Yellow strawberries and red bananas: The influence of object-colour knowledge on emerging object representations in the brain

Lina Teichmann*[1,2], Genevieve L. Quek[5], Amanda Robinson[1,2,3], Tijl Grootswagers[1,2,3], Thomas A. Carlson[2,3], Anina N. Rich[1,2,4]

1l Perception in Action Research Centre & Department of Cognitive Science, Macquarie University, Sydney, Australia
2l ARC Centre of Excellence in Cognition & its Disorders, Macquarie University, Sydney, Australia
3l School of Psychology, University of Sydney, Australia
4l Centre for Elite Performance, Training and Expertise, Macquarie University, Sydney, Australia
5l Donders Institute for Brain, Cognition and Behaviour, Radboud University, Nijmegen, The Netherlands

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

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1 **Abstract**

2   The ability to rapidly and accurately recognise complex objects is a crucial function of

3   the human visual system. Successful object recognition requires binding incoming visual

4   features such as colour and form into specific neural representations that can be compared to

5   our pre-existing knowledge about the world. Some objects have typical or implied colour as a

6   central feature that is useful for recognition; for example, a banana is typically yellow. In the

7   current study, we address two main questions. First, we test how colour representations unfold

8   over time when activated by real colour perception versus the activation of implied colours.

9   Second, we examine how features such as colour and form are bound together. We apply

10   multivariate pattern analyses to time-resolved neuroimaging (magnetoencephalography) data

11   to address these questions. Our results show that colour representations can be accessed

12   both via real colour perception and via implied colour activation in the complete absence of

13   colour in the stimulus. These real and implied colour representations share characteristics but

14   differ in the timing of their neural activation. In addition, our data demonstrate that object

15   representations are influenced by object-colour knowledge at later, but not at initial stages of

16   visual processing. Single object features are processed before feature-binding occurs which

17   allows for a comparison of visual input with existing knowledge about objects. Taken together,

18   these results provide new insights into the integration of incoming visual information with

19   existing conceptual object knowledge.

20   **Introduction**

21   Objects in our environment can be characterised by many different properties including

22   form, colour, surface texture, and motion. For successful object recognition, we need to

23   compare incoming perceptual information with pre-existing object concepts, which contain

24   multiple features. Robust conceptual object representations allow for reliable object

25   recognition under different conditions such as changing light, orientation or size. A central

26   feature of many objects in the environment is colour, which can be a highly informative cue

27   about an object's identity but also varies in certain situations. For example, colour is a crucial

28   clue to distinguish lemons from limes, but can also signify the ripeness of many types of fruit.

29   Here, we use multivariate pattern analyses (MVPA) and Magnetoencephalography (MEG) to

30   examine the way in which incoming sensory information about objects interacts with

31   conceptual object representations, focusing on object-colour knowledge.

32   Colour perception comprises a progression from simple chromatic processing to more

33   complex object-surface colour integration. First, the registration of different wavelengths of

34   light and comparing their intensities occurs in V1 and V2 (Zeki, 1983a, 1983b; Zeki & Marini,

35   1998). Area V4, slightly further on in the visual hierarchy, has been shown to code for more

36   complex aspects of colour perception by comparative processes between surfaces reflecting

37   different amounts of light (Zeki & Marini, 1998). Functional magnetic resonance imaging (fMRI)

38   has shown that colour in a specific retinal position was represented in early visual areas such

39   as V1 but colour bound to form (object surface colour) could only be differentiated later along

40   the visual hierarchy (V4 and beyond) (Seymour, Williams, & Rich, 2015). Increasingly complex

41   colour processing along the visual hierarchy is thus likely to contribute to object identification

42   at higher levels of processing.

43   To recognise objects, we have to be able to integrate incoming perceptual information

44   with what we already know (Albright, 2012; Clarke & Tyler, 2015). Area V4 can distinguish

45   between different surface colours but is not concerned with whether objects are coloured

2

46   correctly or incorrectly (Zeki & Marini, 1998). Results of behavioural studies show that typical

47   or *implied colour* information (e.g., yellow for a banana) facilitates the recognition of objects

48   that are strongly associated with a certain colour (for a meta-analysis see Bramão, Reis,

49   Petersson, & Faísca, 2011). For example, for objects high in colour diagnosticity, participants

50   are faster to identify objects that are congruently coloured (e.g., yellow banana) compared to

51   objects that are incongruently coloured (e.g., red banana) (Nagai & Yokosawa, 2003; Tanaka

52   & Presnell, 1999). This colour congruency effect demonstrates that our representation of

53   canonically-coloured objects inherently includes colour as a strong defining feature, such that

54   conflicting visual information slows recognition. Thus, activating implied object colours

55   appears to interact with processing perceptual object features.

56   A key question about how object-colour knowledge is represented is whether implied

57   colours rely on the same neural mechanisms as perceiving object colours. There is evidence

58   from fMRI of overlap or close proximity in the brain areas activated for both colour perception

59   *and* memory colour activation (Chao & Martin, 1999; Martin, Haxby, Lalonde, Wiggs, &

60   Ungerleider, 1995; Wiggs, Weisberg, & Martin, 1998). For example, Bannert and Bartels

61   (2013) applied multivariate pattern analyses (MVPA) to fMRI data and showed overlapping

62   neural representations for colour perception and implied object colour activation in visual

63   areas V1 and V4. Similarly, Coutanche and Thompson-Schill (2014) showed that brain

64   activation patterns evoked by object-colour and object-shape activated from memory can be

65   distinguished in areas associated with colour (V4) and shape (lateral occipital cortex, LOC)

66   perception, respectively. Their results also demonstrated that the conjunction of colour *and*

67   shape, a 'bound' representation activated from memory, is only represented in the anterior

68   temporal lobe (ATL). This finding corresponds to patient work (Patterson, Nestor, & Rogers,

69   2007) and transcranial magnetic stimulation studies (Chiou, Sowman, Etchell, & Rich, 2014;

70   Pobric, Jefferies, & Lambon Ralph, 2010) that point towards the ATL as a hub for conceptual

71   knowledge (for a recent review see Ralph, Jefferies, Patterson, & Rogers, 2017). Overall,

72 these results suggest that similar processes are utilised for colour processing when it is

73 accessed via real colour and via implied colour.

74 To understand at what stage of processing the activation of colour representations

75 accessed via colour perception and object-colour knowledge interacts, we need to examine

76 the temporal dynamics of this process. In non-human primates, information in V1 is processed

77 at ~50ms after stimulus onset while information reaches visual areas such as V4 after ~70ms

78 (DiCarlo, Zoccolan, & Rust, 2012). Results of the fMRI studies reviewed above suggest that

79 several brain regions are involved in both colour perception *and* the activation of implied

80 colours from memory, but it is possible that these occur at different time scales.

81 Electroencephalography (EEG) studies have investigated the temporal dynamics of

82 object-colour knowledge (Lloyd-Jones, Roberts, Leek, Fouquet, & Truchanowicz, 2012; Lu et

83 al., 2010; Proverbio, Burco, del Zotto, & Zani, 2004). Lloyd-Jones et al. (2012) used images

84 of real objects to show that shape information modulates neural responses at around 170ms

85 (i.e., component N1), the combination of shape and colour affected the signal at 225ms (i.e.,

86 component P2), and the typicality of object-colour pairing modulated components

87 approximately 225 and 350ms after stimulus onset (i.e., P2 and P3). These findings suggest

88 that shape information activates typical object-colour associations and that bound colour *and*

89 shape features are processed later than shape alone. This leads to the question of what effect

90 object-colour knowledge has on colour perception and whether neural activity associated with

91 activating typical colours and perceiving real colours unfolds in a similar way.

92 In the current study, we examine the temporal aspects underlying object-colour

93 processing by applying MVPA to MEG data. First, we compare how neural colour

94 representations evolve over time when accessed via real colour perception and implied colour

95 activation. Second, we examine how object-colour knowledge affects colour and shape

96 binding. We present participants with colour-diagnostic objects that are either coloured

97 congruently (e.g., yellow banana), incongruently (e.g., red banana), or greyscale (e.g., grey

98   banana), and coloured abstract shapes that have no canonical colour. Decoding colour that

99   is triggered by different wavelengths of light (i.e., "real" colour) signifies *colour perception,*

100   whereas decoding a greyscale object's *implied colour*. Decoding a coloured object's colour

101   congruency status is related to colour associations based on *object-colour knowledge*. First,

102   we examine the time-course of real colour perception, which serves as a basis to investigate

103   how the neural response to real colour perception changes over time. In a previous study, we

104   showed that the MEG pattern of activation evoked by red and green can be differentiated

105   70ms after image presentation (Teichmann, Grootswagers, Carlson, & Rich, 2018, *Preprint*).

106   Here, we included the colours orange and yellow to examine how colours are represented

107   across a wider range. Second, we test whether colour representations accessed via real

108   colour perception and object-colour activation are similar. Third, we focus on binding of colour

109   and form to understand the effect of typical colour-form associations on object and colour

110   processing, and examine the timecourse of object-feature binding.

111

112   **Methods**

113   *Participants.* 20 healthy volunteers (11 female, mean age = 28.9 years, SD = 6.9 years,

114   1 left-handed) participated in the study. All participants reported accurate colour-vision and

115   had normal or corrected-to-normal visual acuity. Participants gave informed consent before

116   the experiment started and were financially compensated. The study was approved by the

117   Macquarie University Human Research Ethics Committee.

118   *Stimuli.* We used four different stimulus types: *congruent objects, incongruent objects,*

119   *greyscale objects,* and *abstract shapes* (Figure 1A). All objects exhibited robust form-colour

120   associations in previous studies (Bannert & Bartels, 2013; Joseph, 1997; Lloyd-Jones et al.,

121   2012; Naor-Raz, Tarr, & Kersten, 2003; Tanaka & Presnell, 1999; Therriault, Yaxley, & Zwaan,

122   2009). There were four different colour categories (red, green, yellow, orange) and five

123   different objects per colour. In each category there was one man-made object, one living

124   object, and three fruits or vegetables. We used two different exemplars per object.

125   We did not use naturally coloured photographs of the objects for the congruent objects,

126   as this would introduce a confounding difference between our congruent and incongruent

127   conditions. Instead, we desaturated object photos and equated them in luminance using the

128   SHINE toolbox (Willenbockel et al., 2010). These greyscale, luminance matched images

129   formed the *greyscale* object condition. Then we overlayed different hues of colours over the

130   grey-scale objects. The congruent objects were colour diagnostic objects (e.g., a banana)

131   presented with their canonical colour (e.g., yellow). As incongruent objects, we used the

132   identical objects but coloured in a colour other than the diagnostic colour. This ensured the

133   congruent and incongruent stimuli were well matched in the way the texture and shape of the

134   object interacted with the colour. Every congruent object exemplar had a colour-matched

135   incongruent partner. For example, we used a specific shade of red and added it to the grey-

136   scale images of the strawberries to make the congruent strawberries. We took the identical

137   shade of red and then overlayed it onto the lemons to make the incongruent lemon exemplars.

138   To make the congruent lemon exemplar and the incongruent strawberry exemplar, we

139   overlayed the identical hue of yellow onto the grey scale images. That means, overall, we

140   have the identical shapes and colours in the congruent and the incongruent condition, a factor

141   that is crucial to ensure our results cannot be explained by features other than colour

142   congruency. The only difference between these key conditions is that the colour-shape

143   combination is either typical (congruent) or atypical (incongruent). In the abstract condition,

144   angular abstract shapes were used as stimuli. Each shape occurred equally often in red,

145   green, orange, and yellow. Because the congruent and incongruent objects were made by

146   overlaying the colours from the abstract shape conditions onto the equiluminant greyscale

147   objects, the colours in the congruent and incongruent condition appear darker than the colours

148   in the abstract shapes.

6

149   Image sizes for all conditions were randomly varied on each trial to add visual

150 variability. Participants viewed these stimuli with a distance of 114cm (visual angle: ~4.3 – 6.3

151 degrees). Varying the size of the stimuli reduced the low-level featural differences between

152 images that were not related to colour.

153   *Procedure.* Before entering the magnetically shielded room for MEG recordings, an

154 elastic cap with five marker coils was placed on the participants' heads. We recorded their

155 head shapes with a digitiser pen and used these marker coils to measure the head position

156 within the magnetically shielded room at the start of the experiment, half way through and at

157 the end.

158   In the main task (Figure 1B), participants completed eight blocks of 800 trials each.

159 Each exemplar was repeated 40 times over the course of the experiment. Each stimulus was

160 presented centrally for 450ms with a black fixation dot on top of it. To keep participants

161 attentive, after every 80 trials, there was a target image presented until a response was given

162 indicating whether this stimulus had appeared in the immediately previous block of trials or

163 not (50% present vs absent). The different conditions were randomly intermingled throughout,

164 and the target was randomly selected each time. On average, participants performed with

165 90% (SD=5.4%) accuracy.
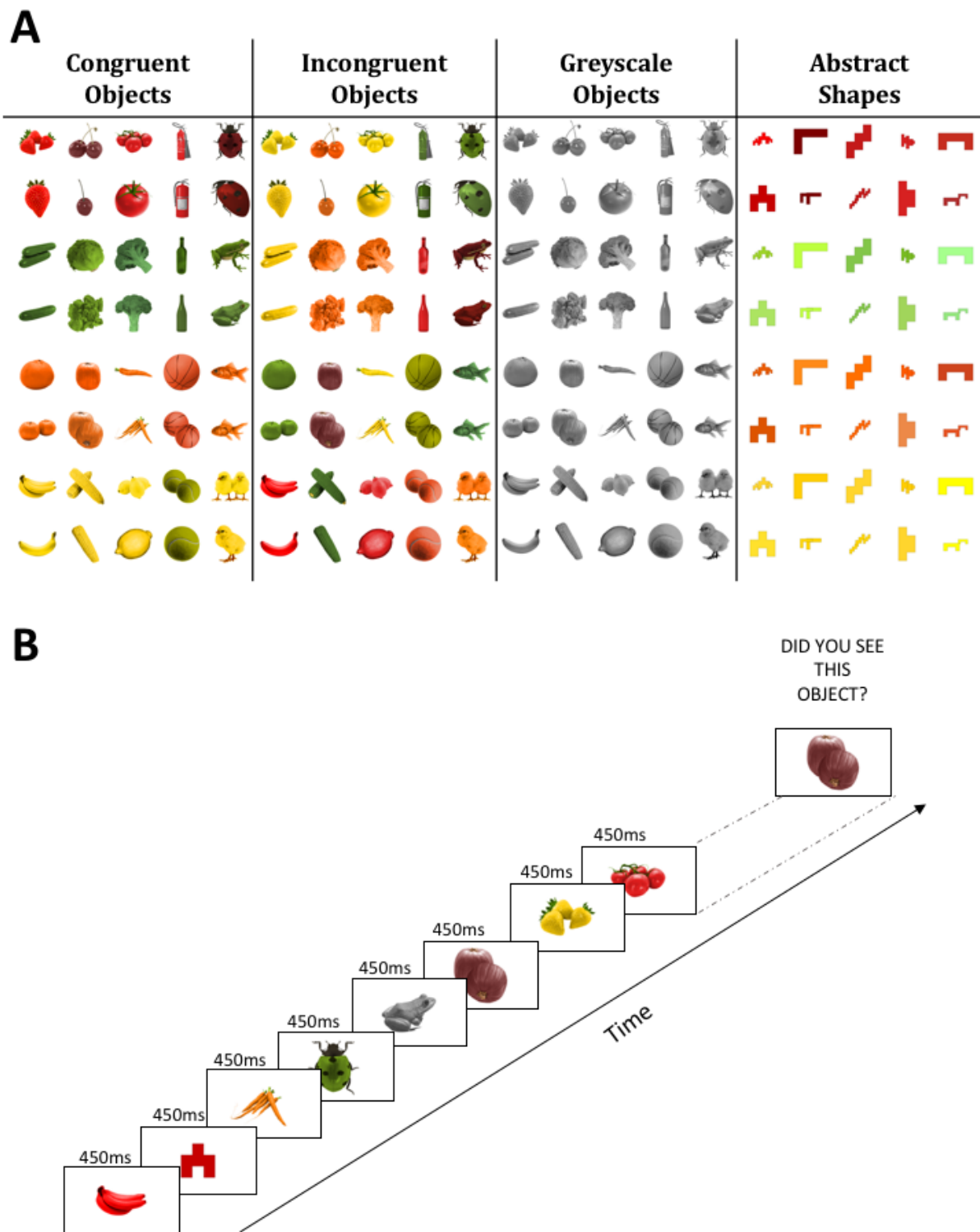
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Figure 1. (A) shows all stimuli used in this experiment. The same objects were used in the congruent, incongruent, and greyscale condition. There were two exemplars of each objects. Colours in the congruent and incongruent condition were matched. The abstract shapes were identical across colour categories. (B) shows an example sequence of the main task. Participants viewed each object for 450ms. After each run one object was displayed and participants had to indicate whether they had seen this object in the previous run or not.

8

173   After completing the main blocks, we collected behavioural object-naming data to test

174   for a behavioural congruency effect with our stimuli. Participants remained in the scanner and

175   a microphone was used to record verbal responses. On the screen, participants saw each of

176   the objects again (congruent, incongruent or grey-scale) in a random order and had to name

177   the objects as quickly as possible. As soon as voice onset was detected, the stimulus

178   disappeared. Stimulus-presentation time was marked with a photodiode and voice-onset was

179   recorded using a microphone. Seventeen participants completed three blocks of this reaction

180   time task, one participant completed two blocks, and for two participants we could not record

181   any reaction times. Each block contained all congruent, incongruent and grey-scale objects

182   presented once.

183   Naming reaction times were defined as the difference between stimulus-onset and

184   voice-onset. Trials containing naming errors and microphone errors (on average 10.1%) were

185   not analysed. We calculated the median naming time for each exemplar for each person and

186   then averaged the naming times for each of the congruent, incongruent and greyscale

187   conditions.

188   *Apparatus.* The neuromagnetic recordings were conducted with a whole-head axial

189   gradiometer MEG (KIT, Kanazawa, Japan), containing 160 axial gradiometers. We recorded

190   the MEG signal with a 1000Hz frequency. An online low-pass filter of 200Hz and a high-pass

191   filter of 0.03Hz were used. All stimuli were projected on a translucent screen mounted on the

192   ceiling of the magnetically shielded room. Stimuli were presented using MATLAB with

193   Psychtoolbox extension (Brainard, 1997; Brainard & Pelli, 1997; Kleiner et al., 2007). Parallel

194   port triggers and the signal of a photodiode were used to mark the beginning and end of each

195   trial. A Bimanual 4-Button Fiber Optic Response Pad (Current Designs, Philadelphia, USA)

196   was used to record the responses. Head shape recordings were completed with a Polhemus

197   Fastrak digitiser pen (Colchester, USA).

198   *Pre-processing.* FieldTrip (Oostenveld, Fries, Maris, & Schoffelen, 2011) was used to

199   pre-process the data. The data were downsampled to 200Hz and then epoched from -100 to

200   450ms relative to stimulus onset. We did not conduct any further pre-processing steps

201   (filtering, channel selection, trial-averaging etc.) to keep the data in its rawest possible form.

202   *Decoding Analyses.* For all our decoding analyses, patterns of brain activity were

203   extracted across MEG sensors at every timepoint, for each participant separately. We used a

204   linear discriminant analysis (LDA) classifier which was trained to distinguish the conditions of

205   interest. We then used independent test data to assess whether the classifier could predict

206   the condition above chance in the new data. We conducted training and testing at every

207   timepoint and corrected for multiple comparisons using random-effects Monte Carlo cluster

208   statistics. Note that our aim was not to achieve the highest possible decoding accuracy (i.e.

209   "classification for prediction", Hebart & Baker, 2017), but rather we were interested in whether

210   the classifier can predict the conditions above chance at any of the timepoints ("classification

211   for interpretation", Hebart & Baker, 2017). Therefore, we followed a minimal preprocessing

212   pipeline and performed our analyses on a single-trial basis. Classification accuracy above

213   chance indicates that the MEG data contains information that is different for the categories.

214   We used the CosmoMVPA toolbox (Oosterhof, Connolly, & Haxby, 2016) to conduct all our

215   analyses.

216   We ran five decoding analyses to (1) enhance our understanding of colour

217   representations activated via real colour perception and implied colour activation; and (2) to

218   examine how the typicality of object-colour combinations influences colour and shape

219   processing over time. We will explain each of these analyses in turn.

220

221   *Decoding colour representations*

222   In a previous study, we showed that MEG data evoked by real colour perception of red

223   and green could be distinguished by a linear classifier at 70ms (Teichmann et al., 2018,

224   *Preprint*). The results of that study further showed that colour representations accessed via

225   perceiving red and green are similar enough to colour representations activated via grey-scale

226   objects associated with red and green to allow cross-generalisation. The first aim of the current

227   study is to replicate and extend these findings by examining how colour representations of a

228   broader range of colours unfolds, both for actual colour and implied colour. While there are

229   luminance differences between the colours we used here, our key comparisons test at which

230   timepoint real and implied colour evoke similar brain activation patterns, and these cannot be

231   driven by overall luminance differences as the greyscale objects are equated for mean

232   luminance. Luminance can, however, contribute to the classifier accuracy in the real colour

233   decoding analysis, but such a driver would not improve cross-generalisation. Nevertheless, it

234   is important to keep in mind that the real colours used here do not only differ in terms of hue

235   but also in terms of luminance.

236   In our first analysis, we examined the time-course of real colour perception for four

237   different colour categories (red, green, orange, yellow). This analysis allows us to determine

238   whether there are different brain activation patterns for these four colour categories, and to

239   test whether certain colour pairs are more decodable than others. Colours that are very

240   dissimilar (e.g., red versus green) might be more decodable than colours that are more similar

241   (e.g., orange versus yellow, see Figure 2A). To test this, we trained a classifier to distinguish

242   between the coloured shapes of two different colours, for each of the possible pairs in turn.

243   To illustrate, for red versus green, we trained the classifier on trials with all red and green

244   shapes except one shape of each colour. We then tested the classifier on trials containing this

245   left-out pair. This process was repeated until all matched shapes had been left out once (5-

246   fold cross validation). This method ensured that the colour classifier always had to generalise

247   to different object forms. We conducted this classification analysis for each of the six possible

248   colour pairs (i.e., red-green, red-orange, red-yellow, green-orange, green-yellow, yellow-

249   orange), and then compared the classification performance over time for the different pairs.

250   Second, we tested whether colour representations accessed via real colour perception

251   and implied object-colour activation are similar. We trained a classifier to distinguish between

252   the pairs of coloured abstract shapes and tested whether it could generalise to the grey-scale

253   colour diagnostic objects. For example, we trained the classifier to distinguish the red from the

254   orange shape trials and then tested the classifier when distinguishing trials where grey-scale

255   objects were shown that are usually associated with red and orange. We used a time-

256   generalisation approach (Carlson, Hogendoorn, Kanai, Mesik, & Turret, 2011; King &

257   Dehaene, 2014) to examine the full time-to-time decoding matrix. As in the first analyses, we

258   split the data into all colour pairs to assess whether colours that are more dissimilar (e.g., red

259   versus green, green versus orange) are more distinct and hence can be better decoded than

260   colours that are more similar (e.g., red versus orange, orange versus yellow, Figure 2A). This

261   analysis is a strong test of the hypothesis that colour representations evoked by real colour

262   perception and implied colour activation share characteristics because the coloured shapes

263   only differ in terms of colour. Although the training set is based on identical shapes that differ

264   in terms of hue and luminance, the test set comprises greyscale objects equated for

265   luminance, so overall luminance cannot drive successful classification. That means successful

266   cross-decoding would show that there is colour information in the signal even in the total

267   absence of colour in the stimulus.

268

269   *Feature binding and object-colour knowledge*

270   The next analyses aim to enhance our understanding of feature binding and the effect

271   of typical colour-form associations on object and colour processing. By examining the

272   timecourse of object-feature binding, these analyses allow us to track the interaction between

273   object-colour knowledge and object representations in the brain.

274   First, we tested whether activation patterns evoked by congruently coloured objects

275   (e.g., red strawberry) differ from activation patterns evoked by incongruently coloured objects

276   (e.g., yellow strawberry). Any differential response that depends on whether a colour is typical

277   or atypical for an object (a congruency effect) requires binding the perceived shape and colour

278   and comparing this input with a conceptual object representation activated from memory. To

279   assess whether there is a congruency effect, we ran a decoding analysis to test for reliable

280   differentiation of congruent and incongruent trials. We trained the classifier on all congruent

281   and incongruent trials *except* for trials in which one pair of matched exemplars was shown

282   (e.g., all instances of congruent and incongruent strawberries and congruent and incongruent

283   bananas). To test the classifier, we only used the left-out exemplar pair. This process was

284   then repeated such that each matched exemplar pair had been left out (used as test data)

285   once. Leaving an exemplar pair out ensures that there are identical shapes and colours for

286   both classes (congruent and incongruent) in both the training and the testing set, and that the

287   stimuli of the test set have different shape characteristics than any of the training objects. That

288   means the only distinguishing feature between the conditions is the conjunction of shape and

289   colour features, which defines congruency. This allows us to compare directly whether (and

290   at which timepoint) object-colour knowledge interacts with object representations.

291   Second, we examined whether the conjunction of object and colour influenced colour

292   perception. It is likely that over the course of our lives we have learned statistical regularities

293   regarding common shape-colour pairings. Perceiving a certain shape might thus lead to a

294   stable colour representation early in the signal. For example, if we see a yellow banana, it is

295   possible that the shape leads to a stable colour representation of yellow earlier than if we see

296   a yellow strawberry. To assess this possibility, we trained the classifier to distinguish between

297   the surface colours of the abstract shapes (i.e., red, orange, yellow, green, chance: 25%). We

298   then tested how well the classifier could predict the colour of the congruent and the

299   incongruent objects. Training the classifier on the same shapes across colour categories

300   makes it unlikely that a certain shape-colour combination drives an effect. Instead, the only

13

301   distinguishing feature is colour. This analysis allows us to compare whether the typicality of

302   colour-form combinations has an effect on colour processing.

303   Third, we tested whether the conjunction of object and colour had an effect on object

304   decoding. If object-colour influences early perceptual processes, we might see a facilitation

305   for decoding objects when they are coloured congruently or interference when the objects are

306   coloured incongruently. We used the greyscale object trials to train the classifier to distinguish

307   between all of the objects. The stimulus set contained two exemplars of each item (e.g.,

308   strawberry 1 and strawberry 2). We used different exemplars for the training and testing set

309   to minimise the effects of low-level visual features. The classifier was trained on one exemplar

310   of all of the greyscale trials. We then tested the classifier's performance on the congruent and

311   incongruent object trials using the exemplars the classifier did not train on. We then swapped

312   the exemplars used for training and testing set until every combination had been used in the

313   testing set. Essentially, this classifier is trained to predict which object was presented to the

314   participant (e.g., was it a strawberry or a frog?).

315

316   *Statistical Tests.* In all our analyses, we used random effects Monte-Carlo cluster

317   statistic using Threshold Free Cluster Enhancement (TFCE, Smith & Nichols, 2009) as

318   implemented in the CosmoMVPA toolbox to see whether the classifier could predict the

319   decisions above chance. The TFCE statistic represents the support from neighbouring time

320   points, thus allowing for detection of sharp peaks and sustained weaker effects over time. We

321   used a permutation test, swapping labels of complete trials, and re-ran the decoding analysis

322   on the data with the shuffled labels 100 times per participant to create subject-level null-

323   distributions. We then used Monte-Carlo sampling to create a group-level null-distribution

324   consisting of 10,000 shuffled label permutations for the time-resolved decoding, and 1000 for

325   the time-generalisation analyses (to limit computation time). The null distributions were then

326   transformed into TFCE statistics. To correct for multiple comparisons, the *maximum* TFCE

327   values across time in each of the null distributions was selected. We then transformed the true

328   decoding values to TFCE statistics. To assess whether the true TFCE value at each timepoint

329   is significantly above chance, we compared it to the 95th percentile of the corrected null

330   distribution. Selecting the maximum TFCE value provides a conservative threshold for

331   determining whether the observed decoding accuracy is above chance, corrected for multiple

332   comparisons.

333

334   **Results**

335   We first present the behavioural data to confirm that our stimuli induce a congruency

336   effect on object naming times. All incorrect responses and microphone errors were excluded

337   from analysis. We then calculated the median reaction time for naming each stimulus. If a

338   participant named a specific stimulus incorrectly across trials (e.g., incongruently coloured

339   strawberry was always named incorrectly), we removed this stimulus completely to ensure

340   that the reaction times in one condition were not skewed. For example, if it took longer to

341   name one stimulus (e.g., "frog") in comparison to the other stimuli and that stimulus was only

342   ever named correctly in one of the conditions, this condition would overall have longer reaction

343   times; hence we would exclude this stimulus from both congruent and incongruent conditions

344   (on average this occurred in 5.4% of cases). At the group level, participants were faster to

345   name the congruently coloured (702ms, 95% CI [663.8 740.2]) than incongruently coloured

346   (750ms, 95% CI [698.5, 801.5]) objects ($t(17) = 4.06$, $p < .001$). This suggests that the objects

347   we used here do indeed have associations with specific canonical colours, and we replicate

348   the effect of colour congruency on recognition of these objects (Bannert & Bartels, 2013;

349   Joseph, 1997; Lloyd-Jones et al., 2012; Naor-Raz et al., 2003; Tanaka & Presnell, 1999;

350   Therriault et al., 2009).

351   In the main task, participants were asked to indicate every 80 trials whether they had

352   seen certain target object or not. The aim of this task was to keep participants motivated and

353   attentive throughout the training session. On average, participants reported whether the

354   targets were present or absent with 90% accuracy (SD = 0.05%, range: 81.25% - 100%).

355

356   *Decoding colour representations*

357   We first examined whether there are differences in brain activation patterns evoked by

358   perceiving different colour categories. For this *real colour* analysis, we trained the classifier to

359   distinguish between MEG data when participants viewed the abstract shapes in different

360   colours and tested its performance on independent real colour trials. We found that most of

361   the colour pairs could be decoded from ~70ms after stimulus onset (Figure 2B). Yellow versus

362   green trials could be differentiated later on in the signal (~115ms) but the colour representation

363   was not stable (Figure 2B). Red versus orange could not be decoded, probably reflecting the

364   high similarity between these colours (Figure 2B). Note that the decoding accuracy might be

365   influenced by luminance differences which are smaller in the case of red versus orange and

366   yellow versus green than in all the other colour pairs. Peak decoding for the remaining real

367   colour pairs was at ~135-150ms after stimulus onset (Figure 2).

16

368
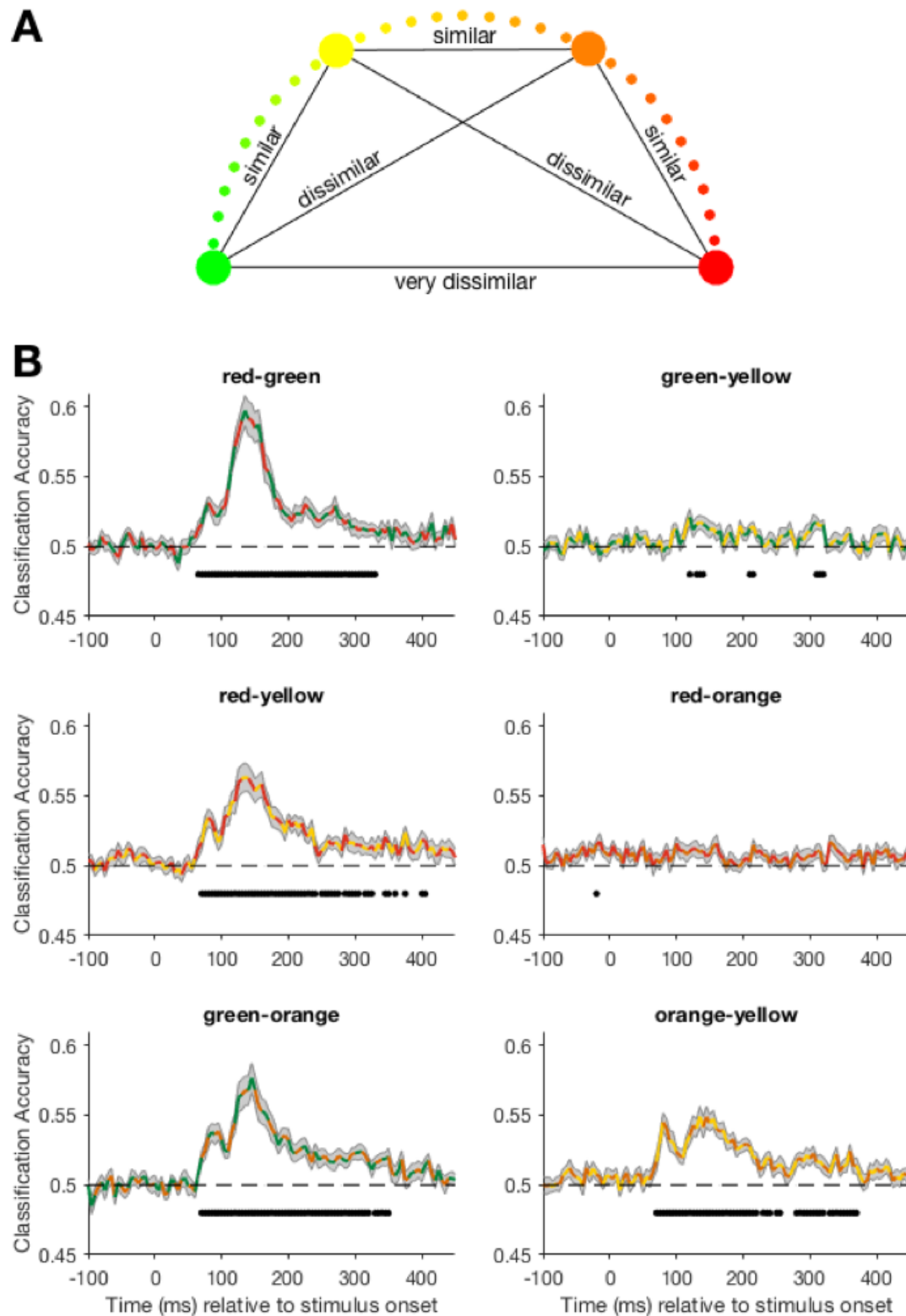
Figure 2. (A) shows the similarity between colour categories based on colour distance. (B) shows the results of the real colour decoding analysis for all colour pairs. The classifier was trained on the abstract shape trials to distinguish between two colours at a time. Each colour category contained identical shapes. The classifier was trained to distinguish between all shapes except one. Testing was done only on the shape that the classifier did not train on.

374　The classification accuracy over time for the real colour decoding analysis for each colour pair

375　is plotted above. Shading represents the standard error. Black dashed line represents chance

376　level (50% - pairwise comparison). Black dots highlight significant timepoints for each pairwise

377　comparison (p<0.05), corrected for multiple comparisons.

378

379　　　　　A controlled approach of testing whether there is any representational overlap between

380　real and implied colours is training a classifier on real colour and testing on implied colour

381　trials. Successful cross-generalisation implies that the brain representation of colour accessed

382　via colour perception and implied colour activation share characteristics. To see whether this

383　is the case we trained a classifier to distinguish between patterns evoked by pairs of our

384　coloured abstract shapes, as in our first analysis. We then tested the classifier on

385　distinguishing between the grey-scale objects that are associated with those colours.

386　Consistent with previous work (Teichmann et al., 2018, *Preprint*), the representational overlap

387　for real and implied colours dynamically evolves over time. We therefore ran this analysis as

388　a time-generalisation analysis, training and testing the classifier at every timepoint

389　combination (Carlson et al., 2011; King & Dehaene, 2014). We ran the analysis separately for

390　each of the colour pairs as the real colour decoding results showed that the classifier cannot

391　reliably distinguish all colour pairs (Figure 2). Across the time-time decoding matrices (Figure

392　3), we can see that the classifier can cross-generalise best between real and implied colours

393　when the colours are most dissimilar (i.e., red and green). Accessing colour via real colour

394　perception and implied colour activation occurred at the same time, around 150ms. For red

395　versus green, there was additional significant decoding off the diagonal, which indicates a

396　temporal difference in the instantiation of a similar pattern. Colour information evoked by real

397　colours from ~150ms-450ms resembles colour information evoked by greyscale objects in a

398　timewindow from ~150-170ms after stimulus onset. This indicates that colour information

399　evoked by association is only briefly in the signal. There also is a reactivation of colour

400　information for the red-green comparison at ~400ms after stimulus onset. For the red versus

401　yellow and green versus orange contrast there is cross-generalisation in a timewindow around

18

402   ~150ms after stimulus onset. In contrast, we did not observe successful cross-generalisation

403   when training and testing on colours that are similar. This is not surprising given that we did

404   not have a reliable model to distinguish between these real colours (i.e., red versus orange,
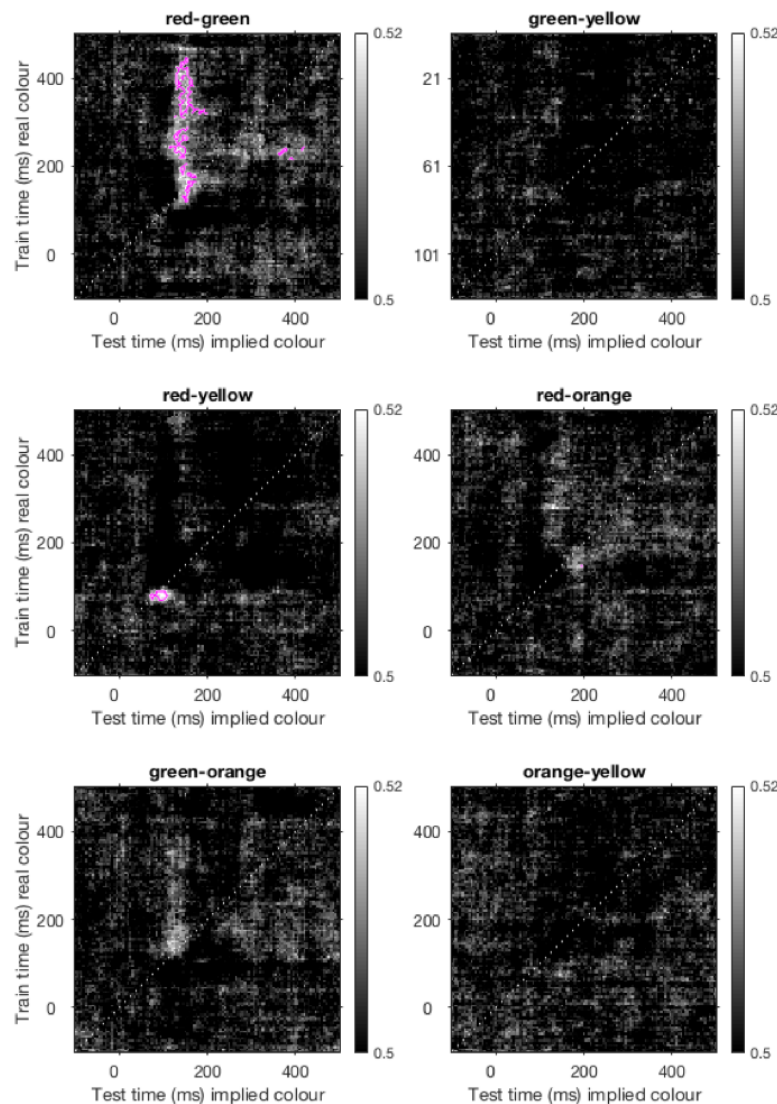
405   Figure 2).

406

407   Figure 3. Time-generalisation for cross-decoding, training the classifier on real colour trials
408   and testing on grey-scale object trials. The analysis was done separately for each pairwise
409   colour comparison. The plots in show the decoding accuracies for every timepoint combination
410   when training on real colour and testing on implied colour trials. Pink highlights show
411   timepoints with decoding significantly above chance (p<0.05), controlled for multiple
412   comparisons.

413

19

414   Overall, our results show that there are representational similarities for real and implied

415   colours but this is only evident for colours that are quite dissimilar (e.g., red and green). It is

416   important to note that there is no colour information at all in the equiluminant greyscale object

417   trials and that the shapes used for training the classifier are identical except in colour and

418   luminance. That means we here have strong evidence for real and implied colour sharing an

419   overlapping brain activation pattern that becomes apparent from around 150 to 200ms after

420   stimulus onset, at least when the colours are dissimilar enough.

421

422   _Feature binding and object-colour knowledge_

423   The aim of our next decoding analyses was to examine the interaction between object-

424   colour knowledge and object representations. First, we examined whether there is a difference

425   in the brain activation pattern for congruently and incongruently coloured objects. Thus, we

426   trained the classifier to distinguish between congruent and incongruent trials. To ensure that

427   neither colour nor shape alone can drive the classifier performance, we used the independent

428   exemplar cross-validation approach, leaving trials out which were matched for colour and

429   shape (Figure 4A). As shown in Figure 4A as an example, in one fold, we trained on all trials

430   except for the congruent strawberries (red), incongruent strawberries (yellow), congruent

431   bananas (yellow), and incongruent bananas (red). The testing set then contained only these

432   exemplars. The left-out exemplars were matched in colour and shape, making congruency the

433   only feature that differed between the classes. We then repeated this for each combination.

434   The results of this analysis show that there are distinct patterns of neural activity for congruent

435   and incongruent objects in a cluster stretching from 265 to 330ms after stimulus onset,

436   highlighting that the signal is modulated by colour congruency in this time window (Figure 4B).

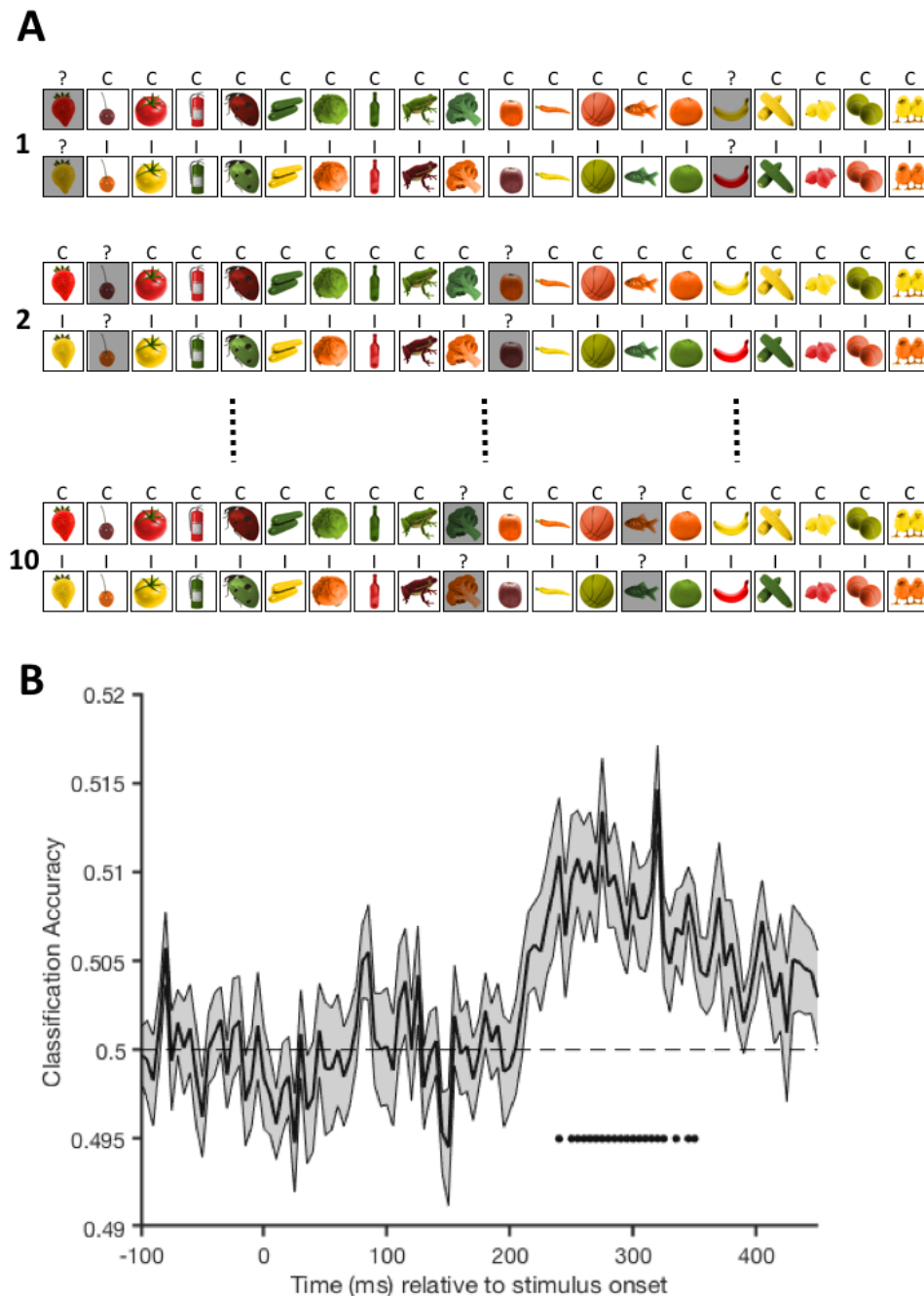437   This indicates that binding of colour and form must have occurred by ~265ms.

Figure 4. Cross-validation and results of the congruency analysis. We are here contrasting trials from the congruent and incongruent conditions. (A) shows the leave-one-matched-exemplar-out cross validation approach used for the congruency decoding analysis. The classifier was trained on all "clear" trials and tested on the trials that are shaded in grey, ensuring that the classifier is not tested on the exemplars that it trained on. This limits the effect features other than congruency can have on classifier performance. (B) shows the classification accuracy over time. Shading represents the standard error. Black dashed line represents chance level (50% - congruent versus incongruent). Black dots highlight significant timepoints, corrected for multiple comparisons.

449   To assess whether the typicality of object-colour combinations influences colour

450   perception, we trained a classifier to distinguish between the colours in the abstract shape

451   condition and then tested it on the congruent and incongruent trials separately. The data show

452   that colour can be successfully classified in a cluster stretching from 75 to 125ms for the

453   congruent and in a cluster stretching from 75 to 185ms for the incongruent trials (Figure 5A).

454   Looking at these results it seems like there is a qualitative difference between the colour

455   information in the congruent and the incongruent trials. To assess how the signal in these two

456   conditions evolved over time, we also looked at the time-generalisation matrices for these

457   analyses (Figure 5B and 5C). Colour category was decodable form both conditions early on

458   (~70ms) but the activation associated with colour seems to be sustained longer for the

459   incongruent (Figure 5C) than for the congruent condition (Figure 5B). This suggests that colour

460   signals are prolonged when object-colour combinations are atypical in comparison to when

461   they are typical.

22

A: Real colour decoding for congruent & incongruent objects

B: Real colour congruent objects

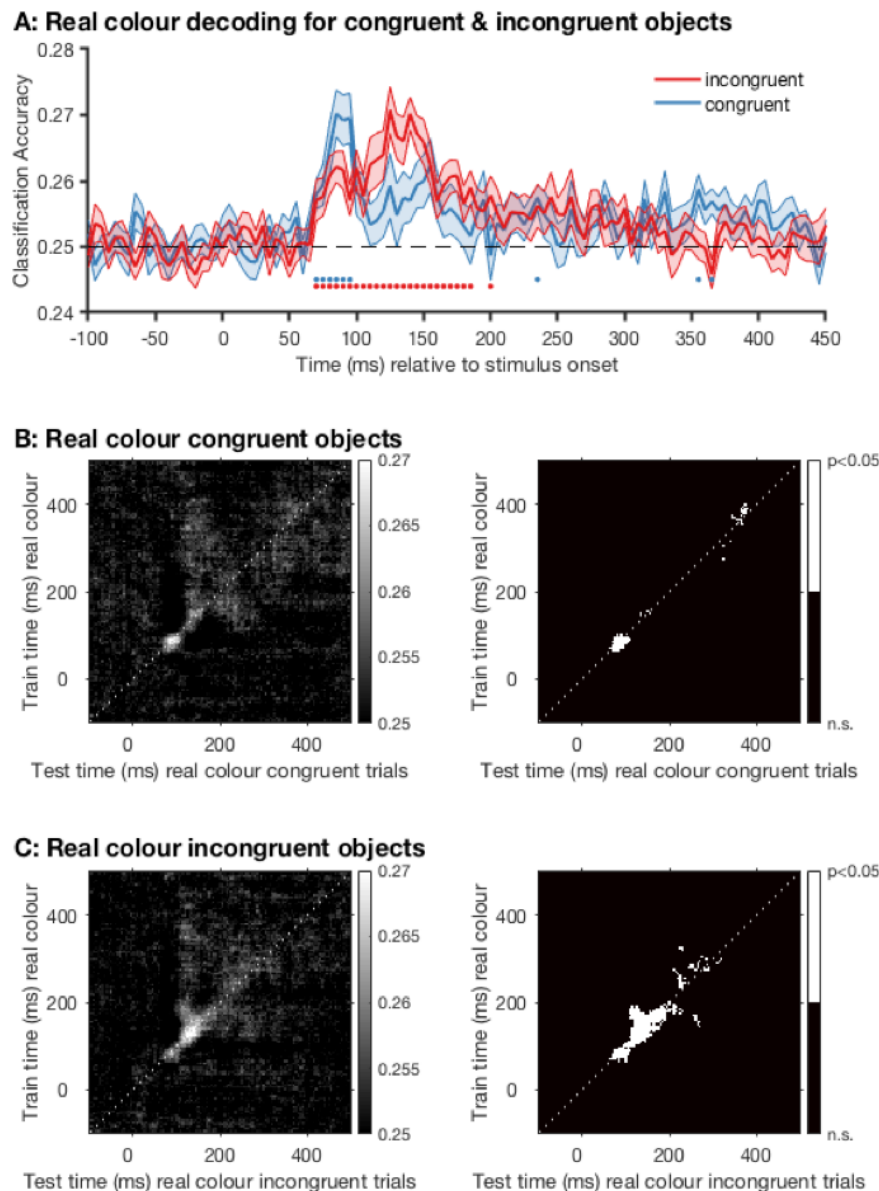**C: Real colour incongruent objects**

462

463   Figure 5. Results of the colour decoding analysis for the congruent and incongruent trials.
464   Here, the classifier was trained to distinguish the colour of all abstract shape trials and tested
465   on the congruent and incongruent trials separately. (A) shows the classification accuracy over
466   time for this analysis. Red indicates the classifier's performance when it was tested on
467   incongruent trials and blue indicates the classifier's performance when it was tested on
468   congruent trials. Shading represents the standard error. Black dashed line indicates chance
469   level (25% - red versus green versus orange versus yellow). Red (incongruent) and blue
470   (congruent) dots highlight significant timepoints, corrected for multiple comparisons. (B) and
471   (C) show the results of the same analysis across all possible training and testing timepoint
472   combinations. These time-time matrices allow to examine how the signal for the congruent
473   colours (B) and incongruent colours (C) evolves over time. The plots on the left show the
474   classification accuracy at every timepoint combination with lighter colours reflecting higher
475   decoding accuracies. The plots on the right show clusters where decoding is significantly
476   above chance, corrected for multiple comparisons.

477

23

478   The goal of the third analysis was to examine whether shape representations are

479   affected by colour congruency. We trained a classifier to distinguish between trials in which

480   the participant saw one of the exemplars of each of the twenty objects in greyscale (e.g.,

481   greyscale strawberry 1, greyscale cherry 1…). We then tested at which timepoint the classifier

482   could successfully cross-generalise to the other exemplar of that object in the congruent and

483   incongruent condition separately. Note that although the exact images are unique, there are

484   shared shape characteristics between exemplars (e.g., frog exemplars share some similar

485   shape aspects despite being different postures). The results show that the classifier can

486   generalise to the other exemplar in a cluster stretching from 80 to 450ms for the congruent

487   test set and from 90 to 450ms for the incongruent test set (Figure 6A). The decoding

488   performance over time for congruently coloured and incongruently coloured exemplars follows

489   a highly similar pattern. These results show that we can decode the object category early on,

490   suggesting that the classifier is driven by low-level visual features such as shape or texture.

491   The timecourses for congruent and incongruent exemplar decoding are very similar,

492   suggesting that colour might not affect the initial processing that contributes to object

493   identification. To test whether the classifier makes the same mistakes when decoding from

494   the congruent and incongruent trials, we looked at the confusion matrices averaged across

495   timepoints where decoding was significant (Figure 6B). To assess the similarity of the

496   confusion matrices over time, we correlated the average matrix across participants at each

497   timepoint (Figure 6C). The high correlation between the matrices suggests that the object

498   representations for the congruent and incongruent condition were similar. Thus, we have no

499   evidence that shape representations are affected by colour congruency.

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A: Exemplar decoding for congruent & incongruent objects

B: Confusion matrices 90-450ms

C: Correlation of confusion matrices

500
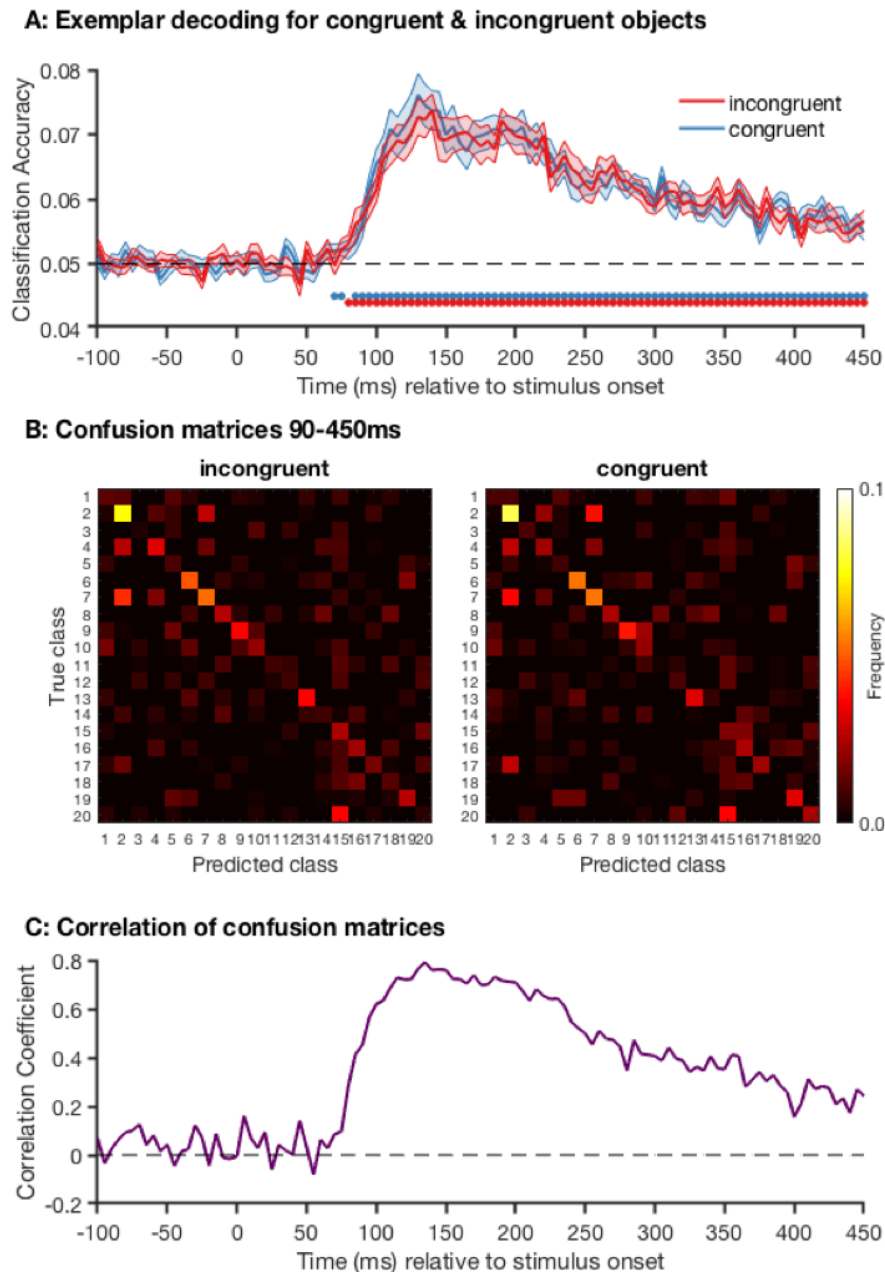
Figure 6. Results of the object exemplar decoding analysis. The classifier was trained on distinguishing between all object classes in the greyscale object condition. We used one exemplar of each class for the training and the other exemplar for testing the classifier. Testing was done for the congruent and incongruent trials separately. (A) shows the classification accuracy over time for the exemplar decoding analysis. The red line shows the classifier accuracy when testing the classifier on incongruent trials and blue shows the classifier accuracy when testing the classifier on congruent trials. Shading represents the standard error. Black dashed line represents chance level (5% - 20 different object classes). Red (incongruent) and blue (congruent) dots highlight significant timepoints ($p<0.05$), corrected for multiple comparisons. (B) shows the confusion matrices for the incongruent (left) and congruent (right) condition. The confusion matrices were averaged across time (90-450ms). The true object classes are plotted on the y-axis and the predicted classes on the x-axis. The colour highlights the frequency of a specific class being predicted in response to a specific

514   class. The diagonal shows accurate classifier prediction (match between predicted and true

515   class. (C) shows the correlation of the two confusion matrices over time.

516

517   **Discussion**

518   A crucial question in object recognition is how incoming visual information interacts

519   with stored object concepts to create meaningful vision under varying situations. The aims of

520   this study were two-fold: First, we examined how the representation of colour unfolds over

521   time when it is accessed via colour perception and implied colour activation. Second, we

522   looked at the temporal dynamics of feature-binding and object-colour knowledge.

523   We found that colour information can be accessed via real colour perception as well

524   as via greyscale objects associated with certain colours, demonstrating that canonical object-

525   colour can be activated in complete absence of colour in the stimulus. Brain activity patterns

526   evoked by real colours that are dissimilar (e.g., red and green) can be generalised to colour

527   representations accessed by implied colour activation. This highlights that there are

528   similarities in the neural representation of real colour and implied colour processing in the

529   brain, replicating our previous finding in an independent sample with different stimuli

530   (Teichmann et al., 2018, *Preprint*). With regard to feature binding and object-colour

531   knowledge, our results demonstrate that object representations are influenced by object-

532   colour knowledge, but only later in the timeseries (i.e., ~260ms and beyond). This is

533   consistent with a hierarchical view that basic visual feature processing has to occur before

534   stored object concepts are activated. The data suggest that the typicality of object-colour

535   binding has an effect on the activation of colour representations. Colour representations

536   appear to be activated longer for objects that are coloured incongruently in comparison to

537   objects that are coloured congruently. In comparison, the typicality of object-colour binding

538   does not have an effect on the representations evoked by different object shapes.

539   The results presented here allow for a differentiation between perceptual and

540   associative processes of activating colour. Decoding the colour of objects presented on a

541   screen is related to colour perception whereas decoding implied colour and colour congruency

542   are related to colour associations based on object-colour knowledge. Overall, we find that

543   colour representations can be decoded earlier when accessed via perception than

544   association. The latencies we report here for early perceptual processing correspond to earlier

545   findings of the time it takes for information to progress through the ventral visual stream (see,

546   for example, DiCarlo et al., 2012). Our data show that information corresponding to higher-

547   level, knowledge-based colour representations can be decoded later (>150ms), consistent

548   with the idea that low-level visual features need to be processed first. In the following, we will

549   first discuss our results of the early, perceptual colour processes and then move on to discuss

550   later, associative processes.

551   In line with our earlier results (Teichmann et al., 2018, *Preprint*), we found that colour

552   categories can be decoded as early as ~70ms after stimulus onset (Figure 2B). This latency

553   corresponds to the time it takes for information to reach colour-sensitive areas such as V4

554   (Nowak & Bullier, 1997; Schmolesky et al., 1998). The brain representations of colour pairs

555   which are highly dissimilar, such as red and green, were more decodable than colours that

556   are more similar, such as red and orange, highlighting that the physical similarity between

557   colours is reflected in the neural signal evoked by perceiving these colours. When comparing

558   real colour decoding for the congruently and incongruently coloured objects, we found

559   decoding onset at a similar time (~70ms). However, colours were decodable longer in the

560   incongruent condition than the congruent condition (Figure 5A). The time-generalisation

561   analyses (Figure 5B) suggest that there is a different dynamic for congruent trials in

562   comparison to incongruent trials. In case of incongruent objects, colour information may be

563   relevant for longer as the combination of low-level features and perceived colours is unusual.

564   One possible explanation is that certain object features (e.g., shape, texture) co-occur more

565   often with certain colours. To facilitate object recognition, the "most likely" colour may get

27

566   activated along with other low-level features which are dominant earlier in the signal. Further

567   work is needed to test this idea.

568   The timecourse of exemplar decoding we present is consistent with previous studies

569   on object recognition. Here, we found that exemplar identity could be decoded at ~90ms

570   (Figure 6A). Similar latencies have been found in other M/EEG decoding studies (Carlson et

571   al., 2013; Cichy et al., 2014; Contini, Wardle, & Carlson, 2017; Grootswagers, Robinson, &

572   Carlson, 2018; Isik, Meyers, Leibo, & Poggio, 2013) and single unit recordings (e.g., Hung,

573   Kreiman, Poggio, & DiCarlo, 2005). Behavioural data, including the reaction times collected

574   here in our participants, show that colour influences object identification speed (e.g., Bramão,

575   Faísca, Petersson, & Reis, 2010). The neural data, however, did not show an effect of object

576   colour on the classifier's performance when distinguishing the neural activation patterns

577   evoked by different objects. For example, the brain activation patterns in response to a

578   strawberry could be differentiated from patterns evoked by a lemon, regardless of the

579   congruency of their colours. This suggests that colour and shape processing affect each other

580   in an asymmetric way: colour representations are influenced by object shape but that shape

581   representations are not influenced by colour. This findings is consistent with previous results

582   (Proverbio et al., 2004) but might seem puzzling because colour congruency has been shown

583   to have a strong effect on object naming (e.g., Chiou et al., 2014; Nagai & Yokosawa, 2003;

584   Tanaka & Presnell, 1999). One possible interpretation of this finding is that the typicality

585   between object and colour combination does not affect early stages of processing but that it

586   has an effect on later stages of processing. For example, it is possible that the source of

587   behavioural congruency effects is at the stage of response selection, which would not show

588   up in these early neural signals. More evidence is needed for this interpretation, but the current

589   data suggest that colour congruency does not have an impact on early stages of shape

590   processing.

28

591   Further evidence for colours influencing object processing at a later stage comes from

592   our findings of congruency and implied colour decoding (Figures 3 and 4). When comparing

593   brain activation patterns of the same objects presented in different colours, there was a

594   decodable difference between congruent and incongruent conditions from 265ms onwards.

595   This is consistent with earlier findings showing that colour congruency modulates the P2

596   (~225ms) and P3 (~350ms) component (Lloyd-Jones et al., 2012). Prior to this time, the signal

597   would primarily be driven by early perceptual features, which were matched for the congruent

598   and incongruent conditions (same objects, same colours, only the binding of colour and shape

599   differed). Thus, we show here that single features such as colour and shape are processed

600   first and that the combined information of colour and shape only becomes distinguishable at

601   a later stage. This is consistent with previous work showing that simple colour processes such

602   as registering the intensity of light occurs in early visual areas such as V1 and V2, while more

603   complex colour-related processes such as distinguishing between object surface colours

604   occurs in V4 and beyond (Seymour et al., 2015; Zeki & Marini, 1998). Activating object colour

605   from memory has been shown to involve the ATL (e.g., Coutanche & Thompson-Schill, 2014).

606   From our data, we cannot draw direct conclusions about which brain areas are involved in the

607   integration of colour and shape information, however, the timecourse of our congruency

608   analysis shows that congruent and incongruent trials can be differentiated later than single

609   feature processing (i.e., differentiation between real colours). Previous work on patients with

610   semantic dementia (e.g., Bozeat, Lambon Ralph, Patterson, & Hodges, 2002) and studies on

611   healthy participants using TMS (e.g., Chiou et al., 2014) and fMRI (e.g., Coutanche &

612   Thompson-Schill, 2014) point to the ATL as candidate region responsible for the integration

613   of information, such as colour and shape, at a conceptual level. The latency of the successful

614   congruency decoding may therefore reflect the process of comparing the combination of

615   perceptual object features with a conceptual template representation of the object.

616   Our data speak to the debate of whether specific object-features activated from

617   memory share similarities with perceiving these object-features. Bannert and Bartels (2013)

618   previously showed that there is an overlapping brain activation pattern in early visual cortex

619   when colour is activated via colour perception and implied colour activation. This finding shows

620   that a similar neural representation is activated via implied colour activation and real colour

621   perception, even in the total absence of real colour in the stimulus. The data here are

622   consistent with this finding but with regard to temporal dynamics rather than brain regions. In

623   line with one of our previous MEG studies (Teichmann et al., 2018, *Preprint*), we showed that

624   the colour representations for red and green accessed via perception and implied colour

625   activation are similar enough to allow for cross-generalisation at ~150-200ms. The data

626   suggest that colour representations accessed via real colour perception and implied colour

627   activation shared similar patterns at the same time (~150-200ms) and that cross-decoding

628   remained stable across a narrow testing time window (~150-450ms). For colour pairs that

629   were more similar (e.g., red versus yellow), decoding was not as stable as for the red-green

630   pair, however, a classifier trained on the brain activation patterns distinguishing between other

631   colours such as red and yellow can still cross-generalise to patterns evoked by grey-scale

632   objects that are associated with these colours. There were not as many timepoints in which

633   cross-generalisation worked in comparison to the red-green distinction and the cross-

634   generalisation is limited to the same time window (~160ms after stimulus onset) rather than

635   being sustained (as it is for red vs green). This difference is partially accounted for by the

636   strength of decoding of the real colour pairs in the first place: real colours that are more similar

637   in colour space are also more similar in neural space and are therefore more difficult to

638   decode. This points to a limitation in the sensitivity of our current methods, such that the subtle

639   differences in patterns for similar colours are beyond our reach at this point. Another potential

640   reason for unsuccessful decoding of similar implied colour is that object representations must

641   be flexible to allow recognition under varying circumstances such as varying lighting. Thus, it

642   is possible that these concepts include a range of colours that would be considered "normal"

643   for the object. This might be why we can differentiate between real colour signals evoked by

644   orange and yellow but not the implied colour signals associated with these colours. Together,

645   the data show that colour representations evoked by real colour perception and implied colour

646   activation are sufficiently similar to allow for cross-generalisation, at least for colour pairs that

647   are quite dissimilar.

648   Overall, our results demonstrate that MVPA applied to time-resolved neural data is a

649   sensitive approach to examine the temporal dynamics of object-colour knowledge. We report

650   two main insights. First, colour representations can be accessed via both real colour

651   perception and via implied colour activation in the complete absence of colour in the stimulus.

652   These colour representations share a sufficient degree of similarity to allow for cross-

653   generalisation, at least when the colours are dissimilar (e.g., red and green). Colour

654   representations activated via implied colours are accessed later than via real colour

655   perception, which could reflect involvement in a later stage of colour processing. Second, our

656   data demonstrate that object representations are influenced by object-colour knowledge but

657   not at the initial stages of visual processes. This shows that single object features are

658   processed before the features are bound into a coherent object that can be compared with

659   existing, conceptual knowledge about objects. However, our data also suggest that the

660   activation of colour may be affected by the conjunction of object and colour, showing later

661   stage interactions between bound objects and single features. Taken together, these results

662   provide new insights into the interaction between our knowledge about the world and incoming

663   visual information.

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