Is perception probabilistic? Clarifying the definitions

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Abstract

A fundamental question for perception research is what sensory information is available for decision making, or, stated differently, what is the output of perception. One answer that has emerged in the last two decades is that perception is probabilistic, meaning that the brain represents probability distributions over world states. However, despite the apparent simplicity of this statement, there are substantial disagreements on exactly what probabilistic perception is and how it should be tested. In this adversarial collaboration, two proponents (Jehee and Denison) and two skeptics (Rahnev and Block) of probabilistic perception deliberate on the terms of the debate and present arguments for or against the notion that perception is probabilistic. We believe that this collaboration helps clarify the critical issues that need to be considered but that further work is required to reach consensus.

Introduction

Our sensory organs generate signals that are both ambiguous and noisy. On one hand, the ambiguity is imposed by the world and the nature of our sensory organs: for example, an infinite number of 3D objects at different distances from the eye with different lighting can create the same 2D image on the retina (Palmer, 1999). On the other hand, the noise is the result of the inherent stochasticity in neuronal signals (Vogels et al., 1989). Together, the ambiguity and noisiness of sensory signals affect the precision with which the state of the outside world can be represented by the brain. Faced with this limitation, how does information come to be represented in the sensory cortex so as to facilitate adaptive cognition and behavior? Most importantly, what information is available at the output of perception to allow us to deal with this uncertainty?

The notion of probabilistic perception

One answer that has emerged in the last two decades is that perception is probabilistic (Drugowitsch & Pouget, 2012; Fiser et al., 2010; Haefner et al., 2016; Jazayeri & Movshon, 2006; Ma et al., 2006; Ma & Jazayeri, 2014; Pouget et al., 2000, 2013; Sahani & Dayan, 2003; Zemel et al., 1998). The probabilistic nature of perception has been defined, for example, as "the brain represents information probabilistically, by coding and computing with probability density functions" (Knill & Pouget, 2004). Probabilistic perception is usually viewed as the idea that the perceptual representation at the output of perception represents a probability distribution over the possible world states (Fiser et al., 2010). However, despite the seeming simplicity of this statement and the fact that the authors agree on many of the issues, we could not thus far reach consensus about what the definition really entails and how it can be tested. This paper is our attempt to address these issues. We structure the rest of the paper in two sections. First, two proponents of probabilistic perception (Jehee & Denison) explain what they see to be the critical components of probabilistic perception and review the empirical evidence for it. Second, two skeptics of probabilistic perception (Rahnev & Block) outline two possible definitions of probabilistic perception that they term "strong" and "weak" probabilistic perception, and argue that the empirical evidence only supports weak but not strong probabilistic perception. We start, however, with a brief introduction to probability theory, which is at the heart of the concept of probabilistic perception.

A very brief introduction to probability theory

Probability is an abstract mathematical notion first formally developed by Kolmogorov (1933). It is defined by three axioms. Informally, the axioms state that probability of any set should be greater or equal to zero, the probability of the whole set should be 1, and that the probability of the union of disjointed sets should be equal to the sum of the probability of each set. Formally, let Ω be a set, $\mathcal{F}$ be a σ-algebra on Ω, and $\mathbb{P}$ be a set function. $\mathbb{P}$ is a probability if and only if the following three axioms are met: (1) $\mathbb{P}(A) \geq 0$ for all $A \in \mathcal{F}$, (2) $\mathbb{P}(\Omega) = 1$, and (3) $\mathbb{P}(\bigcup_{i=1}^{\infty} A_i) = \sum_{i=1}^{\infty} \mathbb{P}(A_i)$ for all countable collections of disjoint sets $A_i \in \mathcal{F}$ where σ-algebra on Ω is a collection of subsets of Ω.

The term "probabilistic" then is defined with respect to a function, $\mathbb{P}$, that conforms to the formal definition of probability. This definition of the term probabilistic is often expressed in more intuitive terms such as "using the tools of probability theory" (Hitchcock, 2021), "reflect the laws of probability" (Moss, 2018), and obey "the Kolmogorov axioms of probability" (Byrne, 2021) with all of these definitions ultimately referencing the formal definition of probability $\mathbb{P}$.

The case for probabilistic perception (Jehee & Denison)

What is a 'world state', when and how is probability 'represented' in neural population activity, and how do we quantify 'uncertainty'? We will start by providing some definitions and intuitions.

<u>What is a world state?</u>

Perception is essentially an inference problem. The brain takes incoming sensory signals and interprets these in terms of what they convey about the environment. Sensory signals convey, for example, information about material properties, surface shape, object movement or identity, and these variables of interest are collectively called the 'world state'. The variables are 'latent'. That is, the brain receives noisy sensory signals, rather than an explicit representation of the variables themselves.

<u>Which probability distribution would be represented in neural activity?</u>

It is important to realize that we are not interested in a representation of probability *per se*, but rather in the probability of a latent variable *s* given the sensory measurement *r*. The probability distribution is obtained using the tools of probability theory and Bayesian statistics, so this is either the likelihood $L(s|r)$ or the posterior distribution $p(s|r)$. The distribution describes the range of possible interpretations of the neural response. The variable *s* can be the orientation of a stimulus, the identity of a face, or any other aspect of the environment that the brain might be interested in. The measurement *r* is the response of a population of neurons. The traditional view is that neurons signal single-valued interpretations, such as an estimate of the orientation of a stimulus. However, because of ambiguity and noise, a given population response hardly ever points to just one interpretation. Rather, neural responses are usually consistent with a whole range of possibilities, with some possibilities more likely than others. The probabilistic view quantifies this notion as a probability distribution, whereby each possible interpretation is assigned a probability. More formally, the distribution can be viewed as a measure of the *amount of information* that is available about the variable in the neural population response, where information is formalized as, for example, Lindley-Shannon information (Lindley, 1956; Shannon, 1948). A broader range of interpretations indicates less information, so the population is said to carry more *uncertainty* about its estimates.

In order to be able to extract information from a neural population response, it is necessary to have some notion of neuronal tuning and noise. Note that this is a general statement – no information can *ever* be extracted without some sort of knowledge of neural response properties, however this knowledge may be implemented in downstream neurons. In the probabilistic framework, this is formalized by the ‘generative model’, which is a statistical description of the link between latent variable and neural response. Importantly, the descriptions of the generative model need not be fully accurate, and probability distributions can still be computed when the model is approximated or incomplete. Interestingly, such imprecision often results in biases and more variable behavior. Thus, biases and suboptimalities in neural representations and behavior are not inconsistent with a probabilistic readout of information; rather, they can arise from approximations in complex neural computations (Beck et al., 2012). Of course, the observer need not be forever stuck with an imperfect statistical description. Additional experience will enable the observer to learn and better capture the true statistical structure of the task. This could, for example, modify neural tuning properties, thereby improving cortical information as well as the observer's task performance.

What is our definition of uncertainty?

Neural signals are necessarily imprecise due to noise and ambiguity in the input, and this imprecision is quantified by a probability distribution. Within the probabilistic framework, 'uncertainty' directly refers to this probability distribution. Specifically, it is a function of the likelihood $L(s|r)$ or posterior $p(s|r)$ that quantifies how much information the neural signals provide about the latent variable. This is sometimes further specified as Shannon entropy. For Gaussian distributions, a measure of statistical dispersion (such as variance) is also used, which is linked to Fisher information (Seung & Sompolinsky, 1993). Of course, information can only be extracted from neurons that are somehow tuned to the variable of interest – after all, nothing can be learned about the orientation of a stimulus from color-tuned neurons. Similarly, uncertainty about an estimated variable is intrinsically linked to neurons that are tuned to this variable. For example, consider the color-tuned neurons. Although it would be technically possible to extract from their response a probability distribution over orientation, the distribution would be flat, signaling no information. Consequently, any orientation estimate derived from the color-tuned signals would simply be a random guess, with maximum associated uncertainty. This scenario contrasts strongly with a distribution that is computed from orientation-tuned neurons. Such a distribution would not be flat, but rather bell shaped, signaling that there is in fact information about orientation. The most likely orientation (the peak of the distribution) could be the estimate, while the width of the distribution can be taken to reflect the degree of uncertainty in this estimate (i.e., the error bars on the estimate). Importantly, because this measure directly reflects the *actual* amount of information contained in the neural population response, it is our best estimate of uncertainty.

For non-probabilistic coding schemes, uncertainty is not derived from the probability distribution. Instead, non-probabilistic uncertainty is based on heuristic strategies. For example, certain physical properties of the stimulus, such as its blurriness or contrast, are often correlated with probabilistic uncertainty (Barthelmé & Mamassian, 2010; Bertana et al., 2020; Honig et al., 2020; van Bergen et al., 2015). Thus, a change in stimulus contrast alters the amount of cortical information available about orientation, and contrast can therefore be taken as a proxy to probabilistic uncertainty in the orientation estimates. Because it is derived from heuristics, however, this strategy does not always reflect the true amount of information available about the variable of interest (Bertana et al., 2020; Dehaene et al., 2021), and it is in this sense suboptimal. As an example, increasing stimulus duration will reduce probabilistic uncertainty, but has no effects on stimulus contrast. Thus, a heuristic strategy based on contrast might track some, but certainly not all cortical changes in orientation information.

How would a probability distribution be represented in neural population activity?

What does it mean for a neural population to 'represent' something? For the purpose of this discussion, our definition is that a variable is represented in neural activity when two requirements are met: 1) the variable can be expressed as a function of the neural population response (indicating there is information about the variable), and 2) this information is read out by downstream areas when required for the task at hand[1]. This definition well matches common intuition. For example, consider neural activity in primary visual cortex (V1). Because neuronal firing rates change as a function of the presented stimulus orientation (also known as a 'neural tuning curve'), it is possible to infer from a given neural response which orientation was likely presented to the observer. This means that orientation can be expressed as a function of the neural population response, and that requirement 1 is satisfied. Furthermore, a change in the response of orientation-tuned V1 neurons causally affects neural activity in downstream areas, as well as the observer's behavior (Seidemann & Geisler, 2018). This means that requirement 2 is also satisfied. Altogether, this means that the definition is met and that the orientation of the stimulus is 'represented' in the activity patterns of V1 neurons. Following the same logic, a neural representation is probabilistic when 1) the likelihood $L(s|r)$ or posterior distribution $p(s|r)$ over the latent variable *s* can be expressed as a function of the neural response *r*. And 2), this information is functionally available in downstream areas. Note that, under this definition, downstream areas have access to more than the first and second

[1]Note that through the information processing inequality (Cover & Thomas, 2006), information can never be created but only lost in processing. As such, retinal neurons necessarily represent information about, say, the orientation of the stimulus, but the readout of this retinal information would require complex nonlinear operations. Additional constraints on the meaning of "representation" would be needed to capture what is often meant when we say "V1 represents orientation" and plot associated neural tuning curves. While a general definition of representation is beyond the scope of the current project, the more minimal definition we provide suffices for our purposes.

moments (i.e., mean and variance) of the distribution; in fact, they would have access to an arbitrary number of moments. The accuracy of higher moments may be limited by the resolution of the downstream read out, but in principle any moment could contribute to downstream computations.

Does the nervous system represent variables probabilistically? There is evidence to suggest that probability distributions are indeed represented in cortical population activity. Several studies in humans (van Bergen et al., 2015; van Bergen & Jehee, 2019) and monkeys (Walker et al., 2020) used novel analysis techniques to extract probability distributions over orientation from population activity in visual cortex (i.e., using the tools of probability theory and Bayesian statistics, the likelihood and posterior were expressed as a function of the cortical population response). Interestingly, the width of the decoded probability distribution predicted the observer's behavioral choices. That is, when information in visual cortex was less precise (as indicated by the decoded distribution), the observer's decisions changed in ways predicted by the ideal strategy. Crucially, the point estimate (e.g., the most likely orientation) did not change with uncertainty, and so could not be used to adjust choice behavior in the way that observers did. This indicates that more information than the point estimate was available for downstream use. The studies also showed that obvious possible heuristic proxies for uncertainty, such as stimulus contrast, could not account for observer behavior. The results are therefore consistent with a probabilistic representation of information about stimulus orientation.

Argument for probabilistic perceptual representations

We will now outline our argument for probabilistic perceptual representations, as defined in the previous section, and present supporting evidence. We will also consider challenges to different parts of the argument and identify issues requiring further study. At the outset, we wish to clarify that we are not here addressing the nature of *conscious* perception, but rather of perceptual processing.

1. More than a point estimate is represented, and this information is reflected in behavior.

A variety of evidence supports the notion that representations of perceptual quantities consist of more information than just point estimates of those perceptual quantities. Again, for information to be *represented*, we mean that this information is functionally available for downstream computations. The most downstream stage of all is behavior, so if certain information is found to influence flexible decision behavior, this is clear evidence that the information is functionally available. Many studies have demonstrated that human behavior depends not just on point estimates, but also on the uncertainty associated with those estimates.

Classic studies in perceptual decision making showed that uncertainty is taken into account when combining different sources of perceptual information (e.g., from vision and audition), a process known as “cue combination” (e.g., Ernst & Banks, 2002; Trommershäuser et al., 2011). In these cases, the perceptual estimate of the observer should be closer to the more reliable cue, which is typically what is observed. Perceptual decisions also take prior information and sensory reliability into account in a probabilistic fashion (e.g., Acerbi et al., 2014; Chalk et al., 2010; Qamar et al., 2013). They also take into account uncertainty that arises not from the stimulus, but from their attentional state (Denison et al., 2018). Although observers do not always adjust their decision behavior optimally in these experiments, their adjustments are systematic over parametric manipulations of reliability. So, it is not merely that observers have some doubt in their mind (colloquial use of “uncertainty”), but rather their behavior appears to be governed by a metric of uncertainty that is statistically appropriate given the levels of internal noise associated with their decisions. Perhaps the strongest empirical links to date between probabilistic information contained in neural responses and behavior are the studies described in the previous section, which show that probabilistic uncertainty can be decoded from visual cortex, and decoded uncertainty correlates with behavior (van Bergen et al., 2015; van Bergen & Jehee, 2019; Walker et al., 2020). Taken together, these studies suggest that uncertainty information that appropriately tracks internal noise is available for use in perceptual decision making.

2. Complex probability distributions can be encoded and are reflected in behavior

Although the kind of evidence described above suggests that probabilistic perceptual information is available for downstream use, it can be argued that such evidence falls short of showing that full probability distributions are available. Most of the studies described so far summarize uncertainty by a single number that quantifies the dispersion of the distribution, such as the standard deviation. So, one could argue that these findings could be explained by only two summary statistics – say the mean and standard deviation of the distribution – being available for downstream use. The entire probability distribution, then, is not needed (Vance, 2020).

This line of thinking raises the question: how much information about a stimulus feature is available for use by downstream computations? The probabilistic view says that, although information may be lost in the course of stimulus processing, what is maintained to the level of decision making can still be fairly rich (i.e., more than two moments) and can support probabilistic computations that use all of the available information in a statistically appropriate way. Because Gaussian distributions are fully characterized by two moments, providing evidence for the probabilistic view therefore requires showing that more complex probability distributions can also be used by downstream computations.

Behavioral work suggests that humans use non-Gaussian priors, for example when judging the orientation of a stimulus (Girshick et al., 2011) or the speed of motion (Stocker & Simoncelli, 2006). Models of perception have also postulated non-Gaussian priors, likelihood functions, and posteriors (Kersten et al., 2004), and shown that they can explain behavior (Wei & Stocker, 2015). We know that the perceptual system performs relatively sophisticated inference, such as estimating the color of a surface by taking into account both the light that is reflected from the surface and the light that is shining on the surface. The way that surface color and illumination interact to determine the color of reflected light is unlikely to be Gaussian. Yet in such cases, perception seems to successfully invert the generative model. Finally, theoretical work has established biologically plausible schemes for the encoding of complex probability distributions by neurons (Fiser et al., 2010; Jazayeri & Movshon, 2006; Ma et al., 2006).

Unresolved issues

The empirical and theoretical findings described above suggest that perceptual inference can incorporate complex probability distributions. However, proponents of a non-probabilistic view may still argue that rich probabilistic information could be encapsulated within circuits dedicated to perception, and the only information available further downstream is summary statistics. That is, probabilistic information is present and used in the brain, but it is trapped inside a kind of perceptual module and inaccessible for flexible decision making. We agree that this kind of account could explain the current available evidence – and an important goal for future research is to design experiments that can assess the availability of non-Gaussian probabilistic information in downstream areas. However, as proponents of the probabilistic view, we think it is more plausible that the kinds of representations and computations involved in perception are not limited to encapsulated perceptual circuits (if those even exist) but are similar throughout cortex. Information may be lost moving from more perceptual to more cognitive processing stages, but we think it would be surprising if the fundamental computations changed qualitatively.

Conclusion

Is perception probabilistic? Here we have cached out the notion of what it means to "represent" probabilistic perceptual information. We then presented evidence and arguments supporting the idea that the human brain represents perceptual information probabilistically. An unresolved issue is how much perceptual information is available at different stages of processing, though it is unclear if there will be a general answer to this question across all stimuli and tasks. A key next step in building the case for probabilistic perceptual decision making is testing the nature of the representation throughout cortex, moving from perceptual to more cognitive stages of processing.

The case against probabilistic perception (Rahnev & Block)

There are two common definitions of probabilistic perception, which are often considered to be equivalent and co-exist in the same papers (Fiser et al., 2010; Knill & Pouget, 2004; Ma, 2010, 2012):

- Standard definition 1: Perception is probabilistic if it represents probability distributions over world states
- Standard definition 2: Perception is probabilistic if it includes a representation of uncertainty that is reflected in behavior

However, the definitions are not equivalent: for example, only Definition 1 mentions probabilities and only Definition 2 mentions behavior. More critically, these definitions leave several issues unaddressed, which we believe is at the heart of many disagreements. We argue that a definition of the term “probabilistic perception” needs to be explicit about three critical factors: (1) whether one takes the brain’s or the experimenter’s perspective, (2) what are the criteria used to judge if a probability distribution exists, and (3) what is the scope of the term "perception." Based on these factors, we define "strong" and "weak" probabilistic perception and give examples of the difference between them. We argue that strong probabilistic perception is unlikely, while weak probabilistic perception is almost trivially true.

Three critical components of a definition of probabilistic perception

There are three factors that, we believe, need to be an explicit part of any definition of probabilistic perception:

- *Factor 1: brain vs. experimenter perspective*. A definition of probabilistic perception can take either the brain's or the experimenter's perspective. That is, the hypothesized probability distributions could be defined either by the brain or by an experimenter observing the brain.
- *Factor 2: criteria for a probability distribution*. A definition of probabilistic perception can use different criteria for determining whether something is a probability distribution. Specifically, one can use the three axioms of probability or a simpler (but much weaker criterion) such as whether the representation consists of more than a point estimate.
- *Factor 3: the scope of perception.* A definition of probabilistic perception can define "perception" as encompassing anything we can perceive including object categories, spatiotemporal relationships between the objects, individual features, etc. Or, alternatively, it can define "perception" more narrowly to encompass only certain simple features like orientation.

Unfortunately, these three factors are almost never explicitly addressed when defining probabilistic perception. In fact, we believe that the two standard definitions of probabilistic perception highlighted above implicitly take different views on these three factors. Below, we provide definitions of probabilistic perception that explicitly address the three factors, resulting in defining "strong" and "weak" versions of probabilistic perception (which, we believe, also correspond to the standard definitions 1 and 2 above).

Strong versus weak probabilistic perception

One possible definition of probabilistic perception takes (1) the brain's perspective, (2) the axioms of probability as the relevant criterion for judging whether something is a probability distribution, and (3) a global perspective on perception. We call this "strong probabilistic perception."

To help make the definition as precise as possible, we also give a formal mathematical definition that explicitly refers to the three factors (note that by using the term "probability distribution," it implies the three axioms of probability):

> *Consider the 2-tuple (S, R) where S is the set of all perceivable stimuli and R is the set of all relevant sensory responses. Strong probabilistic perception entails that for any given response $r \in R$, the brain defines a probability distribution $p(s|r)$ over world states.*

Alternatively, one can take the opposite perspective on each of the three factors and thus arrive at a very different claim that we term "weak probabilistic perception." First, weak probabilistic perception takes the experimenter's point of view: it is the experimenter, not the brain, who defines a probability distribution over world states. Second, weak probabilistic perception makes no reference to probabilities and is instead concerned with whether uncertainty is taken into account. In practice, this typically means that the question is whether the brain "uses" both the mean and variance of the experimenter-defined probability distribution. This definition therefore necessitates that we also define what "using" a probability distribution means. The obvious choice is to observe specific behaviors and determine if they are based on both the mean and variance of the experimenter-defined probability distribution. Third, weak probabilistic perception defines perception more narrowly to encompass only specific stimuli, often a single feature dimension such as orientation, rather than all perceivable stimuli.

Again, we make this definition precise using a formal mathematical formulation:

> *Consider the 4-tuple (S, R, A, f) where S is a stimulus set, R is a response set, A is the set of relevant actions the organism can take, and $f: R \rightarrow A$ is a function that specifies how each response maps onto an action. Weak probabilistic perception is then defined only for specific 4-tuples and entails that (1) for every response $r \in R$, an experimenter can define a probability distribution $p(s|r)$ over S, and (2) the function $f(r)$ that maps sensory responses to actions is equal to $g\big(p(.|r)\big)$ where the function g cannot be derived from a single summary statistic of $p(s|r)$.*

Note the fact that the definition explicitly takes the experimenter's perspective, that it defines the sets S and R much more narrowly than the definition of strong probabilistic perception, and that it also includes a set of actions A and a function f that maps responses to actions. Finally, because mean and variance only exist for probability distributions over continuous variables, the definition above uses the more general formulation of summary statistics.

We believe that strong probabilistic perception is what the debate around probabilistic perception is about. Conversely, weak probabilistic perception is only of interest to the extent to which it provides evidence for strong probabilistic perception. We explore the relationship between the two in greater depth in the next section.

We described three factors and defined strong probabilistic perception in terms of the strongest versions of each of them and weak probabilistic perception in terms of the weakest versions of each of them. Of course, one could mix and match the three factors above to create "intermediate" forms of probabilistic perception. However, we ignore such intermediate possibilities for now as we are not aware of such possibilities having been endorsed by anyone.

<u>Weak probabilistic perception can be true even if strong probabilistic perception isn't</u>

As already mentioned, we believe that the debate around probabilistic perception is really a debate on strong probabilistic perception. Yet, strong probabilistic perception is very difficult to test. Indeed, the challenges in taking the brain's perspective, confirming the three axioms of probability, and of using even a few different object categories or feature dimensions simultaneously are immense. We may need a much greater knowledge of the brain before we can empirically test the notion of strong probabilistic perception.

On the other hand, weak probabilistic perception is eminently testable. Indeed, the existence of weak probabilistic perception for specific 4-tuples (S, R, A, f) is already supported by many studies including research of cue combination (Ernst & Banks, 2002; Trommershäuser et al., 2011) and of uncertainty decoding in sensory areas of the brain (van Bergen et al., 2015; van Bergen & Jehee, 2019; Walker et al., 2020). Given the vast difference in how empirically testable strong and weak probabilistic perception are, it is completely understandable that many researchers have focused on testing weak probabilistic perception. However, the gulf between strong and weak probabilistic perception is so vast that support for weak probabilistic perception provides virtually no support for strong probabilistic perception. We illustrate this point with a concrete example.

Imagine a single-cell organism with two sensors whose output is used in only one way: when their sum exceeds a threshold, the organism initiates an approach behavior. Further, imagine that we, as the experimenters, can determine that sensor 1 detects the concentration of a certain molecule emitted by a particular food X, whereas sensor 2 detects the concentration of a second molecule whose concentration is correlated with the precision of the measurement in sensor 1. Note that sensor 2 may have evolved to detect a different food altogether and the correlation with the reliability of sensor 1 could be purely incidental. Nevertheless, an external observer can interpret the organism's behavior as "approach food X only when you're sure it's there" regardless of whether this is a correct description of the evolution of this behavior.

On one hand, this behavior satisfies the requirements of weak probabilistic perception. Indeed, an experimenter can define a particular set of world states S (e.g., distance to food X), response set R (e.g., activity in the two sensors), actions A (e.g., approach or not), and function f (e.g., approach if sum of activity in the sensors exceeds a threshold). Based on additional measurements, for a given response, an experimenter can define a probability distribution $p(s|r)$ over distances to a given food source with the mean of the distribution determined by the signal from sensor 1 and variance of the distribution determined by the (inverse of the) signal from sensor 2. Thus, f becomes a function of both the mean and the variance of $p(s|r)$, which is more than a single summary statistic. Therefore, the organism meets the criteria for weak probabilistic perception in the context of judging distance to food.

On the other hand, this 2-sensor organism does not have strong probabilistic perception. As defined, it does not have a model of possible world states (e.g., it does not know about distances) and therefore cannot define a probability distribution $p(s|r)$ over them. Moreover, even if we are to equip this organism with knowledge about the possible world states, there is no representation within the organism that meets the three axioms of probability. In fact, in the behaviorist tradition, the organism's behavior would be considered a simple stimulus-response mechanism.

This example demonstrates that weak probabilistic perception is so broad as to apply to 2-sensor organisms with no nervous system. In a similar vein, empirical studies have shown that even plants can somehow register mean and variance of nutrients in the soil (Dener et al., 2016). It should be little surprise that animals with nervous systems meet the criteria of weak probabilistic perception too. This fact, however, has virtually no implication about whether humans have strong probabilistic perception.

Challenges to strong probabilistic perception

In our opinion, all experimental evidence to date concerns weak probabilistic perception. This means that even if strong probabilistic perception is true, we have no evidence for it. Here we also argue that it is unlikely to be true by formulating two specific challenges.

Challenge 1: Define a set S of possible world states

Any theory of strong probabilistic perception has to start with defining the relevant set of world states S. This is much more difficult than it may appear. One option is that S is defined over everything that we could perceive. More specifically, given that perception can represent things like "the green apple is falling on the chair behind the tall table," then one may want to define S as all possible objects (e.g., apples, chairs, tables, etc.), features (green, tall, etc.), spatial relationships (behind, above, etc.) and actions (fall, expand, etc.) (Cavanagh, 2021). A serious difficulty with this definition of S is that the brain can learn arbitrary new object categories (e.g., a "cell phone" or "greeble," Gauthier & Tarr, 1997). Given that there are essentially infinite number of such potential object categories, it appears unlikely that we have a probabilistic perception over all of them. A more plausible option, then, is to define S as the set of all objects, features, spatial relationships and actions that an organism has already encountered rather than all possible ones. However, a serious difficulty here is how items get added to S. If the brain defines a probability distribution $p(s|x)$ over known world states, then how does it determine if a new element should be added to these world states? Finally, another possibility is to define S more narrowly to just some features (e.g., orientation). However, corresponding claims should then be about "probabilistic perception of orientation" rather than "probabilistic perception" in general and it should be clarified whether perception of other items is supposed not to be probabilistic.

Challenge 2: Specify how the brain defines the probability distribution $p(s|r)$

If one is able to define the set of world states S, the second challenge is to specify how the brain may define a probability distribution $p(s|r)$. Several theories have been proposed on how the brain may do so including probabilistic population codes (Beck et al., 2008; Ma et al., 2006), distributed distributional codes (Sahani & Dayan, 2003; Zemel et al., 1998) and neural sampling (Fiser et al., 2010; Haefner et al., 2016). However, it is yet unknown whether these approaches (or any other) can generalize to all of perception, including objects, features, spatial relationships and actions. Further, many sensory computations have been theorized to depend on as little as a single spike per neuron (Rieke et al., 1997; Thorpe et al., 2006; Van Rullen et al., 1998), making the construction of probability distributions with so little neural firing especially difficult.

We acknowledge that neither of these challenges prove that strong probabilistic perception is wrong – they simply highlight some of the reasons for doubting that the brain represents a probability distribution over world states.

Alternatives to strong probabilistic perception

If strong probabilistic perception is not the correct way to describe perception, what is? The two authors of this section favor the possibility that perceptual representations have the relatively simple form of a specific interpretation that is accompanied by uncertainty estimates for that interpretation (Block, 2018; Rahnev, 2017; Yeon & Rahnev, 2020). For example, perception may consist of the content of "green apple" where both "green" and "apple" include accompanying values that reflects the uncertainty in the color or object identity. We note that this simple representation obviates the need to pre-specify a set of world states S besides learning a vocabulary akin to a language vocabulary (Cavanagh, 2021), which is clearly solvable by the brain given that we have language. It also appears to fit well with our conscious experience, including the fact that we only consciously experience a single interpretation of bistable images at a time (Block, 2018). We also note that this "best guess plus uncertainty" representation is another example of a representation that satisfies the criteria of weak probabilistic perception while falling short of strong probabilistic perception because it does not involve probabilities.

The "best guess plus uncertainty" representation could be tested by examining whether more than one interpretation of the world is available at a time. The empirical evidence is mixed with some results suggesting that only a single interpretation is available (Yeon & Rahnev, 2020), while others suggesting that multiple interpretations are available (Chetverikov et al., 2020). Nevertheless, we note that the resolution of this question (which we informally refer as a debate between "simple" and "complex" representations) is independent from the debate about strong probabilistic perception. The reason is that complex representations with more than a single interpretation do not have to include probabilities; conversely, at least in the case of continuous feature dimensions, probability distributions could be represented only with their means and higher moments, which may make strong probabilistic perception consistent with representations that appear to include only one interpretation of the world (i.e., the mean of the distribution).

Conclusion

Is perception probabilistic? It depends on how you define "probabilistic perception." Here we argue that two very different notions of probabilistic perception – what we call "strong" and "weak" probabilistic perception – coexist with little acknowledgment that they are vastly different from each other. We further argue that weak probabilistic perception could apply even to simple single-cell organisms, and that this is the only type of probabilistic perception supported by empirical evidence. On the other hand, strong probabilistic perception – what we consider to be the relevant and controversial claim – has no direct empirical support and faces substantial challenges.

Our approach here was to provide precise definitions for the two notions of probabilistic perception most commonly encountered in the literature. We expect that some researchers may hold views that do not fall under either definition. If so, we invite these researchers to provide alternative, but precise (and, ideally, mathematically rigorous) definitions that explicitly address the three factors highlighted above. We believe that without precise definitions, the term “probabilistic perception” (and related terms such as “probabilistic computation” and “Bayesian brain”) would become a Rorschach test about whether one prefers to view the brain from a Bayesian or a non-Bayesian lens.

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