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Review article

Perceptual reality monitoring: Neural mechanisms dissociating imagination from reality

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ABSTRACT

There is increasing evidence that imagination relies on similar neural mechanisms as externally triggered perception. This overlap presents a challenge for perceptual reality monitoring: deciding what is real and what is imagined. Here, we explore how perceptual reality monitoring might be implemented in the brain. We first describe sensory and cognitive factors that could dissociate imagery and perception and conclude that no single factor unambiguously signals whether an experience is internally or externally generated. We suggest that reality monitoring is implemented by higher-level cortical circuits that evaluate first-order sensory and cognitive factors to determine the source of sensory signals. According to this interpretation, perceptual reality monitoring shares core computations with metacognition. This multi-level architecture might explain several types of source confusion as well as dissociations between simply *knowing* whether something is real and actually *experiencing* it as real. We discuss avenues for future research to further our understanding of perceptual reality monitoring, an endeavour that has important implications for our understanding of clinical symptoms as well as general cognitive function.

1. Introduction

In order to function in complex environments, agents have evolved to move beyond stimulus-triggered responses to actions guided by internal simulations (Mugan and MacIver, 2020). Mental simulation – the ability to imagine alternative scenarios to the one currently perceived – is a cornerstone of human cognition and plays a key role in various cognitive processes such as memory, planning and navigation (Barron et al., 2020, 2013; Epstein, 2008; Redish, 2016; Schacter et al., 2012; Zeidman et al., 2015). While allowing for a vast increase in cognitive sophistication, the existence of stimulus-independent simulation poses a challenge to a nervous system: as soon as an agent has the capacity to engage in offline simulation, there is a need to keep track of what is imagined and what is real.

Research from different fields has repeatedly shown that internally generated imagination relies on similar neural machinery as stimulus-triggered perception (Fazekas et al., 2020). Overlap in sensory processing has been found between veridical perception and working memory (Christophel et al., 2012, 2017; Harrison and Tong, 2009), mental imagery (Dijkstra et al., 2017a,b; Lee et al., 2012; Naselaris et al.,

2015a,b; Reddy et al., 2010), dreaming (Horikawa et al., 2013; Siclari et al., 2017) and hallucinations (Zmigrod et al., 2016). The existence of such overlap emphasises the challenge the brain faces in dissociating the two.

Perceptual reality monitoring – determining whether a current sensory experience reflects perception or imagination – might seem like a trivial process: after all, the phenomenological character of imagination seems so different from that of stimulus-triggered perception (Koenig-Robert and Pearson, 2021; Pearson and Kosslyn, 2015). However, source confusions, wrongfully attributing an internally generated experience to an external source or vice versa, do happen. A clear example is hallucinations. During hallucinations an internally generated experience is erroneously evaluated as being real. Hallucinations form a key symptom in certain psychiatric disorders (McCarthy-Jones and Longden, 2016) but are also prominent in the general population (Honig et al., 1998; Sommer et al., 2010; Tien, 1991; Waters et al., 2014). Another example is dreams, during which we are generally unaware that what we experience is in fact not real (Corlett et al., 2014– with the notable exception of lucid dreaming, discussed in more detail below). Although less common, the reverse also happens: wrongfully attributing

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veridical perception to be the result of imagination. Various studies have shown that participants fail to notice the external presentation of objects when they are simultaneously imagining those objects, suggesting the external signal is mistaken for imagination (Finke, 1986; Okada and Matsuoka, 1992; Reeves, 1981; Segal and Fusella, 1970; Segal and Glicksman, 1967; Segal and Nathan, 1964). This effect is known as the Perky effect after its first description by Mary Cheves West Perky in 1910 (Perky, 1910). The different variants of perceptual source confusion are listed in Table 1.

These examples demonstrate that determining whether a sensory experience has an external or internal source is a non-trivial process that is prone to error in both health and disease. In this article, we outline the neurocognitive mechanisms that might underlie perceptual reality monitoring – deciding in the moment whether a given perceptual experience reflects reality or imagination. We also discuss how it relates to a well-established framework for investigating reality monitoring of memory – deciding after the fact whether an event really happened or was only imagined (Johnson and Raye, 1981a,b; Simons et al., 2017), a process that can explain the existence of false memories (Robin, 2010; Robin and Mahé, 2015). We first provide an overview of neurocognitive factors that might dissociate imagination and perception and that could be used as inputs to a perceptual source attribution system. In this paper, we define imagination as any sensory experience generated in the absence of the corresponding external signals. Next, we will discuss how these factors could be incorporated in a decision-making process that monitors the source of sensory experience. We then discuss differences between perceptual reality monitoring at the level of experience versus belief which is important for explaining phenomena such as lucid dreams. We finish by outlining an integrated framework for perceptual reality monitoring and suggest avenues for future research.

2. What type of evidence can be used for perceptual source attribution?

As outlined above, several lines of research have demonstrated that internally generated sensory experience arising from memory, imagery and dreaming relies on similar neural mechanisms as externally triggered perception (Dijkstra et al., 2019; Horikawa et al., 2013; Pearson, 2019). The system therefore faces a challenge in dissociating imagination from real-world perception. In this section we discuss the differences between perception and imagination in terms of sensory signals and cognitive control. We suggest that these differences are used by a perceptual reality monitoring mechanism to determine the source of sensory experience and dissociate reality from imagination.

2.1. Sensory strength and precision

One of the most striking differences between perception and imagination is that the subjective experience of stimulus-triggered perception is generally much stronger and more detailed than that of internally generated imagery (Fig. 1). In line with this, it has been suggested that imagination is a weak form of perception (Koenig-Robert and Pearson,

2021; Pearson et al., 2015). This implies that one simple way to determine whether a given visual experience reflects veridical perception or imagination would be to monitor its strength and detail: if the signal is strong and contains a high level of detail, it likely reflects external input.

According to the source monitoring framework (SMF), amount of detail is also a key factor in retroactively determining the source of memories (Johnson and Raye, 1981a,b; Simons et al., 2017): memories reflecting true events contain more details than memories based on imagined events. Indeed, it has been shown that more vivid imagery during memory encoding leads to more source attribution errors during recall: i.e. a higher likelihood of misattributing imagined events as real (Markham and Hynes, 1993; Stephan-Otto et al., 2017). Within the source monitoring framework, this is explained by the idea that more vivid imagery is more similar to perception (Johnson and Raye, 1981a,b; Simons et al., 2017).

If the strength of sensory experience also plays a role in perceptual reality monitoring, we would expect that more vivid imagery is more likely to lead to hallucinations. In line with this idea, it has been found that visual imagery vividness is elevated in people with schizophrenia (Sack et al., 2005), and that in both Parkinson's and Alzheimer's disease, more vivid visual imagery is associated with an increased likelihood of experiencing visual hallucinations (El Haj et al., 2019; Shine et al., 2015). Similar effects have also been found within the auditory domain (Badcock and Hugdahl, 2012; Slade, 1976). Furthermore, the Perky effect, mistaking veridical perception for imagination, only happens when the perceptual signal is presented around threshold; once the external signal becomes stronger, participants correctly attribute their sensory experience to perception (Okada and Matsuoka, 1992; Segal and Nathan, 1964).

The strength and precision of both imagined and perceived experiences is related to neural activation in sensory brain areas (Fazekas et al., 2020). The subjective visibility of perception as well as the vividness of imagery correlate positively with the strength of neural signals in visual cortex (Cui et al., 2007; Fu et al., 2017; Ress and Heeger, 2003; Tagliabue et al., 2016). In general, however, neural activation in visual cortex during imagery is lower than during perception (Ganis et al., 2004; Ishai et al., 2000; Kosslyn et al., 2001; Winlove et al., 2018). Furthermore, the amount of information present in the signal, quantified as multivariate decoding accuracy, also tends to be lower during imagery compared to perception, suggesting that imagined representations are also less precise (Dijkstra et al., 2018; Lee et al., 2012; Naselaris et al., 2015a,b; Reddy et al., 2010; Fig. 1).

The different properties of externally and internally generated sensory representations can be explained by a reversal of information flow during imagination compared to perception (Dijkstra et al., 2020; Linde-Domingo et al., 2019). During perception, neural activation is ultimately triggered by external signals from the retina, entering the cortex via the middle layer of V1 and then progressing up the visual hierarchy via feedforward connections (Felleman and Van Essen, 1991; Fracasso et al., 2016; Kok et al., 2016; Lawrence et al., 2018) (Fig. 1). In contrast, signals during imagery have been shown to be generated in high-level visual areas and flow down the visual hierarchy via feedback connections, terminating in the deep layers of V1 (Al-Tahan and Mohsenzadeh, 2020; Bergmann et al., 2019; Dijkstra et al., 2017a,b; Fig. 1).

Feedforward connections strongly *drive* neural activity, i.e. causing downstream neurons to fire action potentials, whereas feedback connections generally *modulate* neural activity, changing existing firing rates via gain control, but usually without driving neurons to fire action potentials in isolation (Aru et al., 2020; Bastos et al., 2012; Crick and Koch, 1998; Klink et al., 2017; Koenig-Robert and Pearson, 2021; Larkum, 2013); but see e.g. (Hupé et al., 1998). This explains why neural activation during perception is stronger than during imagination. Furthermore, two recent studies showed that compared to stimulus-triggered perception, population receptive fields (pRFs) are larger during memory (Favila et al., 2020) and imagery (Breedlove et al., 2020). Instead of increasing in size across increasing levels of the visual

Table 1

Perceptual source confusion. Sensory experience can be triggered internally or externally (true source) and can be inferred to have an internal or external source (attributed source). When the attributed source is different to the true source, this reflects a source confusion.

		Attributed source	
		External	Internal
True source	**External**	Veridical perception	Perky effect
	Internal	Hallucinations	Mental imagery
		Dreaming	Episodic memory
			Working memory
			…
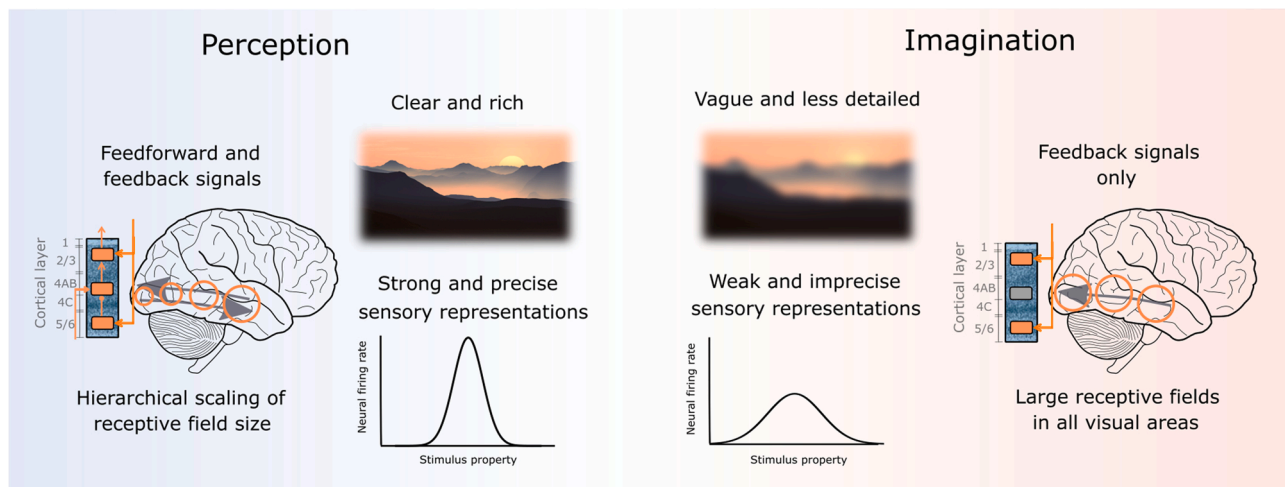
Fig. 1. Differences in sensory processing between perception (left) and imagination (right). Veridical perception is generally experienced as clearer and more detailed compared to imagination, leading to the idea that imagery is like weak perception (Pearson et al., 2015). Neural signals in early sensory areas tend to be lower in amplitude (Ganis et al., 2004; Winlove et al., 2018) and code stimuli less precisely (Dijkstra et al., 2018; Lee et al., 2012; Naselaris et al., 2015a,b; Reddy et al., 2010) during imagination compared to perception. This is likely due to the fact that imagined signals originate from high-level areas with large receptive fields, leading to top-down influences of lower spatial resolution which terminate at the deep and superficial layers of early sensory areas (Lawrence et al., 2018; Van Kerkoerle et al., 2017; Aitken et al., 2020a,b). In contrast, signals during perception originate from the high-resolution retina and enter the cortex via the middle layers of the early visual cortex, leading to a hierarchical organisation in receptive field size from low to high-level visual areas and high amplitude neural activity. Landscape image: https://pxhere.com/en/photo/1599478, brain image: https://commons.wikimedia.org/wiki/File:Elephant_side-view_Kruger.jpg.

hierarchy as they do during perception (Gattass et al., 2005; Fig. 1), during imagery and memory pRFs are as large in lower-level visual areas as they are in higher-level areas (Breedlove et al., 2020; Favila et al., 2020; Fig. 1). This can be explained by the idea that the precision in higher-level areas serves as an upper limit on the precision of internally generated representations, such that these are necessarily less detailed than their feedforward counterparts (Breedlove et al., 2020; Favila et al., 2020).

Together, this suggests that differences in sensory strength and precision between veridical perception and internally generated imagination are due to differences in the origin of the signals and the hierarchical organisation of sensory systems in the brain. Furthermore, this view predicts that neural differences should be most apparent at lower levels of the hierarchy, where high-resolution feedforward signals enter and low-resolution feedback signals terminate. Indeed, overlap in neural representations of imagined and perceived stimuli is most pronounced in high-level visual areas (Dijkstra et al., 2019; Ishai et al., 2000; Lee et al., 2012). Moreover, the vividness of visual imagery has been shown to be predominantly related to activation in low-level visual areas (Albers et al., 2013; Cui et al., 2007; Dijkstra et al., 2017a; Lee et al., 2012), as well as the strength of top-down connections to early visual areas within the visual system (Dijkstra et al., 2017b).

Taken together, these findings reveal that the natural organisation of sensory systems results in feedback-initiated imagination being weaker and less precise than externally triggered perception. This suggests that the strength and precision of sensory signals is a strong candidate factor for inferring the perceptual source. Source confusions would then happen when internally triggered sensory signals are very detailed and strong – i.e. experienced as very vivid (Allen et al., 2008) – or when externally triggered sensory signals are weak – i.e. experienced as being near threshold (Perky, 1910).

### 2.2. Cognitive control and predictability

Sensory strength is not the only factor that determines whether something is experienced as real. This is demonstrated by the existence of extremely strong mental imagery (referred to as 'hyperphantasia'), that is still experienced as imagined rather than real (Zeman et al., 2020) – as well as the existence of very weak externally triggered visual

experience which is still correctly attributed to perception. A distinct factor that may modulate source attribution in these cases is cognitive control: sensory experience during imagination can be voluntarily generated whereas perception is triggered by the external appearance of stimuli (Waters et al., 2021).

Imagination can make sensory information that is currently not present in the environment available to the system in order to execute some cognitive task (Kosslyn et al., 2001). For example, when shopping for new furniture, you might imagine what your living room looks like in order to decide which new couch to buy. In this case, sensory information is voluntarily activated and can be controlled to a high degree: you can easily change the colour, shape and position of the couch in the living room to decide which is the best match. In contrast, perception is mostly determined by what comes into the senses and the amount of control we have over its content is limited (Fig. 2).

Cognitive control has also been identified as an important factor in reality monitoring of memories (Johnson et al., 1993; Johnson and Raye, 1981a,b). In one study, participants were instructed during a recall phase to discriminate whether words had been self-generated or presented by the experimenter (Johnson et al., 1981). When the self-generation process was made more automatic, for example by giving the first letter of a word, participants were more likely to say it was presented by the experimenter. In contrast, when the self-generated words involved more cognitive operations, these were later more likely to be classified as self-generated (Johnson et al., 1981). Furthermore, the absence of control is a key aspect of hallucinations (Badcock et al., 2005; David, 2004; Waters et al., 2006; Waters et al., 2014), suggesting that cognitive control is also an important factor in perceptual reality monitoring.

One hypothesis would therefore be that internally generated experience is associated with stronger cognitive control compared to externally driven perception. The neural mechanisms of cognitive control have long been thought to depend on the frontal cortex (Badre and Nee, 2018; Miller, 2000; Miller and Cohen, 2001; Ridderinkhof et al., 2004). In line with this proposal, studies contrasting activation during imagery and perception tend to find stronger activation in frontal areas during imagery (Dijkstra et al., 2017a,b, 2019; Ishai et al., 2000, 2002; Kosslyn et al., 2001) as well as stronger connectivity from frontal to sensory areas (Dentico et al., 2014; Dijkstra et al., 2017b; Mechelli et al., 2004).
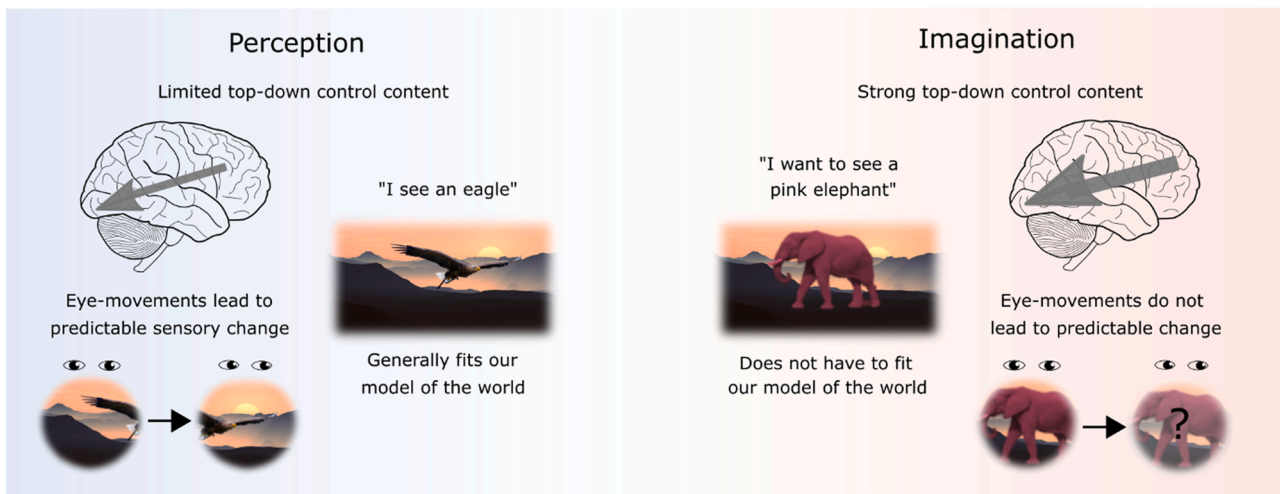
Fig. 2. Differences in cognitive control between perception (left) and imagination (right). The content of perception is under diminished voluntary control compared to the content of imagination: perception is mostly driven by what happens in the environment whereas the content of imagination is largely voluntarily determined, making its content *more* predictable. An alternative perspective is that the content of perception generally fits with our internal model of the world, which is not the case for imagery, making imagery *less* predictable. Furthermore, perceptual content can be manipulated by changing the focus of attention or moving the eyes, which leads to predictable changes in sensory signal. In contrast, while eye-movements appear to play a role in imagination, they might not lead to predictable changes in sensory input. Eagle picture: https://pxhere.com/en/photo/1599478, elephant picture: https://commons.wikimedia.org/wiki/File:Elephant_side-view_Kruger.jpg.

The strength of top-down control could then be another factor that informs perceptual reality monitoring, in addition to sensory precision and strength. In line with this, hallucinations and dreams are associated with changes in frontal activation (Lawrie et al., 2002; Stebbins et al., 2004; Waters et al., 2021).

However, top-down control of sensory representations is also an integral part of perception (Fig. 2). We pay attention to different parts of our visual input depending on our current goals. There is evidence that these attentional operations during perception may even be implemented via the same top-down mechanisms that underlie imagery (Dijkstra et al., 2017b; Gazzaley and Nobre, 2012; Xie et al., 2020). Furthermore, not all internally generated sensory experiences that are outside of voluntary control are incorrectly attributed to perception. For example, the rapid stream of mental images associated with mind-wandering or intrusive images associated with post-traumatic stress disorder are triggered automatically, but are still correctly classified as internally generated (Fazekas, 2021; Pearson, 2014).

Therefore, while cognitive control seems to be higher during internally generated experience, it is not enhanced in all forms of imagination and it also plays an important role in perception. This implies that the level of cognitive control cannot conclusively dissociate internally from externally generated experience. Besides control, one other important cognitive aspect of the self-generated nature of imagination is that imagined sensory signals are highly predictable; after all, they are generated by an internal model (Fletcher and Frith, 2009; Frith et al., 2000; Griffin and Fletcher, 2017; Sterzer et al., 2018). This has led to the proposal that a sense of agency, or ownership, of our actions is partly determined by how predictable they are (Haggard, 2017). Accordingly, perceptual reality monitoring might then be accomplished by evaluating how predictable sensory activation is, with more predictable activation being attributed to an internal source.

However, in contrast to internally versus externally triggered *actions* (Haggard, 2017), externally generated sensory signals are in some ways *more* predictable than internally triggered sensations. This is because, contrary to imagination, externally triggered sensations are spatiotemporally smooth (van Bergen and Jehee, 2019). This means that the spatial configuration of sensory input tends to change little from one moment to the next. Put differently, in contrast to what can happen in our imagination, objects in the real world generally do not pop in and out of existence. Furthermore, external sensations tend to obey our

model of the external world: they follow the rules of physics and are generally in line with what we expect based on the overall context (Press et al., 2020). Together, these considerations suggest an alternative hypothesis, namely, that the larger the prediction error associated with a sensory signal, the higher the probability that it reflects an internal source, i.e. does not reflect veridical perception (Drori et al., 2020). This hypothesis would predict that if a sensory signal appears suddenly and is incongruent with the current context we are more likely to think it is imagined. Indeed, the sudden appearance of a polar bear in your living room would likely make you question whether it was real (hopefully after hiding first, just in case). On the other hand, the content of our imagery is to some extent also constrained by our internal model of the world: while we can combine known features in novel ways in our imagination (e.g. a pink polar bear) we are unable to imagine features we have never seen before (e.g. an ultraviolet polar bear). Our imagery also does generally follow the context of our internal world and stream of thoughts, and its content is therefore likely to be somewhat predictable over time.

A final possible cue for reality monitoring might be how externally versus internally generated signals are altered by (eye) movements (Seth, 2014). When we move our eyes, the objects in the external world tend to remain in the same location, causing the associated visual signals to shift on our retinas. In turn, downstream sensory processing is influenced by the changes in sensory input associated with (eye) movements: if an eye-movement causes an external object to move from the left side of the visual field to the right side, its associated sensory representation is re-mapped from the right to the left hemisphere in the brain. In contrast, signals coming from our sensory apparatus itself, such as the shadows caused by blood vessels on the surface of the retina, or scotomas, move along with our eye movements (i.e., are retinally invariant). Therefore, retinal invariance could provide a cue as to whether signals originate from the outside world. According to the perceptual scotoma hypothesis, this mechanism can explain motion induced blindness – the perceptual disappearance of attended, stationary stimuli when set against a moving background (New and Scholl, 2008, 2018). The idea is that, in the context of globally changing signals, objects that remain stationary are assumed not to represent the external world and can therefore be discarded (New and Scholl, 2008, 2018).

However, while retinal invariance might prove a useful cue to the absence of external input, the presence of eye gaze-contingent effects is

not a reliable cue to its presence. Perhaps surprisingly, mental imagery is often also accompanied by content-specific eye-movements (Gurtner et al., 2021; Martarelli and Mast, 2021; Mast and Kosslyn, 2002) and while the changes in external input associated with eye-movements should not influence purely internally generated sensory representations, recent findings have shown that internally generated representations are also re-mapped during eye-movements (Brincat et al., 2021). This means that the way (eye) movements alter sensory processing might be similar during perception and imagery and unless a reality monitoring system has direct access to what is happening at the retina, this might not tell apart imagination and reality.

In conclusion, top-down control and predictability seem to be different for internally generated versus externally driven sensory experience (Fig. 2). Top-down control is generally higher during imagination compared to perception and this generative nature of imagined sensory signals makes them in some ways more predictable. Furthermore, loss of control and unexpectedness are defining features of hallucinations. This suggests that source confusions might happen when control of internally generated experience is lost, making it feel less predictable, or when externally driven perception erroneously seems to be under voluntary control. However, the content of externally driven perception is to some extent also under top-down control, for example via (covert) attention and action. This, together with the fact that external signals are constrained by the physics of the external world, makes them in some ways more predictable than imagination. Finally, (eye) movements lead to predictable changes in externally generated signals whereas self-generated signals are typically retinally invariant, suggesting this might be a way to dissociate imagination and reality. However, recent evidence suggests that sensory processing of internally generated signals might be altered by eye movements in a similar way to perceived signals. Therefore, while cognitive control and predictability are clearly important in dissociating imagination from reality, it remains unclear exactly how they might each inform perceptual source attributions.

3. How is a perceptual source decision made?

Summarising the evidence above, compared to externally triggered perception, internally generated sensory experience seems to be weaker and less detailed (Fig. 1), under more cognitive control, and less constrained by our model of the world (Fig. 2). However, none of these features exhaustively separates all externally from internally generated sensory experiences. This suggests the need for a reality monitoring mechanism that integrates different types of information about sensory experience to make source attributions. In the following section we first discuss possible neural substrates of such a mechanism and how it relates to metacognition. Then, we will highlight a distinction between different levels of reality monitoring which is necessary to explain phenomena such as lucid dreams.

3.1. Higher-order perceptual reality monitoring

Two recent accounts suggest that deciding whether sensory signals represent reality or imagination is achieved via a higher-order inferential process (Gershman, 2019; Lau, 2019; Fig. 3). One computational framework proposes that reality monitoring is important for learning efficient generative models (Gershman, 2019). In recent advances in artificial intelligence and machine learning, architectures known as generative adversarial networks (GANs) learn internal or generative models of the world with the aid of a discriminator that dissociates input from simulations. In this context, reality monitoring as achieved by such a discriminator is an inherent part of efficient perceptual learning (Gershman, 2019). Another, complementary, account proposes a tight link between reality monitoring and metacognition. In brief, the idea is that metacognitive processes that evaluate confidence in our memories or perceptions – whether they are an accurate reflection of the external world – may also be co-opted to distinguish between reality and imagination. According to this view, perceptual reality monitoring is implemented within a multi-level system where higher, metacognitive levels evaluate the precision or reliability of lower, sensory levels. In Lau's perceptual reality monitoring account of consciousness, for instance,
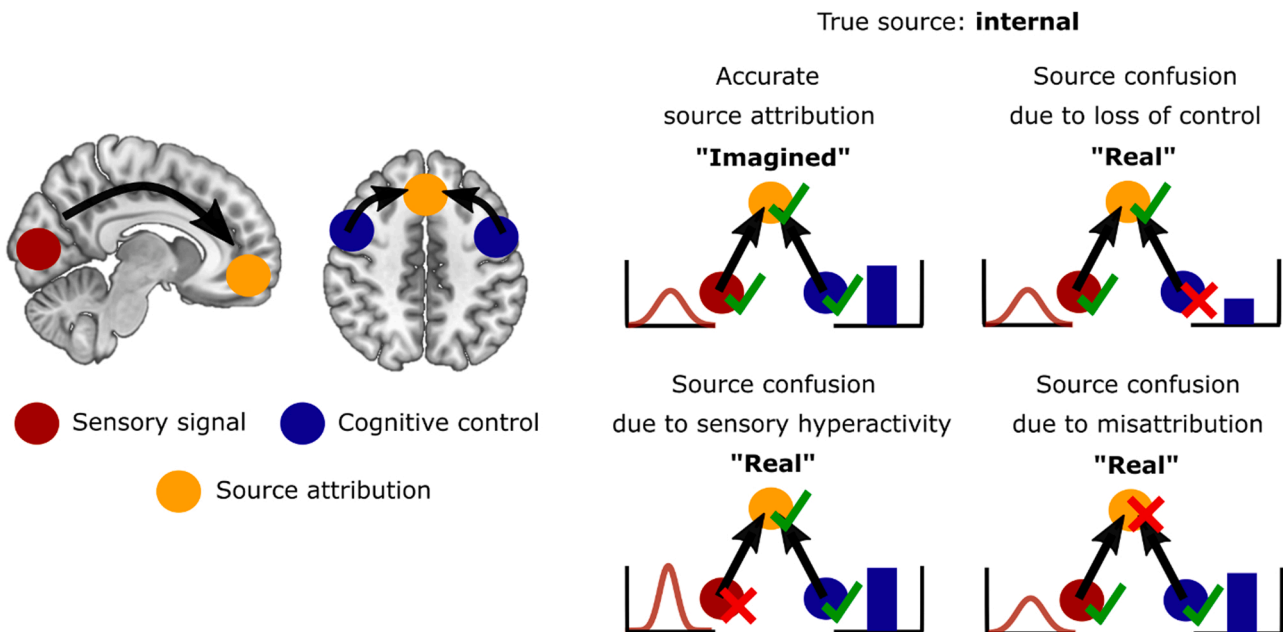

Fig. 3. Potential neural mechanisms for perceptual reality monitoring. The anterior medial prefrontal cortex (amPFC; yellow circle) evaluates sensory (Fig. 1; red circle) and cognitive control (Fig. 2; blue circles) aspects of perception and imagination in order to make a source attribution. For accurate source attribution, the neural basis of first-order perceptual and cognitive processes that distinguish perception and imagination, and the workings of a second-order source attribution process, should both be intact. Source confusions can therefore arise from different combinations of deficits as illustrated by the examples on the right. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

such mechanisms infer whether current sensory signals accurately reflect the external world, our internal imagination, or noise (Lau, 2019).

This latter model implies a tight coupling between perceptual reality monitoring and metacognition, such that we would expect deficits in metacognition to be associated with deficits in reality monitoring and vice versa. In line with this hypothesis, schizophrenia is associated with impaired metacognition about memory (Moritz et al., 2008, 2006), as well as generally decreased metacognitive functioning (Davies and Greenwood, 2020). A recent study found no difference in perceptual metacognition between patients with schizophrenia and healthy controls (Faivre et al., 2019), suggesting potential differences between reality monitoring and metacognition. However, this study did not report whether and to what extent the patients also experienced visual hallucinations, which may be crucial since the above accounts predict that metacognitive deficits would be specifically present in patients suffering from hallucinations.

Furthermore, within such hierarchical architectures, errors in perceptual reality monitoring might be caused by different factors (Fig. 3). First, source confusions could arise due to disturbances in specific first-order sensory or cognitive processes that generally separate perception and imagination. For instance, hallucinations may be related to very strong internally generated sensory signals and/or weak cognitive control signals. Conversely, source confusions could also arise from deficits in the reality monitoring process itself, which performs a source inference on the basis of the strength of these sensory and cognitive control signals (Fig. 3). Indeed, such a multi-factor explanation has been suggested to explain differences in clinical versus non-clinical hallucinations, where non-clinical hallucinations might be solely due to hyperactivation of sensory systems with a generally intact reality monitoring system, whereas hallucinations in schizophrenia might further be associated with malfunctioning reality monitoring (Simons et al., 2017). Deficits at these different levels might also lead to dissociable effects on first-order (e.g. perceptual, d') versus second-order (metacognitive, meta-d') performance respectively, which have often been confounded in previous studies (Fleming and Lau, 2014). Future studies should investigate how deficits in reality monitoring relate to different levels of perceptual and metacognitive processing.

In line with the idea of a higher-order system contributing to reality monitoring, previous research has suggested a unique role for the anterior medial prefrontal cortex (amPFC, Brodmann's area 10) in determining the source of memories. The amPFC has been consistently shown to differentiate between the retrieval of internal versus external aspects of memories (Simons et al., 2017); for example, determining whether an object was previously perceived or imagined (Kensinger and Schacter, 2006). Activation in this area correlates negatively with the tendency to misattribute imagined memories as real (Simons et al., 2006). Furthermore, variation in the size of the paracingulate sulcus (PCS), a cortical fold located within the amPFC, correlates with performance in reality monitoring tasks within the healthy population (Buda et al., 2011), such that a larger amPFC surface is associated with better reality monitoring.

Similar evidence that the amPFC may be important for *perceptual* reality monitoring comes from studies on schizophrenia. Errors in source attribution of memory are greater in patients with schizophrenia who also experience hallucinations compared to patients without hallucinations (Seal et al., 1997; Simons et al., 2017). Furthermore, PCS morphology dissociates patients with schizophrenia from healthy controls (Fornito et al., 2006) and also dissociates patients who experience hallucinations from patients who do not (Garrison et al., 2015). However, the relationship between PCS morphology and hallucinations might not generalise to non-clinical populations (Garrison et al., 2019). Functionally, decreases in amPFC activity are associated with more severe hallucinations in schizophrenia (Yanagi et al., 2020) and several studies have found decreased connectivity between auditory cortex and amPFC in patients with schizophrenia who hear voices (Mechelli et al.,

2007; Wang et al., 2011) as well as reduced global connectivity between amPFC and the rest of the brain in non-clinical voice-hearers (Lin et al., 2020). Furthermore, one study found that both clinical and non-clinical participants who experienced hallucinations in daily life were less likely to engage the amPFC during a detection task compared to clinical and non-clinical participants who did not experience hallucinations (Powers et al., 2017), indicating its importance for accurate perceptual source attributions.

A broader network of prefrontal subregions may also contribute to perceptual reality monitoring. For instance, in the primate brain, signals in lateral prefrontal cortex have been shown to differentiate memorised versus perceived stimuli (Mendoza-Halliday and Martinez-Truijilo, 2017). Furthermore, metacognitive evaluation of sensory signals has repeatedly been shown to engage the medial and lateral anterior PFC, both during perception and imagination (Bang et al., 2020; Bang and Fleming, 2018; Cui et al., 2007; Dijkstra et al., 2017a,b; Fleming et al., 2018; Gherman and Philiastides, 2018; Mazor et al., 2020; Morales et al., 2018; Motes et al., 2008).

Taken together, convergent evidence suggests that perceptual reality monitoring might be achieved by higher-order circuits centred on anterior medial prefrontal cortex evaluating low-level sensory and cognitive aspects of a perceptual experience (Fig. 3). According to this view, perceptual reality monitoring and metacognition are highly related and share common neural mechanisms. Future research should explore this relationship further in clinical as well as non-clinical contexts. Furthermore, according to this account, errors in perceptual reality monitoring can arise from deficits in either first-order processes, second-order processes, or both. In the next section, we discuss how interactions between these different levels could further explain various types of source confusions.

3.2. Recurrence between monitoring and sensory processing

It is now commonly accepted that perception does not only rely on feedforward processing but that perceptual inference is performed iteratively via recurrence between different levels of processing hierarchies (Bastos et al., 2012; Friston, 2005; Hochstein and Ahissar, 2002; Lee and Mumford, 2003). Within this context, higher-level inferences are fed back to lower-levels to regulate low-level processing. In line with this, there is now ample evidence that prior knowledge influences our perception (Aitken et al., 2020a,b; de Lange et al., 2018; Kersten et al., 2004). In contrast, the sketch of reality monitoring outlined above is unidirectional: higher-order frontal areas collect information in a feedforward manner to decide whether a sensory experience is real or imagined. One important question is whether metacognitive processes involved in source attribution are part of a broader recurrent network that exerts top-down influences on perception.

There is some evidence for recurrent interactions between metacognitive judgements and perceptual processing. Two recent studies showed that confidence in a perceptual decision biased subsequent low-level sensory processing in favour of that decision (Balsdon et al., 2020; Rollwage et al., 2020). Furthermore, with respect to reality monitoring, a recent study showed that cultural beliefs about seeing spirits and gods influenced the frequency at which these events were experienced (Luhrmann et al., 2021). Using a cross-cultural, interdisciplinary approach, this study found that people who believed that such visions had religious significance, and that the mind was permeable to the world, were more likely to experience such hallucinations (Luhrmann et al., 2021). These findings suggest that higher-order beliefs about the source of sensory signals can in turn influence sensory processing.

This view suggests that during reality monitoring, the output of a high-level source attribution is sent back to sensory areas to alter sensory processing in an iterative, recurrent loop. One consequence of such an architecture could be that sensory signals that are initially inferred to accurately reflect the external world are amplified whereas signals that are inferred to reflect noise or imagination might be dampened. This

could explain the Perky effect where, during imagination, signals that would have usually been strong enough to be perceived are missed (Okada and Matsuoka, 1992; Perky, 1910; Segal and Gordon, 1969; Whitford et al., 2017). In this case, the belief that one is imagining would dampen sensory activity, leading to lower detection rates. Furthermore, a recent study showed that people have the tendency to remember previously seen scenes as more vivid than they actually were during encoding, suggesting that the sensory signals were amplified after encoding (Rivera-Aparicio et al., 2021).

A recurrent architecture also implies that imbalances at any level of the hierarchy can have large effects throughout the network. For example, a minor dysfunction in a higher-level monitoring system might bias source attribution towards reality, leading to amplification of sensory signals (e.g. sensory hyperactivity, Fazekas, 2021) which are in turn more readily attributed as real in the next iteration (Jardri and Denève, 2013). In line with this, hallucinations and psychoses have been explained as imbalances at different levels within a hierarchical system (Corlett et al., 2019; Fletcher and Frith, 2009; Wengler et al., 2020). Indeed, several studies have found differences in hierarchical perceptual inference to be linked to changes in reality monitoring (Haarsma et al., 2020; Powers et al., 2016; Sterzer et al., 2018). To characterise the recurrent nature of reality monitoring, future research should investigate whether source attribution judgements themselves dynamically influence the strength of sensory activation.

3.3. Knowing versus experiencing something as real

Generally, sensory experiences that are attributed to an internal source (e.g. working memory, imagery, mind-wandering) also do not *feel* real; their phenomenology is very different from veridical perception. In those instances, beliefs about the reality of the experience are in line with its phenomenology. However, this is not always the case. For example, drug-induced hallucinations might feel very real even though the person experiencing them *knows* they are a direct effect of the drug they took and do not reflect external reality. Another striking example is lucid dreaming during which a dreaming person can suddenly realise that they are dreaming and that their current sensory experience therefore is not real (Corlett et al., 2014; Konkoly et al., 2021) (for more examples, see Table 2). These cases show that there are situations in which a belief about the source of a sensory signal and its effect on sensory experience are dissociable.

The existence of a dissociation between reality beliefs and reality experiences suggests that the computation of these two variables might be distinct. One possibility is that this dissociation maps directly onto a distinction between first-order and second-order processes discussed above (Fig. 3). More concretely, this would mean that the quality of perceptual experiences is determined by first-order sensory processes while beliefs about reality are determined by higher-order monitoring

Table 2
Different dimensions of source attribution (irrespective of true source). Source attributions can be made at two distinct levels: whether something is experienced as real or imagined (experience) and whether something is believed to be real or imagined (belief). Usually, these two levels are in line with each other, but in some circumstances, they can be dissociated. 1. Foote et al. (2006).

		Belief	
		External	Internal
Experience	**External**	Veridical perception Hallucinations without insight Non-lucid dreaming	Hallucinations with insight Lucid dreaming Projector synaesthesia Some visual illusions
	Internal	TMS induced phosphenes Dissociative disorders[1]	Mental imagery Memory recall Working memory Associator synaesthesia

mechanisms. Since these are two components of one reality monitoring system, both processes would generally be in line with each other, but because they rely on different neural substrates, they will sometimes dissociate.

In line with the idea that experience is determined by first-order processes, it has been suggested that differences in layer-specific activations in early visual cortex might directly account for whether something is experienced as real or imagined (Bergmann et al., 2019; Lawrence et al., 2018, 2019). However, due to differences in target layers for feedforward and feedback signals, the layer profile of externally and internally triggered signals is very different (Fig. 1), making it unlikely that internally generated signals that are experienced as real (e. g. hallucinations) could evoke the same laminar activity profile as externally presented signals. Alternatively, the general strength and precision of sensory representations might determine the 'feel' of a sensory experience, with stronger and more precise signals feeling more real. In line with the idea that first-order representations determine experience, hallucinations with insight, such as in Charles Bonnet syndrome, have mostly been associated with spontaneous fluctuations in sensory activation (Hahamy et al., 2021), rather than dysfunctional frontal systems.

Furthermore, while research into the neural correlates of lucid dreaming is scarce, initial findings suggest that the involvement of anterior prefrontal cortex is found in lucid but not non-lucid dreams (Baird et al., 2019), despite both types of dreams having more real 'feel' than wakeful imagination. Interestingly, this dissociation between implicit and explicit monitoring has also been suggested to exist for metacognition (Carruthers, 2009; Nicholson et al., 2020), with uncertainty or precision being encoded at various levels of the system (Meyniel et al., 2015; Pouget et al., 2016). For instance, information about confidence might already be represented within first-order visuomotor circuits without requiring the involvement of higher-order frontal areas (Kiani and Shadlen, 2009).

However, as discussed above, first-order mechanisms alone seem to be unable to account for all source confusions. For example, the existence of very weak sensory signals that are still experienced as real as well as strong imagery that is still experienced as imagined suggests that sensory representations alone cannot fully account for the feeling of reality. Accordingly, it has been suggested that both conscious experience as well as knowledge about reality is determined by higher-order frontal monitoring systems (Lau, 2019). The difference between the two might then be how this system is employed: for instance, an automatic, implicit route might determine the *feeling* of reality while a more deliberate, explicit route determines beliefs about reality. These two processes might map unto separate neural systems within the frontal cortex. In terms of metacognitive processes, a relevant distinction can be made between regions of agranular posterior medial PFC (such as the perigenual anterior cingulate cortex; pgACC) and more anterior frontopolar cortex. The former has been shown to track "implicit" or automatic confidence evaluations in simple decisions (Bang and Fleming, 2018; Morales et al., 2018; Wittmann et al., 2016), occurring very early in a trial (as revealed by simultaneous EEG-fMRI; Gherman and Philiastides, 2018). In contrast, frontopolar cortex has been found to track higher-order aspects of metacognitive evaluation, including the need to make explicit judgements (Bang et al., 2020; Gherman and Philiastides, 2018; Fleming et al., 2012), infer on the absence of stimulation (Mazor et al., 2020; Miyamoto et al., 2018) and/or use metacognitive estimates for adjusting decision-making strategy (Donoso et al., 2014). Direct comparisons between the functional anatomy of metacognition and reality monitoring will be required to understand how these potentially distinct metacognitive processes contribute to different aspects of PRM.

Future research is also necessary to determine whether reality experience and belief are determined by mechanisms at different levels of the system (e.g. by first-order sensory versus second-order metacognitive processes respectively) or whether both are supported by a higher-order monitoring system employed in different ways. One

concrete route to dissociating these two hypotheses would be by testing whether sensory signals that are experienced as real but believed to be imagined, such as hallucinations with insight or lucid dreaming, are also accompanied by changes within putative frontal reality monitoring systems and/or whether they reflect hyperactivation of first-order representations.

4. Conclusion

Deciding whether a sensory signal is real or imagined has important implications for behaviour as well as for perceptual processing in general. For example, the sensory representation of a bear will lead to a very different response when it is inferred to reflect reality (being scared and running away) compared to when it is merely imagined (being charmed and staying put). Furthermore, if the bear is real, our internal model of the world should be updated to accommodate the existence of bears in this specific environment, which is not necessary for imagined bears. A wealth of neuroimaging research has shown that imagined and perceived sensory experience employ similar neural mechanisms (Dijkstra et al., 2019; Pearson, 2019; Waters et al., 2021), potentially complicating this perceptual reality monitoring process. Despite its importance for general cognitive functioning, the neurocognitive mechanisms underlying perceptual reality monitoring remain largely unknown.

In this paper we first discussed the differences between internally and externally triggered sensory experiences which might be used to infer the source of sensory signals. We concluded that, in contrast to veridical perception, imagination is associated with weaker and less precise sensory representations, likely as a result of anatomical restrictions associated with running the visual system backwards (Breedlove et al., 2020; Dijkstra et al., 2020; Domingo et al., 2018). Accordingly, internally generated signals that are misattributed as real, e.g. hallucinations, are often associated with hyperactivation in sensory areas (Waters et al., 2021). Furthermore, imagination is associated with stronger cognitive control which renders it in some ways more predictable than veridical perception, resulting in a feeling of agency that dissociates it from externally triggered signals (Dijkstra et al., 2019; Haggard, 2017; Kosslyn et al., 2001). However, cognitive control of sensory signals is also employed during veridical perception; via top-down attention (Dijkstra et al., 2019; Gazzaley and Nobre, 2012). Furthermore, perception is more predictable than imagery in the sense that it is both more constrained by our model of the external world and obeys sensorimotor contingencies, although recent evidence suggests this might also be true of imagery (Brincat et al., 2021; Gurtner et al., 2021). Together these observations suggest that while there are differences in sensory signals and cognitive control, there is no clear neural signature that unambiguously dissociates all imagination from reality.

This ambiguity motivates the need for a perceptual reality monitoring mechanism that evaluates these different factors in order to form a decision about the likely source of sensory signals. Various lines of research suggest that the anterior medial prefrontal cortex (amPFC) might house such machinery (Powers et al., 2017; Simons et al., 2017). Perceptual reality monitoring might then be implemented within a multi-level system as a higher-order evaluation of the quality of sensory processing (Gershman, 2019). According to this view, reality monitoring is tightly linked to metacognition; the process of evaluating our own cognition (Lau, 2019). Within such a system, source confusion can arise from disruptions at different levels. One exciting avenue for future research is to investigate to what extent there is recurrence between different levels of the system such that source attributions are fed back to change sensory processing (e.g. Luhrmann et al., 2021; Rollwage et al., 2020). Furthermore, it remains unclear to what extent this high-level monitoring system is only important for *explicit beliefs* about reality or also determines whether something is *experienced* as real.

In conclusion, due to the overlap in neural machinery used for imagination and perception, determining whether a sensory experience

reflects reality is a non-trivial process. Here, we suggest that perceptual reality monitoring might be implemented within a multi-level system in which higher-levels located in frontal areas monitor sensory signal strength and cognitive control to determine the source of a sensory experience. However, many open questions remain and future research is necessary to fully characterise the different elements of this mechanism. A better understanding of the mechanisms supporting perceptual reality monitoring will have important implications for our understanding of general cognitive function as well as clinical cases of source confusion.

Competing interests

The authors declare that they have no competing interests.

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