

# A novel model of divergent predictive perception

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## Abstract

Predictive processing theories state that our subjective experience of reality is shaped by a balance of expectations based on previous knowledge about the world (i.e. priors) and confidence in sensory input from the environment. Divergent experiences (e.g. hallucinations and synaesthesia) are likely to occur when there is an imbalance between one's reliance on priors and sensory input. In a novel theoretical model, inspired by both predictive processing and psychological principles, we propose that predictable divergent experiences are associated with natural or environmentally induced prior/sensory imbalances: inappropriately strong or inflexible (i.e. maladaptive) high-level priors (beliefs) combined with low sensory confidence can result in reality discrimination issues, a characteristic of psychosis; maladaptive low-level priors (sensory expectations) combined with high sensory confidence can result in atypical sensory sensitivities and persistent divergent percepts, a characteristic of synaesthesia. Crucially, we propose that whether different divergent experiences manifest with dominantly sensory (e.g. hallucinations) or nonsensory characteristics (e.g. delusions) depends on mental imagery ability, which is a spectrum from aphantasia (absent or weak imagery) to hyperphantasia (extremely vivid imagery). We theorize that imagery is critically involved in shaping the sensory richness of divergent perceptual experience. In sum, to predict a range of divergent perceptual experiences in both clinical and general populations, three factors must be accounted for: a maladaptive use of priors, individual level of confidence in sensory input, and mental imagery ability. These ideas can be expressed formally using nonparametric regression modeling. We provide evidence for our theory from previous work and deliver predictions for future research.

"...our conscious experiences of the world around us, and of ourselves within it, are kinds of controlled hallucinations..."  
(Seth 2017)<sup>1</sup>

Divergent perception is the atypical experience, or interpretation, of sensory information. This excludes illusions, as these are consistent and reliably observed across the general population (so do not meet the criterion of "atypical"). One of the most striking examples of divergent perception is complex visual hallucinations, which take the form of meaningful objects and environments and can occur in various neurological and psychiatric disorders (Waters et al. 2014). Another form of divergent perception is synaesthesia, a phenomenon whereby a specific experience (called the inducer) triggers an additional, unrelated experience (called the concurrent); this can be a sensory experience, such as that seen in grapheme-color synaesthesia (experiencing colors

associated with different alphanumeric characters), or a less sensory experience, such as that seen in sequence-space synaesthesia (experiencing information with a specific spatial organization; Simner 2012). An interesting, but little-investigated phenomenon is mental projection (Cavedon-Taylor 2022) or "prophantasia"<sup>2</sup>; this is the voluntary ability to mentally project imagined stimuli into the external environment.

It is currently unknown why people can have different divergent perceptual experiences. For example, hallucinations are defined as being as vivid as real perception, experienced as external, and uncontrollable (Ffytche 2005); however, synaesthesia can have all these qualities, and prophantasia has the first two. The difference is that it is highly unlikely for synaesthesia or prophantasia to be confused with reality. Reality discrimination issues alone do not explain hallucinations; however, they can also lead to delusional thinking and so do not necessarily manifest as a sensory experience (Thoresen et al. 2014). Individuals can have both hallucinations and delusions, or either (Corlett et al., 2019), and

<sup>1</sup> Although this quote is from Anil Seth's 2017 TED Talk, the term "controlled hallucination" purportedly goes back much further, and others have attributed it to Ramesh Jain in 1990 or Hyppolyte Taine in 1870, although attempts to uncover published quotes (translated or otherwise) have been unsuccessful by the authors.

<sup>2</sup> A term coined by citizen scientist Alec J Figueroa, from the Greek *pro-* (before, in front of) and *phantasia* (imagination; personal communication, 16 October 2020).

there is currently no way to predict whether they will occur in combination or isolation in different individuals.

In this paper, we argue that three factors can predict individual differences in divergent perceptual experience: confidence in sensory input, maladaptive use of priors in interpreting sensory input, and mental imagery ability. Although the first two factors have already been proposed to be involved in atypical perception, a crucial—novel—and exploratory aspect of our model is that mental imagery is critically involved in determining the sensory richness of divergent experiences. We will first discuss confidence in sensory input, maladaptive priors, and mental imagery before moving on to the model. Taking inspiration from both predictive processing theory and psychological principles, we present a new model of divergent predictive perception.

## Predictive processing theory

The predictive processing account of perception states that perception is achieved through a balanced weighting of predictions based on prior knowledge about the world (top-down) and incoming sensory information from the environment (bottom-up; [Walsh et al. 2020](#)). In an optimal perceptual system, priors (expectations) about the characteristics of stimuli will be deployed prior to perception, so that the least amount of energy will be spent in updating one's internal model of the environment with the accumulation of sensory evidence. Prediction error (the difference between the predicted and actual sensory input) is inherent to top-down mechanisms of perception, since perception is fundamentally an interpretative process. The system's goal is to minimize prediction error, both in anticipation of and during sensory stimulation.

“Sensory confidence” refers to the weighting of sensory information in perceptual processing, which is usually tied to sensory precision (which we refer to as the clarity or ambiguity of a stimulus). Less precise sensory information (e.g. a stimulus in noise) will typically decrease reliance on sensory information and increase reliance on prior information for perception. Another factor that could influence one's reliance on sensory information is individual sensitivity to sensory input from the environment. If you are very sensitive to sensory information, you may also have more confidence in sensory evidence and assign this more weight during perceptual processing.

In a similar vein, “prior precision” refers to the clarity of a prior ([Haarsma et al. 2022](#)). Priors can be precise or imprecise, strong or weak, and flexible or inflexible (see [Table 1](#) for a summary of definitions). Optimal priors can have any of these characteristics; for example, you may have a precise prior for a friend's face, but if you know your friend shaved their beard since you last saw them, your prior should become less precise, but more flexible, so that you can quickly identify them; alternatively, if you have been tasked with detecting a stimulus that does not change identity but can appear at different contrasts, having a precise, inflexible, and narrow prior for that stimulus would be beneficial. In an optimal Bayesian perceptual system, decreasing prior precision should increase one's reliance on sensory information and decreasing sensory precision should increase one's reliance on precise prior information to fill in the blanks. Inappropriately precise, imprecise, weak, strong, flexible, or inflexible priors are considered “maladaptive.” We emphasize “inappropriate” here, because sometimes optimal priors are, e.g. imprecise (which makes them more flexible, as in the case of identifying a friend with a changed appearance)—but priors become maladaptive when they cannot be optimized for the situation.

**Table 1.** Definitions of prior precision, flexibility, and strength

Prior	Definition
Precision	The clarity or detail of a prior. In Bayesian terms, this is defined as the width of the prior distribution (e.g. a precise prior will have a narrow distribution). For our purposes, we use the psychological definition of this term, rather than Bayesian. Example: your prior for an acquaintance you have met once will be less precise than your prior for a close friend.
Flexibility	How easily a prior can be updated, related to precision. Example: once you see your shaved friend, you can recognize him because your (imprecise) prior of his visual identity can be flexibly updated; if you cannot recognize him, your prior is inflexible (and overly precise for the situation).
Strength	The extent to which you rely on a prior for perception. Example: your prior of your friend will need to be stronger if you are searching for him in poor lighting compared to bright lighting.

Several theories of predictive processing distinguish between two levels of priors that can influence perception: “low-level” sensory expectations (e.g. the predictable visual structure of the world) and “high-level” beliefs (e.g. “What I'm seeing is real”; [Clark 2013](#), [Samaha et al. 2018](#)). Prediction errors can occur at either or both levels. Prediction errors are essential to any kind of perceptual inference, but certain perceptual anomalies can arise when prediction errors are not effective in updating priors. Visual illusions that exploit strong priors based on learned stimulus regularities (such as the Ponzo illusion, where individuals perceive two lines of equal length as different if one seems more distant than the other) are the result of low-level prediction errors in which predictions are so strong that they override sensory evidence ([Yildiz et al. 2022](#)). These occur reliably across most individuals because they defy our extensive previous experience with stimulus regularities; in other words, such predictions are almost always accurate, and such illusions exploit exceptions. Compare this to the rubber-hand illusion, which has much more variable effectiveness across individuals; to believe you can feel touch on a false hand requires a high-level prediction error, and beliefs are nowhere near as regular or concrete as low-level priors ([Hohwy 2017](#)). This suggests that low-level priors are typically more precise than high-level priors, due to their stronger association with sensory evidence (and therefore better likelihood of minimizing prediction error). However, there are individual differences in “prior strength” or the extent to which an individual relies on prior information for perception ([Hohwy 2012](#)), which contributes to the natural balance between the weighting of prior and sensory information at each level ([Corlett et al., 2019](#)).

It is important to stress that illusory visual experience is not indicative of a suboptimal predictive system—indeed, susceptibility to such errors indicates that the system is working as it should and that priors can sometimes override sensory evidence even in nonpathological, nondivergent perception. These examples also demonstrate that persistent prediction errors at different levels may result in different nonveridical percepts (e.g. different types of illusions) and different likelihoods of experiencing those percepts depending on individual reliance on priors (i.e. prior strength)—but for percepts to be divergent (rather than simply nonveridical), priors must also be maladaptive. A system becomes maladaptive when there is an inability to update priors based on

**Table 2.** Definitions of conditions discussed

Condition	Definition
Psychosis	A disordered mental state characterized by an impairment in reality discrimination, which includes positive (e.g. delusions and hallucinations) and disorganized symptoms (e.g. nonsensical communication and unpredictable behaviors), characteristic of schizotypal personality disorder and schizophrenia spectrum disorders.
Synaesthesia	A phenomenon whereby specific stimuli (inducer) trigger an additional experience (concurrent); sensations can trigger other unrelated sensations (e.g. tasting colors), but nonsensory associations are also common (e.g. experiencing time in different spatial quadrants). Synaesthesia can further be experienced as overlaid onto the real world (projector-type) or as a strong feeling of an association (associator-type).
Autism	A spectrum of developmental conditions characterized by challenges in verbal and nonverbal communication, language, and social interaction; social deficits; and exhibiting restricted or repetitive behaviors, which can be accompanied by unusual reactions to sensory stimulation (e.g. hyper- or hyposensitivity).
Savantism	Prodigious skill in a specific domain (e.g. arts, math, and music) that far exceeds the general level of functioning of the individual.

even precise sensory evidence, which is the result of an “imbalance” in the weighting of prior and sensory information; these types of errors are discussed now.

## Theories of atypical predictive processing

Predictive processing theory has been used to explain various characteristics of psychosis, synaesthesia, and autism as the consequence of maladaptive priors, which contribute to persistent imbalances in the weighting of prior and sensory information. Here, we propose that divergent perceptual experiences are generally either psychosis-like or synaesthesia-like, and this can also explain that many of the diverse divergent experiences observed conditions such as autism and savantism, both of which are discussed here. [Table 2](#) presents definitions of the terms that will be used in this section.

### Psychosis

Psychosis is narrowly defined as the presence of delusions, hallucinations, or both, which can occur across a range of psychiatric disorders and stems from reduced reality monitoring ability ([Arciniegas 2015](#), [Garrison et al. 2017](#)). Reality monitoring is a type of source memory ([Brébion et al. 2008](#)) defined as the ability to determine whether information comes from external or internal sources ([Bentall 1990](#)). Hallucinating individuals have an abnormal propensity to make perceptual reality monitoring errors ([Böker et al. 2000](#), [Aleman et al. 2003](#), [van de Ven and Merckelbach 2003](#), [Aleman and de Haan 2004](#), [Brébion et al. 2008](#)) and thus are more likely to attribute internally generated perception to incoming sensory signals from the environment. Reality monitoring errors can also be more abstract, as can be seen in delusional thinking ([Thoresen et al. 2014](#)) such as mind control or thought insertion; in the case of delusions, beliefs are not updated based on new information ([Bronstein et al. 2019](#)). In both cases, reality

monitoring issues are thought to be the result of a lack of confidence in the external world (dismissing sensory signals and new information; [Woodward et al. 2008](#), [Corlett et al. 2009](#), [Fletcher and Frith 2009](#), [Teufel et al. 2015](#), [Garrison et al. 2017](#), [Sterzer et al. 2018](#)).

In the perception and attention deficit model of clinical hallucinations, [Collerton et al. \(2005\)](#) hypothesized that hallucinations occur when expected, yet inaccurate, object representations called “proto-objects” persist in the attended field. The inability to form correct proto-objects from incoming sensory information, combined with weak attentional binding, results in the presence of hallucinations in an otherwise accurately perceived scene. Although this theory does not place hallucinations in the context of predictive processing, the connection is easily made: persistent, inappropriate (maladaptive) priors that are not updated with sensory evidence (lack of sensory confidence) contribute to an imbalance in the weighting of prior and sensory information. [Friston \(2005\)](#) explicitly stated in his commentary on this theory that the perception and attention deficit model is in line with the idea that hallucinations arise from such an imbalance—specifically, too much weight is ascribed to priors from supraordinate cortical levels (i.e. high-level priors), resulting in an inability to update priors based on sensory evidence. The general idea that hallucinations are the result of maladaptive high-level priors is supported by several other predictive processing interpretations of hallucinations ([Corlett et al., 2019](#); [Horga et al. 2014](#), [Powers et al. 2017](#), [Sterzer et al. 2018](#)).

Delusions, by comparison, have been explained as a result of a combination of overly strong (maladaptive) high-level priors and overly weak (maladaptive) low-level priors ([Schmack et al. 2013](#), [Sterzer et al. 2018](#)). The idea is that persistent, imprecise low-level perceptual priors continually result in poor updating mechanisms and a reduced ability to make sense of incoming sensory signals; this reduces confidence in sensory input, increases reliance on high-level interpretations, and leads to a stronger focus on beliefs over sensory evidence (thus resulting in the same predictive processing issues as hallucinations: a combination of maladaptive high-level priors, and a lack of confidence in sensory input).

In making sense of how the same predictive issues can result in hallucinations versus delusions, [Corlett et al. \(2019\)](#) stressed the importance of taking into account different “levels” of priors, which, as we have previously demonstrated, can have different amounts of precision that contribute to prior strength. The authors proposed that imprecise perceptual (i.e. low-level) priors specifically increase the likelihood of delusions, and overly precise cognitive (i.e. high-level) priors specifically increase the likelihood of hallucinations. Individuals can have both (e.g. delusions of conspiracy and hallucinations of conspiring voices) or either (e.g. delusions that are separated from perception, such as delusions of grandeur), and they are not mutually exclusive.

### Synaesthesia

The weighting of prior and sensory information is often seen as a zero-sum process—i.e. a stronger reliance on priors results in a weaker reliance on sensory information. However, there is evidence that a person can have both strong (but, e.g. inflexible, narrow, or otherwise maladaptive) priors and show high sensory confidence (i.e. they have good reality monitoring), which can result in synaesthesia ([van Leeuwen et al. 2020](#)). Synaesthesia is an interesting case because, like hallucinations, synaesthetic experiences

are elicited involuntarily and can seem to occur externally—but unlike hallucinations, they are not confused with reality.<sup>3</sup>

According to the predictive perception theory of sensorimotor contingencies (Seth 2014), perceptual experience is determined by hierarchical generative models that include a variety of priors (with dynamically updating weights based on sensory evidence) that correspond mainly to the interaction between perception and action (called sensorimotor contingencies); specifically, these models inform how we should behave in response to a stimulus. We have generative models at each level of the perceptual hierarchy, from early sensory, secondary, or associative sensory (intermediate-level) to higher-level, cognitive models (e.g. reality monitoring). According to this theory, synaesthesia occurs when strong, intermediate-level priors override sensory evidence (resulting in maladaptive priors, according to our definition). The intact reality monitoring in synaesthesia is explained by a difference in the “counterfactual richness” of veridical stimuli compared to synaesthetic associations; that is, there are many possible ways to interact with real stimuli compared to synaesthetic experiences, which are impossible to interact with or manipulate. We learn over our lifetimes the many ways we can interact with sensory information, and this shapes our experience of richness in reality. This has led to the hypothesis that synaesthesia is the result of both unusually strong perceptual priors and high confidence in sensory evidence, with intact reality monitoring capabilities.

This theory best accounts for sensory forms of synaesthesia, such as grapheme-color (experiencing specific illusory colors for different alphanumeric characters). Nevertheless, there are dozens of known types of synaesthesia, many of which are not necessarily sensory, such as sequence-space (experiencing specific illusory locations in space for different items in a sequence). The inducer (the item that “triggers” a synaesthetic experience) and concurrent (the illusory experience) can also have different levels of abstraction (e.g. the concept of a weekday is an abstract inducer, and many synaesthetic inducers are abstract entities that cannot be physically manipulated), and the subjective perception of the experience can also be more concrete or abstract: projector-type synaesthesia seems to occur in the external world (e.g. the individual can point to a location where the experience occurs), whereas associator-type synaesthesia either seems to occur internally (e.g. in mental imagery) or can be even more abstract, such as a strong feeling that the association is so (for a review, see Hochel and Milán 2008). Perceptual priors do not seem to play a role in these cases, and abstract concepts cannot have counterfactual richness.

Individuals with synaesthesia often experience high sensory sensitivity (Ward et al. 2017, van Leeuwen et al. 2019) and show enhanced perception of sensory information—both at the level of the synaesthetic modality (e.g. colors, touch; Banissy et al. 2009) and generally enhanced processing of local features (Ward et al. 2018, van Leeuwen et al. 2019). All these point to having high sensory confidence. Because we have already established that psychosis results from a combination of maladaptive priors and low sensory confidence, we propose that synaesthesia, although also a consequence of maladaptive priors, is unlikely to be accompanied by psychosis (including psychotic and psychosis-prone disorders, such as schizophrenia and schizotypy, respectively;

<sup>3</sup> There is a known case of an individual with synaesthesia who also experiences reality discrimination issues (Hunt 1994). As we propose that reality discrimination issues and synaesthesia are the result of different kinds of maladaptive priors, we consider this case to be rare, though not impossible within the breadth of human complexity.

Schultze-Lutter et al. 2019) due to intact confidence in sensory evidence.

This incompatibility idea already has some evidence (Carmichael et al. 2019, Nugent and Ward 2022); note, however, that synaesthesia has been associated with higher rates of self-reported schizotypal traits (Banissy et al. 2012, Janik Mcerlean and Banissy 2016), not excluding a relationship between synaesthesia and certain aspects of schizotypy, particularly unusual experiences and cognitive disorganization. A weak genetic link between schizophrenia and synaesthesia has also been reported (Tilot et al. 2019). Speculatively, with regard to our model, these links may actually be related to the fact that both (and indeed all) forms of divergent perception require maladaptive priors; stemming from this logic, there should also be a comparably weak link between these conditions, autism, and other conditions associated with divergent perception. We therefore propose that the critical factor that distinguishes between psychosis-like and synaesthesia-like divergent perception is sensory confidence, which can influence how priors become maladaptive (i.e. inflexible, but strong, perceptual priors in synaesthesia; strong high-level priors in psychosis). For this reason, synaesthesia-like and psychosis-like perceptions are very unlikely to occur in combination (but see Footnote 3).

## Autism

Divergent perceptual characteristics of autism (Van de Cruys et al. 2014) include, for instance, a lack of temporal pattern formation (Coil et al. 2020), less surprise when an item in the pattern is changed (van Laarhoven et al. 2017), less susceptibility to (visual) illusions, and weaker Gestalt binding (Bölte et al. 2007), compared to a general population. Weaker Gestalt binding is related to the precedence of local information over global information in visual displays (Van der Hallen et al. 2015). All these perceptual characteristics point to an altered role of prior information during predictions of sensory input in autistic perception (Cannon et al. 2021).

Different ideas have been put forward to explain the altered influence of priors in autism. One account (Pellicano and Burr 2012) suggests that priors are generally weaker in autism, leading to less accurate predictions of incoming sensory information (e.g. pattern prediction) and resulting in stronger influences of sensory input on perception, which can explain the feelings of sensory salience and sensory overload that can occur in autism. An alternative theory proposes that prior predictions are overly specific, narrow, and inflexible in autism, in which one probable source of sensory information is favored above other options, leading to large prediction errors if predictions are not met (Van de Cruys et al. 2014). The inflexibility of priors is related to the weight that is afforded to prediction errors; it has been proposed that in autism, all prediction errors are weighted with the same, inflexible, high weight, regardless of whether the error should actually be ignored, which makes it difficult to adjust priors in an adaptive way (Lawson et al. 2014, Van de Cruys et al. 2014). This is hypothesized to impair learning and generalization, because all input is regarded as equally important and salient.

Strong prediction errors and heightened salience of sensory information, alongside the earlier mentioned perceptual characteristics, suggest that sensory confidence can be intact or even rather high in autism (e.g. van Leeuwen et al. 2020). However, individuals with autism report both hyposensitivity and hypersensitivity to sensory stimuli (Tomchek and Dunn 2007, Robertson and Simmons 2013), which is an official diagnostic criterion in

the Diagnostic and Statistical Manual of Mental Disorders (American Psychiatric Association, 2013). Hence, individuals with autism do not fit on only one end of the sensory confidence spectrum, and hypersensitivity and hyposensitivity can even occur within the same individual, within one or across multiple modalities.

With regard to divergent perception, autism co-occurs with synaesthesia in ~20% of cases (Baron-Cohen et al. 2013, Neufeld et al. 2013) and is hypothesized to share the strong, narrow, low-level priors that may also drive synaesthetic perception (van Leeuwen et al. 2020). One hypothesis would be that individuals with autism and high sensory confidence would experience synaesthesia relatively often, whereas individuals with autism and low sensory confidence would not experience synaesthesia. Preliminary results of a comparison of autistic individuals with and without synaesthesia suggest that sensory hypersensitivity is stronger when synaesthesia and autism co-occur (van Leeuwen et al. 2022). On the other hand, psychosis is also common in autism, with a prevalence as high as 34% (Ribolsi et al. 2022) compared to the general lifetime prevalence of ~3% (Perälä et al. 2007), although care should be taken not to mistake altered thought patterns in autism with delusions or hallucinations (Cochran et al. 2013). Following from our predictions, it could be the case that individuals with autism and low sensory confidence would be more sensitive to develop psychosis symptoms than those with high sensory confidence.

## Savantism

Savantism is characterized by prodigious skills and can either be sensory (e.g. using mental images of calendar pages to remember date-event associations) or nonsensory (e.g. using automatic time-space synaesthetic associations to enhance the recall of learned date-event memories; Simner et al. 2009). Savantism has a high prevalence in autism and, beyond being rooted in cognitive alterations, could also partly be a consequence of obsessive and repetitive behaviors in those with autism (O'Connor and Hermelin 1991). Savantism occurs more often in individuals with autism who also have synaesthesia (Hughes et al. 2017), and similarly, synaesthetes show advantages in savant skill acquisition (Hughes et al. 2019). The high probability of savantism in individuals with both autism and synaesthesia suggests that autistic individuals who also have savant skills resemble synaesthetes in their high sensory precision and strong, inflexible, and narrow low-level priors. That savants have high sensory confidence also fits with the nature of their prodigious skills, such as producing detailed drawings from memory or absolute pitch.

To sum up provisionally, previous studies point to an imbalance in weighting prior and sensory information as a factor in divergent perception, which manifests in characteristics of psychosis or synaesthesia, as observed in diverse conditions such as autism. The combination of maladaptive priors and low sensory confidence likely results in experiences unraveled from reality such as hallucinations, delusions, weakened pattern formation, and/or sensory hyposensitivity; maladaptive priors combined with high sensory confidence, on the other hand, likely result in an enhanced experience of reality such as synaesthesia, savantism, and/or sensory hypersensitivity.

## Mental imagery determines the sensory richness of divergent experience

In the summary of divergent experiences thus far, we have not yet touched on what determines their “sensory richness,” which contributes to a specifically sensory (as compared to abstract)

experience. We propose that mental imagery ability ultimately determines whether any divergent experience is more sensory or nonsensory in nature. Mental imagery is defined as the simulation of sensory information in the absence of a relevant, external sensory stimulus; ability refers to one's ability to generate mental imagery voluntarily.<sup>4</sup> Throughout the following sections, we use the terms “mental imagery” and “imagery” interchangeably.

As an example of the role of mental imagery in perception, suppose that you are playing a game to find different objects in the clouds. Any objects seen (e.g. a face and a dinosaur) are nonveridical (a form of divergent perception called pareidolia) and can have varying levels of detail: one individual may see an emoji-like face, finding an eyes–nose–mouth pattern, whereas another individual may see a highly detailed and realistic face, mentally injecting new sensory features into the random patterns that can occur in cloud formations.

This is evidenced by a recent study: when asked to find faces in pure noise images, different individuals report a range of percepts: from seemingly incidental face-like patterns (even when computer algorithms could not detect such patterns) to detailed and realistic, sometimes fantastic or grotesque, faces (which cannot be explained exclusively by bottom-up processing; Salge et al. 2020). Importantly, Salge et al. (2020) found strong evidence that the interpretation of pure noise as a meaningful stimulus is correlated with visual mental imagery vividness, suggesting that imagery is used to create illusory structures in the interpretation of unstructured sensory information. In other words, different levels of sensory detail applied to random or unstructured patterns may be predicted by trait-level mental imagery vividness. This feeds into our broader proposal that mental imagery critically determines the sensory richness of divergent experiences.

In setting up our justification for a critical role of mental imagery in different divergent experiences, we must go back to the predictive perception theory of synaesthesia. Seth (2014) proposed that synaesthesia must be associated with intermediate-level generative models that influence the interpretation of sensory signals; however, we instead propose that what critically results in synaesthesia is a combination of maladaptive (in this case, strong and inflexible) low-level priors with intact confidence in sensory input. This may be compounded in a feedback loop: just as individuals with maladaptive high-level priors may have low sensory confidence because they learn over time to mistrust reality (resulting in psychosis symptoms), individuals with maladaptive low-level priors and heightened sensory confidence may learn over time to embellish or enhance reality (resulting in synaesthesia). Tying in with our proposed role of mental imagery in divergent experience, synaesthetes with vivid imagery will be more likely to experience concurrents as sensory and synaesthetes with weak imagery will be more likely to experience concurrents as abstract or less sensory. This idea has already been proposed for different subjective manifestations of grapheme-color synaesthesia (Simner 2013), specifically that synaesthetes with weak imagery report the experience of synaesthesia as more associator-like, even though the occurrence of associator or projector synaesthesia did not differ between those with weak or strong imagery (Dance et al. 2021a). This suggests an influence of mental imagery ability on synaesthetic experience.

Psychosis, synaesthesia, and autism symptoms emerge with different weightings of prior and sensory information, but each

<sup>4</sup> Mental imagery can also be involuntary—e.g. intrusive or hypnagogic imagery—which individuals can experience even if they have an inability to generate imagery voluntarily. We propose that the same mechanism contributes to both; see the Future directions section.

condition can further have sensory and nonsensory symptoms, and there is evidence that the sensory richness of divergent cognition appears to be related to mental imagery ability. Previous studies have found that imagery is more vivid in schizophrenic spectrum disorders compared to a general population (Sack et al. 2005, Oertel et al. 2009, Benson and Park 2013); however, imagery seems to be more vivid specifically in individuals with sensory symptoms (Shine et al. 2015, Aynsworth et al. 2017) and recently was found to be related to only certain complex hallucinatory experiences, rather than schizophrenia symptoms, generally (Wagner and Monzel 2023). Furthermore, although vivid imagery is considered a hallmark of synaesthesia (Barnett and Newell 2008, O'Dowd et al. 2019), recent research suggests that even people without imagery can have synaesthesia (Dance et al. 2021a). Finally, although low imagery is often taken as a feature of autism (e.g. as part of the subscale of “imagination” within the Autism-Spectrum Quotient; Baron-Cohen et al. 2001), there are personal accounts suggesting that at least some autistic individuals can vividly “think in pictures” (Grandin 1995) as well as empirical evidence that some autistic people favor visual thinking in certain situations (Kunda and Goel 2011). We suspect that different individuals with autism simply have different imagery abilities, which result in different levels of abstractness in divergent experiences.

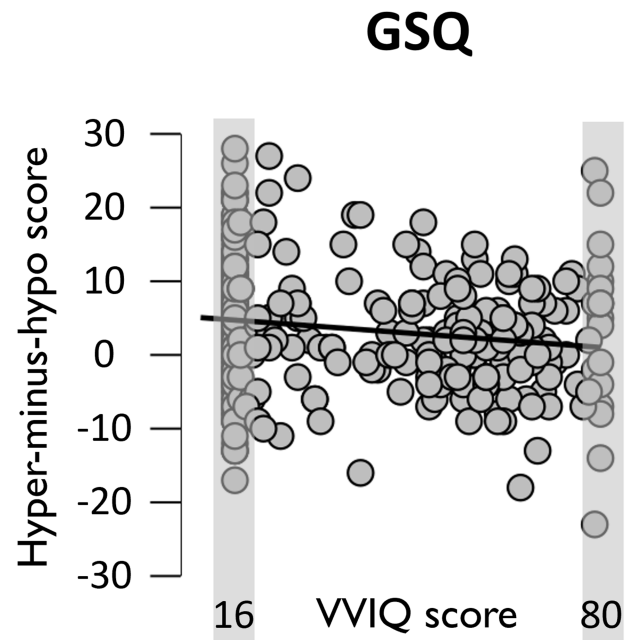
Furthermore, although we do not devote an entire section on imaginative control here (due to the rather few scientific studies on the topic), this can also be highly sensory, as in the case of prophantasia, as described by Galton (1880) (in which a proportion of participants were able to mentally project a stimulus onto a blank piece of paper in their hand) and recently by Cavedon-Taylor (2022). Controlled imaginative information can also be less sensory, such as seen in time-space savantism (Simner et al. 2009).

These all support the hypothesis that mental imagery ability needs to be taken into account to best predict different divergent perceptual experiences.

## Mental imagery extremes

Mental imagery extremes refer to the extreme ends of the mental imagery spectrum, which include aphantasia (the absence of voluntary mental imagery) and hyperphantasia (extremely intense and realistic imagery; Zeman et al. 2020). It is alluring to try to dichotomize the two: hyperphantasia being associated with creativity, openness to experience, and synaesthesia and aphantasia being associated with enhanced mathematical reasoning, autism characteristics, and introversion (Zeman et al. 2020). There is some evidence for these associations: e.g. more vivid imagery is associated with increased fantasy (van de Ven and Merckelbach 2003, Aleman and de Haan 2004), pareidolia (Salge et al. 2020), and hallucination proneness (Shine et al. 2015), and individuals with aphantasia may report reduced imagination and social skills characteristic of autism (Sack et al. 2005, Oertel et al. 2009, Benson and Park 2013, Matthews et al. 2014) and atypical sensory sensitivities (Dance et al. 2021b). We propose that the reality is more nuanced: that as individuals approach more extreme imagery abilities, perceptual divergences of all kinds are more likely. We have already discussed that synaesthesia and autism can co-occur in individuals with both vivid and absent imageries and that schizophrenia does not generally seem to be associated with heightened imagery.

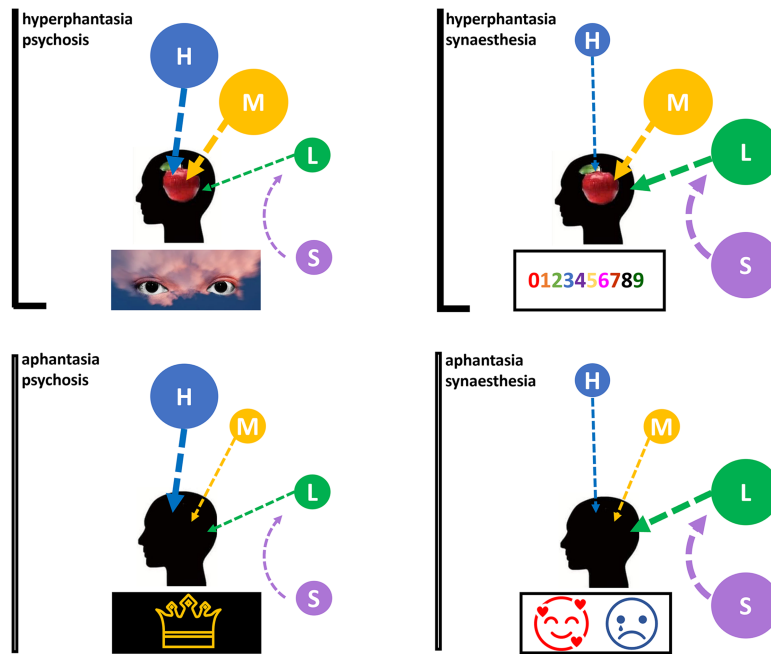
Atypical sensory sensitivity is another important aspect of divergent perception: as mentioned previously, it is a hallmark of both synaesthesia and autism. We propose that individuals with imagery extremes may naturally be more prone to atypical



**Figure 1.** Data reanalyzed with permission from Dr Carla Dance. In the original study of sensory sensitivities in aphantasia versus imagery (Dance et al. 2021b), participants completed the Glasgow Sensory Questionnaire (Robertson and Simmons 2013) which provides two scores related to sensory hyposensitivity and hypersensitivity. Each of these scores is on a range from 0 to 84, with higher scores indicating greater hyper- or hyposensitivity. In our reanalysis, we subtracted hyposensitivity scores from hypersensitivity scores (Y axis), so we could see within-subject differences in hypo- versus hypersensitivity. Individuals with negative scores thus reported more hypo- than hypersensitivity, and individuals with positive scores reported more hyper- than hyposensitivity. We also analyzed individuals with hyperphantasia (Vividness of Visual Imagery Questionnaire (VVIQ) score >75,  $N = 25$ ) as a separate group from typical imagery (highlighted with the gray strip, along with the aphantasia group). From visualizing the figure with a trend line showing the best linear fit, it is clear that both hyperphantasia and aphantasia groups show more variability in responses compared to the typical imagery group, particularly in that more individuals from the extreme groups tend to have either hyposensitivity or hypersensitivity, suggesting that further divergent subgroups are likely hiding within each imagery extreme. To test this increased variability at the extremes inferentially, we performed Breusch–Pagan tests for heteroscedasticity in jamovi. This revealed significant heteroscedasticity with all groups included (statistic = 8.85,  $P = 0.012$ ) and also when individuals with aphantasia (statistic = 4.79,  $P = 0.029$ ) or hyperphantasia (Statistic = 6.76,  $P = 0.009$ ) were selectively tested against individuals with nonextreme VVIQ scores

sensory sensitivities. Recently published data suggest that individuals with aphantasia have lower ratings of (both hypo- and hyper-) sensitivities compared to individuals with typical imagery (Dance et al. 2021b). Although this much is true, there is another interesting effect at work in their data: that individuals at both imagery extremes show more variation in sensory sensitivities than individuals within the typical range of imagery ability (Fig. 1).

It therefore appears that individuals with imagery extremes are more likely to have unbalanced sensory sensitivity scores (either hypo- or hypersensitivity), which is associated with a higher proneness to divergent experiences, compared to those with typical imagery. We propose that this variation is driven by different subgroups at the extremes: specifically, that individuals with sensory hyposensitivity will have more psychosis-like divergent perception and individuals with sensory hypersensitivity will have more synaesthesia-like divergent perception. We have



**Figure 2.** The divergent predictive perception model. This schematic shows the likely characteristics associated with imbalances between reliance on sensory evidence (S) and high- (H) or low-level (L) priors and different mental imagery abilities (M). Large prior bubbles represent a maladaptive over-reliance on priors; large sensory bubbles represent high confidence in sensory input; and large imagery bubbles represent strong imagery. A combination of maladaptive high-level priors, low sensory confidence, and strong mental imagery (represented by the head with an apple in the mind's eye) will likely result in sensory psychosis symptoms such as complex hallucinations (top left, represented by the eyes in the cloud). A combination of maladaptive low-level priors, high sensory confidence, and strong mental imagery will likely result in vivid sensory synaesthesia symptoms (top right, represented by grapheme-color synaesthesia). A combination of maladaptive high-level priors, low sensory confidence, and weak mental imagery (represented by the head without an apple in the mind's eye) will likely result in nonsensory psychosis symptoms such as delusions of grandeur (bottom left, represented by the crown). A combination of maladaptive low-level priors, high sensory confidence, and weak mental imagery will likely result in more abstract synaesthesia symptoms (bottom right, represented by emotion-color synaesthesia). Note that for comparison purposes, low-level priors are included in the psychosis panels and high-level priors are included in the synaesthesia panels of the schematic, but these are not included in our model, as they do not offer additional predictive value

already suggested that individuals with imagery extremes may both be more likely to experience divergent perception compared to individuals with typical imagery: whether that will manifest as more sensory or abstract will depend on whether the extreme is hyperphantasia or aphantasia, respectively.

## Divergent predictive perception model

This concludes the justification for the parameters of our model. The model is inspired by both the predictive processing framework and psychological principles, illustrating predicted divergent perceptual experiences based on different weightings of the three parameters (Fig. 2). The summary of our model is as follows:

Maladaptive priors, combined with high or low confidence in sensory input, contribute to divergent perception, generally. Low sensory confidence combined with maladaptive (high-level) priors is characteristic of psychosis; high sensory confidence combined with maladaptive (low-level) priors is characteristic of synaesthesia. High or low sensory confidence alone may point to the form of divergent perception an individual would likely have if they were to develop maladaptive priors, but without maladaptive priors, they will not likely experience divergent perception. We therefore propose that we can best predict these traits from a “perfect storm” of the first two factors in our model. Finally, mental imagery ability independently contributes to the likelihood of having rich, percept-like divergent experiences. For example, maladaptive high-level priors combined with low confidence in sensory input may result in psychosis

symptoms such as delusions, but delusions can have different levels of abstraction or can be accompanied by hallucinations. Stronger and more vivid imagery will result in a higher likelihood of rich, percept-like experiences such as hallucinations. Mental imagery therefore determines the sensory richness of divergent experiences.

The theoretical model (Fig. 2) can be expressed statistically as a nonparametric regression model. We hypothesize that the way the predictors (i.e. maladaptive priors, sensory confidence, and mental imagery ability) are connected to the outcome variables (i.e. psychosis and synaesthesia) cannot be modeled by standard linear regression models. Because we aim to capture specifically divergent perceptual experiences in our model, we predict outcomes of specifically extreme values: e.g. behavior when priors become maladaptive, when one loses confidence in sensory input, or when one has especially vivid mental imagery. This does not allow us to make predictions about typical perception, e.g. when priors are slightly favored over sensory input or when an individual has average mental imagery vividness. Thus, traditional linear regression models, which assume a linear relationship between predictors (independent variables) and the target variable (dependent variable), may not hold in such scenarios. It is also unlikely that these nonlinear relationships can be linearized via link functions (e.g. identity, log, etc.) commonly employed in generalized linear modeling. Conversely, machine learning models can capture complex and nonlinear relationships. Examples of implementations of nonparametric machine learning regression models include tree-based machine learning and neural networks. We do not

advocate for any specific machine learning algorithm, as long as it is designed for modeling complex (i.e. nonlinear) relationships across variables.

The phenomena at hand can be expressed with the following general equation:

$$g(\mu) = \beta_0 + F(X),$$

where  $F()$  is a set of nonparametric (or semiparametric) functions applied to a matrix of predictors  $X$ ,  $\beta_0$  is the intercept, and  $g()$  is a link function applied to the expected outcome measure  $\mu$ . The application of this class of models on real data will allow us to quantify the additional fit that machine learning modeling may provide over generalized linear modeling.

We can model the likelihood of experiencing symptoms of psychosis ( $\mu_1$ ) or synaesthesia ( $\mu_2$ ) using the following equations, where  $f$  is used instead of  $F$  to denote a specific function:

$$g(\mu_1) = \beta_0 + f_1({}_mH_i, 1 - S_i), \quad (1)$$

$$g(\mu_2) = \beta_0 + f_1({}_mL_i, S_i), \quad (2)$$

where  ${}_mH_i$  is a predictor variable estimating maladaptive ( ${}_m$ ) use of high-level priors ( $H$ ) of the individual ( $i$ ) in (1).  ${}_mL_i$  is a predictor variable estimating maladaptive ( ${}_m$ ) use of low-level priors ( $L$ ) of the individual ( $i$ ) in (2).  $S_i$  is a predictor variable estimating sensory confidence ( $S$ ) of the individual ( $i$ ), which represents that higher sensory confidence will increase the likelihood of experiencing synaesthesia symptoms, and lower sensory confidence ( $1 - S_i$ ) will increase the likelihood of experiencing psychosis symptoms.

The interaction in each equation is included to express the multiplicative increase in the probability of having a divergent experience if an individual has a combination of maladaptive priors and high or low sensory confidence. For example, if sensory confidence is low, but high-level priors are not used maladaptively, this will not likely result in psychosis symptoms.  $\mu_1$  and  $\mu_2$  are expressed in separate equations to indicate independent likelihoods for experiencing psychosis or synaesthesia characteristics based on  ${}_mH_i$  and  ${}_mL_i$ , respectively. This is not to say that, e.g. an individual with psychosis cannot have maladaptive low-level priors (these are a hypothesized hallmark of delusions, as described earlier), but rather they do not add to the predictive quality of that model.

To express the predicted sensory richness of divergent experience, we model a generally linear relationship with  $\mu_3$ :

$$g(\mu_3) = \beta_0 + f_1(M_i), \quad (3)$$

where  $M_i$  is a predictor variable estimating mental imagery ability ( $M$ ) of the individual ( $i$ ), which represents the linear effect of mental imagery ability on the sensory richness of the experience.

Thus far, we have described how our model takes into account pathological imbalances in the weighting of prior and sensory information, but our model can also be applied to the general population (in the absence of, or prior to, a psychiatric diagnosis), provided that conditions are conducive to divergent perception; this requires inducing an imbalance in prior/sensory weighting.

## Manipulating the balance of priors and sensory input

An imbalance between the weighting of prior and sensory information can occur due to pathological, maladaptive priors, but

it can also be modulated by external changes in sensory precision (e.g. the clarity or ambiguity of sensory input, as defined previously) or by manipulating the natural balance in various ways.

Altered states of consciousness can increase this imbalance. Mind-altering substances achieve this by affecting our ability to update priors and interpret sensations accurately. According to a compelling predictive processing account of psychedelic states, psychedelic substances (e.g. psilocybin) influence the production of extra-detailed priors (called “decomposed predictions”), which can either cause sensory information to seem extraordinarily enhanced or be completely dissolved (in the case of hallucinations), depending on the precision of incoming sensory information (Pink-Hashkes et al. 2017). Specifically, a combination of decomposed predictions and increased sensory precision (such as going into nature) may be more likely to elicit enhanced sensory experiences, whereas a combination of decomposed predictions and decreased sensory precision (such as closing one’s eyes or going in a darkened room) may be more likely to elicit hallucinatory experiences. Psychedelics are perhaps the most obvious example of a substance that can cause altered states of consciousness, but there are many other substances in common use that can induce such states to varying degrees, including alcohol, caffeine, and nicotine (Presti 2017). Nonpharmacological altered states of consciousness are thought to work by using techniques that block out sensory input (decreasing sensory precision) and draw focus to internal states (increasing prior weighting; Hove and Stelzer 2018). These can be achieved via yoga, breathwork, meditation, fasting, being in nature, reading spiritual literature (Corneille and Luke 2021), mind-wandering and daydreaming (Abraham 2018), lucid dreaming (Corneille and Luke 2021), or sleep deprivation (Guilleminault et al. 1975), among other things.

“Sensory deprivation” refers to the temporary withdrawal of sensory stimulation either through purposeful implementation such as sensory deprivation chambers (Daniel and Mason 2015) or blindfolding (Boroojerdi et al. 2000) or due to damage to sensory organs, pathways, or brain areas (Abbott et al. 2007, Dotan et al. 2021). Sensory deprivation increases neural sensitivity and plasticity in the affected brain regions as the brain attempts to recover from, or adjust to, the decrease in stimulation (Tan and Sabel 2006, Tan et al. 2006). This can cause spontaneous neural activity and increased proneness to nonveridical perceptual phenomena such as phosphenes (Boroojerdi et al. 2000) or tinnitus (Dotan et al. 2021). If sensory deprivation induces an altered state of consciousness, this may enhance susceptibility to divergent experiences due to an increased reliance on priors in the absence of sensory input. In this environment, spontaneous sensory phenomena are likely to be misinterpreted as meaningful, complex experiences (Merabet et al. 2004).

“Perceptual deprivation” is a related phenomenon achieved via extended exposure to monotonous, impoverished, or unstructured sensory input such as visual or auditory noise, ganzfeld (Lloyd et al. 2012), or Ganzflicker (Sumich et al. 2018, Königsmark, et al., 2021, Reeder 2022). Ganzfeld is defined as a homogeneous visual field, such as a uniformly colored screen (Wackermann et al. 2008, Zdravkovic 2019), whereas Ganzflicker is a rhythmic alternation of two or more ganzfelds. In all these cases, the reduction in the content and richness of sensory stimulation compared to normal perception can induce similar effects as sensory deprivation. Our brains are naturally attuned to find structure in the environment, and the absence of external structure leads to an imbalance in the weighting of prior and sensory information for



perception. For example, several studies have found that people will report having seen faces (behavioral) and show activation of face-related brain areas (neuroimaging) while observing pure visual noise images, if told falsely that faces were embedded in those images (Zhang et al. 2008, Rieth et al. 2011, Zimmermann et al. 2019, Liu and Peng 2020).

Most commonly, sensory precision can be lowered by manipulating stimulus features and quality via degradation (Ramachandran and Gregory 1991), adding noise (Emadi et al. 2013, van Leeuwen et al. 2021), lowering contrast (Gorea and Sagi 2001), or increasing ambiguity in different ways such as using camouflage (Troscianko et al. 2008), bistable images (Meng and Tong 2004), and different levels of occlusion (van Lier et al. 1994). There is a long history of investigating the top-down influence on perception using such methods, which tend to rely on signal detection (i.e. was the stimulus present or absent?) or discrimination (i.e. was it stimulus A or B?). These methods are effective for investigating perception in psychiatric conditions and with different levels of conscious awareness, though are not the optimal tool to investigate subjective divergent experiences or altered states of consciousness.

Therefore, it is possible to increase the likelihood of divergent experiences in the general population by manipulating one's reliance on prior and sensory information in different ways. With this in mind, we can move on to a potential application of our model to the (arguably) starkest example of divergent perception: hallucinations.

## Explaining visual hallucinations in clinical and nonclinical populations

Hallucinations are widely considered to be the most debilitating symptom of divergent perception, yet much about them remains mystifying. Importantly, we still cannot predict who will experience them or not and how they are different from other forms of divergent perception. Ffytche et al. (1998) asserted that hallucinations are different from other forms of nonveridical perception (such as mental imagery) in that they are experienced externally rather than internally, are as vivid as real percepts, and are involuntary. However, individuals with hyperphantasia report that their mental images manifest in as much detail as external stimuli (Marks 1973, Aleman et al. 2000, van de Ven and Merckelbach 2003, Zeman et al. 2020, Milton et al. 2021); additionally, involuntary intrusions of mental images are not uncommon in cases of emotional or traumatic imagery (Hackmann and Holmes 2004, Hirsch and Holmes 2007, Holmes et al. 2008); finally, cases of prophantasia and projector-type synaesthesia suggest that mental images can be experienced externally without being confused with reality.

The one thing that seems to distinguish hallucinations from other related phenomena is reality discrimination. This is not to say that impaired reality discrimination necessarily results in hallucinations—we have already discussed how delusions are also a result of this kind of error. Several researchers have proposed a more specific error resulting from increased confidence in mental imagery over reality (Aleman et al. 2003, Shine et al. 2015, Aynsworth et al. 2017). This fits our account of divergent predictive perception—hallucinations are specifically a result of maladaptive high-level priors and vivid mental imagery.

This raises the question about whether the role of mental imagery in hallucinations is causal or correlational: i.e. whether vivid mental imagery causes maladaptive priors or whether the incidental co-occurrence of vivid imagery and maladaptive priors

results in hallucinatory experience. These ideas may not be mutually exclusive: we propose that individuals with imagery extremes will be more susceptible to forming maladaptive priors, generally, but the co-occurrence of vivid imagery and maladaptive priors, specifically, increases proneness to hallucinations. This remains to be explicitly tested, although two previous studies have shown significant correlations between imagery vividness and hallucinations, specifically, rather than other symptoms of maladaptive priors (i.e. schizophrenia symptoms), more generally (Shine et al. 2015, Aynsworth et al. 2017).

Because there is so much variation in hallucinatory experience (Ffytche 2005) and perceptual experience in general (Dror 2005), debates persist over whether a comprehensive model of hallucinatory experience should even be pursued. Ffytche (2005) asserted that eye and vision disorders account for a large proportion of hallucinatory experiences (in the case of Charles Bonnet syndrome, which is hallucinatory experience following macular degeneration; Schadlu et al. 2009), but hallucinations experienced as a result of these deficits are different from hallucinations experienced in psychiatric and neurological disorders; the former tend to be transient and simple and are not accompanied by other cognitive impairments (also see Ffytche et al. 1998, Burke 2002). Thus, Ffytche proposed a visual deafferentation model of hallucinations, which can account for hallucinations due to degeneration of visual acuity. However, this still does not explain hallucinations in the healthy population, which can occur due to perceptual (Wackermann et al. 2008) or sensory deprivation (Merabet et al. 2004) and pharmaceutical intervention (Barrett et al. 2015, Aday et al. 2020) and on the border of sleep and wakefulness (Ohayon 2000), among many other things. Because these experiences are so pervasive, any comprehensive model of divergent perception should also account for divergences among the wider clinical (e.g. vision loss) and general populations (Waters et al. 2014).

We propose that all these conditions—whether they be neurological, physical, or environmental—decrease confidence in sensory input, either via a lack of trust in reality due to over-reliance on high-level priors (which occurs in psychosis) or a lack of trust in one's ability to interpret a stimulus due to physical (e.g. Charles Bonnet syndrome) or environmental factors (e.g. variations in states of consciousness). A reduction in sensory confidence will lead to an over-reliance on priors. Reduced sensory confidence combined with vivid mental imagery will increase susceptibility to complex and detailed divergent sensory experiences such as hallucinations, whereas reduced sensory confidence combined with weak mental imagery will not likely result in hallucinatory experience but other altered states or delusional phenomena that are less sensory. Therefore, our model of divergent predictive perception explains why hallucinations can occur across all these various conditions, but no condition guarantees hallucinations. Divergent predictive perception specifically models how different combinations of behavioral factors may contribute to the likelihood of experiencing hallucinations in pathology and can be applied to general population models by simulating fluctuations in individual hallucination proneness via manipulation of the weighting of prior/sensory information.

## Ganzflicker as a hallucination simulator

Ganzflicker, as mentioned briefly before, is a tool to induce perceptual deprivation using rhythmically flickering visual stimulation. Related techniques require viewing the flicker through closed eyelids (e.g. using a powerful lamp; Bartossek et al. 2021), but

Ganzflicker can be implemented with eyes open (e.g. using a bright computer screen) (Königsmark et al. 2021, Reeder 2022); in all cases, various colors (Brown 1966) and frequencies (Allefeld et al. 2011, Sumich et al. 2018) can induce robust effects, including altered states of consciousness and pseudo-hallucinatory perception.<sup>5</sup> In terms of pseudo-hallucinations (i.e. induced hallucinations), both simple (e.g. geometric patterns and shapes) and complex visual experiences (e.g. real-world objects and things like faces, animals, and natural environments) can be observed within 1–2 min of continuous stimulation. Altered states of consciousness may span the whole spectrum of experiences, including losing a sense of time or space, altered bodily sensations, visual distortions, intense emotions, and ego dissolution (Schwartzman et al. 2019). Based on these reported experiences, we have proposed that Ganzflicker is a promising technique to simulate psychedelic experiences (MacKisack and Reeder 2022) that could be used to experimentally increase the imbalance between the weighting of prior and sensory information.

Recent Ganzflicker research has already demonstrated that pseudo-hallucination proneness, vividness, and complexity are related to mental imagery ability (Reeder 2022). Preliminary evidence suggests that individuals with aphantasia are much less likely to experience pseudo-hallucinations during Ganzflicker compared to individuals with imagery (~50% compared to ~88%; Königsmark et al. 2021, Reeder 2022); among those who do see pseudo-hallucinations, these experiences are much less likely to be complex in people with aphantasia (3%) compared to people with imagery (33%). The subjective intensity of Ganzflicker experiences is linearly related to mental imagery vividness ( $r=0.40$ ). These all point to a relationship between mental imagery ability and susceptibility to different sensory characteristics (complexity and vividness) of divergent cognition. The observed behavioral patterns in the subjective vividness and complexity of pseudo-hallucinations across different imagery abilities may be related to the interaction between mental imagery and sensory confidence: if mental imagery is vivid and sensory confidence is low, more vivid and complex pseudo-hallucinations will occur (attributed to a stronger influence of imagery on perception); if mental imagery is vivid and sensory confidence is high, vivid but simple pseudo-hallucinations will occur (attributed to a lower-level interpretation of ambiguous sensory input, analogous to certain visual illusions); if mental imagery is generally weak, any pseudo-hallucination will appear nonvivid (with intact sensory confidence) but may never appear at all (in the case of low sensory confidence). Therefore, we can test our divergent predictive perception model in a nonclinical population by simulating hallucinatory experience with this tool.

## Model predictions

The divergent predictive perception model informs specific predictions about susceptibility to perceptual divergences, generalizable across both clinical and general populations. Here, we lay out how we can predict probabilities of experiencing simple pseudo-hallucinations (analogous to certain illusory experiences) or complex pseudo-hallucinations (analogous to complex visual hallucinations; Collerton et al. 2005) in a general population, while observing Ganzflicker. Both synaesthesia characteristics (Cuskey et al. 2019) and psychosis (specifically “schizotypal”

characteristics (van de Ven and Merckelbach 2003, Burch et al. 2006, Smailes et al. 2020) occur in different magnitudes across the general population, and we propose that Ganzflicker can induce psychosis-like (i.e. complex) or synaesthesia-like (i.e. simple) pseudo-hallucinations that simulate divergent characteristics found in clinical populations. Prior strength, in this case, represents a shift in reliance on priors due to environmental manipulation (Ganzflicker) rather than naturally maladaptive priors. We predict that a combination of sensory confidence level (sensory sensitivity), preferred prior level (schizotypal traits), and mental imagery vividness will influence divergent perceptual experiences in Ganzflicker, as summarized in Fig. 3. An interactive version of the model predictions can be accessed at the following webpage: <https://www.reshannereeder.com/interactive-model>.

Because the sensory richness of divergent experiences is dependent on imagery ability (easily assessed by a questionnaire, e.g. Andrade et al. 2014), individuals with weak imagery (i.e. aphantasia) are most unlikely to have rich, percept-like experiences, whereas individuals with strong imagery (i.e. hyperphantasia) are most likely. With the degradation of sensory input due to Ganzflicker, typical sensory confidence levels will be compromised, leading to a temporary imbalance between the weighting of prior and sensory information (simulating the interaction between maladaptive priors and sensory confidence in pathological divergent perception).

Natural sensory confidence levels could be preassessed using a measure of sensory sensitivity (Robertson and Simmons 2013), and natural propensity to rely on (specifically high-level) priors could be preassessed with a measure of schizotypy as a proxy to psychosis-proneness (Merckelbach et al. 2001). If sensory confidence is already natural on the low side, individuals will be unlikely to experience simple pseudo-hallucinations; whereas if sensory confidence is naturally on the higher end, individuals will be most likely to experience simple pseudo-hallucinations. Additionally, reliance on high-level priors to interpret the Ganzflicker will lead to perceptual consequences that are less tethered in reality (e.g. a high probability to experience complex pseudo-hallucinations), whereas a lower reliance on high-level priors will result in a low probability to experience complex pseudo-hallucinations. Therefore, we can predict susceptibility to different types of pseudo-hallucinations in the general population based on scores from three tests: one for sensory confidence (sensory sensitivity), one for prior weighting (schizotypy), and one for mental imagery ability. Finally, we note that although simple pseudo-hallucinations can be reported with a range of subjective vividness, complex pseudo-hallucinations are always reported as vivid (Reeder 2022). Therefore, scores can be input into our non-parametric regression model to predict proneness to complex ( $\mu_4$ ), vivid simple ( $\mu_5$ ), or nonvivid simple ( $\mu_6$ ) pseudo-hallucinations, in the following equations:

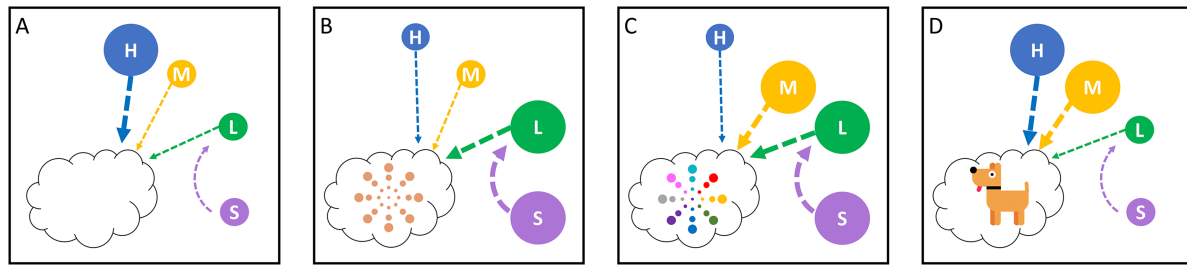
$$g(\mu_4) = \beta_0 + f_1(SZ_i) + f_2(1 - Sen_i) + f_3(M_i), \quad (4)$$

$$g(\mu_5) = \beta_0 + f_1(1 - SZ_i) + f_2(Sen_i) + f_3(M_i), \quad (5)$$

$$g(\mu_6) = \beta_0 + f_1(1 - SZ_i) + f_2(Sen_i) + f_3(1 - M_i), \quad (6)$$

where  $\beta_0$  is the intercept term.  $SZ_i$  is a predictor variable estimating schizotypal (SZ) traits of the individual ( $i$ ), which is the general population analog to maladaptive high-level priors ( ${}_mH_i$ ) in the clinical model expressed in (1) and (2). Higher schizotypal traits will increase the likelihood of experiencing complex

<sup>5</sup> We distinguish pseudo-hallucinations from true hallucinations in that the former are an induced, or simulated, experience; their onset and offset are controlled; and they are known to be unreal. Pharmaceutically induced hallucinations are considered true hallucinations: although they are induced, their onset and offset cannot be completely controlled, and they are often not understood to be unreal in the moment they are experienced.



**Figure 3.** Predictions of the likelihood of having different divergent experiences, based on the model. Individual differences in reliance on high-level (H) and low-level (L) priors, sensory confidence (S), and mental imagery ability (M) will result in different proneness to percept-like divergent experiences. This model explains differences in the likelihood to experience simple or complex pseudo-hallucinations during Ganzflicker stimulation: the empty cloud represents no pseudo-hallucination (A), the dull pattern represents a nonvivid simple pseudo-hallucination (B), the rainbow pattern represents a vivid simple pseudo-hallucination (C), and the dog represents a complex pseudo-hallucination (D)

pseudo-hallucinations, and lower schizotypal traits will decrease the likelihood of complex pseudo-hallucinations.  $Sen_i$  is a predictor variable estimating sensory sensitivity ( $Sen$ ) of the individual ( $i$ ), analogous to sensory confidence ( $S_i$ ) in the clinical model expressed in (1) and (2). This represents that higher sensory sensitivity will increase the likelihood of experiencing simple pseudo-hallucinations and lower sensory sensitivity will decrease the likelihood of experiencing simple pseudo-hallucinations.  $M_i$  is a predictor variable estimating mental imagery ability ( $M$ ) of the individual ( $i$ ), same as in the clinical model. More vivid mental imagery will increase the likelihood of vivid pseudo-hallucinations.

The model can also predict proneness to hallucinations in psychiatric conditions. Individuals with hyperphantasia and psychosis are very likely to have hallucinations, with or without delusions (imagery is not required for delusions, but it is required for hallucinations); hyperphantasia will also increase the likelihood of synchronized delusions and hallucinations (e.g. thoughts of persecution along with persecutory voices). Individuals with aphantasia and psychosis will be very unlikely to have hallucinations but be very likely to have delusions, and delusions will be less sensory in nature (e.g. grandeur). Therefore, there will be different likelihoods to experience rich, percept-like symptoms (only likely with imagery) versus nonsensory symptoms (which can occur in anyone experiencing psychosis).

Therefore, the probability of experiencing hallucinations ( $H$ ) given psychosis (“Psychosis”) can simply be expressed as a linear increase in mental imagery vividness according to (3),

$$p(H|\text{Psychosis}) \propto g(\mu_3).$$

## Future directions

### The relationship between voluntary and involuntary imagery

Mental imagery can either be voluntary (e.g. “think of a horse”) or involuntary (e.g. intrusive images), and a distinction has previously been made between the two (Pearson and Westbrook 2015). Evidence for this distinction stems from studies of individuals with aphantasia, who can experience involuntary imagery such as visual dreams, intrusions, or “flashes” during wakefulness (Zeman et al. 2015). Nevertheless, more recent research suggests that individuals with aphantasia are less likely to experience sensory intrusions associated with previous traumatic events compared to individuals with imagery; they are also less likely to report sensory dreams (Dawes et al. 2020). We therefore speculate that voluntary and involuntary imageries are generated via the same, trait-level mechanism, with voluntary imagery being an additional, effortful

process and involuntary imagery being an effortless process. Due to this difference in effort, we suggest that individuals with weak trait-level imagery will be unable to generate voluntary imagery but may experience involuntary imagery, albeit to a lesser extent than individuals with strong trait-level imagery. To tie this back to our theory, divergent sensory experiences such as hallucinations are involuntary and therefore can be experienced by individuals with aphantasia—but the likelihood is much lower than in individuals with imagery.

One interesting avenue would be to test the controllability of involuntary perceptual experiences. Going back to the example of dreaming, it is known that dreams are often involuntary and uncontrollable; however, there is the phenomenon of “lucid dreaming,” in which one becomes aware that they are currently dreaming and the individual may have a level of control over the progression of the dream (Saunders et al. 2016). Perhaps, then, individuals could learn to control other typically involuntary perceptual experiences, such as pseudo-/hallucinations.

### Experimental manipulation of imagery ability

Is it possible to experimentally reduce imagery in hyperphantasia or boost imagery in aphantasia? Imagery ability is something of a double-edged sword: it can increase susceptibility to severe sensory divergent experiences like hallucinations if the individual develops a psychiatric disorder, but it can also enhance the efficacy of visualization-based therapeutic and wellness techniques in personalized medicine. For example, guided imagery is used widely in meditation, relaxation, pain management, stress reduction, and myriad psychotherapies (Utay and Miller 2006). Preliminary research suggests that imagery can be temporarily enhanced or reduced with transcranial stimulation (Keogh et al. 2020); however, the extent to which this translates to practical outcomes (e.g. decreased hallucination proneness and increased positive response to therapy) remains to be seen.

### What is the role of phenomenological control in divergent perception?

Thus far, we have not discussed the role of phenomenological control, otherwise known as imaginative suggestion, in divergent perceptual experience (Lush et al. 2021). Phenomenological control is the susceptibility for subjective experience to be influenced by suggestions or expectations. This is aptly demonstrated by the placebo effect, which can have powerful physical and psychological consequences, such as feeling and acting inebriated when sober (Bodnár et al. 2021); inducing and relieving nausea (Quinn and Colagiuri 2015) and pain (Turner et al. 1994) and, most related

to the current research, relieving symptoms of psychosis (Hird et al. 2023).

Two important questions for this line of research are how much of susceptibility to divergent experience is driven by expectations and how much does it matter? For example, to what extent can hallucination proneness be controlled simply by telling the participant they will or will not have such experiences? This would be important to know also in evaluating the manipulability of mental imagery vividness.

Finally, there is sparse literature on the relationship between reality monitoring and phenomenological control and their role in hallucinations, although one study (Alganami et al. 2017) found that high-hallucination-prone individuals reported hearing voices in white noise more often than low-hallucination-prone individuals, but only when participants were told they should expect to hear a voice on the majority of trials. This study was inspired by a review of historical research on hallucinations, in which Bentall (1990) described how individuals from nonclinical samples have reported auditory or visual hallucinations following a verbal suggestion. Suggestion may add uncertainty to decisions in individuals with typically high signal detection criteria (i.e. strong reality discrimination), but perhaps it changes signal detection criteria if the individual is naturally uncertain in their perceptual decisions (i.e. weak reality discrimination). The extent to which the perceptual effects of phenomenological control are amplified by weak reality discrimination will need to be investigated further.

## The origin of reality monitoring issues

Although our theory is the most comprehensive, to date, in explaining divergent experiences, because it seeks to provide explanatory value for both clinical and nonclinical populations, we do not go into what compels individuals with psychosis to “lose confidence” in reality in the first place, leading to overly strong high-level priors and creating an imbalance in the weighting of prior and sensory information. We have already demonstrated that we can manipulate sensory confidence to simulate an imbalance in individuals who generally have good functioning reality discrimination, but the root cause of reality discrimination issues (in the absence of a sensory confidence manipulation) is beyond the scope of the model. Nevertheless, we speculate here.

Early warning signs of psychosis (e.g. anxiety, eccentric behavior, and depression; Birchwood et al. 2000) and symptoms during acute experiences (delusions and, hallucinations) may all stem from a breakdown in the ability to discriminate internal and external sources of information. This could be related to having maladaptively inflexible priors, which cannot be updated based on new information and are thought to be the root of delusional thinking in both clinical and nonclinical populations (Woodward et al. 2008, Bronstein et al. 2019). Maladaptively inflexible priors can explain the inability to update priors based on sensory evidence, leading to a breakdown in efficient predictive processing. They can occur in autism without psychosis (inflexible low-level priors may explain characteristics of autism, as described earlier). Psychosis may require inflexible high-level priors that compound in an inability to update belief-related (high-level) prediction errors accurately, a reduced sense of agency, and source attribution errors.

As briefly mentioned earlier, synaesthesia and hallucinations share many defining qualities: they are both uncontrollable, can appear to be embedded in the external world, and are as vivid

as real perception; the key difference seems to be in reality discrimination. This is also the key difference between hallucinations and pseudo-hallucinations. It is the reality factor that seems to ultimately determine impact on quality of life: synaesthesia and pseudo-hallucinations are often considered to be enjoyable and even helpful, whereas hallucinations are overwhelmingly fearful and debilitating. This brings us to speculate that if we could tap into what causes an individual to lose faith in reality, we could even eliminate psychosis symptoms.

As a further point of speculation, it could be that trait-level sensory sensitivity may play a role in reality monitoring. Earlier, we proposed that sensory sensitivity could provide a measure of sensory confidence in the general population: perhaps abnormal sensory sensitivities developed early in life contribute to the formation of maladaptive priors. Individuals with synaesthesia often have sensory hypersensitivity, whereas individuals with schizophrenia spectrum disorders (in which psychosis is a core symptom) are susceptible to experience catatonia (non-responsive to the environment) and flat affect (lack of ability to experience emotional range; Norman et al. 2005), indicative of sensory hyposensitivity. For now, this important factor in hallucination proneness remains a mystery.

## Implementation of the model

We have already demonstrated how our model can be used to predict susceptibility to hallucinations generally, and different kinds of hallucinations specifically, in the absence of (or prior to) a psychiatric diagnosis. Our model stresses mental imagery ability as a crucial factor in predicting the sensory nature of divergent experiences. Therefore, if an individual is referred to a medical professional due to experiencing psychiatric or neurological symptoms, assessing mental imagery ability can assist medical professionals in predicting possible future divergent experiences.

Although we may find a way to reduce or even eliminate hallucinations in the future with this research, this possibility is still far from being realized. In the meantime, if hallucinations can be predicted as proposed, simply telling patients that these may be expected can already eliminate some of the stigma surrounding these mystifying events (Menon et al. 2003, Lannon et al. 2006, Abbott et al. 2007). Due to the stigma surrounding hallucinations, patients are overwhelmingly reluctant to admit having these experiences to medical professionals, so the onus is on the professional to understand and explain them.

## Conclusions

Here, we describe a predictive, testable model of divergent perception, which considers three factors that contribute to different divergent experiences: maladaptive priors, sensory confidence, and mental imagery ability. The model predicts susceptibility to divergent experiences across psychiatric (psychosis), neurodivergent (synaesthesia, autism, and savantism), other clinical (vision loss), and general populations. We propose that there is a necessary combination of these factors that increases susceptibility to debilitating divergent perceptual experiences such as complex hallucinations. This model is the first step toward a comprehensive understanding of divergent perception.

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## Conflict of interest

None declared.

## Data availability

There are no new data associated with this article.

## References

- Abbott EJ, Connor GB, Artes PH et al. Visual loss and visual hallucinations in patients with age-related macular degeneration (Charles Bonnet syndrome). *Invest Ophthalmol Visual Sci* 2007;**48**:1416–23.
- Abraham A. The wandering mind: where imagination meets consciousness. *J Conscious Stud* 2018;**25**:34–52.
- Aday JS, Mitzkovitz CM, Bloesch EK et al. Long-term effects of psychedelic drugs: a systematic review. *Neurosci Biobehav Rev* 2020;**113**:179–89.
- Aleman A, Böcker KBE, Hijman R et al. Cognitive basis of hallucinations in schizophrenia: role of top-down information processing. *Schizophr Res* 2003;**64**:175–85.
- Aleman A, de Haan EHF. Fantasy proneness, mental imagery and reality monitoring. *Pers Individ Dif* 2004;**36**:1747–54.
- Aleman A, Nieuwenstein MR, Böcker KBE et al. Mental imagery and perception in hallucination-prone individuals. *J Nerv Mental Dis* 2000;**188**:830–6.
- Alganami F, Varese F, Wagstaff GF et al. Suggestibility and signal detection performance in hallucination-prone students. *Cogn Neuropsych* 2017;**22**:159–74.
- Allefeld C, Pütz P, Kastner K et al. Flicker-light induced visual phenomena: frequency dependence and specificity of whole percepts and percept features. *Conscious Cogn* 2011;**20**:1344–62.
- American Psychiatric Association. *Diagnostic and statistical manual of mental disorders*. 5th edn, 2013.
- Andrade J, May J, Deeprose C et al. Assessing vividness of mental imagery: the plymouth sensory imagery questionnaire. *Br J Psychol* 2014;**105**:547–63.
- Arciniegas DB. Psychosis. *Continuum* 2015;**21**:715–36.
- Aynsworth C, Nemat N, Collerton D et al. Reality monitoring performance and the role of visual imagery in visual hallucinations. *Behav Res Ther* 2017;**97**:115–22.
- Banissy MJ, Cassell JE, Fitzpatrick S et al. Increased positive and disorganised schizotypy in synaesthetes who experience colour from letters and tones. *Cortex* 2012;**48**:1085–7.
- Banissy MJ, Walsh V, Ward J. Enhanced sensory perception in synaesthesia. *Exp Brain Res* 2009;**196**:565–71.
- Barnett KJ, Newell FN. Synaesthesia is associated with enhanced, self-rated visual imagery. *Conscious Cogn* 2008;**17**:1032–9.
- Baron-Cohen S, Johnson D, Asher J et al. Is synaesthesia more common in autism?. *Mol Autism* 2013;**4**:1–6.
- Baron-Cohen S, Wheelwright S, Skinner R et al. The autism-spectrum quotient (AQ): evidence from Asperger syndrome/high-functioning autism, males and females, scientists and mathematicians. *J Autism Dev Disord* 2001;**31**:5–17.
- Barrett FS, Johnson MW, Griffiths RR. Validation of the revised mystical experience questionnaire in experimental sessions with psilocybin. *J Psychopharmacol* 2015;**29**:1182–90.
- Bartossek MT, Kemmerer J, Schmidt TT. Altered states phenomena induced by visual flicker light stimulation. *PLoS One* 2021;**16**:e0253779.
- Benson T, Park S. Exceptional visuospatial imagery in schizophrenia: implications for madness and creativity. *Front Human Neurosci* 2013;**7**:756.
- Bentall RP. The illusion of reality: a review and integration of psychological research on hallucinations. *Psychol Bull* 1990;**107**:82–95.
- Birchwood M, Spencer E, McGovern D. Schizophrenia: early warning signs. *Adv Psychiatric Treat* 2000;**6**:93–101.
- Bodnár V, Nagy K, Cziboly Á et al. Alcohol and placebo: the role of expectations and social influence. *Int J Ment Health Addict* 2021;**19**:2292–305.
- Böker KBE, Hijman R, Kahn RS et al. Perception, mental imagery and reality discrimination in hallucinating and non-hallucinating schizophrenic patients. *Br J Clin Psychol* 2000;**39**:397–406.
- Bölte S, Holtmann M, Poustka F et al. Gestalt perception and local-global processing in high-functioning autism. *J Autism Dev Disord* 2007;**37**:1493–504.
- Borojerdi B, Bushara KO, Corwell B et al. Enhanced excitability of the human visual cortex induced by short-term light deprivation. *Cereb Cortex* 2000;**10**:529–34.
- Brébion G, Ohlsen RI, Pilowsky LS et al. Visual hallucinations in schizophrenia: confusion between imagination and perception. *Neuropsychology* 2008;**22**:383–9.
- Bronstein MV, Everaert J, Castro A et al. Pathways to paranoia: analytic thinking and belief flexibility. *Behav Res Ther* 2019;**113**:18–24.
- Brown B. Specificity of EEG photic flicker responses to color as related to visual imagery ability. *Psychophysiology* 1966;**2**:197–207.
- Burch GSJ, Pavelis C, Hemsley DR et al. Schizotypy and creativity in visual artists. *Br J Psychol* 2006;**97**:177–90.
- Burke W. The neural basis of Charles Bonnet hallucinations: a hypothesis. *J Neurol Neurosurg* 2002;**73**:535–41.
- Cannon J, O'Brien AM, Bungert L et al. Prediction in autism spectrum disorder: a systematic review of empirical evidence. *Autism Res* 2021;**14**:604–30.
- Carmichael DA, Smees R, Shillcock RC et al. Is there a burden attached to synaesthesia? Health screening of synaesthetes in the general population. *Br J Psychol* 2019;**110**:530–48.
- Cavedon-Taylor D. Predictive processing and perception: what does imagining have to do with it? *Conscious Cogn* 2022;**106**:103419.
- Clark A. Whatever next? Predictive brains, situated agents, and the future of cognitive science. *Behav Brain Sci* 2013;**36**:181–204.
- Cochran DM, Dvir Y, Frazier JA. “Autism-plus” spectrum disorders: intersection with psychosis and the schizophrenia spectrum. *Child Adolesc Psychiatr Clin* 2013;**22**:609–27.
- Collerton D, Perry E, McKeith I. Why people see things that are not there: a novel perception and attention deficit model for recurrent complex visual hallucinations. *Behav Brain Sci* 2005;**28**:737–57, discussion 757–794.
- Coll M-P, Whelan E, Catmur C et al. Autistic traits are associated with atypical precision-weighted integration of top-down and bottom-up neural signals. *Cognition* 2020;**199**:104236.
- Corlett PR, Horga G, Fletcher PC et al. Hallucinations and strong priors. *Trends Cogn Sci* 2019;**23**:114–27.
- Corlett P, Simons J, Pigott J et al. Illusions and delusions: relating experimentally-induced false memories to anomalous experiences and ideas. *Front Behav Neurosci* 2009;**3**:53.
- Corneille JS, Luke D. Spontaneous spiritual awakenings: phenomenology, altered states, individual differences, and well-being. *Front Psychol* 2021;**12**:720579.
- Cuskley C, Dingemans M, Kirby S et al. Cross-modal associations and synesthesia: categorical perception and structure in vowel-color mappings in a large online sample. *Behav Res Methods* 2019;**51**:1651–75.

- Dance CJ, Jaquiere M, Eagleman DM et al. What is the relationship between aphantasia, synaesthesia and autism? *Conscious Cogn* 2021a;**89**:103087.
- Dance CJ, Ward J, Simner J. What is the link between mental imagery and sensory sensitivity? Insights from aphantasia. *Perception* 2021b;**50**:757–82.
- Daniel C, Mason OJ. Predicting psychotic-like experiences during sensory deprivation. *Biomed Res Int* 2015;**2015**:439379.
- Dawes AJ, Keogh R, Andrillon T et al. A cognitive profile of multi-sensory imagery, memory and dreaming in aphantasia. *Sci Rep* 2020;**10**:10022.
- Dotan A, Shriki O, Schaette R. Tinnitus-like “hallucinations” elicited by sensory deprivation in an entropy maximization recurrent neural network. *PLoS Comput Biol* 2021;**17**:e1008664.
- Dror IE. Perception is far from perfection: the role of the brain and mind in constructing realities. *Behav Brain Sci* 2005;**28**:763–763.
- Emadi N, Esteky H, Arabzadeh E. Neural representation of ambiguous visual objects in the inferior temporal cortex. *PLoS One* 2013;**8**:e76856.
- Ffytche DH. Two visual hallucinatory syndromes. *Behav Brain Sci* 2005;**28**:763–4.
- Ffytche DH, Howard RJ, Brammer MJ et al. The anatomy of conscious vision: an fMRI study of visual hallucinations. *Nat Neurosci* 1998;**1**:738–42.
- Fletcher PC, Frith CD. Perceiving is believing: a Bayesian approach to explaining the positive symptoms of schizophrenia. *Nat Rev Neurosci* 2009;**10**:48–58.
- Friston KJ. Hallucinations and perceptual inference. *Behav Brain Sci* 2005;**28**:764–6.
- Galton F. Statistics of mental imagery. *Mind* 1880;**5**:301–18.
- Garrison JR, Bond R, Gibbard E et al. Monitoring what is real: the effects of modality and action on accuracy and type of reality monitoring error. *Cortex* 2017;**87**:108–17.
- Gorea A, and Sagi D. Disentangling signal from noise in visual contrast discrimination. *Nat Neurosci* 2001;**4**:1146–50.
- Grandin T. How people with autism think. In: Schopler E, Mesibov GB (eds), *Learning and Cognition in Autism*. USA: Springer, 1995, 137–56.
- Guilleminault C, Billiard M, Montplaisir J et al. Altered states of consciousness in disorders of daytime sleepiness. *J Neurol Sci* 1975;**26**:377–93.
- Haarsma J, Kok P, Browning M. The promise of layer-specific neuroimaging for testing predictive coding theories of psychosis. *Schizophr Res* 2022;**245**:68–76.
- Hackmann A, Holmes EA. Reflecting on imagery: a clinical perspective and overview of the special issue of memory on mental imagery and memory in psychopathology. *Memory* 2004;**12**:389–402.
- Hird EJ, Diederer K, Leucht S et al. The placebo effect in psychosis: why it matters and how to measure it. *Biol Psych Global Open Sci* 2023;**3**:605–13.
- Hirsch CR, Holmes EA. Mental imagery in anxiety disorders. *Psychiatry* 2007;**6**:161–5.
- Hochel M, Milán EG. Synaesthesia: the existing state of affairs. *Cogn Neuropsychol* 2008;**25**:93–117.
- Hohwy J. Attention and conscious perception in the hypothesis testing brain. *Front Psychol* 2012;**3**:96.
- Hohwy J. Priors in perception: top-down modulation, Bayesian perceptual learning rate, and prediction error minimization. *Conscious Cogn* 2017;**47**:75–85.
- Holmes EA, Geddes JR, Colom F et al. Mental imagery as an emotional amplifier: application to bipolar disorder. *Behav Res Ther* 2008;**46**:1251–8.
- Horga G, Schatz KC, Abi-Dargham A et al. Deficits in predictive coding underlie hallucinations in schizophrenia. *J Neurosci* 2014;**34**:8072–82.
- Hove MJ, Stelzer J. Biological foundations and beneficial effects of trance. *Behav Brain Sci* 2018;**41**:e76.
- Hughes JEA, Gruffydd E, Simner J et al. Synaesthetes show advantages in savant skill acquisition: training calendar calculation in sequence-space synaesthesia. *Cortex* 2019;**113**:67–82.
- Hughes JEA, Simner J, Baron-Cohen S et al. Is synaesthesia more prevalent in autism spectrum conditions? Only where there is prodigious talent. *Multisens Res* 2017;**30**:391–408.
- Hunt T (Director). *Orange Sherbet Kisses*. Horizon. Box of Broadcasts. 1994. <https://learningonscreen.ac.uk/ondemand/index.php/prog/RT450B1D?bcast=120203839> (16 September 2023, date last accessed).
- Janik Mcerlean AB, Banissy MJ. Examining the relationship between schizotypy and self-reported visual imagery vividness in grapheme-color synaesthesia. *Front Psychol* 2016;**7**: 131.
- Keogh R, Bergmann J, Pearson J. Cortical excitability controls the strength of mental imagery. *eLife* 2020;**9**:e50232.
- Königsmark VT, Bergmann J, Reeder RR. The Ganzflicker experience: high probability of seeing vivid and complex pseudo-hallucinations with imagery but not aphantasia. *Cortex* 2021;**141**:522–34.
- Kunda M, Goel AK. Thinking in pictures as a cognitive account of autism. *J Autism Dev Disord* 2011;**41**:1157–77.
- Lannon SP, Stevenson MR, White ST et al. Visual hallucinations in patients with age-related macular degeneration (AMD). *Vis Impair Res* 2006;**8**:9–16.
- Lawson RP, Rees G, Friston KJ. An aberrant precision account of autism. *Front Human Neurosci* 2014;**8**:302.
- Liu S, Peng M. Does scope of attention affect creativity? Testing the attentional priming hypothesis. *J Creat Behav* 2020;**54**:423–35.
- Lloyd DM, Lewis E, Payne J et al. A qualitative analysis of sensory phenomena induced by perceptual deprivation. *Phenomenol Cogn Sci* 2012;**11**:95–112.
- Lush P, Scott RB, Seth AK et al. The phenomenological control scale: measuring the capacity for creating illusory nonvolition, hallucination and delusion. *Collabra* 2021;**7**:29542.
- MacKisack M, Reeder R. *Manipulating light can induce psychedelic experiences – and scientists aren’t quite sure why*. The Conversation. 2022. <http://theconversation.com/manipulating-light-can-induce-psychedelic-experiences-and-scientists-arent-quite-sure-why-192885> (24 October 2022, date last accessed).
- Marks DF. Visual imagery differences in the recall of pictures. *Br J Psychol* 1973;**64**:17–24.
- Matthews NL, Collins KP, Thakkar KN et al. Visuospatial imagery and working memory in schizophrenia. *Cogn Neuropsychol* 2014;**19**:17–35.
- Meng M, Tong F. Can attention selectively bias bistable perception? Differences between binocular rivalry and ambiguous figures. *J Vis* 2004;**4**:2.
- Menon GJ, Rahman I, Menon SJ et al. Complex visual hallucinations in the visually impaired: The Charles Bonnet syndrome. *Surv Ophthalmol* 2003;**48**:58–72.
- Merabet LB, Maguire D, Warde A et al. Visual hallucinations during prolonged blindfolding in sighted subjects. *J Neuroophthalmol* 2004;**24**:109–13.
- Merckelbach H, Horselenberg R, Muris P. The Creative Experiences Questionnaire (CEQ): a brief self-report measure of fantasy proneness. *Pers Individ Dif* 2001;**31**:987–95.

- Milton F, Fulford J, Dance C et al. Behavioral and neural signatures of visual imagery vividness extremes: aphantasia versus hyperphantasia. *Cereb Cortex Commun* 2021;**2**:tgab035.
- Neufeld J, Roy M, Zapf A et al. Is synesthesia more common in patients with Asperger syndrome? *Front Human Neurosci* 2013;**7**:847.
- Norman RMG, Scholten DJ, Malla AK et al. Early signs in schizophrenia spectrum disorders. *J Nerv Mental Dis* 2005;**193**:17–23.
- Nugent M, Ward J. Familial aggregation of synaesthesia with autism (but not schizophrenia). *Cogn Neuropsych* 2022;**27**:373–91.
- O'Connor N, Hermelin B. Talents and preoccupations in idiots-savants. *Psychol Med* 1991;**21**:959–64.
- O'Dowd A, Cooney SM, McGovern DP et al. Do synaesthesia and mental imagery tap into similar cross-modal processes? *Philos Trans R Soc B* 2019;**374**:20180359.
- Oertel V, Rotarska-Jagiela A, van de Ven V et al. Mental imagery vividness as a trait marker across the schizophrenia spectrum. *Psychiatry Res* 2009;**167**:1–11.
- Ohayon MM. Prevalence of hallucinations and their pathological associations in the general population. *Psychiatry Res* 2000;**97**:153–64.
- Pearson J, Westbrook F. Phantom perception: voluntary and involuntary nonretinal vision. *Trends Cogn Sci* 2015;**19**:278–84.
- Pellicano E, Burr D. When the world becomes “too real”: a Bayesian explanation of autistic perception. *Trends Cogn Sci* 2012;**16**:504–10.
- Perälä J, Suvisaari J, Saarni SI et al. Lifetime prevalence of psychotic and bipolar I disorders in a general population. *Arch Gen Psych* 2007;**64**:19–28.
- Pink-Hashkes S, van Rooij I, Kwisthout J. Perception is in the details: A predictive coding account of the psychedelic phenomenon *Proceedings of the 39th Annual Meeting of the Cognitive Science Society* London, UK, 2017, 2907–12.
- Powers AR, Mathys C, Corlett PR. Pavlovian conditioning-induced hallucinations result from overweighting of perceptual priors. *Science* 2017;**357**:596–600.
- Presti DE. Altered States of Consciousness: Drug-Induced States. In: Schneider S, Velmans M. (eds.) *The Blackwell Companion to Consciousness, Second Edition*. John Wiley & Sons, Ltd, 2017, 171–86.
- Quinn VF, Colagiuri B. Placebo interventions for nausea: a systematic review. *Ann Behav Med* 2015;**49**:449–62.
- Ramachandran VS, Gregory RL. Perceptual filling in of artificially induced scotomas in human vision. *Nature* 1991;**350**:699–702.
- Reeder RR. Ganzflicker reveals the complex relationship between visual mental imagery and pseudo-hallucinatory experiences: a replication and expansion. *Collabra* 2022;**8**:36318.
- Ribolsi M, Fiori Nastro F, Pelle M et al. Recognizing psychosis in autism spectrum disorder. *Front Psych* 2022;**13**:768586.
- Rieth CA, Lee K, Lui J et al. Faces in the mist: Illusory face and letter detection. *I-Perception* 2011;**2**:458–76.
- Robertson AE, Simmons DR. The relationship between sensory sensitivity and autistic traits in the general population. *J Autism Dev Disord* 2013;**43**:775–84.
- Sack AT, van de Ven VG, Etschenberg S et al. Enhanced vividness of mental imagery as a trait marker of schizophrenia?. *Schizophr Bull* 2005;**31**:97–104.
- Salge JH, Pollmann S, Reeder RR. Anomalous visual experience is linked to perceptual uncertainty and visual imagery vividness. *Psychol Res* 2020;**85**:1848–65.
- Samaha J, Boutonnet B, Postle BR et al. Effects of meaningfulness on perception: alpha-band oscillations carry perceptual expectations and influence early visual responses. *Sci Rep* 2018;**8**:6606.
- Saunders DT, Roe CA, Smith G et al. Lucid dreaming incidence: a quality effects meta-analysis of 50 years of research. *Conscious Cogn* 2016;**43**:197–215.
- Schadlu AP, Schadlu R, Shepherd JB. Charles Bonnet syndrome: a review. *Curr Opin Ophthalmol* 2009;**20**:219–22.
- Schmack K, de Castro AG-C, Rothkirch M et al. Delusions and the role of beliefs in perceptual inference. *J Neurosci* 2013;**33**:13701–12.
- Schultze-Lutter F, Nenadic I, Grant P. Psychosis and schizophrenia-spectrum personality disorders require early detection on different symptom dimensions. *Front Psych* 2019;**10**:476.
- Schwartzman DJ, Schartner M, Ador BB et al. Increased spontaneous EEG signal diversity during stroboscopically-induced altered states of consciousness. *bioRxiv* 2019;511766.
- Seth AK. A predictive processing theory of sensorimotor contingencies: explaining the puzzle of perceptual presence and its absence in synesthesia. *Cogn Neurosci* 2014;**5**:97–118.
- Seth A. Anil Seth: Your Brain Hallucinates Your Conscious Reality | TED Talk. 2017. [https://www.ted.com/talks/anil\\_seth\\_your\\_brain\\_hallucinates\\_your\\_conscious\\_reality](https://www.ted.com/talks/anil_seth_your_brain_hallucinates_your_conscious_reality) (14 September 2023, date last accessed).
- Shine JM, Keogh R, O'Callaghan C et al. Imagine that: elevated sensory strength of mental imagery in individuals with Parkinson's disease and visual hallucinations. *Proc R Soc B* 2015;**282**:20142047.
- Simner J. Defining synaesthesia. *Br J Psychol* 2012;**103**:1–15.
- Simner J. Why are there different types of synesthete? *Front Psychol* 2013;**4**:558.
- Simner J, Mayo N, Spiller M-J. A foundation for savantism? Visuo-spatial synaesthetes present with cognitive benefits. *Cortex* 2009;**45**:1246–60.
- Smailes D, Burdis E, Gregoriou C et al. Pareidolia-proneness, reality discrimination errors, and visual hallucination-like experiences in a non-clinical sample. *Cogn Neuropsych* 2020;**25**:113–25.
- Sterzer P, Adams RA, Fletcher P et al. The predictive coding account of psychosis. *Biol Psych* 2018;**84**:634–43.
- Sumich A, Anderson JD, Howard CJ et al. Reduction in lower-alpha power during Ganzfeld flicker stimulation is associated with the production of imagery and trait positive schizotypy. *Neuropsychologia* 2018;**121**:79–87.
- Tan C, Sabel B. Dynamic changes in visual acuity as the pathophysiologic mechanism in Charles Bonnet syndrome (visual hallucinations). *Eur Arch Psych Clin Neurosci* 2006;**256**:62–3.
- Tan CSH, Sabel BA, Goh K-Y. Visual hallucinations during visual recovery after central retinal artery occlusion. *Arch Neurol* 2006;**63**:598–600.
- Teufel C, Subramaniam N, Dobler V et al. Shift toward prior knowledge confers a perceptual advantage in early psychosis and psychosis-prone healthy individuals. *Proc Natl Acad Sci USA* 2015;**112**:13401–6.
- Thoresen C, Endestad T, Sigvartsen NPB et al. Frontotemporal hypoactivity during a reality monitoring paradigm is associated with delusions in patients with schizophrenia spectrum disorders. *Cogn Neuropsych* 2014;**19**:97–115.
- Tilot AK, Vino A, Kucera KS et al. Investigating genetic links between grapheme-colour synaesthesia and neuropsychiatric traits. *Philos Trans R Soc B* 2019;**374**:20190026.
- Tomchek SD, Dunn W. Sensory processing in children with and without autism: a comparative study using the short sensory profile. *Am J Occup Ther* 2007;**61**:190–200.
- Troscianko T, Benton CP, Lovell PG et al. Camouflage and visual perception. *Philos Trans R Soc B* 2008;**364**:449–61.
- Turner JA, Deyo RA, Loeser JD et al. The importance of placebo effects in pain treatment and research. *Jama* 1994;**271**:1609–14.

- Utay J, Miller M. Guided imagery as an effective therapeutic technique: a brief review of its history and efficacy research. *J Instr Psychol* 2006;**33**:40–3.
- Van de Cruys S, Evers K, Van der Hallen R et al. Precise minds in uncertain worlds: predictive coding in autism. *Psychol Rev* 2014;**121**:649–75.
- Van der Hallen R, Evers K, Brewaeys K et al. Global processing takes time: a meta-analysis on local-global visual processing in ASD. *Psychol Bull* 2015;**141**:549–73.
- van de Ven V, Merkelbach H. The role of schizotypy, mental imagery, and fantasy proneness in hallucinatory reports of undergraduate students. *Pers Individ Dif* 2003;**35**:889–96.
- van Laarhoven T, Stekelenburg JJ, Eussen M et al. Neural correlates of impaired motor-auditory prediction in Autism Spectrum Disorder. In: *NVP Winter Conference Egmond aan Zee, Netherlands, 2017*. <https://research.tilburguniversity.edu/en/publications/neural-correlates-of-impaired-motor-auditory-prediction-in-autism>.
- van Leeuwen TM, Koolen M, Neufeld J et al. Synaesthesia and its relation to social and sensory aspects of autism. In: *European Conference on Visual Perception Nijmegen, The Netherlands. 2022*.
- van Leeuwen TM, Neufeld J, Hughes J et al. Synaesthesia and autism: different developmental outcomes from overlapping mechanisms? *Cogn Neuropsychol* 2020;**37**:433–49.
- van Leeuwen TM, Sauer A, Jurjut A-M et al. Perceptual gains and losses in synesthesia and schizophrenia. *Schizophr Bull* 2021;**47**:722–30.
- van Leeuwen TM, van Petersen E, Burghoorn F et al. Autistic traits in synaesthesia: atypical sensory sensitivity and enhanced perception of details. *Philos Trans R Soc B* 2019;**374**:20190024.
- van Lier R, van der Helm P, Leeuwenberg E. Integrating global and local aspects of visual occlusion. *Perception* 1994;**23**:883–903.
- Wackermann J, Pütz P, Allefeld C. Ganzfeld-induced hallucinatory experience, its phenomenology and cerebral electrophysiology. *Cortex* 2008;**44**:1364–78.
- Wagner S, Monzel M. Measuring imagery strength in schizophrenia: no evidence of enhanced mental imagery priming. *Brain Behav* 2023;**13**:e3146.
- Walsh KS, McGovern DP, Clark A et al. Evaluating the neurophysiological evidence for predictive processing as a model of perception. *Ann NY Acad Sci* 2020;**1464**:242–68.
- Ward J, Brown P, Sherwood J et al. An autistic-like profile of attention and perception in synaesthesia. *Cortex* 2018;**107**:121–30.
- Ward J, Hoadley C, Hughes JEA et al. Atypical sensory sensitivity as a shared feature between synaesthesia and autism. *Sci Rep* 2017;**7**:41155.
- Waters F, Collerton D, ffytche DH et al. Visual hallucinations in the psychosis spectrum and comparative information from neurodegenerative disorders and eye disease. *Schizophr Bull* 2014;**40**:S233–S245.
- Woodward TS, Moritz S, Menon M et al. Belief inflexibility in schizophrenia. *Cogn Neuropsychol* 2008;**13**:267–77.
- Yildiz GY, Sperandio I, Kettle C et al. A review on various explanations of Ponzo-like illusions. *Psychonomic Bull Rev* 2022;**29**:293–320.
- Zdravkovic S. Ganzfeld. In: Shamey R (ed.), *Encyclopedia of Color Science and Technology*. Berlin, Heidelberg: Springer, 2019, 1–4.
- Zeman A, Dewar M, Della Sala S. Lives without imagery – congenital aphantasia. *Cortex* 2015;**73**:378–80.
- Zeman A, Milton F, Della Sala S et al. Phantasia-the psychological significance of lifelong visual imagery vividness extremes. *Cortex* 2020;**130**:426–40.
- Zhang H, Liu J, Huber DE et al. Detecting faces in pure noise images: a functional MRI study on top-down perception. *NeuroReport* 2008;**19**:229–33.
- Zimmermann KM, Stratil A-S, Thome I et al. Illusory face detection in pure noise images: the role of interindividual variability in fMRI activation patterns. *PLoS One* 2019;**14**:e0209310.



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