

Review

No-Report Paradigms: Extracting the True Neural Correlates of Consciousness

Naotsugu Tsuchiya,^{1,2,*} Melanie Wilke,^{3,4,5} Stefan Frässle,⁶ and Victor A.F. Lamme⁷

The goal of consciousness research is to reveal the neural basis of phenomenal experience. To study phenomenology, experimenters seem obliged to ask reports from the subjects to ascertain what they experience. However, we argue that the requirement of reports has biased the search for the neural correlates of consciousness over the past decades. More recent studies attempt to dissociate neural activity that gives rise to consciousness from the activity that enables the report; in particular, no-report paradigms have been utilized to study conscious experience in the full absence of any report. We discuss the advantages and disadvantages of report-based and no-report paradigms, and ask how these jointly bring us closer to understanding the true neural basis of consciousness.

Looking for Consciousness in All The Wrong Places?

The Hard Problem of consciousness is how to explain the neural basis of phenomenal experience [1]. Why and how does neural activity give rise to conscious perception? Why are some types of activity, such as recurrent and feedback activity, more strongly associated with consciousness than others [2,3]? Why does the activity and integrity of the thalamo-cortical complex seem crucial for consciousness, while the cerebellum, which has fourfold more neurons than the thalamo-cortical complex, does not [4,5]? These results give hints as to where to look for the **neural correlates of consciousness** (see [Glossary](#)). However, the exact neural underpinnings of conscious experience remain a mystery. Why is it that we still seem unable to solve it?

One of the difficulties in tackling the Hard Problem is that the exact functions of conscious phenomenology remain elusive. Unlike other biological functions realized by the brain, it remains unclear what purpose raw conscious experiences (also termed **qualia** or **phenomenal consciousness** [6,118]) serve (for possible biological functions see [7]). On the other hand, once conscious percepts are attended, remembered, and **cognitively accessed**, they become useful for the control of present and future behaviors and reasoning [3,8] (note that we distinguish **accessibility** from the act of cognitively accessing). Even so, when we study these cognitive aspects of consciousness, do we study the right phenomena? In principle, attention, memory, control, or any other cognitive function can be implemented by clever, non-conscious computational algorithms (e.g., [9]). Hence, even if we understand how our brains cognitively access specific contents of consciousness, this approach seems to leave the core problem of how phenomenology arises from neural activity – in other words the Hard Problem – untouched.

In the now almost two decades of ongoing enthusiasm to study the neural correlates of consciousness (NCC) [3,10,11], the main goal was to first establish a neuroscience of

Trends

To study the neural correlates of consciousness (NCC), some forms of behavioral reports from subjects may seem absolutely necessary. However, strong reliance on reports has biased much of the NCC research towards the search for the neural correlates of perceptual reports.

Stringent requirement of behavioral reports not only overestimates the true NCC, owing to the inclusion of the neural correlates of reports, but also underestimates it because there are some aspects of real conscious experience that are fundamentally difficult to report.

Recent fMRI, EEG, and neurophysiological recordings studies that utilized no-report paradigms successfully purified the putative NCC.

Advantages and disadvantages of report-based and no-report paradigms are discussed. A combination of both will significantly advance the field.

¹School of Psychological Sciences, Faculty of Biomedical and Psychological Sciences, Monash University, Melbourne, VIC 3800, Australia

²Monash Institute of Cognitive and Clinical Neurosciences, Monash University, Melbourne, VIC 3800, Australia

³Department of Cognitive Neurology, University Medicine Goettingen, Robert-Koch-Strasse 40, 37075 Goettingen, Germany

⁴German Primate Center, Leibniz Institute for Primate Research, Kellnerweg 4, 37077 Goettingen, Germany

consciousness, and worry about such more philosophical issues, including the Hard Problem, later [12]. In typical NCC paradigms, researchers record and contrast neural activity between one perceptual state and the other. One of the most powerful NCC methodologies is to hold the sensory input constant while observing how consciousness fluctuates. Fluctuating phenomenology with a constant input can be induced, for example, using perceptual threshold paradigms such as backward masking [13], where subjects discriminate the properties of masked stimuli (e.g., present vs absent, or left vs right orientation). At discrimination threshold, subjective reports vary across trials despite the constant visual input, such that neural activity can be contrasted depending on the reports [14,15]. Another method is the use of ambiguous stimuli [16], where continuous viewing of physically constant stimuli leads to spontaneous alternations of phenomenology over time. In these paradigms, any perceptual changes would not reflect changes in the sensory input. By correlating the reports indicating perceptual changes with fluctuating neural activity, it is assumed that the NCC can be isolated [17]. Although influential, this strategy crucially relies on the subjects' reports that allow experimenters to assess the fluctuating phenomenology of physically constant stimuli.

Recently, however, evidence has been mounting that contrasting two conditions with distinct reports may confound a potential NCC with various cognitive components [18–20], such as attention [21–23], working memory [24,25], or expectation [26,27]. In such cases, the putative NCC is overestimated, in the sense that neural mechanisms not directly generating the experience, but only necessary to report it, are included. There are several ways to control for such report-related confounds [28], including manipulation of the decision threshold of the report [14], changing the report modality from usual verbal reports and button presses to more rare forms of reports, such as finger-pointing, blinks, or eye movements, or using memory-based reports [29,30]. This article highlights 'no-report' paradigms, which avoid these confounds altogether. The results from no-report paradigms suggest that the previously proposed NCCs overestimate the true NCC.

No-Report Paradigms

How can the contents of conscious experience be assessed without reports? Employing decoding of neural signals, researchers have recently assessed the contents of consciousness in the absence of explicit reports from subjects. Some conscious visual contents – images in particular – can be decoded accurately in healthy subjects [31–34] and in some non-responsive patients who are unable to communicate verbally [35]. In these cases it is important to ask to what extent we can be sure that such decoded contents reflect conscious experience – as opposed to unconscious stimulus processing. This means that we run the risk of overestimating the NCC in the other direction, by including unconscious neural processes. We argue that both report-based and no-report paradigms may suffer from over- and underestimation, and for various reasons (Table 1 and Box 1). Thus, each method should be used with caution, and with these potential confounds in mind.

As we argue throughout this article, there are potentially many ways that can bypass the need of overt reports to investigate whether the decoded contents are conscious or not. For example, subjects' perceptual contents can be reliably inferred from physiological measures, such as eye movements or pupil size [36], and they can be reliably manipulated by subtle stimulus changes [37] or by instructions [38,39]. Refining these psychophysical techniques, and applying them to a variety of experimental situations of ambiguous conscious/non-conscious perception, will be an important and fruitful research endeavor for the future (see Outstanding Questions). Once no-report paradigms are established, they will provide extremely powerful tools for studying the neural correlates of conscious perception, compensating for some of the disadvantages of report-based paradigms.

⁵German Research Foundation (DFG) Center for Nanoscale Microscopy and Molecular Physiology of the Brain (CNMPB), Georg-August-Universität Göttingen, 37073 Göttingen, Germany

⁶Laboratory for Multimodal Neuroimaging (LMN), Department of Psychiatry, University of Marburg, 35039 Marburg, Germany

⁷Brain and Cognition, Department of Psychology, University of Amsterdam, Amsterdam Brain and Cognition (ABC), The Netherlands

*Correspondence:
naotsugu.tsuchiya@monash.edu
(N. Tsuchiya).

Table 1. Under- and Overestimation of the NCC in Report-Based and No-Report Paradigms

	Traditional, Report-Based Paradigm	No-Report Paradigm
Possible underestimation of the NCC	Conscious, but forgotten (inattentional amnesia). Conscious, but not reportable (e.g., aphasia, minimally conscious state). Conscious, but below decision criterion. Experience without access.	Some percepts may be experienced only when report is attempted. Contrast of conditions (e.g., not reported percept A vs B) may heavily rely on subsequent memory-based trial categorizations (e.g., later reports of A vs B).
Possible overestimation of the NCC	Inclusion of post-perceptual processes (e.g., executive processes, self-monitoring, report, access). Inclusion of pre-perceptual processes (e.g., prior exposure, attention).	Inclusion of non-conscious processing.
Advantages	Ambiguous stimuli and threshold stimuli can remove stimulus-related confounds.	Can be applied to situations where reports are difficult to obtain (patients, babies, animals, anesthesia, and sleep).

No-Report Paradigms with Ambiguous Stimuli

Binocular rivalry provides an excellent opportunity for researchers to isolate the NCC, discounting the neural correlates of basic stimulus processing [17,40]. Previous fMRI studies have established that perceptual states (i.e., perceiving one or the other stimulus) are correlated with neural activation across various levels of visual processing, as early as the lateral geniculate nucleus [41,42], through V1 [43] and high-level visual areas [44]. Perceptual switches (i.e., the moment the percept is reported to alternate) are correlated with activity in right-lateralized fronto-parietal areas [45–47].

Binocular rivalry is often contrasted with a ‘replay’ condition where perceptual alternations are mimicked by a movie, without inducing genuine rivalry. During replay, right fronto-parietal areas show severely diminished activity as compared to rivalry [45–47], which has been taken as evidence that their contribution is crucial for triggering perceptual alternations. Crucially, when comparing the neural activation between genuine rivalry and its physical replay, there are two possible confounds, both associated with the act of reporting. First, there can be a difference between what subjects actually experience and what experimenters infer subjects to experience based on their reports. Here the problem is that the full variety of perceptual combinations of the two stimuli during genuine rivalry is compressed to a set of two or three response options (buttons). Second, owing in part to the difference in perceptual complexity between genuine rivalry and replay, there is a difference between the two conditions with respect to cognitive demands. Although the motor aspect of reports is equally present in the replay, other factors that minimally affect phenomenal experience (e.g., introspection) can evoke spurious differential neural activity. Two recent fMRI studies have addressed these issues.

Reasoning that the phenomenological complexity of binocular rivalry is not very well captured by traditional replay, a recent fMRI study [48] implemented a more realistic and complex version of the replay, where subjects experienced phenomenology of similar variety as during genuine rivalry. By comparing neural activity during improved replay and rivalry, they found that the right fronto-parietal areas were similarly activated. This suggests that previously reported higher fronto-parietal activation during genuine rivalry may be related to differences between genuine rivalry and poor replay, such as different appearance of the stimuli, attentional allocation, and task demands.

An independent fMRI study [36] arrived at a similar conclusion by first establishing that eye movements (i.e., **optokinetic nystagmus**) correlate tightly with conscious reports of perceptual

Glossary

Accessibility: sensory information is accessible if it can be accessed by other mechanisms in the future.

Accessibility does not imply reportability (e.g., in patients with locked-in syndrome). Broadly speaking, accessibility or neural connectivity between areas imply integrated information between areas.

Binocular rivalry: a phenomenon that arises when two distinct physical stimuli are projected to the corresponding retinal locations of the two eyes. Despite the constant physical input, the conscious percept alternates over time.

Cognitive access: conscious contents that are voluntarily accessed for flexible use in other cognitive operations, for storage in working memory, or for reports.

Conscious phenomenology: the way conscious experiences look to ‘us’, and how these conscious experiences are structured. See also qualia.

Event-related potential (ERP): field potentials that are time-locked to a particular event, which could be either sensory or a behavioral response. Typically, the average across many trials is considered as the ERP.

Flash suppression: a phenomenon in which an image that suddenly appears renders the previously presented and perceived one perceptually invisible. The most effective condition is when the newly flashed image is presented to the other eye. Thus, in flash suppression paradigms the perception is determined by the temporal sequence of the stimuli, and not by spontaneous perceptual fluctuations as in other multistable perception paradigms.

Gamma band response: traditionally, 30–80 Hz oscillatory power in field potentials generated by a population of neurons. It can be measured from a single microelectrode inside the brain, at the cortical surface as electrocorticography (ECoG), or at the scalp as electroencephalography (EEG) [109].

Inattentional blindness: when subjects are not told in advance that particular stimuli will be presented, these task-irrelevant stimuli often pass by completely unnoticed. Well-known examples of inattentional

Box 1. Underestimation of the NCC by Exclusive Reliance on Report-Based Paradigms?

How much of conscious phenomenology can we report? In the main text we discussed how the requirement of reports overestimate the NCC by including report-related neural activity that is not related to conscious phenomenology. However, the converse may be true as well; the NCC is underestimated by report-based paradigms because we have a richer phenomenal experience than we can report. The difficulty in generating a proper replay of binocular rivalry [48] already points to a shortcoming of reports.

Indeed, Block [6,75,119] has argued that phenomenally conscious states overflow cognitive access, including reports. In his view, conscious experience is too rich to flow all at once through the bottleneck of access and report. Direct evidence comes from change detection experiments, where arrays of objects are presented, followed by an interval, and then a test array. When one of the objects changes in this array, subjects can fail to notice the change, yielding the estimated capacity of conscious access to be about 2–4 objects. However, when a cue is given to direct their attention to a specific location after disappearance of the memory array, but before the test array, estimated capacity is much higher, typically about 60–90% of the memory array [77,78,120]. This indicates that a visual representation exists that has high capacity, exceeding the capacity to access and store items in working memory. This visual representation is very fragile, however, because it is overwritten once new visual information enters the visual cortex [79]. One can interpret these findings as spatial attentional cueing protecting the fragile memory against being overwritten by the newer information.

Some have argued that these pre-attentive, rich representations are mere 'gists' in the sense that 'some array of objects is out there', but lack the true phenomenal aspects of attended and fully conscious representations [76], which remain non-conscious until they are accessed [73]. However, this has been falsified by experiments showing that these pre-attentive representations are exactly as precise and detailed as attended ones [80] (Figure I). In addition, a recent study found that the global impression of colorfulness of a display remains available even when an attention-demanding task is performed concurrently [121]. Collectively, these findings suggest that indeed conscious experience may be much richer than acknowledged via report.

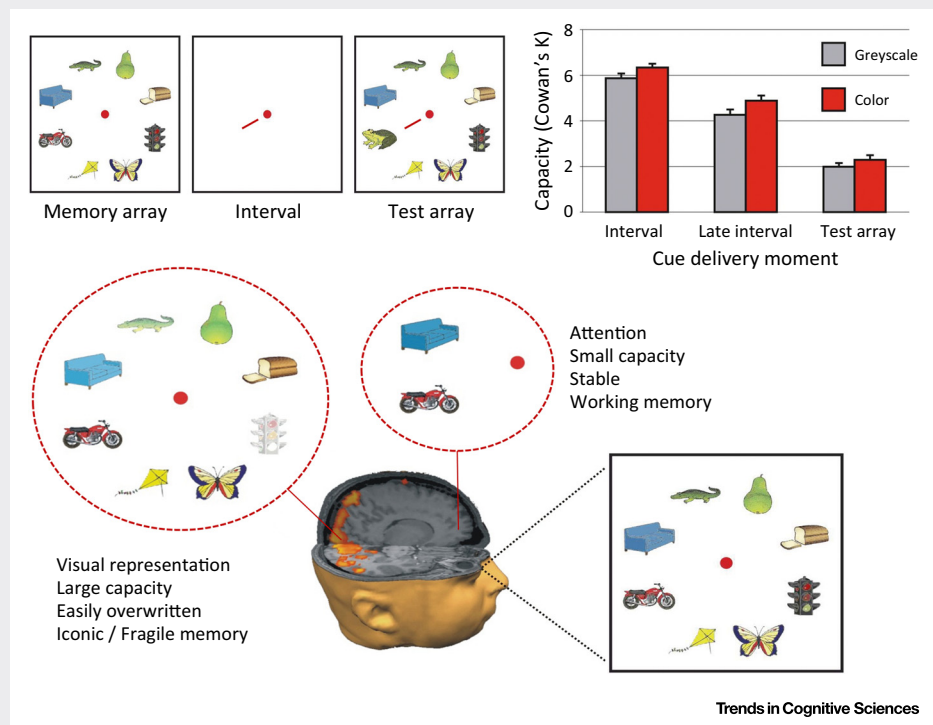


Figure I. Change Detection Tasks Reveal Two Mental Representations. A typical change detection task is shown, where a memory array is presented, followed by an interval (that may last up to several seconds), and then a test array. One of the items of the test array may have changed or not. A pointer is directed to this item, and the subject is required to indicate whether there was a change or not. In this version (test array cue), performance is typically very poor (~60% correct where chance is 50%), and this converts to a capacity (Cowan's K) of about two objects that subjects can store in working memory (independently of the number of items shown). However, when the cue is delivered during the interval, performance is much higher and subjects have a capacity of 4–6 items (which typically scales linearly with the number of items presented). This reveals a fragile visual memory that has much higher capacity, but which is easily overwritten by new visual objects [24].

blindness include the 'man in the gorilla suit' that walks amidst a bunch of people playing basketball (of which their number of passes needs to be counted), and is not noticed by many subjects, despite his obvious saliency [110].

Integrated information theory (IIT) of consciousness: a theory of consciousness which starts from consideration of the essential properties of conscious phenomenology, such as existence, information, integration, composition, and exclusion. IIT proposes what types of physical substrates can support these properties, arriving at some mathematical structure that is equivalent to the structure of conscious phenomenology [85,86].

Kanizsa configurations: one of the most famous configurations that induce an illusory contour. When several PacMan-like shapes are aligned such that the edges form a shape, such as a triangle, the shape is vividly experienced despite the lack of physical contours.

Local field potential (LFP): an electrophysiological signal representing the summed electric current from multiple nearby neurons, as measured using microelectrodes embedded within a small volume of neuronal tissue. The LFP is believed to represent the synchronized input into an observed area, as opposed to action potentials which represent the output from the area [111].

Neural correlates of consciousness (NCC): The neural correlates of consciousness is the minimal set of neuronal mechanisms jointly sufficient for any one specific conscious percept [112,113].

Optokinetic nystagmus (OKN): a type of eye movement that is elicited when a subject is presented with a surface that moves relative to the subject. OKN comprises a slow phase, where the eyes follow the movement, and a fast phase, which goes against the movement direction to reset the position of the eyes. In the context of ambiguous visual stimulation, OKN usually follows the direction of the movement that is consciously perceived [114–116].

P3 component: late component of ERP, which is observed around 300 ms after an event. Some authors have suggested that it is a signature of conscious perception of the event. In our article we propose that it is

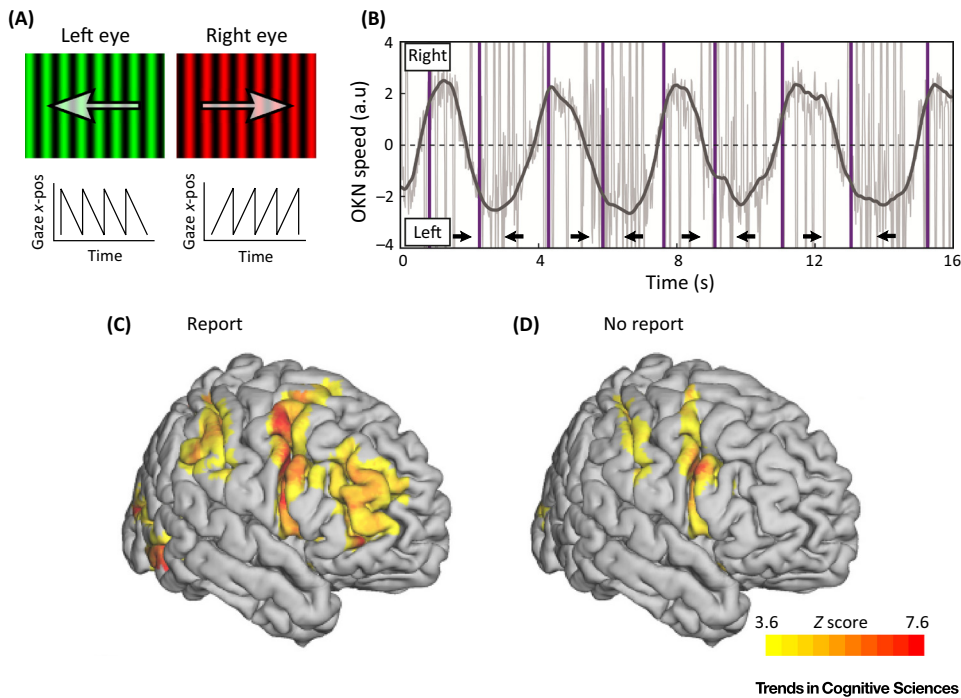


Figure 1. A No-Report Paradigm Applied to Binocular Rivalry. (A) Green and red vertical gratings moving to the left or the right were presented to the left and right eyes, respectively. This not only induces vigorous binocular rivalry between the two stimuli but also an optokinetic nystagmus (OKN), with characteristic slow and fast eye movements. (B) The speed of the OKN slow phase (thick grey line) can be used to infer subjects' perceptual contents (arrows at the bottom), which nicely coincides with their perceptual reports signaled via button presses (purple vertical lines). That is, when the subject reports seeing a red and rightward-moving grating, both eyes execute the slow phase of the OKN to the right. Abbreviation: a.u., arbitrary units. (C,D) fMRI blood oxygen level-dependent (BOLD) contrasts at the time of perceptual transitions during rivalry compared with those during replay when subjects either (C) reported or (D) did not report their percept. Most of the right dorsolateral prefrontal cortex activation disappeared when subjects passively experienced rivalry without reports, implying that the right frontal activation is not a core neural correlate of consciousness but may be a consequence of the need to report it. Adapted from [36] with permission from the Society for Neuroscience.

dominance during binocular rivalry in which the competing stimuli have opposing motion directions [49] (Figure 1). Based on the eye movements, the authors then inferred the timing of perceptual switches in the absence of reports from subjects. Note that, even in the absence of reports, subjects continued to experience vivid rivalry. In this no-report condition, occipital and parietal areas continued to be correlated with the inferred perceptual contents. However, frontal regions were similarly activated time-locked to a perceptual switch in genuine rivalry and replay, whereas they showed stronger activation in genuine rivalry than replay during the report condition. Similar results were obtained using pupil size as a perceptual readout during binocular rivalry between static gratings of low and high luminance.

These studies point to the possibility that previously described switch-related activity in frontal cortices may be largely related to introspection and self-monitoring [50,51], associated with the difficulty of reporting ambiguous percepts, but not directly related to switching between conscious percepts *per se*. Although activation in frontal areas is suggested to be crucial for visual consciousness [3,52–54], activation of the same frontal regions is consistently reported in other types of studies, investigating cognitive and executive processing such as working memory, self-monitoring, and attention, without substantial changes in **conscious phenomenology**. Causal involvement of frontal areas has also been questioned by a transcranial

more related to the report of the event.

Phenomenal consciousness: typically used as distinct from access consciousness, a distinction coined by Ned Block [6,75]. In the domain of vision, phenomenal consciousness would be the mere experience of seeing, whereas access consciousness would be the act of using visual information for other cognitive operations. See also Qualia.

Qualia: quality of conscious experience. What it is like to have a given experience. It can mean a specific aspect (e.g., redness of a rose) or a whole experience extending across all modalities (e.g., seeing a sunset at the sea) [117,118].

Trends in Cognitive Sciences

magnetic stimulation (TMS) study, where stimulation of frontal areas did not reveal any disruption of conscious perception [55] but only impaired voluntary control of rivalry. Similarly, a recent study used a magnetic resonance spectroscopy (MRS) technique to measure GABA (γ -aminobutyric acid) concentrations in the human brain, and found that GABA concentrations in visual, but not frontal, cortex correlated with individual switch-rates for three different types of ambiguous stimuli [56]. Furthermore, a massive bilateral frontal lesion in a human patient did not abolish conscious perception, but led to deficits in cognitive, executive, visuomotor, and motivational functions [57]. Thus, given the currently available evidence, activation and structural integrity of the frontal areas seems to be neither necessary nor sufficient for conscious perception.

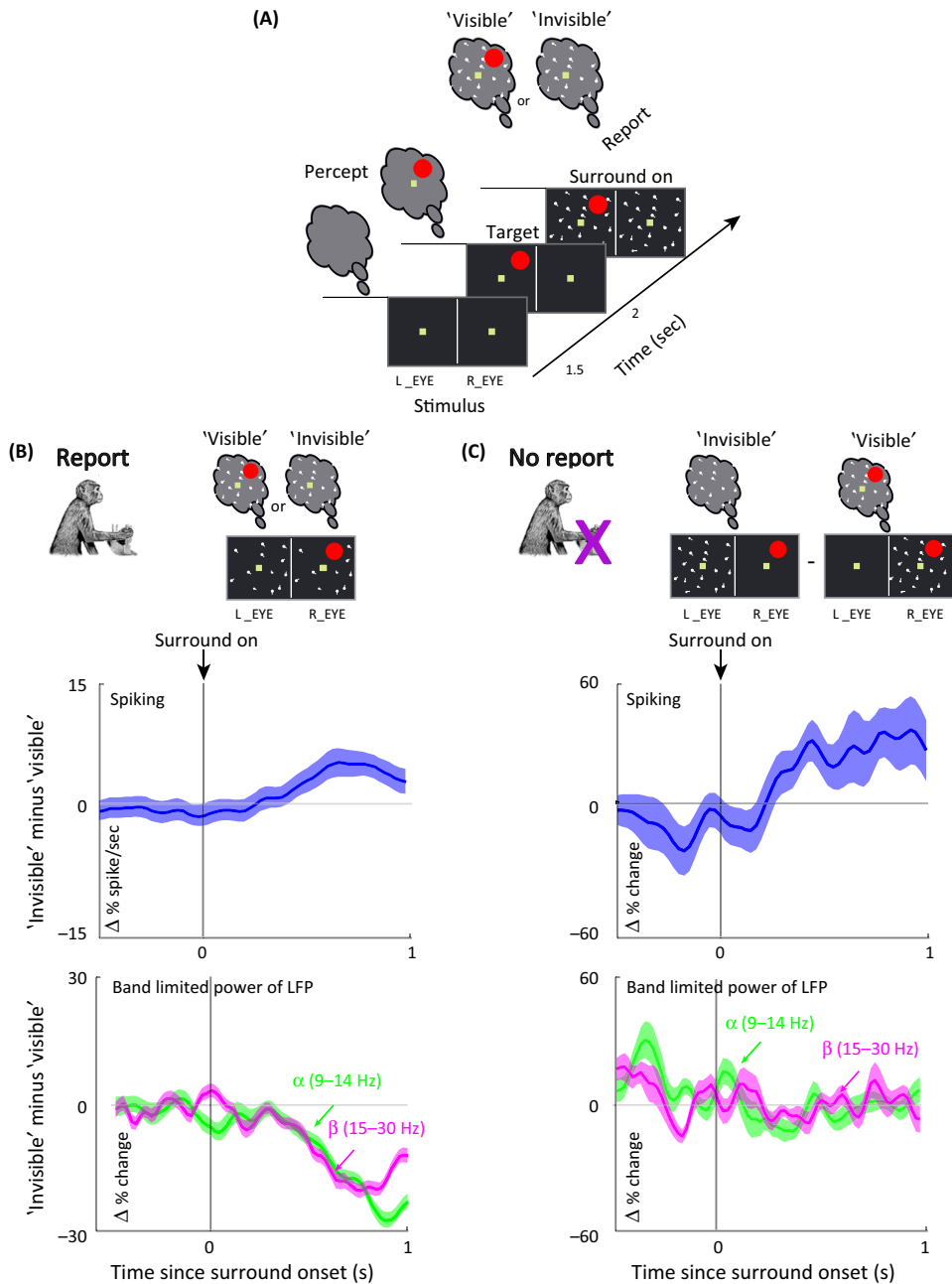
Effects of Reports at Electrophysiological Levels

The effects of reports manifest not only at the macroscopic fMRI scales but also at more refined microscopic electrophysiological levels. Single-cell recording studies in animals such as cats and monkeys have traditionally relied more on no-report paradigms than human studies, mostly to reduce the time associated with behavioral training of the animals. Besides the above-mentioned approach using binocular rivalry combined with eye movements as a perceptual readout [58,59], **flash suppression** paradigms [60,61] are a popular no-report paradigm in animal experiments. In these paradigms, induced perceptual suppression has been shown to correlate with neural spiking activity from visual to frontal areas, with a strong gradient towards more perception-related activity in higher-order association areas [62–66]. The higher in the visual processing hierarchy, the higher the proportion of neurons that modulate activity depending on the inferred conscious percept, and the stronger the amplitude of such perceptual modulation. This conclusion is consistent with those drawn from traditional report-based paradigms employing binocular rivalry or related multistable perception paradigms in either monkeys or humans (see [11,67] for review).

Striking dissociations between report-based and no-report paradigms emerge when different types of electrophysiological signals are compared. Specifically, one study [37] (Figure 2A) found a dissociation between perceptual modulation in the low frequencies of **local field potential** (LFP) in the thalamic pulvinar between the report and no-report conditions when both were compared in the same monkeys, using a visual illusion termed generalized flash suppression (GFS) [61]. In GFS, the onset of a moving surround pattern adjacent to a visual target stimulus triggers the perceptual disappearance of the target. By inserting a spatial gap between target and surround, the probability of subjective target suppression can be systematically varied to render the stimulus ambiguous. Even with small target–surround distances, when the suppressing surrounds are presented to the same eye as the target, the target reliably remains visible, regardless of reports. When the surrounds and the target are presented to different eyes, the target reliably perceptually disappears, regardless of reports. Note that these manipulations of which eyes receive the stimuli are not consciously accessible. Using these properties of GFS, the authors first established that simultaneously recorded spikes and LFPs were strongly correlated with monkeys' percepts in the ambiguous condition that required reports from the monkeys [37] (Figure 2A). In the no-report condition, monkeys passively viewed the stimuli. Without report, the low-frequency LFP power no longer followed the percept, whereas spiking activity continued to do so. A similar dissociation in visual cortices was also recently demonstrated in a human magnetencephalography (MEG) study [68]. Hence, even in electrophysiological signals, different aspects of neural activity (i.e., spiking outputs vs synaptic activity inferred from low-frequency LFP [69]) can depend differentially on the act of reporting.

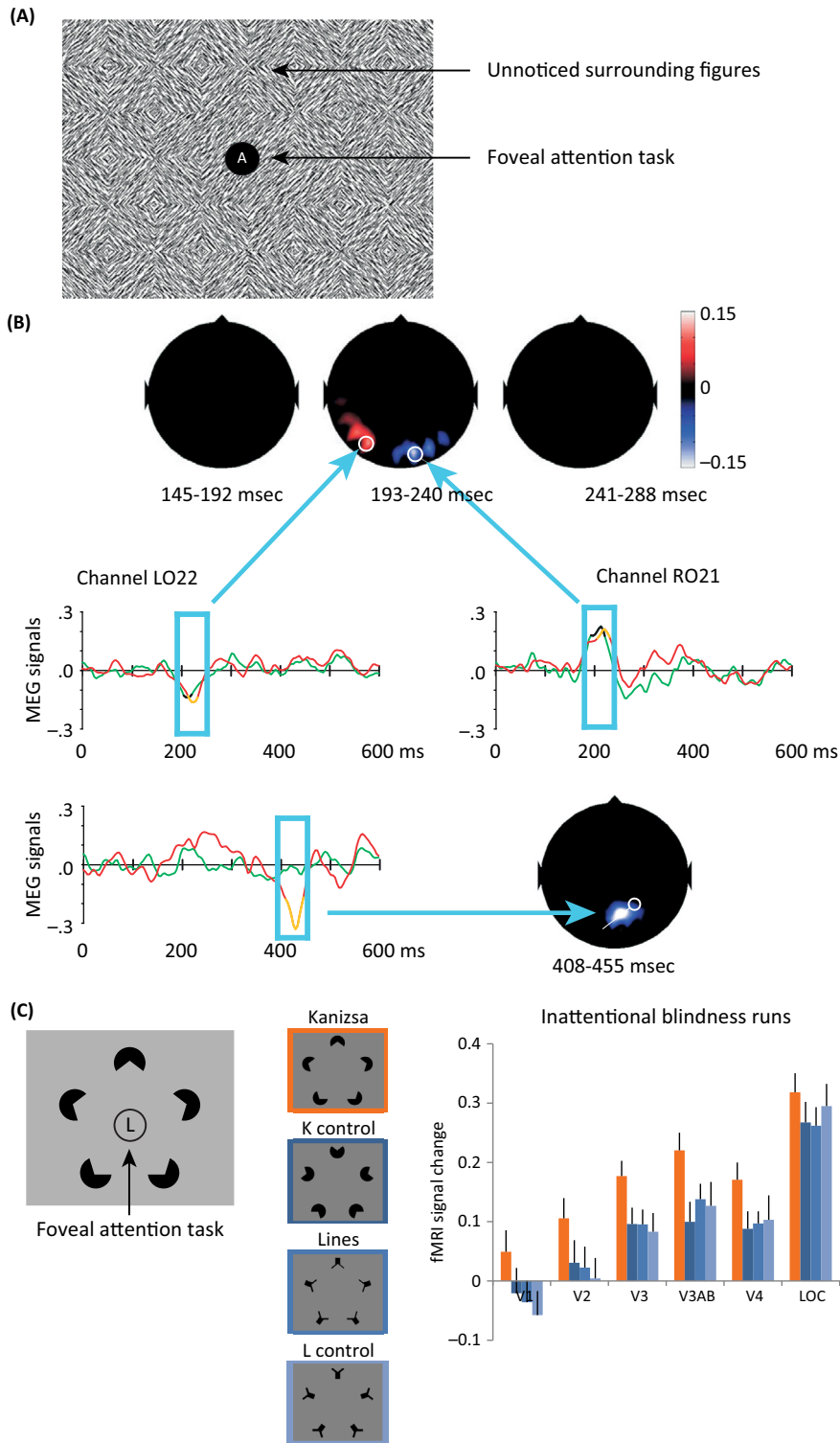
Inattentional Blindness: The Full Absence of Cognitive Access

Whenever subjects become aware of stimuli, it can be argued that some form of 'report' is the consequence. Even when no buttons need to be pushed, stimuli may draw attention, or may be unwillingly pondered, and hence are cognitively accessed, or 'reported to the self'. To avoid such



Trends in Cognitive Sciences

Figure 2. Neural Correlates of Reports and Phenomenology. (A) Generalized flash suppression [61] allows manipulation of the visibility of a salient target stimulus. Monkeys fixated a central spot before the target appeared at a parafoveal position, followed by the onset of a moving surround 2 s later. (B) In the report condition, the onset of the surround triggered the perceptual disappearance of the target in about 50% of the trials. Monkeys pulled a lever as long as the target was visible. If the target became perceptually invisible, monkeys released the lever. In the thalamic pulvinar, spiking activity (top row) as well as α (9–14 Hz) and β (15–30 Hz) power of the local field potential (LFP) (bottom row) showed reliable modulation according to the perceptual reports of the monkeys. Plots show the mean differential time-courses between the 'invisible' and 'visible' condition induced by either perceptual suppression. Shaded areas represent the continuous standard error of the mean between recording sites (± 1 SEM). (C) In the no-report condition, invisibility was induced by slight changes in the ocular configuration of the stimulus (see main text). Without report, only spiking, but not α and β power, shows modulation according to the visibility of the stimuli. Adapted from [37].



Trends in Cognitive Sciences

Figure 3. Inattention Does Not Change Perceptual Organization, Perceptual Inference, and Amodal Completion. (A) Subjects were shown texture defined checkerboards while being engaged in a foveal N-back letter task. (B) Image segmentation specific signals were obtained by subtracting the electroencephalography (EEG) responses to

post-perceptual attention or access, **inattentional blindness** paradigms have been devised. Inattentional blindness depends crucially on two factors: the diverting of attention by some task, and not telling people in advance about a task-irrelevant stimulus. The latter is crucial because once people know, the detection of the stimulus is often easy, even as a dual task together with the primary attention task.

Inattentional blindness paradigms ensure that no attention, cognition, or access is drawn by the stimulus, and that any processing of it is purely sensory. Nevertheless, inattended stimuli are processed up to high levels. One electroencephalography (EEG) study [70] measured responses to attended and inattended texture-defined checkerboards (Figure 3A). As a result, many subjects did not notice the inattended checkerboards. Occipitally localized EEG responses (Figure 3B) were evoked by the figure-ground segregation of the stimuli under the inattention condition, and these signals did not change when checkerboards became task-relevant. However, task relevance added more centrally localized EEG responses. Using a visual illusion, a separate fMRI study [71] arrived at a similar conclusion. Here, PacMan-like shapes are configured in a specific way which can induce illusory contours – a phenomenon dubbed the Kanizsa illusion (Figure 3C) or amodal completion. The **Kanizsa configurations** yielded a stronger fMRI signal across visual cortex in comparison to control stimuli, regardless of whether the subjects noticed the Kanizsa shapes. Apparently the amodal completion and perceptual inference that is typical for the Kanizsa illusion is also processed in the full absence of the act of attending, accessing, and reporting.

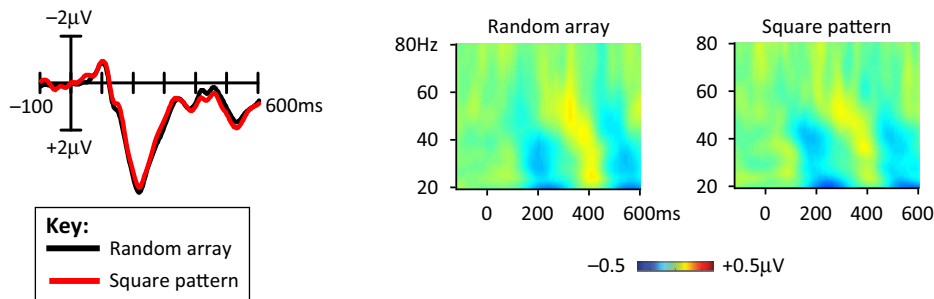
These findings beg an obvious question: if subjects do not notice the objects, should we not call the associated neural findings correlates of unconscious processing? Recent EEG experiments [38,39] addressed this issue in a three-phase version of the inattentional blindness paradigm, to disentangle the role of attention and expectancy, and to dissociate not attending from not seeing (Figure 4). In the first phase, the authors presented unexpected, task-irrelevant stimuli while subjects performed the primary task, which resulted in inattentional blindness in some subjects. In the second phase, as a result of expectation, most subjects, including previously inattentively blind subjects, became aware of the task-irrelevant stimuli. In the third phase, subjects paid attention to and performed the task on the previously task-irrelevant stimuli. By comparing the EEG responses in the first and second phases, they isolated the neural activity that was associated with awareness of the task-irrelevant stimuli under the no-report conditions. By comparing the second and third phases, they distinguished those that reflected post-perceptual-, report-, and task-related activity. These comparisons revealed that **gamma band responses** as well as the **P3 component** of the **event-related potential** (ERP), both of which were proposed as putative NCC in previous studies [3], were correlated with the requirement of report and task-relevance, but not with awareness of the task-irrelevant stimuli [39] (Figure 4). This indicates that neural processes during inattentional blindness can be decomposed into those that reflect non-conscious processing, perceptual and conscious processing that is quickly forgotten [72] or not accessed for report, and post-perceptual processes related to reports.

No Report, No Consciousness?

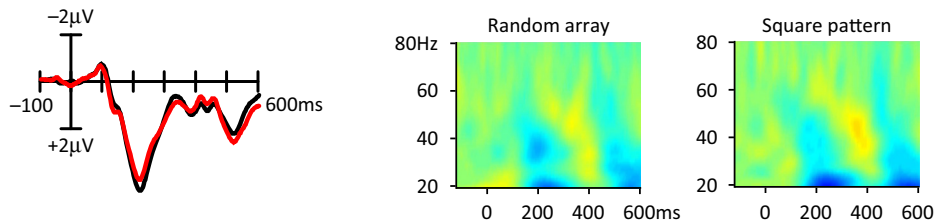
It has been argued that, if one takes away all attention, access, and report (including ‘reporting to the self’), nothing conscious remains and, without any of these, one should talk about

homogeneous textures from the checkerboard responses. The segmentation specific early signal in the visual cortex (left and right visual occipital cortices, LO and RO, 190–240 ms, top row) did not differ between subjects that had not noticed the checkerboards (inattentively blind, green lines) and subjects that had noticed them (aware, red lines). Noticing the checkerboards just added an additional, more central EEG response at a later latency (400–450 ms). Adapted from [70]. (C) Subjects were shown Kanizsa-type pentagons and various other shapes while performing a foveal N-back letter task (left). The Kanizsa patterns evoked distinct patterns of blood oxygen level-dependent (BOLD) responses across visual areas regardless of whether subjects were inattentively blind or aware of the pentagons (right). Adapted from [71].

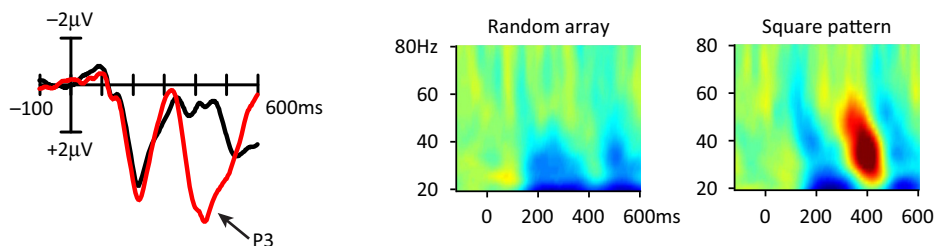
Phase 1: Inattentional blindness and no report



Phase 2: Aware and no report



Phase 3: Aware and report



Trends in Cognitive Sciences

Figure 4. Inattentional Blindness Paradigm Dissociates Consciousness-Related Activity From Report-Related Activity. In the first phase, unexpected, task-irrelevant stimuli were presented while subjects performed the primary task, which resulted in inattentional blindness in some subjects. In the second phase, as a result of expectation, most subjects, including previously inattentively blind subjects, became aware of the task-irrelevant stimuli. In the third phase, subjects paid attention to and performed the task on the previously task-irrelevant stimuli. The P3 component of the event-related potential (ERP recorded at the vertex) and gamma activation correlated with requirement of reports (or task-relevance) but not with the stimulus awareness [39]. ERPs (left column) and time-frequency spectrograms (center and right columns) are shown for phase 1, 2, and 3. Gamma activation behaved similarly to the P3 component. Adapted from [39].

unconscious processing. Even more strongly, some consider the notion of conscious experience without access and report to be unfalsifiable and unscientific [73]. How can such an argument be countered [24,74]?

The key motivation to dissociate the 'true' NCC from report-related neural activity is that – in the end – we want to explain conscious experience. By including processes related to attention, working memory, access, and report we run the risk of barking up the wrong tree: we explain these cognitive functions, and the Hard Problem remains unanswered. It is therefore crucial to address what aspects of conscious experience are in need of explaining.

Introspectively, conscious experiences appear to be 'unified': features are integrated into objects, objects into scenes, scenes into developing stories. This all happens so fast and automatically that it easily overflows anything we can cognitively access and report [75]. Some aspects of visual experience are even hard to describe, such as texture, gloss, or shading. Moreover, this multilevel, rich sensorial experience has been shown not to be an illusion, as suggested by the access-proponents [76], but to be a veridical representation in our minds [77–80] (also Box 1).

Psychological experiments have revealed the properties of visual representations that change when one transitions from unconscious to conscious experience. A masked stimulus, for example, may be represented at the level of its physical properties such as wavelength, whereas once visible its representation shifts to that of perceived color [81], which depends on surrounding colors, scene and object context [82]. In the Kanizsa illusion we observe illusory contours and an illusory brightness increase that are perceptually inferred, and are not represented when masked [83]. Many more illusions are only present in the conscious mind, and are not represented unconsciously. A review of such findings [7] arrived at the conclusion that the key transition from unconscious to conscious representations occurs at the level where isolated features start to be integrated into perceptual 'wholes' [84].

An important theoretical advance in understanding consciousness comes from the **integrated information theory** (IIT) [85,86]. This theory states as one of its axioms that the key to understanding consciousness is to define it as the integration of information. From that, it builds a mathematical and quantitative account of what makes a system conscious. In doing so, the theory explains many puzzling findings, such as that consciousness does not require the cerebellum, and is absent in epileptic states or during anesthesia. Moreover, it has provided a quantitative way of measuring consciousness in (neural) systems that seems to converge very well with the observed levels of consciousness in those systems [87].

In IIT, consciousness is directly related to the potential repertoires of states the system can take in representing information. In other words, provided that there is the possibility that one part of the system can influence the other, the information in the two parts can belong to a single conscious experience. That implies that accessibility (mediated by connectivity across areas) has more explanatory power for conscious phenomenology than the act of cognitive accessing itself. The theory predicts that removing the act of cognitively accessing information (as is done in no-report paradigms) does not remove the accessibility of that information, and hence will not remove the phenomenal experience associated with it[‡].

Introspective phenomenology and systematic psychological investigation, as well as more theoretical approaches, thus seem to converge on the same conclusion: the transition from unconscious to conscious processing is marked by a massive increase in the integration of information. This integration is what seems to define consciousness, and it hence is the phenomenon that needs to be explained by the NCC. So far, understanding attention, access, and report have done very little in this respect. They have great explanatory power in explaining how people can store, use, and communicate conscious information, but have very little explanatory power in how the information became conscious in the first place. Pre-access

[‡]Anatomical disconnection of two parts of a conscious system, as is done in split-brain patients [88], or in Cohen and Dennett's 'perfect experiment' [73], will result in two separate conscious systems, each with their own phenomenology, and each (obviously) without any experience of information present in the other. The interesting question in such cases is which of the two systems is the real 'you'.

activity, such as the interactions between sensory areas, seems to be more successful and promising [24,89].

Concluding Remarks

To explain anything about consciousness, we need to look for functions that explain key features of phenomenology [7,89,90]. The empirical investigation of phenomenology will require a thorough understanding of how parts of the system affect, and are affected by other parts of the system. How nerve cells interact is becoming an ever more important focus of study, and how such interactions relate to conscious experience [14,91] remains a fruitful avenue for future research on the neural basis of consciousness.

The aim of cognitive neuroscience should be to combine all available techniques, paradigms, and theoretical options to tackle one of the few remaining big mysteries of science. In our view, to study consciousness, one of these options is to go beyond the report-based paradigm and search for the true neural basis of consciousness. As a nice side-benefit, the avenue opened by the no-report paradigm may shed light on understanding consciousness in subjects who cannot report their conscious experience, such as animals, non-responsive patients, and babies.

Acknowledgments

We thank three anonymous reviewers and the participants of the 19th Annual Meeting of the Association for the Scientific Study of Consciousness (ASSC) 2015; our manuscript improved through their inputs. N.T. is supported by Future Fellowship (FT120100619) and Discovery Project (DP130100194) from Australian Research Council (ARC). M.W. is supported by the Herman and Lilly Schilling Foundation and the German Research Foundation (DFG). S.F. is supported by the Research Foundation of the University of Marburg (PhD fellowship).

References

- Chalmers, D.J. (1995) Facing up to the problem of consciousness. *J. Conscious. Stud.* 2, 200–219
- Lamme, V.A. and Roelfsema, P.R. (2000) The distinct modes of vision offered by feedforward and recurrent processing. *Trends Neurosci.* 23, 571–579
- Dehaene, S. and Changeux, J.P. (2011) Experimental and theoretical approaches to conscious processing. *Neuron* 70, 200–227
- Tononi, G. and Koch, C. (2015) Consciousness: here, there and everywhere? *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 370
- Lemon, R.N. and Edgley, S.A. (2010) Life without a cerebellum. *Brain* 133, 652–654
- Block, N. (2007) Consciousness, accessibility, and the mesh between psychology and neuroscience. *Behav. Brain Sci.* 30, 481–499
- Lamme, V.A.F. (2015) The crack of dawn—perceptual functions and neural mechanisms that mark the transition from unconscious processing to conscious vision. In *Open MIND: 22(7)* (Metzinger, T. and Windt, J.M., eds), pp. 1–34, MIND Group
- Baars, B.J. et al. (2013) Global workspace dynamics: cortical 'binding and propagation' enables conscious contents. *Front. Psychol.* 4, 200
- Mnih, V. et al. (2015) Human-level control through deep reinforcement learning. *Nature* 518, 529–533
- Koch, C. (2004) *The Quest for Consciousness*, Roberts and Publishers
- Boly, M. et al. (2013) Consciousness in humans and non-human animals: recent outstanding advances, and possible future directions. *Front. Psychol.* 4, 1–20
- Crick, F. and Koch, C. (1998) Consciousness and neuroscience. *Cereb. Cortex* 8, 97–107
- Breitmeyer, B.G. and Ogmen, H. (2007) Visual masking. *Scholarpedia* 2, 3330
- Super, H. et al. (2001) Two distinct modes of sensory processing observed in monkey primary visual cortex (V1). *Nat. Neurosci.* 4, 304–310
- Ress, D. et al. (2000) Activity in primary visual cortex predicts performance in a visual detection task. *Nat. Neurosci.* 3, 940–945
- Blake, R. and Logothetis, N.K. (2002) Visual competition. *Nat. Rev. Neurosci.* 3, 13–21
- Tong, F. et al. (2006) Neural bases of binocular rivalry. *Trends Cogn. Sci.* 10, 502–511
- Aru, J. et al. (2012) Distilling the neural correlates of consciousness. *Neurosci. Biobehav. Rev.* 36, 737–746
- de Graaf, T.A. et al. (2012) The 'correlates' in neural correlates of consciousness. *Neurosci. Biobehav. Rev.* 36, 191–197
- Blake, R. et al. (2014) Can binocular rivalry reveal neural correlates of consciousness? *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 369, 20130211
- Lamme, V.A. (2003) Why visual attention and awareness are different. *Trends Cogn. Sci.* 7, 12–18
- Koch, C. and Tsuchiya, N. (2007) Attention and consciousness: two distinct brain processes. *Trends Cogn. Sci.* 11, 16–22
- Tsuchiya, N. and Koch, C. (2014) On the relationship between consciousness and attention. In *The Cognitive Neurosciences* (Gazzaniga, M.S., ed.), pp. 839–853, MIT Press
- Lamme (2010) How neuroscience will change our view on consciousness. *Cogn. Neurosci.* 1–57
- Soto, D. and Silvanto, J. (2014) Reappraising the relationship between working memory and conscious awareness. *Trends Cogn. Sci.* 18, 520–525
- Melloni, L. et al. (2011) Expectations change the signatures and timing of electrophysiological correlates of perceptual awareness. *J. Neurosci.* 31, 1386–1396
- Kok, P. et al. (2012) Attention reverses the effect of prediction in silencing sensory signals. *Cereb. Cortex* 22, 2197–2206
- van Boxtel, J. and Tsuchiya, N. (2015) De-confounding the neural constitution of phenomenal consciousness from attention, report and memory. In *The Constitution of Phenomenal Consciousness* (Miller, S.M., ed.), pp. 81–103, John Benjamins Publishing Company

Outstanding Questions

In the main text we featured techniques that allow us to accurately infer conscious contents through implicit physiological measures (e.g., eye movements and pupil size [36]), ocular configuration [61], and expectation [38,39]. Are there other effective measures and manipulations? Can other implicit measures, such as skin conductance, heart rate, and respiration, or other stimulus/experimental manipulations, such as adaptation, prior exposure of a subset of stimuli [92], order of presentation [26], and perceptual stabilization [93], be used as no-report paradigms and deepen our insights into the NCC?

What type of neural mechanism supports the integrated information that is generated by the system [85,86]? To understand these processes, it is essential to assess how brain regions interact with each other [94]. Although the empirical application is still scarce [95–98], integrated information theory provides a promising venue to explain how conscious phenomenology is supported by interacting mechanisms [85,86]. It will thus become important to combine no-report paradigms with measures of integrated information or effective connectivity, such as dynamic causal modeling [99] and Granger causality [100].

Electrophysiological recordings from feature-selective neurons in the lateral prefrontal cortex showed that they are correlated with conscious perception, inferred from a flash suppression paradigm without reports [66,101]. This result is apparently inconsistent with the above-mentioned fMRI study [36]. A direct comparison of these findings is limited by the different research approaches (e.g., species, flash suppression vs rivalry). Will there be dissociations in neural correlates of consciousness with report-based and no-report paradigms in the prefrontal cortex when comparing fMRI BOLD with spiking/LFP signals? Do different regions in the frontal cortex, such as frontal eye fields (FEF), dorsolateral prefrontal cortex (dlPFC), or orbitofrontal cortex, relate to different aspects of access or consciousness?

Is parietal cortex directly related to conscious perception, or merely to cognitive functions associated with perceptual reports? Electrophysiological research indicated that the parietal cortex is involved in selective attention and

29. Marcel, A.J. (1993) Slippage in the unity of consciousness. *Ciba Found. Symp.* 174, 168–180
30. Imamoglu, F. *et al.* (2012) Changes in functional connectivity support conscious object recognition. *Neuroimage* 63, 1909–1917
31. Haynes, J.D. (2009) Decoding visual consciousness from human brain signals. *Trends Cogn. Sci.* 13, 194–202
32. Garcia, J.O. *et al.* (2013) Near-real-time feature-selective modulations in human cortex. *Curr. Biol.* 23, 515–522
33. Horikawa, T. *et al.* (2013) Neural decoding of visual imagery during sleep. *Science* 340, 639–642
34. Nishimoto, S. *et al.* (2011) Reconstructing visual experiences from brain activity evoked by natural movies. *Curr. Biol.* 21, 1641–1646
35. Monti, M.M. *et al.* (2010) Willful modulation of brain activity in disorders of consciousness. *N. Engl. J. Med.* 362, 579–589
36. Frässle, S. *et al.* (2014) Binocular rivalry: frontal activity relates to introspection and action but not to perception. *J. Neurosci.* 34, 1738–1747
37. Wilke, M. *et al.* (2009) Neural activity in the visual thalamus reflects perceptual suppression. *Proc. Natl. Acad. Sci. U.S.A.* 106, 9465–9470
38. Pitts, M.A. *et al.* (2012) Visual processing of contour patterns under conditions of inattention blindness. *J. Cogn. Neurosci.* 24, 287–303
39. Pitts, M.A. *et al.* (2014) Gamma band activity and the P3 reflect post-perceptual processes, not visual awareness. *Neuroimage* 101, 337–350
40. Maier, A. *et al.*, eds (2012) *Binocular Rivalry: A Gateway to Consciousness*, Frontiers Media
41. Haynes, J.D. *et al.* (2005) Eye-specific effects of binocular rivalry in the human lateral geniculate nucleus. *Nature* 438, 496–499
42. Wunderlich, K. *et al.* (2005) Neural correlates of binocular rivalry in the human lateral geniculate nucleus. *Nat. Neurosci.* 8, 1595–1602
43. Polonsky, A. *et al.* (2000) Neuronal activity in human primary visual cortex correlates with perception during binocular rivalry. *Nat. Neurosci.* 3, 1153–1159
44. Tong, F. *et al.* (1998) Binocular rivalry and visual awareness in human extrastriate cortex. *Neuron* 21, 753–759
45. Lumer, E.D. *et al.* (1998) Neural correlates of perceptual rivalry in the human brain. *Science* 280, 1930–1934
46. Lumer, E.D. and Rees, G. (1999) Covariation of activity in visual and prefrontal cortex associated with subjective visual perception. *Proc. Natl. Acad. Sci. U.S.A.* 96, 1669–1673
47. Sterzer, P. *et al.* (2009) The neural bases of multistable perception. *Trends Cogn. Sci.* 13, 310–318
48. Knapen, T. *et al.* (2011) The role of frontal and parietal brain areas in bistable perception. *J. Neurosci.* 31, 10293–10301
49. Naber, M. *et al.* (2011) Perceptual rivalry: reflexes reveal the gradual nature of visual awareness. *PLoS ONE* 6, e20910
50. Gusnard, D.A. *et al.* (2001) Medial prefrontal cortex and self-referential mental activity: relation to a default mode of brain function. *Proc. Natl. Acad. Sci. U.S.A.* 98, 4259–4264
51. Goldberg, I.I. *et al.* (2006) When the brain loses its self: prefrontal inactivation during sensorimotor processing. *Neuron* 50, 329–339
52. Rees, G. (2001) Neuroimaging of visual awareness in patients and normal subjects. *Curr. Opin. Neurobiol.* 11, 150–156
53. Bor, D. and Seth, A.K. (2012) Consciousness and the prefrontal parietal network: insights from attention, working memory, and chunking. *Front. Psychol.* 3, 63
54. Naghavi, H.R. and Nyberg, L. (2005) Common fronto-parietal activity in attention, memory, and consciousness: shared demands on integration? *Conscious. Cogn.* 14, 390–425
55. de Graaf, T.A. *et al.* (2011) On the functional relevance of frontal cortex for passive and voluntarily controlled bistable vision. *Cereb. Cortex* 21, 2322–2331
56. van Loon, A.M. *et al.* (2013) GABA shapes the dynamics of bistable perception. *Curr. Biol.* 23, 823–827
57. Mataro, M. *et al.* (2001) Long-term effects of bilateral frontal brain lesion: 60 years after injury with an iron bar. *Arch. Neurol.* 58, 1139–1142
58. Fries, P. *et al.* (2002) Oscillatory neuronal synchronization in primary visual cortex as a correlate of stimulus selection. *J. Neurosci.* 22, 3739–3754
59. Leopold, D.A. *et al.* (2002) Visual processing in the ketamine-anesthetized monkey. Optokinetic and blood oxygenation level-dependent responses. *Exp. Brain Res.* 143, 359–372
60. Wolfe, J.M. (1984) Reversing ocular dominance and suppression in a single flash. *Vision Res.* 24, 471–478
61. Wilke, M. *et al.* (2003) Generalized flash suppression of salient visual targets. *Neuron* 39, 1043–1052
62. Keilari, G.A. *et al.* (2010) The role of the primary visual cortex in perceptual suppression of salient visual stimuli. *J. Neurosci.* 30, 12353–12365
63. Bahmani, H. *et al.* (2014) Binocular flash suppression in the primary visual cortex of anesthetized and awake macaques. *PLoS ONE* 9, e107628
64. Maier, A. *et al.* (2007) Context-dependent perceptual modulation of single neurons in primate visual cortex. *Proc. Natl. Acad. Sci. U.S.A.* 104, 5620–5625
65. Maier, A. *et al.* (2008) Divergence of fMRI and neural signals in V1 during perceptual suppression in the awake monkey. *Nat. Neurosci.* 11, 1193–1200
66. Panagiotaropoulos, T.I. *et al.* (2012) Neuronal discharges and gamma oscillations explicitly reflect visual consciousness in the lateral prefrontal cortex. *Neuron* 74, 924–935
67. Panagiotaropoulos, T.I. *et al.* (2014) Subjective visual perception: from local processing to emergent phenomena of brain activity. *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 369, 20130534
68. Kloosterman, N.A. *et al.* (2015) Top-down modulation in human visual cortex predicts the stability of a perceptual illusion. *J. Neurophysiol.* 113, 1063–1076
69. Logothetis, N.K. (2002) The neural basis of the blood-oxygen-level-dependent functional magnetic resonance imaging signal. *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 357, 1003–1037
70. Scholte, H.S. *et al.* (2006) The influence of inattention on the neural correlates of scene segmentation. *Brain Res.* 1076, 106–115
71. Vandenbroucke, A.R. *et al.* (2014) Seeing without knowing: neural signatures of perceptual inference in the absence of report. *J. Cogn. Neurosci.* 26, 955–969
72. Wolfe, J.M. (1999) Inattention blindness. In *Fleeting Memories* (Coltheart, V., ed.), pp. 71–94, MIT Press
73. Cohen, M.A. and Dennett, D.C. (2011) Consciousness cannot be separated from function. *Trends Cogn. Sci.* 15, 358–364
74. Fahrenfort, J.J. and Lamme, V.A. (2012) A true science of consciousness explains phenomenology: comment on Cohen and Dennett. *Trends Cogn. Sci.* 16, 138–139 author reply 139–140
75. Block, N. (2011) Perceptual consciousness overflows cognitive access. *Trends Cogn. Sci.* 15, 567–575
76. Kouider, S. *et al.* (2010) How rich is consciousness? The partial awareness hypothesis. *Trends Cogn. Sci.* 14, 301–307
77. Sligte, I.G. *et al.* (2008) Are there multiple visual short-term memory stores? *PLoS ONE* 3, e1699
78. Sligte, I.G. *et al.* (2009) V4 activity predicts the strength of visual short-term memory representations. *J. Neurosci.* 29, 7432–7438
79. Landman, R. *et al.* (2004) The role of figure-ground segregation in change blindness. *Psychon. Bull. Rev.* 11, 254–261
80. Sligte, I.G. *et al.* (2010) Detailed sensory memory, sloppy working memory. *Front. Psychol.* 1, 175
81. Breitmeyer, B.G. *et al.* (2004) Unconscious color priming occurs at stimulus- not percept-dependent levels of processing. *Psychol. Sci.* 15, 198–202
82. Olkkonen, M. *et al.* (2008) Color appearance of familiar objects: effects of object shape, texture, and illumination changes. *J. Vis.* 8, 13 11–16
83. Harris, J.J. *et al.* (2011) Contextual illusions reveal the limit of unconscious visual processing. *Psychol. Sci.* 22, 399–405

perceptual decision-making [102–104], and that different parietal regions [e.g., lateral intraparietal sulcus (LIP) vs middle intraparietal sulcus (MIP)] specialize in different effectors such as eye and hand movements [105]. Consistent with lesion studies in parietal cortex of humans and monkeys [106–108], this raises the possibility that neural activity in parietal regions may be directly related to effector-specific visuomotor transformations associated with perceptual reports, rather than to conscious perception *per se*. Are different regions within parietal cortex, such as area 7, more related to perceptual contents regardless of reports, while other areas, such as LIP and MIP, depend more on the exact report modalities, regardless of conscious perception? In addition to no-report paradigms, using different effectors for perceptual report (e.g., saccade vs reaching movement, dissociation of stimulus location and report location [29,30]) may further clarify the role of different subregions within parietal cortex for consciousness.

84. Murray, S.O. *et al.* (2002) Shape perception reduces activity in human primary visual cortex. *Proc. Natl. Acad. Sci. U.S.A.* 99, 15164–15169
85. Tononi, G. (2004) An information integration theory of consciousness. *BMC Neurosci.* 5, 42
86. Oizumi, M. *et al.* (2014) From the phenomenology to the mechanisms of consciousness: Integrated Information Theory 3.0. *PLoS Comput. Biol.* 10, e1003588
87. Casali, A.G. *et al.* (2013) A theoretically based index of consciousness independent of sensory processing and behavior. *Sci. Transl. Med.* 5, 198ra105
88. Gazzaniga, M.S. (2005) Forty-five years of split-brain research and still going strong. *Nat. Rev. Neurosci.* 6, 653–659
89. Lamme, V.A. (2006) Towards a true neural stance on consciousness. *Trends Cogn. Sci.* 10, 494–501
90. Seth, A.K. (2010) The grand challenge of consciousness. *Front. Psychol.* 1, 5
91. Fahrenfort, J.J. *et al.* (2012) Neuronal integration in visual cortex elevates face category tuning to conscious face perception. *Proc. Natl. Acad. Sci. U.S.A.* 109, 21504–21509
92. Aru, J. *et al.* (2012) Local category-specific gamma band responses in the visual cortex do not reflect conscious perception. *J. Neurosci.* 32, 14909–14914
93. Leopold, D.A. *et al.* (2002) Stable perception of visually ambiguous patterns. *Nat. Neurosci.* 5, 605–609
94. Deco, G. *et al.* (2015) Rethinking segregation and integration: contributions of whole-brain modelling. *Nat. Rev. Neurosci.* 16, 430–439
95. Lee, U. *et al.* (2009) Propofol induction reduces the capacity for neural information integration: implications for the mechanism of consciousness and general anesthesia. *Conscious. Cogn.* 18, 56–64
96. Chang, J.Y. *et al.* (2012) Multivariate autoregressive models with exogenous inputs for intracerebral responses to direct electrical stimulation of the human brain. *Front. Hum. Neurosci.* 6, 317
97. Oizumi, M. *et al.* (2015) Measuring integrated information from the decoding perspective. *arXiv* 15, 849–853
98. Barrett, A.B. and Seth, A.K. (2011) Practical measures of integrated information for time-series data. *PLoS Comput. Biol.* 7, e1001052
99. Friston, K.J. *et al.* (2003) Dynamic causal modelling. *Neuroimage* 19, 1273–1302
100. Roebroeck, A. *et al.* (2005) Mapping directed influence over the brain using Granger causality and fMRI. *Neuroimage* 25, 230–242
101. Safavi, S. *et al.* (2014) Is the frontal lobe involved in conscious perception? *Front. Psychol.* 5, 1063
102. Bisley, J.W. and Goldberg, M.E. (2010) Attention, intention, and priority in the parietal lobe. *Annu. Rev. Neurosci.* 33, 1–21
103. Shadlen, M.N. and Kiani, R. (2013) Decision making as a window on cognition. *Neuron* 80, 791–806
104. Williams, Z.M. *et al.* (2003) Parietal activity and the perceived direction of ambiguous apparent motion. *Nat. Neurosci.* 6, 616–623
105. Andersen, R.A. and Cui, H. (2009) Intention, action planning, and decision making in parietal-frontal circuits. *Neuron* 63, 568–583
106. Ro, T. *et al.* (2001) Ipsilesional biases in saccades but not perception after lesions of the human inferior parietal lobule. *J. Cogn. Neurosci.* 13, 920–929
107. Hwang, E.J. *et al.* (2012) Inactivation of the parietal reach region causes optic-ataxia-like symptoms impairing reaches but not saccades. *Neuron* 76, 1021–1029
108. Kubanek, J. *et al.* (2015) Motor role of parietal cortex in a monkey model of hemispatial neglect. *Proc. Natl. Acad. Sci. U.S.A.* 112, E2067–E2072
109. Buzsáki, G. and Wang, X.J. (2012) Mechanisms of gamma oscillations. *Annu. Rev. Neurosci.* 35, 203–225
110. Simons, D.J. and Rensink, R.A. (2005) Change blindness: past, present, and future. *Trends Cogn. Sci.* 9, 16–20
111. Einevoll, G.T. *et al.* (2013) Modelling and analysis of local field potentials for studying the function of cortical circuits. *Nat. Rev. Neurosci.* 14, 770–785
112. Mormann, F. and Koch, C. (2007) Neural correlates of consciousness. *Scholarpedia* 2, 1740
113. Crick, F. and Koch, C. (1990) Some reflections on visual awareness. *Cold Spring Harb. Symp. Quant. Biol.* 55, 953–962
114. Fox, R. *et al.* (1975) Optokinetic nystagmus as an objective indicator of binocular rivalry. *Vision Res.* 15, 849–853
115. Leopold, D.A. *et al.* (1995) The role of attention in binocular rivalry as revealed through optokinetic nystagmus. *A. I. Memo* 1554
116. Logothetis, N.K. and Schall, J.D. (1990) Binocular motion rivalry in macaque monkeys: eye dominance and tracking eye movements. *Vision Res.* 30, 1409–1419
117. Balduzzi, D. and Tononi, G. (2009) Qualia: the geometry of integrated information. *PLoS Comput. Biol.* 5, e1000462
118. Kanai, R. and Tsuchiya, N. (2012) Qualia. *Curr. Biol.* 22, R392–R396
119. Block, N. (2013) The grain of vision and the grain of attention. *Thought J. Philos.* 1, 170–184
120. Landman, R. *et al.* (2003) Large capacity storage of integrated objects before change blindness. *Vision Res.* 43, 149–164
121. Bronfman, Z.Z. *et al.* (2014) We see more than we can report: 'cost free' color phenomenality outside focal attention. *Psychol. Sci.* 25, 1394–1403