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Current Opinion in Neurobiology

Perspective

Surprise and novelty in the brain

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Abstract

Notions of surprise and novelty have been used in various experimental and theoretical studies across multiple brain areas and species. However, 'surprise' and 'novelty' refer to different quantities in different studies, which raises concerns about whether these studies indeed relate to the same functionalities and mechanisms in the brain. Here, we address these concerns through a systematic investigation of how different aspects of surprise and novelty relate to different brain functions and physiological signals. We review recent classifications of definitions proposed for surprise and novelty along with links to experimental observations. We show that computational modeling and quantifiable definitions enable novel interpretations of previous findings and form a foundation for future theoretical and experimental studies.

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Current Opinion in Neurobiology 2023, **82:**102758

This review comes from a themed issue on **Computational Neuroscience 2023**

Edited by **Jeanette Hellgren Kotaleski** and **Tatjana Tchumatchenko**

For a complete overview see the Issue and the Editorial

Available online xxx

https://doi.org/10.1016/j.conb.2023.102758

Introduction

An unexpected video interruption strengthens human memory of the video's content [1], mismatches between visual flow and locomotion facilitate synaptic changes in the mouse visual cortex [2], monkeys show faster saccades to unseen objects than to familiar ones [3], and mice have a higher breathing frequency when sniffing new odors than those already known [4].

What these four statements have in common is that they all concern situations where words like 'surprise' and 'novelty' seem applicable: The first two statements assess neural responses to violation of expectations, potentially caused by a feeling of surprise, whereas the second two statements assess behavioral responses to unfamiliar stimuli, potentially triggered by novelty of the stimuli. It hence feels tempting to rephrase the first two statements to 'surprise strengthens memory and modulates learning' and the second two to 'novelty attracts attention and drives curiosity'. However, the rephrased statements imply notably more than the original statements: They suggest common mechanisms for different experimental phenomena across different species. Such generalisations are important for moving towards a unified understanding of the brain, but they can be misleading if not justified.

Intuitive usage of 'surprise' and 'novelty' is common practice in neuroscience [5], psychology [6], and machine learning [7]. However, it has remained a mystery how humans' self-reported degree of 'surprise' when entering a new and unexpected room [8] relates to the brain activity of monkeys seeing 'surprising' fractals [9]. This is particularly worrisome as the words 'surprise' and 'novelty', sometimes used interchangeably, refer to different measurable variables in different studies [10,11]. Moreover, neural and behavioral signatures of several novelty- or surprise-related variables have been found simultaneously in single experiments [12–16].

If there are indeed common principles of how 'surprise' and 'novelty' contribute to different brain functions across brain areas and species, then we need systematic studies that enable neuroscientists to distinguish between different 'aspects' of surprise and novelty. In this paper, we argue that computational modeling and quantifiable definitions are necessary first steps for such systematic studies.

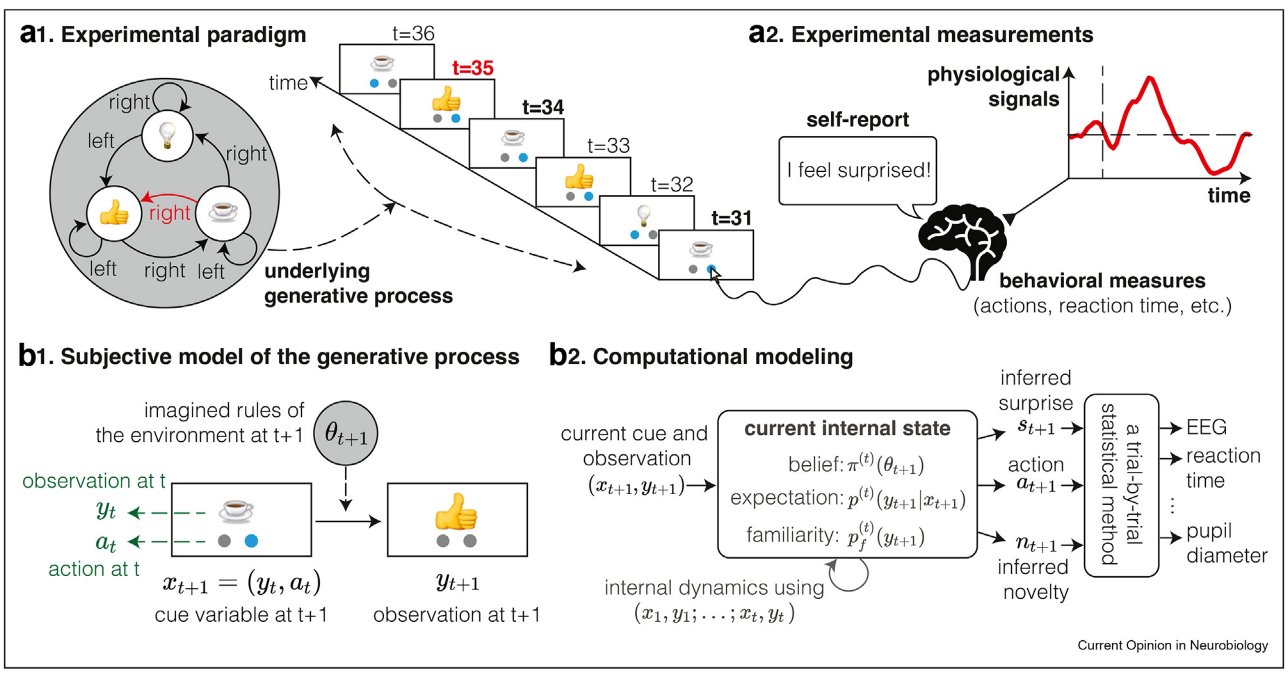
A unifying computational framework

In experimental paradigms for studying surprise and novelty, experimental subjects (human participants or animals) are presented with unlikely or infrequent observations [17,18], observations violating repeating patterns [19–22], or, in general, any observation that can *intuitively* be called 'novel' or 'surprising' (e.g., Figure 1a1). The goal of these experiments is to study how novel or surprising observations influence physiological brain signals [13,23] and action choices [16,24] (Figure 1a2).

In an example of human multi-step decision-making [16], participants see an image on a computer screen and are instructed to select an action by clicking on one of the disks below the image (Figure 1a1). The next image to appear on the screen depends on the current image and the selected action and is determined by some underlying rules that are unknown to the participants. After several trials, participants associate a particular action with a particular outcome, e.g., clicking on the right action below the coffee cup yields the light bulb as the next image ($t = 31$ and $t = 32$ in Figure 1a1). Participants will feel surprised if they see a different image than the expected one (e.g., the thumb at $t = 35$ in Figure 1a1). The experimental design is based on the idea that measurable changes in, e.g., EEG, pupil dilation, or reaction time after seeing the unexpected image can be attributed to surprise.

Computational models and quantifiable definitions allow us to go beyond mere ideas. A computational model consists of two parts: (i) an abstract description of the experimental paradigm (from the perspective of experimental subjects; Figure 1b1) and (ii) a formal description of subjects' perception and behavior (Figure 1b2). We can describe most existing experiments on surprise and novelty by using only three variables at time $t+1$ (Figure 1b1): The observation y_{t+1}, a potential cue x_{t+1}, and a set of hidden parameters θ_{t+1} (Box 1) [11].

Figure 1



Computational modeling of experimental paradigms studying surprise and novelty. a. The goal of experiments on surprise and novelty is to study the influence of 'novel' or 'surprising' observations (a1) on various behavioral and physiological measurements (a2). The example in a1 shows a simplified version of the task of [16]: In each trial, human participants see an image on a computer screen and select one of the two available actions (i.e., disks below the image; selected actions are shown in blue). The next image depends on the current image and the selected action and is determined by the underlying rules of the experiment that are unknown to participants (i.e., the graph on the left side; the black arrows correspond to available actions and the red one to a potentially surprising transition after an unannounced change of rules). Assuming all transitions have been experienced in the first 30 trials, observing the 'light bulb' at $t = 32$ is expected, whereas observing the 'thumb' at $t = 35$ is unexpected and potentially surprising (after taking action 'right' when seeing the 'coffee cup'). See Figure 2a and [11] for other examples. **b.** A computational model of an experiment consists of an abstract description of the experimental paradigm (b1) and a formal description of the subjects' behavior (b2). **b1.** The great majority of experiments can be described using three variables for the trial at time $t + 1$: The observation y_{t+1}, the cue x_{t+1}, and the parameter set θ_{t+1} [11]. For the example in a1, y_{t+1} is the image at time $t + 1$, $x_{t+1} = (y_t, a_t)$ is the pair of the last image y_t and action a_t, and θ_{t+1} models the transitions according to the rules imagined by the subject. **b2.** A subject is modeled by an algorithm that receives a cue x_{t+1} and an observation y_{t+1} as inputs and gives an inferred surprise value s_{t+1}, an inferred novelty value n_{t+1}, and, when required, an action a_{t+1} as outputs. The algorithm has an internal state that is iteratively updated according to some internal dynamics by using the past cues and observations $(x_1, y_1; \ldots; x_t, y_t)$. In general, the internal state includes a belief $\pi^{(t)}(\theta_{t+1})$ about the parameter set θ_{t+1}, a predictive model $p^{(t)}(y_{t+1}|x_{t+1})$ to summarise the subject's expectations (e.g., Equation (1)), and a familiarity measure $p_f^{(t)}(y_{t+1})$ to quantify the familiarity of observations (e.g., Equation (2)); see Box 1. Novelty and surprise values of each observation are evaluated according to the internal state of the algorithm as in Equation (3) and Equation (4), respectively. These values are used for trial-by-trial prediction of experimental measurements (e.g., using linear regression). See [11,16] for precise definitions and [13,25] for some examples.

The cue x_{t+1} summarises all information in time step $t+1$ that subjects may consider for predicting y_{t+1}, e.g., the pair (y_t, a_t) of observation y_t and action a_t (Figure 1b1). We always include the action a_t in the cue variable x_{t+1}; this allows us to use the same mathematical formulation for experiments with or without the possibility of selecting actions. The set of parameters θ_{t+1} summarises the hidden rules (for example action-dependent transitions in Figure 1b1) that subjects, potentially unconsciously, imagine to explain the observation y_{t+1} given x_{t+1}. The imagined rules are estimates of the 'real' rules of the experiment.

Defining novelty and surprise for the observation y_{t+1} needs a formal model of how experimental subjects perceive y_{t+1}, which is described by the second part of a computational model. All modeling studies on surprise and novelty assume that subjects use their past experiences $(x_1, y_1; \ldots; x_t, y_t)$ and some internal update dynamics to make a prediction of the next observation $\widehat{y}_{t+1}$ (Box 1) and, if required, select an action a_t accordingly (Figure 1b2) [26–29]. Depending on the model assumptions, the internal dynamics can have different levels of abstractions [30], ranging from algorithmic implementations of Bayesian inference [31–34] to detailed models of biological neural networks [35–38]. In the most general setting, the model describes (i) the belief $\pi^{(t)}(\theta_{t+1})$ of the subject about the unknown set of parameters θ_{t+1} and (ii) a predictive distribution of the next observation $p^{(t)}(y_{t+1}|x_{t+1})$ based on that belief (Box 1). The belief $\pi^{(t)}(\theta_{t+1})$ indicates the probability of θ_{t+1} to be the 'real' rule of the experiment at time $t+1$ according to the subjects' past experience up to time t. The predictive distribution $p^{(t)}(y_{t+1}|x_{t+1})$ summarises subjects' expectations of what they might observe next (Box 1). For example, in a simple case where x_{t+1} and y_{t+1} take discrete values, we can define the predictive distribution as [29,39]

$$p^{(t)}\left(y_{t+1}|x_{t+1}\right) = \frac{C^{(t)}\left(y_{t+1}|x_{t+1}\right) + \text{constant}}{C^{(t)}\left(x_{t+1}\right) + \text{constant}}, \qquad (1)$$

where $C^{(t)}(x_{t+1})$ is the count of how many times a subject has received cue x_{t+1} until time t, $C^{(t)}(y_{t+1}|x_{t+1})$ is the count of those trials that were followed by observation y_{t+1}, and constants are added to avoid having zero probabilities.

Novelty is not surprise

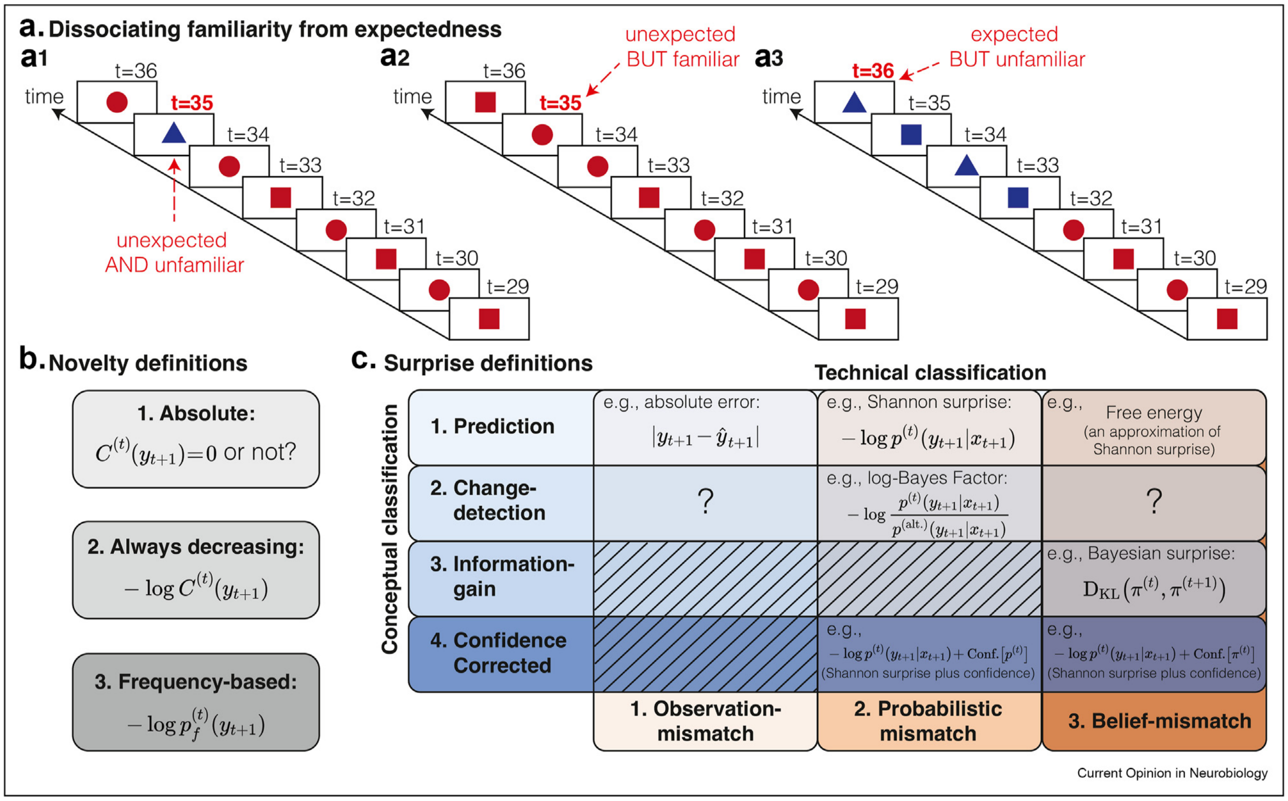
Homann et al. (2022) [22] identify a population of neurons in the mouse primary visual cortex that shows strong responses to novel stimuli but not to familiar stimuli even if the latter violate highly predictable observation patterns (Figure 2a1 versus Figure 2a2; Box 1). In the computational framework described above, this means that the physiological variables studied by [22] do not depend on the unexpectedness of y_{t+1} given the cue x_{t+1} (i.e., preceding stimuli in this case) but only on the unfamiliarity of y_{t+1} independently of any inferred regularities in the sequence of observations (Box 1).

These experimental results support the earlier proposition of Xu et al. (2021) [16] to separate notions of

Box 1. Glossary. Explanation of technical terms used to describe experiments, experimental subjects, and observations.

- When describing an **experiment**
  - **Cue** refers to information that subjects use to predict the next observation. The previously selected action (Figure 1a1) or the previous observation (Figure 2a) can be used as cues.
  - **Hidden parameters** describe the rules that generate experimental observations. A rule may imply that observation B always comes after observation A (Figure 2a). The rules are called hidden because they are not known by the subject but need to be inferred from observations. The rule in the mind of a subject may not be the same as the 'real' rule of the experiment.
  - A **Volatile experiment** is an experiment where the 'real' rule changes at unknown moments in time, e.g., [19,24].
- When describing an **experimental subject**
  - The **Belief** summarises the subject's guess about the hidden rules, based on past observations. Belief forms a probability distribution over all possible rules of the experiment.
  - **Expectations** summarise a subject's guess about possible next observations, based on the current *cue* and the current *belief.* Expectations form a probability distribution over all possible next observations.
  - A **Prediction** condenses a subject's *expectations* into a single guess for the next observation.
  - **Confidence** quantifies the certainty of a subject about either (i) the hidden rule or (ii) the next observation.
  - **Familiarity** quantifies how often a specific observation has occurred or how similar it is to other frequent observations. Familiarity does not depend on *cues.*
- When describing an **observation**
  - **Predictable** observations can in principle (i.e., if experimental rules are known) be predicted with high probability from *cues.* For example, observations in repeating or regular patterns are predictable (Figure 2a).
  - **Unexpected** observations are either unlikely given the subject's *expectations* or predicted inaccurately given the subject's *prediction.* Given sufficient experience, *predictable* observations are on average less unexpected than *unpredictable* ones. Whether an observation is unexpected depends on the *cue.*
  - **Unfamiliar** observations are those that have been encountered rarely by subjects and are not similar to other frequent observations (i.e., low *familiarity*). An *expected* observation can be unfamiliar (Figure 2a3), while a familiar observation can be *unexpected* (Figure 2a2). Whether an observation is unfamiliar does not depend on the *cue.*

Figure 2



A taxonomy of surprise and novelty definitions. Novelty quantifies the unfamiliarity of an observation (Equation (3)), whereas surprise quantifies its unexpectedness conditioned on the cue variable x_{t+1} (Equation (4)) [16]. **a.** Average familiarity and expectedness can be manipulated in an experimental paradigm where each observation $y_t = x_{t+1}$ is the predictor of the next observation y_{t+1} (e.g., [9,14,22]; Box 1). A blue triangle in the middle of a repeating sequence of red squares and circles is unexpected and unfamiliar (high surprise, high novelty; a1), whereas a misplaced red circle is unexpected although familiar (high surprise, low novelty; a2). A blue triangle observed for the second time after a switch in the observation pattern from repeating red square-red circle to repeating blue square-blue triangle is expected but not familiar (low surprise, high/medium novelty; a3). **b.** Most definitions of novelty can be classified into three groups: 1. 'Absolute novelty' considers novel observations as those never observed before ($C^{(t)}$ (y_{t+1}): the count of y_{t+1} until time t). 2. 'Always decreasing novelty' is a decreasing function of the count $C^{(t)}$ (y_{t+1}). 3. 'Frequency-based novelty' is a decreasing function of the observation-frequency $p_f^{(t)}(y_{t+1})$ (e.g., Equation (2)). **c.** A technical classification of surprise definitions (columns) [11]: 1. Observation-mismatch surprise needs only a prediction $\hat{y}_{t+1}$ of the next observation. 2. Probabilistic mismatch surprise needs the full predictive distribution $p^{(t)}$ $(y_{t+1}|x_{t+1})$. 3. Belief-mismatch surprise needs the subject's full belief distribution $\pi^{(t)}$ (θ_{t+1}); $\mathrm{D_{KL}}$ denotes Kullback-Leibler divergence. An additional conceptual classification of surprise definitions (rows) [11]: 1. Prediction surprise defines surprising events as those that violate predictions. 2. Change-detection surprise quantifies possibility of changes in θ_{t+1} and defines surprising events as those predicted inaccurately *in comparison* with an alternative predictive model $p^{(\mathrm{alt.})}$ $(y_{t+1}|x_{t+1})$ [33]. 3. Information-gain surprise defines surprising events as those that change a subject's belief. 4. Confidence-corrected surprise adds an explicit measure of confidence into a definition of surprise, e.g., Shannon surprise plus a measure of confidence; note that the categorisation as probabilistic or belief-mismatch also depends on the definition of confidence. While the two classifications are complementary, they are not fully independent: One needs $\pi^{(t)}$ to evaluate an information-gain surprise, and it is not possible to define confidence without access to $\pi^{(t)}$ or $p^{(t)}$ (hatched boxes). Question marks: Categories without any example in the literature. See [11] for a detailed mathematical treatment of different definitions, their placement in the categories, and their relationships.

surprise and novelty based on their relation to unexpectedness and familiarity: Surprising stimuli violate expectations; hence, *surprise is a measure of the unexpectedness* of y_{t+1} according to the predictive model $p^{(t)}$ $(y_{t+1}|x_{t+1})$. Novel stimuli, however, violate familiarity; hence, *novelty is a measure of the unfamiliarity* of y_{t+1} according to the familiarity $p_f^{(t)}(y_{t+1})$ (Box 1 and Figure 2). The familiarity $p_f^{(t)}(y_{t+1})$ quantifies how frequent y_{t+1} (e.g., a specific image) has been up to time t independently of the cue x_{t+1} and potential regularities in observations (see [40] for similar ideas in machine learning). For example, in cases where x_{t+1} and y_{t+1} take discrete values (same assumption as in Equation (1)), one can define familiarity as the observation frequency

$$p_f^{(t)}(y_{t+1}) = \frac{C^{(t)}(y_{t+1}) + \text{constant}}{t + \text{constant}}, \tag{2}$$

where $C^{(t)}$ (y_{t+1}) is the count of how many times a subject has observed y_{t+1} until time t, and constants are added to avoid having zero frequencies. Novelty of observation y_{t+1} defined as $n_{t+1} = -\log\ p_f^{(t)}\ (y_{t+1})$ ('frequency-based novelty'; Figure 2b) explains some significant trial-by-trial variabilities of human EEG signals [16]. More generally, novelty of y_{t+1} can be defined as

$$n_{t+1} = N^{(t)}(y_{t+1}), \tag{3}$$

where $N^{(t)}$ is a general function that (i) takes y_{t+1} as its argument, (ii) is *independent* of the cue x_{t+1}, and (iii) depends on the subject's current internal state at time t (Figure 1b2).

The central criterion proposed by Xu et al. is that definitions of surprise quantify the *unexpectedness* of y_{t+1} and must be *conditioned* on x_{t+1}, whereas definitions of novelty quantify the *unfamiliarity* of y_{t+1} and must be *independent* of x_{t+1}. Almost all existing definitions of novelty in neuroscience and psychology meet this criterion and can be written as in Equation (3) [5,10]. For example, two alternative approaches to defining novelty are to (i) consider only the first encounter of a specific observation as novel ('absolute novelty'; Figure 2b) [41,42] or (ii) define the novelty of y_{t+1} as a decreasing function of the count $C^{(t)}$ (y_{t+1}) ('always decreasing novelty'; Figure 2b) [43,44]. Note that according to novelty definitions based on observation frequency (e.g., Equation (2)), the novelty of the observation y_{t+1} increases if it has not been observed for some time.

The distinction proposed by Xu et al. enables new interpretations of earlier results: For example, the separate MEG signatures found by [13] for 'frequency-based' and 'transition-based' surprise can alternatively be interpreted as separate signatures for novelty and surprise, respectively; what has been called 'expected surprise' by [45] can be seen as novelty; and what has been called 'contextual novelty' in neuroscience [5] is a form of surprise and not novelty. These interpretations help connect otherwise separate experimental phenomena in a single coherent framework.

Finally, the perceived novelty of a stimulus does not only depend on how often the exact same stimulus has been experienced. For example, a familiar image with an altered contrast level is a novel stimulus per se, but it may be perceived as a familiar one if the subject cares only about the image identity [46]; similarly, some novel stimuli may be perceived less novel than others if they look similar to familiar stimuli. Many experimental studies support such feature-dependency in novelty responses in the brain [9,22,47]. Novelty definitions based on the simple observation frequency in Equation (2) can be generalised to account for feature-dependent novelty estimation as the familiarity measure $p_f^{(t)}$ (y_{t+1}) can be an arbitrary (non-negative and normalised) function of the stimulus. Analogously, count-based novelty definitions can account for feature-dependent novelty estimation by turning to frequency-based pseudo-counts [40,48].

A taxonomy of surprise definitions

Surprise is caused by a violation of expectations. However, even if we agree that surprise quantifies the unexpectedness of y_{t+1} conditioned on x_{t+1}, there are multiple possibilities for quantifying unexpectedness [10,12,31–33,49–51]. In general, surprise of y_{t+1} can be written as

$$s_{t+1} = S^{(t)}(y_{t+1}|x_{t+1}), \tag{4}$$

where $S^{(t)}$ is a general function that (i) takes both y_{t+1} and x_{t+1} as arguments (in contrast to Equation (3)) and (ii) depends on the subject's current internal state at time t (Figure 1b2) [11]. A recent systematic taxonomy of commonly used definitions of surprise proposes two classification schemes for these definitions [52] (Figure 2c).

The first classification is based on the minimal information, about the subject's internal state, that is needed for computing surprise with a given definition (columns in Figure 2c): 1. *Observation-mismatch* surprise is defined based on the assumption that, at each time t, an experimental subject makes a prediction $\hat{y}_{t+1}$ of the upcoming observation y_{t+1}. Observation-mismatch surprise quantifies surprise as a mismatch between y_{t+1} and $\hat{y}_{t+1}$; an example is the absolute difference $s_{t+1} = |y_{t+1} - \hat{y}_{t+1}|$, where $\hat{y}_{t+1}$ is, e.g., the mean of the predictive distribution [53]. 2. *Probabilistic mismatch* surprise depends on the full distribution $p^{(t)}$ $(y_{t+1}|x_{t+1})$ of possible outcomes and, hence, requires more information than a single prediction $\hat{y}_{t+1}$; an example is the Shannon surprise or surprisal $s_{t+1} = -\log p^{(t)}$ $(y_{t+1}|x_{t+1})$ [10]. 3. *Belief-mismatch* surprise can be evaluated only by having access to the full belief $\pi^{(t)}$ (θ_{t+1}) about the hidden parameter set θ_{t+1} and requires even more information than the full distribution $p^{(t)}$ $(y_{t+1}|x_{t+1})$; an example is the Bayesian surprise $s_{t+1} = \mathrm{D_{KL}}(\pi^{(t)}, \pi^{(t+1)})$, where $\mathrm{D_{KL}}$ denotes Kullback-Leibler divergence [31,32].

The second classification is a conceptual one (rows in Figure 2c): 1. *Prediction* surprise defines surprising events as those that violate predictions, e.g., the Shannon surprise $s_{t+1} = -\log p^{(t)}$ $(y_{t+1}|x_{t+1})$. 2. *Change-detection* surprise also defines surprising events as those that violate predictions but only *in comparison* with an alternative predictive model; an example is the difference in the Shannon surprise $s_{t+1} = \log[p^{(t)}(y_{t+1}|x_{t+1}) \,/\, p^{(\text{alt.})}(y_{t+1}|x_{t+1})]$, where $p^{(\text{alt.})}$ $(y_{t+1}|x_{t+1})$ is a prior or naive predictive model [33]. According to change-detection surprise definitions, if the observation y_{t+1} is unlikely according to both the predictive model $p^{(t)}$ and its alternative, then it is not perceived as surprising. Hence, change-detection surprise can be interpreted as a measure of relative surprise. Importantly, change-detection surprise is optimal to modulate learning in volatile environments [11,33] (Box 1), in agreement with experimental observations [19, 24, 63].

3. *Information-gain* surprise defines surprising events as those that change a subject's belief about the world, e.g., the Bayesian surprise $s_{t+1} = \mathrm{D}_{\mathrm{KL}}(\pi^{(t)}, \pi^{(t+1)})$. We note, however, that only a handful of information-gain measures [64] have been previously interpreted as measures of surprise [12,31,32]. 4. *Confidence-corrected* surprise is defined based on the argument that a given error in prediction should feel more surprising if it is made with higher confidence (Box 1); examples have been suggested both in neuroscience [50] and psychology [51].

The two classifications together propose a refined terminology necessary for a systematic study of surprise in the brain. The first classification is important to judge whether surprise computation based on different definitions can be biologically plausible. For example, evaluating observation-mismatch surprise in a recurrent network of spiking neurons might be simpler than evaluating probabilistic mismatch and belief-mismatch surprise under similar biological constraints [35,36,38]; see [65,66] for different views on the neural implementation of probabilistic inference. The first classification can thus help studies to bridge the gap between algorithmic and mechanistic neural models of 'surprise-driven' attention [67], exploration [68], and learning [28].

The second classification is important as it suggests that observations that *intuitively* feel surprising can do so because of different aspects of surprise. Importantly, experimental studies of surprise have found separate neural signatures for different definitions (Table 1). For example, Gijsen et al. (2021) [14] found independent EEG signatures of prediction, information-gain, and confidence-corrected surprise in an experimental paradigm using somatosensory roving stimuli. Similarly, Kolossa et al. (2015) [12] showed in an earlier study that even different definitions in the same surprise category (e.g., information-gain surprise) can have different neural signatures. These results suggest that the experimental phenomena previously attributed to a single broad notion of 'surprise' might relate to very different but precise definitions of surprise.

The proposed taxonomy can also provide new interpretations of existing experiments: Beyond the comparison of trial types (e.g., expected versus unexpected trials), mathematical definitions of surprise and novelty enable trial-by-trial data analysis (Table 1). For example, Zhang et al. (2022) [9] observe in monkeys that neural responses to an unexpected stimulus are different depending on whether the stimulus appears in a random unpredictable sequence or in a regular predictable sequence (Box 1). The observed difference may be an indication that surprise signals in different brain areas relate to different surprise categories rather than a single notion of surprise. Such a hypothesis can be tested by trial-by-trial data analysis combined with computational modeling.

Finally, surprise can also quantify the unexpectedness of a scalar (or low dimensional) summary signal extracted from the (high dimensional) observation y_{t+1} instead of y_{t+1} itself. For example, the unsigned reward prediction error (uRPE) [69,70] measures the mismatch between the reward $r(y_{t+1})$ associated with stimulus y_{t+1} and a prediction $\widehat{r}_{t+1}$ thereof (see [11]). Similarly, an unsigned novelty prediction error (uNPE) measures the unexpectedness of the novelty value $N^{(t)}$ (y_{t+1}) of an observation y_{t+1} [16,71]. We can think of uRPE and uNPE as secondary surprise signals since they are derived from a scalar summary signal. When interpreting neural responses to 'novel' stimuli, it is hence important to consider that responses correlated with novelty may in fact be caused by errors in novelty prediction [16,71]. Moreover, subjects may assume potential associations between novelty (or similarly between surprise) and threats or rewards [43,60], which can lead to confounding effects of threats and rewards on neural responses to novelty (or surprise); hence, ideal experimental paradigms for studying neural and behavioral signatures of novelty and surprise require a dissociation of these signals from threats and rewards.

In addition, there can be multiple forms of neural responses to surprise and novelty of an abstract observation y_{t+1} depending on how it is neurally represented regarding, for example, sensory modality (e.g., auditory versus visual [59]) or the hierarchy of representations (e.g., image identity [16,46] versus primary visual features [2,22]). For example, a repeating sequence of binary observation as in Figure 2a can be presented as either a sequence of tones or a sequence of images (i.e., different modalities); Grundei et al. (2023) [59] found separate modality-specific and modality-independent EEG signatures of surprise in an experimental paradigm using somatosensory, auditory, and visual roving stimuli. Moreover, a sequence of images could consist of meaningless fractals, sketches of meaningful objects, or different visual drawing styles of always the same object, which results in the same temporal sequence of stimuli in the visual domain but at different levels of abstraction.

Towards a systematic study of surprise and novelty

Different computational roles in learning [34,72] and decision-making [73–75], broadly attributed to 'surprise' and 'novelty, may correspond to different but mathematically precise definitions of novelty and surprise and ultimately also to distinct physiological signals. This leaves us with two main questions: 1. How many fundamentally distinct physiological signals are involved in brain computations related to surprise and novelty? 2.

Table 1

Example experimental papers with more than one signal related to surprise and novelty. 'T-by-T' indicates whether trial-by-trial data analysis is performed. 'Compared signals' lists precise mathematical definitions (for trial-by-trial analysis) or the description of trial types (otherwise) that are compared. Animal studies with trial-by-trial analysis exist (e.g., [**54**,**55**]) but none with more than one definition of surprise or novelty. *Abbrevations:* CI: Calcium Imaging. Conf.: Confidence. Cort.: Cortex. DA: Dopamine. EEG: Electroencephalography. EP: Electrophysiology. Exp.: Expected. fMRI: Functional Magnetic Resonance Imaging. FP: Fiber Photometry. MEG: Magnetoencephalography. OG: Optogenetic. Seq.: Sequence. Unexp.: Unexpected.

	T-by-T	Compared signals	Subjects	Stimulus modality	Measurements
Macedo et al. (2004) [51]	Yes	1. Six definitions of prediction surprise 2. Two definitions Conf.-Corrected surprise	Humans	Questionnaire	1. Self-report
O'Reilly et al. (2013) [56]	Yes	1. Shannon surprise 2. Bayesian surprise	Humans	Visual	1. fMRI 2. Pupillometry 3. Reaction time
Kolossa et al. (2015) [12]	Yes	1. Shannon surprise 2. Bayesian surprise 3. Postdictive surprise	Humans	Visual	1. EEG
Maheu et al. (2019) [13]	Yes	1. Shannon surprise 2. Frequency-based novelty	Humans	Auditory	1. MEG
Visalli et al. (2019 & 2021 & 2023) [15,57,58]	Yes	1. Shannon surprise 2. Bayesian surprise	Humans	Visual	1. EEG [15,58] 2. fMRI [57] 3. Reaction time
Dubey and Griffiths (2019) [44]	Yes	1. Information-gain 2. Always decreasing novelty	Humans	Questionnaire	1. Action choices
Xu et al. (2021) [16]	Yes	1. Shannon/Bayes Factor surprise 2. Frequency-based novelty	Humans	Visual	1. EEG 2. Action choices
Gijsen et al. (2021) [14] and Grundei et al. (2023) [59]	Yes	1. Shannon surprise 2. Bayesian surprise 3. Conf.-Corrected surprise	Humans	1. Somatosensory [14,59] 2. Auditory [59] 3. Visual [59]	1. EEG
Modirshanechi et al. (2023) [52]	Yes	1. Shannon surprise 2. Postdictive surprise 3. Frequency-based novelty	Humans	Visual	1. Action choices
Morrens et al. (2020) [4]	No	1. New stimuli in a random seq. 2. Rare stimuli in a random seq.	Mice	Olfactory	1. FP recording of DA 2. Breathing frequency
Zhang et al. (2022) [9]	No	1. Unexp. new stimuli 2. Unexp. familiar stimuli in a random seq. 3. Unexp. familiar stimuli in a regular seq.	Monkeys	Visual	1. EP in 22 brain areas 2. Pupillometry 3. Saccade latency
Homann et al. (2022) [22]	No	1. New stimuli in a regular seq. 2. Switch of stimuli in a regular seq.	Mice	Visual	1. CI in the visual cort.
Akiti et al. (2022) [60]	No	1. Novel objects 2. Familiar objects in unexp. context	Mice	Visual	1. OG recording of DA 2. Action choices
Garrett et al. (2023) [61] (see also [62])	No	1. Exp. new stimuli 2. Unexp. new stimuli 3. Unexp. familiar stimuli 4. Omission of exp. stimuli	Mice	Visual	1. CI in the visual cort. 2. Action choices

What is the role of each physiological signal in each brain function? Addressing these questions requires interactions of theory and experiments.

Recent years have seen an increasing interest in this line of research. For example, Akiti et al. (2021) [60] show that mice exhibit different behavioral patterns when inspecting novel versus surprising objects and that striatal dopamine release modulates the inspection of novel objects differently from the inspection of surprising ones. Dubey and Griffiths (2019) [44] show that seeking novelty and information-gain (i.e., two distinct curiosity-related behavioral patterns) can be considered special cases of seeking a single 'curiosity signal' that is 'optimal' for exploration and depends on experimental conditions. Another study on exploratory behavior, on the other hand, shows that novelty-driven algorithms explain the human search for rewarding states better than algorithms driven by prediction surprise or information-gain, even when novelty-seeking is suboptimal [52]. Similar approaches can be applied to studying the influence of different aspects of surprise and novelty on learning, memory, and attention.

In conclusion, different aspects of surprise and novelty can be captured and quantified by precise definitions and well-designed experiments. The classifications in Figure 2 offer a foundation for future experimental and theoretical studies on surprise and novelty.

Author contributions

A.M. Conceptualization, Methodology, Formal analysis, Writing- Original draft, Writing-Review and Editing., S.B. Conceptualization, Writing-Review and Editing., J.B. Conceptualization, Writing-Review and Editing. W.G. Conceptualization, Writing-Review and Editing, Supervision.

Declaration of competing interest

The authors declare no competing interests.

Data availability

No data was used for the research described in the article.

Acknowledgement

A.M. thanks Vasiliki Liakoni, Martin Barry, and Valentin Schmutz for useful discussions on related topics. This research was supported by the Swiss National Science Foundation No. 200020_207426.

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