

Opinion

A leaky evidence accumulation process for perceptual experience

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The neural correlates supporting our perceptual experience of the world remain largely unknown. Recent studies have shown how stimulus detection and related confidence involve evidence accumulation (EA) processes similar to those involved in perceptual decision-making. Here, we propose that independently from any tasks, percepts are not static but fade in and out of consciousness according to the dynamics of a leaky evidence accumulation process (LEAP), and that confidence corresponds to the maximal evidence accumulated by this process. We discuss the implications and limitations of our proposal, assess how it may qualify as a neural correlate of consciousness, and illustrate how it brings us closer to a mechanistic understanding of phenomenal aspects of perceptual experience like intensity and duration, beyond mere detection.

From evidence accumulation to perceptual experience

When we admire a distant star, how does our brain integrate the tenuous stream of photons over time to produce a conscious percept, known as the specific feel of what it is like to have a visual experience? In perceptual decision-making, EA (see Glossary) refers to the integration of noisy sensory signals until a threshold is crossed, leading to a decision enacted by a motor command. Computational accounts of EA [1,2] are supported by decades of electrophysiological recordings in non-human primates [3] and rodents [4] and are now considered a biologically plausible model of perceptual decision-making [5]. Because the majority of studies rely on discrimination tasks where participants make decisions about stimuli that are always consciously perceived, the extent to which the dynamics of perceptual consciousness are tied to the decisional process of EA remains largely unexplored (Box 1). Answering this question requires fusing computational models, electrophysiological recordings, and subjective reports. This feat is becoming more accessible to consciousness researchers as new toolboxes allow more flexibility to fit EA models [6] and powerful optimization tools enable the development of new models [7].

Here, based on seminal work in perceptual decision-making, previous theoretical works on consciousness [8,9] and our recent empirical study [10], we propose that a specific form of EA called the **LEAP** can account for two key components of **perceptual experience**, namely perceptual consciousness and perceptual monitoring. As we describe later, the specificity of LEAP is that it is leaky in nature, occurs continuously irrespective of stimulus onset or task demands, and continues after reaching a threshold. While our proposal does not qualify as a mechanistic theory that explains why consciousness occurs, the dynamics of LEAP may predict the dynamics of perceptual experience, that is if, when, for how long, how intensely, and with what confidence a given percept becomes conscious (Figure 1A, Key figure). It can thus shed light on the neural correlates of perceptual experience, that is, the phenomenal aspects of conscious percepts and metacognitive feelings of confidence. With the goal of rendering our claims amenable to empirical evidence, we discuss the computational and neurobiological implementations of LEAP and its explanatory power for key findings in consciousness and metacognition. We also

Highlights

Evidence accumulation enables accurate perceptual decisions based on noisy sensory evidence. Here, we explore how leaky evidence accumulation processes (LEAPs) could determine perceptual consciousness.

We propose that a stimulus fades in and out of consciousness according to the dynamics of the corresponding accumulated evidence. A percept is held to become conscious when accumulated evidence exceeds a threshold, increases in intensity until maximal evidence is reached, and ceases to be conscious when accumulated evidence drops below threshold due to a leaky accumulation regime.

We account for perceptual monitoring by proposing a proxy for perceptual reliability: confidence in having perceived or not a stimulus is defined as the distance between the maximum of accumulated evidence and the detection threshold, thereby enabling metacognition for conscious and unconscious percepts.

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Box 1. Neural correlates of consciousness and subjective reports

The quest for the NCC [79] does not search for a mechanistic model that explains how consciousness arises from physical processes, but seeks to identify a minimal set of neural activity that predict the occurrence of conscious states [79-81]. This set is required to be minimal to exclude neural activity on which the NCC itself depends. Neglecting this requirement would lead to overestimating NCCs to almost the whole brain [80,82]. To find NCCs, researchers typically contrast brain activity when human volunteers consciously perceive a stimulus to when they do not, while keeping the physical properties of the stimulus constant. Neural activity that distinguishes the presence versus absence of a conscious percept can thereby be uncovered during detection tasks with perithreshold stimuli. Additionally, neural activity that distinguishes two conscious contents can be uncovered by contrasting different conscious reports during discrimination tasks (e.g., bistable stimuli). As LEAP addresses the dynamics of perceptual consciousness rather than its content, we focus here on detection tasks. To probe whether a stimulus is consciously perceived or not participants are asked to report whether a stimulus was 'present' versus 'absent', or use subjective report scales. Although they do not directly probe consciousness, confidence ratings are often added as a proxy to the type of metacognitive processes that higherorder theories posit to determine consciousness [52,83].

The contrastive approach to find NCCs has some caveats [46]. Brain processes supporting the occurrence of perceptual consciousness but devoid of actual conscious content can be included in the contrast (NCC prerequisite). For example, pre-stimulus activity can bias perception but does not relate to conscious content [84]. Likewise, cognitive processes (e.g., related to the task of reporting conscious perception) could be included in the NCC (NCC consequence). This is why no-report conditions are often added to experimental paradigms to find the NCC proper, devoid of task-dependent activity. This is done by inferring the conscious percept of task-irrelevant stimuli through oculometric signals instead of subjective reports [76], or by testing whether stimuli elicit brain activity resembling a putative NCC irrespective of a task [85]. Interestingly, many candidate NCCs found in report conditions were not observed in no-report conditions, illustrating how the act of reporting may confound the NCC [76]. To further complicate the matter, the interpretation of brain activity as a NCC prerequisite or consequence may depend on the theory of consciousness one ascribes to [86,87].

provide two empirically verifiable predictions about how conscious percepts unfold in time, a property left aside by most theoretical accounts. This way, we hope to move toward a better, neurophysiologically rooted mechanistic understanding of perceptual experience.

How could evidence accumulation govern perceptual consciousness?

To isolate the neural correlates of consciousness (NCC), researchers often rely on a contrastive approach comparing distinct conscious percepts induced by constant sensory stimulation [11], for instance by presenting a stimulus at threshold and asking participants to detect its presence. Compared with discrimination tasks, such detection tasks have been rarely studied in relation to EA [12], possibly due to the difficulties of fitting computational models without response times when stimuli are not detected. As a consequence, much of the neurophysiological and computational underpinnings of EA have been inferred from discrimination tasks with suprathreshold stimuli [2,3,13,14], less suited for a contrastive approach, which is the focus of the present article (Box 1). One notable exception reported electrophysiological signatures of EA in non-human primates for detected versus missed stimuli similar to those found in classical discrimination tasks [15]. At the computational level, the findings were consistent with EA models encoding stimulus presence, and considering a stimulus as absent if accumulated evidence did not reach a threshold. Similar findings were found in humans using scalp electroencephalography (EEG) [16]. However, until recently empirical evidence was lacking to support a link between EA and perceptual consciousness in the absence of task demands, as when participants become conscious of a stimulus irrespective of any task [17]. In the rest of this section, we discuss empirical and theoretical attempts to posit a link between EA and perceptual consciousness. While they endow EA with the role of a mere prerequisite for perceptual consciousness, we will argue that some specific forms of EA are a candidate for an NCC proper, in the sense that conscious contents occur and vary according to them.

Among the rare studies that have attempted to assess the link between EA and perceptual consciousness empirically, one found that the subjective latency of discrimination decisions during a

Glossarv

Drift rate: in the evidence accumulation (EA) mechanism, the rate at which noisy sensory evidence is accumulated. An increase in drift rate (e.g., due to high stimulus intensity or attention) leads to an average increase in the slope of the accumulated evidence.

Evidence accumulation (EA): the

process by which evidence toward one of several possible alternatives is gathered over time through the sequential sampling of noisy signals. Leakage: in the EA mechanism, the forgetting rate of the EA process. Leakage is inversely related to the integration time and drives an EA process back to zero in the absence of incoming sensory information. Increasing this parameter reduces the probability of noise being accumulated above a threshold – which in LEAP leads to a hallucination - at the expense of slower EA.

LEAP: an evidence accumulation process that is leaky in nature, occurs continuously irrespective of stimulus onset or task demands and continues after reaching a threshold.

Neural correlates of consciousness (NCC): the minimal neuronal mechanisms jointly sufficient for any one specific conscious percept.

Perceptual consciousness: the sensory component of an experience. such as the phenomenal character of shapes, colors, spatial layout of the items of which a perceived scene is composed.

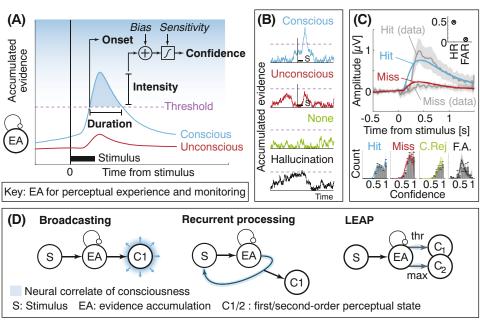
Perceptual experience: integration of the phenomenality issuing from first-order processes (perceptual consciousness in LEAP) and the phenomenality issuing from second-order processes (the metacognitive feeling of confidence in

Perceptual monitoring: evaluation of the quality of a sensory signal. This so-called metacognitive evaluation can be either a slow, explicit, and controlled process, or a fast, implicit, and automatic process. In its latter form, in particular, perceptual monitoring consists of unconscious detection and interpretation of cues whose conscious upshot are metacognitive feelings, for example, feeling confident that something has been detected. Sufficiency: a neural state is sufficient for a certain state of consciousness to occur if and only if, given the laws of the



Key figure

Linking evidence accumulation to perceptual experience



Trends in Cognitive Sciences

Figure 1. (A) Leaky evidence accumulation processes (LEAP) for perceptual consciousness and monitoring. Average evidence accumulation (EA) traces locked on stimulus onset. A conscious percept occurs when accumulated evidence (blue trace) reaches a threshold (broken line) and lasts until leakage pulls it back below threshold. The perceived intensity is proportional to the maximal accumulated evidence above the threshold, as indicated by the blue gradient in the background. The stimulus remains unconscious when accumulated evidence (red trace) fails to reach the threshold. Early differences in accumulated evidence represent pre-stimulus EA, which can already differentiate consciously perceived from unconscious stimuli. Input to perceptual monitoring is read out from the distance between maximal evidence and detection threshold and transformed through bias and sensitivity parameters to produce explicit confidence estimates. (B) Dynamics of EA for various percepts at the single-trial level. A percept is conscious when accumulated evidence reaches the threshold (blue) or unconscious when it does not (red). When no stimulus is present, there is no conscious perception (green), unless EA reaches the threshold and triggers a hallucination (black). (C) Model fits for 18 participants, adapted from [10]. Top: the EEG proxy to EA (gray) is reproduced by a LEAP model for hits (blue) and misses (red). The inset shows the corresponding data (o) and model fits (x) for the hit-rates (HR) and false-alarm rates (FAR). Bottom: the confidence histograms (gray) were reproduced by the maximal evidence rule for hits, misses, correct rejections (C.Rej.), and false alarms (F.A.). (D) Evidence accumulation and neural correlates of consciousness (blue color) for three neural mechanisms. Leakage is represented by the self-inhibitory connection within each EA module. Within the Global Neuronal Workspace (GNW), EA may operate as the trigger of global broadcasting through neural ignition. Within Recurrent Processing Theory (RPT), EA may be the upshot of the recurrent activity that enables perceptual consciousness. According to LEAP, perceptual consciousness is enabled by a thresholding of accumulated evidence (thr), while metacognitive feelings are derived from the maximally accumulated evidence (max).

Libet-like paradigm was well predicted by an EA model [18], while another established that the relation between stimulus intensity and an EEG marker of EA was mediated by conscious reports [19]. Similar electrophysiological markers have been proposed to relate to perceptual consciousness [20], suggesting that it could occur when accumulated evidence reaches a threshold. Besides, the classical phenomenon of binocular rivalry is well explained by an EA model [21] and involves single neurons with a gradual buildup of activity prior to switches in perceptual content [22].

normal functioning of the brain, if the neural state occurs, then the state of consciousness occurs too. On a close to standard definition, sufficiency provides the defining criterion for being a NCC.



The neural implementation of EA is unclear and probably comprises a hierarchy of EA processes that need to be collapsed into a unique process in mathematical models of behavior [13] (Box 2). Notably, neurons representing accumulated evidence have been mainly reported in regions related to motor planning such as the lateral intraparietal area, frontal eye field, or superior colliculus [3,23]. Before any conclusions can be made regarding a specific role of EA for perceptual consciousness, it is important to identify which types of EA processes contribute to perceptual consciousness per se, which arguably involves more than the preparation of an action following the detection of a stimulus. EEG studies have shown that some neural correlates of EA are tied to motor preparation but others represent a more abstract signal independent from motor preparation [17]. Likewise, in the lateral intraparietal area, some neurons seem to track evolving decisions irrespective of motor preparation ([24], but see [25]) (unlike in the dorsal premotor cortex [26]) and even accumulate task-irrelevant evidence, albeit with a lower gain [27]. The involvement of EA beyond motor planning is further supported by the fact that neurons instantiating EA were found in other brain regions such as the caudate nucleus [28], the cerebellum [29], or the posterior parietal cortex [10]. More generally, hemodynamic correlates of EA have been found in the fusiform, occipital, and inferior frontal gyri [30]. In sum, there is ample evidence suggesting that EA occurs broadly in the brain and sometimes irrespective of motor output and could therefore relate to perceptual consciousness as one can be conscious without any overt behavior.

The links between EA and consciousness have also been discussed at a theoretical level [8,9,31]. Among first-order theories which assume that consciousness depends on the properties of first-order representations alone, the global neuronal workspace theory of consciousness [32] postulates that several unconscious perceptual representations compete for conscious access according to a winner-take-all rule. Such competition may be arbitrated considering that separate EA processes take place for each representation and possibly inhibit each other. Then, conscious access is granted to the strongest representation when its corresponding sensory evidence reaches a threshold, and the information is ignited into the workspace. As suggested before, EA could serve as the mechanism triggering the broadcasting of perceptual signals throughout the brain (i.e., neural ignition) and thereby providing them with conscious access (Figure 1D) [8,9]. Likewise, if recurrent processing of neuronal activity underlies consciousness, as proposed by the recurrent processing theory [33], EA could enable perceptual consciousness by triggering recurrent processing between different specialized cortical regions (Figure 1D). This possibility is

Box 2. Biases in evidence accumulation

Apart from sensory evidence, our choices are influenced by multiple factors such as expectations, past choices, reward probabilities, or attention [88]. Some biases such as expectations are implemented through a change in the baseline rate of evidence accumulating neurons [89,90], determining the starting point of EA [91]. Choice history and preference also affect baseline firing rates, although an effect on the drift rate was also found [92], confirmed by computational work [93]. Temporal uncertainty could also modulate response threshold [94]. It is unclear which of these biases in reporting also affect perceptual consciousness. At one extreme, punishing false alarms rather than misses in a detection task induces a conservative bias for decisions [95]. It is however unclear whether such a bias also affects perceptual consciousness [96]. There could be a dissociation between the threshold associated with report and the one associated with perceptual consciousness, which could be achieved by having a lower threshold for perceptual consciousness than for decisions. Such a dissociation would explain how modulations of drift rate might affect decisions more than perceptual consciousness [47]. Alternatively, perceptual consciousness and decisions could be represented in different subspaces of the neuronal population, akin to task-relevant and -irrelevant information [97]. In the latter case, any bias on the EA process could selectively modulate perceptual consciousness depending on their projection onto the readout. Prior expectations are a particularly interesting type of bias since it relates to Bayesian theories of perception [98] and consciousness [99]. Based on Bayesian principles, normative accounts of EA posit that sensory signals are integrated with prior beliefs on their reliability [100], a property which was recently verified with magnetoencephalographic recordings [101]. In sum, biases and priors could be integrated at various stages of EA and may in turn affect perceptual consciousness beyond decision-making, as well as explain altered states of consciousness including hallucinations [102] or blindsight [103].



notably supported by the fact that EA could be implemented by recurrent circuits [34]. EA may also be considered within higher-order theories of consciousness, according to which a state becomes conscious in case a second-order representation of that state is formed. It is conceivable that accumulated first-order evidence is the input for second-order representations, which would provide a mechanism to assess the reliability of first-order representations: a first-order representation is considered reliable, and therefore becomes conscious when a higher-order evidence accumulator reaches a threshold [35]. This is particularly relevant given that EA is known to be involved in the computation of confidence estimates, which serve as proxy to second-order representations (see later).

Thus, as illustrated by these empirical and theoretical studies, in its weakest form, EA could play a role for consciousness, but would be nonsufficient, serving as a mere trigger that brings about the very process determining perceptual consciousness (e.g., global broadcasting, recurrent processing, or higher-order representation). More ambitiously, in the next section, we discuss three specific properties whose possession by an EA process suggest it could play a primary role as a mechanism **sufficient** for perceptual experience to occur.

A leaky evidence accumulation process for perceptual consciousness

In a recent study, we recorded brain activity in a patient with epilepsy while the patient detected weak and unpredictable stimuli, and isolated posterior parietal neurons with ramping activity reaching similar levels prior to the detection response, and therefore instantiating EA [10]. Importantly, similar neuronal responses were found when stimuli were reported after a delay with a different effector, or even when stimuli were presented but no overt reporting was required. These findings confirm that EA could be involved in perceptual consciousness per se, irrespective of motor preparation and task relevance. To better understand how EA could trigger perceptual consciousness, we developed a computational model of EA implementing three properties [10]. It is these specific properties of EA models we now discuss as LEAP.

First, accumulated evidence is constantly driven back to zero by a leakage factor [36]. Although some models of EA assume no leakage during discrimination decisions [37], in detection tasks, the leakage factor avoids continuously accumulating noise when stimuli are absent and thereby reaching the threshold through random fluctuations (i.e., false alarms). This leakage parameter may be adapted to the average length of the stimuli to be detected [38] or to their reliability [39]. Second, unlike classic EA models, evidence gathered through LEAP is continuously accumulated from the beginning of each trial, irrespective of stimulus onset [40], and irrespective of a task to be performed. Therefore, the drift rate, indexing how much sensory information is available as input to EA, is zero except while the stimulus is presented. We thus assume the existence of a variety of (content-specific) accumulators spontaneously fluctuating under the threshold for perceptual consciousness and reaching that threshold only following the onset of their corresponding content (i.e., stimulus) ([9], but see [41]). Third, unlike neurons in motor areas that stop accumulating evidence upon reaching the decisional threshold [42], EA was allowed to continue after crossing the threshold, notably to account for confidence as described later. Similar models were developed to account for change-of-minds [43] and are supported by EEG studies [44]. While in discrimination tasks different possible choices can be represented by distinct accumulators, LEAP reproduces detection rates using only one accumulator, ignoring negative evidence that could possibly signal stimulus absence [10,45]. It is still possible, however, that in some situations, different contentspecific accumulators could compete through mutual inhibition [36] to reach the threshold for perceptual consciousness, as it has been proposed for binocular rivalry [21].

With this computational model of LEAP, we were able to reproduce EEG and behavioral data from healthy participants, as well as the average firing rate of EA neurons (Figure 1C) [10]. Interestingly,



the three specific properties of LEAP listed previously lead to explicit predictions on the dynamics of EA following the crossing of the threshold. Indeed, leakage and postdecisional EA imply that accumulated evidence only remains above threshold for a limited amount of time, depending on a combination of the physical duration and intensity of the stimulus. Thus, a percept may become conscious as a LEAP reaches a threshold, increase in intensity until a maximal level of accumulated evidence, and remain conscious for as long as accumulated evidence remains above that threshold (Figure 1A,B). Under this assumption, the onset, intensity, and duration [108] of a conscious percept would directly derive from LEAP. This would suggest that although LEAP does not account for the contents of perceptual experience in their categorical specificity (e.g., the color in an image), it provides a mechanism sufficient to predict the occurrence of conscious experience as well as some of its phenomenal aspects, which can be defined as a NCC proper [46] (Box 1). Should our proposal turn out to be right, it would bring the NCC approach forward by pointing out a relation between LEAP and fine-grained features of perceptual consciousness so far left aside by theories of consciousness.

The hypothesis that LEAP predicts the dynamics of conscious percepts including their onset, duration, and intensity over time leads to two simple - yet non-trivial - predictions. It is worth noting that both these predictions have been empirically observed but left unaccounted by most current theories of consciousness.

Prediction 1: stronger stimuli lead to longer conscious percepts

Because stronger stimuli increase the drift rate of LEAP, accumulated evidence reaches the threshold earlier and then rises higher above it, which in turn leads to intense conscious percepts with early onsets. Interestingly, the leakage also needs more time to drive the accumulated evidence back below threshold, leading to longer perceived durations. In line with this prediction, increasing stimulus intensity was associated with earlier [47], clearer [48], and longer conscious percepts [49].

Prediction 2: for similar stimulus strength, earlier conscious percepts are clearer

Two identical stimuli evoke conscious percepts with latencies that depend on stochastic fluctuations taking place either before or after stimulus onset. Earlier threshold crossings imply that drift rate will remain positive for a longer time, leading accumulated evidence to reach higher levels. In line with this prediction, subjective reports of clearer conscious percepts are associated with shorter response times [50]. Similar effects were reported for confidence [51] although the link between confidence and perceptual consciousness is debated, as we will see later.

A leaky evidence accumulation process for perceptual monitoring

Perceptual decisions usually come with a sense of confidence which is considered by some as a proxy for the intensity of perceptual consciousness [52] and is also a useful metric to quantify perceptual monitoring [53,54]. In what follows, we describe how EA generates confidence estimates in discrimination tasks and explore with LEAP how similar mechanisms apply to detection tasks. Different readouts of EA have been used to describe opt-out behavior from non-human primates [55] and explain the dependence of confidence on choice, stimulus intensity, and time [56]. Some works assume that the confidence is read out of the losing accumulator at the time of the decision [57]. Other works assume that confidence is based on a postdecisional readout of choice-congruent evidence only [58,59]. The latter models assume that evidence continues to be accumulated after reaching the threshold (postdecisional EA) [43,44].

These rules cannot be directly generalized to detection tasks since they rely on accumulated evidence reaching a threshold that does not occur for missed stimuli. One solution is to assume



that confidence in the absence of stimulus is based on a different mechanism, such as the monitoring of attention [60]. Alternatively, we previously proposed that confidence scales with the distance between the maximum amount of accumulated evidence and the detection threshold (Figure 1A,B; [10], see also [61]). This simple rule is sufficient to explain various features of confidence estimates that are computed automatically during a detection task (i.e., perceptual confidence, see [53]). Because this distance can be defined even if the threshold is not crossed, the maximal evidence rule provides a simple mechanism to monitor the absence of evidence (but not evidence of absence, see [62]), such as cases when one is sure that no stimulus was presented [60]. It also explains how contents remaining inaccessible to consciousness may still be subject to self-monitoring, such as cases where confidence tracks the accuracy of decisions about unseen stimuli [63,64]. This implies that metacognitive monitoring may operate automatically [65], provided that a readout of the maximum of accumulated evidence is available. This notion departs from a previous proposal in which conscious percepts only are accompanied by confidence estimates [66]. Tagging both conscious and unconscious percepts with a confidence estimate may help compare or weight signals across domains, confidence being considered in that context as a common currency on which comparisons can operate [67,68]. In addition, this definition of confidence instantiates a form of metacognitive noise through the influence of leakage [69] on postdecisional evidence readouts. In the presence of strong leakage, accumulated evidence decays fast so that maximum evidence accurately reflects perceptual strength. With little leakage, accumulated evidence keeps fluctuating irrespective of perceptual processes, possibly reaching new maxima which are less accurately related to decision accuracy. Last, but most importantly, by deriving both detection and confidence from the same EA process, we posit that perceptual consciousness and perceptual monitoring result alike from basic computations (i.e., thresholding, maximum) applied to accumulated evidence. As we develop later, these two steps may relate to two key components of perceptual experience, namely the phenomenal character of the sensory content and of the metacognitive feeling of confidence.

Implications for perceptual consciousness and monitoring

We have outlined the neurophysiological and computational implementations of LEAP accounting for detection and confidence reports. Building on this, we have argued for the hypothesis that LEAP may qualify as a NCC proper. By way of three implications of our hypothesis, in this section we refine how it accounts for perceptual consciousness and perceptual monitoring, two key components of perceptual experience. We consider some limitations of our proposal in Box 3.

Perceptual consciousness as none-or-graded

A first implication concerns the dichotomous or graded nature of conscious experience, an issue that remains debated today [70]. In our proposal, the thresholding of accumulated evidence implies that a given stimulus remains unconscious until the corresponding evidence reaches a threshold, which corresponds to conscious access. Following this all-or-none rule for conscious access, the by-now conscious percept is held to increase in intensity in a graded manner, proportional to the maximum of accumulated evidence. Thus, perceptual consciousness is a none-orgraded phenomenon. Importantly, the graded nature of a conscious percept once the threshold is reached does not result from a set of all-or-none steps at different levels of the perceptual hierarchy as proposed before [71], but reflects the existence of gradual states of experience produced by a given feature eliciting distinct levels of maximal evidence. Note that while there probably are perithreshold fluctuations in some experimental settings, in line with ordinary cases of weak stimuli like seeing a distant star, such fluctuations remain unknown as the vast majority of studies on consciousness consider conscious experience to be constant within a trial, and ask participants to report conscious experiences at the end of a trial only.



Box 3. Limitations

We consider three main critiques against LEAP. The first is that such a mechanism could lead perceptual consciousness to fluctuate when accumulated evidence oscillates around the threshold [104]. This issue does not apply for suprathreshold stimuli for which accumulated evidence is far above the threshold. It is valid, however, for perithreshold stimuli, although it applies to any model considering conscious access as all-or-none, assuming noisy sensory signals. Further research will be needed to characterize whether perceptual consciousness for such weak stimuli is fleety and fluctuating, notably through new experimental paradigms considering the dynamics of perceptual consciousness beyond simple binary reports of stimulus presence. The second critique is that the proposed mechanism is only based on decisional mechanisms and therefore only valid in the case of overt reports. Mounting evidence has shown that EEG markers of awareness that are similar to EA markers [105] tend to vanish for task-irrelevant stimuli or in the absence of report [106,107]. These null results based on scalp EEG suggest that the size or response magnitude of the neuronal population involved in EA is reduced in comparison to when stimuli are task-relevant, although single neuron recordings indicate it remains present [10]. To link perceptual consciousness with EA, we will need to produce more evidence supporting the existence of neurons that still accumulate evidence in the absence of task demands [10]. A third limitation is that the current implementation of LEAP does not allow a change of mind to occur once a stimulus is detected [43]. Because confidence is always defined as the maximum of accumulated evidence, it will be considered as high even if it drops dramatically after the maximum is reached. Additional mechanisms encoding evidence in support of the absence of a stimulus may enable the revision of such confidence judgments. Finally, from a practical point of view, because it is by definition impossible to collect informative response times for undetected stimuli, and because the effect of leakage on response times can be explained by a combination of the other parameters, LEAP benefits greatly from additional information such as the shape of EEG responses distinguishing detected versus undetected stimuli [10] (see also [93]).

A single mechanism for perceptual consciousness and metacognitive feelings

As a second implication, we provide the basis for a parsimonious account for both components of perceptual experience. It is often assumed that perceptual experience boils down to having a phenomenal experience, while it actually comprises two components at least. As we perceive an object, it does not merely appear with its sensory qualities but also elicits additional feelings - for example, the 'feeling of presence' [72], the 'sense of reality' [73] or the 'assertoric force' [74]. Importantly, the feeling of confidence counts among these additional feelings. Recently, some have suggested that the second component of perceptual experience formed of such feelings is metacognitive in nature [35,73]. Due to metacognitive monitoring, a first-order state with its sensory content would be imbued with the aforementioned feelings. For most proponents of this view, however, the two components of perceptual experience are attributed to two separate mechanisms, one that would determine its perceptual qualities and the other the additional feeling. For instance, it has been proposed [73] that the sensory content of perceptual experience is due to sensory processing, while the feeling of reality is due to the detection and interpretation of processing cues like fluency [74]. As far as LEAP is concerned, perceptual monitoring involves the same EA mechanism as perceptual consciousness, so that one single mechanism would give rise to perceptual experience broadly construed. In support of first-order theories, LEAP enables the possibility that accumulated evidence corresponding to a feature of the first-order information is sufficient to predict perceptual consciousness, with no need of a second-order representation that renders it conscious [35,75]. But in line with higher-order theories, the existence of LEAP would suggest that beyond perceptual consciousness, perceptual experience is formed of a second-order component, namely a metacognitive feeling of confidence that assesses perceptual consciousness as having actually occurred.

Absence of evidence but no evidence for absence

LEAP only considers a single accumulator collecting positive evidence in favor of the presence of a stimulus. However, some findings suggest that negative evidence supporting the absence of a stimulus may also be encoded in the brain, notably in the prefrontal cortex of non-human primates during the delay period following a missed stimulus [45] and time-locked to stimulus onset in the human posterior parietal cortex as we reported recently [10]. How these neurons influence the decision process is actually unknown. Given their activity profile characterized by late latencies, one could speculate that such 'miss neurons' modulate late EA at the postdecisional



level (i.e., after the threshold for detection is reached), which could help explain complex behaviors such as changes of mind whereby participants indicate a posteriori that their report of having perceived a stimulus was in fact a mistake (see Box 3).

Concluding remarks

We discussed electrophysiological and computational evidence supporting LEAP as a prime mechanism triggering perceptual consciousness and monitoring. We also argued that several properties of LEAP are susceptible to explain the dynamics of conscious percepts (intensity, onset, and duration, as well as the metacognitive feeling of confidence associated with them). Although there is strong evidence that EA is involved at one stage or another in conscious perception, it remains unclear whether it should be seen merely as a prerequisite mechanism within current theories of consciousness, or rather as a sufficient mechanism for perceptual experience to arise. And if it is sufficient, it remains unclear for which aspects of perceptual experience exactly it should be considered so, even though we have offered reasons to be optimistic about LEAP being a NCC proper. Through LEAP, we provide a computational mechanism to describe the quality of dynamic features of perceptual experience, which is directly testable experimentally.

To further support this hypothesis, we will need experimental paradigms that provide proxies to the dynamics of perceptual experience such as its onset, intensity, and duration [18,47], features which are ignored by most paradigms in the study of consciousness. Another major challenge when testing this mechanism resides in the difficulty to access the content of perceptual consciousness in the absence of reports [76]. LEAP also provides a way of smoothing noisy sensory signals into stable conscious percepts, which could also be applied in other types of experimental paradigms like binocular rivalry [22] that are more appropriate to infer the content of perceptual consciousness in the absence of report [77,78]. Finally, delineating the contribution of LEAP to existing theories of consciousness will require future research fusing behavioral, neuronal, and computational data (see Outstanding questions).

Acknowledgments

M.P. is supported by a Postdoc. Mobility fellowship from the Swiss National Science Foundation (P400PM_199251). N.F. has received funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation program (grant agreement no. 803122). We thank Jérôme Dokic, Elisa Filevich, Vincent de Gardelle, Louise Goupil, Liad Mudrik, Roy Salomon, and Frédérique de Vignemont for their insightful comments.

Declaration of interests

No interests are declared.

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Outstanding questions

How is activity from EA neurons readout to account for perceptual experience? Documenting the population dynamics at play toward perceptual experience will require simultaneous recordings of multiple neurons at multiple locations in humans capable of conscious reports.

Does the prefrontal cortex accumulate evidence? Given the current debates regarding the role of the prefrontal cortex for perceptual consciousness among first- and second-order theories of consciousness, it will be important to measure whether neuronal populations in the prefrontal cortex accumulate evidence to encode the subjective presence versus absence of sensory stimuli irrespective of reports.

How do multiple stimulus features integrate with LEAP? The combination of multiple features possibly originating from distinct sensory modalities and resulting in a unified multisensory experience remains a mystery for most theories of consciousness, including EA models. Likewise, these models account for perceptual experience associated with the detection of isolated, temporally well-defined stimuli, and do not consider the stream of consciousness produced by more naturalistic stimulation whereby percepts fade in and out of consciousness in rapid succession.

How do biases in EA result in perceptual experience in the absence of stimuli, similar to hallucinations? Future research comparing hallucinators and nonhallucinators or using pharmacological manipulations may determine how the different parameters of EA contribute to hallucinations and the metacognitive feelings of confidence associated with them.

Where anatomically is confidence conditioned to stimulus detection? The definition of confidence we proposed is conditional to stimulus detection, as the difference between the maximal accumulated evidence and the detection threshold will take opposite signs for detected and undetected stimuli. The neural implementation of this conditionalization remains to be defined.



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