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1 **The influence of object-colour knowledge on
2 emerging object representations in the brain**

4 Abbreviated Title: Colour knowledge and object representations

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42

Abstract

43 The ability to rapidly and accurately recognise complex objects is a crucial function of the
44 human visual system. To recognise an object, we need to bind incoming visual features
45 such as colour and form together into cohesive neural representations and integrate these
46 with our pre-existing knowledge about the world. For some objects, typical colour is a central
47 feature for recognition; for example, a banana is typically yellow. Here, we applied
48 multivariate pattern analysis on time-resolved neuroimaging (magnetoencephalography)
49 data to examine how object-colour knowledge affects emerging object representations over
50 time. Our results from 20 participants (11 female) show that the typicality of object-colour
51 combinations influences object representations, although not at the initial stages of object
52 and colour processing. We find evidence that colour decoding peaks later for atypical object-
53 colour combinations in comparison to typical object-colour combinations, illustrating the
54 interplay between processing incoming object features and stored object-knowledge. Taken
55 together, these results provide new insights into the integration of incoming visual
56 information with existing conceptual object knowledge.

57

58

59 **Significance Statement**

60 To recognise objects, we have to be able to bind object features such as colour and shape
61 into one coherent representation and compare it to stored object knowledge. The
62 magnetoencephalography data presented here provide novel insights about the integration
63 of incoming visual information with our knowledge about the world. Using colour as a model
64 to understand the interaction between seeing and knowing, we show that there is a unique
65 pattern of brain activity for congruently coloured objects (e.g., a yellow banana) relative to
66 incongruently coloured objects (e.g., a red banana). This effect of object-colour knowledge
67 only occurs after single object features are processed, demonstrating that conceptual
68 knowledge is accessed relatively late in the visual processing hierarchy.

69

Introduction

70 Successful object recognition depends critically on comparing incoming perceptual
71 information with existing internal representations (Albright, 2012; Clarke & Tyler, 2015). A
72 central feature of many objects is colour, which can be a highly informative cue in visual
73 object processing (Rosenthal et al., 2018). Although we know a lot about colour perception
74 itself, comparatively less is known about how object-colour knowledge interacts with colour
75 perception and object processing. Here, we measure brain activity with
76 magnetoencephalography (MEG) and apply multivariate pattern analyses (MVPA) to test
77 how stored object-colour knowledge influences emerging object representations over time.

78

79 Colour plays a critical role in visual processing by facilitating scene and object recognition
80 (Gegenfurtner & Rieger, 2000; Tanaka et al., 2001), and by giving an indication of whether
81 an object is relevant for behaviour (Conway, 2018; Rosenthal et al., 2018). Objects that
82 include colour as a strong defining feature have been shown to activate representations of
83 associated colours (Bannert & Bartels, 2013; Hansen et al., 2006; Olkkonen et al., 2008;
84 Teichmann et al., 2019; Vandenbroucke et al., 2014; Witzel et al., 2011), leading to slower
85 recognition when there is conflicting colour information (e.g., a red banana; Nagai &
86 Yokosawa, 2003; Tanaka & Presnell, 1999; for a meta-analysis, see Bramão, Reis,
87 Petersson, & Faísca, 2011). Neuroimaging studies on humans and non-human primates
88 have shown that there are several colour-selective regions along the visual ventral pathway
89 (Lafer-Sousa et al., 2016; Lafer-Sousa & Conway, 2013; Seymour et al., 2010, 2015; Zeki &
90 Marini, 1998). While the more posterior colour-selective regions do not show a shape bias,
91 the anterior colour-selective regions do (Lafer-Sousa et al., 2016), supporting suggestions
92 that colour knowledge is represented in regions associated with higher-level visual
93 processing (Simmons et al., 2007; Tanaka et al., 2001). A candidate region for the
94 integration of stored knowledge and incoming visual information is the anterior temporal lobe
95 (ATL; Chiou et al., 2014; Papinutto et al., 2016; Patterson et al., 2007). In one study
96 (Coutanche & Thompson-Schill, 2014), for example, brain activation patterns evoked by
97 recalling a known object's colour and its shape could be distinguished in a subset of brain
98 areas that have been associated with perceiving those features, namely V4 and lateral
99 occipital cortex, respectively. In contrast, recalling an object's particular conjunction of colour
100 and shape, could only be distinguished in the ATL, suggesting that the ATL processes
101 conceptual object representations.

102

103 Time-resolved data measured with electroencephalography (EEG) or MEG can give an
104 understanding of how conceptual-level processing interacts dynamically with perception.

105 Previous EEG studies have examined the temporal dynamics of object-colour knowledge as
106 an index of the integration of incoming visual information and prior knowledge (Lloyd-Jones
107 et al., 2012; Lu et al., 2010; Proverbio et al., 2004). For example, Lloyd-Jones et al. (2012)
108 showed that shape information modulates neural responses at ~170ms (component N1), the
109 combination of shape and colour affected the signal at 225ms (component P2), and the
110 typicality of object-colour pairing modulated components approximately 225 and 350ms after
111 stimulus onset (P2 and P3). These findings suggest that the initial stages of object
112 recognition may be driven by shape, with the interactions with object-colour knowledge
113 coming into play at a much later stage, perhaps as late as during response selection.

114

115 Using multivariate methods for time-resolved neuroimaging data, we can move beyond
116 averaged measures (i.e., components) to infer what type of information is contained in the
117 neural signal on a trial-to-trial basis. In the present study, we used MVPA to determine the
118 timepoint at which neural activity evoked by congruently (e.g., yellow banana) and
119 incongruently (e.g., red banana) coloured objects differs, which indicates when stored
120 knowledge is integrated with incoming visual information. Furthermore, we examined
121 whether existing knowledge about an object's colour influences perceptual processing of
122 surface colour and object identity. Overall, using colour as a model, our findings elucidate
123 the timecourse of interactions between incoming visual information and prior knowledge in
124 the brain.

125

126

127 Materials and Methods

128 Participants

129 20 healthy volunteers (11 female, mean age = 28.9 years, SD = 6.9 years, 1 left-handed)
130 participated in the study. All participants reported accurate colour-vision and had normal or
131 corrected-to-normal visual acuity. Participants gave informed consent before the experiment
132 started and were financially compensated. The study was approved by the Macquarie
133 University Human Research Ethics Committee.

134

135 Stimuli

136 We identified five real world objects that previous studies have shown to be strongly
137 associated with each of four different colours (red, green, orange and yellow; see Figure 1)
138 (Bannert & Bartels, 2013; Joseph, 1997; Lloyd-Jones et al., 2012; Naor-Raz et al., 2003;
139 Tanaka & Presnell, 1999; Therriault et al., 2009). Each colour category had one manmade
140 object (e.g., fire hydrant), one living object (e.g., ladybird), and three fruits or vegetables

141 (e.g., strawberry, tomato, cherry). We sourced two exemplar images for each object class,
142 resulting in 10 images for each colour, 40 individual images in total. We then created
143 incongruently coloured objects by swapping the colours (e.g., yellow strawberry, red
144 banana). For both congruent and incongruent stimuli, we did not use the native colours from
145 the images themselves, but instead overlayed pre-specified hues on desaturated (greyscale)
146 images that were equated for luminance using the SHINE toolbox (Willenbockel et al.,
147 2010). A greyscale image overlayed with its canonically associated colour (e.g., yellow hue
148 applied to greyscale banana) resulted in a congruent object; a greyscale image overlayed
149 with a colour different from its canonically associated colour (e.g., red hue applied to
150 greyscale banana) resulted in an incongruent object. Every congruent object exemplar had a
151 single colour-matched incongruent partner. For example, we used a specific shade of red
152 and added it to the grey-scale images of the strawberry to make the congruent strawberry
153 and overlayed it onto the lemon to make the incongruent lemon. We then took a specific
154 shade of yellow and overlayed it on the lemons to make the congruent lemon exemplar, and
155 onto the strawberry to make the incongruent strawberry exemplar. That means, overall, we
156 have the identical objects and colours in the congruent and the incongruent condition, a
157 factor that is crucial to ensure our results cannot be explained by features other than colour
158 congruency. The only difference between these key conditions is that the colour-object
159 combination is either typical (congruent) or atypical (incongruent).

160

161 This procedure resulted in 40 congruent objects (10 of each colour), and 40 incongruent
162 objects (10 of each colour, Figure 1). We added two additional stimulus types to this set: the
163 full set of 40 greyscale images, and a set of 10 different angular abstract shapes, coloured in
164 each of the four hues for a set of 40 (see Figure 1). As is clear in Figure 1, the colours of the
165 abstract shapes appeared brighter than the colours of the objects, this is because the latter
166 were made by overlaying hue on greyscale, whereas the shapes were simply coloured. As
167 our principle goal was to ensure that the congruent objects appeared to have their typical
168 colouring, we did not match the overall luminance of the coloured stimuli. For example, if we
169 equated the red of a cherry with the yellow of a lemon, neither object would look typically
170 coloured. Thus, each specific colour pair is not equated for luminance; however, we have
171 the same colours across different conditions.

172

173 All stimuli were presented at a distance of 114cm. To add visual variability, which reduces
174 the low-level featural overlap between the images, we varied the image size from trial to trial
175 by 2 degrees of visual angle. The range of visual angles was therefore between ~4.3 – 6.3
176 degrees.

177

178 **Experimental Design and Statistical Analysis**

179 *Experimental tasks*

180 In the main task (Figure 1C), participants completed eight blocks of 800 stimulus
181 presentations each. Each individual stimulus appeared 40 times over the course of the
182 experiment. Each stimulus was presented centrally for 450ms with a black fixation dot on top
183 of it. To keep participants attentive, after every 80 stimulus presentations, a target image
184 was presented until a response was given indicating whether this stimulus had appeared in
185 the last 80 stimulus presentations or not (50% present vs absent). The different conditions
186 (congruent, incongruent, grey-scale, abstract shape) were randomly intermingled throughout
187 each block, and the target was randomly selected each time. On average, participants
188 performed with 90% (SD=5.4%) accuracy.

189

190 After completing the main blocks, we collected behavioural object-naming data to test for a
191 behavioural congruency effect with our stimuli. On the screen, participants saw each of the
192 objects again (congruent, incongruent or greyscale) in a random order and were asked to
193 name the objects as quickly as possible. As soon as voice onset was detected, the stimulus
194 disappeared. We marked stimulus-presentation times with a photodiode and recorded voice-
195 onset with a microphone. Seventeen participants completed three blocks of this reaction
196 time task, one participant completed two blocks, and for two participants we could not record
197 any reaction times. Each block contained all congruent, incongruent and grey-scale objects
198 presented once.

199

200 Naming reaction times were defined as the difference between stimulus-onset and voice-
201 onset. Trials containing naming errors and microphone errors were not analysed. We
202 calculated the median naming time for each exemplar for each person and then averaged
203 the naming times for each of the congruent, incongruent and greyscale conditions.

204

205 [Figure 1]
206

207

208

209 *MEG data acquisition*

210 While participants completed the main task of the experiment, neuromagnetic recordings
211 were conducted with a whole-head axial gradiometer MEG (KIT, Kanazawa, Japan),
212 containing 160 axial gradiometers. We recorded the MEG signal with a 1000Hz frequency.
213 An online low-pass filter of 200Hz and a high-pass filter of 0.03Hz were used. All stimuli
214 were projected on a translucent screen mounted on the ceiling of the magnetically shielded

215 room. Stimuli were presented using MATLAB with Psychtoolbox extension (Brainard, 1997;
216 Brainard & Pelli, 1997; Kleiner et al., 2007). Parallel port triggers and the signal of a
217 photodiode were used to mark the beginning and end of each trial. A Bimanual 4-Button
218 Fiber Optic Response Pad (Current Designs, Philadelphia, USA) was used to record the
219 responses.

220

221 Before entering the magnetically shielded room for MEG recordings, an elastic cap with five
222 marker coils was placed on the participant's head. We recorded head shape with a
223 Polhemus Fastrak digitiser pen (Colchester, USA) and used the marker coils to measure the
224 head position within the magnetically shielded room at the start of the experiment, halfway
225 through and at the end.

226

227 *MEG data analysis: Preprocessing*

228 FieldTrip (Oostenveld et al., 2011) was used to preprocess the MEG data. The data were
229 downsampled to 200Hz and then epoched from -100 to 500ms relative to stimulus onset.
230 We did not conduct any further preprocessing steps (filtering, channel selection, trial-
231 averaging etc.) to keep the data in its rawest possible form.

232

233 *MEG data analysis: Decoding Analyses*

234 For all our decoding analyses, patterns of brain activity were extracted across all 160 MEG
235 sensors at every timepoint, for each participant separately. We used a regularised linear
236 discriminant analysis (LDA) classifier which was trained to distinguish the conditions of
237 interest across the 160-dimensional space. We then used independent test data to assess
238 whether the classifier could predict the condition above chance in the new data. We
239 conducted training and testing at every timepoint and tested for significance using random-
240 effects Monte Carlo cluster (TFCE; Smith & Nichols, 2009) statistics, corrected for multiple
241 comparisons using the max statistic across time points (Maris & Oostenveld, 2007). Note
242 that our aim was not to achieve the highest possible decoding accuracy, but rather to test
243 whether the classifier could predict the conditions above chance at any of the timepoints
244 (i.e., "classification for interpretation", Hebart & Baker, 2017). Therefore, we followed a
245 minimal preprocessing pipeline and performed our analyses on a single-trial basis.
246 Classification accuracy above chance indicates that the MEG data contains information that
247 is different for the categories. We used the CoSMoMVPA toolbox (Oosterhof et al., 2016) to
248 conduct all our analyses.

249

250 We ran several decoding analyses which can be divided in three broad themes. First, we
251 tested when we can differentiate between trials where congruently and incongruently

252 coloured objects were presented. This gives us an indication of the timecourse of the
253 integration of visual object representations and stored conceptual knowledge. Second, we
254 examined single feature processing focusing on colour processing and how the typicality of
255 object-colour combinations influences colour processing over time. Third, we looked at
256 another single feature, shape, and tested whether object-colour combinations influence
257 shape processing over time.

258

259 For the congruency analysis (Figure 2A), we tested whether activation patterns evoked by
260 congruently coloured objects (e.g., red strawberry) differ from activation patterns evoked by
261 incongruently coloured objects (e.g., yellow strawberry). Any differential response that
262 depends on whether a colour is typical or atypical for an object (a congruency effect)
263 requires the perceived shape and colour to be bound and compared to a conceptual object
264 representation activated from memory. We trained the classifier on all congruent and
265 incongruent trials *except* for trials corresponding to one pair of matched exemplars (e.g., all
266 instances of congruent and incongruent strawberries and congruent and incongruent
267 bananas). We then tested the classifier using only the left-out exemplar pairs. We repeated
268 this process until each matched exemplar pair had been left out (i.e., used as test data)
269 once. Leaving an exemplar pair out ensures that there are identical objects and colours for
270 both classes (congruent and incongruent) in both the training and the testing set, and that
271 the stimuli of the test set have different shape characteristics than any of the training objects.
272 As such, the only distinguishing feature between the conditions is the *conjunction* of shape
273 and colour features, which defines congruency. This allows us to compare directly whether
274 (and at which timepoint) stored object representations interact with incoming object-colour
275 information.

276

277 Next, we focused on the timecourse of colour processing. First, we examined the timecourse
278 of colour processing independent of congruency (Figure 3A). For this analysis, we trained
279 the classifier on distinguishing between the four different colour categories of the abstract
280 shapes and tested its performance on an independent set of abstract shape trials. We
281 always left one block out for the cross-validation (8-folds). The results of this analysis give
282 an indication about the emergence of when the representations differ between different
283 surface colours, but as we did not control the colours to be equal in luminance or have the
284 same hue difference between each pair, this is not a pure chromatic measure. We did not
285 control luminance because we used these colours to create our coloured objects, which
286 needed to look as realistic as possible. Thus, the colour decoding analysis includes large
287 and small differences in hue *and* in luminance between the categories. To look at the

288 differences between each colour pair, we also present confusion matrices showing the
289 frequencies of the predicted colour categories at peak decoding.

290

291 Our second colour processing analysis was to examine whether the conjunction of object
292 and colour influenced colour processing (Figure 4A). Perceiving a strongly associated object
293 in the context of viewing a certain colour might lead to a more stable representation of that
294 colour in the MEG signal. For example, if we see a yellow banana, the banana shape may
295 facilitate a representation of the colour yellow earlier than if we see a yellow strawberry. To
296 assess this possibility, we trained the classifier to distinguish between the surface colours of
297 the abstract shapes (i.e., red, orange, yellow, green; chance: 25%). We then tested how well
298 the classifier could predict the colour of the congruent and incongruent objects. Training the
299 classifier on the same abstract shapes across colour categories makes it impossible that a
300 certain shape-colour combination drives an effect, as the only distinguishing feature between
301 the abstract shapes is colour. This analysis allows us to compare whether the typicality of
302 colour-form combinations has an effect on colour processing.

303

304 In our final set of analyses, we examined the timecourse of shape processing. First, to
305 assess the timecourse of shape processing independent of congruency, we trained a
306 classifier to distinguish the five different abstract shapes in a pairwise fashion (Figure 5A).
307 We always used one independent block of abstract shape trials to test the classifier
308 performance (8-fold cross-validation). The results of this analysis indicate when information
309 about different shapes are present in the neural signal, independent of other object
310 features (e.g., colour) or congruency. Second, we tested whether the conjunction of object
311 and colour has an effect on object decoding (Figure 6A). If object-colour influences early
312 perceptual processes, we might see a facilitation for decoding objects when they are
313 coloured congruently or interference when the objects are coloured incongruently. We used
314 the greyscale object trials to train the classifier to distinguish between all of the objects. The
315 stimulus set contained two exemplars of each item (e.g., strawberry 1 and strawberry 2). We
316 used different exemplars for the training and testing set to minimise the effects of low-level
317 visual features, however, given that there are major differences in object shapes and edges,
318 we can still expect to see strong differences between the objects. The classifier was trained
319 on one exemplar of all of the greyscale trials. We then tested the classifier's performance on
320 the congruent and incongruent object trials using the exemplars the classifier did not train
321 on. We then swapped the exemplars used for training and testing set until every combination
322 had been used in the testing set. Essentially, this classifier is trained to predict which object
323 was presented to the participant (e.g., was it a strawberry or a frog?) and we are testing

324 whether there is a difference depending on whether the object is congruently or
325 incongruently coloured.

326

327 *Statistical Inferences*

328 In all our analyses, we used random effects Monte-Carlo cluster statistic using Threshold
329 Free Cluster Enhancement (TFCE, Smith & Nichols, 2009) as implemented in the
330 CoSMoMVPA toolbox to see whether the classifier could predict the condition of interest
331 above chance. The TFCE statistic represents the support from neighbouring time points,
332 thus allowing for detection of sharp peaks and sustained small effects over time. We used a
333 permutation test, swapping labels of complete trials, and re-ran the decoding analysis on the
334 data with the shuffled labels 100 times per participant to create subject-level null-
335 distributions. We then used Monte-Carlo sampling to create a group-level null-distribution
336 consisting of 10,000 shuffled label permutations for the time-resolved decoding, and 1000
337 for the time-generalisation analyses (to reduce computation time). The null distributions were
338 then transformed into TFCE statistics. To correct for multiple comparisons, the *maximum*
339 TFCE values across time in each of the null distributions was selected. We then transformed
340 the true decoding values to TFCE statistics. To assess whether the true TFCE value at each
341 timepoint is significantly above chance, we compared it to the 95th percentile of the corrected
342 null distribution. Selecting the maximum TFCE value provides a conservative threshold for
343 determining whether the observed decoding accuracy is above chance, corrected for
344 multiple comparisons.

345

346 To assess at which timepoint the decoding accuracy peaks, we bootstrapped the
347 participants' decoding accuracies for each analysis 10,000 times and generated 95%
348 confidence intervals for peak decoding. For the analyses in which we are comparing colour
349 and exemplar decoding for congruent and incongruent trials, we also compared the above
350 chance decoding durations. To test for the duration of above chance decoding, we
351 bootstrapped the data (10,000 times) and ran our statistics. At each iteration we then looked
352 for the longest period in which we have above chance decoding in consecutive timepoints.
353 We plotted the bootstrapped decoding durations and calculated medians to compare the
354 distributions for the congruent and the incongruent condition.

355

356

357 **Results**

358 **Behavioural results**

359 We first present the data from our behavioural object-naming task to confirm that our stimuli
360 induce a congruency effect on object naming times. All incorrect responses and microphone
361 errors were excluded from the analysis (on average across participants: 10.1%). We then
362 calculated the median reaction time for naming each stimulus. If a participant named a
363 specific stimulus incorrectly across trials (e.g., incongruently coloured strawberry was always
364 named incorrectly), we removed this stimulus completely to ensure that the reaction times in
365 one condition were not skewed. We ran a repeated measures ANOVA to compare the
366 naming times for the different conditions in the behavioural object naming task using JASP
367 (Love et al., 2015). Naming times were significantly different between the conditions ($F(2,34)$
368 = 12.8; $p < 0.001$). Bonferroni-corrected post hoc comparisons show that participants were
369 faster to name the congruently coloured (701ms) than the incongruently coloured (750ms)
370 objects ($p_{\text{bonf}} < 0.001$; 95%CI for mean difference [23.8, 72.8]). It took participants on
371 average 717ms to name the greyscale objects which was significantly faster than naming
372 the incongruently coloured objects ($p_{\text{bonf}} = 0.007$; 95%CI for mean difference [7.8, 56.8]) but
373 not significantly slower than naming the congruently coloured objects ($p_{\text{bonf}} = 0.33$; 95%CI
374 for mean difference [-40.5, 8.5]). These results suggest that the objects we used here do
375 indeed have associations with specific canonical colours, and we replicate that these objects
376 are consistently associated with a particular colour (Bannert & Bartels, 2013; Joseph, 1997;
377 Lloyd-Jones et al., 2012; Naor-Raz et al., 2003; Tanaka & Presnell, 1999; Therriault et al.,
378 2009).

379

380 In the main task, participants were asked to indicate every 80 trials whether they had seen a
381 certain target object or not. The aim of this task was to keep participants motivated and
382 attentive throughout the training session. On average, participants reported whether the
383 targets were present or absent with 90% accuracy ($SD = 5\%$, range: 81.25% - 100%).

384

385 **MEG results**

386 The aim of our decoding analyses was to examine the interaction between object-colour
387 knowledge and object representations. First, we tested for a difference in the brain activation
388 pattern for congruently and incongruently coloured objects. The results show distinct
389 patterns of neural activity for congruent compared to incongruent objects in a cluster of
390 consecutive timepoints stretching from 250 to 325ms after stimulus onset, demonstrating
391 that brain activity is modulated by colour congruency in this time window (Figure 2B). Thus,
392 binding of colour and form must have occurred by ~250ms and stored object-colour
393 knowledge is integrated with incoming information. An exploratory searchlight (Carlson et al.,
394 2019; Collins et al., 2018; Kaiser et al., 2016) across small clusters (9 at a time) of MEG

395 sensors suggests that this effect is driven a range of frontal, temporal and parietal sensor
396 clusters (Figure 2C).

397

398 [Figure 2]

399

400 To examine the timecourse of colour processing separately from congruency, we decoded
401 the surface colours of the abstract shapes (Figure 3A). Consistent with earlier results
402 (Teichmann et al., 2019), we found that colour can be decoded above chance from the
403 abstract shape trials in a cluster stretching from 70 to 350ms (Figure 3B). Looking at data
404 from an exploratory sensor searchlight analysis across small clusters of sensors shows that
405 colour information at peak decoding is mainly distinguishable from occipital and parietal
406 sensors. To examine whether all colours could be dissociated equally well, we also looked at
407 confusion matrices displaying how frequently each colour category was predicted for each
408 colour (Figure 3D). The results show that at the decoding peak (140ms), red and green are
409 most easily distinguishable and that the prediction errors are not equally distributed: Red
410 trials are more frequently misclassified as being orange than green or yellow and green trials
411 are more frequently misclassified as being yellow than orange or red. This indicates that
412 colours that are more similar evoke a more similar pattern of activation than colours that are
413 dissimilar (Figure 3E).

414

415 [Figure 3]

416

417 To assess whether congruency influences colour processing, we trained a classifier to
418 distinguish between the colours in the abstract shape condition and then tested it on the
419 congruent and incongruent trials separately (Figure 4A). Colour can be successfully
420 classified in a cluster stretching from 75 to 125ms for the congruent condition and in a
421 cluster stretching from 75 to 185ms for the incongruent trials (Figure 4B). These results
422 suggest there may be a difference in the way colour information is processed depending on
423 the congruency of the image, specifically evident in the decoding peaks and decoding
424 duration. To test whether there is a true difference in decoding timecourses, we
425 bootstrapped the data and looked at the peak decoding and the longest consecutive streak
426 of above chance decoding. Comparing the peak decoding times for the congruent and the
427 incongruent condition, we find that they are different from each other (Figure 4C, top).
428 However, comparing the confidence intervals of the decoding durations we find no
429 consistent differences between the congruent and the incongruent condition (Figure 4C,
430 bottom). This could be due to the fact that on- and offsets in above chance decoding are
431 affected by signal strength and thresholds (cf. Grootswagers et al., 2017). The peak

432 differences are a more robust measure and suggest that colour stronger colour decoding
433 occurs later in the incongruent compared to congruent condition. To get a complete picture
434 of how these signals evolve over time, we used time-generalisation matrices (Figure 4D and
435 4E). To create time-generalisation matrices, we trained the classifier on each timepoint of
436 the training dataset and then tested it on all timepoints of the test set. The diagonal of these
437 matrices corresponds to the standard time-resolved decoding results (e.g., training at 100ms
438 and testing at 100ms). A decodable off-the-diagonal effect reflects a temporal asynchrony in
439 information processing in the training and testing set (cf. Carlson et al., 2011; King &
440 Dehaene, 2014). Our data show that colour category was decodable from both conditions
441 early on (~70ms). In the incongruent condition, the activation associated with colour seems
442 to be sustained longer (Figure 4E) than for the congruent condition (Figure 4D), but for both,
443 decoding above chance occurs mainly along the diagonal. This suggests that the initial
444 pattern of activation for colour signals occurs at the same time but that the signals
445 associated with colour are prolonged when object-colour combinations are unusual relative
446 to when they are typical.

447

[Figure 4]

449

450 In an exploratory colour analysis, we also examined which errors the classifier made when
451 predicting the colour of the incongruently coloured objects. We looked at whether the implied
452 object colour is predicted more often than the surface colour or the other colours. However,
453 as errors were not equally distributed across the incorrect labels in the training (abstract
454 shape) dataset, we need to compare the misclassification results for the incongruent
455 condition to the results from the congruent condition, to take these differing base rates into
456 account. For each object in the incongruent condition (e.g., yellow strawberry), we have a
457 colour-matched object in the congruent condition (e.g., yellow banana). We made use of
458 these matched stimuli by looking at misclassifications and checking how frequently the
459 implied colour of an incongruent object (e.g., red for a yellow strawberry) was predicted in
460 comparison to the matched congruent object (e.g., red for a yellow banana). If the implied
461 colour of incongruently coloured objects was activated along with the surface colour, we
462 should see a higher rate of implied colour predictions (e.g., red) for the incongruent object
463 (e.g., yellow strawberry) than for the colour-matched congruent object (e.g., yellow banana).

464 The results (Figure 5) do not show this pattern: at the first peak (~80-110ms), the “other”
465 colours are actually more likely to be chosen by the classifier than the implied colour, for
466 both the congruent and incongruent condition. A possible explanation for not seeing an
467 effect of implied colour in the colour decoding analysis is that the decoding model is based

468 on the actual colour pattern, whereas the timing and mechanisms of implied colour activation
469 may be different (Teichmann et al., 2019).

470 [Figure 5]

471

472

473 The goal of the third analysis was to examine whether shape representations are affected by
474 colour congruency. It could be the case, for example, that the representation of banana-
475 shapes compared to strawberry-shapes is enhanced when their colours are correct. First,
476 we tested when shape representations can be decoded independent of colour congruency.
477 We trained the classifier to distinguish between the five different abstract shapes in a
478 pairwise fashion and then tested its performance on independent data (Figure 6A). The data
479 show that shape information can be decoded in a cluster stretching from 60 to 500ms
480 (Figure 6B). Running an exploratory searchlight analysis on small clusters of sensors (9 at a
481 time) shows that shape information at peak decoding is mainly driven by occipital sensors
482 (Figure 6C).

483

[Figure 6]

485

486 To examine whether colour affects object processing, we trained a classifier to distinguish
487 between trials in which the participant saw one of the exemplars of each of the twenty
488 objects in greyscale (e.g., greyscale strawberry 1, greyscale cherry 1, etc.). We then tested
489 at which timepoint the classifier could successfully cross-generalise to the other exemplar of
490 that object in the congruent and incongruent condition separately (Figure 7A). If object
491 representations (e.g., banana) are influenced by the typicality of their colours, then cross-
492 generalisation should be different for congruent and incongruent trials. Note that although
493 the exact images are unique, there are shared shape characteristics between exemplars
494 (e.g., the two frog exemplars share some shape aspects despite being different postures),
495 which can be expected to drive an effect. The results show the neural data has differential
496 information about the object in a cluster stretching from 65 to 500ms for both the congruent
497 and the incongruent test sets (Figure 7B). These results show that we can decode the
498 object class early on, at a similar time to when we can decode the abstract shape conditions,
499 suggesting that the classifier here is driven strongly by low-level features (like shape), rather
500 than being influenced by colour congruency. The timecourse for congruent and incongruent
501 object decoding is very similar in terms of peak decoding and decoding duration (Figure 7C).
502 Thus, our data suggest that there is no effect of colour congruency on object processing.

503

504

[Figure 7]

505

506 Overall, the results here show that single features present within the incoming visual stimuli
507 are decodable earlier than the congruency between them, which can be seen as an index for
508 accessing stored conceptual knowledge (Figure 8). When we compare colour and shape
509 decoding for abstract shapes and for congruently and incongruently coloured objects, the
510 decoding onsets are very similar, suggesting the initial processes of single feature
511 processing are not influenced by congruency. However, peak colour decoding occurs later
512 for incongruently coloured in comparison to congruently coloured objects suggesting that
513 colour congruency influences colour processing to some degree.

514

[Figure 8]

515

516

517

518 Discussion

519 A crucial question in object recognition concerns how incoming visual information interacts
520 with stored object concepts to create meaningful vision under varying situations. The aims of
521 the current study were to examine the temporal dynamics of object-colour knowledge and to
522 test whether activating object-colour knowledge influences the early stages of colour and
523 object processing. Our data provide three major insights: First, congruently and
524 incongruently coloured objects evoke a different neural representation after ~250ms
525 suggesting that, by this time, visual object features are bound into a coherent representation
526 and compared to stored object representations. Second, colour can be decoded at a similar
527 latency (~70ms) irrespective of whether participants view coloured abstract shapes, or
528 congruently and incongruently coloured objects. However, peak decoding occurs later when
529 viewing incongruently coloured objects compared to congruent ones. Third, we do not find
530 an influence of colour congruency on object processing, which may suggest that behavioural
531 congruency effects are due to conflict at a later stage in processing.

532

533 Colour congruency can act as an index to assess when prior knowledge is integrated with
534 bound object features. When comparing brain activation patterns of the same objects
535 presented in different colours, there was a decodable difference between congruent and
536 incongruent conditions from ~250ms onwards suggesting a stored object representation that
537 contains information about the typical colour of an object must have been activated by this
538 stage. Prior to this time, the signal is primarily driven by processing of early perceptual
539 features such as colour and shape, which were matched for the congruent and incongruent
540 conditions (same objects, same colours, only the combination of colour and shape differed).

541 Although from our data we cannot draw direct conclusions about which brain areas are
542 involved in the integration of incoming visual information and stored object knowledge, our
543 congruency analysis adds to the fMRI literature by showing the relative timecourse at which
544 a meaningful object representation emerges. Activating object-colour knowledge from
545 memory has been shown to involve the ATL (e.g., Coutanche & Thompson-Schill, 2014) and
546 there is evidence that object-colour congruency coding occurs in perirhinal cortex (Price et
547 al., 2017). Further support on the involvement of the ATL in the integration of incoming
548 sensory information and stored representations comes from work on patients with semantic
549 dementia (e.g., Bozeat et al., 2002) and studies on healthy participants using TMS (e.g.,
550 Chiou et al., 2014). Higher level brain areas in the temporal lobe have also been shown to
551 be part of neuronal circuits involved in implicit imagery, supporting visual perception by
552 augmenting incoming information with stored conceptual knowledge (e.g., Albright, 2012;
553 Miyashita, 2004). The latency of congruency decoding here may thus reflect the time it takes
554 to compare visual object representations with conceptual templates in higher-level brain
555 areas such as the ATL, or the time it takes for feedback or error signals about colour
556 congruency to arrive back in early visual areas.

557

558 Our results also show that colour congruency has an effect on colour processing. We found
559 colour decoding onset at a similar time (~70ms) for abstract shapes and congruently and
560 incongruently coloured objects. This indicates that colour signals are activated initially
561 independently of object shape, consistent with previous work showing that single features
562 are processed first and that the conjunction of colour and shape occurs at a later stage (e.g.,
563 Seymour et al., 2015). However, we also found differences between colour processing in
564 congruent and incongruent conditions: The colour signal peaked later in the incongruent
565 relative to the congruent condition, suggesting that congruency influences the timecourse of
566 colour processing to some degree. Our time-generalisation analysis (Figure 4D) supports
567 this by showing that there is a different dynamic for congruent and incongruent trials. One
568 possible explanation for this finding is that unusual feature pairings (e.g., shape and colour
569 or texture and colour) might lead to local feedback signals that prolong colour processing.
570 Alternatively, consistent with the memory colour literature (e.g., Hansen et al., 2006;
571 Olkkonen et al., 2008; Witzel et al., 2011), it is possible that typical colours are co-activated
572 along with other low-level features. For incongruent trials, this would then lead to two
573 potential colours needing to be distinguished, extending the timeframe for processing and
574 delaying the peak activation for the surface colour of the object.

575

576 The timecourse of exemplar decoding we present is consistent with previous studies on
577 object recognition. Here, we found that exemplar identity could be decoded at ~65ms.

578 Similar latencies have been found in other M/EEG decoding studies (Carlson et al., 2013;
579 Cichy et al., 2014; Contini et al., 2017; Grootswagers et al., 2019; Isik et al., 2013) and
580 single unit recordings (e.g., Hung, Kreiman, Poggio, & DiCarlo, 2005). Behavioural data,
581 including the reaction times collected from our participants, show that colour influences
582 object identification speed (e.g., Bramão, Faísca, Petersson, & Reis, 2010). The neural data,
583 however, did not show an effect of object colour on the classifier's performance when
584 distinguishing the neural activation patterns evoked by different object exemplars. For
585 example, the brain activation pattern in response to a strawberry could be differentiated from
586 the pattern evoked by a lemon, regardless of the congruency of their colours. This finding is
587 consistent with previous results (Proverbio et al., 2004) but might seem puzzling because
588 colour congruency has been shown to have a strong effect on object naming (e.g., Chiou et
589 al., 2014; Nagai & Yokosawa, 2003; Tanaka & Presnell, 1999). One plausible possibility is
590 that the source of behavioural congruency effects may be at the stage of response selection,
591 which would not show up in these early neural signals. More evidence is needed, but there
592 is no evidence in the current data to suggest colour congruency influences early stages of
593 object processing.

594

595 Our data demonstrate that object representations are influenced by object-colour knowledge
596 but not at the initial stages of visual processes. Consistent with a traditional hierarchical
597 view, we show that visual object features are processed before the features are bound into a
598 coherent object that can be compared with existing, conceptual object representations.
599 However, our data also suggest that the temporal dynamics of colour processing are
600 influenced by the typicality of object-colour pairings. Building on the extensive literature on
601 visual perception, these results provide a timecourse for the integration of incoming visual
602 information with stored knowledge, a process that is critical for interpreting the visual world
603 around us.

604

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605

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- 751
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- 753

Figure Legends

Figure 1. (A) shows all stimuli used in this experiment. The same objects were used in the congruent, incongruent, and greyscale conditions. There were two exemplars of each object. Colours in the congruent and incongruent condition were matched. The abstract shapes were identical across colour categories. (B) shows the mean chromaticity coordinates for the 2° observer under D65 illumination for each colour category (top) as well as the mean lightness of all coloured stimuli used in this experiment (bottom). The colours were transformed into CIELUV space using the OptProp toolbox (Wagberg, 2007). (C) shows an example sequence of the main task. Participants viewed each object for 450ms. After each sequence, one object was displayed and participants had to indicate whether they had seen this object in the previous sequence or not.

Figure 2. Cross-validation and results of the congruency analysis contrasting trials from the congruent and incongruent conditions. (A) shows the leave-one-matched-exemplar-out cross validation approach for a single fold for the congruency decoding analysis. The classifier was trained on the trials shown on the left and tested on the trials on the right, 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 across participants. Black dashed line represents chance level (50% - congruent versus incongruent). Filled dots highlight significant timepoints, corrected for multiple comparisons. The horizontal bar above the curve shows the 95% confidence interval of the peak. (C) is an exploratory sensor searchlight analysis in which we run the same analysis across small clusters of sensors. The colours highlight the decoding accuracy for each sensor cluster averaged over the 95% confidence interval of the peak timepoints.

Figure 3. (A) depicts the colour decoding analysis when training the classifier to distinguish between the different colour categories of the abstract shapes and testing on a block of independent abstract shape trials. (B) shows the decoding accuracy for the colour decoding analysis over time. Shading represents the standard error across participants. Black dashed line represents chance level (25% - red versus green versus orange versus yellow). Filled dots highlight significant timepoints, corrected for multiple comparisons. The horizontal bar above the curve shows the 95% confidence interval of the peak. (C) shows the results of a exploratory searchlight analysis over small sensor clusters averaged across the timepoints of the 95% confidence interval for peak decoding. Colours indicate the decoding accuracies at each sensor. (D) depicts a confusion matrix for peak decoding (140ms) showing the frequencies at which colour categories were predicted given the true class. (E) shows the similarity of the colour categories which might underlie the results in (D).

Figure 4. Results of the colour decoding analysis for the congruent and incongruent trials. Here, the classifier was trained to distinguish the colour of all abstract shape trials and tested on the congruent and incongruent trials separately (A). (B) shows the classification accuracy over time for the congruent (blue) and incongruent (green) trials. Shading represents the standard error across participants. Black dashed line indicates chance level (25% - red versus green versus orange versus yellow). Blue (congruent) and green (incongruent) dots highlight timepoints at which we can decode the surface colour significantly above chance, corrected for multiple comparisons. (C) shows the bootstrapped differences in peak time (top) and the bootstrapped differences in decoding duration (bottom) for the congruent and the incongruent conditions. (D) shows the results of the same analysis across all possible training and testing timepoint combinations. These time-time matrices allow us to examine how the signal for the congruent colours (left) and incongruent colours (right) evolves over time. The top row shows the classification accuracy at every timepoint combination with lighter pixels reflecting higher decoding accuracies. The bottom

808 row shows clusters where decoding is significantly above chance (yellow), corrected for
809 multiple comparisons.

810
811 Figure 5. (A) shows the frequency of a predicted class when the classifier is trained on
812 distinguishing colours in the abstract shape condition and tested on trials from the congruent
813 (dotted lines) and incongruent (full lines) conditions. Shading represents the standard error
814 across participants. There are clear peaks for the correct prediction of the surface colour
815 between 100and 150ms (purple lines). In cases where the classifier makes an error, there is
816 no evidence that the classifier picks the implied object colour (blue lines) more frequently
817 than the other incorrect colours (green lines). Note that the classifier is trained on the
818 abstract shape condition which has an uneven colour similarity, the errors in the incongruent
819 condition have to be interpreted in relation to how often the matched implied colour in the
820 congruent condition is predicted. (B) shows the difference of the classifier predicting the
821 implied over the other colours for the congruent (purple) and incongruent (blue) conditions.
822

823
824 Figure 6. (A) depicts the shape decoding analysis when training the classifier to distinguish
825 between the different categories of the abstract shapes and testing on a block of
826 independent abstract shape trials. (B) shows the decoding accuracy for the shape decoding
827 analysis over time. Shading represents the standard error across participants. Black dashed
828 line represents chance level (50% - pairwise comparison of all shapes). Filled dots highlight
829 significant timepoints, corrected for multiple comparisons. The horizontal bar above the
830 curve shows the 95% confidence interval of the peak. (C) shows the results of an
831 exploratory searchlight analysis over small sensor clusters averaged across the timepoints
832 of the 95% confidence interval for peak decoding. Colours indicate the decoding accuracies
833 at each sensor.

834
835 Figure 7. Results of the object exemplar decoding analysis. The classifier was trained to
836 distinguish between all pairwise object categories in the greyscale object condition. We used
837 one exemplar of each class for the training and the other exemplar for testing the classifier.
838 Testing was done for the congruent and incongruent trials separately (A). (B) shows the
839 classification accuracy over time for the object decoding analysis when testing the
840 classifier's performance on congruent (blue) and incongruent (green) trials. Shading
841 represents the standard error across participants. Black dashed line represents chance level
842 (50% - pairwise decoding for all 20 different object categories). Blue (congruent) and green
843 (incongruent) dots highlight significant timepoints ($p < 0.05$), corrected for multiple
844 comparisons. (C) shows the bootstrapped differences in peak time (top) and the
845 bootstrapped differences in decoding duration (bottom) for the congruent and the
846 incongruent conditions.

847
848 Figure 8. Overview of the findings. Each coloured bar shows the onset (x axis) and
849 duration (length of coloured bar) at which feature and conjunction information was contained
850 in the neural signal. Darker shadings surrounded by dotted black lines show the
851 bootstrapped 95% confidence interval for peak decoding. The dotted vertical line represents
852 stimulus onset.















