

A leaky evidence accumulation process for perceptual experience

Michael Pereira¹, Denis Perrin², Nathan Faivre¹

Affiliations

1 Univ. Grenoble Alpes, Univ. Savoie Mont Blanc, CNRS, LPNC, 38000 Grenoble, France

2 Univ. Grenoble Alpes, IPhiG, 38000 Grenoble, France

Corresponding author:

Michael Pereira

Laboratoire de Psychologie et Neurocognition

CNRS UMR 5105

UGA BSHM

1251 Avenue Centrale

38058 Grenoble Cedex 9

Keywords: evidence accumulation, perceptual consciousness, perceptual monitoring, decision-making, electrophysiology, neural correlates of consciousness.

Abstract (100 - 120 words)

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 overtime to produce a conscious percept, known as the specific feel of what it is like to have a visual experience? In perceptual decision-making, evidence accumulation (EA) 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** is 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 **Leaky Evidence Accumulation Process** (LEAP) can account for two key components of **perceptual experience**, namely perceptual consciousness and **perceptual monitoring**. As we describe below, 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). 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 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 towards 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 to 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 does 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 (**BOX 1**).

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 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].

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 108] (unlike in the dorsal premotor cortex [25]) and even accumulate task-irrelevant evidence, albeit with a lower gain [26]. 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 [27], the cerebellum [28] or the posterior parietal cortex [10]. More generally, hemodynamic correlates of EA have been found in the fusiform, occipital, and inferior frontal gyri [29]. 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 [8,9,30]. Among first-order theories which assume that consciousness depends on the properties of first-order representations alone, the global neuronal workspace theory of consciousness [31] 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 and 8,9]. Likewise, if recurrent processing of neuronal activity underlies consciousness, as proposed by the recurrent processing theory [32], EA could enable perceptual consciousness by triggering recurrent processing between different specialized cortical regions (Figure 1D). This possibility is notably supported by the fact that EA could be implemented by recurrent circuits [33]. Evidence accumulation 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 [34]. 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 below).

Thus, as illustrated by these empirical and theoretical studies, in its weakest form, EA could play a role for consciousness, but would be non-sufficient, 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 they 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 [35]. Although some models of EA assume no leakage during discrimination decisions [36], 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 [37] or to their reliability [38]. Second, unlike classic EA models, evidence gathered through LEAP is continuously accumulated from the beginning of each trial, irrespective of stimulus onset [39], 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 [40]. Third, unlike neurons in motor areas that stop accumulating evidence upon reaching the decisional threshold [41], EA was allowed to continue after crossing the threshold, notably to account for

confidence as described below. Similar models were developed to account for change-of-minds [42] and are supported by EEG studies [43]. 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 [44,10]. It is still possible, however, that in some situations, different content-specific accumulators could compete through mutual inhibition [35] 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 and 10]. Interestingly, the three specific properties of LEAP listed above lead to explicit predictions on the dynamics of EA following the crossing of the threshold. Indeed, leakage and post-decisional 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 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 [45] (**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 [46], clearer [47], and longer conscious percepts [48].

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 [49]. Similar effects were reported for confidence [50] although the link between confidence and perceptual consciousness is debated, as we will see below.

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 [51] and is also a useful metric to quantify perceptual monitoring [52,53]. 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 [54] and explain the dependence of confidence on choice, stimulus intensity and time [55]. Some works assume that the confidence is read out of the losing accumulator at the time of the decision [56]. Other

works assume that confidence is based on a post-decisional readout of choice-congruent evidence only [57,58]. The latter models assume that evidence continues to be accumulated after reaching the threshold (post-decisional EA) [42,43].

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 [59]. Alternatively, we previously proposed that confidence scales with the distance between the maximum amount of accumulated evidence and the detection threshold (Figure 1A-B and [10], see also [60]). 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 [52]). 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 [61]), such as cases when one is sure that no stimulus was presented [59]. 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 [62,63]. This implies that metacognitive monitoring may operate automatically [64], 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 [65]. 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 [66,67]. In addition, this definition of confidence instantiates a form of metacognitive noise through the influence of leakage [68] on post-decisional 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 below, 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 [69]. 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-or-graded 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 [70], 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.

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—e.g. the “feeling of presence” [71], the “sense of reality” [72] or the “assertoric force” [73]. 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 [34,73]. 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 [74] 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 [73]. 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 [34,75]. 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 [44] 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 evidence accumulation at the post-decisional 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 [18,46], 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).

Box 1. NCC and subjective reports

The quest for the neural correlates of consciousness (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 vs. 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 higher-order theories posit to determine consciousness [51,83].

The contrastive approach to find NCCs has some caveats [45]. Brain processes supporting the occurrence of perceptual consciousness but devoid of actual conscious content can be included in the contrast (*NCC prerequisite*). For example, prestimulus 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-dependant 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].

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 affect also 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 [46]. 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].

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 fleetly 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 [42]. 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 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 vs. undetected stimuli [10] (see also [93]).

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.

Glossary

Evidence accumulation: the process by which evidence toward one of several possible alternatives is gathered over time through the sequential sampling of noisy signals.

Drift rate: in the 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.

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

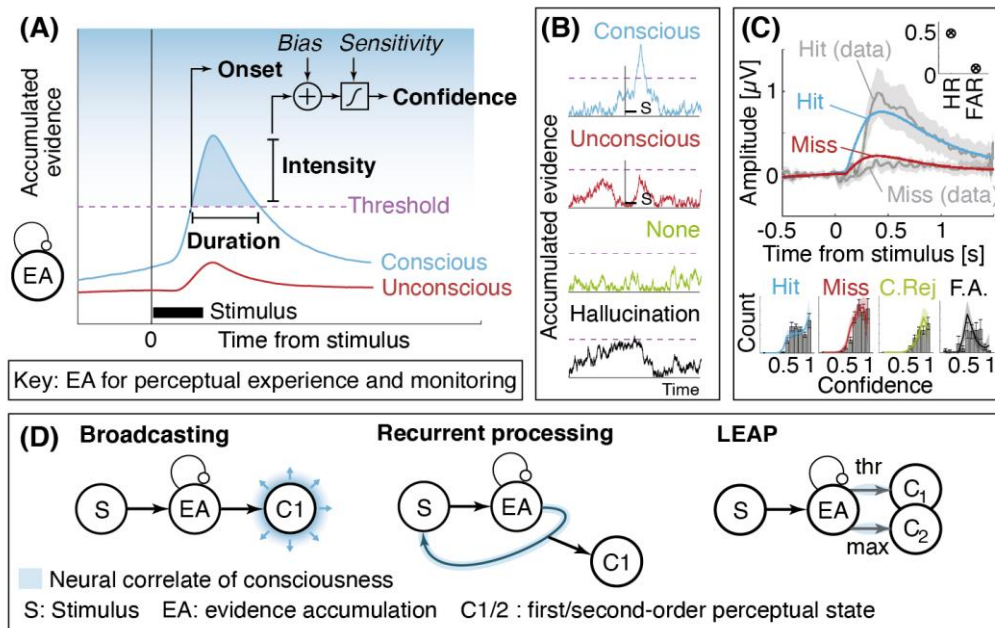
Neural Correlates of Consciousness: the minimal neuronal mechanisms jointly sufficient for any one specific conscious percept.

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 LEAP).

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, e.g. 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 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.



Key Figure. Linking evidence accumulation to perceptual experience.

(A) LEAP for perceptual consciousness and monitoring. Average EA traces locked on stimulus onset. A conscious percept occurs when accumulated evidence (blue trace) reaches a threshold (dashed 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 readout 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 (grey) 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 (grey) 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 evidence accumulation (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).

Reference

- 1 Busemeyer, J.R. and Townsend, J.T. (1993) Decision field theory: A dynamic-cognitive approach to decision making in an uncertain environment. *Psychological Review* 100, 432–459
- 2 Ratcliff, R. *et al.* (2016) Diffusion Decision Model: Current Issues and History. *Trends in Cognitive Sciences* 20, 260–281
- 3 Gold, J.I. and Shadlen, M.N. (2007) The Neural Basis of Decision Making. *Annu. Rev. Neurosci.* 30, 535–574
- 4 Hanks, T.D. *et al.* (2015) Distinct relationships of parietal and prefrontal cortices to evidence accumulation. *Nature* 520, 220–223
- 5 Shadlen, M.N. *et al.* (2016) Comment on “Single-trial spike trains in parietal cortex reveal discrete steps during decision-making.” *Science* 351, 1406–1406
- 6 Shinn, M. *et al.* (2020) A flexible framework for simulating and fitting generalized drift-diffusion models. *eLife* 9, e56938
- 7 Acerbi, L. (2020) Variational Bayesian Monte Carlo with Noisy Likelihoods. *arXiv:2006.08655 [cs, q-bio, stat]* at <<http://arxiv.org/abs/2006.08655>>
- 8 Dehaene, S. (2011) Conscious and Nonconscious Processes: Distinct Forms of Evidence Accumulation? In *Biological Physics* (Rivasseau, V., ed), pp. 141–168, Springer Basel
- 9 Moutard, C. *et al.* (2015) Spontaneous Fluctuations and Non-linear Ignitions: Two Dynamic Faces of Cortical Recurrent Loops. *Neuron* 88, 194–206
- 10 Pereira, M. *et al.* (2021) Evidence accumulation relates to perceptual consciousness and monitoring. *Nat Commun* 12, 3261
- 11 Baars, B.J. (1994) A Thoroughly Empirical Approach To Consciousness. *Psyche* 1, 1–18
- 12 Ratcliff, R. and Van Dongen, H.P.A. (2011) Diffusion model for one-choice reaction-time tasks and the cognitive effects of sleep deprivation. *Proceedings of the National Academy of Sciences* 108, 11285–11290
- 13 O’Connell, R.G. *et al.* (2018) Bridging Neural and Computational Viewpoints on Perceptual Decision-Making. *Trends in Neurosciences* 41, 838–852
- 14 Schall, J.D. (2019) Accumulators, Neurons, and Response Time. *Trends in Neurosciences* DOI: 10.1016/j.tins.2019.10.001
- 15 Cook, E.P. and Maunsell, J.H.R. (2002) Dynamics of neuronal responses in macaque MT and VIP during motion detection. *Nat Neurosci* 5, 985–994
- 16 O’Connell, R.G. *et al.* (2012) A supramodal accumulation-to-bound signal that determines perceptual decisions in humans. *Nat Neurosci* 15, 1729–1735
- 17 Twomey, D.M. *et al.* (2016) Abstract and Effector-Selective Decision Signals Exhibit Qualitatively Distinct Dynamics before Delayed Perceptual Reports. *Journal of Neuroscience* 36, 7346–7352
- 18 Kang, Y.H.R. *et al.* (2017) Piercing of Consciousness as a Threshold-Crossing Operation. *Current Biology* 27, 2285–2295.e6
- 19 Tagliabue, C.F. *et al.* (2019) The EEG signature of sensory evidence accumulation during decision formation closely tracks subjective perceptual experience. *Sci Rep* 9, 4949
- 20 Salti, M. *et al.* (2015) Distinct cortical codes and temporal dynamics for conscious and unconscious percepts. *eLife* 4, e05652

- 21 Cao, R. *et al.* (2021) Binocular rivalry reveals an out-of-equilibrium neural dynamics suited for decision-making. *eLife* 10, e61581
- 22 Gelbard-Sagiv, H. *et al.* (2018) Human single neuron activity precedes emergence of conscious perception. *Nat Commun* 9, 2057
- 23 de Lafuente, V. *et al.* (2015) Representation of Accumulating Evidence for a Decision in Two Parietal Areas. *Journal of Neuroscience* 35, 4306–4318
- 24 Bennur, S. and Gold, J.I. (2011) Distinct Representations of a Perceptual Decision and the Associated Oculomotor Plan in the Monkey Lateral Intraparietal Area. *Journal of Neuroscience* 31, 913–921
- 25 Wang, M. *et al.* (2019) Macaque dorsal premotor cortex exhibits decision-related activity only when specific stimulus–response associations are known. *Nat Commun* 10, 1793
- 26 Kumano, H. *et al.* (2016) Context-Dependent Accumulation of Sensory Evidence in the Parietal Cortex Underlies Flexible Task Switching. *Journal of Neuroscience* 36, 12192–12202
- 27 Ding, L. and Gold, J.I. (2010) Caudate Encodes Multiple Computations for Perceptual Decisions. *Journal of Neuroscience* 30, 15747–15759
- 28 Devereitt, B. *et al.* (2018) Cerebellar involvement in an evidence-accumulation decision-making task. *eLife* 7, e36781
- 29 Tremel, J.J. and Wheeler, M.E. (2015) Content-specific evidence accumulation in inferior temporal cortex during perceptual decision-making. *NeuroImage* 109, 35–49
- 30 Shadlen, M.N. and Kiani, R. (2011) Consciousness as a Decision to Engage. In *Characterizing Consciousness: From Cognition to the Clinic?* (Dehaene, S. and Christen, Y., eds), pp. 27–46, Springer Berlin Heidelberg
- 31 Mashour, G.A. *et al.* (2020) Conscious Processing and the Global Neuronal Workspace Hypothesis. *Neuron* 105, 776–798
- 32 Lamme, V.A.F. (2006) Towards a true neural stance on consciousness. *Trends in Cognitive Sciences* 10, 494–501
- 33 Wang, X.-J. (2008) Decision Making in Recurrent Neuronal Circuits. *Neuron* 60, 215–234
- 34 Lau, H. (2019) *Consciousness, Metacognition, and Perceptual Reality Monitoring*, PsyArXiv.
- 35 Usher, M. and McClelland, J.L. (2001) The time course of perceptual choice: The leaky, competing accumulator model. *Psychological Review* 108, 550–592
- 36 Kiani, R. *et al.* (2008) Bounded Integration in Parietal Cortex Underlies Decisions Even When Viewing Duration Is Dictated by the Environment. *Journal of Neuroscience* 28, 3017–3029
- 37 Ossmy, O. *et al.* (2013) The Timescale of Perceptual Evidence Integration Can Be Adapted to the Environment. *Current Biology* 23, 981–986
- 38 Piet, A.T. *et al.* (2018) Rats adopt the optimal timescale for evidence integration in a dynamic environment. *Nat Commun* 9, 4265
- 39 Devine, C.A. *et al.* (2019) The role of premature evidence accumulation in making difficult perceptual decisions under temporal uncertainty. *eLife* 8, e48526
- 40 Loughnane, G.M. *et al.* (2016) Target Selection Signals Influence Perceptual Decisions by Modulating the Onset and Rate of Evidence Accumulation. *Current Biology* 26, 496–502
- 41 Roitman, J.D. and Shadlen, M.N. (2002) Response of Neurons in the Lateral Intraparietal Area during a Combined Visual Discrimination Reaction Time Task. *J. Neurosci.* 22, 9475–9489
- 42 Resulaj, A. *et al.* (2009) Changes of mind in decision-making. *Nature* 461, 263–266
- 43 Desender, K. *et al.* (2021) Understanding neural signals of post-decisional performance monitoring: An integrative review. *eLife* 10, e67556
- 44 Merten, K. and Nieder, A. (2012) Active encoding of decisions about stimulus absence in primate prefrontal cortex neurons. *Proceedings of the National Academy of Sciences* 109,

6289–6294

- 45 Aru, J. *et al.* (2012) Distilling the neural correlates of consciousness. *Neuroscience & Biobehavioral Reviews* 36, 737–746
- 46 Miller, J. and Schwarz, W. (2006) Dissociations between reaction times and temporal order judgments: A diffusion model approach. *Journal of Experimental Psychology: Human Perception and Performance* 32, 394–412
- 47 Sandberg, K. *et al.* (2011) Measuring consciousness: Task accuracy and awareness as sigmoid functions of stimulus duration. *Consciousness and Cognition* 20, 1659–1675
- 48 Brigner, W.L. (1986) Effect of Perceived Brightness on Perceived Time. *Percept Mot Skills* 63, 427–430
- 49 Koivisto, M. *et al.* (2014) Recurrent Processing Enhances Visual Awareness but Is Not Necessary for Fast Categorization of Natural Scenes. *Journal of Cognitive Neuroscience* 26, 223–231
- 50 Baranski, J.V. and Petrusic, W.M. (1998) Probing the locus of confidence judgments: Experiments on the time to determine confidence. *Journal of Experimental Psychology: Human Perception and Performance* 24, 929–945
- 51 Morales, J. and Lau, H. (2021) *Confidence Tracks Consciousness*,
- 52 Mamassian, P. (2016) Visual Confidence. *Annu. Rev. Vis. Sci.* 2, 459–481
- 53 Rahnev, D. *et al.* (2020) The Confidence Database. *Nat Hum Behav* 4, 317–325
- 54 Kiani, R. and Shadlen, M.N. (2009) Representation of Confidence Associated with a Decision by Neurons in the Parietal Cortex. *Science* 324, 759–764
- 55 Kiani, R. *et al.* (2014) Choice Certainty Is Informed by Both Evidence and Decision Time. *Neuron* 84, 1329–1342
- 56 Moreno-Bote, R. (2010) Decision Confidence and Uncertainty in Diffusion Models with Partially Correlated Neuronal Integrators. *Neural Computation* 22, 1786–1811
- 57 Zylberberg, A. *et al.* (2012) The construction of confidence in a perceptual decision. *Front. Integr. Neurosci.* 6:79
- 58 Pereira, M. *et al.* (2020) Disentangling the origins of confidence in speeded perceptual judgments through multimodal imaging. *Proc Natl Acad Sci USA* 117, 8382–8390
- 59 Mazor, M. *et al.* (2020) Distinct neural contributions to metacognition for detecting, but not discriminating visual stimuli. *eLife* 9, e53900
- 60 Pereira, M. *et al.* (2021) *Optimal confidence for unaware visuomotor deviations*, bioRxiv 2021.10.22.465492.
- 61 Mazor, M. and Fleming, S.M. (2020) Distinguishing absence of awareness from awareness of absence. *PhiMiSci*, 1(II). <https://doi.org/10.33735/phimisci.2020.II.69>
- 62 Charles, L. *et al.* (2014) Decoding the Dynamics of Action, Intention, and Error Detection for Conscious and Subliminal Stimuli. *Journal of Neuroscience* 34, 1158–1170
- 63 Kanai, R. *et al.* (2010) Subjective discriminability of invisibility: A framework for distinguishing perceptual and attentional failures of awareness. *Consciousness and Cognition* 19, 1045–1057
- 64 Aguilar-Lleyda, D. *et al.* (2021) Confidence can be automatically integrated across two visual decisions. *Journal of Experimental Psychology: Human Perception and Performance* 47, 161–171
- 65 Shea, N. and Frith, C.D. (2019) The Global Workspace Needs Metacognition. *Trends in Cognitive Sciences* 23, 560–571
- 66 de Gardelle, V. *et al.* (2016) Confidence as a Common Currency between Vision and Audition. *PLoS ONE* 11, e0147901
- 67 Faivre, N. *et al.* (2018) Behavioral, Modeling, and Electrophysiological Evidence for Supramodality in Human Metacognition. *J. Neurosci.* 38, 263–277
- 68 Yu, S. *et al.* (2015) Dynamics of postdecisional processing of confidence. *Journal of Experimental Psychology: General* 144, 489–510

- 69 Windey, B. and Cleeremans, A. (2015) Consciousness as a graded and an all-or-none phenomenon: A conceptual analysis. *Consciousness and Cognition* 35, 185–191
- 70 Kouider, S. *et al.* (2010) How rich is consciousness? The partial awareness hypothesis. *Trends in Cognitive Sciences* 14, 301–307
- 71 Matthen, M. (2010) Two Visual Systems and the Feeling of Presence. In *Perception, Action, and Consciousness* Oxford University Press
- 72 Dokic, J. and Martin, J.-R. (2015) Felt Reality and the Opacity of Perception. *Topoi* 36, 299–309
- 73 Chasid, A. and Weksler, A. (2020) Belief-like imaginings and perceptual (non-)assertoricity. *Philosophical Psychology* 33, 731–751
- 74 Dokic, J. and Martin, J.-R. (2017) Felt Reality and the Opacity of Perception. *Topoi* 36, 299–309
- 75 Gennaro, R.J. (2004) Higher-Order Theories of Consciousness: An Overview. In *Higher-order Theories of Consciousness. An Anthology* pp. 1–13, John Benjamins Publishing Company
- 76 Tsuchiya, N. *et al.* (2015) No-Report Paradigms: Extracting the True Neural Correlates of Consciousness. *Trends in Cognitive Sciences* 19, 757–770
- 77 Hesse, J.K. and Tsao, D.Y. (2020) A new no-report paradigm reveals that face cells encode both consciously perceived and suppressed stimuli. *eLife* 9, e58360
- 78 Kapoor, V. *et al.* (2020) *Decoding the contents of consciousness from prefrontal ensembles*, bioRxiv 2020.01.28.921841
- 79 Koch, C. *et al.* (2016) Neural correlates of consciousness: progress and problems. *Nat Rev Neurosci* 17, 307–321
- 80 Chalmers, D.J. (2000) What is a Neural Correlate of Consciousness? In *Neural correlates of consciousness* pp. 17–39, MIT Press
- 81 Owen, M. and Guta, M.P. (2019) Physically Sufficient Neural Mechanisms of Consciousness. *Front. Syst. Neurosci.* 13, 24
- 82 Morales, J. and Lau, H. (2020) The Neural Correlates of Consciousness. In *The Oxford Handbook of the Philosophy of Consciousness*
- 83 Peters, M.A.K. (2021) *Towards Characterizing the Canonical Computations Generating Phenomenal Experience*, PsyArXiv. April 27. doi:10.31234/osf.io/bqfr6.
- 84 Busch, N.A. and VanRullen, R. (2010) Spontaneous EEG oscillations reveal periodic sampling of visual attention. *Proceedings of the National Academy of Sciences* 107, 16048–16053
- 85 Pitts, M.A. *et al.* (2014) Gamma band activity and the P3 reflect post-perceptual processes, not visual awareness. *NeuroImage* 101, 337–350
- 86 Boly, M. *et al.* (2017) Are the Neural Correlates of Consciousness in the Front or in the Back of the Cerebral Cortex? Clinical and Neuroimaging Evidence. *J. Neurosci.* 37, 9603–9613
- 87 Odegaard, B. *et al.* (2017) Should a Few Null Findings Falsify Prefrontal Theories of Conscious Perception? *J. Neurosci.* 37, 9593–9602
- 88 Rahnev, D. and Denison, R. (2018) Suboptimality in perceptual decision making. *Behavioral and Brain Sciences* 41, 1–66
- 89 Hanks, T.D. *et al.* (2011) Elapsed Decision Time Affects the Weighting of Prior Probability in a Perceptual Decision Task. *Journal of Neuroscience* 31, 6339–6352
- 90 Rao, V. *et al.* (2012) Neural Correlates of Prior Expectations of Motion in the Lateral Intraparietal and Middle Temporal Areas. *Journal of Neuroscience* 32, 10063–10074
- 91 Mulder, M.J. *et al.* (2012) Bias in the Brain: A Diffusion Model Analysis of Prior Probability and Potential Payoff. *Journal of Neuroscience* 32, 2335–2343
- 92 Mochol, G. *et al.* (2021) Prefrontal cortex represents heuristics that shape choice bias and its integration into future behavior. *Current Biology* 31, 1234-1244.e6

- 93 Kelly, S.P. *et al.* (2020) Neurocomputational mechanisms of prior-informed perceptual decision-making in humans. *Nat Hum Behav* DOI: 10.1038/s41562-020-00967-9
- 94 Carnevale, F. *et al.* (2015) Dynamic Control of Response Criterion in Premotor Cortex during Perceptual Detection under Temporal Uncertainty. *Neuron* 86, 1067–1077
- 95 Kloosterman, N.A. *et al.* (2019) Humans strategically shift decision bias by flexibly adjusting sensory evidence accumulation. *eLife* 8, 1–27
- 96 Peters, M.A.K. *et al.* (2016) Who's afraid of response bias? *Neurosci Conscious* 2016, niw001
- 97 Mante, V. *et al.* (2013) Context-dependent computation by recurrent dynamics in prefrontal cortex. *Nature* 503, 78–84
- 98 Summerfield, C. and de Lange, F.P. (2014) Expectation in perceptual decision making: neural and computational mechanisms. *Nat Rev Neurosci* 15, 745–756
- 99 Hohwy, J. and Seth, A. (2020) Predictive processing as a systematic basis for identifying the neural correlates of consciousness. *PhiMiSci* 1(II).
<https://doi.org/10.33735/phimisci.2020.II.64>
- 100 Glaze, C.M. *et al.* (2015) Normative evidence accumulation in unpredictable environments. *eLife* 4, e08825
- 101 Murphy, P.R. *et al.* (2021) Adaptive circuit dynamics across human cortex during evidence accumulation in changing environments. *Nat Neurosci* DOI: 10.1038/s41593-021-00839-z
- 102 Corlett, P.R. *et al.* (2019) Hallucinations and Strong Priors. *Trends in Cognitive Sciences* 23, 114–127
- 103 Weiskrantz, L. *et al.* (1974) VISUAL CAPACITY IN THE HEMIANOPIC FIELD FOLLOWING A RESTRICTED OCCIPITAL ABLATION. *Brain* 97, 709–728
- 104 Denison, R.N. *et al.* (2020) *What do models of visual perception tell us about visual phenomenology?*, PsyArXiv, <https://doi.org/10.31234/osf.io/7p8jg>.
- 105 Twomey, Deirdre M. *et al.* (2015) The classic P300 encodes a build-to-threshold decision variable. *European Journal of Neuroscience* 42, 1636–1643
- 106 Cohen, M.A. *et al.* (2020) Distinguishing the Neural Correlates of Perceptual Awareness and Postperceptual Processing. *J. Neurosci.* 40, 4925–4935
- 107 Dembski, C. *et al.* (2021) Perceptual awareness negativity: a physiological correlate of sensory consciousness. *Trends in Cognitive Sciences* 25, 660–670
- 108 Shushruth S, Mazurek M, Shadlen MN. Comparison of Decision-Related Signals in Sensory and Motor Preparatory Responses of Neurons in Area LIP. *J Neurosci.* 2018 Jul 11;38(28):6350-6365.