Modelling perception as a hierarchical competition differentiates imagined, veridical, and hallucinated percepts

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Abstract

Mental imagery is a process by which thoughts become experienced with sensory characteristics. Yet, it is not clear why mental images appear diminished compared to veridical images, nor how mental images are phenomenologically distinct from hallucinations, another type of non-veridical sensory experience. Current evidence suggests that imagination and veridical perception share neural resources. If so, we argue that considering how neural representations of externally-generated stimuli (i.e. sensory input) and internally-generated stimuli (i.e. thoughts) might interfere with one another can sufficiently differentiate veridical, imaginary, and hallucinatory perception. We here use a simple computational model of a serially-connected, hierarchical network with bidirectional information flow to emulate the primate visual system. We show that modelling even first-approximations of neural competition can more coherently explain imagery phenomenology than non-competitive models. Our simulations predict that, without competing sensory input, imagined stimuli should ubiquitously dominate hierarchical representations. However, with competition, imagination should dominate high-level representations but largely fail to outcompete sensory inputs at lower processing levels. To interpret our findings, we assume low-level stimulus information (e.g. in early visual cortex) contributes most to the sensory aspects of perceptual experience, while high-level stimulus information (e.g. towards temporal regions) contributes most to its abstract aspects. Our findings therefore suggest that ongoing bottom-up inputs during waking life may prevent imagination from overriding veridical sensory experience. In contrast, internally-generated stimuli may be hallucinated when sensory input is dampened or eradicated. Our approach can explain individual differences in imagery, along with aspects of daydreaming, hallucinations, and non-visual mental imagery.

Keywords: mental imagery, hallucinations, aphantasia, hyperphantasia, daydreaming, perception

Introduction

Mental images are internally-generated thoughts which can be seen, heard, or in some way perceived with sensory qualities. Yet, how does the brain generate sensory experiences without a real sensory stimulus in the environment to perceive? One answer might be that mental imagery involves similar processes to those used during veridical perception, yet with an opposite direction of information flow. Instead of pooling together sensory information to extract abstract knowledge from a real stimulus, mental imagery may involve retrohierarchically reconstructing the sensory features of an imagined stimulus from abstract knowledge we already possess. In line

46 with this idea, mental imagery seems to use the same neural machinery as that used
47 during veridical perception (Cichy et al., 2012; Dijkstra et al., 2017, 2018; Dijkstra,
48 Bosch, et al., 2019; Ishai, 2010; Kosslyn et al., 1993; Xie et al., 2020), yet with neural
49 activity during the early stages of veridical visual perception resembling neural activity
50 during the later stages of visual mental imagery and vice versa (Breedlove et al., 2020;
51 Dentico et al., 2014; Dijkstra et al., 2020; Linde-Domingo et al., 2019).

52 However, mental imagery is unlikely to be an exact reverse of feedforward processes
53 in veridical perception given that individuals reliably report that their mental images
54 are experienced with some form of reduced sensory quality (termed *vividness*)
55 compared to real images (Galton, 1880; Marks, 1973). Some researchers have
56 proposed that this difference follows from differences between feedforward and
57 feedback processes, the latter of which are believed to be responsible for propagating
58 mental images. For instance, information about mental imagery content tends to be
59 most detectable in superficial and deep cortical layers, but not granular mid-layers, in
60 contrast to information about environmental stimulus content which can be detected
61 across all cortical layers (Bergmann et al., 2019; Lawrence et al., 2018). Other
62 accounts speculate that imagery could be propagated using weak feedback
63 connections in the visual system, in contrast to feedforward connections which
64 stereotypically drive, rather than modulate, action potentials (Koenig-Robert &
65 Pearson, 2021). However, feedback to early visual regions can drive action potentials
66 depending on local neurochemistry (Aru et al., 2020). Further, neither of these
67 differences between feedforward and feedback processes can explain the unique
68 experience of mental imagery without a framework specifying what it means for a
69 mental image to be a quasi-sensory experience to begin with.

70 A more readily-interpretable explanation is that mental images appear impoverished
71 simply because the features of the images they depict are distorted relative to those
72 of real images. That is, mental images might merely have less-precise image statistics
73 (e.g. spatial frequency, location, size) compared to real images, but are otherwise just
74 as visible. Breedlove et al. (2020) provide an account which allows for this possibility,
75 finding that representations of mental images in early visual cortices are deficient in
76 detailed sensory information compared to real images. As hierarchical feedforward
77 processes combine multiple pieces of sensory information (e.g. edges) to form fewer
78 pieces of more abstract information (e.g. a shape), reconstructing sensory information
79 using retrohierarchical feedback requires extrapolating from a relatively information-
80 deficient source material. This process should distort imagined stimuli in predictable
81 ways such that neural populations which represent mental images in early visual
82 cortices have lower spatial frequency preferences, more foveal receptive fields, and
83 larger receptive fields than when responding to real images (Breedlove et al., 2020).

84 Ultimately, many factors may distinguish between veridical and mental percepts given
85 that the former are externally-generated while the latter are internally-generated.
86 However, any complete explanation of the unique appearance of mental images must
87 also account for how the quasi-sensory experience of mental imagery might be
88 differentiated from other internally-generated, yet unambiguously-sensory
89 experiences, such as which occur in hallucinations, many dreams, and eidetic mental
90 imagery. Regardless of the image statistics of the internally-generated content being
91 depicted, these latter phenomena tend to involve a sensory experience of internally-
92 generated content which is entirely equivalent to the subjective experience of

93 externally-generated content (Chiu, 1989; Ffytche et al., 1998) except that the content
94 experienced is non-veridical and is not typically experienced as part of normal waking
95 life. For the purposes of this article, we refer to the internally-generated,
96 unambiguously-sensory experience common to each of hallucinations, dreams, and
97 eidetic imagery as hallucinatory imagery, or a hallucination generally, regardless of
98 whether such imagery is voluntary or involuntary, regardless of whether it is believed
99 to be real or unreal, and regardless of where exactly within the visual field it is
100 perceived to be located. Crucially, while mental imagery is quasi-sensory, seemingly
101 seen yet unseen, hallucinatory imagery is definitively visible. This should require that
102 non-veridical internally-generated sensory content or features replace veridical
103 sensory content or features, overwriting them in a given region of the visual field. For
104 instance, seeing a hallucinatory cat on this page instead of text, or seeing the text on
105 this page as moving instead of still, or seeing anything at all during a dream instead of
106 merely the back of our eyelids.

107 Here, we propose that imagined, veridical, and hallucinated percepts can be clearly
108 distinguished by considering perception as a competitive process. While mental
109 imagery generation can be modelled without competition from veridical perception
110 (e.g. Breedlove et al., 2020), mental imagery almost never occurs in isolation. Instead,
111 mental images are invariably generated while we are awake and receiving sensory
112 input from the external world. If mental imagery and veridical perception share neural
113 resources, then both processes should interact such that neural representations of
114 imagined and real stimuli interfere or compete with one another.

115 Interactions between real and imagined stimuli have been previously demonstrated,
116 lending support to the idea that perception may be a competitive process, although
117 the exact outcome and nature of this interaction seems to vary. For instance, mental
118 images can constructively interfere with real image content, depending on stimulus
119 congruency (Dijkstra et al., 2022), and can induce priming or adaptation to veridical
120 stimuli, depending on the individual (Dijkstra et al., 2021; Dijkstra, Hinne, et al., 2019;
121 Keogh & Pearson, 2017). Increasing environmental luminance can also impede the
122 priming effects of mental imagery (Keogh & Pearson, 2017), while real modality-
123 specific distractors reduce the recall of modality-specific information (Vredeveldt et al.,
124 2011; Wais et al., 2010), potentially reflecting competitive interference.

125 We sought to predict whether perceptual interference could account for the quasi-
126 sensory, rather than hallucinatory, experience of mental imagery. Yet, any valid
127 explanation of the quasi-sensory experience of mental imagery must first clearly
128 specify what it means to have a quasi-sensory experience at all. Such an experience
129 may be possible under a framework where perceptual experience itself is considered
130 as a multifaceted phenomenon, composed of both sensory and abstract experiences
131 at any given time. In vision, this entails having an experience of the low-level features
132 of an image, such as its hues and edge orientations, while also having an experience
133 of the high-level features of what the image actually depicts, such as recognising that
134 an image is depicting a duck. Usually, low- and high-level features of an image seem
135 intertwined such that it is unintuitive to consider them as separate components of
136 perceptual experience. Yet, these aspects become clearly separable when we
137 consider bistable percepts (e.g. the rabbit-duck illusion), where the same low-level
138 information can give rise to different abstract experiences. These abstract experiences

feel perceptually distinct from one another even though the spatial pattern of light in our visual field, and our purely low-level visual experience of it, remains unchanged.

To anchor these experiences to physical processes, we assume that the sensory and abstract aspects of experience are dependent on neural systems encoding each respective type of information in the brain, such as those along the visual ventral stream. However, as neural representations of externally- and internally-generated stimuli are not explicitly sensory or abstract, but distributed on a spectrum, so too may perceptual experience itself be composed of a spectrum of sensory and abstract aspects. Given that internally-generated perceptual experiences also seem to use similar neural resources to their externally-generated counterparts, including in a feature-specific manner (Ffytche et al., 1998), then mental and hallucinatory imagery processes may also be experienced with a spectrum of abstract and sensory features. Under this framework, the quasi-sensory experience of mental imagery can be clearly conceptualised as the experience arising from the activation of high-level to mid-level, but not low-level, feature representations of internally-generated content, regardless of the content itself. Hallucinatory imagery, in contrast, may invoke low-level sensory representations, with or without more abstract components, whilst veridical percepts should at least invoke low-level featural representations given their bottom-up entryway into the visual system.

Under these assumptions, we constructed simple computational model of a serially-connected network with bidirectional information flow as a first-approximation to simulating the hierarchical interaction of internally- and externally-generated stimulus representations (Figure 1). We used this model to evaluate the degree to which internally-generated (i.e. imagined) stimulus representations are able to spread throughout a hierarchical system, with and without competition from externally-generated stimuli. We demonstrate that competition from external sensory input could prevent internally-generated content from ever recruiting the low-level neural infrastructure best suited to representing highly-sensory, highly-modal information. In doing so, we show that accounting for perceptual interference, even with preliminary models, can provide an arguably more coherent explanation for the unique phenomenology of mental imagery than approaches which consider mental imagery in isolation. We explore the perceptual implications of such predictions on the subjective experience of mental imagery, provide a neurochemically-grounded hypothesis for variance in imagery across individuals and states, and delineate how perceptual interference may relate to hallucinations and mental imagery in non-visual modalities. Ultimately, we demonstrate that reconceptualising mental imagery as an intrinsically competitive process can resolve major lingering questions in imagery research.

Methods

Computational model

Our goal was to assess the degree and extent to which internally-generated stimuli are able to spread throughout a hierarchical system, with and without competition from externally-generated stimuli. To do this, a dynamic, serially-connected, five-layer computational network was constructed as a simple model of how stimulus information

184 may flow bidirectionally in the hierarchical human visual system (Figure 1). Each layer
185 *l* encoded a representation *r* consisting of a square matrix of values. The number of
186 units available to represent information (i.e. dimensionality) in each layer decreased
187 linearly in size from 256 x 256 matrix elements at the lowest layer (*l = 0*) to 208 x 208
188 elements at the higher layer (*l = 4*). This mimics feedforward dimensionality reduction
189 in the visual system such that upper layers encode more abstract stimulus information
190 than lower layers, analogous to neural structures towards the parietal and temporal
191 lobes (Binder, 2016). Each element in the matrix could vary in value along a single
192 dimension, from 0 to 1, encoding the variation of an arbitrary stimulus feature. The
193 lowest layer acted as an input layer for externally-generated stimuli and never received
194 feedback, analogous to the retina in visual perception.

195

196 **Figure 1**

197 *A hierarchical network modelling interference between externally- and internally-*
198 *generated stimuli*

199
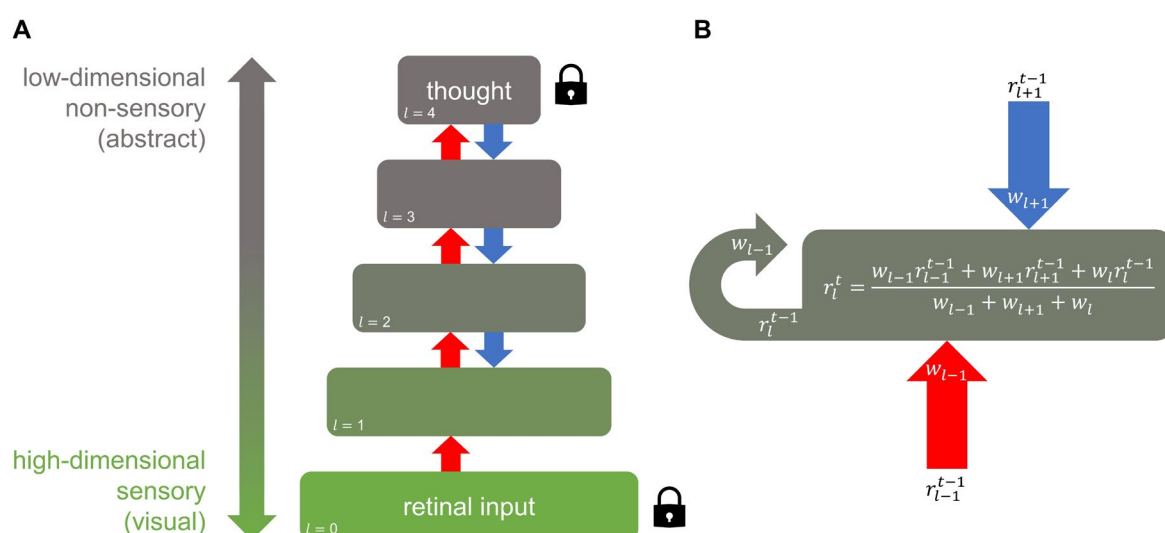
200 *Note.* **A.** A hierarchical network model of visual perception. Layer size indicates the relative
201 dimensionality of the encoded representation. Information is pooled via feedforward processes
202 (red) and extrapolated via feedback processes (blue). Lock icons indicate input layers with
203 clamped representations during simulations where mental imagery is attempted during veridical
204 perception. Clamped representations do not evolve with time. Note that a "thought" here could be
205 any internally-generated representation. **B.** Evolution rule for unclamped layers. Each value *r* in
206 the representational matrix of each layer *l* evolves at each timepoint *t* according to a weighted
207 average of the adjacent layers and the current layer at the previous timestep with weights *w*. The
208 ascending value array was convolved with an averaging kernel before being weighted to facilitate
209 feedforward dimensionality reduction.

210

211 The network allowed representations to propagate between layers, and for bottom-up
212 processes to interact with top-down processes. Hence, the representation *r* of each
213 layer *l* was updated at each timestep *t* according to a weighted average of the
214 ascending representation r_{l-1} from the layer below, descending representation r_{l+1} from
215 the layer above, and representation r_l of the current layer, each at the previous
216 timestep *t-1* (Figure 1B). We note that despite the simplicity of this approach, weighted

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217 averaging is approximately equivalent to the biologically-plausible additive
218 combination of neural inputs, followed by a decay of activity proportional to the
219 strength of activation. However, unlike in real neurons, decay here occurs
220 instantaneously. We allow for this simplification given that we simulate the perception
221 of static images only and are therefore most concerned with the steady-state, rather
222 than moment-to-moment, profile of the system.

223 Each layer was updated sequentially, first as part of a feedforward sweep, then as part
224 of a feedback sweep, and then alternating with every subsequent iteration. Weightings
225 w_{l-1}, w_{l+1}, and w_l for the ascending, descending, and current representations
226 respectively were each equal to one except where the effect of weighting ratios was
227 explicitly investigated. However, if a layer acted as a constant source of information in
228 the network (representing either an internally- or externally-generated stimulus), the
229 values in its representational matrix were locked in place (clamped) by setting the
230 weightings of ascending and/or descending inputs to that layer to zero. Given that the
231 retina is always receiving visual input in an awake state, the lowest layer of the network
232 was always clamped to some predetermined set of input values. Drawing from
233 modelling by Breedlove et al. (2020), the highest layer in the network was also
234 clamped to a fixed set of input values to simulate an internally-generated stimulus (i.e.
235 a thought) during mental imagery.

236 To simulate feedforward information pooling in the visual ventral stream, ascending
237 representations were combined using a 13 x 13 square convolutional kernel such that
238 each element of the layer above received the average of inputs from multiple elements
239 from the layer below. Hence, from $l = 0$ to $l = 4$, the receptive field size of each element
240 in each representation increased while layer dimensionality decreased. Because
241 forming a mental image of an object first requires at some point seeing the object or
242 its constituent parts, internally-generated stimulus representations were formed from
243 externally-generated (e.g. retinal) stimulus inputs first processed through a single
244 complete feedforward sweep from layer 0 to layer 4.

245 To assess the degree to which mental imagery was able to compete with veridical
246 sensory input, we allowed the network to evolve under three main sets of initial
247 conditions: veridical perception without imagination, imagination without veridical
248 perception, and imagination during veridical perception. In the first case, to simulate a
249 scenario where externally-generated visual input is present without competition, only
250 the bottom layer was clamped to a stimulus representation (veridical perception
251 without imagination). Secondly, to simulate a scenario where an internally-generated
252 stimulus is present without competition, the top layer was clamped to an imagined
253 stimulus representation (imagination without veridical perception). The ascending
254 input from the base layer was down-weighted to zero in this scenario to enforce a state
255 of sensory disconnection. Thirdly, in what we consider a more realistic mental imagery
256 scenario, both the top and bottom layers were simultaneously clamped to different
257 stimulus representations to simulate mental imagery occurring in the presence of
258 competing sensory input (imagination during veridical perception). All intervening or
259 non-input layers were initialised with white noise.

260 In each scenario, we measured the steady-state contribution of top-down
261 representations relative to bottom-up representations at each layer. This was achieved
262 by taking the average value of all elements in each layer for the case where the initial
263 low-level or high-level input representations were set homogenously to zeros or ones,

264 respectively (Figure 2D-F). Each scenario was also replicated using images as inputs
265 with each element of a representation corresponding to one pixel in the image such
266 that the collective pixel values of each image equate to a simulated neural activity
267 pattern (Figure 2A-C). A 256 x 256 greyscale image of a camel was used for sensory
268 input, and a 256 x 256 greyscale image of a hat was used for imagined input after
269 conversion to a reduced dimensionality of 208 x 208 via feedforward pooling. Both
270 were sourced from the BOSS image database (Brodeur et al., 2010). The similarity
271 between layer activity patterns and the original imagined or veridical stimulus patterns
272 can be quantified by calculating the absolute mean pixel difference between the
273 images. We also separately explored how varying the ascending and descending
274 weighting schemes affected competition between simulated imagined and veridical
275 stimulus representations (Figure 3). For each scenario in Figure 3, all mid-layer
276 feedforward or feedback weightings were ≤ 1 with the ratio specified in the figure for
277 the duration of the simulation.

278

279 **Model interpretation**

280 Our model can be interpreted as analogous to a simplified model of the human visual
281 processing hierarchy, with a basal layer encoding externally-generated retinal input
282 and an apical layer housing more abstract internally-generated stimulus
283 representations encoded by neural structures towards the parietal and temporal lobes
284 (Binder, 2016). To interpret simulation outcomes phenomenologically, we considered
285 that a single perceptual experience can contain a distribution of information, spanning
286 from highly-sensory (modal) in nature to highly-abstract (amodal). We assume that
287 each representational layer in the visual hierarchy which receives both feedforward
288 and feedback input contributes information to the construction of conscious perceptual
289 experience. We also assume that the type of information provided by each layer aligns
290 with the layer's dimensionality such that high-dimensional representations contribute
291 most to the sensory aspects of the experience while low-dimensional representations
292 contribute most to the non-sensory aspects of the experience. Hence, low-level
293 representations would be most influential in determining the literal image content of a
294 visual experience (e.g. the exact location, orientation, and contrast of high-spatial
295 frequency edges), while high-level representations would contribute most to the
296 abstract understanding of what is being thought about or observed (e.g. knowing
297 whether the edges in a scene form a hat or a camel), with a spectrum of quasi-sensory
298 or quasi-abstract features in between.

299 Crucially, this implies that a perceptual experience *gains* sensory or abstract
300 properties depending on how well neural regions with the corresponding high- or low-
301 dimensional structure, respectively, are recruited during that experience. Therefore,
302 the further an internally-generated stimulus representation is able to spread towards
303 the primary visual cortex, for instance, the more it may be experienced with properties
304 approaching that of an actual visual image (i.e. a true mental image) rather than
305 something pondered without sensory qualia (i.e. a non-sensory thought). This
306 approach can therefore maintain consistency with traditional accounts implicating the
307 primary visual cortex in mental imagery (Kosslyn, 2005; Kosslyn & Thompson, 2003;
308 Pearson, 2019; Pearson & Kosslyn, 2015).

309 Note that, given hallucinatory visual experience is possible without corresponding
310 retinal activity, we consider the lowest level in the hierarchy purely as a non-conscious
311 input layer to the rest of the network. We also note that while there's compelling
312 evidence that some high-level representations are stored in a largely amodal form (e.g.
313 Popham et al., 2021), they are not necessarily completely non-sensory. Late-stage
314 object representations can still contain some degree of sensory information (e.g. see
315 DiCarlo & Cox, 2007), albeit in a considerably more low-dimensional form relative to
316 primary sensory areas. Our model only requires higher-level representations to be less
317 sensory than low-level representations rather than completely non-sensory.

318

Results

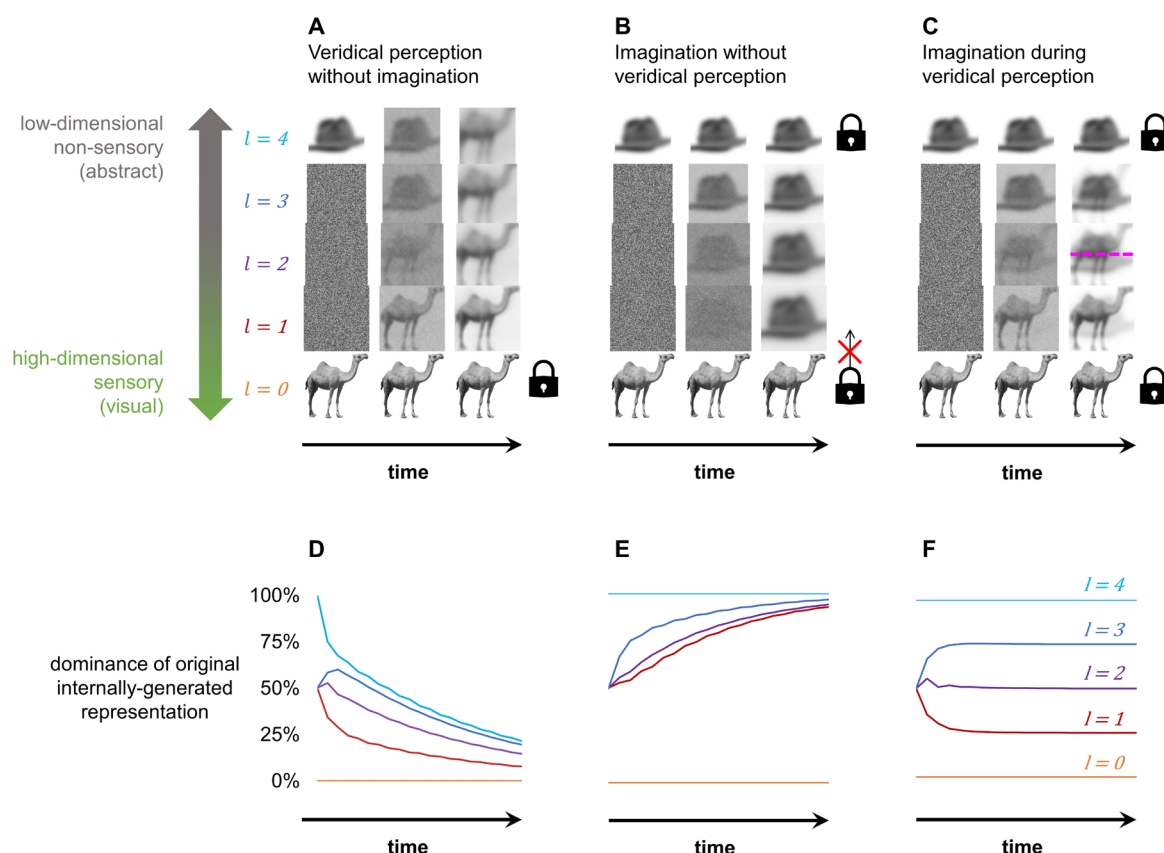### Perception without competition

321 Two scenarios were simulated where competition was not present: veridical
322 perception without imagination, and imagination without veridical perception. Initiation
323 of veridical perception was simulated by allowing the lowest representational layer to
324 have a non-zero contribution to the layer above. Imagination was simulated by
325 preventing the highest layer from being affected by feedforward inputs below such that
326 it provided a constant source of top-down information to the system. In both cases,
327 only one fixed source of perceptual information was present within the network, either
328 an externally- or internally-generated stimulus representation. An example simulation
329 is shown in Figure 2 using an image of a camel as the externally-generated veridical
330 stimulus input (i.e. retinal activity pattern), and a compressed image of a hat as the
331 internally-generated imagined stimulus input (i.e. high-level neural activity pattern).

332 Without competition from imagination, all freely-evolving (unclamped) layers in the
333 network converged asymptotically to a representation dominated by the externally-
334 generated stimulus representation (Figure 2A). Conversely, without competition from
335 veridical perception, all unclamped layers converged to a representation dominated
336 by the internally-generated stimulus representation (Figure 2B). As all unclamped
337 representations are eventually dominated by the original externally- or internally-
338 generated source stimulus, both scenarios each result in a state corresponding to
339 having a visual experience of the same stimulus which is being thought about
340 abstractly. In the case of pure veridical perception, the system evolves to emulate a
341 common perceptual experience: seeing an object while also knowing what it is. Yet,
342 where the internally-generated stimulus is uncontested, the sensory characteristics of
343 the imagined stimulus should completely dominate visual experience, resulting in the
344 perception of what was imagined and not what was present in the environment. Hence,
345 pure imagination imitates hallucinating the object one is thinking about.

346 Although in both cases, layer $l = 1$ is entirely dominated by one stimulus, each state
347 occurred through a distinct formation route. Note that the top-down, but not bottom-
348 up, formation route resulted in substantial distortions at lower layers, reflecting the
349 findings of Breedlove et al. (2020). Yet, these distortions only affect the *content* of the
350 imagined stimulus, not the degree to which that stimulus is able to commandeer a
351 hierarchical layer in this model.

352

Figure 2

Veridical stimuli outcompete imagined stimuli at low-level sensory representations, but not high-level abstract representations

Note. How simulated neural representations of an internally-generated (imagined) hat and an externally-generated (veridical) camel spread through a perceptual processing hierarchy with and without competition. **A-C.** Simulated neural activity patterns, coded as image pixel values, evolving over 0, 2, and 20 alternating feedforward or feedback sweeps. Initial activity patterns are the same in each scenario, and mimic thinking about a hat while receiving a retinal image of a camel. Lock icons indicate clamped representations which do not evolve. The crossed arrow indicates disconnected sensory input ($w_{l = 0} = 0$). **A.** All layers except the base layer are free to evolve, causing activity patterns to be dominated by the initial veridical input. **B.** Mid-layers are free to evolve only. Sensory input is present but disconnected. All evolving activity patterns become dominated by the initial imagined input. **C.** Mid-layers are free to evolve only, and sensory input is present and connected. Imagined content dominates upper layers and veridical content dominates lower layers. The magenta line indicates the *representational equilibrium point* where the internally- and externally-generated stimuli equally contribute to a layer. **D-F.** One-dimensional simulations of each scenario above in A-C illustrating how the character of each layer evolves over time. The dominance of the original externally-generated stimulus representation at $l = 0$ can be obtained by subtracting the internally-generated stimulus dominance from 100%.

Perception with competing imagined and veridical stimuli

Where two fixed sources of information are simultaneously present within the network, neither the imagined nor veridical stimulus can dominate every unclamped layer in the system (Figure 2C). Instead, the network represents both stimuli simultaneously at the steady state. However, the further a given layer is from an externally- or internally-

379 generated stimulus input layer, the smaller the contribution of the original veridical or
380 imagined stimulus to the representation held by the given layer. This is shown in Figure
381 2F for the case where feedforward and feedback weightings are equal ($w_{l-1} = w_{l+1} = 1$).

382 Consequently, where imagination occurs in the presence of sensory input, the
383 externally-generated veridical stimulus dominates low-level representations while the
384 internally-generated imagined stimulus dominates high-level representations. Such a
385 system is therefore representing two distinct stimuli, yet at largely separate
386 hierarchical levels. As lower levels are more suited for representing sensory
387 information, and higher levels for abstract, this state corresponds to a situation where
388 an individual has a visual experience of their veridical environment despite
389 simultaneously having relatively non-sensory thoughts about what they are imagining.
390 Hence, the simulation suggests that external sensory input outcompetes imagination
391 at the low-level regions most likely to contribute to the most sensory aspects of
392 perceptual experience.

393

Modelling variation in imagery quality (e.g. aphantasia and hyperphantasia) as
a shift in representational equilibrium

396 This model can also be used to understand states where thoughts are experienced in
397 a highly sensory way (hyperphantasia) or in a non-sensory or weakly-sensory way
398 (aphantasia; Figure 3). When sensory input and imagination compete, our simulation
399 showed that spanning along the perceptual hierarchy from bottom to top corresponded
400 to transitioning from primarily representing a veridical stimulus to primarily
401 representing an imagined stimulus. The exact point where the two stimuli are
402 represented in equal proportion is here dubbed the *representational equilibrium point*
403 for the system. Representations contain more veridical stimulus character below this
404 point and more imagined stimulus character above it.

405 The location of the representational equilibrium point can summarise how far an
406 imagined representation can penetrate towards lower layers before it is outcompeted
407 by the veridical stimulus, or how far a veridical stimulus representation can penetrate
408 towards upper layers before it is outcompeted by the imagined stimulus. Where
409 ascending and descending information is weighted equally ($w_{l-1} = w_{l+1} = 1$; Figure 3B),
410 the equilibrium point lies at the middle layer in the centre of the hierarchy such that
411 lower layers (e.g. towards the primary visual cortex) are dominated by externally-
412 generated sensory input and upper layers (e.g. towards the temporal lobe) are
413 dominated by internally-generated thoughts, symmetrically. However, overweighting
414 feedforward information ($w_{l-1}/w_{l+1} > 1$) elevates the equilibrium point such that the
415 imagined stimulus is restricted to only the highest, least-modal hierarchical layers,
416 corresponding to a state of aphantasia (Figure 3A). In contrast, overweighting
417 feedback information ($w_{l-1}/w_{l+1} < 1$) lowers the equilibrium point such that the imagined
418 stimulus dominates the majority of the hierarchy, corresponding to a state of
419 hyperphantasia (Figure 3C). Feedforward-to-feedback weighting ratio variation could
420 therefore account for between-person and moment-to-moment differences in the
421 apparent sensory quality of mental imagery experiences.

422

423   **Figure 3**

424   *Decreasing feedforward-to-feedback weighting ratio induces more sensory mental*
425   *imagery*
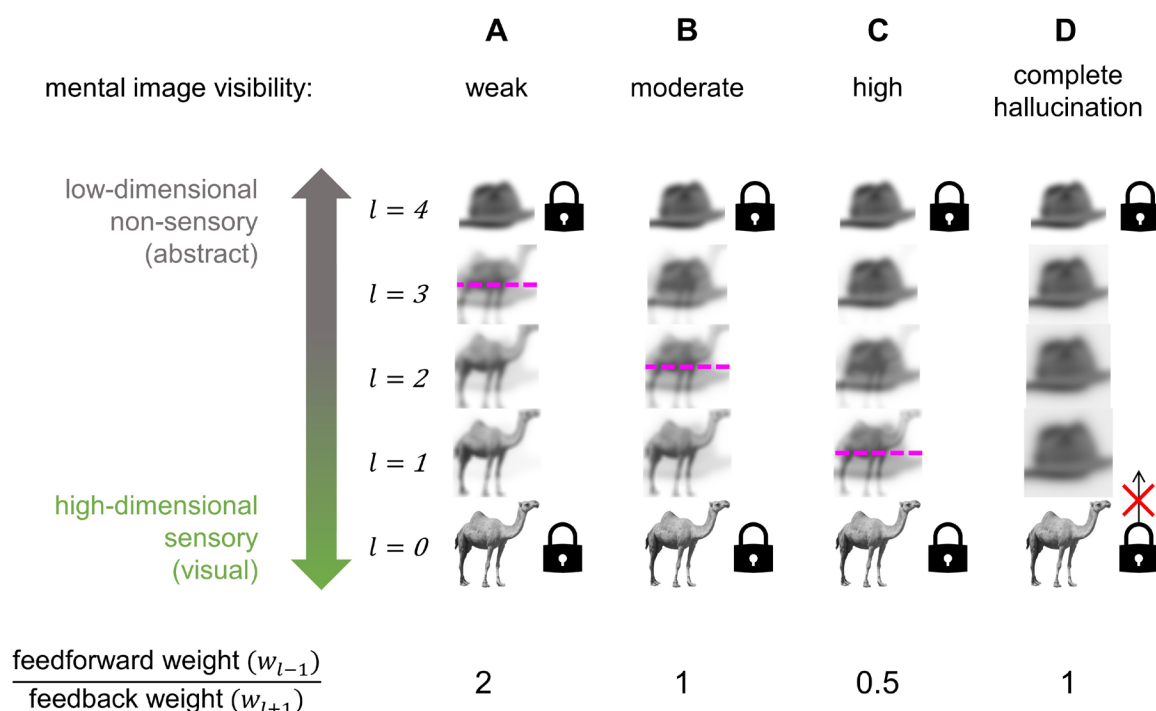
427   *Note.* Hierarchical competition between simulated neural representations of an internally-
428   generated (imagined) hat and an externally-generated (veridical) camel modelled under different
429   feedforward-to-feedback weighting ratios. Simulated neural activity patterns, coded as image pixel
430   values, are depicted after 20 alternating feedforward or feedback sweeps. Initial activity patterns
431   are the same in each scenario, and mimic thinking about a hat while receiving a retinal image of a
432   camel. Lock icons indicate clamped representations which do not evolve. The crossed arrow
433   indicates disconnected sensory input ($w_{l=0} = 0$). The magenta line indicates the *representational*
434   *equilibrium point* where the internally- and externally-generated stimuli contribute equally to a layer.
435   **A-C.** Globally varying the ratio of bottom-up (w_{l-1}) and top-down (w_{l+1}) weightings affects
436   representational equilibrium and the extent to which thoughts should be experienced visually (e.g.
437   weak, moderate, or high). **D.** All unclamped layers converge towards the original internally-
438   generated stimulus representation once sensory input is disconnected.

439

440   **Discussion**

441   **Distinguishing imagined, veridical, and hallucinatory percepts**

442   In this study, we aimed to explain the apparent differences in vividness between
443   veridical, imagined, and hallucinated percepts. We show that, for a hierarchical system
444   with bidirectional information flow, the presence of competing sensory input can
445   prevent internally-generated stimuli from dominating low-level regions most suited for
446   supporting a modal, highly-sensory neural representation. We interpret this finding as
447   suggesting that, when competing sensory input is present, the sensory content of
448   imagination does not supersede the sensory content of veridical perception. That is,
449   for instance, even if we imagine a hat, our mental image of the hat does not replace
450   the image of a real camel in our visual field: the camel is still more visible. In contrast,
451   the attenuation or abolition of competing external sensory input could facilitate

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452 internally-generated stimuli becoming the dominant contributor to sensory experience,
453 creating hallucinatory imagery. Our model therefore illustrates that the apparent
454 difference in reported vividness between veridical and imagined percepts could be
455 explained by the degree to which imagined and veridical stimulus representations
456 spread hierarchically, and that this difference can arise due to external sensory input
457 competing with our internally-generated thoughts.

458

Neurological consequences of perceptual competition

460 Our model results in some counterintuitive implications. Despite the suitability of the
461 early visual cortex for representing retinotopic, visual information, our account
462 suggests that hierarchically low-level neural regions (e.g. primary sensory cortices)
463 may be less involved in representing an imagined stimulus than any other region in
464 the corresponding perceptual hierarchy. However, this implication is consistent with
465 existing findings. Individuals still report being able to create mental images despite
466 near-complete bilateral lesions to primary visual cortex, suggesting that the primary
467 visual cortex is not necessary for visual mental imagery (Bridge et al., 2012; Chatterjee
468 & Southwood, 1995; de Gelder et al., 2015; Zago et al., 2010). Even mid-level
469 impairments to the visual system, a potential cause of visual agnosia, can leave visual
470 mental imagery preserved (Behrmann et al., 1994). Further, a meta-analysis of the
471 neural correlates of visual mental imagery by Spagna et al. (2021) found that the left
472 fusiform gyrus, a high-level region within the visual ventral stream, was reliably
473 involved during mental imagery across studies while early visual cortices were not.

474 These findings are entirely in line with the predictions of our model: while primary
475 sensory cortices can be involved in mental imagery, the only essential component of
476 the experience is the internal generation of a non-veridical stimulus representation,
477 which in our model occurs at the hierarchical apex, corresponding, for instance, to late
478 in the visual ventral stream. This may be why subjective vividness ratings better
479 correlate to how distinctly imagined information is represented in retinotopic, rather
480 than associative, neural regions (S.-H. Lee et al., 2012). Under our model, activation
481 at levels below the clamped internally-generated representation can add progressively
482 more sensory components to the experience of imagining, although at what stage a
483 relatively amodal, abstract thought formally becomes a truly sensory mental image
484 may be an arbitrary distinction.

485 Our simulations predict that the dominance of internally-generated stimuli should
486 increase from posterior to anterior regions of the visual hierarchy. Supporting this
487 prediction, VanRullen & Reddy (2019) used a mental imagery decoding paradigm to
488 show that more information about imagined face images was present in temporal
489 regions than occipital regions. Lee et al. (2012) likewise showed that less information
490 about imagined object images could be decoded towards more posterior, retinotopic
491 areas of the visual system. Both studies also found that externally- and internally-
492 generated stimulus representations became more similar towards higher-level
493 regions, aligning with the notion that imagined content is propagated from areas active
494 during late-stage veridical perception.

495

Phenomenological consequences of perceptual competition

Our model has implications for the functional and subjective characteristics of imagery. For instance, the relegation of imagination to relatively high-level representations suggests that thinking in a non-sensory way may be more commonplace than manifesting thoughts in a sensory way (e.g. as an actual visual image). This makes pragmatic sense in everyday life: thinking about what you are seeing is often favourable during veridical visual perception, yet it may be quite unfavourable to see what you are thinking about given that such hallucinations may supersede important survival-relevant environmental information. However, this process could involve a functional trade-off as the semantic content of sensory input may be processed poorly if high-level regions are already occupied by unrelated thoughts. Mental imagery could push internally-generated high-level representations towards mid-level regions, interfering with the ascending processing of externally-generated stimuli. This could explain why internal attention can affect the processing of environmental stimuli, such as during daydreaming (Schooler et al., 2011; Smallwood, 2011). States of immersive mental imagery (e.g. daydreaming) might then loosely and transiently share phenomenological similarities with agnosia given that high-level processing of externally-generated stimuli may be impeded despite low-level visual feature processing being relatively unaffected. For instance, when reading text while distracted by other thoughts, one may find themselves rereading the same paragraph repeatedly, seeing the words each time, yet failing to process the meaning of the text.

Another effect of abstract representations being activated without any significant low-level representation during imagery is that a perceiver might plausibly even *feel* like they have seen their imagined thought without ever experiencing it in any substantially visual way. That is, units involved in the recognition of an object may be activated despite minimal low-level activation. Hence people could theoretically report being able to visualise objects yet fail to be able to reconstruct the details of these imagined stimuli accurately.

Additionally, experiencing imagery on a spectrum from highly-abstract to highly-sensory may explain why the unique quasi-sensory experience of mental imagery may be difficult to describe. While the *content* of mental imagery could be described in terms of objectively-quantifiable stimulus properties (e.g. contrast, size, duration), the *experience* of such content is modified by the degree to which a mental image gains sensory features as well as just abstract features. This modulation, encapsulated by the aforementioned concept of a representational equilibrium point, could be the underlying variable commonly measured (albeit somewhat indistinctly) by subjective ratings of imagery vividness. If so, this would justify why vividness ratings are generally only investigated concerning imagined, not veridical, experiences: veridical percepts are maximally sensory by default.

Hallucinations

Our model also delineates conditions for hallucinations. Visually, a hallucination entails seeing a non-veridical percept in a given region of the visual field *instead of* a percept that reflects external reality. Under our model, for any modality, the most perceptually compelling hallucinations would then be those where a non-veridical stimulus dominates most, if not all, low-level representations. The notion of non-veridical

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information penetrating sensory systems top-down to cause hallucinations has been previously explored in depth under a predictive coding framework (Powers et al., 2016). In our model, it can occur from overweighting top-down information relative to bottom-up information. However, hallucinations could also occur simply if aberrant low-level activity is fed through an otherwise normal perceptual system (Hahamy et al., 2021). Note that, in both cases, our model only accounts for the perceptual experience of imagery, hallucinated or otherwise, and not whether it was induced voluntarily (as imagery tends to be), or involuntarily (as hallucinations tend to be).

In the first possible route to hallucinations, top-down information becomes overweighted such that non-veridical thoughts can permeate low-level areas to nearly the same extent as uncontested bottom-up veridical input. In this case, hallucinations are modelled as an anomalous case of mental imagery with an extremely low representational equilibrium point, similar to hyperphantasia. If our model is correct, then individuals with hallucinatory disorders should tend to have improved mental imagery abilities. Accordingly, Parkinson's hallucinators tend to have stronger mental imagery priming effects than non-hallucinating controls, with the degree of imagery-induced priming predicting hallucination frequency (Shine et al., 2015). Parkinson's hallucinators also mind-wander more than non-hallucinators, corresponding to increased connectivity to the early visual cortex from default network regions (Walpola et al., 2020). Additionally, although individuals with schizophrenia can have impaired memory, their abilities on visuospatial mental imagery manipulation tasks are enhanced compared to neurotypical controls (Benson & Park, 2013; Matthews et al., 2014). However, note that some individuals are able to complete mental imagery manipulation tasks while reporting no visual mental imagery (Zeman et al., 2010).

Hallucinations should also occur when sensory input is disconnected altogether such that internally-generated percepts are entirely uncontested. If feedforward information is downweighted completely ($w_{l-1} = 0$) to any layer, then that layer and any layer above it are free to be commandeered by any high-level internally-generated stimulus present. Representations at such layers will then inevitably converge towards the internally-generated stimulus representation (Figure 2B, 2E, & 3D). This could contribute to hallucinations in disorders of afferent visual processing (e.g. Charles Bonnet Syndrome; Reichert et al., 2013). Hallucinations are reasonably common following cortical blindness (Aldrich et al., 1987), and in one such reported case, hallucinations could be induced directly from attempting voluntary mental imagery (Wunderlich et al., 2000). Dampening external sensory input might also contribute to hypnagogic hallucinations, which occur during sleep onset. When falling asleep, the cortex remains active several minutes after the thalamus begins silencing external sensory information (Magnin et al., 2010), potentially providing a window of time in which internally-generated cortical activity has reduced competition from the external environment.

These types of top-down influences likely aren't the only contributor to hallucinatory perception, however. Hallucinations can be visually detailed, and sometimes reportedly even clearer than veridical percepts (Ffytche et al., 1998; Manford & Andermann, 1998; Teunisse et al., 1996). This implies hallucinations may not be a purely top-down phenomenon given that retrohierarchically extrapolating high-level information into low-level regions should result in a degradation of visual information (Breedlove et al., 2020). Many hallucinations are therefore likely to also involve

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589 aberrant low-level cortical activity (Hahamy et al., 2021; Manford & Andermann, 1998)
590 perhaps independent of, or in tandem with, amplified feedback signals.

591

Eyes-open versus eyes-closed imagery

593 We note that the model proposed in this paper does not presume any difference
594 between an eyes-closed and eyes-open state apart from the change to the content of
595 the sensory input each act produces. Though closing one's eyes might be ostensibly
596 interpreted as disconnecting sensory input, if this were the case, our model would
597 predict that closing one's eyes would immediately result in hallucinations. While
598 hallucinations can happen when the eyes are deprived of light, such phenomena
599 generally require either drugs (Fisher, 1991), or multiple hours (if not days) of light
600 deprivation to manifest (Merabet et al., 2004). It could be that darkness constitutes a
601 genuine sensory disconnection, yet with neural activity adapting to a lack of
602 competition on slow timescales, or it could be that sensory deprivation alone does not
603 equate to a true sensory disconnection. A formal disconnection or down-weighting of
604 sensory input could instead require large-scale neurochemical or neurophysiological
605 changes, such as which occur when shifting between different states of arousal. Such
606 potential changes are described in the section below. This may be why eyes-closed
607 hallucinations in neurotypical individuals are generally isolated to sleep onset and
608 offset (i.e. hypnagogic and hypnopompic hallucinations) or while asleep (i.e.
609 dreaming), but not while awake, and why hallucinations which occur in blind individuals
610 become most likely later in the day when drowsy, regardless of light perception
611 (Manford & Andermann, 1998).

612 Closing one's eyes (at least on short time-scales) might then be most aptly interpreted
613 as changing sensory input to a diffuse, dark, and generally unremarkable stimulus
614 image rather than disconnecting it altogether. Still, visual mental imagery is more likely
615 to be reported when eyes are closed rather than open (Sulfaro et al., 2023). However,
616 while eye-closure tends to aid the recall of fine-grained sensory information, potentially
617 by improving mental imagery, recall is not significantly improved compared to merely
618 looking at blank space (Vredeveldt et al., 2011). Yet, we acknowledge that our
619 conceptualisation of eye-closure may be a simplification given that neural activity
620 patterns between eyes-closed and eyes-open states can differ substantially even
621 when both occur in darkness (Marx et al., 2003, 2004). Even so, an eyes-closed state
622 could still improve mental imagery simply due to the signal-to-noise ratio advantage
623 gained by pitting an imagined stimulus representation against a homogenous closed-
624 eye scene, with the additional benefit of hiding attentional distractors.

625

Serotonin and acetylcholine: neurologically-plausible bottom-up and top-down weighting agents

628 This model implies that neural agents exist which modulate the relative contribution of
629 top-down and bottom-up processes. Given that this model predicts that weighting
630 schemes affect veridical and hallucinatory perception as well as mental imagery,
631 agents which modulate these processes might also be apt candidate weighting agents
632 in our current model.

633 Serotonin may be one such agent that modulates the contribution of bottom-up
634 information during visual experience. Classic hallucinogens act on the serotonergic
635 system via 5HT2A receptors (Nichols, 2016), and cortical serotonin levels are
636 dependent on plasma levels of tryptophan, serotonin's blood-brain-barrier-permeable
637 precursor (Fernstrom & Wurtman, 1971). Plasma tryptophan increases over the
638 course of the day, peaking in the late evening (Rao et al., 1994), approximately
639 corresponding to the most common time of hallucination onset for individuals with
640 Charles Bonnet Syndrome, peduncular hallucinosis, and Parkinson's Disease,
641 including for those without any light perception ability (Manford & Andermann, 1998).
642 Further, 5HT2A receptor expression in the ventral visual pathway of Parkinson's
643 Disease hallucinators is elevated compared to non-hallucinators (Ballanger et al.,
644 2010; Huot et al., 2010), while inverse agonists for this receptor are used to treat
645 Parkinson's Disease hallucinations (Yasue et al., 2016). Outside of hallucinatory
646 states, serotonin administered in the primary visual cortex of awake macaques acts
647 as a gain modulator, dampening cell responses to external sensory input without
648 affecting stimulus tuning or selectivity profiles (Seillier et al., 2017). In mice, this
649 dampening in V1 was mediated by a 5HT2A receptor agonist (Michaiel et al., 2019).

650 Additionally, acetylcholine may modulate the contribution of top-down information
651 during visual experience. The ratio of acetylcholine to serotonin is a factor in
652 hallucination aetiology (Manford & Andermann, 1998), and both serotonin and
653 acetylcholine target layer-five cortical pyramidal neurons, cells which have been
654 proposed as essential for manifesting conscious sensory perception (Aru et al., 2019).
655 High concentrations of acetylcholine can transition the activity of layer-five cortical
656 pyramidal neurons from being driven by feedforward inputs to feedback inputs, which
657 may mediate the hallucinatory experience of dreaming (Aru et al., 2020). The
658 concentration of cortical acetylcholine peaks during rapid-eye-movement sleep, where
659 dreaming is most likely, higher than during wakefulness and higher still than during
660 non-rapid-eye-movement sleep where consciousness is greatly impaired (M. G. Lee
661 et al., 2005). Hence, cortical acetylcholine concentrations may modulate feedback
662 connectivity in sensory cortices.

663 Given their actions in the visual system, serotonin and acetylcholine levels could be
664 plausible factors accounting for contextual and inter-individual differences in the
665 sensory experiences of mental imagery. Accordingly, they could also be considered
666 as factors which modulate inter-layer weightings within our proposed model. However,
667 ascertaining the role of such neurotransmitters in mental imagery research is
668 challenged by a reliance on human models for self-report, indistinct measurement
669 constructs (e.g. vividness ratings), and the restricted access of psychoactive
670 serotonergic drugs. Ultimately, there are many mechanisms by which our model can
671 facilitate hallucinations and such mechanisms may work in tandem. Note that in all
672 cases, our model does not explain how the initial internally-generated source stimulus
673 might be produced, only how it may be represented, regardless of whether it was
674 generated as part of a voluntary thought, involuntary hallucination, or otherwise.

675

Mental imagery as a dynamic process

677 So far, our predictions have been based on simulations where imagery, once
678 generated, continues to be generated indefinitely and without interruption. Under

these conditions, internally-generated content can continue to spread downwards until it reaches an equilibrium point and can spread no further. Yet, if imagery is interrupted or generated intermittently, it may never be generated for a period long enough for it to spread to its maximum possible extent, even if the balance of top-down and bottom-up processes favours a very low equilibrium point (i.e. highly-sensory mental imagery). Analogously, even though the maximum possible speed of a sportscar may be faster than that of a van, the sportscar will be outpaced if the van driver keeps the pedal floored while the sportscar driver only taps the pedal on and off. If mental image content can be generated continuously, or supported by a stream of simulated sensory information at lower levels, then the chances of that content spreading to its maximum possible extent are increased.

Visual versus auditory mental imagery

Though we have focused on visual mental imagery, mental imagery can occur in other sensory modalities, presumably through similar generative feedback. A complete account of mental imagery should be able to predict and explain modality-specific differences in imagined experience. Auditory hallucinations are roughly twice as common as visual hallucinations in schizophrenia and bipolar disorder (Waters et al., 2014), although how experiences differ between modalities specifically for mental imagery is not well understood. Comparisons generally rely on mental image vividness ratings (e.g. Andrade et al., 2014; Betts, 1910; Gissurarson, 1992; Schifferstein, 2009; Sheehan, 1967; Switras, 1978; Talamini et al., 2022). Yet, as such rating systems are ambiguously defined and difficult to meaningfully interpret (Richardson, 1988), findings have been understandably mixed. Here we make predictions about how the quality of mental imagery may differ between visual and auditory mental imagery, perhaps the two most-studied imagery modalities, based on differences in the brain's ability to synthesise sensory information in each modality.

Unlike with visual stimuli, our bodies are readily capable of producing their own auditory stimuli, using speech. Self-initiated movements, including the act of speech, produce signals (e.g. efference copies) which carry temporally-precise predictions of the sensory consequences of such movements (Curio et al., 2000). Sensory predictions related to motor movements have been suggested to aid mental imagery when they are produced in the absence of real movements (Gelding et al., 2019; Jack et al., 2019; Pruitt et al., 2019; Scott, 2013; Whitford et al., 2017). This could occur by supplying imagination with the sensory content needed to generate a mental image or by supporting existing mental imagery with a stream of sensory predictions linked to real or simulated movements. As discussed previously, anchoring mental images to continuous sensory information should improve the quality of mental imagery under our model.

While visual mental images could be supported by sensory predictions from real or simulated eye movements, eye movements generally contain information about *where* imagined content is, was or will be (e.g. Fourtassi et al., 2017). However, they are far less informative about *what* is actually being imagined in a given region of the visual field. In comparison, consider inner speech, a type of auditory imagery specifically relating to the imagination of oral sound content like words. If auditory imagery can be expressed as inner speech, such as through converting imagined sounds to

725 onomatopoeia, then real or simulated vocal movements could produce a stream of
726 temporally-precise sensory information not just informing *when* a particular imagined
727 sound should be heard, but also *what* the imagined sound content should be. In
728 essence, using motor systems, the brain could have a greater capacity to simulate
729 sensory features of imagined sounds compared to images, provided the imagined
730 sounds are somewhat possible to replicate vocally. Yet, even when not readily
731 imitable, sounds could still be imagined as some form of onomatopoeia, sacrificing
732 real-world accuracy in order to boost the sensory quality of the imagery experience.
733 Consequently, we expect that auditory mental imagery may often be a more
734 compelling sensory experience than visual mental imagery.

735

Limitations and future directions

737 The primary intention of this article is to highlight that competition from externally-
738 generated sensory input could be a major factor which explains the unique
739 phenomenology of mental imagery. Our modelling is mainly intended merely to provide
740 a simple example of how treating perception as a competitive process can explain
741 aspects of imagery, supporting the larger theoretical argument that mental imagery
742 should always be considered in tandem with cooccurring veridical perceptual
743 processes. Nonetheless, both our argument and our suggested model rely on some
744 assumptions.

745 Our most crucial restraint is that we require that internally- and externally-generated
746 perceptual processes utilise the same neural substrates such that interference can
747 occur. Our current understanding is that these processes do overlap (Dijkstra et al.,
748 2017, 2020; Ffytche et al., 1998), down to the laminar cortical (Bergmann et al., 2019;
749 Lawrence et al., 2018), if not cellular (Aru et al., 2020), level. However, differences
750 between each process may mean that overlap might vary across the visual hierarchy
751 (e.g. Lawrence et al., 2018), influencing the degree or nature of interference. Yet, even
752 if these processes do overlap, imagined representations may not necessarily
753 propagate smoothly along a serial, retrohierarchical cascade. If imagery utilises direct
754 feedback connections from associative cortices to primary sensory cortices, rather
755 than via a series of intermediate cortical units, interference may have radically different
756 outcomes.

757 We also rely on assumptions about how neural activity translates into subjective
758 experience. Namely, we assume that lower and higher levels of processing
759 respectively contribute to sensory and abstract features of perceptual experience. Yet,
760 encoding along the visual hierarchy may only correlate with the degree to which
761 semantic content of a perceptual experience is simple or complex, rather than the
762 degree to which such content is experienced in a sensory and modality-specific, rather
763 than non-sensory, way at all. Of course, ascertaining the neural substrates of
764 subjective experience is an immense area of investigation.

765 Although we make broad predictions about the decaying influence of internally-
766 generated stimuli towards primary sensory regions, the exact balance of this influence,
767 and its dynamics, would likely vary substantially with more neurologically-plausible
768 methods of simulating interference beyond the simple weighted-averaging rule used
769 to approximate interference in our model. Note also that our model does not comment
770 on any of the nonlinear transformations necessary to encode a representation within

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a layer, but only makes assumptions about how such representations, once formed, may be transmitted and combined. Modelling a more neurologically-plausible system would be a logical next step for investigating mental imagery as a competitive process. Further, it is entirely plausible that other mechanisms aside from competition could account for the segregated distributions of internally- and externally-generated content in the visual system. We merely show that simple models of competition can account for these distributions and many other imagery phenomena.

Our simulations also use retinal inputs (and generally imagined stimulus inputs) which are static and constant, so our simulations cannot account for the effects of neural adaptation on perceptual interference. In reality, retinally-stabilised images tend to induce a reversible blindness, greying-out the visual field. However, such blindness is suspected to be a very early, low-level effect, at or near the retina (Martinez-Conde et al., 2004). Within our model, this state should then be roughly equivalent to feeding in a homogenous field as a real stimulus input, such that the same logic regarding the imagery improvements (or lack thereof) associated with eye-closure and the perception of a dark room would also apply to the perceptual greying-out that occurs with retinally-stabilised images. However, neural adaptation could have many more consequential effects on mental imagery which future studies could explore.

Our model also assumes that feedforward and feedback processes are computationally equivalent. However, Koenig-Robert & Pearson (2021) argue that while feedforward signals initiated from visual input may drive action potentials in the visual cortex, feedback signals terminating in early visual areas tend to be more modulatory, guiding but not overriding activity induced by sensory input. They suggest that this asymmetry could account for the apparent difference in vividness between veridical and mental imagery. However, weak feedback could also be a logical consequence of competition within our model. Our simulations predict that the influence of internally-generated stimulus information should gradually diminish towards lower levels in the presence of bottom-up competition. At some point, this declining influence could fall below a threshold such that it can no longer drive action potentials. Yet, our model still uniquely predicts that feedback should remain influential when external competition is not present. Evidence supports this prediction, as feedback can drive action potentials in the visual cortex of neurotypical individuals during dreaming (Aru et al., 2020), including in neurons which are arguably crucial for manifesting conscious sensory perception (Aru et al., 2019). Hence, it's plausible that weak feedback follows from perceptual competition. Our model may then supplement the account of Koenig-Robert & Pearson (2021) which could otherwise be interpreted as precluding the possibility of purely top-down hallucinations. Asymmetries in feedforward and feedback processing can still be operationalised in our model by manipulating bottom-up and top-down weightings, but our model distinctly predicts that imagined percepts should be experienced in a less sensory manner than veridical percepts, even if feedforward and feedback processes are computationally equivalent, due to the interference caused by competing sensory input.

Overall, vindicating or falsifying competition as the origin of the quasi-sensory experience of mental imagery will ultimately require a detailed understanding of how neural representations of internally- and externally-generated perceptual content interact. Future studies may seek to explore the predicted impact of hierarchical competition on neural activity using alternative models of feedforward-feedback

818 interference, although our model still capably emulates findings on how imagined and
819 veridical information is distributed in real human brains (e.g. Lee et al., 2012; Spagna
820 et al., 2021; VanRullen & Reddy, 2019).

821

Conclusion

823 Overall, this work provides a formal framework for explaining the unique quasi-sensory
824 experience of mental imagery. We propose that internally-generated thoughts are
825 experienced along an axis from highly-abstract to highly-sensory in nature, aligning
826 with the degree of dimensionality that a given thought is represented in. Under this
827 assumption, we show that competition from bottom-up sensory input may prevent
828 imagined stimuli from being perceived in any substantially sensory way. Accounting
829 for competition in a hierarchical system can therefore provide sufficient conditions for
830 distinguishing imagined, veridical, and hallucinatory perception, as well as variation
831 within these phenomena. As modelling imagery competitively may resolve major
832 lingering questions in imagery research, we recommend future studies investigate the
833 exact manner by which internally- and externally-generated stimuli may be combined
834 in the brain. Ultimately, we conclude that mental imagery is most logically understood
835 as an intrinsically competitive process and should be largely considered as such in
836 ongoing research.

837

Acknowledgements

843

Data availability

845 No data was collected as part of this study.

846

References

848 Aldrich, M. S., Alessi, A. G., Beck, R. W., & Gilman, S. (1987). Cortical blindness: Etiology,
849   diagnosis, and prognosis. *Annals of Neurology*, *21*(2), 149–158.
850   https://doi.org/10.1002/ana.410210207
851 Andrade, J., May, J., Deeprose, C., Baugh, S.-J., & Ganis, G. (2014). Assessing vividness of
852   mental imagery: The Plymouth Sensory Imagery Questionnaire. *British Journal of
853   Psychology*, *105*(4), 547–563. https://doi.org/10.1111/bjop.12050
854 Aru, J., Siclari, F., Phillips, W. A., & Storm, J. F. (2020). Apical drive—A cellular mechanism of
855   dreaming? *Neuroscience & Biobehavioral Reviews*, *119*, 440–455.
856   https://doi.org/10.1016/j.neubiorev.2020.09.018
857 Aru, J., Suzuki, M., Rutiku, R., Larkum, M. E., & Bachmann, T. (2019). Coupling the State and
858   Contents of Consciousness. *Frontiers in Systems Neuroscience*, *13*.
859   https://doi.org/10.3389/fnsys.2019.00043

860   Ballanger, B., Strafella, A. P., van Eimeren, T., Zurowski, M., Rusjan, P. M., Houle, S., & Fox, S.
861   H. (2010). Serotonin 2A Receptors and Visual Hallucinations in Parkinson Disease. *Archives*
862   *of Neurology*, *67*(4), 416–421. https://doi.org/10.1001/archneurol.2010.35

863   Behrmann, M., Moscovitch, M., & Winocur, G. (1994). Intact visual imagery and impaired visual
864   perception in a patient with visual agnosia. *Journal of Experimental Psychology: Human*
865   *Perception and Performance*, *20*, 1068–1087. https://doi.org/10.1037/0096-1523.20.5.1068

866   Benson, T., & Park, S. (2013). Exceptional visuospatial imagery in schizophrenia; implications for
867   madness and creativity. *Frontiers in Human Neuroscience*, *7*.
868   https://doi.org/10.3389/fnhum.2013.00756

869   Bergmann, J., Morgan, A. T., & Muckli, L. (2019). Two distinct feedback codes in V1 for 'real' and
870   'imaginary' internal experiences. *BioRxiv*, 664870. https://doi.org/10.1101/664870

871   Betts, G. H. (1910). Review of: The Distribution and Functions of Mental Imagery. *Psychological*
872   *Bulletin*, *7*(10), 351–352. https://doi.org/doi:10.1037/h0064277

873   Binder, J. R. (2016). In defense of abstract conceptual representations. *Psychonomic Bulletin &*
874   *Review*, *23*(4), 1096–1108. https://doi.org/10.3758/s13423-015-0909-1

875   Breedlove, J. L., St-Yves, G., Olman, C. A., & Naselaris, T. (2020). Generative Feedback
876   Explains Distinct Brain Activity Codes for Seen and Mental Images. *Current Biology*.
877   https://doi.org/10.1016/j.cub.2020.04.014

878   Bridge, H., Harrold, S., Holmes, E. A., Stokes, M., & Kennard, C. (2012). Vivid visual mental
879   imagery in the absence of the primary visual cortex. *Journal of Neurology*, *259*(6), 1062–
880   1070. https://doi.org/10.1007/s00415-011-6299-z

881   Brodeur, M. B., Dionne-Dostie, E., Montreuil, T., & Lepage, M. (2010). The Bank of Standardized
882   Stimuli (BOSS), a New Set of 480 Normative Photos of Objects to Be Used as Visual Stimuli
883   in Cognitive Research. *PLOS ONE*, *5*(5), e10773.
884   https://doi.org/10.1371/journal.pone.0010773

885   Chatterjee, A., & Southwood, M. H. (1995). Cortical blindness and visual imagery. *Neurology*,
886   *45*(12), 2189–2195. https://doi.org/10.1212/WNL.45.12.2189

887   Chiu, L. P. W. (1989). Differential Diagnosis and Management of Hallucinations. *Journal of Hong*
888   *Kong Medical Association*, *41*(3), 292–297.

889   Cichy, R. M., Heinzle, J., & Haynes, J.-D. (2012). Imagery and Perception Share Cortical
890   Representations of Content and Location. *Cerebral Cortex*, *22*(2), 372–380.
891   https://doi.org/10.1093/cercor/bhr106

892   Curio, G., Neuloh, G., Numminen, J., Jousmäki, V., & Hari, R. (2000). Speaking modifies voice-
893   evoked activity in the human auditory cortex. *Human Brain Mapping*, *9*(4), 183–191.
894   https://doi.org/10.1002/(SICI)1097-0193(200004)9:4<183::AID-HBM1>3.0.CO;2-Z

895   de Gelder, B., Tamietto, M., Pegna, A. J., & Van den Stock, J. (2015). Visual imagery influences
896   brain responses to visual stimulation in bilateral cortical blindness. *Cortex*, *72*, 15–26.
897   https://doi.org/10.1016/j.cortex.2014.11.009

898   Dentico, D., Cheung, B. L., Chang, J.-Y., Guokas, J., Boly, M., Tononi, G., & Van Veen, B.
899   (2014). Reversal of cortical information flow during visual imagery as compared to visual
900   perception. *NeuroImage*, *100*, 237–243. https://doi.org/10.1016/j.neuroimage.2014.05.081

901   DiCarlo, J. J., & Cox, D. D. (2007). Untangling invariant object recognition. *Trends in Cognitive*
902   *Sciences*, *11*(8), 333–341. https://doi.org/10.1016/j.tics.2007.06.010

903   Dijkstra, N., Ambrogioni, L., Vidaurre, D., & van Gerven, M. (2020). Neural dynamics of
904   perceptual inference and its reversal during imagery. *ELife*, *9*, e53588.
905   https://doi.org/10.7554/eLife.53588

906   Dijkstra, N., Bosch, S. E., & Gerven, M. A. J. van. (2017). Vividness of Visual Imagery Depends
907   on the Neural Overlap with Perception in Visual Areas. *Journal of Neuroscience*, *37*(5),
908   1367–1373. https://doi.org/10.1523/JNEUROSCI.3022-16.2016

909   Dijkstra, N., Bosch, S. E., & van Gerven, M. A. J. (2019). Shared Neural Mechanisms of Visual
910   Perception and Imagery. *Trends in Cognitive Sciences*, *23*(5), 423–434.
911   https://doi.org/10.1016/j.tics.2019.02.004

912   Dijkstra, N., Hinne, M., Bosch, S. E., & van Gerven, M. A. J. (2019). Between-subject variability
913   in the influence of mental imagery on conscious perception. *Scientific Reports*, *9*(1), Article
914   1. https://doi.org/10.1038/s41598-019-52072-1

915   Dijkstra, N., Kok, P., & Fleming, S. M. (2022). Imagery adds stimulus-specific sensory evidence
916   to perceptual detection. *Journal of Vision*, *22*(2), 11. https://doi.org/10.1167/jov.22.2.11

917   Dijkstra, N., Mazor, M., Kok, P., & Fleming, S. (2021). Mistaking imagination for reality:
918   Congruent mental imagery leads to more liberal perceptual detection. *Cognition*, *212*,
919   104719. https://doi.org/10.1016/j.cognition.2021.104719

920 Dijkstra, N., Mostert, P., Lange, F. P. de, Bosch, S., & van Gerven, M. A. (2018). Differential
921   temporal dynamics during visual imagery and perception. *ELife*, *7*, e33904.
922   https://doi.org/10.7554/eLife.33904
923 Fernstrom, J. D., & Wurtman, R. J. (1971). Brain serotonin content: Physiological dependence on
924   plasma tryptophan levels. *Science*, *173*(3992), 149–152.
925   https://doi.org/10.1126/science.173.3992.149
926 Ffytche, D. H., Howard, R. J., Brammer, M. J., David, A., Woodruff, P., & Williams, S. (1998).
927   The anatomy of conscious vision: An fMRI study of visual hallucinations. *Nature*
928   *Neuroscience*, *1*(8), 738–742. https://doi.org/10.1038/3738
929 Fisher, C. M. (1991). Visual Hallucinations on Eye Closure Associated with Atropine Toxicity. A
930   Neurological Analysis and Comparison with other Visual Hallucinations. *Canadian Journal of*
931   *Neurological Sciences*, *18*(1), 18–27. https://doi.org/10.1017/S0317167100031255
932 Fourtassi, M., Rode, G., & Pisella, L. (2017). Using eye movements to explore mental
933   representations of space. *Annals of Physical and Rehabilitation Medicine*, *60*(3), 160–163.
934   https://doi.org/10.1016/j.rehab.2016.03.001
935 Galton, F. (1880). Statistics of Mental Imagery. *Mind*, *5*(19), 301–318.
936 Gelding, R. W., Thompson, W. F., & Johnson, B. W. (2019). Musical imagery depends upon
937   coordination of auditory and sensorimotor brain activity. *Scientific Reports*, *9*(1), Article 1.
938   https://doi.org/10.1038/s41598-019-53260-9
939 Gissurarson, L. R. (1992). Reported auditory imagery and its relationship with visual imagery.
940   *Journal of Mental Imagery*, *16*(3–4), 117–122.
941 Hahamy, A., Wilf, M., Rosin, B., Behrmann, M., & Malach, R. (2021). How do the blind 'see'? The
942   role of spontaneous brain activity in self-generated perception. *Brain*, *144*(1), 340–353.
943   https://doi.org/10.1093/brain/awaa384
944 Huot, P., Johnston, T. H., Darr, T., Hazrati, L.-N., Visanji, N. P., Pires, D., Brotchie, J. M., & Fox,
945   S. H. (2010). Increased 5-HT2A receptors in the temporal cortex of parkinsonian patients
946   with visual hallucinations. *Movement Disorders*, *25*(10), 1399–1408.
947   https://doi.org/10.1002/mds.23083
948 Ishai, A. (2010). Seeing faces and objects with the "mind's eye." *Archives Italiennes de Biologie*,
949   *148*(1), Article 1. https://doi.org/info:doi/10.5167/uzh-46897
950 Jack, B. N., Le Pelley, M. E., Han, N., Harris, A. W. F., Spencer, K. M., & Whitford, T. J. (2019).
951   Inner speech is accompanied by a temporally-precise and content-specific corollary
952   discharge. *NeuroImage*, *198*, 170–180. https://doi.org/10.1016/j.neuroimage.2019.04.038
953 Keogh, R., & Pearson, J. (2017). The perceptual and phenomenal capacity of mental imagery.
954   *Cognition*, *162*, 124–132. https://doi.org/10.1016/j.cognition.2017.02.004
955 Koenig-Robert, R., & Pearson, J. (2021). Why do imagery and perception look and feel so
956   different? *Philosophical Transactions of the Royal Society B: Biological Sciences*,
957   *376*(1817), 20190703. https://doi.org/10.1098/rstb.2019.0703
958 Kosslyn, S. M. (2005). Mental images and the Brain. *Cognitive Neuropsychology*, *22*(3–4), 333–
959   347. https://doi.org/10.1080/02643290442000130
960 Kosslyn, S. M., Alpert, N. M., Thompson, W. L., Maljkovic, V., Weise, S. B., Chabris, C. F.,
961   Hamilton, S. E., Rauch, S. L., & Buonanno, F. S. (1993). Visual Mental Imagery Activates
962   Topographically Organized Visual Cortex: PET Investigations. *Journal of Cognitive*
963   *Neuroscience*, *5*(3), 263–287. https://doi.org/10.1162/jocn.1993.5.3.263
964 Kosslyn, S. M., & Thompson, W. L. (2003). When is early visual cortex activated during visual
965   mental imagery? *Psychological Bulletin*, *129*(5), 723–746. https://doi.org/10.1037/0033-
966   2909.129.5.723
967 Lawrence, S. J. D., van Mourik, T., Kok, P., Koopmans, P. J., Norris, D. G., & de Lange, F. P.
968   (2018). Laminar Organization of Working Memory Signals in Human Visual Cortex. *Current*
969   *Biology: CB*, *28*(21), 3435-3440.e4. https://doi.org/10.1016/j.cub.2018.08.043
970 Lee, M. G., Hassani, O. K., Alonso, A., & Jones, B. E. (2005). Cholinergic Basal Forebrain
971   Neurons Burst with Theta during Waking and Paradoxical Sleep. *Journal of Neuroscience*,
972   *25*(17), 4365–4369. https://doi.org/10.1523/JNEUROSCI.0178-05.2005
973 Lee, S.-H., Kravitz, D. J., & Baker, C. I. (2012). Disentangling visual imagery and perception of
974   real-world objects. *NeuroImage*, *59*(4), 4064–4073.
975   https://doi.org/10.1016/j.neuroimage.2011.10.055
976 Linde-Domingo, J., Treder, M. S., Kerrén, C., & Wimber, M. (2019). Evidence that neural
977   information flow is reversed between object perception and object reconstruction from
978   memory. *Nature Communications*, *10*(1), Article 1. https://doi.org/10.1038/s41467-018-
979   08080-2

980 Magnin, M., Rey, M., Bastuji, H., Guillemant, P., Mauguière, F., & Garcia-Larrea, L. (2010).
981   Thalamic deactivation at sleep onset precedes that of the cerebral cortex in humans.
982   *Proceedings of the National Academy of Sciences*, *107*(8), 3829–3833.
983   https://doi.org/10.1073/pnas.0909710107
984 Manford, M., & Andermann, F. (1998). Complex visual hallucinations. Clinical and
985   neurobiological insights. *Brain*, *121*(10), 1819–1840.
986   https://doi.org/10.1093/brain/121.10.1819
987 Marks, D. F. (1973). Visual Imagery Differences in the Recall of Pictures. *British Journal of*
988   *Psychology*, *64*(1), 17–24. https://doi.org/10.1111/j.2044-8295.1973.tb01322.x
989 Martinez-Conde, S., Macknik, S. L., & Hubel, D. H. (2004). The role of fixational eye movements
990   in visual perception. *Nature Reviews Neuroscience*, *5*(3), Article 3.
991   https://doi.org/10.1038/nrn1348
992 Marx, E., Deutschländer, A., Stephan, T., Dieterich, M., Wiesmann, M., & Brandt, T. (2004). Eyes
993   open and eyes closed as rest conditions: Impact on brain activation patterns. *NeuroImage*,
994   *21*(4), 1818–1824. https://doi.org/10.1016/j.neuroimage.2003.12.026
995 Marx, E., Stephan, T., Nolte, A., Deutschländer, A., Seelos, K. C., Dieterich, M., & Brandt, T.
996   (2003). Eye closure in darkness animates sensory systems. *NeuroImage*, *19*(3), 924–934.
997   https://doi.org/10.1016/S1053-8119(03)00150-2
998 Matthews, N. L., Collins, K. P., Thakkar, K. N., & Park, S. (2014). Visuospatial imagery and
999   working memory in schizophrenia. *Cognitive Neuropsychiatry*, *19*(1), 17–35.
1000   https://doi.org/10.1080/13546805.2013.779577
1001 Merabet, L. B., Maguire, D., Warde, A., Alterescu, K., Stickgold, R., & Pascual-Leone, A. (2004).
1002   Visual hallucinations during prolonged blindfolding in sighted subjects. *Journal of Neuro-*
1003   *Ophthalmology: The Official Journal of the North American Neuro-Ophthalmology Society*,
1004   *24*(2), 109–113. https://doi.org/10.1097/00041327-200406000-00003
1005 Michaiel, A. M., Parker, P. R. L., & Niell, C. M. (2019). A Hallucinogenic Serotonin-2A Receptor
1006   Agonist Reduces Visual Response Gain and Alters Temporal Dynamics in Mouse V1. *Cell*
1007   *Reports*, *26*(13), 3475-3483.e4. https://doi.org/10.1016/j.celrep.2019.02.104
1008 Nichols, D. E. (2016). Psychedelics. *Pharmacological Reviews*, *68*(2), 264–355.
1009   https://doi.org/10.1124/pr.115.011478
1010 Pearson, J. (2019). The human imagination: The cognitive neuroscience of visual mental
1011   imagery. *Nature Reviews Neuroscience*, *20*(10), Article 10. https://doi.org/10.1038/s41583-
1012   019-0202-9
1013 Pearson, J., & Kosslyn, S. M. (2015). The heterogeneity of mental representation: Ending the
1014   imagery debate. *Proceedings of the National Academy of Sciences*, *112*(33), 10089–10092.
1015   https://doi.org/10.1073/pnas.1504933112
1016 Popham, S. F., Huth, A. G., Bilenko, N. Y., Deniz, F., Gao, J. S., Nunez-Elizalde, A. O., &
1017   Gallant, J. L. (2021). Visual and linguistic semantic representations are aligned at the border
1018   of human visual cortex. *Nature Neuroscience*, *24*(11), Article 11.
1019   https://doi.org/10.1038/s41593-021-00921-6
1020 Powers, A. R., Kelley, M., & Corlett, P. R. (2016). Hallucinations as Top-Down Effects on
1021   Perception. *Biological Psychiatry: Cognitive Neuroscience and Neuroimaging*, *1*(5), 393–
1022   400. https://doi.org/10.1016/j.bpsc.2016.04.003
1023 Pruitt, T. A., Halpern, A. R., & Pfordresher, P. Q. (2019). Covert singing in anticipatory auditory
1024   imagery. *Psychophysiology*, *56*(3), e13297. https://doi.org/10.1111/psyp.13297
1025 Reichert, D. P., Seriès, P., & Storkey, A. J. (2013). Charles Bonnet Syndrome: Evidence for a
1026   Generative Model in the Cortex? *PLOS Computational Biology*, *9*(7), e1003134.
1027   https://doi.org/10.1371/journal.pcbi.1003134
1028 Richardson, J. E. (1988). Vividness and unvividness: Reliability, consistency, and validity of
1029   subjective imagery ratings. *Journal of Mental Imagery*, *12*(3–4), 115–122.
1030 Schifferstein, H. N. J. (2009). Comparing Mental Imagery across the Sensory Modalities.
1031   *Imagination, Cognition and Personality*, *28*(4), 371–388. https://doi.org/10.2190/IC.28.4.g
1032 Schooler, J. W., Smallwood, J., Christoff, K., Handy, T. C., Reichle, E. D., & Sayette, M. A.
1033   (2011). Meta-awareness, perceptual decoupling and the wandering mind. *Trends in*
1034   *Cognitive Sciences*, *15*(7), 319–326. https://doi.org/10.1016/j.tics.2011.05.006
1035 Scott, M. (2013). Corollary Discharge Provides the Sensory Content of Inner Speech.
1036   *Psychological Science*, *24*(9), 1824–1830. https://doi.org/10.1177/0956797613478614
1037 Seillier, L., Lorenz, C., Kawaguchi, K., Ott, T., Nieder, A., Pourriahi, P., & Nienborg, H. (2017).
1038   Serotonin Decreases the Gain of Visual Responses in Awake Macaque V1. *Journal of*
1039   *Neuroscience*, *37*(47), 11390–11405. https://doi.org/10.1523/JNEUROSCI.1339-17.2017

23

Sheehan, P. W. (1967). A shortened form of Betts' questionnaire upon mental imagery. *Journal of Clinical Psychology*, *23*(3), 386–389. https://doi.org/10.1002/1097-4679(196707)23:3<386::AID-JCLP2270230328>3.0.CO;2-S

Shine, J. M., Keogh, R., O'Callaghan, C., Muller, A. J., Lewis, S. J. G., & Pearson, J. (2015). Imagine that: Elevated sensory strength of mental imagery in individuals with Parkinson's disease and visual hallucinations. *Proceedings. Biological Sciences*, *282*(1798), 20142047. https://doi.org/10.1098/rspb.2014.2047

Smallwood, J. (2011). Mind-wandering While Reading: Attentional Decoupling, Mindless Reading and the Cascade Model of Inattention. *Language and Linguistics Compass*, *5*(2), 63–77. https://doi.org/10.1111/j.1749-818X.2010.00263.x

Spagna, A., Hajhajate, D., Liu, J., & Bartolomeo, P. (2021). Visual mental imagery engages the left fusiform gyrus, but not the early visual cortex: A meta-analysis of neuroimaging evidence. *Neuroscience & Biobehavioral Reviews*, *122*, 201–217. https://doi.org/10.1016/j.neubiorev.2020.12.029

Sulfaro, A. A., Robinson, A. K., & Carlson, T. A. (2023). *Comparing mental imagery experiences across visual, auditory, and other sensory modalities* (p. 2023.05.15.540306). bioRxiv. https://doi.org/10.1101/2023.05.15.540306

Switras, J. E. (1978). An Alternate-Form Instrument to Assess Vividness and Controllability of Mental Imagery in Seven Modalities. *Perceptual and Motor Skills*, *46*(2), 379–384. https://doi.org/10.2466/pms.1978.46.2.379

Talamini, F., Vigl, J., Doerr, E., Grassi, M., & Carretti, B. (2022). Auditory and visual mental imagery in musicians and non-musicians. *Musicae Scientiae*, 10298649211062724. https://doi.org/10.1177/10298649211062724

Teunisse, R. J., Zitman, F. G., Cruysberg, J. R. M., Hoefnagels, W. H. L., & Verbeek, A. L. M. (1996). Visual hallucinations in psychologically normal people: Charles Bonnet's syndrome. *The Lancet*, *347*(9004), 794–797. https://doi.org/10.5555/uri:pii:S0140673696908697

VanRullen, R., & Reddy, L. (2019). Reconstructing faces from fMRI patterns using deep generative neural networks. *Communications Biology*, *2*(1), Article 1. https://doi.org/10.1038/s42003-019-0438-y

Vredeveldt, A., Hitch, G. J., & Baddeley, A. D. (2011). Eyeclosure helps memory by reducing cognitive load and enhancing visualisation. *Memory & Cognition*, *39*(7), 1253–1263. https://doi.org/10.3758/s13421-011-0098-8

Wais, P. E., Rubens, M. T., Boccanfuso, J., & Gazzaley, A. (2010). Neural Mechanisms Underlying the Impact of Visual Distraction on Retrieval of Long-Term Memory. *Journal of Neuroscience*, *30*(25), 8541–8550. https://doi.org/10.1523/JNEUROSCI.1478-10.2010

Walpola, I. C., Muller, A. J., Hall, J. M., Andrews-Hanna, J. R., Irish, M., Lewis, S. J. G., Shine, J. M., & O'Callaghan, C. (2020). Mind-wandering in Parkinson's disease hallucinations reflects primary visual and default network coupling. *Cortex; a Journal Devoted to the Study of the Nervous System and Behavior*, *125*, 233–245. https://doi.org/10.1016/j.cortex.2019.12.023

Waters, F., Collerton, D., Ffytche, D. H., Jardri, R., Pins, D., Dudley, R., Blom, J. D., Mosimann, U. P., Eperjesi, F., Ford, S., & Larøi, F. (2014). Visual Hallucinations in the Psychosis Spectrum and Comparative Information From Neurodegenerative Disorders and Eye Disease. *Schizophrenia Bulletin*, *40*(Suppl_4), S233–S245. https://doi.org/10.1093/schbul/sbu036

Whitford, T. J., Jack, B. N., Pearson, D., Griffiths, O., Luque, D., Harris, A. W., Spencer, K. M., & Le Pelley, M. E. (2017). Neurophysiological evidence of efference copies to inner speech. *ELife*, *6*, e28197. https://doi.org/10.7554/eLife.28197

Wunderlich, G., Suchan, B., Volkmann, J., Herzog, H., Hömberg, V., & Seitz, R. J. (2000). Visual Hallucinations in Recovery From Cortical Blindness: Imaging Correlates. *Archives of Neurology*, *57*(4), 561–565. https://doi.org/10.1001/archneur.57.4.561

Xie, S., Kaiser, D., & Cichy, R. M. (2020). Visual Imagery and Perception Share Neural Representations in the Alpha Frequency Band. *Current Biology*, *30*(13), 2621-2627.e5. https://doi.org/10.1016/j.cub.2020.04.074

Yasue, I., Matsunaga, S., Kishi, T., Fujita, K., & Iwata, N. (2016). Serotonin 2A Receptor Inverse Agonist as a Treatment for Parkinson's Disease Psychosis: A Systematic Review and Meta-analysis of Serotonin 2A Receptor Negative Modulators. *Journal of Alzheimer's Disease: JAD*, *50*(3), 733–740. https://doi.org/10.3233/JAD-150818

Zago, S., Corti, S., Bersano, A., Baron, P., Conti, G., Ballabio, E., Lanfranconi, S., Cinnante, C., Costa, A., Cappellari, A., & Bresolin, N. (2010). A Cortically Blind Patient With Preserved

1099   Visual Imagery. *Cognitive and Behavioral Neurology*, *23*(1), 44–48.

1100   https://doi.org/10.1097/WNN.0b013e3181bf2e6e

1101 Zeman, A. Z. J., Della Sala, S., Torrens, L. A., Gountouna, V.-E., McGonigle, D. J., & Logie, R.

1102   H. (2010). Loss of imagery phenomenology with intact visuo-spatial task performance: A

1103   case of 'blind imagination.' *Neuropsychologia*, *48*(1), 145–155.

1104   https://doi.org/10.1016/j.neuropsychologia.2009.08.024

1105