Seeing versus Knowing: The Temporal Dynamics of Real and Implied Colour Processing in the Human Brain

Abbreviated title: Real and Implied Colour Processing in the Brain

Lina Teichmann*[1,2], Tijl Grootswagers[1,2,3], Thomas Carlson[2,3], Anina N. Rich[1,2,4]

1| Perception in Action Research Centre & Department of Cognitive Science, Macquarie University, Sydney, Australia

2| ARC Centre of Excellence in Cognition & its Disorders, Macquarie University, Sydney, Australia

3| School of Psychology, University of Sydney, Australia

4| Centre for Elite Performance, Training and Expertise, Macquarie University, Sydney, Australia

Corresponding author's email: lina.teichmann@mq.edu.au

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1 **Abstract**

2   Colour is a defining feature of many objects, playing a crucial role in our ability to

3 rapidly recognise things in the world around us and make categorical distinctions. For example,

4 colour is a useful cue when distinguishing lemons from limes or blackberries from raspberries.

5 That means our representation of many objects includes key colour-related information. The

6 question addressed here is whether the neural representation activated by *knowing* that

7 something is red is the same as that activated when we *actually see* something red, particularly

8 in regard to timing. We addressed this question using neural timeseries

9 (magnetoencephalography, MEG) data to contrast real colour perception and implied object

10 colour activation. We applied multivariate pattern analysis (MVPA) to analyse the brain

11 activation *patterns* evoked by colour accessed via real colour perception and implied colour

12 activation. Applying MVPA to MEG data allows us here to focus on the temporal dynamics of

13 these processes. Male and female human participants (N=18) viewed isoluminant red and green

14 shapes and grey-scale, luminance-matched pictures of fruits and vegetables that are red (e.g.,

15 tomato) or green (e.g., kiwifruit) in nature. We show that the brain activation pattern evoked

16 by real colour perception is similar to implied colour activation, but that this pattern is

17 instantiated at a later time. These results suggest that a common colour representation can be

18 triggered by activating object representations from memory and perceiving colours.

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Introduction

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22   Throughout our lives, we learn statistical regularities about objects in our environment.

23 We acquire knowledge about their typical perceptual features, which motor actions are required

24 to interact with them, and in which context they usually appear. For example, we know that a

25 tomato is round and red, we can eat it and it appears in the wider context of food. Our neural

26 representations of objects therefore need to encompass a conceptual combination of these learnt

27 attributes spanning from perception to action and semantic knowledge (A. Martin, Haxby,

28 Lalonde, Wiggs, & Ungerleider, 1995). The activation of object representations is likely to

29 involve a widespread, distributed activation of several brain regions (Patterson, Nestor, &

30 Rogers, 2007) with some brain areas responding preferentially to object colour (e.g., Seymour,

31 Williams, & Rich, 2015). Several neuroimaging studies have compared perceiving colour and

32 accessing object-colour knowledge from memory, finding evidence that similar brain areas are

33 involved in these two processes (e.g., Bannert & Bartels, 2013; A. Martin et al., 1995;

34 Vandenbroucke, Fahrenfort, Meuwese, Scholte, & Lamme, 2014). Using

35 magnetoencephalography (MEG), we look at the neural timecourse of 'real' (by which we

36 mean 'induced by wavelengths of light') colour perception versus implied object-colour

37 activation from memory.

38   Associations between objects and typical or *implied* colours are acquired through

39 experience (Bartleson, 1960; Hering, 1920) and are activated effortlessly and involuntarily

40 (Bramão, Faísca, Petersson, & Reis, 2010; Chiou & Rich, 2014). The activation of object-

41 colour knowledge is part of the dynamic interaction between perceptual processes and

42 activation of prior conceptual knowledge to evaluate sensory input (Collins & Olson, 2014;

43 Engel, Fries, & Singer, 2001; Goldstone, de Leeuw, & Landy, 2015). One of the central

44 questions is how object-colour knowledge interacts or overlaps with colour representations

45 generated by external stimuli. There is behavioural evidence that object-colour knowledge can

46   influence colour perception. Hansen, Olkkonen, Walter, & Gegenfurtner (2006) found that

47   participants overcompensated for implied colours when they were asked to change the colour

48   of colour-diagnostic objects to be achromatic. For example, a banana would be adjusted

49   towards the blue side of grey, showing the influence of the implied colour yellow. Similarly,

50   Witzel (2016) showed that participants selected an image of an object as achromatic more often

51   when its colour was modified to be the opposite of its implied colour (e.g., a bluish-grey

52   banana). These results suggest that colour perception can be influenced by previously learnt

53   object-colour associations (see Firestone and Scholl, (2016) for debates about the extent to

54   which activation of colour from memory is identical to colour perception). Brain-imaging data,

55   recorded with functional magnetic resonance imaging (fMRI), suggest that brain activation

56   corresponding to implied object colour activation shares characteristics with real colour

57   perception: Retrieving the knowledge that a banana is yellow activates brain areas in or around

58   the V4 complex, which is involved in colour perception (Bannert & Bartels, 2013; Barsalou,

59   Simmons, Barbey, & Wilson, 2003; Chao & Martin, 1999; Rich et al., 2006; Simmons et al.,

60   2007; Vandenbroucke et al., 2014). This suggests that activation of implied colour rests on a

61   similar neural architecture as real colour perception.

62   These results suggest that similar brain areas are active when perceiving colour and

63   accessing implied colour, which may drive the behavioural interactions between the two (e.g.,

64   Hansen et al., 2006). Real colour activations occur very early in visual processing, whereas

65   implied colour presumably is only activated once the object is processed at a higher level.

66   Hence, there could be a temporal delay for activity driven by implied colour in comparison to

67   activity driven by perceived colour. As the signal measured by fMRI is slow, it is not a suitable

68   method to distinguish fine temporal differences between real and implied object colour

69   processing. In the current study, we use multivariate pattern analysis (MVPA) on MEG data

70   (Grootswagers, Wardle, & Carlson, 2017) to compare the brain activation patterns evoked by

71 colour perception and implied object colour activation. MEG has fine temporal resolution, and

72 with MVPA we can detect patterns across the sensors at each time point that are reliable enough

73 to train an algorithm to classify different categories of stimulus. Here, we use these methods to

74 test whether a classifier trained on 'real colour' can successfully decode 'implied colour'. Such

75 cross-generalisation can only occur if there is sufficient similarity in the neural signals. This

76 approach enables us to contrast the temporal dynamics of real and implied colour processing,

77 shedding light on the interaction between perceptual processing and activation of object

78 representations.

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80
81   **Methods**

82   *Participants*. 20 healthy volunteers (12 female, mean age = 27.6 years, SD = 6.6 years)

83 completed the study. All participants reported normal or corrected-to-normal vision including

84 normal colour vision. Participants gave informed consent before the experiment and were

85 reimbursed with $20/hour. During the MEG recording, participants were asked to complete a

86 target-detection task to ensure they were attentive. Two participants performed more than three

87 standard deviations below the group mean on this task, suggesting they did not pay attention

88 to the stimuli, and were therefore excluded from analysis, leaving 18 participants in total. The

89 study was approved by the Macquarie University Human Research Ethics Committee.

90   *Procedure*. While lying in the magnetically shielded room (MSR) for MEG recordings,

91 participants first completed a colour flicker task (Kaiser, 1991) to equate the coloured stimuli

92 in perceptual luminance. Then they completed the main target-detection task. We used only

93 two colours to increase the power of our analysis. If there are luminance differences between

94 the colour categories, the classifier can use this strong signal to discriminate the categories

95 instead of relying on colour. While previous studies have shown the greatest behavioural

96 effects for colours along the daylight axis (yellow-blue, Hansen et al., (2006)), these are not

97   feasible colours for the current design: equiluminant blue and yellow stimuli no longer look

98   clearly blue and yellow. We chose red and green as the two colours as they can be matched for

99   luminance, and we included varying exemplars of these two hue categories to ensure any

100   potential remaining slight differences in luminance could not be used by a classifier to

101   distinguish the colour categories.

102   *Colour Flicker Task*. In the colour flicker task, participants were presented with red and

103   green circles (5x5 degrees visual angle) in the centre of the screen. The colours alternated at a

104   rate of 30Hz. Participants completed 2 runs of 5 trials each. In each trial, one red-green

105   combination was used. The red colour was kept consistent throughout each trial while

106   participants were asked to use a button box to adjust the luminance level of green and report

107   when they perceived the least amount of flickering. The HSV (hue, saturation, value) values

108   for each green shade were then recorded. This procedure was repeated in the second run. The

109   average HSV values between the two runs was then computed, yielding five shades of red and

110   green equated for perceptual luminance. Using different shades of red and green which were

111   each equated for perceptual luminance minimises the degree that any luminance difference

112   between the categories could influence the results (see Table 1 [supplementary materials]

113   summarising individual HSV values used).

114   *Target-Detection Task*. In the main target-detection task (Figure 1A), participants

115   completed eight blocks of 440 trials each. There were two different types of blocks: *implied*

116   *colour* and *real colour*. Block types alternated for each participant and the overall order was

117   counterbalanced across participants. In the *implied colour* blocks, participants viewed

118   luminance-equated (SHINE toolbox Willenbockel et al. (2010)) grey-scale images of colour

119   diagnostic objects (see Figure 1A). Equating the overall luminance ensures that differences in

120   MEG response patterns are not caused by luminance differences between the 'usually red' and

121   'usually green' categories. To increase variability in the stimulus set, half the stimuli depicted

122   a single item on the screen (e.g., one strawberry) and the other half were multiple, partially

123   overlapping items (e.g., three strawberries). Having several different stimuli in each category

124   helps to minimise the influence of low-level features such as edges and shapes on the results.

125   In the *real colour* blocks, participants viewed five different abstract shapes. Each shape was

126   filled in one of the red and green shades which had been equated for perceptual luminance with

127   the colour flicker task. Each shape occurred equally often in red and green. To match the stimuli

128   presented in the *implied colour* block, half of the shapes were single shapes (e.g., one square)

129   on the screen while the other half consisted of partially overlapping shapes (e.g., three squares).

130   All stimuli (objects and shapes) contained the same number of pixels (Figure 1A).

131   In both block types, presentation location varied randomly by ~1 degree visual angle

132   around the central fixation cross. Changing the spatial location of the stimulus images adds

133   variability to the retinal image, again reducing the influence low-level visual features have on

134   the results. Participants were asked to press a button when they saw an image of the target

135   shape (cross) or target object (capsicum). Every block had 40 target trials. All target trials were

136   discarded before the MEG data analysis. On average, participants detected 98.51% (SD =
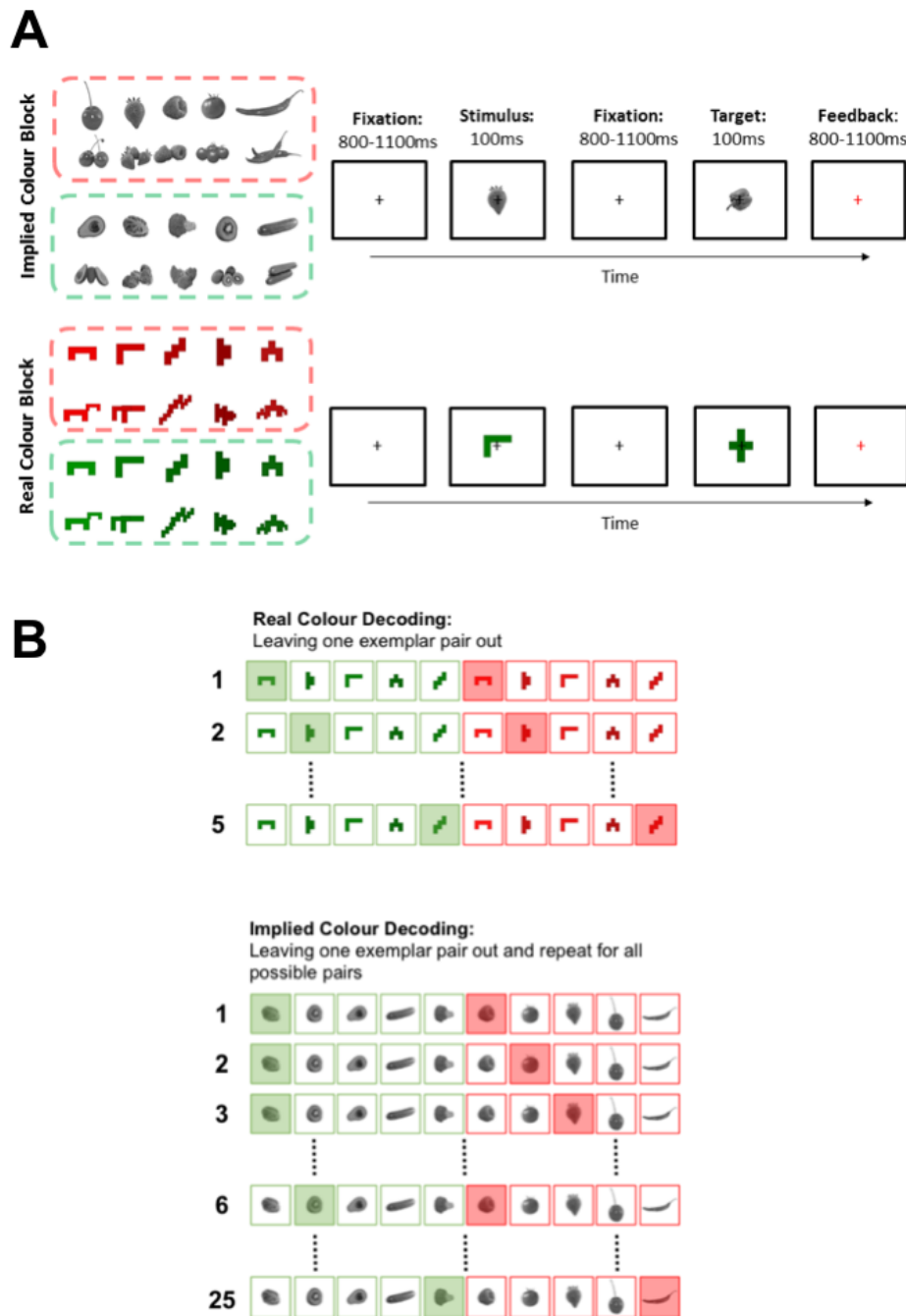
137   0.013%) of target stimuli.

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Figure 1: (A) Target-detection task and stimuli for both implied colour (top panel) and real colour (bottom panel) blocks. Participants were asked to press a button as soon as they saw the target (capsicum or cross). If they pressed the button after a target (correct detection) the fixation cross would turn green briefly, if they missed the target it would turn red. (B) Cross-validation approach used for real (top) and implied (bottom) colour decoding analyses. Every row shows which trials were used for the training set (clear) and which trials were used for the testing set (shaded). Trials with the same exemplar are never in the training and the testing set. In the real colour decoding analysis, we split the data in 5 different ways, always leaving one pair of the same shape with matched luminance out. In the implied colour decoding analysis, we split the data in 25 different ways, leaving all possible exemplar pairs out once. The classification accuracy is an average of the classifier performance for each of these divisions.

139   *Apparatus and Pre-processing*. The stimuli had a visual angle of approximately 5 x 5

140   degrees and were projected onto a translucent screen mounted in the magnetically shielded

141   room. The stimulus display system used was an Epsom projector (EB-G7400U) with a refresh

142   rate of 60Hz. The projector display size had approximately 10.02 x 19.9 degrees visual angle

143   and the resolution of the display was set to 1280 x 720 pixels. Stimuli were presented using

144   MATLAB with Psychtoolbox extension (Kleiner et al., 2007; Pelli, 1997). The neuromagnetic

145   recordings were obtained with a whole-head axial gradiometer MEG (KIT, Kanazawa, Japan),

146   containing 160 axial gradiometers. The frequency of recording was 1000Hz. FieldTrip

147   (Oostenveld, Fries, Maris, & Schoffelen, 2011) was used to pre-process the data. We used a

148   low-pass filter of 200Hz and a high-pass filter of 0.03Hz online. Stimulus onsets were

149   determined with a photodiode that detected light change when a stimulus came on the screen.

150   Trials were epoched from -100 to 800ms relative to stimulus onset and downsampled to 200Hz

151   (5ms resolution). All target trials were removed. We performed no further preprocessing steps

152   (e.g., channel selection, artefact correction), leaving our data in the rawest possible form. This

153   choice was motivated by recent work showing that traditional preprocessing choices can

154   introduce artefacts in the data that have a strong effect on multivariate analyses (van Driel,

155   Olivers, & Fahrenfort, 2019).

156   *Decoding Analysis*. We conducted four separate decoding analyses using linear

157   discriminant classifiers (LDA) implemented in CoSMoMVPA (Oosterhof, Connolly, &

158   Haxby, 2016). First, to test whether we can decode perception of red versus green, we analysed

159   the data from the real colour (shape) blocks. We tested whether we could decode the colour of

160   our abstract shapes for each person. The classifier was trained on distinguishing the activity

161   patterns evoked by red versus green shapes at each timepoint using 80% of the real colour data.

162   We then used the classifier to predict the colour of each stimulus at every timepoint in the

163   remaining 20% of the real colour data. To divide the data into training and testing set, we used

164   an independent exemplar cross-validation approach (Carlson, Tovar, Alink, & Kriegeskorte,

165   2013), leaving out one exemplar pair with matched luminance (e.g., red and green L-shape,

166   matched for perceptual luminance). This process was repeated over all folds so that each

167   exemplar pair was in the training and the testing set once (5-fold cross-validation). Hence, the

168   colours in each fold were balanced (Figure 1B).

169   Second, to assess whether we can decode implied colour from grey-scale objects, we

170   trained a classifier to distinguish trials of grey-scale objects that are associated with red versus

171   green. As in the analysis described above, we used an independent cross-validation approach

172   and trained the classifier on 80% of the implied colour data and tested its performance on the

173   remaining 20% of implied colour data. Because the greyscale objects in the red and green

174   condition varied in more ways than just their implied colours, we left out both possible

175   exemplar pairs for each object in the implied colour decoding analysis to minimise the degree

176   to which visual features such as shape would be used by the classifier. We selected trials based

177   on label for both colour categories (e.g., all strawberry and kiwifruit trials). Note that there

178   were two instances of each stimulus (e.g., an image of one strawberry and an image of three

179   strawberries) and these were considered the same object for the leave-one-out procedure. We

180   trained our classifier to distinguish between activity patterns evoked by all stimuli except the

181   selected stimuli and tested its performance on the left-out trials. We repeated this process to

182   have every possible combination of green and red objects used once as the testing set (25-fold

183   cross-validation), and report the average classification performance over all these combinations

184   (Figure 1B). Although the independent cross-validation approach reduces the risk of features

185   other than implied colour driving the effect, we still have to be cautious with the interpretation

186   as there may be overall low-level differences across all the red and green objects. This is

187   unavoidable when using natural objects.

188   Last, we conducted a cross-decoding analysis across the two different block types,

189   training the classifier on all real colour trials and testing on all implied colour trials. This cross-

190   decoding analysis is highly conservative as *everything* about the stimuli differs between real

191   colour and object colour trials, the only potential link is the implied colour of the objects to the

192   real colour of the abstract shapes. If there are any low-level differences in the real colour

193   decoding other than chromaticity (e.g., overall luminance difference), this would only decrease

194   the likelihood of finding significant cross-generalisation to the implied colour trials. In

195   addition, any differences in between the greyscale objects cannot drive an effect in the cross-

196   decoding analysis, as the classifier is trained to distinguish the real colour shapes which are the

197   same in the red and the green condition.

198   It is possible that a similar pattern is elicited by the two colour types but it occurs at

199   different times, thus, we may not see it in a direct cross-decoding analysis. We therefore also

200   conducted a time-generalisation analysis (Carlson, Hogendoorn, Kanai, Mesik, & Turret, 2011;

201   King & Dehaene, 2014), training the classifier at each timepoint on the real colour trials and

202   then testing on each timepoint in implied colour trials, yielding an accuracy score for all pairs

203   of training and testing timepoints. This technique allows us to test for similar activation patterns

204   that do not occur at the same time.

205   *Statistical Tests Classification Analyses*. To assess whether the classifier could

206   distinguish between red and green trials significantly above chance, we used random effects

207   Monte-Carlo cluster statistic (Maris & Oostenveld, 2007) using Threshold Free Cluster

208   Enhancement (TFCE, Smith & Nichols, 2009) as implemented in CoSMoMVPA (Oosterhof

209   et al., 2016). The TFCE statistic represents the support from neighbouring time points, allowing

210   optimal detection of sharp peaks, as well as sustained weaker effects. First, a permutation test

211   was conducted by swapping the labels of complete trials and then we re-ran the analysis on the

212   data with the shuffled labels. This was repeated 100 times per participant to generate subject-

213   level null-distributions. Second, Monte-Carlo sampling was used to create a group-level null-

214   distribution consisting of 10,000 shuffled label permutations for the time-resolved decoding,

215   and 1000 for the time-generalisation analysis (to limit computation time). Third, these group-

216   level null-distributions were transformed into TFCE statistics (Smith & Nichols, 2009). To

217   correct for multiple comparisons, we then selected the maximum TFCE value across time in

218   each of the null distributions. Finally, to assess whether decoding was above chance, we

219   transformed the true decoding values to TFCE statistics and compared them to the 95th

220   percentile of the corrected null distribution.

221   *Behavioural data collection*. In addition to our MEG experiment, we collected colour

222   categorisation accuracies and reaction times on our stimuli from a new sample of 100

223   participants on Amazon's Mechanical Turk. Participants were presented with the red and green

224   shapes and the grey-scale objects, each presented individually for 100ms, randomly

225   intermingled. On the instructions screen, participants were told that they would see images that

226   can be categorised as red or green. They were informed that some images would be shown in

227   greyscale, but that these objects were typically associated with red or green. Their task was to

228   categorise the images into these two categories as fast and as accurately as possible by

229   responding with either "m" or "z" using a keyboard. This allowed us to first confirm that the

230   objects we had selected were indeed typically associated with red or green, and second, to test

231   whether there was a reaction time difference between real and implied colour categorisation.

232   Response-key mappings were randomly determined for each participant. Participants each

233   completed 6 practice trials on objects that were not used in the experiment before the actual

234   data collection began. Each participant was presented with each of the objects once. We

235   calculated the mean accuracy and reaction times for the real and implied colour condition.

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Results

238   For our real colour decoding analysis, we trained the classifier to distinguish red from

240   green shapes and then tested whether it could distinguish red from green shapes in an

241   independent set of data. The classifier was able to predict the colour above chance in a cluster

242   stretching from 65 to 315 ms, reflecting a signal modulated by colour (Figure 2, orange).

243   To examine whether we can decode implied object colour, the classifier was trained on

244   a subset of the object trials and then tested on an independent set. The testing set included only

245   exemplars (e.g., all strawberry and kiwifruit trials) that the classifier did not train on. Our data

246   show that the classifier can distinguish between the objects belonging to the red and green

247   category significantly above chance in a cluster stretching from 190 to 215 ms and from 270

248   to 290 ms (Figure 2, blue). While this suggests that there is categorical difference between

249   objects associated with red and green, the results of this particular analysis could be driven by

250   an overall difference in object characteristics other than colour (e.g., if red objects tend to have

251   more round edges than green objects), and we therefore do not interpret this further.

252   Our key analysis to test whether there is a representational overlap of real and object

253   colour processing depends on cross-decoding: training a classifier on real colour stimuli and

254   testing on grey-scale objects that have implied colours. We trained the classifier to distinguish

255   between the red and green shapes and tested its performance on the grey-scale objects to see

256   whether direct cross-generalisation between real and implied object colour is possible. In this

257   analysis, the classifier is trained on identical shapes that only vary in terms of colour. Hence,

258   this is the most conservative way of testing whether there is a representational overlap between

259   real and implied colours. The cross-colour decoding was not significant at any point in the

260   timeseries (Figure 2, yellow). Accessing implied colour, however, presumably requires first

261   accessing the general concept of the object. Therefore, real and implied colours may have a

262   similar representation but colour information could be accessed later when activated via objects

263   in comparison to when colour is perceived. We therefore tested whether this is the case using

264   a cross-decoding time-generalisation analysis. We trained a classifier to distinguish between

265   red and green shapes at every timepoint and then tested whether it could cross-generalise to the

266   grey-scale objects at any timepoint. The results of key cross-generalisation analyses are

267   summarised in Figure 3, showing a cluster of significant cross-generalisation with a time-shift.
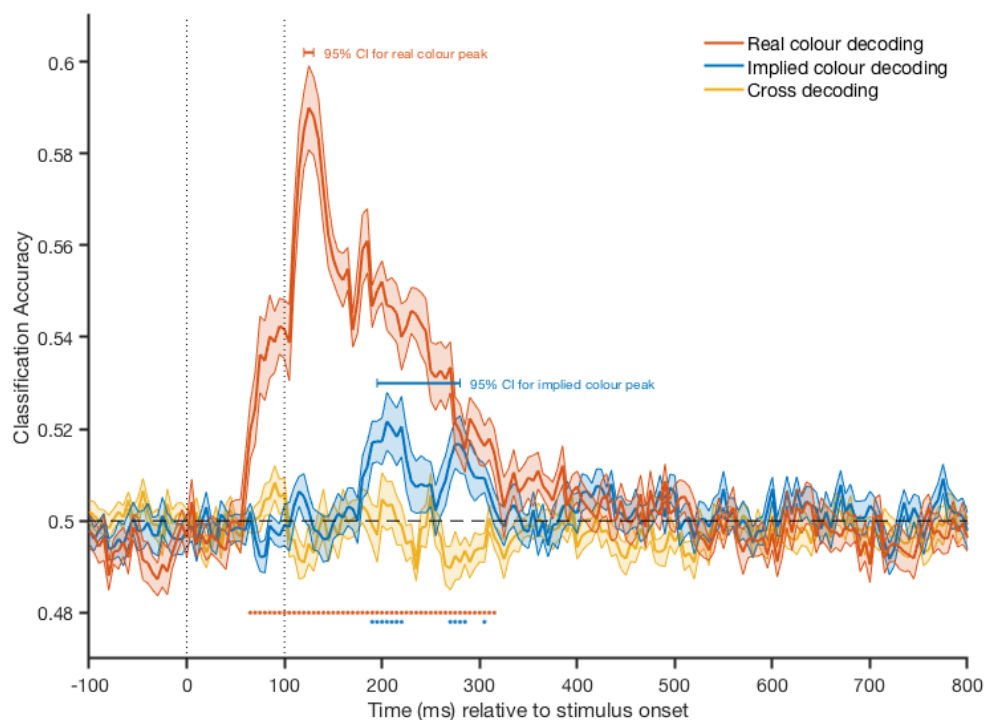
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Figure 2: Classification accuracies for real colour (orange), implied colour (blue), and direct cross-colour (yellow) decoding over time. Vertical, dotted lines show stimulus on- and offset. Dashed line indicates chance level (50%). Shading indicates error bars around the mean (standard deviation of decoding accuracies across participants divided by the square root of the number of participants). Coloured dots depict significant timepoints corrected for multiple comparisons. The 95% confidence intervals for peak decoding latencies are plotted above the classification accuracies.

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270   The time-generalisation analysis revealed similar activation patterns between real and implied

271   colours when the classifier is trained on real colour at an earlier timepoint and tested on implied

272   colour at a later one (Figure 3A and 3B). These generalisation accuracies were statistically

273   above chance, even with our conservative correction for multiple comparisons (Figure 3C).

274   Inspecting the training timepoint with maximum decoding (140 ms) indicates that there is

275   above-chance decoding at later testing timepoints with peak decoding at 200 ms after stimulus

276   onset (Figure 3B). The results show that we can cross-decode between real and implied colours

277   when we *train* the classifier on *real* colours at timepoints between 140 to 160 ms and *test* it on

278   *implied* colours at a cluster from 200 to 215 ms (Figure 3C). Combining the off-diagonal shift

279   of the significant timepoints shows a median delay of 55 ms for implied colour testing times

280   compared to real colour training times (Figure 3D). Importantly, these results are unlikely to

281   be driven by anything else than colour as the classifier is trained on real colour trials in which

282   the only different stimulus characteristic was colour and tested on implied colour trials which

283   were achromatic. As a check, we also performed the reverse analysis (i.e., training the classifier

284   on implied colour trials and testing it on real colour trials) which showed the same results,

285   mirrored across the diagonal. The results highlight that there are similarities between real

286   colour and implied object colour patterns but this pattern is instantiated later for implied object

287   colours than for real colours. Note that above-chance cross-decoding does not mean we can

288   interpret that the processes involved in real and implied colour processing are identical.

289   However, the results show that there are sufficient similarities for the classifier to cross-

290   generalise from brain activation patterns evoked by perceiving red and green to brain activation

291   patterns evoked by viewing grey-scale images of objects that are associated with red and

292   green[1].

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[1]Please note that these results are stable across different analysis parameters. For example, the effect remains when using a different classifier, a wider sliding time windows, and when averaging across trials in the training data, normalising the training data, and using principal component analysis.
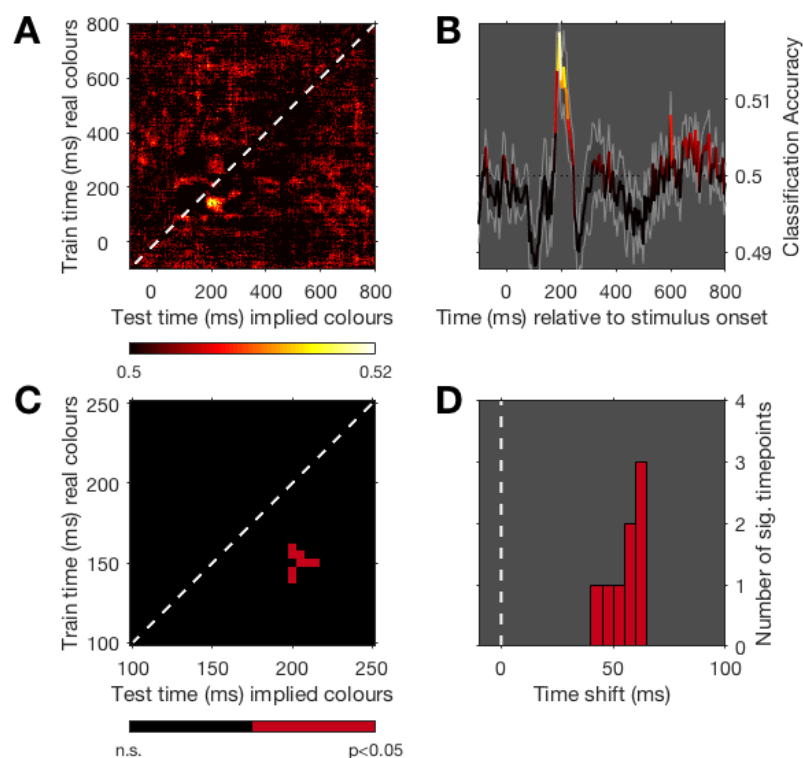
Figure 3: Results of the time-generalisation analysis. In this analysis, the classifier was trained on the real colour trials and tested on the implied colour trials. Panel A shows the classification accuracy at every possible train-test-time combination. Lighter colours indicate higher classification accuracy. Panel B shows the timecourse of the classification accuracy when the classifier relies on the training data at 140ms (peak decoding at 200ms). Shading indicates error bar around the mean (standard deviation of decoding accuracies across participants divided by the square root of the number of participants). Panel C shows all training-testing-timepoint combinations where classification is significantly above chance (based on permutation, corrected for multiple comparisons). Note that the axes in C are different to show the significant timepoints. Panel D shows the time shift of all significant timepoints from the diagonal. The delay of colour representations activated via implied colour activation in comparison to real colour perception is ~55ms .

293   These results predict that it takes more time to access implied colour than real colour,

294   presumably because one first has to access the concept of the object. We decided post-hoc to

295   test this prediction behaviourally. 100 mTurk participants were presented with the red and

296   green shapes and the grey-scale objects, each presented individually for 100ms, and were asked

297   to indicate as quickly and accurately as possible whether the stimulus was (typically) red or

298   green. Four participants were excluded from the analysis as their accuracy scores were more

299   than 2 standard deviations below the group mean. For the remaining 96 participants, we

300   excluded all the incorrect responses and compared the correct reaction times to the real and

301   implied colour trials. Responding correctly to a real colour shape was on average ~136ms (SD

302   = 85ms) faster than responding correctly to an implied colour of an object (t(95) = 15.9, p<0.05,

303   95% CI [121.08, 155.64]). Real colour responses were also more accurate (M = 91.5%, SD =

304   0.08) than implied colour responses (M=80.4%, SD=0.13). The accuracy scores for the real

305   and implied colour condition were significantly different (t(95)=8.07, p<0.05, 95% CI [8.3

306   13.8]). Using mTurk introduces variance to the experimental setup, including monitor settings

307   for colour, computer and internet speeds, all of which will increase the noise in the data; we do

308   not, therefore, interpret the specific difference in timing. Despite the variability, there is a clear

309   difference between the time taken for categorising colour in the two conditions. These results

310   are consistent with real colour perception being faster and easier than recalling implied colours,

311   in line with the prediction from our decoding results.

312   To test the relationship between the neural data and behavioural data further, we also

313   ran an exploratory analysis correlating the neural data of our sample with the behavioural data

314   of the independent set of mTurk participants. We correlated the stimulus-wise behavioural

315   categorisation data with the stimulus-wide MEG decoding accuracies for the implied colour

316   decoding analysis and examined how this correlation unfolds over time (Figure 4). The results

317   show that the neural data can be linked to the behavioural data from ~200ms after stimulus

318   onset which suggests that the information we decode can be used to generate behaviour (cf. de-

319   Wit, Alexander, Ekroll, & Wagemans, 2016; Grootswagers, Cichy, & Carlson, 2018; Williams,
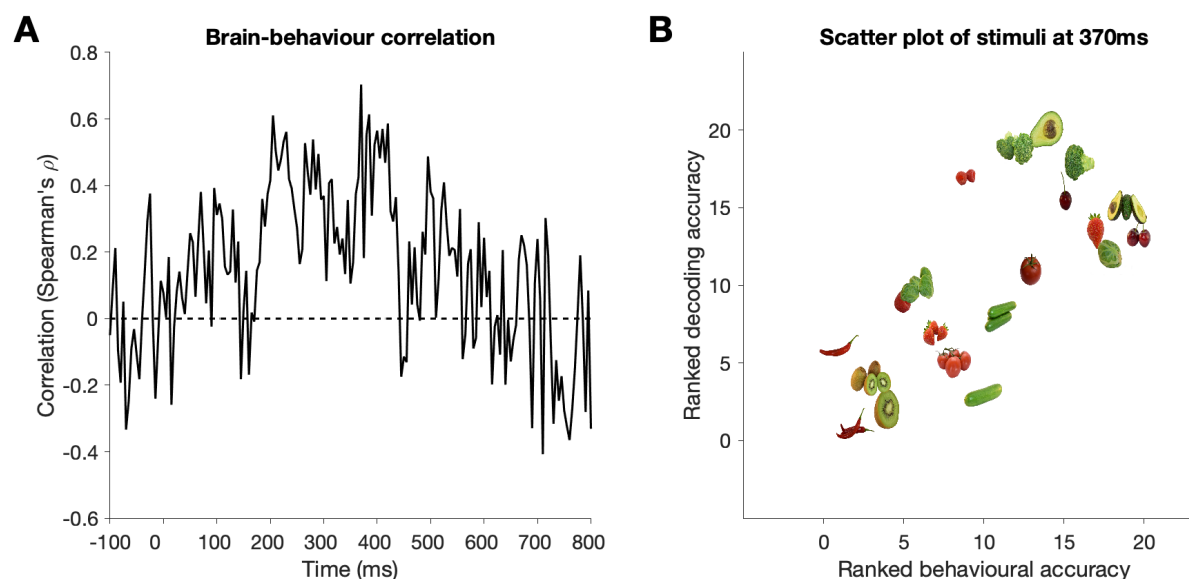
320   Dang, & Kanwisher, 2007).

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Figure 4: **Panel A shows the correlation between the stimulus-wise behavioural accuracies in the independent colour categorisation task and the stimulus-wise MEG decoding accuracies over time. Panel B shows a scatterplot for the ranked behavioural accuracies and the ranked decoding accuracies for each stimulus at the peak timepoint of Panel A (370ms).**

Discussion

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323   In this study, we compared the temporal activation patterns of colour perception and implied

324   colour to examine the interaction between perceptual processing and access to object

325   representations. We applied MVPA to time-series MEG data and show that both real and

326   implied colour can be decoded, with some caveats around implied colour decoding due to

327   potential visual stimulus differences. Our key results indicate that real and implied colour

328   processing share a sufficient degree of similarity to allow for cross-generalisation with a

329   temporal shift. The activity pattern distinguishing colours was instantiated ~55ms later for

330   implied colours than for real colour, highlighting that there are similarities between colour

331   representations accessed via 'real' colour and via implied colour, but that there is a temporal

332   asynchrony between these processes.

333   We interpret our cross-decoding results as evidence that the representation of implied

334   colour involves some of the same mechanisms as those involved in colour perception. This is

335   in line with previous studies showing that the same brain regions are active when retrieving

336   object representations from memory and perceiving those object features (for reviews see A.

337   Martin, 2007; Patterson et al., 2007) For example, Vandenbroucke et al. (2014) and Bannert

338   and Bartels (2013) showed that early visual cortex is involved when real and implied colour

339   are processed. Using fMRI, Vandenbroucke et al. (2014) trained a classifier on data recorded

340   while participants viewed red and green shapes, and then tested the classifier on data recorded

341   while participants viewed line-drawings of colour-diagnostic objects filled with ambiguous

342   colours between red and green. Behavioural results suggested participants were slightly more

343   likely to respond 'red' to the ambiguous colour presented on a line drawing of a typically red

344   object than a line drawing of a typically green object. In their fMRI data, the classifier

345   categorised the colour consistent with what the participant perceived. That means the classifier

346   categorised colours to be red when shown on objects that are typically red, and green for objects

347   that are typically green, at above chance levels. They interpret these data as evidence for an

348   influence of implied object colours on the creation of a subjective experience of colour.

349   Consistent with this study, Bannert and Bartels (2013) trained a classifier to distinguish fMRI

350   data from trials where four different colours were presented. They showed that the classifier

351   can cross-generalise to grey-scale colour-diagnostic objects. Both fMRI studies highlight that

352   there are similar activation patterns across voxels in the visual cortex for real and implied

353   colour processing. Our results provide further evidence that object-colour knowledge and

354   colour perception instantiate similar patterns, this time in the temporal domain.

355   There are several possible explanations for a temporal difference between accessing

356   colour representations via real colour and implied colour. One possibility is that the time

357   difference reflects greater individual variability in the temporal activation profile of implied

358   colours in comparison to real colours. Implied colours may be accessed at slightly different

359   timepoints for different people and thus the cross-decoding accuracy that is above chance for

360   each participant only overlaps at a later timepoint. There are also more interesting potential

361   explanations. First, it could be due to actual differences in neural processes. Colour

362   representations accessed via colour perception are immediately available whereas implied

363   colour activation presumably only happens once the object is processed to some higher level.

364   Thus, the delay could reflect differences between bottom-up and top-down access to colour

365   representations. It might be, for example, that processing an object with a typical colour

366   involves the activation of information about the object's implied colour which is fed-back to

367   earlier visual areas to compare incoming information with stored object-knowledge. In

368   comparison, the shapes used in the real colour trials are not associated with a typical colour

369   and thus do not evoke such as signal. This is a plausible interpretation of the temporal delay

370   and corresponds with earlier findings of early visual areas being involved in implied colour

371   activation (Bannert & Bartels, 2013; Vandenbroucke et al., 2014). Second, it is possible that

372   the binding of colour and shape information happens later in the visual processing hierarchy

373   compared to initial processing of separate features, and that the comparison of typical and

374   perceived colour can therefore only happen later once shape-colour binding is complete. This

375   view is consistent with results of a recent fMRI study, which showed that object-colour and

376   object-shape activated from memory can be distinguished in areas associated with colour (V4)

377   and shape (lateral occipital cortex, LOC) perception, respectively, but that the conjunction of

378   colour *and* shape can be decoded only later along the visual hierarchy (anterior temopral lobe,

379   ATL; Coutanche & Thompson-Schill, 2014). Similarly, Seymour et al. (2015) showed that

380   colour *per se* can be decoded in early visual areas but object surface colour (bound to form)

381   can only be decoded in areas further along the ventral visual stream. These findings also

382   correspond to patient work (Patterson et al., 2007) and previous transcranial magnetic

383   stimulation studies (Chiou, Sowman, Etchell, & Rich, 2014) which point towards the ATL as

384   the hub for object-knowledge (for a review see Lambon Ralph, Jefferies, Patterson, & Rogers,

385   2017). Besides the ATL, other brain areas along the processing stream such as the medial

386   temporal lobe (e.g., Rey et al., 2018), and the parahippocampal cortex (e.g., C. B. Martin,

387   Douglas, Newsome, Man, & Barense, 2018) are also involved in retrieving long-term

388   associations. Thus, it is possible that the temporal delay reflects the time it takes to activate

389   these long-term colour associations. Finally, it could also be that the delay reflects the greater

390   complexity of the grey-scale objects relative to the abstract shapes, hence binding the features

391   may take slightly longer. From the data we cannot disentangle these interpretations. Our results

392   clearly highlight, however, that there is a similar structure to the brain response to externally

393   perceived and internally activated colour representations, and that time seems to be the key

394   difference.

395   What is driving the successful decoding performance? For the real colour decoding, we

396   used shapes that were identical across colour categories and used five different levels of

397   stimulus luminance for each category that were perceptually matched. Therefore, the only

398   distinguishing feature between the stimuli was colour. That means that for the real-colour

399   decoding analysis *and* the cross-generalisation (i.e., training on shapes and testing on objects),

400   we can rule out visual differences other than colour as a driving factor. Our results show that

401   we can successfully decode real colour from ~65ms onwards. The within-implied colour

402   decoding results show that implied colour is decodable at ~190ms after stimulus onset and then

403   again a bit later at ~270ms. This double-peak may occur because of variance between stimuli,

404   such that accessing colour representations might be quicker for some images with stronger

405   colour associations (for example) than others, or between participants in the speed with which

406   they activate these representations. Alternatively, it may relate to differences in feedforward

407   and feedback processes. For this within-implied colour classification analysis, visual

408   differences could potentially contribute, as natural objects cannot be perfectly matched for the

409   different conditions (i.e., red and green), unlike in our real colour condition. Previous studies

410 have used line-drawings instead of photos of objects to reduce local low-level differences

411 between stimuli (e.g., Vandenbroucke et al., 2014). Line-drawings can reduce some of these

412 differences (e.g., local luminance differences due to texture) but also cannot completely rule

413 out any contribution of low-level effects (e.g., shapes). In addition, there is a considerable

414 trade-off between line-drawings in terms of similarity of the objects to real world objects which

415 can slow down recognition and implied colour effects (Olkkonen, Hansen, & Gegenfurtner,

416 2008; Vurro, Ling, & Hurlbert, 2013). We therefore used isoluminant, grey-scale photos of

417 objects and dealt with differences in low-level features (e.g., edges) by using an independent

418 exemplar cross-validation approach. We trained the classifier to distinguish typically red and

419 green objects using all objects except one typically-red and one typically-green object (each

420 with two exemplars, which were both left out). The classifier was then tested on the left-out

421 pair. We thereby considerably reduced the likelihood of the implied colour classification being

422 driven by low-level features as the classifier never trained and tested on the same objects. While

423 limiting the influence low-level features could have on the implied object colour decoding, it

424 is still possible that the results in this particular analysis are driven by object features other than

425 colour. To test this, we ran the same classification analysis on the output of a deep

426 convolutional neural network which showed that it is unlikely that low-level visual differences

427 account for all of the within-implied classification results (see supplementary material).

428 Crucially, however, visual differences are not a concern for the key cross-decoding analysis.

429 Here, we used identical red and green shapes in the training set, making low-level shape or

430 texture features a highly unlikely source of contribution to classifier performance and colour

431 hue being the primary predictor of category for the classifier (red vs green).

432 Our time-generalisation analysis shows that there are sufficient similarities in neural

433 representation when perceiving real colour and activating implied colour for cross-

434 generalisation. In addition, these results speak to the important aspect of temporal differences

435   between colour evoked by external stimulation and internal activation. Activating conceptual

436   knowledge of objects from memory is thought to involve a widespread network of brain areas

437   involved in perception and action of different object features (A. Martin, 2007; Patterson et al.,

438   2007). To access the implied colour of an object requires that the conceptual representation of

439   that object is activated first. Using time-generalisation methods (King & Dehaene, 2014), we

440   show here that in comparison to real colour perception, which can be decoded rapidly,

441   accessing object-colour knowledge takes ~55ms longer. This is consistent with our behavioural

442   data showing that real colour judgments are faster than implied colour judgments. The

443   behavioural data do not, however, speak to the neural similarity between real and implied

444   colour activation patterns, which are observed in the time-generalisation analyses. Our MEG

445   results increase our existing knowledge of how real and implied colour are processed by

446   showing that aspects of colour representations via external stimulation are also instantiated

447   during internal activation, but with a delay. Applying MVPA to our MEG data allows us to

448   capture the similarity of representations of real colour perception and implied colour activation,

449   but also allow us to examine temporal differences, highlighting the value of this method for

450   dissociating activation of memory of object features from perception of object features in the

451   real world.

452   Our results highlight that the activation of implied colours can occur independent of a

453   task that focuses on colour. Participants completed a target-detection task in which attending

454   to colour was not a useful strategy. The targets were ambiguous in colour (e.g., a capsicum can

455   be either red or green), and this avoided biasing participants towards deliberately thinking

456   about the implied colour of the objects. Using a task that is irrelevant to the classifier

457   performance allowed us to explore the involuntary activation of implied colours rather than the

458   signals associated with perhaps actively imagining colours or retrieving colour names. Not

459   attending to the feature that is relevant for the classifier probably reduced our decoding

460   accuracy in general (e.g., Brouwer & Heeger, 2013; Jackson, Rich, Williams, & Woolgar,

461   2017), but clearly supports previous studies showing that there is an *involuntary* activation of

462   object-colour independent of task demands (Bannert & Bartels, 2013; Vandenbroucke et al.,

463   2014).

464   Overall, the decoding accuracies across our analyses are low but significantly above

465   chance with conservative statistics. As outlined above, this is probably partially due to colour

466   being irrelevant for the task. In addition, it is important to note that we did not use extensive

467   pre-processing, meaning we ran our analyses on effectively raw data. We use our multivariate

468   decoding analyses for *interpretation* (Hebart & Baker, 2017)– if decoding is above chance, this

469   means there is a signal that allows a categorical distinction between the conditions. Minimal

470   pre-processing (e.g., no trial averaging, filtering, channel-selection, trial-selection) ensures that

471   there is no potential influence of plurality of methods or specific pre-processing choices; it also

472   means that the data overall are noisier which can result in relatively low decoding accuracies.

473   However, it is crucial to note that low decoding accuracies does not necessarily mean that the

474   effects are weak, as decoding accuracies are not effect sizes (cf. Hebart & Baker, 2017). Here,

475   we show with rigorous methodological controls and strict correction for multiple comparisons

476   that there is significant cross-generalisation from real colour to implied colour.

477   Previous fMRI studies showed that early visual areas are involved in real colour

478   perception and implied colour activation (Bannert & Bartels, 2013; Rich et al., 2006;

479   Vandenbroucke et al., 2014), but other studies implicate anterior temporal regions in object

480   colour knowledge. For example, a transcranial magnetic stimulation study showed that the

481   behavioural effects of implied colour knowledge on object recognition are disrupted when

482   stimulating the anterior temporal lobe (Chiou et al., 2014), complementing patient studies

483   suggesting this area holds conceptual object information (e.g., Lambon Ralph & Patterson,

484   2008). This highlights that activating object attributes, including implied colour, goes beyond

485   low-level visual areas. Our study adds time as a novel aspect to this discussion by comparing

486   the temporal profiles of colour representations accessed via real colour perception and implied

487   colour activation.

488   In conclusion, our data show that there is a common representation of real and implied

489   colour but that this representation is accessed later when triggered by activating implied colour

490   than by perceiving real colour. This is in line with previous studies suggesting that the same

491   brain areas are involved in object-feature activation from memory *and* object-feature

492   perception. Our results highlight that applying MVPA to time-series MEG data is a valuable

493   approach to exploring the interaction between object-feature inputs and predictions or

494   representations based on prior knowledge. This opens multiple avenues for future studies

495   examining the dynamic interactions between perceptual processes and activation of prior

496   conceptual knowledge.

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