et al., 2011) and in another through attention (Wyart and Tallon-Baudry, 2008). Which neural processes resulting from the contrast ⟨consciously perceived⟩ vs. ⟨not consciously perceived⟩ are *similar* and which ones are *different* in these two conditions? Neural signatures that differ between conditions should belong to the NCC-pr; neural signatures common to both comparisons are likely to be related to the NCC. Using such an approach, it was recently shown that short-latency event-related potentials previously related to conscious perception (Pins and Ffytche, 2003) most likely represent signatures of the NCC-pr (Melloni et al., 2011) as opposed to NCC. Contrasting attention with expectations might be particularly revealing, as these processes are proposed to have opposite effects on neural activity – attention increases sensory responses whereas expectation decreases them (Summerfield and Egner, 2009). Thus, neural processes that increase with attention but decrease with expectation under similar subjective experience and objective performance are unlikely to reflect the NCC proper.

In addition to cognitive factors, one could affect NCC-pr in a similar vein with TMS. In a recent experiment it was observed that when the visual cortex was stimulated 100–120 ms after a near-threshold visual stimulus with TMS intensity below the phosphene threshold, the thresholds for explicit perception of the visual stimulus were decreased (Abrahamyan et al., 2011). In line with the experimental strategies proposed above, one could combine this TMS-related

improvement of perception with an independent cognitive manipulation (e.g. of attention or expectation) that also has a beneficial effect on perception and measure the neural correlates of conscious perception with the same logic as presented previously: only neural signatures related to perceptual enhancement common to both manipulations are likely to be related to the NCC.

3.2. Disentangling NCC-co from NCC

As with NCC-pr, one cannot straightforwardly rely on a strict temporal distinction between NCC and NCC-co. Probably correlates that appear 2 s after the onset of a 30 ms stimulus indeed represent NCC-co, however, the critical question refers to neural correlates appearing earlier than 500 ms post-stimulus as the bulk of studies have related those to NCC (Del Cul et al., 2007; Fisch et al., 2009; Gaillard et al., 2009; Koivisto et al., 2008; Melloni et al., 2011; Sergent et al., 2005). Neurons in the MTL have a latency of about 300 ms MTL (Quiroga et al., 2008). If we are right in stating that the activity of MTL neurons, even when apparently closely following the subjective report, is not the NCC but constitutes the NCC-co, it becomes evident that the NCC-co can be present already in a time window that is often investigated for the NCC.

According to the definition, the NCC-co corresponds to the aftereffects of conscious perception. Thus, it is logically possible to observe NCC even when NCC-co is not elicited. In the normal brain such a dissociation might not occur very often; however, lesion studies might be revealing: if an area can be lesioned or removed without any effect on conscious perception, then activation of this area can be regarded as NCC-co. This approach allowed, for instance, ruling out activity in MTL as a direct NCC (Crick and Koch, 1990; Postle, 2009). Importantly, the tests applied to identify NCC-cos have to be sensitive enough to capture subtle effects on conscious perception. For instance, although the view that prefrontal cortex (PFC) is causally relevant for conscious perception (Dehaene and Changeux, 2011) could at first have been rejected based on lesion studies (Pollen, 1999), it has gained support from carefully conducted studies exploiting the masking paradigm in patients with PFC lesions (Del Cul et al., 2009). Nonetheless, the fact that the psychophysical threshold for conscious access is elevated in patients with PFC lesions cannot be taken as direct evidence of PFC having a central role in conscious perception. Instead, PFC could provide top-down support for either strengthening or maintaining the (cognitive results of the) conscious percept (Gazzaley et al., 2007; Miller et al., 2011). This is a likely possibility as patients could perform the difficult masking task relatively well and were reporting conscious perception despite their PFC lesion.

Lesion studies can be complemented with interventional techniques in healthy subjects, such as TMS (see also de Graaf et al., 2012) and/or transcranial direct or alternating current stimulation (tDCS or tACS). This approach offers several advantages over lesion studies. First, it allows for comparisons within the same individual, as TMS can be applied in an on–off manner. Second, due to the transient nature of the intervention, profound reorganization of brain networks is not to be expected. This allows dissociating effects related to lesioning a particular area from alterations at the level of the network resulting from compensatory plasticity. Third, virtual lesions can be made with a precision not comparable even when performing probabilistic lesion mapping studies in patients. Furthermore, virtual lesions can be made not only of a single region, but also in several regions at the same or at varying times. Combined with neuroimaging, one could first find a neural signature X that correlates with conscious perception in the contrastive analysis (e.g. the activity in the frontal cortex) and then in a second step test whether perturbation of this signature X (e.g. by TMS) has an effect on conscious perception. If such perturbation produces no effects on conscious perception, the respective process or area is a prime candidate for NCC-co. However, to firmly conclude that, evidence has to be provided that such manipulation has a behavioral effect. Otherwise, it is unclear whether the effect was not observed because the perturbation is simply ineffective, or it specifically does not affect conscious perception. The feasibility of such selective manipulation has been recently shown: theta-burst TMS to bilateral dorsolateral PFC interfered with metacognitive aspects of visual awareness but not with discrimination performance (Rounis et al., 2010).

Besides interventional approaches, much progress could be made by (i) obtaining comprehensive data on the sequence of cognitive events distinguishing conscious from unconscious processing, assuming that causes precede effects, and by (ii) considering theoretical approaches which clearly disclose some cognitive processes (e.g. working memory) as dependent on conscious perception (Baars, 1989). This is particularly relevant as it allows for contrasts in which not only consciousness is manipulated (e.g., aware vs. unaware trials) but also its consequences (e.g., conditions in which encoding in working memory is present or absent). Following such an approach, it was recently shown that late electrical signatures of consciousness, in particular the P3 event-related potential typically associated with conscious access (Dehaene and Changeux, 2011), does not follow conscious perception when subjects already have a conscious working memory representation of the target stimulus (Melloni et al., 2011). This result points to the tantalizing possibility that late waves of EEG activity such as the P3 might reflect NCC-cos, and not the NCC itself.

4. The 3 NCCs and previous results

In light of the ideas proposed here, an important question is whether previous findings reflect NCC or rather NCC-pr, NCC-co or even a compound of these different processes. Since little is known about the NCC-pr and NCC-co and how they interact with the NCC proper, it is currently not straightforward to determine which results indeed relate to NCC and which ones do not. A first step is to identify and recognize the neuronal signatures of processes that might *not* reflect the NCC.

Importantly, many current theories of consciousness are founded on empirical findings, assuming that these genuinely reflect the NCC. As shown, this assumption might not hold true. Thus, it is possible that some theories about the NCC are actually based on NCC-prs or NCC-cos. Clarifying this issue will hopefully lead to better agreement among theories of consciousness. Note that we do not suggest that all previous findings are necessarily wrong or doubtable, nor do we claim that all theories are based on the wrong assumptions about the previous results; we simply point to the worrisome possibility that follows the theoretical distinction between the 3 NCCs. In the next paragraphs we link this theoretical problem to existing results from the contrastive analysis with the hope that the recognition of the 3 NCC problem will contribute constructively to the disputes about the timing and neuroanatomical locus of conscious perception.

4.1. The 3 NCCs and the temporal course of conscious perception

The distinction between the three NCCs could prove valuable to resolve some controversies regarding the question whether conscious perception happens early (Aru and Bachmann, 2009b; Melloni et al., 2007; Pins and Ffytche, 2003) or late (Del Cul et al., 2007; Gaillard et al., 2009; Sergent et al., 2005), as some of the studies observing early correlates might reflect NCC-pr while those reporting late correlates might reflect NCC-co. In a recent study, such an approach was purposely followed: the processes related to NCC-pr and NCC-co were manipulated in an attempt
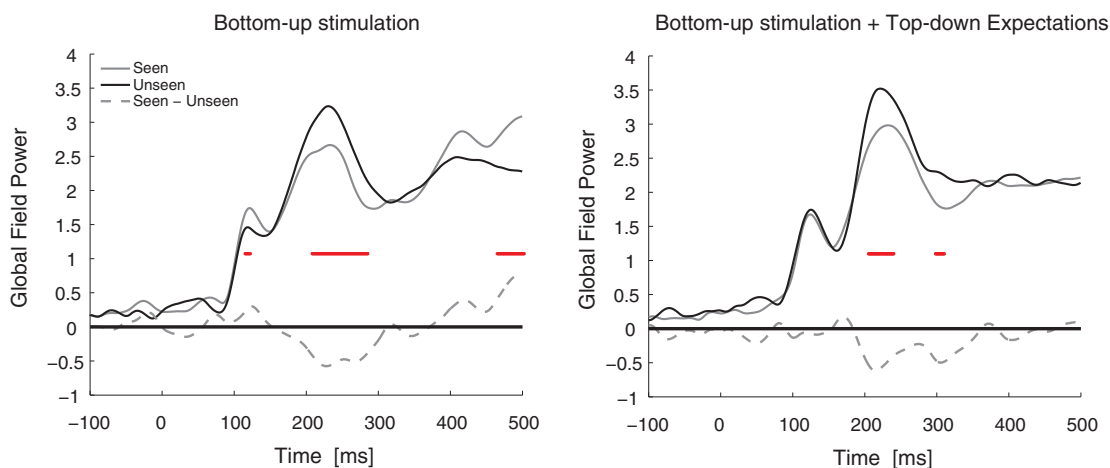
Fig. 4. Neural signatures of conscious perception: NCC-pr, NCC and NCC-co. In the study of Melloni et al. (2011), both the pre-requisites and the after-effects of conscious perception were manipulated. Subjects had to rate the visibility of a stimulus embedded in noise. Visibility could either arise because of the strength of sensory evidence (left panel) or because of the presence of perceptual expectations (right panel). In these conditions, the prerequisites (NCC-pr) differed, but conscious perception was identical. Furthermore, a conscious working memory representation of the target could already be present (left panel) or absent (right panel). Here, conscious perception was again equalized, but the consequences (NCC-co) differed, since in the latter case, a new representation needed to be encoded in working memory. The red bars indicate the periods of significant difference between the aware and unaware trials. The only component differentiating consciously perceived from not consciously perceived trials independently of differences in NCC-pr or NCC-co was a mid latency component, likely reflecting neuronal processes directly involved in the NCC. In contrast, early processes differentiating seen from unseen stimuli were not present when consciousness resulted from an interaction between sensory evidence and top-down expectations. Also, the late ERP component was only present when a working memory representation had to be established. The fact that some neural signatures of consciousness disappeared when either the prerequisites or consequences of consciousness were manipulated questions the general involvement of these processes in conscious perception.

to more directly address neuronal processes related to the NCC itself (Melloni et al., 2011). To investigate NCC-prs, Melloni et al. (2011) examined how sensory evidence and top-down expectations, respectively, influence the threshold of awareness, and whether the two factors modulate brain activity differently. This allowed contrasting brain states with and without expectations and with perceived and non-perceived stimuli for identical stimulation conditions. To investigate NCC-cos, conditions based on whether the target was or was not present in working memory were compared. As in previous studies (Mathewson et al., 2009; Pins and Ffytche, 2003) it appeared that in the absence of expectations an early event-related potential (ERP), already present around 100 ms in occipital sensors, distinguished conscious from unconscious trials (Fig. 4). Perception under those circumstances is known to depend on bottom-up stimulation (the amount of sensory evidence) and stochastic fluctuations in the prestimulus period which jointly determine whether a target will or will not be consciously perceived (Busch et al., 2009; Mathewson et al., 2009). However, in the presence of expectations, that is, when perception depends not only on bottom-up information but also on top-down expectations, this early component was not different between the consciously perceived and not perceived targets. As both conditions resulted in similar rates of visibility, this finding suggests that early processes differentiating seen from unseen stimuli – previously interpreted as a NCC – were actually not directly related to subjective experience, but reflect differences in NCC-pr (Fig. 4). Along the same lines, a late ERP (P300) distinguishing consciously perceived from not consciously perceived trials was only observed in trials where the target had to be encoded in working memory but not when subjects already had a conscious working memory representation of the target. This suggests that late effects like the P300 can index processes related to the NCC-co instead of the NCC proper under certain conditions (Fig. 4). At threshold, the component most consistently related to conscious perception was the P200, arising at about 200 ms over occipitoparietal sensors. This study also revealed that the electrophysiological signatures of conscious perception are not bound to processes with a strict latency, but depend on how consciousness comes about: earlier electrophysiological signatures were observed in the presence of top-down expectations (P200)

than in their absence (P300). This further complicates the search of the NCC, as they might change in time depending on which NCC-pr determines perception.

Converging evidence for the proposed temporal relationships between NCC-pr, NCC and NCC-co comes from studies with intermittent binocular rivalry. In this paradigm, epochs of binocular rivalry stimulation alternate with blank intervals, which allows to study neural processes locked to the stimulus onset and to delineate the sequence of neural events related to bistable perception. Interestingly, Pitts and Britz (2011) when reviewing recent studies employing such methodology come to similar three time windows related to conscious perception as we did based on a different experimental paradigm described above (Melloni et al., 2011): (1) early processes around 130–160 ms after stimulus onset that vary with conscious perception but probably constitute a preconscious state (in the current terms the NCC-pr), as although this component varies with the subjective percept (Pitts et al., 2010), the stable perceptual representation of the target has not emerged yet (Pitts and Britz, 2011), (2) the "reversal negativity" around 200–300 ms that is a "primary candidate for a neural correlate of awareness" (Pitts and Britz, 2011), as there the stable representation has been established and (3) the late positive complex around 400–600 ms that might reflect further processing of the perceptual information or processes related to working-memory maintenance (NCC-co in the current terms).

4.2. The 3 NCCs and the activity of different brain areas

Regarding the neural locus of consciousness it is also debated whether conscious perception is associated with activity in sensory areas (Hesselmann et al., 2011; Lamme, 2006; Zeki, 2001) or whether higher non-sensory areas are directly involved in conscious perception (Dehaene et al., 2006; Lau and Rosenthal, 2011). In this context, several previous studies are directly relevant for understanding whether particular brain areas such as the prefrontal cortex serve a crucial role in conscious perception, as proposed in some theories (Dehaene and Naccache, 2001; Lau, 2008), or whether they reflect other cognitive processes, such as top-down control, report, or performance on a task. The

available evidence relating PFC activity with consciousness has been obtained by contrasting conscious vs. non-conscious trials (Dehaene and Changeux, 2011). The key message of our proposal is that by solely relying on the contrast between trials with and without conscious perception of a particular content it is undetermined whether such activation indeed constitutes an NCC or rather a consequence of conscious perception (NCC-co). In line with this conjecture, when subjects do not need to report the stimuli, differential activity between conscious and non-conscious stimuli is not observed in the prefrontal cortex but only in occipital visual areas downstream of V1/V2 (Tse et al., 2005). In addition, activity in prefrontal cortex is suppressed when subjects are engaged in a demanding perceptual categorization task, although they are presumably fully conscious of their rapidly changing visual or auditory world during that time (Goldberg et al., 2006). Finally, although TMS over frontal cortex affected voluntary control of bistable perception, TMS had no influence on passive bistable perception (de Graaf et al., 2011), which conforms nicely with the approach proposed in Section 3.2: TMS had a measurable effect on one process (voluntary control) but not on conscious perception. These results directly support the thesis that prefrontal activity might not be a part of the NCC but could rather represent processes that follow conscious perception as consequences.

In another relevant study, Eriksson and colleagues (Eriksson et al., 2008) found that prefrontal activity and coupling between prefrontal and occipital areas decreased after training in an identification task. This result might imply that at least part of the prefrontal activity observed in contrastive analysis could be attributable to the fact that in such paradigms, conscious recognition is often made difficult (e.g. by masking or by lowering the contrast of the stimuli) and PFC might be recruited to aid the recognition process under poor sensory evidence (Eriksson et al., 2008). From this perspective PFC activity could constitute a NCC-pr, as prefrontal activity would determine whether the target reaches consciousness or not. This idea agrees with theories and empirical evidence suggesting that short-latency prefrontal activity facilitates perception (Bar, 2003; Bar et al., 2006). Alternatively, it could be argued that PFC activity represents NCC-co (instead or in addition to the NCC-pr) that change as a function of perceptual training. In particular, extensive experience with the stimulus could lead to established memory representations such that there is no need to create working memory representations on each trial, leading to decreased prefrontal activity with training.

All these results challenge the notion that prefrontal cortex is directly involved in visual awareness but suggest instead that it could reflect executive functions, top-down facilitation and/or top-down control under conditions of increased effort. As a number of theories of consciousness (Crick and Koch, 2003; Dehaene and Changeux, 2011; Dehaene and Naccache, 2001; Lau, 2008) assert that activation of prefrontal cortex is part of the NCC, it is clear that the question whether PFC activity is indeed a NCC or rather a NCC-pr or NCC-co is central for further research on the neural correlates of consciousness.

Similar caveats hold true for the involvement of parietal cortex in consciousness. In fact, when using the contrastive method in visual versus auditory tasks, it was found that activity in parietal cortex is correlated with visual but not with auditory conscious perception (Eriksson et al., 2007), questioning its general, modality-independent role in conscious perception. Even further, it is known from the neurological literature that bilateral lesions of the parietal cortex do not abolish conscious perception: although patients exhibiting such lesions are only able to perceive one object at a time (simultagnosia), this one object is nevertheless consciously experienced (Friedman-Hill et al., 1995; Robertson, 2003). These results suggest that the activity of the parietal cortex might not be a part of the NCC. As substantial empirical evidence links the activity of the

parietal cortex to perceptual alternations in paradigms with multistable perception (Kleinschmidt et al., 1998; Lumer et al., 1998), it is likely that the processes in the parietal cortex constitute an essential prerequisite for NCC. This claim is substantiated by recent evidence that TMS to parietal cortex affects the dominance durations during binocular rivalry (Carmel et al., 2010; Zaretskaya et al., 2010) and that the structure of the parietal cortex is correlated with the intraindividual differences in the perceptual alternation rate of a bistable stimulus (Kanai et al., 2010).

Finally, there is a long-standing controversy about the role of primary visual cortex (V1) in conscious perception. Even if V1 lesions lead to loss of awareness in the corresponding parts of the visual field, it constitutes no strong argument for the NCC being in V1, as V1 lesions also disrupt information flow to higher order visual areas. Empirical and theoretical arguments in the mid-1990s suggested that V1 might not be necessary for visual conscious experience (Barbur et al., 1993; Crick and Koch, 1995) but further research and theoretical positions generally favored the idea that cortical feedback to V1 is indeed necessary for visual conscious perception and therefore part of the NCC (Lamme, 2001; Pascual-Leone and Walsh, 2001; Tong, 2003). We believe that the division between the three types of NCC can be fruitful in solving such controversies, as it offers the possibility that although V1 activity correlates with conscious perception (Tong, 2003), it might constitute a NCC-pr rather than be a part of the NCC. Indeed, a recent experiment revisited the issue whether patients with V1 lesion lack visual consciousness (Ffytche and Zeki, 2011) and contrary to what is commonly believed the authors showed that these patients do have visual experiences. Furthermore, clinical studies have shown that conscious vision can recover after a V1 lesion (Silvanto and Rees, 2011). These results imply that neither activity in V1 nor the cortical feedback to V1 is necessary for visual conscious perception. In the current terminology, intact V1 would be an important prerequisite for visual conscious experience, but not part of the NCC. However, it is possible that V1 is not necessary for *all* visual experiences but those involving the *fine-tuned* spatial contrast distribution in the experienced image due to the functional capabilities of V1. Thus, whether some brain area is necessarily involved in NCC may depend not only on its neuroanatomical locus, but also on the specific details of the experience (Haynes, 2009).

Taken together, the tripartite distinction of NCCs calls for a reappraisal of previous results and theories, but also highlights the need of further studies that put emphasis on investigating and distinguishing the pre-conscious determinants of conscious perception (NCC-pr) and its consequences (NCC-co) from the NCC proper.

5. Conclusions

Despite its original simplicity and appeal, the traditional method, contrasting trials with and without conscious perception of a particular target, by itself does not appear to have the necessary specificity to reveal the NCC. Instead, processes that precede (NCC-pr) and follow (NCC-co) conscious perception are confounded with the NCC proper. Here we relied on the theoretical distinction between those processes (Bachmann, 2009; de Graaf et al., 2012; Melloni and Singer, 2010) and suggested tentative experimental paradigms aimed at disentangling these processes from each other.

An important way to circumvent the specificity problem altogether is to move away from mere correlates and focus the search on mechanisms of conscious experience, as correlates which do not have explanatory power can be excluded a priori (Melloni and Singer, 2010). However, the key to success in unraveling the NCC will ultimately lie in combining such mechanistic models that generate testable predictions (Bachmann, 2007; Dehaene and Changeux, 2011; Lamme, 2006; Melloni and Singer, 2010) with

suitable experimental paradigms. Only then we will be capable of putting theoretical proposals to the test. We thus hope that future work, adopting the distinction between NCC, NCC-pr and NCC-co and following the empirical strategies proposed here, will allow us to re-assess previous studies and theories, focus on the NCC, and distill the crucial neural processes that underlie our conscious experience.

Acknowledgments

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