Research into the neural correlates of individual differences in imagery vividness point to an important role of the early visual cortex. However, there is also great fluctuation of vividness within individuals, such that only looking at differences between people necessarily obscures the picture. In this study, we show that variation in moment-to-moment experienced vividness of visual imagery, within human subjects, depends on the activity of a large network of brain areas, including frontal, parietal, and visual areas. Furthermore, using a novel multivariate analysis technique, we show that the neural overlap between imagery and perception in the entire visual system correlates with experienced imagery vividness. This shows that the neural basis of imagery vividness is much more complicated than studies of individual differences seemed to suggest.

**Key words:** mental imagery; multivariate analyses; neural overlap; perception; working memory

**Introduction**

Visual imagery allows us to think and reason about objects that are absent in the visual field by creating a mental image of them. This ability plays an important role in several cognitive processes, such as working memory, mental rotation, reasoning about future events, and many more (Kosslyn et al., 2001). The vividness of visual imagery seems to be a key factor in these cognitive abilities, with more vivid imagery being linked to better performance on tasks requiring imagery (Keogh and Pearson, 2011, 2014; Albers et al. 2013).

There are great individual differences in how vividly people can generate a mental image (Cui et al., 2007; Lee et al., 2012; Bergmann et al., 2016). However, within individuals there is also variation in imagery vividness: in some instances, imagery is much more vivid than in other instances (Pearson et al., 2008).

To date, the neural mechanisms underlying this moment-to-moment variation in experienced imagery vividness have remained unclear.

Previous work has shown that people who have more vivid visual imagery, as measured by the Vividness of Visual Imagery Questionnaire (VVIQ) (Marks, 1973), show higher activity in early visual cortex during imagery (Cui et al., 2007). Furthermore, individual differences in imagery precision and strength, as measured by the effect on subsequent binocular rivalry, are related to the size of V1, whereas individual differences in subjective imagery vividness correlate with prefrontal cortex volume but not with visual cortex anatomy (Bergmann et al., 2016). Studies using multivariate analysis techniques have shown that there is overlap in stimulus representations between imagery and perception across the whole visual hierarchy, with more overlap in higher visual areas (Reddy et al., 2010; Lee et al., 2012). However, only the overlap between perception and imagery in the primary visual cortex correlates with VVIQ scores and with imagery ability as measured by task performance (Lee et al., 2012; Albers et al., 2013).

It remains unclear which of these neural correlates are important in determining moment-to-moment vividness of visual imagery and whether V1, especially the neural overlap with perception in V1, also relates to the variation of vividness within
participants. In the current study, we investigated this question by having participants perform a retro-cue imagery task in the MRI scanner and rate their experienced vividness in every trial. First, we explored where in the brain activity correlates with vividness. Second, we investigated the overlap of category representations of perceived and imagined stimuli and in which areas this overlap is modulated by imagery vividness.

Materials and Methods

Participants. Twenty-nine healthy adult volunteers with normal or corrected to normal vision gave written informed consent and participated in the experiment. Three participants were excluded: two because of insufficient data caused by scanner problems and one because of not finishing the task. Twenty-six participants (mean ± SD age = 24.31 ± 3.05 years; 18 female) were included in the reported analyses. The study was approved by the local ethics committee (CMO Arnhem-Nijmegen).

Experimental paradigm. Before scanning we asked participants to fill in the VVIQ. This 16-item scale is summarized in a vividness score between 1 and 4 for each participant, where a score of 1 indicates low vividness and 4 indicates high vividness. The experimental paradigm is depicted in Figure 1. We adapted a retro-cue working memory paradigm (Harrison and Tong, 2009). In each trial, participants were shown two objects successively, followed by a cue indicating which of the two they subsequently should imagine. During imagery, a frame was presented within which subjects were asked to imagine the cued stimulus as vividly as possible. After this, they indicated their experienced vividness on a scale from 1 to 4, where 1 was low vividness and 4 was high vividness. Previous research has shown that such a subjective imagery rating shows high test-retest reliability and correlates with objective measures of imagery vividness (Pearson et al., 2011; Bergmann et al., 2016).

There were 20 of these trials per block. Each stimulus was perceived 60 times and imagined 30 times over the course of the whole experiment, resulting in nine blocks in total and a total scanner time of approximately 1.5 hours per participant.

Stimuli. Six images obtained from the World Wide Web were used as stimuli: 2 faces (Barack Obama and Emma Watson), 2 letters (‘D’ and ‘I’), and 2 kinds of fruit (banana and apple). These three categories were chosen because they had, respectively, high, medium, and low Kolmogorov complexity, which is a measure that describes the complexity of an image in terms of its shortest possible description and can be approximated by its normalized compressed file size. It has been shown that the neural response in visual cortex is influenced by the Kolmogorov complexity of the stimulus (Güch and van Gerven, 2015). Furthermore, the within-category exemplars were chosen to be maximally different, such as to allow potential within-class differentiation. For the letters, this was quantified as the pair of images with the least pixel overlap.

fMRI acquisition. Each block was recorded in a separate fMRI run, leading to 9 runs in total. In between runs, the participant had a break and indicated by means of a button press when they were ready for the experiment to continue. fMRI data were recorded on a Siemens 3T Prisma scanner with a Multiband 4 sequence (TR, 1.5 s; voxel size, 2 × 2 × 2 mm; TE, 39.6 ms) and a 32 channel head coil. For all participants, the field of view was tilted −25° from the transverse plane, using the Siemens AutoAlign Head software, resulting in the same tilt relative to the individual participant’s head position. T1-weighted structural images (MPRAGE; voxel size, 1 × 1 × 1 mm; TR, 2.3 s) were also acquired for each participant.

fMRI data preprocessing. Data were preprocessed using SPM8 (RRID: SCR_007037). Functional imaging data were motion corrected and coregistered to the T1 structural scan. No spatial or temporal smoothing was performed. A high-pass filter of 128 s was used to remove slow signal drift.

Univariate GLM analysis. Before the multivariate analyses, we first ran a standard GLM in SPM8 in which we modeled the different regressors separately for each fMRI run. We modeled, per category, the perception events, imagery events, and the parametric modulation of the imagery response by vividness each in a separate regressor. The intertrial intervals were modeled as a baseline regressor during which there was no imagery. The visual cues, the presentation of the vividness instruction screen and the button presses, were included in separate nuisance regressors, along with subject movement in six additional regressors. This analysis gave us the β weight of each regressor for each voxel separately. Significance testing for univariate contrasts was done on the normalized smoothed t maps using FSL’s cluster-based permutation technique (FSL, RRID: SCR_002823). To illustrate the parametric influence of vividness, a separate GLM was run in which the imagery response per vividness level was...
modeled in a separate regressor, collapsed over stimulus categories, and concatenated over runs.

Searchlight-based cross-validated MANOVA. Numerous studies have shown that information about complex cognitive processes, such as visual imagery, is often more clearly present in patterns of neural responses than in the mean response amplitude pooled over voxels (Kok et al., 2012; Tong et al., 2012; Albers et al., 2013; Bosch et al., 2014). Therefore, in this study, we focused on effects in the multivariate patterns of voxel responses.

We used the multivariate searchlight-based analysis technique developed by Allefeld and Haynes (2014). This analysis takes the parameter estimates of the GLM regressors per run as input and computes the multivariate “pattern distinctness” of any given contrast per searchlight. We chose a searchlight with a radius of 4 mm, leading to 33 voxels per sphere, in line with the findings of Kriegeskorte et al. (2006), who showed that this size is optimal for most brain regions.

The pattern distinctness $D$ of the two conditions in any contrast is defined as the magnitude of the between-condition covariance compared with the within-condition covariance (Allefeld and Haynes, 2014). When there are only two conditions, which is the case in all our contrasts, $D$ has a clear relationship to the Mahalanobis distance. Let

$$\Delta = \sqrt{(\mu_2 - \mu_1)^T \Sigma (\mu_2 - \mu_1)}$$

denote the Mahalanobis distance, where $\mu_1$ and $\mu_2$ are $p \times 1$ vectors representing the means of the two conditions and $\Sigma$ is a $p \times p$ matrix representing the data covariance, where $p$ is the number of voxels per searchlight. The distinctness is related to the Mahalanobis distance as follows:

$$D = \frac{1}{4} \Delta^2 \times \frac{n_1 + n_2}{n}$$

where $n_1$ and $n_2$ are the number of data points per condition.

As defined here, $D$ is a squared distance measure and therefore cannot take on values smaller than zero. If $\Delta$ is close to zero or zero, estimation errors mostly increase the estimate. This problem is solved by implementing a leave-one-run-out cross-validation. This leads to the final, unbiased estimator of pattern distinctness as follows:

$$\hat{D} = \frac{(m - 1) f_k - p - 1}{(m - 1) m} \times \frac{1}{m} \sum_{i=1}^{m} D_i$$

where $m$ is the number of runs, $p$ a correction for the searchlight size and $f_k$ the residual degrees of freedom per run.

Parametric modulation by vividness analysis. We first wanted to investigate where in the brain the neural response was modulated by trial-by-trial differences in experienced imagery vividness. To this end, we used the above-mentioned technique with the contrast of the imagery × vividness parametric regressor per category versus the implicit baseline (i.e., the main effect of the parametric regressor). This analysis reveals for each category in which areas the pattern of voxel responses is modulated by the experienced vividness.

Representational overlap imagery and perception analysis. Second, we were interested in revealing the similarity in neural category representations between perception and imagery and subsequently investigating where this was modulated by vividness. Previous studies used cross-decoding for this purpose (Reddy et al., 2010; Lee et al., 2012; Albers et al., 2013). The rationale behind this technique is that, if stimulus representations are similar across two conditions (e.g., imagery and perception), you can use a classifier trained to decode the stimulus in one condition to decode the stimulus in the other condition. The accuracy of this cross-decoding is then interpreted as a measure of similarity or stability in representations over the two conditions. However, this is a rather indirect approach and depends highly on the exact classifier used.

Within the cross-validated MANOVA (cvMANOVA) framework (see above) representational overlap can be calculated much more directly. Overlap between two conditions can be seen as the complement of an interaction. An interaction tries to show that the representations or differences between conditions of one factor change under the conditions of another factor. When investigating overlap, we try to show that the representations remain stable under the levels of another factor. In the context of cvMANOVA, the pattern stability of one factor over the levels of another factor is defined as the main effect of that factor minus the interaction effect with the other factor. In the current analysis, the pattern stability of category over the levels of modality (perception vs imagery) is defined as follows:

$$\hat{D}(C,M) = \hat{D}(C) - \hat{D}(M \times C)$$

where $\hat{D}(C)$ is the main effect of category over all levels of modality (perception and imagery trials together) and $\hat{D}(M \times C)$ is the interaction between category and modality. $\hat{D}(C,M)$ then reveals in which voxels the effect of category remained stable during imagery compared with perception.

Modulation of overlap by vividness analysis. To investigate where the overlap between perception and imagery was influenced by the experienced imagery vividness, we had to identify those voxels that (1) represented the stimulus category during both perception and imagery and (2) are modulated by vividness. This effect is found in the stability in category effect between the perception response and the imagery × vividness response. This stability is calculated in a similar way as the stability of the category effect between the perception and imagery response as described above, but now instead of using the imagery regressor we used the imagery × vividness regressor.

Pooled permutation testing group statistics. Stelzer et al. (2013) argued that the application of standard second-level statistics, including $t$ tests, to MVPA measures is in many cases invalid due to violations of assumptions. Instead, they suggest permutation testing to generate the empirical null-distribution, thereby circumventing the need to rely on assumptions about this distribution. We followed their approach and performed permutation tests.

Single-subject permutations were generated by a sign-permutation procedure adapted for cross-validation as described by Allefeld and Haynes (2014). Because of computational limits, we generated 25 single-subject permutations per contrast. The permuted maps were subsequently normalized to MNI space. Second-level permutations were generated by randomly drawing (with replacement) 1 of the 25 permutation maps per subject and then averaging this selection to a group permutation (Stelzer et al., 2013). For each voxel position, the empirical null-distribution was generated using 10,000 group permutation maps. $p$ values were calculated per voxel as the right-tailed area of the histogram of permuted distinctness from the mean over subjects. Cluster correction was performed, ensuring that voxels were only identified as significant if they belonged to a cluster of at least 50 significant voxels. We corrected for multiple comparisons using FDR correction with a $q$ value cutoff of 0.01.

Because the vividness regressor was not estimable in every run due to lack of variation in some runs, there were fewer runs available to estimate these contrasts. Therefore, these significance maps are based on 10 instead of 25 single subject permutations, but still 10,000 group-level permutations. Furthermore, two participants were removed from this analysis because they did not have enough variation in their responses to even produce 10 permutations. For this analysis, the $q$ value cutoff was set to 0.05.

Results

Behavioral results

Before the experiment, participants filled out the VVIQ, which is a self-report measure of people’s ability to vividly imagine scenes and objects (Marks, 1973; Cui et al., 2007). During the experiment, participants imagined previously seen, cued images and rated their vividness after each trial. First, we investigated whether the reported averaged vividness ratings and VVIQ scores were related. There was a significant negative correlation between the VVIQ and the averaged vividness ratings over trials ($r = -0.45$, $p = 0.02$). Because the polarity of the two scales is reversed, this indicates that subjects with a higher imagery vividness as mea-
Averaged by the VVIQ also experienced on average more vivid imagery during the experiment.

Next, we explored whether experienced imagery vividness was influenced by stimulus category. We performed t-tests between the vividness scores of the different stimulus categories. As shown in Figure 2, there was a significant difference in vividness between letters (3.12 ± 0.59; p = 0.006, t(25) = 3.01) and between faces and fruit (2.99 ± 0.53; p = 0.012, t(25) = 2.71). There was a nonsignificant difference between fruit and letters (p = 0.076, t(25) = 1.85). Because the categories were of different complexity levels, this shows that vividness was modulated by stimulus complexity, such that imagery of simple stimuli was experienced as more vivid than imagery of more complex stimuli. This means that any effect of vividness on the neural responses aggregated over categories may be influenced by the effect of stimulus category. Therefore, we performed subsequent vividness analyses separately for each stimulus category.

Univariate fMRI results
To investigate which brain areas were activated by the different phases in the imagery task, we contrasted activity during perception versus baseline. Both perception and imagery activated large parts of the visual cortex (Fig. 3). Here activity is pooled over all imagery and perception trials so these results are not informative about overlap in stimulus representations.

To directly compare activity between perception and imagery, we contrasted the two conditions (Fig. 4). Even though both conditions activated visual cortex with respect to baseline, we observed stronger activity during perception than imagery throughout the whole ventral visual stream. In contrast, imagery led to stronger activity in more anterior areas, including insula, left dorsal lateral prefrontal cortex, and medial frontal cortex.

Parametric modulation by vividness
We first investigated where in the brain activity was modulated by experienced imagery vividness. To this end, we used the cvMANOVA analysis technique developed by Allefeld and Haynes (2014) (see Materials and Methods). This analysis investigates per searchlight whether the pattern of voxel responses is influenced by the experienced imagery vividness. In all three categories, there was large overlap between imagery and perception in the lateral occipital complex. For both the letter and face category, there was also high overlap in parietal and premotor areas (Fig. 6, red-yellow). Vividness

Overlap between perception and imagery and modulation by vividness
Subsequently, we investigated the overlap in category representations between imagery and perception and where in the brain this overlap was influenced by experienced vividness. Within the cvMANOVA framework, overlap is defined as that part of the category effect that was similar for imagery and perception (see Materials and Methods). In all categories, there was large overlap between imagery and perception in the lateral occipital complex. For both the letter and face category, there was also high overlap in parietal and premotor areas (Fig. 6, red-yellow). Vividness

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modulated the overlap in all categories in the superior parietal cortex, in the fruit and face category in the entire visual cortex, and in the letter category in right inferior temporal cortex and left intraparietal sulcus (Fig. 6, blue-green).

To illustrate this finding more clearly, we ran a new GLM in which we modeled the imagery response for each vividness level separately. In Figure 7, we plotted the difference between the main effect of perception and the main effect of imagery in early visual cortex, for each vividness level. More vivid imagery was associated with a smaller difference between perception and imagery.

**Discussion**

In the present study, we investigated (1) in which brain areas activity was modulated by variation in experienced vividness and (2) where the overlap between perception and imagery was influenced by vividness. There was an effect of vividness on activation in the precuneus, right parietal cortex, medial frontal cortex, and parts of early visual cortex in all categories. We found overlap in category representations between imagery and perception in lateral occipital complex in all categories, and in inferior parietal and premotor cortex in the letter and face category. Furthermore, we found an effect of vividness on the overlap over the whole visual cortex for both the fruit and face categories, and in the superior parietal cortex for all categories. For letters, also the overlap in left intraparietal sulcus and right inferior temporal cortex was modulated by vividness.

Previous work has shown that individual differences in visual imagery vividness correlate with activation of early visual cortex during imagery (Cui et al., 2007). Here, we show that this is also the case for trial-by-trial variation of imagery vividness. Furthermore, previous studies showed a correlation between imagery ability and overlap of neural representations with perception in early visual cortex (Lee et al., 2012; Albers et al., 2013). In contrast, we found that within-participant fluctuations in vividness are related to the amount of overlap in the entire visual cortex as well as the parietal cortex. A possible explanation for this discrepancy is that previous studies defined the overlap across stimulus categories and looked at general imagery ability. In contrast, our
current approach allowed us to define overlap within each stim-
ulus category and relate it directly to the experienced vividness 
of those stimuli. This technique is much more sensitive and can 
reveal more fine-grained effects. The results indicate that the 
overlap of the neural representation in the entire visual system 
is important for participants’ subjective experience.

We did not find a clear modulation of the overlap in the visual 
cortex in the letter category. In this category, the overlap in intra-
parietal sulcus and inferior temporal cortex was modulated in 
stead. An explanation for this is that vividness of letters means 
something different from vividness of other stimuli. Letters were 
the least complex and so had the least visual details: a key factor in 
determining vividness (Marks, 1973). This could therefore mean 
that other factors, such as semantic association or auditory imag-
ery, determined vividness in the letter category.

In addition to effects in the visual cortex, we found that, in all 
categories the activity, but not the overlap, was modulated by 
vividness in precuneus, medial frontal, and right parietal cortex. 
Previous studies have also reported activation in these areas dur-
ing visual imagery (Ishai et al., 2000; Ganis et al., 2004; Mechelli et 
al., 2004; de Borst et al., 2012). It has been suggested that the 
precuneus is important for selecting relevant details during im-
agery (Ganis et al., 2004). This is in line with our current findings 
because the amount of detail experienced during imagery plays 
an important role in judging experienced vividness. Further-
more, medial frontal activity has been associated with imagery 
performance (de Borst et al., 2012), which in turn has been linked 
to experienced imagery vividness (Keogh and Pearson, 2014). It 
has been suggested that the medial frontal cortex is important for 
the retrieval and integration of information during both working 
memory and imagery via connections to parietal and visual areas 
(Onton et al., 2005; de Borst et al., 2012). Finally, right parietal 
cortex has been associated with attention, visual inspection, and 
percept stabilization, all factors that could influence the experi-
enced vividness (Trojano et al., 2000; de Borst et al., 2012; Zarets-
kaya et al., 2010).

Our findings crucially depend on the fluctuations in imag-
ery vividness and associated overlap and activity over time. 
This begs the question what the origin of these fluctuations is. 
Fluctuations may be driven by variation in cortical excitability 
or large-scale reconfigurations of resting-state networks. For 
example, spontaneous changes within the default mode net-
work and frontoparietal networks correlate with switches be-
tween an internal versus an external focus (Smallwood et 
al., 2012; Van Calster et al., 2016). Furthermore, resting state os-
cillations within visual and motor cortices are related to 
changes in cortical excitability, which have an effect on behav-
ior (Fox et al., 2007; Romei et al., 2008). These spontaneous 
fluctuations could underlie the observed variability in experi-
enced vividness within participants. More research is neces-
sary to investigate this idea.

In addition to the neural correlates of imagery vividness, this 
study also provides novel insights with regard to the overlap in 
nerval representations of imagined and perceived stimuli. We 
reveal a large overlap between perception and imagery in visual 
cortex. This is consistent with previous work showing that work-
ning memory, perception, and visual imagery have common rep-
resentations in visual areas (Reddy et al., 2010; Lee et al., 2012; 
Albers et al., 2013; Bosch et al., 2014). However, our study is the 
first to look at overlap between neural representations of imagery 
and perception beyond the visual cortex. Unexpectedly, we also 
found strong overlap in category representations for the letter 
and face category in inferior parietal and premotor cortex. Previ-
ous studies have already reported representations in parietal cor-
text of stimuli held in working memory (Christophel et al., 2015; 
Lee and Kuhl, 2016). It may be the case that different cognitive 
functions rely on the same representations in both visual and 
parietal cortex.

Furthermore, premotor cortex activity during visual imagery 
have been associated with the spatial transformation of a mental 
object (Sack et al., 2008; Oshio et al., 2010). However, we now 
show that stimulus representations in premotor cortex are shared 
between perception and imagery during a task that does not in-
volve spatial transformations. This overlap also cannot be ex-
plained by motor preparation of the vividness response because 
during perception participants did not yet know which stimulus 
they had to imagine. One possible explanation for the overlap in 
the letter category is the fact that letters have a sensorimotor 
representation, such that the perception of letters activates areas 
in premotor cortex involved in writing (Longcamp et al., 2003). 
Our results would imply that imagery of letters also activates 
premotor areas. However, this explanation is less likely to hold 
for faces. Because the overlap is more anterior for faces, this could 
also indicate the involvement of inferior frontal gyrus, a region 
that is known to be involved in the imagery of faces (Ishai et al., 
2002).

The fact that we did not find overlap in more anterior areas for 
the fruit category can be explained by the fact that the neural 
representation of the fruit category was less distinctive than that 
of the other categories. We calculated overlap as that part of the 
main category effect that was not different between perception 
and imagery. The main effect of the fruit category (how distinct-
tive it was from the other categories) was much smaller than the 
main effect of the other categories, especially in more anterior 
brain areas. Therefore, the overlap in these areas was necessarily 
also smaller. This suggests that the fact that we did not find over-
lap in these areas is more likely due to low sensitivity than to true 
absence of overlap in these areas.

Because of the nature of our experimental task, it could be the 
case that our overlap findings are mainly driven by the imagery 
trials in which the second stimulus was cued. This could point to 
spillover of the BOLD response from the perception part of the 
trial, which would pose a problem for the general overlap results. 
To investigate this, we performed the overlap analysis separately 
for first and second cue trials (Harrison and Tong, 2009). The 
peak activations for the first cue dataset were centered around 
lateral occipital complex, parietal, and premotor regions, which 
matches the main results. Furthermore, no salient differences 
were observed when comparing the results for the first and sec-
ond cue. This shows that the effects cannot be explained by spill-
over effects of bottom-up perceptual processing. The modulation 
of overlap by vividness cannot be caused by spillover effects be-
cause these two are completely unrelated in our setup.

In conclusion, we showed that a network of areas, including 
both early and late visual areas, precuneus, right parietal cortex, 
and medial frontal cortex, is associated with the experienced viv-
idness of visual imagery. The more anterior areas seem to be 
important for imagery-specific processes, whereas visual areas 
represent the visual features of the experience. This is apparent 
from the relation between experienced vividness and overlap 
with perception in these areas. Furthermore, our results show 
that the overlap in neural representations between imagery and 
perception, regardless of vividness, extends beyond the visual 
cortex to include also parietal and premotor/frontal areas.
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