



Special issue: Research report

The neural correlates of visual imagery vividness — An fMRI study and literature review



Jon Fulford^a, Fraser Milton^b, David Salas^c, Alicia Smith^c, Amber Simler^c,
Crawford Winlove^d and Adam Zeman^{c,*}

^a NIHR Exeter Clinical Research Facility, University of Exeter Medical School, St Luke's Campus, Exeter, UK

^b Discipline of Psychology, University of Exeter, Washington Singer Laboratories, Exeter, UK

^c Cognitive Neurology Research Group, University of Exeter Medical, School, College House, St Luke's Campus, Exeter, UK

^d University of Exeter Medical, School, College House, St Luke's Campus, Exeter, UK

ARTICLE INFO

Article history:

Received 28 February 2017

Reviewed 19 June 2017

Revised 11 August 2017

Accepted 13 September 2017

Published online 3 October 2017

Keywords:

Visual imagery

Vividness

Aphantasia

Imagination

fMRI

ABSTRACT

Using the Vividness of Visual Imagery Questionnaire we selected 14 high-scoring and 15 low-scoring healthy participants from an initial sample of 111 undergraduates. The two groups were matched on measures of age, IQ, memory and mood but differed significantly in imagery vividness. We used fMRI to examine brain activation while participants looked at, or later imagined, famous faces and famous buildings. Group comparison revealed that the low-vividness group activated a more widespread set of brain regions while visualising than the high-vividness group. Parametric analysis of brain activation in relation to imagery vividness across the entire group of participants revealed distinct patterns of positive and negative correlation. In particular, several posterior cortical regions show a positive correlation with imagery vividness: regions of the fusiform gyrus, posterior cingulate and parahippocampal gyri (BAs 19, 29, 31 and 36) displayed exclusively positive correlations. By contrast several frontal regions including parts of anterior cingulate cortex (BA 24) and inferior frontal gyrus (BAs 44 and 47), as well as the insula (BA 13), auditory cortex (BA 41) and early visual cortices (BAs 17 and 18) displayed exclusively negative correlations. We discuss these results in relation to a previous, functional imaging study of a clinical case of 'blind imagination', and to the existing literature on the functional imaging correlates of imagery vividness and related phenomena in visual and other domains.

© 2018 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

* Corresponding author. Cognitive Neurology Research Group, University of Exeter Medical, School, College House, St Luke's Campus, Exeter, EX1 2LU, UK.

E-mail addresses: j.fulford@exeter.ac.uk (J. Fulford), F.N.Milton@exeter.ac.uk (F. Milton), savedalas@me.com (D. Salas), alicia64@hotmail.co.uk (A. Smith), amber.c.simler@gmail.com (A. Simler), C.I.P.Winlove@exeter.ac.uk (C. Winlove), a.zeman@exeter.ac.uk (A. Zeman).

<https://doi.org/10.1016/j.cortex.2017.09.014>

0010-9452/© 2018 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

1. Introduction

The ability to imagine is a defining feature of human cognition (Dunbar, 2004). It enables us to represent items and events in their absence, allowing us to escape from the limitations of our current perspective into a limitless range of virtual worlds. While we can simulate many aspects of our experience and behaviour, for most of us, visual imagery – ‘visualisation’ – is a particularly prominent component of our imaginative lives. The capacity to visualise deliberately – for example the look of an apple or of our front door – presupposes several more basic cognitive functions. These include i) executive processes required to select, initiate, maintain and monitor visualisation, ii) memory processes, required to supply information about the items which are to be visualised and iii) quasi-perceptual processes which are thought to give the visual image its ‘visual’ qualities (Daselaar, Porat, Huijbers, & Pennartz, 2010; Zvyagintsev, Clemens, Chechko, Mathiak, Sack, & Mathiak, 2013). Studies of visual imagery impairments (Farah, 1984), and, more recently functional imaging studies of visualisation (Ishai, 2010; Kosslyn, Ganis, & Thompson, 2001; Pearson, Naselaris, Holmes, & Kosslyn, 2015), have broadly supported a neurocognitive model of imagination with these three major components. Thus there is evidence that visual imagery is linked to activation of supramodal, frontoparietal, areas associated with attention and cognitive control (Ishai, Ungerleider, & Haxby, 2000; Zvyagintsev et al., 2013), regions of the default mode network, associated with introspective cognition and memory (Daselaar et al., 2010; Zvyagintsev et al., 2013), and visual cortical regions most strongly activated by visual perception itself (Ishai et al., 2000). Although there is a broad consensus on these conclusions from functional imaging studies of visual imagery, aspects of the underlying processing remain controversial. For example, the relative importance of the individual cortical visual areas to imagery, especially area V1 (Cui, Jeter, Yang, Montague, & Eagleman, 2007; Daselaar et al., 2010; Pearson et al., 2015), and the precise role of supramodal brain systems, such as the default mode network, in visual imagery continue to be debated (Amedi, Malach, & Pascual-Leone, 2005; Daselaar et al., 2010; Zvyagintsev et al., 2013).

The majority of such studies have focussed on the neural basis of visualisation without regard to individual differences in imagery vividness. However, there is well-established evidence for such differences (Faw, 2009, 1997; Galton, 1880; McKelvie, 1995). A handful of studies (Amedi et al., 2005; Belardinelli et al., 2009; Cui et al., 2007; Daselaar et al., 2010; Dijkstra, Bosch, & Van Gerven, 2017; Lee, Kravitz, & Baker, 2012; Logie, Pernet, Buonocore, & Della Sala, 2011; Motes, Malach, & Kozhevnikov, 2008; Schienle, Schafer, Pignaneli & Vaitl, 2009) have specifically investigated the neural correlates of imagery vividness, with somewhat variable findings. Most studies, however, have found a correlation between imagery vividness and activation in higher-order occipito-temporal and limbic regions [including e.g., medial temporal lobe (MTL), retrolimbic cortex (BA 30), occipital cortex (BA 19) and posterior temporal cortex (BA 37), more fully discussed below]. Differences between the findings of these studies, for example relating to the role of early visual cortices, are likely

to be due, at least in part, to differences in the tasks used to elicit imagery, the approaches to quantifying and contrasting differences in imagery vividness and the functional imaging analyses.

The current study is inspired by our previous report of a clinical case, MX (Zeman et al., 2010). MX abruptly lost the ability to visualise following a cardiac procedure. His dreams became avidual. Unexpectedly, he performed normally on standard measures of visual imagery, but appeared to do so in the absence of any conscious experience of imagery. This combination of findings led us to describe his case in terms of ‘blind imagination’ by analogy with ‘blindsight’ (Weiskrantz, 1998). A functional MRI study revealed that while his brain activation during face perception was identical to that of controls, his brain activity during imagination of famous faces was markedly different. In particular, by comparison with controls, he hypoactivated the fusiform gyri and other temporo-occipital regions while hyperactivating a group of predominantly anterior regions, in particular the right anterior cingulate cortex. Since our initial description of the case of MX, we have described a group of individuals with a lifelong absence of visualisation, a phenomenon we have termed ‘aphantasia’ (Zeman, Dewar & Della Sala, 2015, 2016). The neural basis of aphantasia has yet to be determined.

In the present study we extend the exploration of the neural basis of inter-individual variation in imagery vividness. Our study is the first to contrast brain activation during visual imagery among individuals preselected on the basis of low or high scores on a standard measure of imagery vividness, the Vividness of Visual Imagery Questionnaire (VVIQ) (Marks, 1973) (though see Motes et al., 2008 for a related approach). Our study had two key aims: firstly, to investigate whether activity in the regions identified in our work with MX is modulated by the degree of imagery vividness in healthy individuals. We ask a) whether there are any detectable differences in brain activation during visual imagery tasks between individuals within high and low vividness groups; b) whether there are any correlations between brain activation and the vividness of individual visual images, as reported by participants during the scanning procedure. Our second aim was to review existing studies of the neural correlates of imagery vividness, placing our own results in context, identifying common ground across studies and understanding the reasons for discrepancies between them.

2. Material and methods

2.1. Participants and subjective vividness rating

One hundred and eleven students from the University of Exeter were recruited and gave written informed consent in accordance with ethical guidelines. Each subject completed a modified VVIQ to measure vividness of visual imagery. The VVIQ was a version of a standardised battery of 16 visualisation questions which assesses the general experience of imagery (Marks, 1973). Participants were asked to create a mental image (e.g., a rising sun) and rate its vividness on a 5-point Likert scale. On the modified scale high scores indicate vivid, low scores faint visual imagery. Ratings across these

items were averaged to produce an imagery vividness score. Twenty nine individuals with the highest and lowest VVIQ scores were selected for the experimental and neuropsychological phases of the study; this resulted in a high-vividness group ($N = 14$) and a low-vividness group ($N = 15$).

2.2. Neuropsychological assessment

Standard neuropsychological tests were used to assess general intelligence [Wechsler Abbreviated Scale of Intelligence (WASI) (Wechsler, 1999)], verbal and visual memory abilities (WMS) (Wechsler Memory Scale-IIIIR (Wechsler, 1997). Depression and anxiety were measured using the Hospital Anxiety and Depression Scale (HADS) (Zigmond & Snaith, 1983).

2.3. fMRI protocol: experimental task

Scanning was performed using a 1.5 T system (Intera, Philips, The Netherlands) at the Exeter University Magnetic Resonance Research Centre (Exeter, UK). fMRI was undertaken using a T2* weighted single shot echoplanar (EPI) scanning sequence (Repetition time (TR) = 3 sec, Echo time (TE) = 50 msec, resolution $2.88 \times 2.88 \times 3.5$ mm, 35 slices) and comprised two imaging runs each of 330 dynamics, resulting in a scanning time of 16.5 min per run. Following completion of the fMRI protocol a high-resolution T1-weighted anatomical image with a resolution $0.9 \times 0.9 \times 0.9$ mm was acquired.

During the fMRI protocol participants undertook a modified version of the task performed by MX (Zeman et al., 2010) which consisted of stimuli belonging to four different classes, grouped into blocks, presented in each run: 'Perception', involving presentation of black and white images of either famous faces or places, one category presented in each run, with the run order randomized; 'Perception control', involving the presentation of very low resolution inverted versions of the same famous faces/places images; 'Imagery', involving presentation of the names of previously presented faces or places with the intention that the participant imagines these; 'Imagery control', involving the presentation of letter strings with the request that the participants should not undertake any visual imagery. An example image presented alongside its low resolution control version is illustrated in Fig. 1. In total 36 famous face and 36 famous place stimuli were used.

Each block began with a presentation of the block's identity e.g., 'Imagery' for 1s duration. In the 'Perception' blocks four different images were sequentially presented per block, each

lasting for 7 sec. In the 'Imagery' block text stimuli corresponding to the name of a famous face or place whose image was shown in the previous 'Perception' block were presented for 800 msec. This was then followed by a 5.2 sec period where a fixation cross was presented and participants attempted to imagine the face or place specified in the text, with the sequence repeated four times within the block. The control conditions were identical to the imagery and perception ones in terms of timings and number of stimuli presented. However, for the 'Perception control' the images presented were the very low resolution inverted versions of the famous faces/places images and for the 'Imagery control' a nonsense text stream was presented followed by the same fixation cross as for the 'imagery' block. A schematic timeline of the procedure is shown in Fig. 2. The block sequence cycle in Fig. 2 was repeated 9 times with different stimuli within each cycle and with the same block order being applied, namely: Perception, Imagery, Perception control, Imagery control. No stimulus was repeated in the experiment. Following the scanning session, immediately after participants had been removed from the scanner, they were shown the same images on a laptop that they had previously been presented, and asked to rate the intensity of the visual imagery the image had provoked during the fMRI protocol (on a 1–5 scale, with 5 corresponding to the most intense visual imagery) with individual results recorded and an average for each participant determined.

2.4. fMRI protocol: data analysis

All data analysis was undertaken using SPM5 software (www.fil.ion.ucl.ac.uk/spm). The data from the two separate fMRI runs were treated as separate sessions within the analysis, which consisted of images being realigned, coregistered to the T1 structural images, normalized to the Montreal Neurological Institute template (MNI305) and smoothed using a Gaussian kernel of 8 mm full-width half-maximum. Following estimation using a general linear model employing a hemodynamic response function together with temporal and dispersion derivatives to model the blood oxygen level dependent response and including 6 head movement parameters as regressors, statistical analysis was carried out to compare activation patterns associated with the 'Perception'-'Perception control' and 'Imagery'-'Imagery control' conditions for each individual. Comparisons were then undertaken at a groupwise level comparing the responses between the high- and low-vividness groups. Clusters were anatomically identified by



Fig. 1 – Example of an image presented within the fMRI protocol alongside its control version.

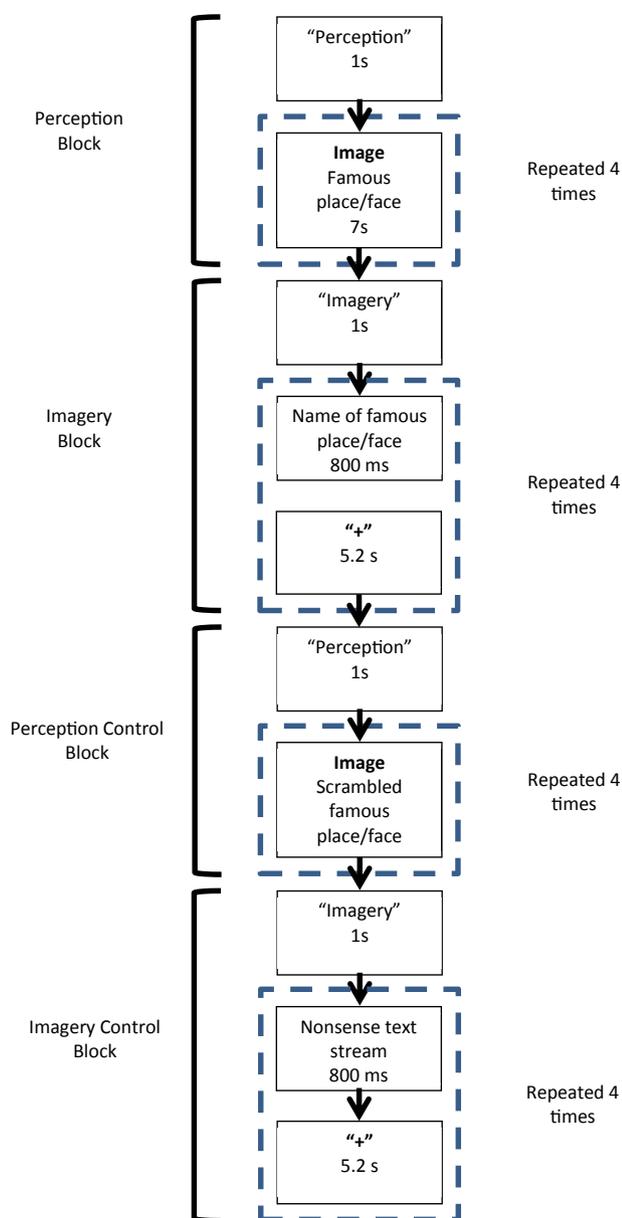


Fig. 2 – Schematic illustrating the timeline of the fMRI protocol. Text in speech marks (“”) indicates text that is presented to the participant. Text in bold is indicative of an image that is presented to the participant, with an explanation of the image contents described beneath. Dotted lines around a section indicate it is repeated a number of times as described by the text immediately to its right. Times illustrate the length of time each section is presented.

initially converting their MNI coordinates into Talairach space and then using Talairach Daemon software (Lancaster, Rainey, et al., 1997; Lancaster, Woldorff et al., 2000) to determine their location.

In addition, the first-order linear parametric analysis option integrated in SPM5 was employed to identify regions both positively and negatively correlated with increased vividness. These analyses were undertaken at the whole group level,

combining individuals from the high- and low-vividness groups in order to increase power to determine those brain regions whether there was a relationship between the vividness of reported imagery and brain activation.

As a result of an uneven distribution in reported scores, the 1–5 scale used to rate the intensity of the visual imagery the image had provoked during the fMRI protocol was collapsed to a three point scale within the parametric analysis. Under such a system, reported scores of 1 or 2 were combined to give a new score of 1 (low vividness), a reported score of 3 was redefined as 2 (medium vividness) and scores of 4 or 5 were combined to give a new score of 3 (high vividness).

All contrasts were set at an uncorrected threshold of $p < 0.001$ and a minimum cluster size of 20 voxels. The use of both a height and a cluster threshold to correct for multiple comparisons has been shown to be an effective way of safeguarding against Type I whilst ensuring sensitivity to avoid Type II errors (e.g., Forman et al., 1995; Poline, Worsley, Evans, & Friston, 1997). Indeed, employing both height and cluster thresholds have been shown to lead to more replicable results than applying a height threshold alone (Thirion et al., 2007).

2.5. Statistical analysis of neuropsychological results

Between group analyses of demographic data and neuropsychological test scores were performed in the Statistical Package for Social Sciences (version 21.0; SPSS Inc., Chicago, USA). Inspection of Q-Q Plots and Levene’s Test for Equality of Variances respectively revealed that scores were normally distributed and there was homogeneity of variance; therefore independent *t*-tests were run on the data. The correlation between VVIQ scores and self-reported levels of visual imagery during the fMRI protocol were assessed using the Pearson correlation coefficient. All statistical analyses were performed with a significance level of $p \leq .05$.

3. Results

3.1. Participant characteristics

Table 1 shows the characteristics of the two study groups. The groups were matched for age ($p = .200$), IQ ($p = .550$) and gender ($p = .893$). There was no difference between groups on the abbreviated WMS-III-R ($p = .804$). On the HADS, there was no significant difference in anxiety scores ($p = .304$) or depression scores ($p = .576$) between the two groups. There was a highly significant difference in VVIQ scores between the high and low imagery groups [respective means/item 4.05 (Range 3.63–4.80) (Averages: Males 3.93, Females 4.12) vs 3.11 (Range 2.57–3.61) (Averages: Males 3.36, Females 2.99), $p < .001$]. Likewise, there was a highly significant difference in the average self-reported post-scanning imagery scores between the high and low imagery groups [respective means/item 2.75 (Range 2.51–2.99) (Averages: Males 2.75, Females 2.74) vs 2.06 (Range 1.60–2.63) (Averages: Males 2.26, Females 1.97), $p < .001$]. When the average self-reported post-scanning imagery scores for each individual over all images was correlated with their average VVIQ results, across all individuals from both groups, there was a significant positive

Table 1 – Demographic and neuropsychological profile for high and low imaginers.

	Low imaginers (N = 15) Mean (SD)	High imagers (N = 14) Mean (SD)
Age (years)	22.00 (4.02)	21.27 (3.93)
Sex ratio (M/F)	5/10	5/9
WAIS full scale IQ	119.87 (12.11)	122.79 (13.60)
AbbrevWMS-IIIR	110.07 (9.77)	108.86 (15.38)
VVIQ total score ^a	46.08 (4.8)	67.36 (5.6)
HADS		
Anxiety score	5.27 (2.69)	4.21 (2.72)
Depression score	1.87 (1.36)	1.57 (1.45)

WASI – Wechsler Abbreviated Scale of Intelligence (Wechsler, 1999).
WMS – Wechsler Memory Scale-IIIR (Wechsler, 1997).
VVIQ – Vividness of Visual Imagery questionnaire.
HADS – Hospital Anxiety and Depression Scale (Zigmond & Snaith, 1983).
^a Significant group difference (independent t-test, $p < .001$).

correlation [$r(29) = .953, p < .0001$]. There were also significant positive relationships when place and face images were considered separately [Faces: $r(29) = .957, p < .001$; Places $r(29) = .943, p < .001$].

3.2. Activation differences between high and low vividness groups during imagination

In a whole brain analysis, numerous regions, widely distributed across both hemispheres, were activated more strongly during imagination in the low vividness group than in the high vividness group (Table 2, Fig. 3). The reverse subtraction revealed that only brain regions, in the medial frontal lobe and insula were activated more strongly during imagination in the high than the low imagery group (Table 3, Fig. 4).

3.3. Relationship between brain activation and reported vividness of visual images

We asked whether there were brain regions in which activation correlated, positively or negatively, with imagery

Table 2 – Neural correlates of imagination: Brain areas where activation was greater in the low vividness group than the high vividness group during the imagery task.

Anatomical area	BA	Hemi	Co-ordinates			K	Z-score
			X	Y	Z		
Supramarginal Gyrus	40	L	-46	-41	33	24	5.08
Superior Frontal Gyrus	10	L	-18	56	-5	30	4.99
Middle Frontal Gyrus	8/9/10	L	-36	31	30	72	4.90
Cingulate Gyrus	32	L	-14	6	40	59	4.90
Middle Occipital Gyrus	18	L	-28	-78	4	31	4.77
Superior temporal gyrus	22	L	-38	-50	21	52	4.71
Insula	13	L	-34	-9	24	25	4.46
Precentral Gyrus	6	L	-53	1	26	46	4.35
Cingulate Gyrus	23	L	-10	-14	32	20	4.21
Inferior Parietal Lobule	40	L	-50	-48	45	25	4.20
Cingulate Gyrus	24	L	-18	-16	38	26	4.11
Caudate	-	L	-20	-18	26		3.45
Middle Temporal Gyrus	39	L	-36	-65	20	31	3.93
Medial Frontal Gyrus	9/10	L	-4	53	18	27	3.68
Middle Temporal Gyrus	39	L	-36	-65	20	31	3.93
Medial Frontal Gyrus	9/10	L	-4	53	18	27	3.68
Superior temporal gyrus	22/41	R	46	-18	-3	76	4.78
Insula	13	R	45	-13	8		4.19
Middle Frontal Gyrus	6/9/10/46	R	34	42	33	126	4.75
Superior Frontal Gyrus	9/10	R	38	38	28		4.62
Middle Occipital Gyrus	18	R	18	-85	15	30	4.66
Cuneus	17	R	22	-86	23		3.35
Lentiform Nucleus	-	R	18	10	9	30	4.51
Inferior frontal gyrus	9	R	48	3	22	28	4.49
Precuneus	7/31	R	20	-57	32	39	4.37
Anterior cingulate	24	R	10	28	17	45	4.30
Declive	-	R	30	-61	22	23	3.90
Anterior cingulate	32	R	2	38	20	25	3.89

BA: Brodmann area(s).

Hemi: Hemisphere activation present in-left (L) or right (R).

K: Cluster size.

Z-score: peak Z-score.

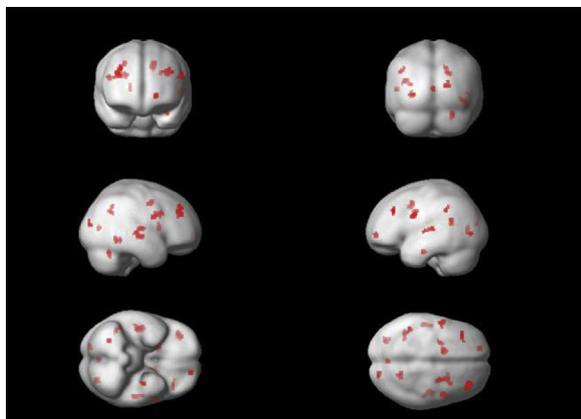


Fig. 3 – Brain regions activated more strongly during imagination in the low-vidviness group than in the high-vidviness group.

vidviness judged, image by image, across the entire group of participants. Areas of positive correlation are shown in Table 4 (Fig. 5), areas of negative correlation in Table 5 (Fig. 6). A series of posterior brain regions, extending from the occipital to the parietal and temporal lobes, show a positive correlation with vividness. These areas include the superior occipital gyrus (SOG) (BA 19), superior (BA 39) and middle temporal gyri (BAs 21, 22), precuneus (BAs 7, 19) and posterior cingulate (BAs 30, 31), fusiform (BAs 19, 37) and parahippocampal gyri (BAs 19, 31, 37). A largely contrasting set of areas displayed a negative

Table 3 – Neural correlates of imagination: Brain areas where activation was greater in the high vividness group than the low vividness group during the imagery task.

Anatomical area	BA	Hemi	Co-ordinates			K	Z-score
			X	Y	Z		
Medial frontal lobe	6	L	-6	-24	60	50	4.95
Insula	13	L	-28	-36	20	24	4.78

BA: Brodmann area(s).
Hemi: Hemisphere activation present in-left (L) or right (R).
K: Cluster size.
Z-score: peak Z-score.

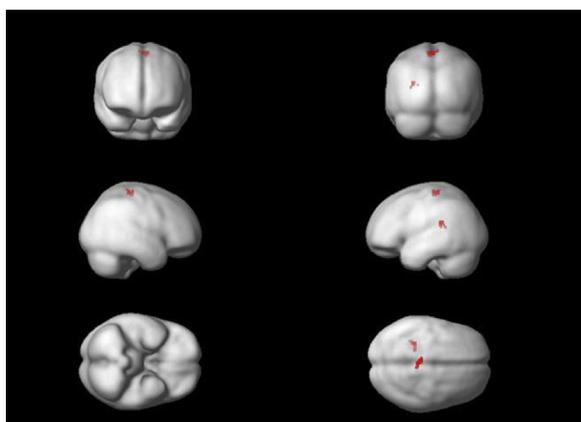


Fig. 4 – Brain regions activated more strongly during imagination in the high-vidviness group than in the low-vidviness group.

correlation with vividness including the cuneus (BAs 17, 18), inferior and middle occipital gyri (BA 18), precentral (BA 44) and inferior frontal gyri (BAs 9, 44, 45, 47) insula (BA 13) and the anterior cingulate (BA 24).

While a small number of brain areas contain subregions with both positive and negative correlations [e.g., in the pre-cuneus (BA 7), superior temporal gyrus [STG] (BA 39) and inferior frontal gyrus (BA 45)], the overall profiles are distinct, with several salient differences: in particular, BA 19, the area with the most extensive positive correlation with vividness, including parts of SOG and fusiform gyrus, shows an exclusively positive correlation, as do posterior cingulate and parahippocampal cortices (BAs 29, 31 and 36). An exclusively negative correlation is seen in BAs 17 and 18. Anterior cingulate (BA 24) also shows an exclusively negative correlation, and in general frontal regions show more negative (BAs 9, 24, 44, 45, 47) than positive (BAs 45, 46) correlations with imagery vividness.

3.4. Activation differences between high vividness and low vividness groups during perception

No brain region was activated more strongly during perception in the high vividness group than in the low vividness group. One small cluster in the Middle Occipital Gyrus activated more strongly during perception in the low vividness than in the high vividness group (see Table 6).

3.5. Review of previous studies (Tables 7 and 8)

We identified ten other functional imaging studies in which the neural correlates of imagery vividness were explicitly examined, together with one additional study in which a similar analysis compared brain activation during imagery before and after ingestion of an hallucinogen, Ayahuasca. These contrast with one another in numerous respects, including participant numbers, the task used to elicit visual imagery, the time allowed to visualise, the baseline condition, the modality of task instructions, the conditions compared in the analysis, the method used to quantify imagery vividness, the use of whole brain versus region of interest analysis, whether the eyes were open or closed during visualisation and whether imagery was investigated in the visual modality alone or in the visual and other modalities. These characteristics of the studies are summarised in Table 7.

Six studies (including the current one) used whole brain analysis to investigate the correlates of imagery vividness in static tasks (i.e., visualisation of an image or scene rather than visualisation in a task requiring mental rotation of images). The regions of brain activation in these studies are compared in Table 8. Despite the methodological differences between these studies, some consistent findings emerge: activity in BA 19 and the adjacent BA 30, in posterior cingulate cortex, correlated positively with vividness in five of the six studies, while activity in the MTLs (including BAs 35 and 36, largely overlapping with perirhinal cortex) and in BA 37 at the occipito-temporal junction correlated positively in four. Activity in the precuneus (BA 7), posterior cingulate (BA 31) and BA 18 correlated positively with vividness in three studies. The recent study by Dijkstra et al. (2017) does not tabulate areas of activation in detail but produced broadly consistent

Table 4 – Areas in which BOLD signal was positively correlated with vividness of individual images.

	BA	Hemi	Co-ordinates			K	Z-score
			X	Y	Z		
Superior occipital gyrus	19	L	−42	−76	24	443	5.85
Middle Temporal Gyrus	22	L	−35	−55	19		4.90
Superior temporal gyrus	39	L	−44	−55	19		4.52
Precuneus	7/19	L	−2	−53	38	768	5.52
Precuneus	7	R	2	−48	54		5.31
Posterior cingulate	29	R	6	−48	8	75	5.33
Fusiform gyrus	19/37	L	−38	−71	−13	121	5.24
Posterior cingulate	31	L	−10	−55	18	164	4.66
Cingulate Gyrus	31	L	−18	−53	26		4.40
Parahippocampal Gyrus	31	L	−10	−47	25		3.53
Parahippocampal Gyrus	19/36	R	25	−41	−6	186	4.32
Culmen		R	20	−33	−15		4.09
Caudate		R	38	−44	10	135	4.20
Superior temporal gyrus	39	R	42	−53	21		3.43
Middle Frontal Gyrus	46	R	55	49	21		2.92
Fusiform gyrus	19/37	R	26	−74	−11	42	4.13
Posterior cingulate	30	R	24	−54	10		2.85
Cingulate Gyrus	31	L	−18	−49	30	32	4.05
Superior temporal gyrus	39	R	53	−55	23		2.82
Middle Temporal Gyrus	21/39	R	58	−6	−10	108	3.94
Inferior frontal gyrus	45	R	48	22	14	48	3.63

BA: Brodmann area(s).
Hemi: Hemisphere activation present in-left (L) or right (R).
K: Cluster size.
Z-score: peak Z-score.

results with evidence for modulation of brain activity by vividness in early visual cortex and precuneus as well as medial frontal and right parietal cortex. Overall these studies highlight the roles of the precuneus, posterior cingulate, MTLs and higher order visual association cortex in mediating the vividness of visual imagery, with some evidence for associations in regions of lateral temporal, parietal, and frontal lobes.

4. Discussion

4.1. Main findings

In this fMRI study of the neural correlates of imagery vividness, we found that a group of healthy participants scoring

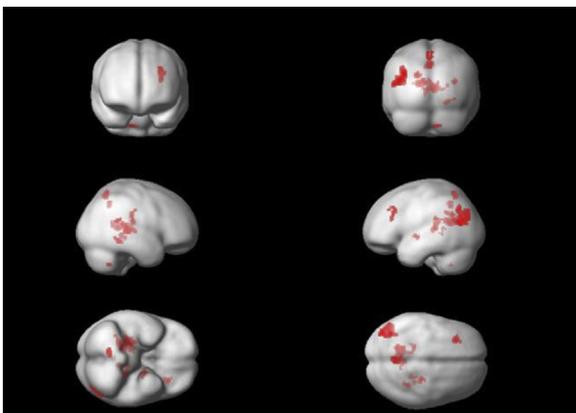


Fig. 5 – Brain regions in which activity was positively correlated with vividness of visual imagery across all participants.

low on the VVIQ activated a diffuse set of brain regions to a greater extent than high-scoring participants when undertaking a visual imagery task. In contrast, areas that were activated more in the high-scoring participants than low-scoring participants were much more restricted. A linear parametric analysis of the neural correlates of the vividness of individual images across the entire group of participants revealed contrasting patterns of positive and negative correlation. In particular, several posterior cortical areas showed a positive correlation with imagery vividness: regions of SOG, fusiform and parahippocampal gyri, posterior cingulate and precuneus (BAs 19, 29, 36, 37) displayed an exclusively positive correlation. By contrast anterior cingulate cortex (BA 24), other frontal regions (BAs 9, 44, 47) and BAs 17 and 18 displayed negative correlations. These results are broadly consistent with our previous single case study of a patient who lost his ‘mind’s eye’ (Zeman et al., 2010). Attempted visualisation in MX was associated with hyperactivation of anterior cingulate cortex but hypoactivation of posterior regions belonging to the group of areas mainly showing a positive correlation with imagery vividness in this study. These results are also substantially in line with previous reports highlighting correlations between vividness of visual imagery and activation of MTLs, posterior cingulate cortex, the precuneus, and higher order visual association cortices. We discuss these key findings below in turn.

4.2. High-vividness group versus low-vividness group contrast

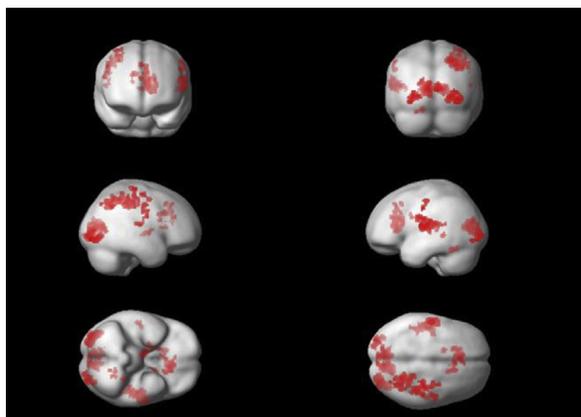
A large number of areas revealed greater brain activation in participants who rate themselves as poor imagers on the VVIQ compared to participants who rate themselves more highly.

Table 5 – Areas in which BOLD signal was negatively correlated with vividness of individual images.

	BA	Hemi	Co-ordinates			K	Z-score
			X	Y	Z		
Cuneus	17	L	−10	−75	15	1805	6.54
Cuneus	18	R	8	−72	13		6.43
Anterior cingulate	24	L	−8	30	10	961	5.89
Superior temporal gyrus	22	L	−50	−13	8	431	5.42
Insula	13	L	−48	−38	15		4.14
Middle Occipital Gyrus	18	R	34	−86	−2	159	5.38
Inferior Occipital Gyrus	18	R	25	−90	−4		3.02
Precuneus	7	R	26	−52	52	288	4.96
Inferior frontal gyrus	9/44/45	R	48	27	9	164	4.86
Transverse Temporal Gyrus	41	R	50	−21	12		3.21
Superior temporal gyrus	22/41	R	50	−16	7	67	4.70
Insula	13	R	44	−19	−1		3.35
Inferior frontal gyrus	9/47	L	−42	3	29	256	4.53
Precentral Gyrus	44	L	−50	−1	18		4.40
Hippocampus		L	−28	−41	0	82	4.48
Precuneus	7	L	−26	−58	51	48	4.35
Superior Parietal Lobule	7	L	−24	−55	41		3.19
Middle Temporal Gyrus	37	R	42	−64	9	36	4.24
Superior temporal gyrus	39	L	−52	−54	8	35	3.63

BA: Brodmann area(s).
Hemi: Hemisphere activation present in-left (L) or right (R).
K: Cluster size.
Z-score: peak Z-score.

For those regions that also showed significant activation within the parametric analysis, discussed below, the majority (nine) were in regions negatively correlated with vividness inferior frontal gyrus (BA9), insula (BA 13), STG (BA 22/41), cuneus (BA 17/18), anterior cingulate (BA 24) while only two were in areas positively correlated with vividness precuneus (BA 7/31), Middle Frontal Gyrus (BA 46). As discussed below, the activations, in the low vividness group, in regions negatively correlated with vividness in the parametric analysis may be explained by either a failure to suppress activity that can interfere with vividness, for example in auditory cortex (BA 41), or by consequential or compensatory activation of executive regions with potential to drive the imagery process: this possibility is consistent with the prominence of frontal regions.

**Fig. 6 – Brain regions in which activity was negatively correlated with vividness of visual imagery across all participants.**

In contrast to the more widespread regions that display increased activation in the low vividness group relative to the high vividness group, only two areas show increased activation in the high vividness group compared to the low vividness group. This is in keeping with evidence from other domains where greater task proficiency tends to be associated with reduced brain activation. This has been reported in the context of processing of syntactic and lexical information (Friederici, Meyer, & von Cramon, 2000), the acquisition of a multifrequency bimanual task (Puttemans, Wenderoth, & Swinnen, 2005), mental strategy (Peres et al., 2000), sequence learning (Gobel, Parrish, & Reber, 2011), category learning (Milton & Pothos, 2011), learning more generally (Chein & Schneider, 2005) and motor imagery (Guillot, Collet, Nguyen, Malouin, Richards, & Doyon, 2008) (discussed more fully below). Some previous evidence has pointed specifically to a similar relationship between performance and brain activation during imagery tasks, with more restricted or less intense

Table 6 – Neural correlates of perception: Brain areas where activation was greater in the low vividness group than the high vividness group during the perception component of the imagery task.

Anatomical area	BA	Hemi	Co-ordinates			K	Z-score
			X	Y	Z		
Middle Occipital Gyrus	37	R	51	−65	−9	24	3.72

BA: Brodmann area(s).
Hemi: Hemisphere activation present in-left (L) or right (R).
K: Cluster size.
Z-score: peak Z-score.

Table 7 – Methodology of previous studies specifically examining the neural correlates of vividness of visual imagery.

Study	n	VT	Modality of instructions	Analysis	Vividness quantification	ROI/WB	Eyes	Modality of imagery	Special features
(1)	9	3 Familiar objects (not stated)	Auditory	Versus rest versus perception	VVIQ (subjects)	ROI + WB	Closed	Visual	
(2)	8	Bench pressing or stairclimbing (10 sec)	Auditory	ROI – rest of brain	VVIQ (subjects)	ROI	Closed	Visual	
(3)	17	Recently seen object drawings (4 sec)	Auditory	Comparison condition unclear	VVIQ, OSIQ, PFT	WB + ROI (ROI for group contrast)	Open	Visual	
(4)	9	96 Multimodal sentences (4.5 sec)	Auditory	Versus abstract	QMI (item)	WB	Open	Multimodal (7 modalities)	
(5)	19	40 Recently seen pictures 20 positive 20 aversive (6 sec)	Visual	Parametric	1–3 rating (item)	ROI	Closed	Visual	Aversive imagery related to worry tendency
(6)	16	456 Multimodal words (3 sec)	Visual	Versus perception parametric	1–4 rating (item)	WB (viv corrln in id areas)	Open	Multimodal (auditory + visual)	
(7)	10	7 Recently seen pictures (21 sec)	?	(Im pre-Im post) – (Perc pre – perc post)	BPRS YMRS (pre/post)	WB	Closed	Visual	Imagery pre/post Ayahuasca ingestion
(8)	21	Mental rotation (<8 sec)	Pre-scan only	Rotation versus non-rotation control	VVIQ (subjects)	ROI + WB	Open	Visual	
(9)	11	10 Familiar objects	Auditory	Split-half correlation, SVM, MDS, parametric	VVIQ (subjects)	ROI	Open	Visual	Multivoxel pattern analysis
(10)	15	8 Familiar objects (28 sec)	Visual	Versus baseline versus auditory	1–4 rating (item)	WB + ROI	?	Visual and auditory	
(11)	26	2 Letters, 2 faces, 2 fruit	Visual	Parametric univariate + cross-validated MANOVA versus perception	VVIQ (subjects) + 1–4 rating (items)	WB	Open	Visual	Multivar. analysis
This study	29	72 Recently seen pictures (5.2 sec)	Visual	Versus imagination control parametric	VVIQ (subjects) + 1–5 rating (item)	WB	Open	Visual	

n: number of participants.

VT: visualization task and length of time visualization carried out for in brackets.

VVIQ: Vividness of visual imagery questionnaire.

OSIQ: Object-spatial imagery questionnaire.

PFT: Paper folding test.

QMI: Questionnaire upon mental imagery.

BPRS: Brief psychiatric ratings scale.

YMRS: Young mania ratings scale.

ROI/WB: analysis done on whole brain (WB) or selective regions of interest (ROI).

Eyes: Whether the instructions due the imagination part of the task specified keeping eyes open or closed.

Study references: (1) [Amedi et al. \(2005\)](#), (2) [Cui et al. \(2007\)](#), (3) [Motes et al. \(2008\)](#) (4) [Belardinelli et al. \(2009\)](#), (5) [Schienle et al. \(2009\)](#), (6) [Daselaar et al. \(2010\)](#) (7) [De Araujo et al. \(2012\)](#) (8) [Logie et al. \(2011\)](#), (9) [Lee et al. \(2012\)](#), (10) [Zvyagintsev et al. \(2013\)](#), (11) [Dijkstra et al. \(2017\)](#).

Table 8 – Brain regions showing positive correlations with imagery vividness in studies closely comparable to the current one.

Study	BA																				
	Frontal						Cingulate				Temporal				Parietal			Occipital			
	10	9	8	6	45	46	32	24	31	29	30	21	22	37	MTL	7	40	39	17	18	19
(1)										>				~	~35 36				>	>	<
(2)	~	<		~	~		<	>	<	<						~				<	~
(3)	<	~	~	<			<		>	>						~	~	~			~
(4)						> ^a					> ^a			~ ^a	>						
(5)	<									~				<	~30	>			~	~	~
This study					<	<			>	<	<	>		<	~36	~		~		~	~
N	3	2	1	2	2	2	2	1	3	2	5	2	1	4	4	3	2	2	2	3	5

BA: Brodmann area.
 >left sided activation, <right sided activation, ~bilateral activation.
 N = number of studies reporting activation in this Brodmann area.
 MTL – medial temporal lobe.
 Study references: (1) Amedi et al. (2005), (2) Belardinelli et al. (2009), (3) Daselaar et al. (2010) (4) Zvyagintsev et al. (2013), (5) De Araujo et al. (2012).
^a BAs inferred from paper.

activation in higher performing participants, in keeping with the neural efficiency hypothesis (Lamm, Bauer, Vitouch, & Gstättner, 1999; Motes et al., 2008; Reichle, Carpenter, & Just, 2000; Vitouch, Bauer, Gittler, Leodolter, & Leodolter, 1997). It is also possible, however, that the differences seen between the two groups reflect a more fundamental difference in strategy rather than a simple unidimensional difference in skill (Belardinelli et al., 2009; Logie et al., 2011): thus, for example, in comparison to high imagers, low imagers may draw on different, non-visual, sources of knowledge when asked to visualise.

There is an alternative interpretation of the difference in brain activation between the low and high vividness groups: that participants in the high vividness group undertake more involuntary imagery during the imagery control condition than participants in the low vividness group, leading to an artefactual reduction in ‘imagery’ activation when the control condition is subtracted from the imagery condition in the vivid imagers. While we cannot exclude this entirely, the fact that the difference between the two groups is especially marked in regions with a negative correlation with imagery vividness would not be predicted by this explanation.

4.3. Parametric analysis of the neural correlates of imagery vividness

The linear parametric analysis correlating imagery vividness with brain activation revealed contrasting patterns of positive and negative correlation over extensive, largely distinct, regions of cortex.

Positive correlations were seen in i) a left lateral temporo-occipital region, extending from the SOG into the Middle Temporal Gyrus (MTG) and STG, encompassing parts of BAs 19, 22 and 39, and in a smaller, comparable right-sided region, involving right MTG and STG (BAs 21/39). These regions are associated with higher order visual and semantic processing, and are likely to be involved in mediation between the verbal stimuli used in our paradigm and the visual representations

they excited (Huth, de Heer, Griffiths, Theunissen, & Gallant, 2016; Ralph, Jefferies, Patterson, & Rogers, 2017); ii) a left parietal region centred on the precuneus, encompassing parts of BAs 7, and 19 and in a smaller, comparable right-sided region (BA 7): the precuneus, one of the key nodes of the default mode network (Buckner, Andrews-Hanna, & Schacter 2008), has repeatedly been associated with visuospatial imagery in functional imaging studies and may also be involved in shifts of visual attention (Cavanna & Trimble, 2006); iii) in regions of the posterior cingulate and retrosplenial cortex bilaterally (BAs 29, 30, 31): the posterior cingulate (BA 31), in particular its ventral portion, is strongly associated, like the precuneus, with internally directed thought (Leech & Sharp, 2014); the retrosplenial cortex (BAs 29,30), which is closely connected to both the precuneus and the posterior cingulate, is implicated in episodic memory and spatial processing, particularly of permanent landmarks like the ‘famous places’ used in this study (Auger, Mullally, & Maguire, 2012); iv) in the fusiform gyrus bilaterally (BAs 19,37), a region strongly associated with face perception (Kanwisher, McDermott, & Chun, 1997), and the visualisation of faces both as images and as hallucinations (Ffytche et al., 1998; O’Craven & Kanwisher, 2000); v) in the right Parahippocampal Gyrus (BAs 19/36), a MTL region linked to memory, particularly spatial memory (Bohbot & Dahmani, 2012). There were only two areas of positive correlation in the frontal lobe, in the right MFG and IFG (BAs 45, 46): interestingly right IFG has been associated with ‘directing attention to or active selection of perceptual, rather than conceptual, representations during retrieval’ (Daselaar et al., 2008, p 225–226).

In contrast, increased brain activity linked to decreasing vividness was seen distinctively i) in a set of frontal brain regions, including the left anterior cingulate (BA 24) and inferior frontal gyrus (left BAs 9, 47, right BAs 9, 44, 45): these areas are broadly executive regions, contributing, for example, to the frontoparietal control network (Vincent, Kahn, Snyder, Raichle, & Buckner, 2008) ii) the superior and middle temporal gyri (left BA 22, 39, right BAs 22, 37, 41): parts of these

regions are associated with audition and deactivation has been observed here during visual imagery in previous studies (see below). Their involvement in semantic memory could also be relevant (Ralph et al., 2017); iii) precuneus (BA 7) bilaterally, discussed above; iv) in left BA 17 and right BA 18, discussed further below; v) in a small cluster within the hippocampus.

4.4. Literature review: i) current findings in relation to previous studies of visual imagery vividness

Table 8 indicates some convergence between the findings of this study and five previous studies reporting correlations between imagery vividness and activation in whole brain analyses. Taken together these studies point to activation positively correlated with vividness in the occipital lobes, with more prominent involvement of higher than lower order visual association cortices; positively correlated activation in the MTLs, most likely related to memory retrieval; positively correlated activation in regions of the precuneus and posterior cingulate which participate in internally directed cognition within the default mode network (Buckner, Andrews-Hanna, & Schacter, 2008). The more prominent correlations with higher than lower order visual cortices are mirrored in the region of interest study of Lee et al. (2012) which focussed on the similarities and difference between imagery and perception in visual cortices. This demonstrated that while the identity of perceived objects can be ‘decoded’ more readily from earlier than later visual areas, this gradient is reversed for visual imagery. Positive correlations with frontal, parietal and lateral temporal regions are less consistent, suggesting that activity here is less intimately related with the experience of vividness.

Our study, which focussed exclusively on visual imagery, does not allow us to comment on the question of whether the regions showing a positive correlation with imagery vividness are specific to the visual modality or related generically to the process of ‘imagination’ regardless of modality. The recent studies by Daselaar and Zvyagintsev support the view that imagination involves both modality-specific and supramodal networks, and that activity within both correlates to some degree with imagery vividness (Daselaar et al., 2010; Zvyagintsev et al., 2013).

The negative correlations observed in our study between imagery vividness and activity in STG (BAs 22, 37, 41), containing early auditory cortices, concur with previous findings. Amedi et al. (2005) reported a negative correlation between visual imagery vividness and activity in STG and STS (BAs 21, 22, 41, 42); similarly Zvyagintsev et al. (2013) observed deactivations in STG (BAs 22/41/42) during visual imagery. Some other studies have also reported deactivation of early visual cortices during visual imagery: in BAs 17 and 18, in the study by Daselaar et al. (2010), by comparison with auditory imagery; in BA 18 in the study by Zvyagintsev et al. (2013), by comparison with an active baseline involving serial subtractions. Belardinelli et al. (2009), in contrast, reported a positive correlation between visual imagery vividness and activity in Area 18, and Cui et al. (2007) found evidence for a complex modulation of activity in Area 17, varying with participant's overall vividness scores. The explanation for the

apparently variable contribution of early visual areas to imagery vividness is uncertain, but higher order areas are implicated more consistently.

The negative correlations with imagery vividness observed in our study in frontal areas are not strongly anticipated by these previous studies, although Zvyagintsev et al. (2013) reported deactivation of BA 6 (precentral and medial frontal gyri) during visual imagery. Other work, however, discussed below, is consistent with the hypothesis of an inverse relationship between anterior and posterior activity in the modulation of imagery vividness. We suspect that the deliberate inclusion of a ‘low imagery’ group in our study may have revealed activation of executive frontal regions in our visual imagery task, high levels of activity probably reflecting less successful and more effortful attempts at imagery generation.

A novel recent line of work has recently added a further dimension to the study of imagery vividness, both providing a behavioural measure of imagery strength and suggesting that it may have structural as well as functional correlates in the brain. Preceding imagery has been shown to bias the results of subsequent perception using binocular rivalry (Pearson, Clifford, & Tong, 2008). Subjective estimates of imagery strength, both using the VVIQ and on a trial by trial basis, predict the strength of this effect (Pearson, Rademaker, & Tong, 2011). Parameters of visual imagery have been linked both to the area of primary visual cortex, which has an inverse relationship with imagery strength, and to the volume of prefrontal cortex, which is positively correlated with imagery vividness (Bergmann, Genc, Kohler, Singer, & Pearson, 2016).

4.5. Literature review: ii) current findings in relation to previous studies in linked domains

Findings in several related research areas are relevant to the interpretation of our results. ‘Vividness’ has been a variable of interest in functional imaging studies of autobiographical memories (AMs). While AMs are multimodal, visual imagery makes a particularly important contribution to them (Rubin & Greenberg, 1998). It is therefore of interest to compare the neural correlates of vividness identified in this memory domain with those emerging from the studies reviewed above. AMs are generally richer in sensory details than laboratory memories: comparisons between them indicate stronger activation of the cuneus and parahippocampal cortex by AMs (Cabeza & St Jacques, 2007; Gardini, Cornoldi, De Beni, & Venneri, 2006). Activity in the precuneus/posterior cingulate (BA 31) correlates with the vividness ratings of AMs (Gilboa, Winocur, Grady, Hevenor, & Moscovitch, 2004); Gilboa et al.'s study also pointed to the involvement of lingual and fusiform cortices (BAs 19, 37) in rich ‘autobiographical re-experiencing’. Daselaar et al. (2010) similarly, found a relationship between a measure of ‘relying’ and activity in BA 19 and cingulate cortices (BAs 31, 32). The greater vividness of recent AMs is likely to account for stronger hippocampal activation by recent than more remote memories (Addis, Moscovitch, Crawley, & McAndrews, 2004; Gilboa et al., 2004). Investigation of everyday recognition memory has produced some evidence for graded MTL activation related to the strength of recollection (Milton, Muhlert, Butler, Benattayallah, & Zeman, 2011). Thus these findings from studies of autobiographical memory are consistent with

those from the imagery domain, reviewed above, in suggesting that greater vividness is associated with stronger activation of visual cortices, regions strongly associated with memory processing (hippocampus, parahippocampal cortex) and the posterior cingulate/precuneus.

Imagery vividness can be influenced exogenously by psychedelic drugs. Several recent studies have examined the neural correlates of the heightening of visual imagery by drugs including Ayahuasca (active ingredient N,N-dimethyltryptamine, DMT), psilocybin (a pro-drug of DMT) and Lysergic acid diethylamide (LSD), all of which are potent serotonergic agonists and hallucinogens. Cerebral blood flow and resting state functional connectivity of primary visual cortex are both increased by LSD (Carhart-Harris et al., 2016). These increases correlate with ratings of complex visual imagery. Similarly, Ayahuasca increases brain activation in visual cortices (BAs 17, 18, 19) during visual imagery to levels seen during visual perception (De Araujo et al., 2012 – though cf. Carhart-Harris et al. (2012) for an apparently divergent result). De Araujo et al. found significant correlation between psychotic symptoms and activation of BA 17, with alteration of connectivity between V1 and other brain regions (BAs 7 and 37). These findings mirror the evidence from studies of natural imagery, discussed above, suggesting a relationship between imagery vividness and activation of visual cortices. A second theme emerging from these studies of hallucinogens is the modulation of cerebral connectivity by hallucinogens, and in particular the importance to the psychedelic experience of the uncoupling of connections between hub regions such as the medial prefrontal and posterior cingulate cortices (Carhart-Harris et al., 2012, 2016; De Araujo et al., 2012). As discussed below, the results from our single case (Zeman et al., 2010) and the current study point to a parallel relationship in the context of natural imagery.

Exceptionally vivid imagery occurs also in the context of hallucinations. No studies, to date, have probed the neural correlates of the vividness of hallucinations, but their occurrence, per se, is associated with elevated activity in modality-specific cortices – auditory in the case of auditory hallucinations, visual in the case of visual, in keeping with the evidence, from the studies discussed above, that non-pathological imagery vividness correlates with activity in relevant sensory cortices (Allen, Laroi, McGuire, & Aleman, 2008; Zmigrod, Garrison, Carr, & Simons, 2016). There is recent evidence that imagery strength influences the risk of hallucinations in patients with Parkinson's disease, adding to the evidence for common ground between the neural basis of imagery and hallucinations (Shine et al., 2015). A recent meta-analysis pointed to a role for MTL activation in auditory but not visual hallucinations (Zmigrod et al., 2016). This literature also implicates altered interactions between anterior and posterior brain regions in the genesis of hallucinations (Allen et al. 2008; Zmigrod et al., 2016), a theme developed further below.

Finally, a small number of studies has examined the neural correlates of normal imagery vividness in modalities other than the visual. Guillot et al. (2008) compared brain activations associated with motor imagery in two groups of participants selected on the basis of high and low motor imagery ability. They found that low imagery participants activated a more extensive network of regions than high imagery participants, though in both cases the activated regions predominantly

belonged to well-recognised motor networks (motor and premotor cortices, basal ganglia, cerebellum, inferior and superior parietal lobules). A subtraction analysis indicated differing patterns of activation within the two groups, with evidence that the low imagery group more strongly activated areas, such as BA 10 and the cuneus, which are not classically associated with motor imagery. Using a within-subject analysis, Lorey et al. (2011) identified a parametric relationship between the vividness of motor imagery and strength of activation in sensorimotor regions including the premotor cortex, putamen and cerebellum bilaterally together with left posterior parietal and left somatosensory cortex. Negative relationships between vividness of motor imagery and strength of activation were observed in several predominantly non-motor regions in the frontal and temporal lobes. These findings broadly mirror those we report in the visual domain, with more extensive brain activation in the low imagery group, positive correlations between imagery vividness and areas classically associated with visual imagery and negative correlations between imagery vividness and areas which, in the main, are less clearly associated with visual imagery.

In the auditory domain, Halpern (2012) reported that activity in the right putamen/globus pallidus and left inferior frontal gyrus/ventral premotor cortex correlated with vividness of auditory imagery, judged trial by trial, in a task involving anticipation of a melody by trained musicians. Zatorre, Halpern, and Bouffard (2010) found a correlation between vividness of auditory imagery as judged using the Bucknell Auditory Imagery Scale and activation in a region of right auditory cortex, with a further correlation with a region of the intraparietal sulcus in a task requiring mental reversal of a melody, somewhat analogous to tasks requiring mental rotation of images in the visual domain (Logie et al., 2011).

4.6. *Blind imagination: current findings in relation to patient MX and 'aphantasia'*

This study was motivated by our previous case report of a patient, MX, who lost the ability to visualise in mid-life, following a cardiac procedure (Zeman et al., 2010). Functional imaging revealed that while his brain activation during a perceptual task – looking at famous faces – was indistinguishable from that of controls, during attempted imagery of faces MX hypoactivated regions including the calcarine cortex bilaterally, the right IOG, the fusiform cortex bilaterally, parts of the middle and superior temporal gyri/sulci bilaterally and a small cluster in the right precuneus. He hyperactivated the right anterior cingulate cortex, together with small clusters in the IFG bilaterally, left precuneus and right MTG.

These findings are broadly consistent with the results of the current study and the other previous studies of the neural correlates of visual imagery vividness discussed above and summarised in Table 8. Posterior occipito-temporal activations, variably involving Areas 17, 18, 19 and 37, have been correlated positively with imagery vividness in the majority of these studies. The increased frontal activation in MX, particularly in the anterior cingulate, is mirrored by our current finding that a range of frontal activations, including activation of the anterior cingulate, are negatively correlated with imagery vividness. We cannot be sure whether the inverse

relationship between frontal activations and imagery vividness seen both in our single case study and the current report reflects a causal relationship – frontal activity inhibiting imagery – or a consequential one – frontal activity responding to difficulty in generating imagery. Stimulation of frontal regions during visual imagery, for example using transcranial magnetic stimulation, could help to clarify this relationship.

The evidence from studies of hallucinogens, that vivid imagery occurs when posterior brain regions are unconstrained by anterior areas, is potentially relevant to this question. However, it is likely that there are two dissociable neural routes to vivid imagery: one involving spontaneous imagery occurring in an ‘unconstrained’ brain, the other involving deliberately generated imagery in a highly connected brain (see Pearson & Westbrook (2015) for a related distinction). It could be that the relationship between frontal activation and imagery vividness differs for these two types of imagery.

In future, investigation of structural and functional connectivity in individuals with widely varying imagery vividness may shed further light on the relative roles of fronto-parietal control systems and posterior visual cortices in the generation of visual imagery. In particular, a group of individuals lying at the low extreme of the vividness spectrum have recently been described using the term ‘aphantasia’ (Zeman et al., 2015, 2016). One estimate suggests that approximately 2% of the normal population lacks the ability deliberately to summon visual imagery to the mind’s eye (Faw, 2009). The current study did not include any individuals at the far extreme of the imagery vividness spectrum, but the studies of the neural correlates of visual imagery summarised here suggest a range of hypotheses for the neural basis of aphantasia.

5. Conclusion

We have shown that a group of individuals with high visual imagery vividness activate the brain more selectively than individuals with low vividness. Areas positively associated with vividness lie mainly in posterior brain regions including higher order visual association cortices, regions of posterior cingulate and precuneus and the MTL, while the areas in which activation is inversely associated with imagery vividness lie particularly in the frontal lobes, and auditory cortices. Many of the areas activated in the low but not the high imagery group displayed an inverse relationship with imagery vividness.

Other studies directly examining visual imagery vividness have reported broadly similar findings, suggesting the conclusion that vividness is associated with activity in both modal and supramodal regions, the latter including parts of the default mode network. Our review of these studies highlights conflicting results on the relative contribution of earlier and later visual areas to imagery vividness: in general activity in higher order visual cortices is more strongly associated with imagery vividness than activity in lower order areas. The results of studies of autobiographical memory, visual experiences induced by hallucinogenic drugs, spontaneous hallucinations and imagery vividness in other modalities also point

to the importance of activations in modal cortices and MTLs in determining imagery vividness. There is tentative evidence for an inverse relationship between activity in some frontal regions and imagery vividness, but it is unclear whether this is causal or consequential.

Our previous study of a patient who had lost the ability to visualise in mid-life (Zeman et al., 2010) revealed comparable findings, with hypoactivation of posterior occipito-temporal cortices and hyperactivation of the anterior cingulate in an imagery task. Further work is required to elucidate the neural basis of lifelong ‘aphantasia’. The most general implication of our work, consistent with other recent findings (Pearson et al., 2011), is that metacognition for the vividness of visual imagery, both on summary measures and on a trial by trial basis, is meaningful, and has observable neural correlates.

Acknowledgements

Jonathan Fulford's salary was supported via an NIHR grant.

REFERENCES

- Addis, D. R., Moscovitch, M., Crawley, A. P., & McAndrews, M. P. (2004). Recollective qualities modulate hippocampal activation during autobiographical memory retrieval. *Hippocampus*, 14, 752–762.
- Allen, P., Laroi, F., McGuire, P. K., & Aleman, A. (2008). The hallucinating brain: A review of structural and functional neuroimaging studies of hallucinations. *Neuroscience and Biobehavioral Reviews*, 32, 175–191.
- Amedi, A., Malach, R., & Pascual-Leone, A. (2005). Negative BOLD differentiates visual imagery and perception. *Neuron*, 48, 859–872.
- Auger, S. D., Mullally, S. L., & Maguire, E. A. (2012). Retrosplenial cortex codes for permanent landmarks. *PLoS One*, 7, e43620.
- Belardinelli, M. O., Palmiero, M., Sestieri, C., Nardo, D., Di Matteo, R., Londei, A., et al. (2009). An fMRI investigation on image generation in different sensory modalities: The influence of vividness. *Acta Psychologica (Amst)*, 132, 190–200.
- Bergmann, J., Genc, E., Kohler, A., Singer, W., & Pearson, J. (2016). Smaller primary visual cortex is associated with stronger, but less precise mental imagery. *Cerebral Cortex*, 26, 3838–3850.
- Bohbot, V., & Dahmani, L. (2012). Epilepsy and the study of spatial memory using virtual reality. In A. Zeman, N. Kapur, & M. Jones-Gotman (Eds.), *Epilepsy and memory* (pp. 209–224). Oxford: Oxford University Press. Ch. 12.
- Buckner, R. L., Andrews-Hanna, J. R., & Schacter, D. L. (2008). The brain's default network: Anatomy, function, and relevance to disease. *Annals of the New York Academy of Sciences*, 1124, 1–38.
- Cabeza, R., & St Jacques, P. (2007). Functional neuroimaging of autobiographical memory. *Trends in Cognitive Sciences*, 11, 219–227.
- Carhart-Harris, R. L., Erritzoe, D., Williams, T., Stone, J. M., Reed, L. J., Colasanti, A., et al. (2012). Neural correlates of the psychedelic state as determined by fMRI studies with psilocybin. *Proceedings of the National Academy of Sciences of the United States of America*, 109, 2138–2143.
- Carhart-Harris, R. L., Muthukumaraswamy, S., Roseman, L., Kaelen, M., Droog, W., Murphy, K., et al. (2016). Neural correlates of the LSD experience revealed by multimodal neuroimaging. *Proceedings of the National Academy of Sciences of the United States of America*, 113, 4853–4858.

- Cavanna, A. E., & Trimble, M. R. (2006). The precuneus: A review of its functional anatomy and behavioural correlates. *Brain*, 129, 564–583.
- Chein, J. M., & Schneider, W. (2005). Neuroimaging studies of practice-related change: fMRI and meta-analytic evidence of a domain-general control network for learning. *Brain Research Cognitive Brain Research*, 25, 607–623.
- Cui, X., Jeter, C. B., Yang, D., Montague, P. R., & Eagleman, D. M. (2007). Vividness of mental imagery: Individual variability can be measured objectively. *Vision Research*, 47, 474–478.
- Daselaar, S. M., Porat, Y., Huijbers, W., & Pennartz, C. M. (2010). Modality-specific and modality-independent components of the human imagery system. *NeuroImage*, 52, 677–685.
- Daselaar, S. M., Rice, H. J., Greenberg, D. L., Cabeza, R., LaBar, K. S., & Rubin, D. C. (2008). The spatiotemporal dynamics of autobiographical memory: Neural correlates of recall, emotional intensity, and reliving. *Cerebral Cortex*, 18, 217–229.
- De Araujo, D. B., Ribeiro, S., Cecchi, G. A., Carvalho, F. M., Sanchez, T. A., Pinto, J. P., et al. (2012). Seeing with the eyes shut: Neural basis of enhanced imagery following Ayahuasca ingestion. *Human Brain Mapping*, 33, 2550–2560.
- Dijkstra, N., Bosch, S. E., & Van Gerven, M. A. J. (2017). Vividness of visual imagery depends on the neural overlap with perception in isual areas. *The Journal of Neuroscience*, 37, 1367–1373.
- Dunbar, R. (2004). *The human story: A new history of mankind's evolution*. London: Faber and Faber.
- Farah, M. J. (1984). The neurological basis of mental imagery: A componential analysis. *Cognition*, 18, 245–272.
- Faw, B. (1997). Outlining a brain model of mental imaging abilities. *Neuroscience and Biobehavioral Reviews*, 21, 283–288.
- Faw, B. (2009). Conflicting intuitions may be based on differing abilities – evidence from mental imaging research. *Journal of Consciousness Studies*, 16, 45–68.
- Ffytche, D. H., Howard, R. J., Brammer, M. J., David, A., Woodruff, P., & Williams, S. (1998). The anatomy of conscious vision: An fMRI study of visual hallucinations. *Nature Neuroscience*, 1, 738–742.
- Forman, S. D., Cohen, J. D., Fitzgerald, M., Eddy, W. F., Mintun, M. A., & Noll, D. C. (1995). Improved assessment of significant activation in functional magnetic resonance imaging (fMRI): Use of a cluster-size threshold. *Magnetic Resonance in Medicine*, 33, 636–647.
- Friederici, A. D., Meyer, M., & Von Cramon, D. Y. (2000). Auditory language comprehension: An event-related fMRI study on the processing of syntactic and lexical information. *Brain and Language*, 75, 289–300.
- Galton, F. (1880). Statistics of mental imagery. *Mind*, 5, 301–318.
- Gardini, S., Cornoldi, C., De Beni, R., & Venneri, A. (2006). Left mediotemporal structures mediate the retrieval of episodic autobiographical mental images. *NeuroImage*, 30, 645–655.
- Gilboa, A., Winocur, G., Grady, C. L., Hevenor, S. J., & Moscovitch, M. (2004). Remembering our past: Functional neuroanatomy of recollection of recent and very remote personal events. *Cerebral Cortex*, 14, 1214–1225.
- Gobel, E. W., Parrish, T. B., & Reber, P. J. (2011). Neural correlates of skill acquisition: Decreased cortical activity during a serial interception sequence learning task. *NeuroImage*, 58, 1150–1157.
- Guillot, A., Collet, C., Nguyen, V. A., Malouin, F., Richards, C., & Doyon, J. (2008). Functional neuroanatomical networks associated with expertise in motor imagery. *NeuroImage*, 41, 1471–1483.
- Halpern, A. R. (2012). Dynamic aspects of musical imagery. *Annals of the New York Academy of Sciences*, 1252, 200–205.
- Huth, A. G., de Heer, W. A., Griffiths, T. L., Theunissen, F. E., & Gallant, J. L. (2016). Natural speech reveals the semantic maps that tile human cerebral cortex. *Nature*, 532, 453–458.
- Ishai, A. (2010). Seeing faces and objects with the “mind’s eye”. *Archives italiennes de biologie*, 148, 1–9.
- Ishai, A., Ungerleider, L., & Haxby, J. V. (2000). Distributed neural systems for the generation of visual images. *Neuron*, 28, 979–990.
- Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *The Journal of Neuroscience*, 17, 4302–4311.
- Kosslyn, S. M., Ganis, G., & Thompson, W. L. (2001). Neural foundations of imagery. *Nature Reviews Neuroscience*, 2, 635–642.
- Lamm, C., Bauer, H., Vitouch, O., & Gstättner, R. (1999). Differences in the ability to process a visuo-spatial task are reflected in event-related slow cortical potentials of human subjects. *Neuroscience Letters*, 269, 137–140.
- Lancaster, J. L., Rainey, L. H., Summerlin, J. L., Freitas, C. S., Fox, P. T., Evans, A. C., et al. (1997). Automated labeling of the human brain: A preliminary report on the development and evaluation of a forward-transform method. *Human Brain Mapping*, 5, 238–242.
- Lancaster, J. L., Woldorff, M. G., Parsons, L. M., Liotti, M., Freitas, C. S., Rainey, L., et al. (2000). Automated Talairach atlas labels for functional brain mapping. *Human Brain Mapping*, 10, 120–131.
- Leech, R., & Sharp, D. J. (2014). The role of the posterior cingulate cortex in cognition and disease. *Brain*, 137, 12–32.
- Lee, S.-H., Kravitz, D. J., & Baker, C. I. (2012). Disentangling visual imagery and perception of real-world objects. *NeuroImage*, 59, 4064–4073.
- Logie, R. H., Pernet, C. R., Buonocore, A., & Della, S. S. (2011). Low and high imagers activate networks differentially in mental rotation. *Neuropsychologia*, 49, 3071–3077.
- Lorey, B., Pilgramm, S., Bischoff, M., Stark, R., Vaitl, D., Kindermann, S., et al. (2011). Activation of the parieto-premotor network is associated with vivid motor imagery – a parametric fMRI study. *Plos One*, 6, e20368.
- Marks, D. F. (1973). Visual imagery differences in the recall of pictures. *British Journal of Psychology*, 64, 17–24.
- Mckelvie, S. (1995). The VVIQ as a psychometric test of individual differences in visual imagery vividness: A critical quantitative review and plea for direction. *Journal of Mental Imagery*, 19, 1–106.
- Milton, F., Muhlert, N., Butler, C. R., Benattayallah, A., & Zeman, A. Z. (2011). The neural correlates of everyday recognition memory. *Brain and Cognition*, 76, 369–381.
- Milton, F., & Pothos, E. M. (2011). Category structure and the two learning systems of COVIS. *The European Journal of Neuroscience*, 34, 1326–1336.
- Motes, M. A., Malach, R., & Kozhevnikov, M. (2008). Object-processing neural efficiency differentiates object from spatial visualizers. *NeuroReport*, 19, 1727–1731.
- O’Craven, K. M., & Kanwisher, N. (2000). Mental imagery of faces and places activates corresponding stimulus-specific brain regions. *Journal of Cognitive Neuroscience*, 12, 1013–1023.
- Pearson, J., Clifford, C. W., & Tong, F. (2008). The functional impact of mental imagery on conscious perception. *Current Biology: CB*, 18, 982–986.
- Pearson, J., Naselaris, T., Holmes, E. A., & Kosslyn, S. M. (2015). Mental imagery: Functional mechanisms and clinical applications. *Trends in Cognitive Sciences*, 19, 590–602.
- Pearson, J., Rademaker, R. L., & Tong, F. (2011). Evaluating the mind’s eye: The metacognition of visual imagery. *Psychological Science*, 22, 1535–1542.
- Pearson, J., & Westbrook, F. (2015). Phantom perception: Voluntary and involuntary nonretinal vision. *Trends in Cognitive Sciences*, 19, 278–284.
- Peres, M., Van De Moortele, P. F., Pierard, C., Lehericy, S., Satabin, P., Le Bihan, D., et al. (2000). Functional magnetic resonance imaging of mental strategy in a simulated aviation performance task. *Aviation, Space, and Environmental Medicine*, 71, 1218–1231.

- Poline, J. B., Worsley, K. J., Evans, A. C., & Friston, K. J. (1997). Combining spatial extent and peak intensity to test for activations in functional imaging. *NeuroImage*, 5, 83–96.
- Puttemans, V., Wenderoth, N., & Swinnen, S. P. (2005). Changes in brain activation during the acquisition of a multifrequency bimanual coordination task: From the cognitive stage to advanced levels of automaticity. *The Journal of Neuroscience*, 25, 4270–4278.
- Ralph, M. A., Jefferies, E., Patterson, K., & Rogers, T. T. (2017). The neural and computational bases of semantic cognition. *Nature Reviews Neuroscience*, 18, 42–55.
- Reichle, E. D., Carpenter, P. A., & Just, M. A. (2000). The neural bases of strategy and skill in sentence-picture verification. *Cognitive Psychology*, 40, 261–295.
- Rubin, D. C., & Greenberg, D. L. (1998). Visual memory-deficit amnesia: A distinct amnesic presentation and etiology. *Proceedings of the National Academy of Sciences of the United States of America*, 95, 5413–5416.
- Schienze, A., Schafer, A., Pignatelli, R., & Vaitl, D. (2009). Worry tendencies predict brain activation during aversive imagery. *Neuroscience Letters*, 461, 289–292.
- 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 of the Royal Society B*, 282, 20142047.
- Thirion, B., Pinel, P., Meriaux, S., Roche, A., Dehaene, S., & Poline, J. B. (2007). Analysis of a large fMRI cohort: Statistical and methodological issues for group analyses. *NeuroImage*, 35, 105–120.
- Vincent, J. L., Kahn, I., Snyder, A. Z., Raichle, M. E., & Buckner, R. L. (2008). Evidence for a frontoparietal control system revealed by intrinsic functional connectivity. *Journal of Neurophysiology*, 100, 3328–3342.
- Vitouch, O., Bauer, H., Gittler, G., Leodolter, M., & Leodolter, U. (1997). Cortical activity of good and poor spatial test performers during spatial and verbal processing studied with Slow Potential Topography. *International Journal of Psychophysiology*, 27, 183–199.
- Wechsler, D. (1997). *Wechsler memory scale III*. San Antonio, Texas: The Psychological Corporation.
- Wechsler, D. (1999). *Wechsler abbreviated scale of intelligence (WASI)*. Psychological Corporation.
- Weiskrantz, L. (1998). *Blindsight – a case study and implications*. Oxford: Clarendon Press.
- Zatorre, R. J., Halpern, A. R., & Bouffard, M. (2010). Mental reversal of imagined melodies: A role for the posterior parietal cortex. *Journal of Cognitive Neuroscience*, 22, 775–789.
- Zeman, A. Z., Della Sala, S., Torrens, L. A., Gountouna, V. E., Mcgonigle, D. J., & Logie, R. H. (2010). Loss of imagery phenomenology with intact visuo-spatial task performance: A case of 'blind imagination'. *Neuropsychologia*, 48, 145–155.
- Zeman, A., Dewar, M., & Della Sella, S. (2016). Reflections on aphantasia. *Cortex*, 74, 336–337.
- Zeman, A., Dewar, M., & Della Sella, S. (2015). Lives without imagery – congenital aphantasia. *Cortex*, 73, 378–380.
- Zigmond, A. S., & Snaith, R. P. (1983). The hospital anxiety and depression scale. *Acta Psychiatrica Scandinavica*, 67, 361–370.
- Zmigrod, L., Garrison, J. R., Carr, J., & Simons, J. S. (2016). The neural mechanisms of hallucinations: A quantitative meta-analysis of neuroimaging studies. *Neuroscience and Biobehavioral Reviews*, 69, 113–123.
- Zvyagintsev, M., Clemens, B., Chechko, N., Mathiak, K. A., Sack, A. T., & Mathiak, K. (2013). Brain networks underlying mental imagery of auditory and visual information. *The European Journal of Neuroscience*, 37, 1421–1434.