Authors' Response

Still PADing along: Perception and attention remain key factors in understanding complex visual hallucinations

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Abstract: Commentators agree that the Perception and Attention Deficit (PAD) model is a promising model for accounting for recurrent complex visual hallucinations (RCVH) across several disorders, though with varying detailed criticisms. Its central tenets are not modified, but further consideration of generative models of visual processing and the relationship of proto-objects and memory systems allows the PAD model to deal with variations in phenomenology. The commentaries suggest new ways to generate evidence that will test the model.

R1. Introduction

We first developed the Perception and Attention Deficit (PAD) model to understand the constraints in the visual system that led many, but not all, of our patients with dementia with Lewy bodies to experience visual hallucinations of a particular character. It was with some trepidation that we extended its coverage to recurrent complex visual hallucinations (RCVH) in other disorders, and subjected it to peer commentary from colleagues whose expertise in their fields far exceeds our own. We are extremely appreciative of their constructive engagement, challenges, elaborations, developments, and occasional corrections.

We have organised the response to commentaries by the key predictions of the PAD model from section 7.3 of the target article. For ease of reference, Table R1 indicates which commentators have focussed on which areas.

R2. Scope of the PAD model: Is there more than one syndrome of repetitive complex visual hallucinations?

In the target article, we set out to account for "repetitive involuntary images of people, animals, or objects that are experienced as real during the waking state but for which there is no objective reality" (sect. 2, para. 1). We agree with **Castelo-Branco** that it does not apply to phenomena such as polyopia or tesselopsia, although it does apply to palinopsia, given that this is simply a hallucination over a short timescale. However, this leaves the question of whether the PAD model applies to all hallucinations that fit the definition above. In answering this question, it is important to bear in mind that the visual system is, in important ways, probabilistic rather than deterministic (Friston 2002b). There are never certainties to be found. Therefore, the search is for factors that influence the probability of RCVH, not ones that always (or never) cause them. Hence, contrary examples to the PAD model will always be available. It is the balance between consistent and inconsistent evidence that is critical.

Samsonovich makes the point that whether RCVH across disorders are considered the same or different depends upon the basis for the comparison. In his example, social agency groups the visual hallucinations of schizophrenia with the auditory hallucinations of that disorder, not with the visual hallucinations of other disorders.

ffytche similarly uses different bases for comparison to

Table R1. *Themes addressed by commentators*

Commentator	Scope of the PAD model	Cognitive and sensory risk factors	Factors influencing phenomenology	Physiological constraints
Badcock & Maybery		✓		
Behrendt		✓		✓
Carroll & Carroll			✓	
Castelo-Branco	✓	✓	✓	✓
Dolgov & McBeath		✓		
Dror			✓	
ffytche	✓		✓	
Friston		✓		✓
Gottesmann			✓	✓
Halliday		✓		✓
Ingle			✓	
Kirov				✓
Mast			✓	
Morrison & David	✓	✓	✓	
Pace-Schott				✓
Samsonovich	✓	✓		
Smythies	✓			✓
Spencer & McCarley		✓		✓
Tadin et al.		✓		

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group together the simple and complex hallucinations in eye disease. He argues for two separate visual hallucination syndromes, with the complex visual hallucinations of eye disease being distinct from those of other disorders, and suggests that we had to do some Procrustean violence to the evidence to make them appear similar. Without wishing to act as Lycomedes to his Theseus,[1] we believe that there are sound grounds for maintaining the original grouping together of all RCVH, at least until more data become available.

To support his view, **ffytche** cites four differences between the hallucinations of eye disease and what he groups as the PAD disorders. Compared to the PAD disorders, hallucinations in eye disease tend to be associated with simple hallucinations, to recover, to be more bizarre, and to not be associated with other psychiatric symptoms.

One major problem with the suggestion that RCVH and other visual hallucinations in eye disease stem from the same cause, namely de-afferentation, is that rates of complex hallucinations in eye disease are much lower than rates of simple hallucinations (Table 1 of the target article). This suggests that de-afferentation alone is an insufficient explanation. In the target article's section 3.1, we argued for two hallucinatory syndromes based on the double dissociation between the rates of simple and complex hallucinations in disorders of visual input and those with more distributed pathology. Double dissociation is the classic, though not infallible, neuropsychological argument for separable mental phenomena, so perhaps the separation of simple from complex hallucinations is not so Procrustean.

Because the people who do have complex hallucinations tend to be more cognitively impaired and prone to fatigue (Table 2 of the target article; but see Menon [2005] for some contrary evidence), consistent with the PAD model, our present inclination is to continue to group them within this, though perhaps in a boundary zone with de-afferentation cases (Fig. R1). If this hypothesis is correct, the overlap group will have both simple and complex hallucinations, as **ffytche** reports.

This leaves the other distinctions that **ffytche** highlights. We have already suggested the progressive visual loss of eye disease as the reason why visual hallucinations become less common as time goes on in those disorders (target article, sect. 7.5.2). We think distorted faces, bizarre figures, and machines are conceptually variations on object representations (as are all other complex hallucinations), rather than variations on simple hallucinations. We will propose later how bizarreness might be accounted for within the PAD framework.

Regarding the association with other symptoms, our present position is that of parsimonious lumpers. Because we believe that, across syndromes, the commonalities of RCVH, as symptoms, outweigh their differences, our position is that they do have a common cause until proven otherwise. Hence, as we discuss in section 5.3, associated symptoms reflect different causes. Circumstances will therefore determine which grouping RCVH are best lumped with. To clinicians in an eye clinic or in mental health services, they may be most helpfully viewed as part of the spectrum of visual abnormalities following de-afferentation or as part of a personally relevant psychosis, but to a researcher trying to understand why they occur in only some people, the PAD model may have more to offer.

As **Morrison & David** say, evidence from direct comparisons across disorders is needed.

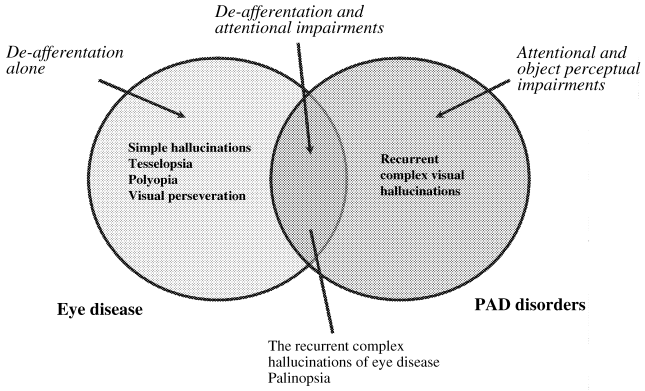


Figure R1. Relationship between the phenomenology of hallucinations in PAD and de-afferentation disorders.

R3. Cognitive and perceptual constraints that increase the risk of RCVH

We predicted that the frequency of RCVH varies with the frequency of the coexistence of attentional dysfunction and object perception impairments.

Commentators **Badcock & Maybery**, **Dolgov & McBeath**, **Friston**, **Halliday**, **Morrison & David**, and **Spencer & McCarley** share our focus on attentional and perceptual factors, though there is variation in the significance attached to these.

R3.1. The role of attentional factors

Spencer & McCarley present data from a reanalysis of their 2004 study on hallucinations in schizophrenia (Spencer et al. 2004). They report a lack of relationship with the presence of visual hallucinations (VH) and clinical ratings of attentional function (except poor impulse control), or with reaction time or error rates on a visual task that involved responding or not responding to a stimulus that was, or was not, a gestalt square. In contrast, there was a clear relationship between occipital gamma band oscillations and visual hallucinations. Spencer & McCarley conclude that this argues against the application of the PAD model to schizophrenia.

However, before attaching high weight to this evidence, we would like to enter several caveats. First, we suggest that attentional impairment alone will not be associated with RCVH (sect. 7.4.1 of the target article). It is clear from Figure 1 in Spencer et al.'s (2004) paper that all of the people with schizophrenia have impaired attentional performance. In order to reject the PAD model, they would need to show that poor perceptual performance in the context of this generally poor attentional performance did not distinguish between the hallucinators and non-hallucinators. Furthermore, Figure R2 shows the results from a small pilot study of ours looking at visual and attentional performance in hallucinating and non-hallucinating patients with dementia. Impaired performance is seen only on some visual tasks – those testing higher-order object recognition. Whether the gestalt recognition of a square would be that type of task, or whether it has more in common with simple visual recognition tasks where there is less difference between hallucinating and non-hallucinating groups, is not clear to us.

Morrison & David and **Tadin**, **Wong**, **Mebane**, **Berkowitz**, **Trott & Park** (**Tadin et al.**) ask for greater

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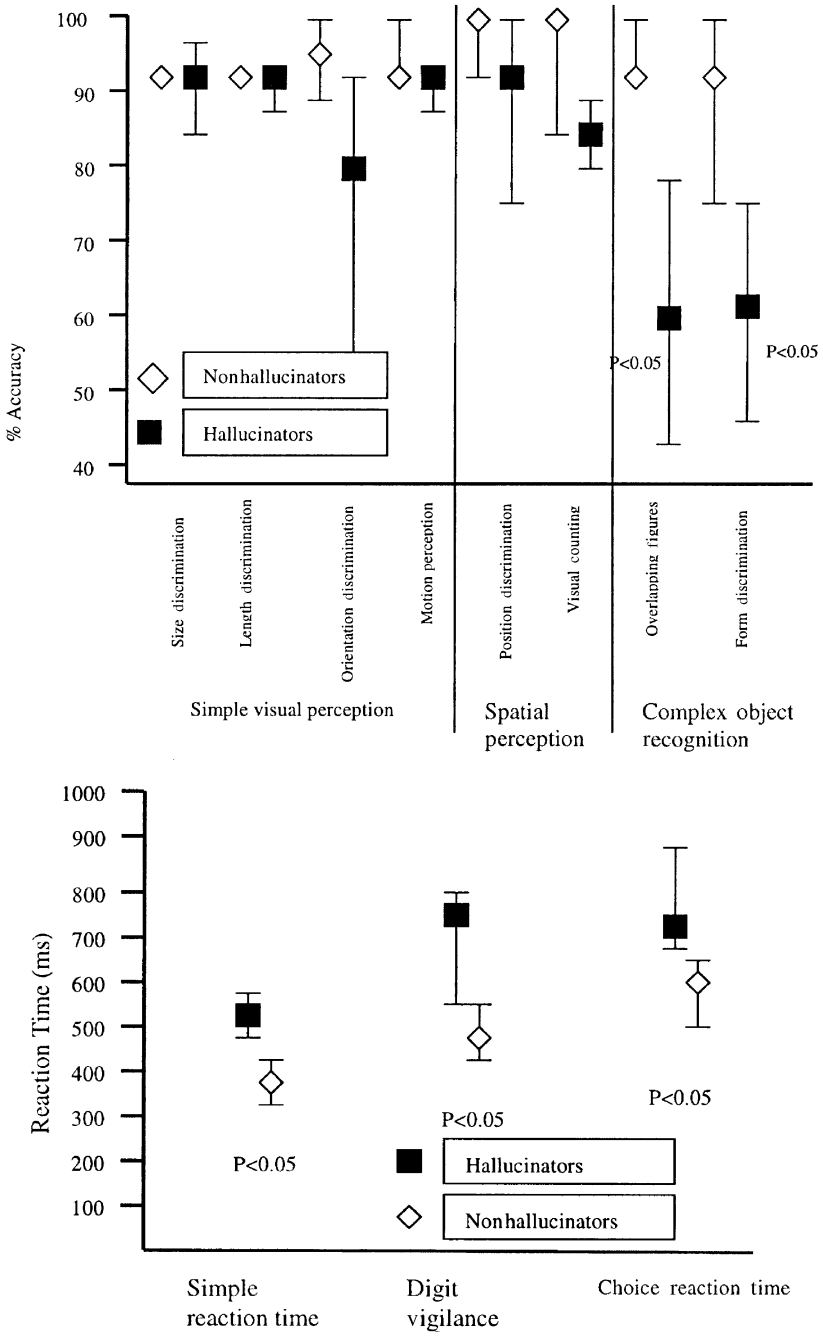


Figure R2. Data from a pilot study comparing hallucinating (N = 7) and non-hallucinating (N = 13) patients with dementia on a range of attentional and visual perceptual tasks. Median scores and interquartile ranges are shown (Bowen, McKeith, Mosimann & Collerton, unpublished data).

specificity in which particular aspects of attention are impaired. This perfectly reasonable request points out the very variable present data. The studies that we featured in the target article's Figure 4 used well over 160 separate measures, very few of them more than once. Additionally, many patient groups with high levels of RCVH do poorly on all attentional tasks. Thus, there is not the experimental evidence to support any specific area of attentional impairment, though we argue on theoretical grounds for impaired dynamic binding. We agree that gathering more specific data is a necessary task.

Morrison & David and **Castelo-Branco** also question the attentional focus that we suggest is important for the perception of the hallucination. As counter-evidence, Morrison & David cite patient reports of seeing hallucinations while doing other activities, and the lack of effect of attending to other things on eradicating active hallucinations. (Menon [2005] similarly reports that this is an infrequently used strategy.) Castelo-Branco additionally queries why hallucinations should be more frequent in areas of the visual field where vision is impaired.

Both of these possibilities need further exploration, particularly because the evidence is not consistent – most reports suggest that hallucinations are seen in the centre of the visual field regardless of aetiology (target article, sect. 4.1.2). However, neither is yet a fatal objection in our eyes.

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There is a well-established distinction between being apparently aware of an object in the visual environment and attending to it (see, e.g., Rensink 2002). The models of scene perception that we draw upon (target article, sect. 7.1, Fig. 3) are based upon the extensive evidence of change blindness and other phenomena that highlight this distinction. Since a key feature of the model is that hallucinations are incorporated into the abstracted scene perception (sect. 7.3), it would actually run counter to our hypothesis if patients did not sometimes appear to be aware of them when attending to something else. Data on attentional function during hallucinations is needed to resolve this issue.

Turning to the patients' lack of use of the coping mechanism of attending to something else, we think that it is equally plausible that they fail to do this because it is hard to attend to something else when hallucinating – the opposite of **Morrison & David**'s interpretation, but entirely in keeping with the PAD model. Further evidence is needed.

R3.2. The role of object perception

Tadin et al. ask that we specify the level at which the primary impairment of the visual system lies. It seems probable that, given the highly interactive nature of visual processing with significant forwards, backwards, and lateral connectivity, there is no single locus of abnormality. However, we would locate functional impairments both upstream and downstream of image generating areas. If dysfunction extends into the image generating areas – for example, central loss of colour vision – hallucinations will reflect this. Loss of the ability to generate images would also abolish hallucinations.

Morrison & David stress the thinness of the evidence for object perception impairments compared to attentional impairments in delirium in our citations. However, Mach et al. (1996) showed specific impairments in Object Assembly and Visual Reproduction in patients who were matched for scores on the Mini Mental Status Examination (MMSE), suggesting that the evidence is not entirely lacking. We agree that delirium has many potential advantages as a disorder to study, though there are some practical difficulties with cooperation and consent. Looking at the existing literature, Inouye et al. (1993) showed in a proportional hazards analysis that, out of 15 potential risk factors for the development of delirium, the only significant ones were severe illness (relative risk [RR] 3.5), high blood urea nitrogen/creatinine ratio (a marker for dehydration, RR 2.0), and *cognitive* (RR 2.8) and *visual* (RR 3.5) impairments. In the absence of the PAD model, it would be difficult to explain *a priori* why these two latter risks should stand out.

R3.3. The need for combined impairments

Castelo-Branco echoes our comments that attentional and perceptual impairments co-vary in Figure 4 of the target article (sect. 7.4.1), and that direct rather than meta-analytic tests would be preferable. Covariation of impairments reflects the nature of dementing illnesses, in which the severity of specific cognitive impairments correlates almost by definition. Rather than using analysis of covariance to control for this, as he suggests, a more powerful test is to look at the rates of RCVH in patients with either attentional or perceptual impairments. Section 6.3 of the target article indicates that the rates are low in both these groups.

The need for combined impairments is supported by analogy with **Badcock & Maybery**'s HEAR model for auditory hallucinations in schizophrenia. In slightly different language, this also posits the need for a combination of attentional binding (intentional inhibition) and sensory impairments (context binding of auditory sensation). In contrast to the PAD model, it has directly supporting data (Waters et al., in press). Badcock & Maybery suggest, and we agree, that consistent attentional impairments coupled with different modally specific perceptual impairments could account for the propensity within some disorders (e.g., schizophrenia, delirium, and dementia with Lewy bodies) for hallucinations in more than one modality. Consistent with this, all these disorders have pathology that is, to varying degrees, distributed across several perceptual systems. Functional imaging combined with tests of specific cognitive areas would allow this to be tested.

Friston uses empirical Bayesian modelling of visual perception to demonstrate the need for interactive impairments in top-down priors (proto-objects, as we have called them) and bottom-up sensory processes to produce hallucinatory perceptions. Though these models do not address attention per se, since attention acts to increase top-down activation of a specific prior, an attentional impairment will cause lesser activation of the correct prior. Bayesian approaches also explicitly model the effects of context – the scene representation – on perception. Given that the PAD model couples lesser activation of the correct prior with normal or, over time, excessive activation of a specific incorrect prior, it can provide an account of how excessive top-down weight may interact with sensory impairments, as hypothesized by **Tadin et al**.

Staying with mathematical models, **Dolgov & McBeath** use signal detection theory to show that hallucinatory perceptions need not always be associated with relatively poorer perception. This is a striking reminder of the multiplicity of ways in which a complex, dynamic set of systems may produce an erroneous result and usefully broadens our perspective to include not just deficit models. However, this specific relationship is mainly likely when the noise and true distributions are highly overlapping (their Fig. 1). Both erroneous "hits" and "misses" are improbable in normal sensory function; otherwise, we would not have functional sensory systems. We therefore suspect that these distributions are usually highly separated. They do overlap when perception is impaired, hence the association within the PAD model of perceptual impairments and hallucinations. In this case, higher rates of hallucinations may be a trade-off to reduce agnosia. This is a fascinating possibility that merits further investigation.

Such statistical models may provide the answer to **Behrendt**'s wish for us to explain *precisely* how top-down and bottom-up processes interact within PAD. Static words and diagrams, no matter how eloquent or how carefully drawn, cannot convey the realities of the intensely dynamic systems of the brain. However, given the highly nonlinear properties of these systems, clarifying their interaction is not trivial. It is not clear that, for example, an increase in the severity of object perceptual impairment for a given severity of attentional impairment, or vice versa, will necessarily lead to an increase in the frequency of hallucinations in an individual case. The striking linear relationship in the target article's Figure 4 may simply reflect a group average rather than each individual case.

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Halliday draws attention to Diederich et al.'s (2005) model for visual hallucinations in Parkinson's disease. This model envisages recurrent hallucinations resulting from a disturbance in a conceptual space defined within Hobson's AIM (Activation, Input, and Modulation) model of consciousness (Hobson et al. 2000). Hobson sees conscious experience as modulated by *activation* (speed of information processing), *input* (the balance between external and internal stimuli), and *modulation* (the dynamic integration of these over time). Diederich and co-authors suggest that hallucinations are most likely when the balance of input is disturbed, with activation and modulation acting as influences. Consistent with the PAD model, the key focus is on the interactivity of the visual system, though the PAD model gives a somewhat more elaborate account of the nature of the impaired interactivity.

R3.4. Summary of cognitive and perceptual risk factors

In our estimation, the balance of the evidence continues to point towards a dysfunctional interaction between top-down and bottom-up visual processes as the genesis of visual hallucinations. Though the exact contribution of each of these may vary from person to person, and there may be occasions when either alone may produce hallucinations, we would maintain that, in practice, such a dysfunction is much more likely when there are impairments in both.

R4. The phenomenology of RCVH – What is hallucinated, and where and when

We hypothesized that the phenomenology of RCVH primarily reflects the nature of scene perception: in particular, the role of scene-based expectations in influencing the attentional focus (what), and environmental and temporal cues in triggering a scene representation that biases processing towards a hallucination (where and when).

Dror, **Carroll & Carroll**, **Friston**, and **Smythies** agree that we are right to place the experience of hallucinations within a dynamic system that actively seeks to reconcile top down representations and bottom-up sensory input within the context provided by the visual environment and its history.

R4.1. Bizarreness and relationship to the environment

Castelo-Branco, **ffytche**, **Morrison & David**, and **Samsonovich** question our characterisations of RCVH as generally in keeping with the environment (though see Merabet et al. 2004 for some examples in which there are very clear links). Even accepting Morrison & David's factual correction, the safest summary of the evidence is that some are in keeping and some are not. Section 1 and Table 3 of the target article show that there are sizable numbers of exceptions to all of the common features of hallucinations. We used the consistencies with the environment to guide us in developing the PAD model. Can the same framework also account for bizarre hallucinations that apparently lack a relationship? We believe that it can if it takes account of the specific effects of eye disease on visual context and visual input.

Empirical Bayesian models of visual processing, described by **Friston** as most consistent with the PAD model, see perception as the least erroneous match between the actual state of visual inputs and a prediction of those visual inputs deriving from an internal model of the visual environment. In eye disease, visual input is necessarily distorted. Hence, the least bad match may be an internally generated visual environment, which, even though bizarre, is still the best reconciliation with actual activity in occipital cortex. In contrast, visual abnormalities in dementia and other illnesses stem from pathology in higher association cortices. This suggests that occipital function is relatively undisturbed and the least erroneous match will be prosaic. One might add to this the role of the scene representation, or contextual information in generative terms. If this is reduced in eye disease, as we suggested in the target article's section 4.1.2 to account for the relatively high prevalence of panoramic hallucinations, this may also place less constraint on bizarre visual experiences. Thus, the PAD model may not be falsified by variations in bizarreness.

R4.2. Individual differences

Behrendt, **Carroll & Carroll**, **Dror**, and **Samsonovich** stress that phenomenology not only depends upon general expectancies from the environment, but also needs to take account of individual goals, desires, and wishes. Although we did acknowledge this area within the PAD model (see the extreme left box of Fig. 3 and sect. 7.4.1 in the target article), our primary focus was on commonalities of experiences. We are therefore grateful for their proposals.

Carroll & Carroll introduce the idea of the proto-object of rest from catatonia, suggesting that one proto-object may, over time, become the default perception when others are not active. **Behrendt** argues eloquently for an understanding of the person's central concerns and wishes, and their potential link to the development of visual hallucinations and further symptoms. Consistent with these roles of top-down processes in the generation of personally relevant hallucinations, ffytche et al. (2004) have reported a fascinating case of a woman with alexia who knew the meanings of text hallucinations which she could not read.

Samsonovich argues that the generation of visual hallucinations in schizophrenia stems from the same roots as auditory hallucinations in a failure of integration of representations of self and others in the mind. He suggests that abnormalities in theory of mind in schizophrenia in conjunction with the PAD model would suggest asocial rather than all too personally relevant hallucinations. We are not altogether convinced of this. It seems equally plausible that aberrant theory of mind would lead people to imbue non-socially relevant stimuli with social relevance, as the other way around. Reasoning only from people with schizophrenia, or indeed any single hallucinatory syndrome, seems to us risky. People with schizophrenia receive that diagnosis in part because of their interpretations of their hallucinations. To argue that these interpretations are causal may prove to be circular. As with so many of these questions, we need more evidence before we can choose between these alternatives.

We fully accept that individual factors are critical in understanding the personal experience of visual hallucinations, though within these we place a high premium on the person's post hoc interpretations (Collerton & Dudley 2004). Gauntlett-Gilbert and Kuipers (2005) and Menon (2005) have shown that distress is not so much due to the phenomenology of the hallucination, but to what the hallu-

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cinator thinks will be the personal consequences of having hallucinations – going mad, for example.

Mast draws attention to the similarities between internally generated images and visual hallucinations. Individual differences in images may provide a route for investigating variations in hallucinations. For example, patients with distorted hallucinations might also have distortions in volitional images.

R4.3. Relationship to memory systems

As **Halliday** and **Ingle** point out, one area that needs further development is the proto-object. As this is conceptualised, it is a potential rather than a real thing, corresponding to potential brain states rather than actual ones. Although interference experiments can clarify this in psychological terms, this unreality has serious implications for the physiological testability that Halliday asks for. It highlights the gap between psychological concepts and the limited temporal, spatial, and neurochemical and neuroanatomical resolution of the techniques that we presently have.

However, we can speculate on which systems hold these potentials. Several commentators produce evidence that procedural rather than episodic memory systems are primarily related to visual hallucinations. **Ingle** uses the qualities of hypnagogic hallucinations, hallucinations induced by blindfolding, and visual persistences to argue that these are canonical representations. He points out that hypnagogic hallucinations are not diminished in people with severe episodic memory impairments, suggesting these are stored in procedural rather than declarative memory systems. This may answer **Morrison & David**'s query why hallucinations are not always familiar if they are biased by the environment. If the activated representation is procedural, its familiarity will depend upon the level of abstraction that it is based on.

This distinguishes hallucinations from the episodic memories replayed by stimulation of the medial temporal lobes, and supports **Carroll & Carroll**'s points that, in posttraumatic stress disorder, flashbacks are episodic memories, and that patients may know that images are not genuine but feel that they are. We have argued (sect. 6.5) that flashbacks are not the same as hallucinations.

If hallucinatory images are generated from procedural rather than episodic memories, this might argue against models that see a causal link between lack of insight or source misattribution. These are features of all procedural memories, and, as **Mast** says, images are rarely confused with percepts. Further grounds for caution come from the consideration of bizarreness and insight in eye disease. If we accept that hallucinations in eye disease are generally bizarre, then there should be more likelihood of recognition of these as hallucinations from the start. In reality, though, insight seems to develop gradually (Menon 2005).

R4.4. Hallucinations and the phenomenology of dreams

Gottesmann, **Pace-Schott**, and **Smythies** draw attention to the overlap between the phenomenology of dreams and visual hallucinations. For the reasons that we outline in section 6.4 of the target article, we do not think that hallucinations are simply waking dreams, even in an attenuated form as Gottesmann suggests. We agree with Pace-Schott, however, that there is much to be learnt from the similarities between the two in the constraints that they place on the visual system. His proposal of "boot strapping" self-organisation within dreams is very appealing and may provide a means of further investigating individual variation in hallucinations. It strikes us that, phenomenologically, the visual experience of dreams is most like the hallucinations of eye disease (bizarreness, full field), despite the different physiology. As with eye disease, there is an impoverishment of the visual environment in the case of dreams by eye closure and low light. Dreams and visual hallucinations produced by blindfolding (**Ingle**) may therefore allow a closer investigation of the effects of contextual scene representations on hallucinatory content.

R4.5. Summary of phenomenology

The PAD model was developed to account for the phenomenology of visual hallucinations at the group level, not to predict the experiences of specific individuals. However, it does provide a framework that can be extended to account for variations, as we have illustrated with bizarreness. Still, before proceeding too far along this road, we do need more evidence to support its core propositions, though there is a degree of support from commentators for them.

R5. Physiological constraints that lead to complex visual hallucinations

The PAD model proposed that because object-based attention depends primarily upon the function of lateral frontal cortex, and because object perception depends primarily upon the ventral visual stream, disorders associated with high levels of RCVH will have a common end stage of both lateral frontal cortex and ventral stream dysfunction. This might be due to intrinsic or extrinsic pathology.

R5.1. Location of abnormalities in the visual network

Behrendt, **Carroll & Carroll**, **Friston**, **Halliday**, and **Smythies** agree that disturbances in a distributed brain network underlie the generation of visual hallucinations. Although most commentators recognise that we have identified the correct ventral system, several suggest that the primary causes of dysfunction lie elsewhere: Behrendt, in the coordinating thalamic reticular system; **Spencer & McCarley**, in hyper-excitability of sensory cortex; and Smythies, in general abnormalities of synaptic connectivity. However, as we argued in the target article, these may well be secondary to abnormalities in our areas of interest or, as Friston suggests, have their functional effect in these areas. Nor are they necessarily exclusive. Careful imaging and other studies will produce the data to distinguish between these possibilities.

Halliday rightly points out the overlap between some of the common physiological factors that we have identified, and those of Diederich et al. (2005). However, with the wider range of disorders that we have considered, we would regard some that they proposed (abnormalities in the ponto-geniculo-occipital system, fluctuating vigilance, intrusion of REM dreaming imagery, and overactivity of the mesolimbic systems) as neither necessary nor sufficient – if there are perceptual and attentional impairments and their underpinning biological dysfunctions.

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R5.2. The role of cholinergic function

Friston and **Smythies** both agree that the role we assign to cholinergic dysfunction in modulating the uncertainty in top-down activity is predictable from models of normal cholinergic function, with the proviso from Smythies that this can be more closely specified as more is understood about the contributions of muscarinic and nicotinic receptors. We accept also that only a proportion of projections from the laterodorsal tegmental nuclei are cholinergic, though this does not greatly weaken the overall point that cholinergic function is intimately connected with many aspects of the visual system.

To resolve the question of how broad-spectrum muscarinic antagonists induce visual hallucinations, we need subtype selective drugs. Receptor knockout animals that can be subjected to appropriate tests of visual processing may also be useful. From the limited knowledge available on the distribution and function of different muscarinic receptor subtypes in mammalian brain, M4 antagonist activity may be most relevant to the induction of hallucinations. m4 receptor proteins are concentrated in visual cortex (Tigges at al. 1997), and M4 (and M2) binding is increased in the cingulate cortex of patients with dementia with Lewy bodies and hallucinations (Teaktong et al. 2005). Additionally, in vivo imaging of muscarinic receptors in schizophrenia has shown widespread reductions in availability, as we summarised in section 7.6.2.2. M4 receptors also modulate dopaminergic transmission (Tzavara et al. 2004), providing a link with the secondary role that we assign to dopaminergic function.

Smythies provides some fascinating new ideas on the role of cholinergic function in balancing top-down and bottom-up representation, particularly during saccades. During a saccade, information from the retina is suppressed in favour of the top-down model of the visual environment (Kleiser et al. 2004). Smythies goes on to argue that saccades during REM sleep are not in response to visual images but may actually be responsible for them and for promoting the dream state of "free wheeling." If verified, this concept could be highly relevant in visual hallucinations in the waking state, although in dementia with Lewy bodies, no relation between saccade execution and hallucinations has been noted (Mosimann et al. 2005).

Gottesmann, **Kirov**, and **Pace-Schott** highlight that cholinergic function is *increased* during REM sleep. This poses some problems if hallucinations are equivalent to the dreams experienced during REM sleep; particularly since serotonergic and noradrenergic changes during sleep also diverge from those seen in hallucinatory syndromes. However, as dreams are not invariably associated with REM sleep (Solms 2000), and as we have suggested that hypnopompic and hypnagogic hallucinations occur in the transition between waking and non-REM sleep, this is less problematic for the PAD model. So long as transitions between sleep and waking and changes in cholinergic function are not fully synchronised, the hallucinator could experience low cholinergic function while partially awake.

R5.3. Other neurochemical abnormalities

Kirov and **Morrison & David** support the argument in sections 3.2 and 7.4.2 for an additional role for dopaminergic hyperactivity based on pharmacology and the changes seen during sleep. Despite their arguments, we see this as having a role mainly in the context of cholinergic dysfunction; the difference in the effects of dopaminergic and cholinergic manipulations on the induction and treatment of hallucinations, and the neurochemical findings from patients with visual hallucinations, do not seem to us to admit to another interpretation.

Consideration of the functional roles of dopaminergic transmission can clarify why dopamine has only a contributory role. Dopamine has a functional role in attention but contributes much less to visual object perception (Nieoullon 2002). Therefore, it could be significant only if there was another cause of impaired visual function. Additionally, as **Friston** suggests, dopamine may also have a role in emotional learning, perhaps accounting for why people with schizophrenia develop distress in the context of their hallucinations but people with eye disease develop insight.

R5.4. Dorsal function and the PAD model

The PAD model gave only passing mention to the role of the dorsal, spatial visual stream, seeing this as normal. This probably underplays its importance.

Pace-Schott's assignment of dorsal function to the integration of hallucinatory objects produced by ventral dysfunction into a whole visual environment (the PAD hallucinatory scene representation) is appealing and might account for some of the differences in the subjective experiences of dreams and hallucinations, and for the laterality effects noted by **Castelo-Branco**. **Tadin et al**. additionally suggest some intriguing methods for testing the relationship within visual hemifields, although we caution that spatial and object attention will need to be separately addressed. Tadin et al. argue as well for greater abnormality in the dorsal, spatial stream of the visual system of people with schizophrenia, citing normal N1 visual evoked potentials (VEPs) in support. However, **Spencer & McCarley** cite abnormal N1 VEPs to bolster their argument of sensory cortex hyperactivity in the same disorder. Not being experts in this field, we will await a consensus on the experimental findings before being able to assess their implications for the PAD model.

R5.5. Summary of physiological constraints

Commentators have reinforced the centrality of cholinergic function for many disorders associated with RCVH. However, it is clear that other neurochemical and functional systems may also play modulatory or constraining roles, although none appear necessary or sufficient in themselves.

R6. Future directions

One indication of a useful model is that it is testable. By that standard, PAD has succeeded. Specific tests have been suggested by **Badcock & Maybery** (multimodal hallucinations), **Dolgov & McBeath** (trade-offs in visual processing), **Ingle** (visual persistences), **Mast** (volitional images), **Morrison & David** (delirium), **Spencer & McCarley** (attentional function), and **Tadin et al**. (visual hemifields).

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R7. Conclusions

Winston Churchill (1947) famously described democracy as the worst form of government – except for all those others that had been tried from time to time. This remark neatly makes the point that it is not just the imperfections in a model that matter, but also how the model measures up against the alternatives.

Our view is that the PAD model remains more potentially predictive than the alternatives. There are still many questions that need new, reliable, unambiguous data in order to be answered. However, no commentator has advanced an alternative model that meets the requirements that we set out in section 5 of the target article. If there can be a grand unified theory of recurrent complex visual hallucinations, we conclude that PAD, despite its many limitations, best fits the present data. Many commentators have proposed specific tests of aspects of it. If we achieve nothing other than to stimulate these tests and the development of a better model, we will be satisfied.

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NOTES

1. For those unfamiliar with Greek mythology, it was Theseus who slew the wicked Procrustes, and Lycomedes who, in some versions of the tale, ultimately threw Theseus to his doom off a cliff.

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Letters "a" and "r" appearing before authors' initials refer to target article and response respectively.

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