

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.

Keywords: perception, imagination, reality monitoring, metacognition

1 **1. Introduction**

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

11 Research from different fields has repeatedly shown that internally generated imagination
12 relies on similar neural machinery as stimulus-triggered perception (Fazekas, Nemeth, & Overgaard,
13 2020). Overlap in sensory processing has been found between veridical perception and working
14 memory (Christophel, Hebart, & Haynes, 2012; Christophel, Klink, Spitzer, Roelfsema, & Haynes,
15 2017; Harrison & Tong, 2009), mental imagery (Dijkstra, Bosch, & van Gerven, 2017; Lee, Kravitz, &
16 Baker, 2012; Naselaris, Olman, Stansbury, Ugurbil, & Gallant, 2015; Reddy, Tsuchiya, & Serre, 2010),
17 dreaming (Horikawa, Tamaki, Miyawaki, & Kamitani, 2013; Siclari et al., 2017) and hallucinations
18 (Zmigrod, Garrison, Carr, & Simons, 2016). The existence of such overlap emphasizes the challenge
19 the brain faces in dissociating the two.

20 Perceptual reality monitoring – determining whether a current sensory experience reflects
21 perception or imagination – might seem like a trivial process: after all, the phenomenological
22 character of imagination seems so different from that of stimulus-triggered perception (Koenig-
23 Robert & Pearson, 2021; Pearson & Kosslyn, 2015). However, source confusions, wrongfully
24 attributing an internally generated experience to an external source or vice versa, do happen. A clear
25 example is hallucinations. During hallucinations an internally generated experience is erroneously
26 evaluated as being real. Hallucinations form a key symptom in certain psychiatric disorders

1 (McCarthy-Jones & Longden, 2016) but are also prominent in the general population (Honig et al.,
 2 1998; Sommer et al., 2010; Tien, 1991; Waters et al., 2014). Another example is dreams, during
 3 which we are generally unaware that what we experience is in fact not real (Corlett, Canavan,
 4 Nahum, Appah, & Morgan, 2014 - with the notable exception of lucid dreaming, discussed in more
 5 detail below). Although less common, the reverse also happens: wrongfully attributing veridical
 6 perception to be the result of imagination. Various studies have shown that participants fail to
 7 notice the external presentation of objects when they are simultaneously imagining those objects,
 8 suggesting the external signal is mistaken for imagination (Finke, 1986; Okada & Matsuoka, 1992;
 9 Reeves, 1981; Segal & Fusella, 1970; Segal & Glicksman, 1967; Segal & Nathan, 1964). This effect is
 10 known as the Perky effect after its first description by Mary Cheves West Perky in 1910 (Perky,
 11 1910). The different variants of perceptual source confusion are listed in Table 1.

12
 13 **Table 1. Perceptual source confusion.** Sensory experience can be triggered internally or externally (true
 14 source) and can be inferred to have an internal or external source (attributed source). When the attributed
 15 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 Dreaming	Mental imagery Episodic memory Working memory ...

16
 17
 18 These examples demonstrate that determining whether a sensory experience has an external or
 19 internal source is a non-trivial process that is prone to error in both health and disease. In this
 20 article, we outline the neurocognitive mechanisms that might underlie perceptual reality monitoring
 21 – deciding in the moment whether a given perceptual experience reflects reality or imagination. We

1 also discuss how it relates to a well-established framework for investigating reality monitoring of
2 memory – deciding after the fact whether an event really happened or was only imagined (Johnson
3 & Raye, 1981; Simons, Garrison, & Johnson, 2017), a process that can explain the existence of false
4 memories (Robin, 2010; Robin & Mahé, 2015). We first provide an overview of neurocognitive
5 factors that might dissociate imagination and perception and that could be used as inputs to a
6 perceptual source attribution system. In this paper, we define imagination as any sensory experience
7 generated in the absence of the corresponding external signals. Next, we will discuss how these
8 factors could be incorporated in a decision-making process that monitors the source of sensory
9 experience. We then discuss differences between sensory and cognitive perceptual reality
10 monitoring which are important for explaining phenomena such as lucid dreams. We finish by
11 outlining an integrated framework for perceptual reality monitoring and suggest avenues for future
12 research.

13

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

15 As outlined above, several lines of research have demonstrated that internally generated sensory
16 experience arising from memory, imagery and dreaming relies on similar neural mechanisms as
17 externally triggered perception (Dijkstra, Bosch, & van Gerven, 2019; Horikawa et al., 2013; Pearson,
18 2019). The system therefore faces a challenge in dissociating imagination from real-world
19 perception. In this section we discuss the differences between perception and imagination in terms
20 of sensory signals and cognitive control. We suggest that these differences are used by a perceptual
21 reality monitoring mechanism to determine the source of sensory experience and dissociate reality
22 from imagination.

23

24 **2.1. Sensory strength and precision**

25 One of the most striking differences between perception and imagination is that the subjective
26 experience of stimulus-triggered perception is generally much stronger and more detailed than that

1 of internally generated imagery (Fig. 1). In line with this, it has been suggested that imagination is a
2 weak form of perception (Koenig-Robert & Pearson, 2021; Pearson, Naselaris, Holmes, & Kosslyn,
3 2015). This implies that one simple way to determine whether a given visual experience reflects
4 veridical perception or imagination would be to monitor its strength and detail: if the signal is strong
5 and contains a high level of detail, it likely reflects external input.

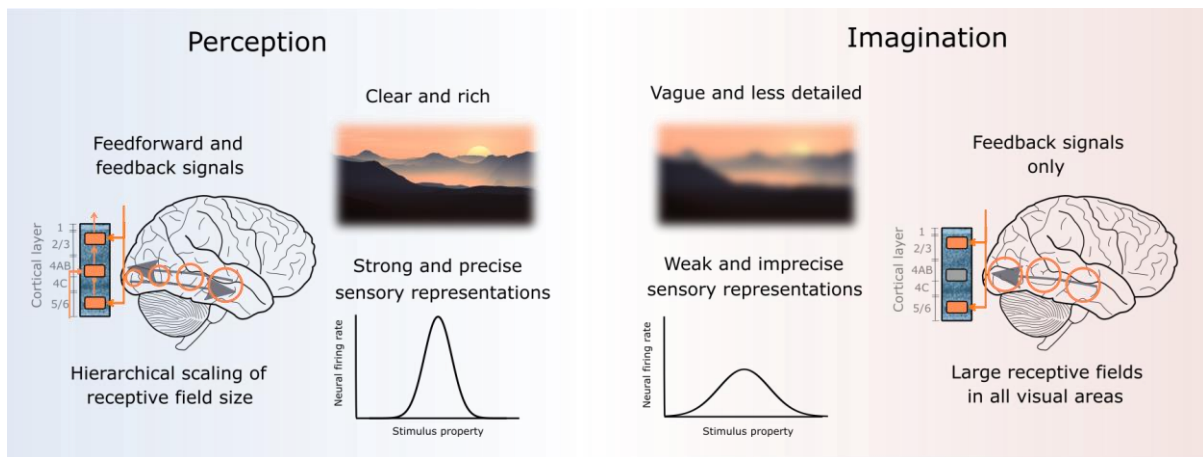
6 According to the source monitoring framework (SMF), amount of detail is also a key factor in
7 retroactively determining the source of memories (Johnson & Raye, 1981; Simons et al., 2017):
8 memories reflecting true events contain more details than memories based on imagined events.
9 Indeed, it has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

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

24 The strength and precision of both imagined and perceived experiences is related to neural
25 activation in sensory brain areas (Fazekas et al., 2020). The subjective visibility of perception as well
26 as the vividness of imagery correlate positively with the strength of neural signals in visual cortex

1 (Cui, Jeter, Yang, Montague, & Eagleman, 2007; Fu et al., 2017; Ress & Heeger, 2003; Tagliabue,
 2 Mazzi, Bagattini, & Savazzi, 2016). In general, however, neural activation in visual cortex during
 3 imagery is lower than during perception (Ganis, Thompson, & Kosslyn, 2004; Ishai, Ungerleider, &
 4 Haxby, 2000; Kosslyn, Ganis, & Thompson, 2001; Winlove et al., 2018). Furthermore, the amount of
 5 information present in the signal, quantified as multivariate decoding accuracy, also tends to be
 6 lower during imagery compared to perception, suggesting that imagined representations are also
 7 less precise (Dijkstra, Mostert, de Lange, Bosch, & van Gerven, 2018; Lee et al., 2012; Naselaris et al.,
 8 2015; Reddy et al., 2010; Fig. 1).

9



10

11

12 **Figure 1. Differences in sensory processing between perception (left) and imagination (right).** Veridical
 13 perception is generally experienced as clearer and more detailed compared to imagination, leading to the idea
 14 that imagery is like weak perception (Pearson et al., 2015). Neural signals in early sensory areas tend to be
 15 lower in amplitude (Ganis et al., 2004; Winlove et al., 2018) and code stimuli less precisely (Dijkstra, Mostert,
 16 de Lange, Bosch, & van Gerven, 2018; Lee et al., 2012; Naselaris, Olman, Stansbury, Ugurbil, & Gallant, 2015b;
 17 Reddy et al., 2010) during imagination compared to perception. This is likely due to the fact that imagined
 18 signals originate from high-level areas with large receptive fields, leading to top-down influences of lower
 19 spatial resolution which terminate at the deep and superficial layers of early sensory areas (Lawrence et al.,
 20 2018; Van Kerkoerle, Self, & Roelfsema, 2017; Aitken et al., 2020). In contrast, signals during perception
 21 originate from the high-resolution retina and enter the cortex via the middle layers of the early visual cortex,
 22 leading to a hierarchical organization in receptive field size from low to high-level visual areas. Landscape
 23 image: [link](#), brain image: [link](#).

24

25 The different properties of externally and internally generated sensory representations can be
 26 explained by a reversal of information flow during imagination compared to perception (Dijkstra,
 27 Ambrogioni, Vidaurre, & van Gerven, 2020; Linde-Domingo, Treder, Kerren, & Wimber, 2019).

1 During normal perception, neural activation is ultimately triggered by external signals from the
2 retina, entering the cortex via the middle layer of V1 and then progressing up the visual hierarchy via
3 feedforward connections (Felleman & Van Essen, 1991; Fracasso, Petridou, & Dumoulin, 2016; Kok,
4 Bains, Van Mourik, Norris, & De Lange, 2016; Lawrence et al., 2018) (Fig. 1). In contrast, signals
5 during imagery have been shown to be generated in high-level visual areas and flow down the visual
6 hierarchy via feedback connections, terminating in the deep layers of V1 (Al-Tahan & Mohsenzadeh,
7 2020; Bergmann, Morgan, & Muckli, 2019; Dijkstra, Zeidman, Ondobaka, van Gerven, & Friston,
8 2017; Fig 1).

9 Feedforward connections strongly *drive* neural activity, i.e. causing downstream neurons to
10 fire action potentials, whereas feedback connections generally *modulate* neural activity, changing
11 existing firing rates via gain control, but usually without driving neurons to fire action potentials in
12 isolation (Bastos et al., 2012; Crick & Koch, 1998; Klink, Dagnino, Gariel-Mathis, & Roelfsema, 2017;
13 Koenig-Robert & Pearson, 2021; Larkum et al., 2013; but see e.g. Hupé et al, 1998). This explains why
14 neural activation during perception is stronger than during imagination. Furthermore, two recent
15 studies showed that compared to stimulus-triggered perception, population receptive fields (pRFs)
16 are larger during memory (Favila, Kuhl, & Winawer, 2020) and imagery (Breedlove, St-Yves, Olman,
17 & Naselaris, 2020). Instead of increasing in size across increasing levels of the visual hierarchy as
18 they do during perception (Gattass et al., 2005; Fig. 1), during imagery and memory pRFs are as large
19 in lower-level visual areas as they are in higher-level areas (Breedlove et al., 2020; Favila et al., 2019;
20 Fig. 1). This can be explained by the idea that the precision in higher-level areas serves as an upper
21 limit on the precision of internally generated representations, such that these are necessarily less
22 detailed than their feedforward counterparts (Breedlove et al., 2020; Favila, Kuhl, & Winawer, 2020).

23 Together, this suggests that differences in sensory strength and precision between veridical
24 perception and internally generated imagination are due to differences in the origin of the signals
25 and the hierarchical organisation of sensory systems in the brain. Furthermore, this view predicts
26 that neural differences should be most apparent at lower levels of the hierarchy, where high-

1 resolution feedforward signals enter and low-resolution feedback signals terminate. Indeed, overlap
2 in neural representations of imagined and perceived stimuli is most pronounced in high-level visual
3 areas (Dijkstra, Bosch, & van Gerven, 2019; Ishai et al., 2000; Lee et al., 2012). Moreover, the
4 vividness of visual imagery has been shown to be predominantly related to activation in low-level
5 visual areas (Albers, Kok, Toni, Dijkerman, & De Lange, 2013; Cui et al., 2007; S.-H. Lee et al., 2012) ,
6 as well as the strength of top-down connections to early visual areas within the visual system
7 (Dijkstra, Zeidman, Ondobaka, Van Gerven, & Friston, 2017)

8 Taken together, these findings reveal that the natural organisation of sensory systems
9 results in feedback-initiated imagination being weaker and less precise than externally triggered
10 perception. This suggests that the strength and precision of sensory signals is likely a key factor in
11 inferring the perceptual source. Source confusions would then happen when internally triggered
12 sensory signals are very detailed and strong – i.e. experienced as very vivid (Allen, Larøi, McGuire, &
13 Aleman, 2008) – or when externally triggered sensory signals are very weak – i.e. experienced as
14 being near threshold (Dijkstra, Mazor, Kok & Fleming, 2021).

15

16 **2.2. Cognitive control and predictability**

17 Sensory strength is not the only factor that determines whether something is experienced as real.
18 This is demonstrated by the existence of extremely strong mental imagery (referred to as
19 ‘hyperphantasia’), that is still experienced as imagined rather than real (Zeman et al., 2020) – as well
20 as the existence of very weak externally triggered visual experience which is still correctly attributed
21 to perception. A distinct factor that may modulate source attribution in these cases is cognitive
22 control: sensory experience during imagination can be voluntarily generated whereas perception is
23 triggered by the external appearance of stimuli (Waters, Barnby, & Blom, 2021).

24 Imagination can make sensory information that is currently not present in the environment
25 available to the system in order to execute some cognitive task (Kosslyn et al., 2001). For example,
26 when shopping for new furniture, you might imagine what your living room looks like in order to

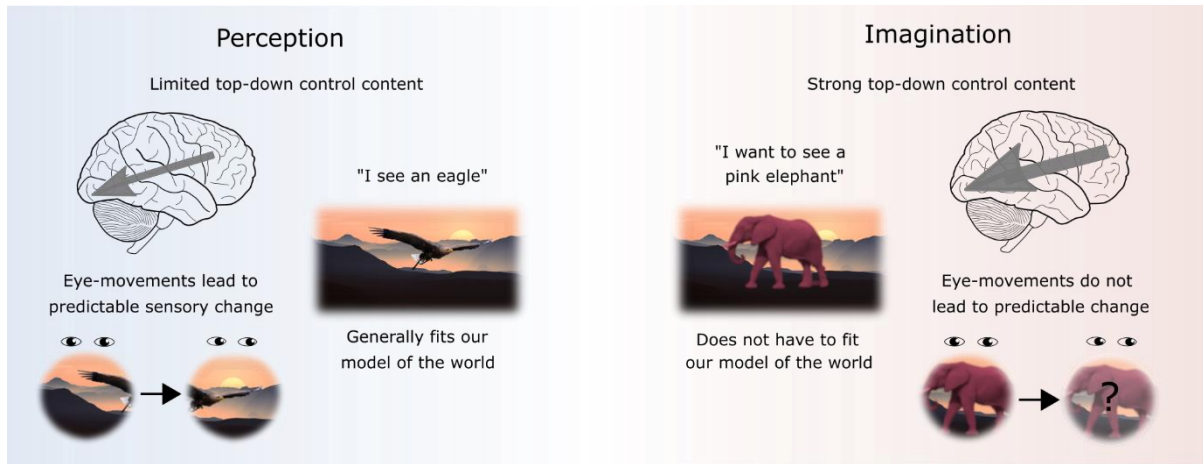
1 decide which new couch to buy. In this case, sensory information is voluntarily activated and can be
2 controlled to a high degree: you can easily change the colour, shape and position of the couch in the
3 living room to decide which is the best match. In contrast, perception is mostly determined by what
4 comes into the senses and the amount of control we have over its content is limited (Fig. 2).

5 Cognitive control has also been identified as an important factor in reality monitoring of
6 memories (Johnson, Hashtroudi, & Lindsay, 1993; Johnson & Raye, 1981). In one study, participants
7 were instructed during a recall phase to discriminate whether words had been self-generated or
8 presented by the experimenter (Johnson, Raye, Foley, & Foley, 1981). When the self-generation
9 process was made more automatic, for example by giving the first letter of a word, participants were
10 more likely to say it was presented by the experimenter. In contrast, when the self-generated words
11 involved more cognitive operations, these were later more likely to be classified as self-generated
12 (Johnson et al., 1981). Furthermore, the absence of control is a key aspect of hallucinations
13 (Badcock, Waters, Maybery, & Michie, 2005; David, 2004; Waters, Badcock, Michie, & Maybery,
14 2006; Waters et al., 2014), suggesting that cognitive control is also an important factor in perceptual
15 reality monitoring.

16 One hypothesis would therefore be that internally generated experience is associated with
17 stronger cognitive control compared to externally driven perception. The neural mechanisms of
18 cognitive control have long been thought to depend on the frontal cortex (Badre & Nee, 2018;
19 Miller, 2000; Miller & Cohen, 2001; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004). In line
20 with this proposal, studies contrasting activation during imagery and perception tend to find
21 stronger activation in frontal areas during imagery (Dijkstra et al., 2017; Dijkstra et al., 2019; Ishai,
22 Haxby, & Ungerleider, 2002; Ishai, Ungerleider, & Haxby, 2000a; Kosslyn et al., 2001) as well as
23 stronger connectivity from frontal to sensory areas (Dentico et al., 2014; Dijkstra, Zeidman,
24 Ondobaka, Van Gerven, & Friston, 2017; Mechelli et al., 2004). The strength of top-down control
25 could then be another factor that informs perceptual reality monitoring, in addition to sensory

1 precision and strength. In line with this, hallucinations and dreams are associated with changes in
2 frontal activation (Lawrie et al., 2002; Stebbins et al., 2004; Waters et al., 2021).

3



4

5

6 **Figure 2. Differences in cognitive control between perception (left) and imagination (right).** The content of
7 perception is under diminished voluntary control compared to the content of imagination: perception is
8 mostly driven by what happens in the environment whereas the content of imagination is largely voluntarily
9 determined, making its content *more* predictable. An alternative perspective is that the content of perception
10 generally fits with our internal model of the world, which is not the case for imagery, making imagery *less*
11 predictable. Furthermore, perceptual content can be manipulated by changing the focus of attention or
12 moving the eyes, which leads to predictable changes in sensory signal. In contrast, while eye-movements
13 appear to play a role in imagination, they do not lead to predictable changes in sensory input. Eagle picture:
14 [link](#), elephant picture: [link](#)

15

16 However, top-down control of sensory representations is also an integral part of perception (Fig. 2).

17 We pay attention to different parts of our visual input depending on our current goals. There is

18 evidence that these attentional operations during perception may even be implemented via the

19 same top-down mechanisms that underlie imagery (Dijkstra, Zeidman, et al., 2017; Gazzaley &

20 Nobre, 2012; Xie, Kaiser, & Cichy, 2020). Furthermore, not all internally generated sensory

21 experiences that are outside of voluntary control are incorrectly attributed to perception. For

22 example, the rapid stream of mental images associated with mind-wandering or intrusive images

23 associated with post-traumatic stress disorder are triggered automatically, but are still correctly

24 classified as internally generated (Fazekas, 2021; Pearson, 2014).

25 Therefore, while cognitive control seems to be higher during internally generated

26 experience, it is not enhanced in all forms of imagination and it also plays an important role in

1 perception. This implies that the level of cognitive control cannot conclusively dissociate internally
2 from externally generated experience. Besides control, one other important cognitive aspect of the
3 self-generated nature of imagination is that imagined sensory signals are highly predictable; after all,
4 they are generated by an internal model (Fletcher & Frith, 2009; Frith, Blakemore, & Wolpert, 2000;
5 Griffin & Fletcher, 2017; Sterzer et al., 2018). This has led to the proposal that a sense of agency, or
6 ownership, of our actions is partly determined by how predictable they are (Haggard, 2017).
7 Accordingly, perceptual reality monitoring might then be accomplished by evaluating how
8 predictable sensory activation is, with more predictable activation being attributed to an internal
9 source.

10 However, in contrast to internally versus externally triggered *actions* (Haggard, 2017),
11 externally generated sensory signals are in some ways *more* predictable than internally triggered
12 sensations. This is because, contrary to imagination, externally triggered sensations are
13 spatiotemporally smooth (van Bergen & Jehee, 2019). This means that the spatial configuration of
14 sensory input tends to change little from one moment to the next. Put differently, in contrast to
15 what can happen in our imagination, objects in the real world generally do not pop in and out of
16 existence. Furthermore, external sensations tend to obey our model of the external world: they
17 follow the rules of physics and are generally in line with what we expect based on the overall context
18 (Press, Kok, & Yon, 2020). Together, these considerations suggest an alternative hypothesis, namely,
19 that the larger the prediction error associated with a sensory signal, the higher the probability that it
20 reflects an internal source, i.e. does not reflect veridical perception (Drori, Bar-Tal, Stern,
21 Zvilichovsky, & Salomon, 2020). This hypothesis would predict that if a sensory signal appears
22 suddenly and is incongruent with the current context we are more likely to think it is imagined.
23 Indeed, the sudden appearance of a polar bear in your living room would likely make you question
24 whether it was real (hopefully after hiding first, just in case). On the other hand, the content of our
25 imagery is to some extent also constrained by our internal model of the world: while we can
26 combine known features in novel ways in our imagination (e.g. a pink polar bear) we are unable to

1 imagine features we have never seen before (e.g. an ultraviolet polar bear). Our imagery also does
2 generally follow the context of our internal world and stream of thoughts, and its content is
3 therefore likely to be somewhat predictable over time.

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

19 However, while retinal invariance might prove a useful cue to the absence of external input,
20 the presence of eye gaze-contingent effects is not a reliable cue to its presence. Perhaps surprisingly,
21 mental imagery is often also accompanied by content-specific eye-movements (Gurtner, Hartmann,
22 & Mast, 2021; Martarelli & Mast, 2021; Mast & Kosslyn, 2002) and while the changes in external
23 input associated with eye-movements should not influence purely internally generated sensory
24 representations, recent findings have shown that internally generated representations are also re-
25 mapped during eye-movements (Brincat et al., 2021). This means that the way (eye) movements
26 alter sensory processing might be similar during perception and imagery and unless a reality

1 monitoring system has direct access to what is happening at the retina, this might not tell apart
2 imagination and reality.

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

19

20 **3. How is a perceptual source decision made?**

21 Summarizing the evidence above, compared to externally triggered perception, internally generated
22 sensory experience seems to be weaker and less detailed (Fig. 1), under more cognitive control, and
23 less constrained by our model of the world (Fig. 2). However, none of these features exhaustively
24 separates externally from internally generated sensory experiences. This suggests the need for a
25 reality monitoring mechanism that integrates information about sensory experience to make source
26 attributions. In the following section we first discuss possible neural substrates of such a mechanism

1 and how it relates to metacognition. Then, we will highlight a distinction between different levels of
2 reality monitoring which is necessary to explain phenomena such as lucid dreams.

3

4 **3.1. Higher-order perceptual reality monitoring**

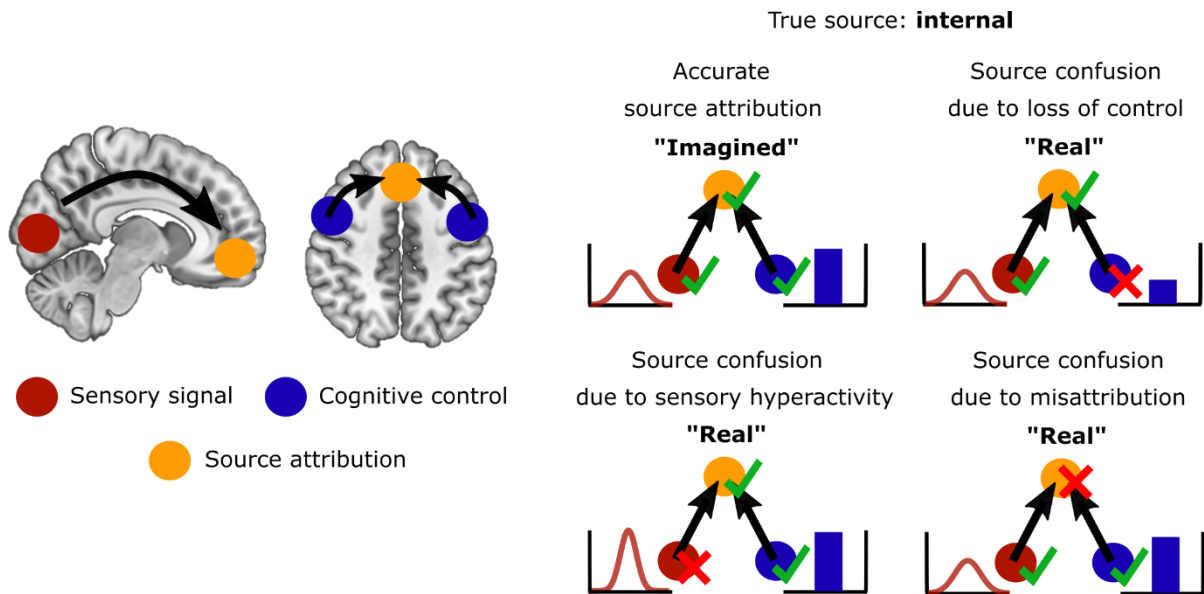
5 Two recent accounts suggest that deciding whether sensory signals represent reality or imagination
6 is achieved via a higher-order inferential process (Gershman, 2019; Lau, 2019; Fig. 3). One
7 computational framework proposes that reality monitoring is important for learning efficient
8 generative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

21 This latter model implies a tight coupling between perceptual reality monitoring and
22 metacognition, such that we would expect deficits in metacognition to be associated with deficits in
23 reality monitoring and vice versa. In line with this hypothesis, schizophrenia is associated with
24 impaired metacognition about memory (Moritz, Woodward, Jelinek, & Klinge, 2008; Steffen Moritz,
25 Woodward, & Rodriguez-Raecke, 2006), as well as generally decreased metacognitive functioning
26 (Davies & Greenwood, 2020). A recent study found no difference in perceptual metacognition

1 between patients with schizophrenia and healthy controls (Faivre et al., 2019), suggesting potential
2 differences between reality monitoring and metacognition. However, this study did not report
3 whether and to what extent the patients also experienced visual hallucinations, which may be crucial
4 since the above accounts predict that metacognitive deficits would be specifically present in patients
5 suffering from hallucinations.

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

21



1
2 **Figure 3. Potential neural mechanisms for perceptual reality monitoring.** The anterior medial prefrontal
3 cortex (amPFC; yellow circle) evaluates sensory (Fig. 1; red circle) and cognitive control (Fig. 2; blue circles)
4 aspects of perception and imagination in order to make a source attribution. For accurate source attribution,
5 the neural basis of first-order perceptual and cognitive processes that distinguish perception and imagination,
6 and the workings of a second-order source attribution process, should both be intact. Source confusions can
7 therefore arise from different combinations of deficits as illustrated by the examples on the right.
8

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

19 Similar evidence that the amPFC may be important for *perceptual* reality monitoring comes
20 from studies on schizophrenia. Errors in source attribution of memory are greater in patients with
21 schizophrenia who also experience hallucinations compared to patients without hallucinations (Seal,
22 Crowe, & Cheung, 1997; Simons et al., 2017). Furthermore, PCS morphology dissociates patients

1 with schizophrenia from healthy controls (Fornito et al., 2006) and also dissociates patients who
2 experience hallucinations from patients who do not (Garrison et al., 2015). However, the
3 relationship between PCS morphology and hallucinations might not generalize to non-clinical
4 populations (Garrison, Fernyhough, McCarthy-Jones, Simons, & Sommer, 2019). Functionally,
5 decreases in amPFC activity are associated with more severe hallucinations in schizophrenia (Yanagi
6 et al., 2020) and several studies have found decreased connectivity between auditory cortex and
7 amPFC in patients with schizophrenia who hear voices (Mechelli et al., 2007; Wang, Metzak, &
8 Woodward, 2011) as well as reduced global connectivity between amPFC and the rest of the brain in
9 non-clinical voice-hearers (Lin et al., 2020). Furthermore, one study found that both clinical and non-
10 clinical participants who experienced hallucinations in daily life were less likely to engage the amPFC
11 during a detection task compared to clinical and non-clinical participants who did not experience
12 hallucinations (Powers, Mathys, & Corlett, 2017), indicating its importance for accurate perceptual
13 source attributions.

14 A broader network of prefrontal subregions may also contribute to perceptual reality
15 monitoring. For instance, in the primate brain, signals in lateral prefrontal cortex have been shown
16 to differentiate memorized versus perceived stimuli (Mendoza-Halliday & Martinez-Trujillo, 2017).
17 Furthermore, metacognitive evaluation of sensory signals has repeatedly been shown to engage the
18 medial and lateral anterior PFC, both during perception and imagination (Bang, Ershadmanesh, Nili,
19 & Fleming, 2020; Bang & Fleming, 2018; Cui et al., 2007; Dijkstra, Bosch, et al., 2017; Fleming, Van
20 Der Putten, & Daw, 2018; Gherman & Philiastides, 2018; Mazor, Friston & Fleming, 2020; Morales,
21 Lau, & Fleming, 2018; Motes, Malach, & Kozhevnikov, 2008).

22 Taken together, convergent evidence suggests that perceptual reality monitoring might be
23 achieved by higher-order circuits centred on anterior medial prefrontal cortex evaluating low-level
24 sensory and cognitive aspects of a perceptual experience (Fig. 3). According to this view, perceptual
25 reality monitoring and metacognition are highly related and share common neural mechanisms.
26 Future research should explore this relationship further in clinical as well as non-clinical contexts.

1 Furthermore, according to this account, errors in perceptual reality monitoring can arise from
2 deficits in either first-order processes, second-order processes, or both. In the next section, we
3 discuss how interactions between these different levels could further explain various types of source
4 confusions.

5

6 **3.2. Recurrence between monitoring and sensory processing**

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

18 There is some evidence for recurrent interactions between metacognitive judgements and
19 perceptual processing. Two recent studies showed that confidence in a perceptual decision biased
20 subsequent low-level sensory processing in favour of that decision (Balsdon, Wyart, & Mamassian,
21 2020; Rollwage et al., 2020). Furthermore, with respect to reality monitoring, a recent study showed
22 that cultural beliefs about seeing spirits and gods influenced the frequency at which these events
23 were experienced (Luhmann et al., 2021). Using a cross-cultural, interdisciplinary approach, this
24 study found that people who believed that such visions had religious significance, and that the mind
25 was permeable to the world, were more likely to experience such hallucinations (Luhmann et al.,

1 2021). These findings suggest that higher-order beliefs about the source of sensory signals can in
2 turn influence sensory processing.

3 This view suggests that during reality monitoring, the output of a high-level source
4 attribution is sent back to sensory areas to alter sensory processing in an iterative, recurrent loop.
5 One consequence of such an architecture could be that sensory signals that are initially inferred to
6 accurately reflect the external world are amplified whereas signals that are inferred to reflect noise
7 or imagination might be dampened. This could explain the Perky effect where, during imagination,
8 signals that would have usually been strong enough to be perceived are missed (Okada & Matsuoka,
9 1992; Perky, 1910; Segal & Gordon, 1969; Whitford et al., 2017). In this case, the belief that one is
10 imagining would dampen sensory activity, leading to lower detection rates. Furthermore, a recent
11 study showed that people have the tendency to remember previously seen scenes as more vivid
12 than they actually were during encoding, suggesting that the sensory signals were amplified after
13 encoding (Rivera-Aparicio, Yu, & Firestone, 2021).

14 A recurrent architecture also implies that imbalances at any level of the hierarchy can have
15 large effects throughout the network. For example, a minor dysfunction in a higher-level monitoring
16 system might bias source attribution towards reality, leading to amplification of sensory signals (e.g.
17 sensory hyperactivity, Fazekas, 2021) which are in turn more readily attributed as real in the next
18 iteration (Jardri & Denève, 2013). In line with this, hallucinations and psychoses have been explained
19 as imbalances at different levels within a hierarchical system (Corlett et al., 2019; Fletcher & Frith,
20 2009; Wengler, Goldberg, Chahine, & Horga, 2020). Indeed, several studies have found differences in
21 hierarchical perceptual inference to be linked to changes in reality monitoring (Haarsma et al., 2020;
22 Powers lii, Kelley, & Corlett, 2016; Sterzer et al., 2018). To characterize the recurrent nature of
23 reality monitoring, future research should investigate whether source attribution judgements
24 themselves dynamically influence the strength of sensory signals.

25

26 **3.3. Knowing versus experiencing something as real**

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

11
 12 **Table 2. Perceptual versus cognitive source attribution (irrespective of true source).** Source attributions can
 13 be made at two distinct levels: whether something is experienced as real or imagined (experience) and
 14 whether something is believed to be real or imagined (belief). Usually, these two levels are in line with each
 15 other, but in some circumstances, they can be dissociated. 1. Foote, Smolin, Kaplan, Legatt, & Lipschitz, 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

16
 17
 18 The existence of a dissociation between reality beliefs and reality experiences suggests that the
 19 computation of these two variables might be distinct. One possibility is that this dissociation maps
 20 directly onto a distinction between first-order and second-order processes discussed above (Fig. 3).
 21 More concretely, this would mean that the quality of perceptual experiences is determined by first-

1 order sensory processes while beliefs about reality are determined by higher-order monitoring
2 mechanisms. Since these are two components of one reality monitoring system, both processes
3 would generally be in line with each other, but because they rely on different neural substrates, they
4 will sometimes dissociate.

5 In line with the idea that experience is determined by first-order processes, it has been
6 suggested that differences in layer-specific activations in early visual cortex might directly account
7 for whether something is experienced as real or imagined (Bergmann et al., 2019; Lawrence et al.,
8 2018; Lawrence, Norris, & De Lange, 2019). However, due to differences in target layers for
9 feedforward and feedback signals, the layer profile of externally and internally triggered signals is
10 very different (Fig. 1), making it unlikely that internally generated signals that are experienced as real
11 (e.g. hallucinations) could evoke the same laminar activity profile as externally presented signals.
12 Alternatively, the general strength and precision of sensory representations might determine the
13 'feel' of a sensory experience, with stronger and more precise signals feeling more real. In line with
14 the idea that first-order representations determine experience, hallucinations with insight, such as in
15 Charles Bonnet syndrome, have mostly been associated with spontaneous fluctuations in sensory
16 activation (Hahamy, Wilf, Rosin, Behrmann, & Malach, 2021), rather than dysfunctional frontal
17 systems.

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

1 However, as discussed above, first-order mechanisms alone seem to be unable to account
2 for all source confusions. For example, the existence of very weak sensory signals that are still
3 experienced as real as well as strong imagery that is still experienced as imagined suggests that
4 sensory representations alone cannot account for the feeling of reality. Accordingly, it has been
5 suggested that both conscious experience as well as knowledge about reality is determined by
6 higher-order frontal monitoring systems (Lau, 2019). The difference between the two might then be
7 how this system is employed: for instance, an automatic, implicit route might determine the *feeling*
8 of reality while a more deliberate, explicit route determines beliefs about reality. These two
9 processes might map unto separate neural systems within the frontal cortex. In terms of
10 metacognitive processes, a relevant distinction can be made between regions of agranular posterior
11 medial PFC (such as the perigenual anterior cingulate cortex; pgACC) and more anterior frontopolar
12 cortex. The former has been shown to track “implicit” or automatic confidence evaluations in simple
13 decisions (Bang & Fleming, 2018; Morales et al., 2018; Wittmann et al., 2016), occurring very early in
14 a trial (as revealed by simultaneous EEG-fMRI; (Gherman & Philiastides, 2018). In contrast,
15 frontopolar cortex has been found to track higher-order aspects of metacognitive evaluation,
16 including the need to make explicit judgments (Bang et al., 2020; Gherman & Philiastides, 2018;
17 Fleming, Huijgen, & Dolan, 2012), infer on the absence of stimulation (Mazor, Friston, & Fleming,
18 2020; Miyamoto, Setsuie, Osada, & Miyashita, 2018) and/or use metacognitive estimates for
19 adjusting decision-making strategy (Donoso, Collins, & Koechlin, 2014). Direct comparisons between
20 the functional anatomy of metacognition and reality monitoring will be required to understand how
21 these potentially distinct metacognitive processes contribute to different aspects of PRM.

22 Future research is also necessary to determine whether reality experience and belief are
23 determined by mechanisms at different levels of the system (e.g. by first-order sensory versus
24 second-order metacognitive processes respectively) or whether both are supported by a higher-
25 order monitoring system employed in different ways. One concrete route to dissociating these two
26 hypotheses would be by testing whether sensory signals that are experienced as real but believed to

1 be imagined, such as hallucinations with insight or lucid dreaming, are also accompanied by changes
2 within putative frontal reality monitoring systems and/or whether they reflect hyperactivation of
3 first-order representations.

4

5 **4. Conclusion**

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

17 In this paper we first discussed the differences between internally and externally triggered
18 sensory experiences which might be used to infer the source of sensory signals. We concluded that,
19 in contrast to veridical perception, imagination is associated with weaker and less precise sensory
20 representations, likely as a result of anatomical restrictions associated with running the visual
21 system backwards (Breedlove et al., 2020; Dijkstra et al., 2020; Domingo, 2018). Accordingly,
22 internally generated signals that are misattributed as real, e.g. hallucinations, are often associated
23 with hyperactivation in sensory areas (Waters et al., 2021). Furthermore, imagination is associated
24 with stronger cognitive control which renders it in some ways more predictable than veridical
25 perception, resulting in a feeling of agency that dissociates it from externally triggered signals
26 (Dijkstra et al., 2019; Haggard, 2017; Kosslyn et al., 2001). However, cognitive control of sensory

1 signals is also employed during veridical perception; via top-down attention (Dijkstra et al., 2019;
2 Gazzaley & Nobre, 2012). Furthermore, perception is more predictable than imagery in the sense
3 that it is both more constrained by our model of the external world and obeys sensorimotor
4 contingencies, although recent evidence suggests this might also be true of imagery (Brincat et al.,
5 2021; Gurtner et al., 2021). Together these observations suggest that while there are differences in
6 sensory signals and cognitive control, there is no clear neural signature that unambiguously
7 dissociates imagination from reality.

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

21 In conclusion, due to the overlap in neural machinery used for imagination and perception,
22 determining whether a sensory experience reflects reality is a non-trivial process. Here, we suggest
23 that perceptual reality monitoring might be implemented within a multi-level system in which
24 higher-levels located in frontal areas monitor sensory signal strength and cognitive control to
25 determine the source of a sensory experience. However, many open questions remain and future
26 research is necessary to fully characterize the different elements of this mechanism. A better

1 understanding of the mechanisms supporting perceptual reality monitoring will have important
2 implications for our understanding of general cognitive function as well as clinical cases of source
3 confusion.

4

5

6 **Acknowledgements**

7 N.D. is supported by a Rubicon grant from the Netherlands Organization for Scientific Research
8 (NWO) [019.192SG.003], P.K. is supported by a Wellcome/Royal Society Sir Henry Dale Fellowship
9 [218535/Z/19/Z], S.M.F. is supported by a Wellcome/Royal Society Sir Henry Dale Fellowship
10 [206648/Z/17/Z] and a Philip Leverhulme Prize from the Leverhulme Trust. The Wellcome Centre for
11 Human Neuroimaging is supported by core funding from the Wellcome Trust [206648/Z/17/Z]. For
12 the purpose of Open Access, the author has applied a CC-BY copyright license to any author
13 accepted manuscript version arising from this submission.

14

15 **Competing interests**

16 The authors declare that they have no competing interests.

17

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