How disrupted interoception could lead to disturbances in perceptual reality monitoring

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Reality and imagination are intermixed in all brains

Most people can experience things that are not there: when dreaming, remembering the past or imagining the future. Contemporary theories of brain function propose that such internally generated perceptual experience relies on similar neural machinery to that engaged by externally driven perception (Bastos et al., 2012; Friston et al., 2006). In line with this, several lines of research have demonstrated overlapping patterns of activity in sensory cortices during imagination and perception. For example, activity in early visual cortices can be used to decode the content of dreams (Horikawa et al., 2013; Siclari et al., 2017); sensory patterns are reinstated in early visual regions during memory (Bosch et al., 2014; Harrison & Tong, 2009); and decoders trained on visual cortex activity during perception can predict what people imagine (Albers et al., 2013; Lee et al., 2012; Ragni et al., 2020), especially when they imagine very vividly (Dijkstra et al., 2017). Given this overlap in neural activation patterns, how does our brain keep apart sensory activity representing reality from that representing imagination?

Perceptual reality monitoring – determining whether what we see is real or imagined - is prone to error in all brains (Dijkstra et al., 2022; Lau, 2019). The first experimental demonstration of confusion between imagination and perception in participants form the general population was reported by Mary Cheves West Perky in 1910 (Perky, 1910). Participants were asked to imagine objects while looking at a specific location on the wall. At the same time, Perky projected faint images of those same objects at the same location on the wall. Rather than noticing these projections, participants marvelled at how vivid their imagination was. Most subjects even expressed astonishment when Perky asked whether they had really imagined everything they saw (Perky, 1910, pp 431, 433). More recently, we demonstrated that healthy participants can also confuse vivid imagination for perception (Dijkstra & Fleming, 2023) and that they are unaware of these confusions, as indicated by high reported confidence (Dijkstra et al., 2024). Furthermore, there is a large group of people who regularly experience hallucinations, but have otherwise no disruptive symptoms and never seek any professional help (Beavan et al., 2011; Toh et al., 2020; Waters et al., 2012). What makes it that these cases of confusing imagination and reality are associated with preserved brain health whereas in other cases they are characteristic of debilitating psychiatric conditions? In this editorial, we speculate that the difference might be (partly) caused by differences in interoception.

Theories of perceptual reality monitoring without a heart

Several prominent theories of psychosis and hallucinations take a cognitive neuropsychiatric approach (David, 2004; Frith, 2008; Surguladze & David, 1998): they explain perceptual reality monitoring pathologies in terms of models of normal brain functioning. For example, one well-known theory proposes that hallucinations arise due to abnormalities in the brain's forward model which predicts the sensory consequences of actions. Disruptions in the forward model are hypothesized to lead to a failure to accurately predict the sensory consequences of internally generated thoughts and imaginations, leading them to be erroneously attributed to external reality (Fig. 1A; Frith, 2005). Another prominent family of theories explains hallucinations within predictive coding models of perception which state that we perceive the world through combining prior knowledge with incoming sensory evidence (Clark, 2013; Friston et al., 2006). Within this framework, perceptual reality monitoring failures are hypothesized to be caused by aberrant weighting of top-down prior knowledge versus bottom-up sensory evidence (Fig. 1B; Corlett et al., 2019; Fletcher & Frith, 2009; Sterzer et al., 2018). Other theoretical frameworks have focused more on high-level monitoring aspects, proposing that reality monitoring errors such as hallucinations are caused by sub-optimally functioning prefrontal circuits involved in source monitoring (Fig. 1C; Griffin & Fletcher, 2017; Simons et al., 2017).

More recent theories combine both perceptual and monitoring aspects and suggest that perceptual reality monitoring is implemented in a hierarchical system where prefrontal regions monitor perceptual processing to determine whether is source. Within these hierarchical frameworks, errors could arise at either perceptual or monitoring levels, or both (Dijkstra et al., 2022; Gershman, 2019; Lau, 2019).

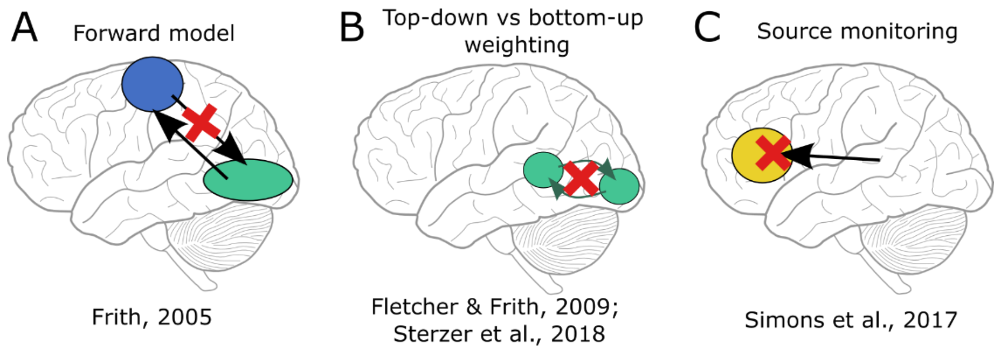

Figure 1. Overview theories perceptual reality monitoring failures. (**A**) Hallucinations are caused by abnormalities in the forward model that usually predicts the sensory consequences of actions. This causes self-generated sensory signals to be misattributed to an external source. (**B**) Over weighting of either top-down prior precision or bottom-up prediction error precision will lead to incorrect perceptual inferences about reality. Examples in (A) and (B) are for visual hallucinations (perceptual processing in visual cortex) but mechanisms are hypothesized to be the same for other modalities with the locus of the perceptual processing changed accordingly. (**C**) Disruptions in reality monitoring mechanisms located in prefrontal areas will lead to incorrect source attributions – confusing imagination for perception and vice versa.

While these frameworks neatly explain experimental results, it is unclear how they can explain the difference between reality monitoring failures in clinical and non-clinical populations. As Stephen Kosslyn already discussed in one of the first editorials of this journal, a process in the "normal" brain might not be "functionally the same with different types of meanings" (Kosslyn, 1996, p. 92). The most commonly reported difference between hallucinations in the general population and those in clinical groups is the emotional valence of the hallucinations (de Leede-Smith & Barkus, 2013). In one study, the negative emotional valence of the content of hallucinations in both clinical and non-clinical groups could predict the presence of a psychotic disorder with an accuracy of 88% (Daalman et al., 2011). Most of the aforementioned perceptual reality monitoring theories do not explicitly consider the role of emotional valence. However, the neural mechanisms responsible for perceptual reality monitoring failures with high emotional valence might be different to those underlying those that are emotionally neutral. If this is indeed the case, not incorporating the influence of emotions will reduce the clinical relevance of these theories. Indeed, if most hallucinations in clinical populations are negatively valanced (Strawson et al., 2022), then maybe there is something fundamental about the emotional nature of hallucinations that is key to understanding their core aetiology. In the remainder of this editorial, we propose how disruptions in interoceptive processing might cause the unique characteristics of clinical cases of reality monitoring failures.

The role of interoception in emotional processing

Emotions are coupled to interoceptive signals from within the body (James, 1884; Nummenmaa et al., 2014; Tsakiris & Critchley, 2016). As James put it: "Without the bodily states following on the perception, the latter would be purely cognitive in form, pale, colourless, destitute of emotional warmth" (James, 1890, pp. 449–450). Interoception is defined as the process by which the nervous system senses, interprets, and integrates signals originating from within the body, providing a moment-by-moment mapping of the body's internal landscape across conscious and unconscious levels (Khalsa et al., 2018). Empirical evidence highlights the importance of interoceptive signals in emotional processing (Critchley & Garfinkel, 2017). For example, the accuracy with which interoceptive signals are sensed is associated with ratings of emotional intensity (Wiens et al., 2000) and emotional regulation success (Füstös et al., 2013; Garfinkel & Critchley, 2016), while mood and anxiety disorders have been linked to failures to anticipate changes in interoceptive signals (Paulus & Stein, 2010).

The brain receives interoceptive signals from many different bodily systems (Nord and Garfinkel, 2022) but to date, most interoceptive research has focused on the heart. Interoception can be delineated into different dimensions, including the nature of the afferent signals (e.g. such as heart rate and heart rate variability), the neural processing of interoceptive signals (e.g. such as the heartbeat evoked potential for the cortical processing of heartbeats), the accuracy with which afferent signals can be sensed, and the potential for afferent signals to change the way stimuli are processed (Suksasilp & Garfinkel, 2022).

Disruptions in interoceptive processing in perceptual reality monitoring disorders

Schizophrenia, associated with perceptual reality monitoring failures in the form of hallucinations in 60 to 80% of diagnosed patients (Bentall et al., 1989; Wing & Nixon, 1975), is also associated with changes in cardiac signals as well as the interoceptive processing of these signals. Compared to controls, individuals with schizophrenia exhibit increased heart rates and reduced heart rate variability (HRV), both of which cannot be explained by medication (Akar et al., 2015; Ardizzi et al., 2016; Chung et al., 2013; Clamor et al., 2016; Mathewson et al., 2012). Furthermore, resting-state heart rates in individuals with a high risk for psychosis positively correlate with subthreshold psychotic symptoms (Kocsis et al., 2020) and HRV negatively correlates with the severity of positive symptoms in patients with schizophrenia (Cella et al., 2018; Kimhy et al., 2017), again also after controlling for effects of medication.

In terms of interoceptive processing, individuals with schizophrenia consistently show reduced interoceptive accuracy in detecting their heartbeats (Ardizzi et al., 2016; Jeganathan et al., 2024; Koreki et al., 2021; Torregrossa et al., 2022), even more so than individuals with other psychiatric disorders (Critchley et al., 2023). Schizophrenia is also associated with reduced confidence in interoceptive reports (Critchley et al., 2023), although interestingly, metacognitive insight, which reflects the association between confidence ratings (lower in patients) and (impaired) accuracy, remains intact (Critchley et al., 2023; Torregrossa et al., 2022). Interoceptive sensibility - the self-rated sensitivity to bodily sensations - also seems to be different in schizophrenia: with some studies reporting increased sensibility (Barbato et al., 2021; Koreki et al., 2021; Torregrossa et al., 2022) and others reporting decreased sensibility (Critchley et al., 2023) compared to controls. Findings concerning the relationship between interoceptive processing and symptom severity are mixed: in one study, interoceptive accuracy was negatively correlated with positive as well as negative symptoms in schizophrenia, while interoceptive metacognition was specifically negatively correlated with positive symptoms, especially delusions. (Koreki et al., 2021). In contrast, in another study, interoceptive accuracy was positively correlated with delusions of grandeur (Ardizzi et al., 2016), and other studies found no relationship between interoceptive accuracy and symptom severity (Torregrossa et al., 2021; Jegenathan et al., 2024). Finally, individuals with schizophrenia also display aberrant heartbeat evoked potentials (Koreki et al., 2024), suggesting altered heart-brain interactions.

Besides schizophrenia, other disorders associated with reality monitoring failures also display changes in interoception. For example, both patients with frontotemporal dementia, which is associated with psychosis in 13-14% of cases (Velakoulis et al., 2009), as well as individuals with Parkinson's disease (PD), which is associated with visual (28.2%) and auditory (8.9%) hallucinations (Eversfield & Orton, 2019), also show reduced interoceptive accuracy (Hazelton et al., 2023; Salamone et al., 2021; Santangelo et al., 2018). More research is needed to determine whether these changes are predictive of reality monitoring symptoms or are related to other symptoms.

Explaining perceptual reality monitoring failures through interoception

Taken together, schizophrenia, as well as other conditions associated with failures in perceptual reality monitoring, are associated with both a chronically elevated low-grade arousal state (as indexed by the increase in resting heart rate and reduction in HVR) as well as a reduced precision in interoceptive processing (as indexed by lower interoceptive accuracy). These changes have the potential to alter any of the processes thought to be essential for successful perceptual reality monitoring. Firstly, changes in cardiac signals might change the content of perception. An elevated arousal state is associated with increased processing of threat-related signals, often at the expense of other types of stimulus processing (Garfinkel & Critchley, 2016). In the case of chronically elevated arousal, this could lead to pervasive biases in sensory sampling towards threat-related signals (Fig. 2A; Allen et al., 2022).

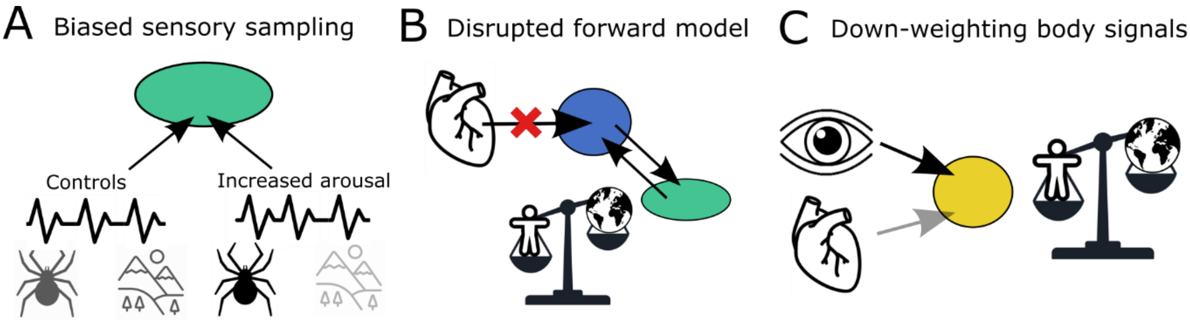

Figure 2. Possible influences of interoception on perceptual reality monitoring. (**A**) An elevated low-grade arousal state, characterized by increased heart rate and reduced HRV, could bias sensory sampling towards threat-related signals, changing the content of perception. (**B**) Disruptions in interoceptive processing could lead to disruptions in forward modelling, leading to an incorrect bias towards attributing self-generated signals to external reality. (**C**) Reduced precision of interoceptive signals could lead to down-weighting body signals and biasing high-level inferences towards exteroceptive signals, leading again to an incorrect bias towards external attribution.

Furthermore, there is evidence that decreased interoceptive accuracy is associated with a decrease in the brain's ability to accurately predict the sensory consequences of actions. Specifically, interoceptive accuracy is found to be positively correlated with sense of agency (Koreki et al., 2022). The sense of agency - the feeling of being in control of one's actions and their consequences - is thought to be created by comparing the brain's predicted sensory consequences of actions with the observed sensory consequences through the forward model. If the predicted and observed sensory signals match, the brain attributes the sensory consequences to the self, reinforcing the sense of agency (Haggard, 2017). As mentioned above (Fig. 1A), one prominent theory of psychosis states that hallucinations are caused by disruptions in accurately predicting self-caused sensory signals, leading to a reduced sense of agency and an increased tendency to misattributed signals to external causes (Frith, 2005; Haggard, 2017). The decrease in interoceptive precision found in schizophrenia and other disorders might therefore somehow disrupt the forward model's predictions, leading to an increase in attributing internal sensory signals to external reality (Fig. 2B).

Finally, the increased uncertainty caused by disruptions in interoceptive processing could lead to pervasive failures in reality monitoring due to the brain's attempt to resolve this uncertainty (Yao & Thakkar, 2022). Interoceptive and exteroceptive signals are assumed to be integrated at higher levels of processing based on their relative precision (Ainley et al., 2016; Ondobaka et al., 2017; Pezzulo et al., 2015). Therefore, reduced interoceptive precision could bias inference towards the exteroceptive modality, leading to attributing these threat-related body signals to external reality instead of the internal bodily states (Fig. 2C). Over time, this could lead to a global and pervasive feeling of something ominous pending (Mishara, 2010; Pezzulo, 2014). In an attempt to discover the cause of this feeling, the brain might furthermore ascribe more salience to neutral external stimuli, eventually leading the world-model to move increasingly further away from consensual reality towards a fear-based model of reality (Corlett et al., 2019; Jardri & Denève, 2013; Yao & Thakkar, 2022). Over time, the content of internally generated imagination will also align to this world-model. Importantly, emotionally valent imagery is experienced as more vivid (Bywaters et al., 2004; Mathews et al., 2013) and more vivid imagery is more likely to be mistaken for reality (Dijkstra & Fleming, 2023; Shine et al., 2015), leading to more emotionally valent perceptual reality monitoring failures.

Conclusion

To summarize, while all brains sometimes confuse imagination and reality, perceptual reality monitoring disturbances in psychiatric conditions tend to be associated with a much higher emotional valence. Here, we hypothesized that this difference could be caused by disruptions in interoception: an increased arousal state combined with decreased interoceptive precision could lead to biased sensory sampling, disruptions in forward-modelling and a bias towards attributing signals to external causes, which together could lead to vivid and emotionally valent hallucinations.

It is important to emphasize speculative nature of this piece. The goal of this editorial is to function as a starting point for future research in this area and to highlight the importance of the body when trying to explain core processes of the mind. For example, the interoception hypothesis outlined here suggests that medication that targets bodily dysregulation might also reduce hallucinations. There is preliminary evidence that this might indeed be the case (Peng et al., 2024). However, the effectiveness of this intervention might depend on the timing: once the internal world-model has been changed, contradictive interoceptive signals might have less of an effect (Jardri & Denève, 2013). Future research is needed to further test to what extent disrupted interoception could lead to disturbances in perceptual reality monitoring.

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