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

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Abstract

The ability to rapidly and accurately recognise complex objects is a crucial function of the human visual system. Successful object recognition requires binding incoming visual features such as colour and form into specific neural representations that can be compared to our pre-existing knowledge about the world. Some objects have typical or implied colour as a central feature that is useful for recognition; for example, a banana is typically yellow. In the current study, we address two main questions. First, we test how colour representations unfold over time when activated by real colour perception versus the activation of implied colours. Second, we examine how features such as colour and form are bound together. We apply multivariate pattern analyses to time-resolved neuroimaging (magnetoencephalography) data to address these questions. Our results show that colour representations can be accessed both via real colour perception and via implied colour activation in the complete absence of colour in the stimulus. These real and implied colour representations share characteristics but differ in the timing of their neural activation. In addition, our data demonstrate that object representations are influenced by object-colour knowledge at later, but not at initial stages of visual processing. Single object features are processed before feature-binding occurs which allows for a comparison of visual input with existing knowledge about objects. Taken together, these results provide new insights into the integration of incoming visual information with existing conceptual object knowledge.

Introduction

Objects in our environment can be characterised by many different properties including form, colour, surface texture, and motion. For successful object recognition, we need to compare incoming perceptual information with pre-existing object concepts, which contain multiple features. Robust conceptual object representations allow for reliable object recognition under different conditions such as changing light, orientation or size. A central feature of many objects in the environment is colour, which can be a highly informative cue about an object's identity but also varies in certain situations. For example, colour is a crucial clue to distinguish lemons from limes, but can also signify the ripeness of many types of fruit. Here, we use multivariate pattern analyses (MVPA) and Magnetoencephalography (MEG) to examine the way in which incoming sensory information about objects interacts with conceptual object representations, focusing on object-colour knowledge.

Colour perception comprises a progression from simple chromatic processing to more complex object-surface colour integration. First, the registration of different wavelengths of light and comparing their intensities occurs in V1 and V2 (Zeki, 1983a, 1983b; Zeki & Marini, 1998). Area V4, slightly further on in the visual hierarchy, has been shown to code for more complex aspects of colour perception by comparative processes between surfaces reflecting different amounts of light (Zeki & Marini, 1998). Functional magnetic resonance imaging (fMRI) has shown that colour in a specific retinal position was represented in early visual areas such as V1 but colour bound to form (object surface colour) could only be differentiated later along the visual hierarchy (V4 and beyond) (Seymour, Williams, & Rich, 2015). Increasingly complex colour processing along the visual hierarchy is thus likely to contribute to object identification at higher levels of processing.

To recognise objects, we have to be able to integrate incoming perceptual information with what we already know (Albright, 2012; Clarke & Tyler, 2015). Area V4 can distinguish between different surface colours but is not concerned with whether objects are coloured

correctly or incorrectly (Zeki & Marini, 1998). Results of behavioural studies show that typical or *implied colour* information (e.g., yellow for a banana) facilitates the recognition of objects that are strongly associated with a certain colour (for a meta-analysis see Bramão, Reis, Petersson, & Faísca, 2011). For example, for objects high in colour diagnosticity, participants are faster to identify objects that are congruently coloured (e.g., yellow banana) compared to objects that are incongruently coloured (e.g., red banana) (Nagai & Yokosawa, 2003; Tanaka & Presnell, 1999). This colour congruency effect demonstrates that our representation of canonically-coloured objects inherently includes colour as a strong defining feature, such that conflicting visual information slows recognition. Thus, activating implied object colours appears to interact with processing perceptual object features.

A key question about how object-colour knowledge is represented is whether implied colours rely on the same neural mechanisms as perceiving object colours. There is evidence from fMRI of overlap or close proximity in the brain areas activated for both colour perception *and* memory colour activation (Chao & Martin, 1999; Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995; Wiggs, Weisberg, & Martin, 1998). For example, Bannert and Bartels (2013) applied multivariate pattern analyses (MVPA) to fMRI data and showed overlapping neural representations for colour perception and implied object colour activation in visual areas V1 and V4. Similarly, Coutanche and Thompson-Schill (2014) showed that brain activation patterns evoked by object-colour and object-shape activated from memory can be distinguished in areas associated with colour (V4) and shape (lateral occipital cortex, LOC) perception, respectively. Their results also demonstrated that the conjunction of colour *and* shape, a 'bound' representation activated from memory, is only represented in the anterior temporal lobe (ATL). This finding corresponds to patient work (Patterson, Nestor, & Rogers, 2007) and transcranial magnetic stimulation studies (Chiou, Sowman, Etchell, & Rich, 2014; Pobric, Jefferies, & Lambon Ralph, 2010) that point towards the ATL as a hub for conceptual knowledge (for a recent review see Ralph, Jefferies, Patterson, & Rogers, 2017). Overall,

these results suggest that similar processes are utilised for colour processing when it is accessed via real colour and via implied colour.

To understand at what stage of processing the activation of colour representations accessed via colour perception and object-colour knowledge interacts, we need to examine the temporal dynamics of this process. In non-human primates, information in V1 is processed at ~50ms after stimulus onset while information reaches visual areas such as V4 after ~70ms (DiCarlo, Zoccolan, & Rust, 2012). Results of the fMRI studies reviewed above suggest that several brain regions are involved in both colour perception *and* the activation of implied colours from memory, but it is possible that these occur at different time scales.

Electroencephalography (EEG) studies have investigated the temporal dynamics of object-colour knowledge (Lloyd-Jones, Roberts, Leek, Fouquet, & Truchanowicz, 2012; Lu et al., 2010; Proverbio, Burco, del Zotto, & Zani, 2004). Lloyd-Jones et al. (2012) used images of real objects to show that shape information modulates neural responses at around 170ms (i.e., component N1), the combination of shape and colour affected the signal at 225ms (i.e., component P2), and the typicality of object-colour pairing modulated components approximately 225 and 350ms after stimulus onset (i.e., P2 and P3). These findings suggest that shape information activates typical object-colour associations and that bound colour *and* shape features are processed later than shape alone. This leads to the question of what effect object-colour knowledge has on colour perception and whether neural activity associated with activating typical colours and perceiving real colours unfolds in a similar way.

In the current study, we examine the temporal aspects underlying object-colour processing by applying MVPA to MEG data. First, we compare how neural colour representations evolve over time when accessed via real colour perception and implied colour activation. Second, we examine how object-colour knowledge affects colour and shape binding. We present participants with colour-diagnostic objects that are either coloured congruently (e.g., yellow banana), incongruently (e.g., red banana), or greyscale (e.g., grey

banana), and coloured abstract shapes that have no canonical colour. Decoding colour that is triggered by different wavelengths of light (i.e., "real" colour) signifies *colour perception,* whereas decoding a greyscale object's *implied colour*. Decoding a coloured object's colour congruency status is related to colour associations based on *object-colour knowledge*. First, we examine the time-course of real colour perception, which serves as a basis to investigate how the neural response to real colour perception changes over time. In a previous study, we showed that the MEG pattern of activation evoked by red and green can be differentiated 70ms after image presentation (Teichmann, Grootswagers, Carlson, & Rich, 2018, *Preprint*). Here, we included the colours orange and yellow to examine how colours are represented across a wider range. Second, we test whether colour representations accessed via real colour perception and object-colour activation are similar. Third, we focus on binding of colour and form to understand the effect of typical colour-form associations on object and colour processing, and examine the timecourse of object-feature binding.

Methods

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

Stimuli. We used four different stimulus types: *congruent objects, incongruent objects, greyscale objects,* and *abstract shapes* (Figure 1A). All objects exhibited robust form-colour associations in previous studies (Bannert & Bartels, 2013; Joseph, 1997; Lloyd-Jones et al., 2012; Naor-Raz, Tarr, & Kersten, 2003; Tanaka & Presnell, 1999; Therriault, Yaxley, & Zwaan, 2009). There were four different colour categories (red, green, yellow, orange) and five

different objects per colour. In each category there was one man-made object, one living object, and three fruits or vegetables. We used two different exemplars per object.

We did not use naturally coloured photographs of the objects for the congruent objects, as this would introduce a confounding difference between our congruent and incongruent conditions. Instead, we desaturated object photos and equated them in luminance using the SHINE toolbox (Willenbockel et al., 2010). These greyscale, luminance matched images formed the *greyscale* object condition. Then we overlayed different hues of colours over the grey-scale objects. The congruent objects were colour diagnostic objects (e.g., a banana) presented with their canonical colour (e.g., yellow). As incongruent objects, we used the identical objects but coloured in a colour other than the diagnostic colour. This ensured the congruent and incongruent stimuli were well matched in the way the texture and shape of the object interacted with the colour. Every congruent object exemplar had a colour-matched incongruent partner. For example, we used a specific shade of red and added it to the grey-scale images of the strawberries to make the congruent strawberries. We took the identical shade of red and then overlayed it onto the lemons to make the incongruent lemon exemplars. To make the congruent lemon exemplar and the incongruent strawberry exemplar, we overlayed the identical hue of yellow onto the grey scale images. That means, overall, we have the identical shapes and colours in the congruent and the incongruent condition, a factor that is crucial to ensure our results cannot be explained by features other than colour congruency. The only difference between these key conditions is that the colour-shape combination is either typical (congruent) or atypical (incongruent). In the abstract condition, angular abstract shapes were used as stimuli. Each shape occurred equally often in red, green, orange, and yellow. Because the congruent and incongruent objects were made by overlaying the colours from the abstract shape conditions onto the equiluminant greyscale objects, the colours in the congruent and incongruent condition appear darker than the colours in the abstract shapes.

Image sizes for all conditions were randomly varied on each trial to add visual variability. Participants viewed these stimuli with a distance of 114cm (visual angle: ~4.3 – 6.3 degrees). Varying the size of the stimuli reduced the low-level featural differences between images that were not related to colour.

Procedure. Before entering the magnetically shielded room for MEG recordings, an elastic cap with five marker coils was placed on the participants' heads. We recorded their head shapes with a digitiser pen and used these marker coils to measure the head position within the magnetically shielded room at the start of the experiment, half way through and at the end.

In the main task (Figure 1B), participants completed eight blocks of 800 trials each. Each exemplar was repeated 40 times over the course of the experiment. Each stimulus was presented centrally for 450ms with a black fixation dot on top of it. To keep participants attentive, after every 80 trials, there was a target image presented until a response was given indicating whether this stimulus had appeared in the immediately previous block of trials or not (50% present vs absent). The different conditions were randomly intermingled throughout, and the target was randomly selected each time. On average, participants performed with 90% (SD=5.4%) accuracy.

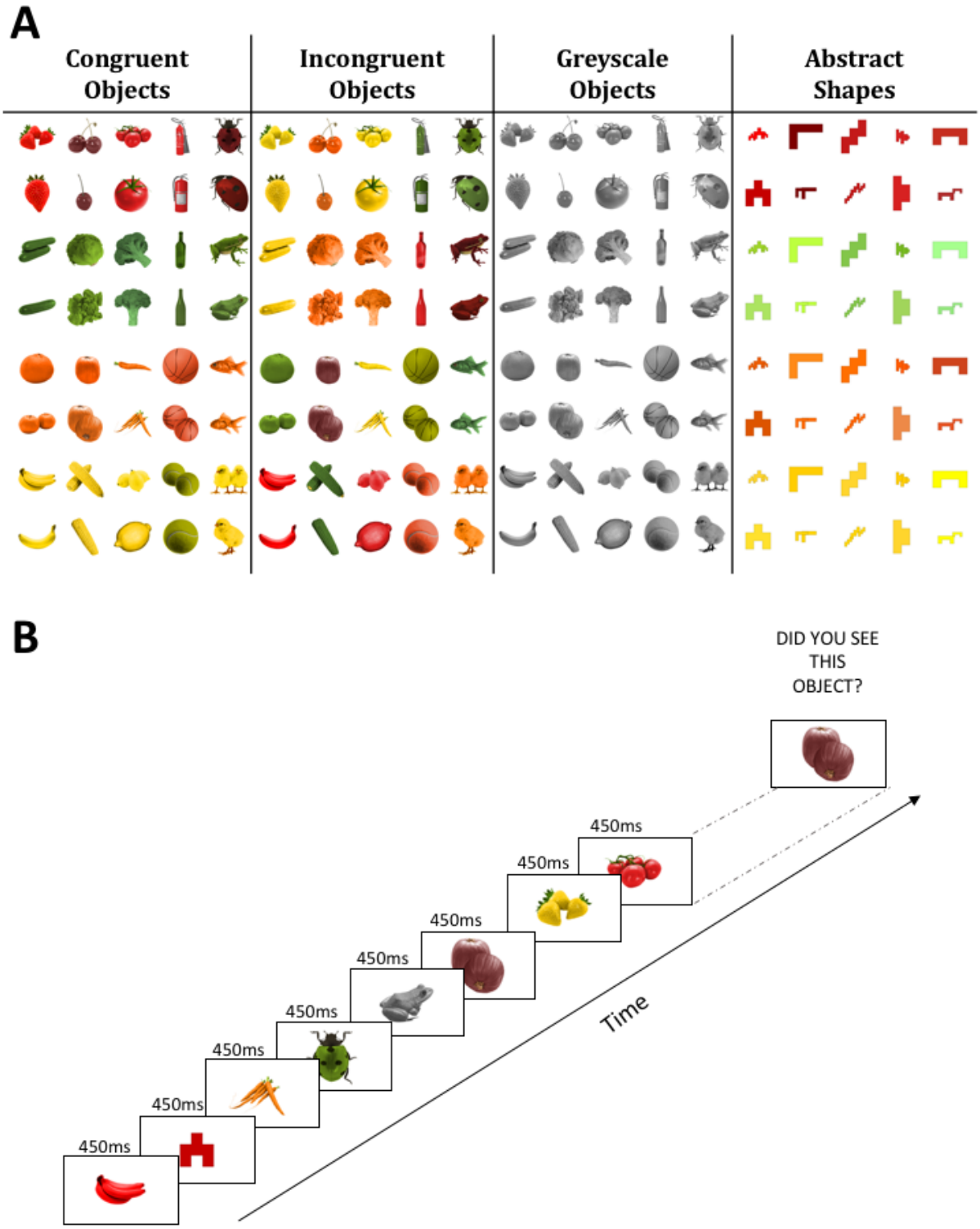

Figure 1. (A) shows all stimuli used in this experiment. The same objects were used in the congruent, incongruent, and greyscale condition. There were two exemplars of each objects. Colours in the congruent and incongruent condition were matched. The abstract shapes were identical across colour categories. (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.

After completing the main blocks, we collected behavioural object-naming data to test for a behavioural congruency effect with our stimuli. Participants remained in the scanner and a microphone was used to record verbal responses. On the screen, participants saw each of the objects again (congruent, incongruent or grey-scale) in a random order and had to name the objects as quickly as possible. As soon as voice onset was detected, the stimulus disappeared. Stimulus-presentation time was marked with a photodiode and voice-onset was recorded using a microphone. Seventeen participants completed three blocks of this reaction time task, one participant completed two blocks, and for two participants we could not record any reaction times. Each block contained all congruent, incongruent and grey-scale objects presented once.

Naming reaction times were defined as the difference between stimulus-onset and voice-onset. Trials containing naming errors and microphone errors (on average 10.1%) were not analysed. We calculated the median naming time for each exemplar for each person and then averaged the naming times for each of the congruent, incongruent and greyscale conditions.

Apparatus. The neuromagnetic recordings were conducted with a whole-head axial gradiometer MEG (KIT, Kanazawa, Japan), containing 160 axial gradiometers. We recorded the MEG signal with a 1000Hz frequency. An online low-pass filter of 200Hz and a high-pass filter of 0.03Hz were used. All stimuli were projected on a translucent screen mounted on the ceiling of the magnetically shielded room. Stimuli were presented using MATLAB with Psychtoolbox extension (Brainard, 1997; Brainard & Pelli, 1997; Kleiner et al., 2007). Parallel port triggers and the signal of a photodiode were used to mark the beginning and end of each trial. A Bimanual 4-Button Fiber Optic Response Pad (Current Designs, Philadelphia, USA) was used to record the responses. Head shape recordings were completed with a Polhemus 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,

Preprint). The results of that study further showed that colour representations accessed via perceiving red and green are similar enough to colour representations activated via grey-scale objects associated with red and green to allow cross-generalisation. The first aim of the current study is to replicate and extend these findings by examining how colour representations of a broader range of colours unfolds, both for actual colour and implied colour. While there are luminance differences between the colours we used here, our key comparisons test at which timepoint real and implied colour evoke similar brain activation patterns, and these cannot be driven by overall luminance differences as the greyscale objects are equated for mean luminance. Luminance can, however, contribute to the classifier accuracy in the real colour decoding analysis, but such a driver would not improve cross-generalisation. Nevertheless, it is important to keep in mind that the real colours used here do not only differ in terms of hue but also in terms of luminance.

In our first analysis, we examined the time-course of real colour perception for four different colour categories (red, green, orange, yellow). This analysis allows us to determine whether there are different brain activation patterns for these four colour categories, and to test whether certain colour pairs are more decodable than others. Colours that are very dissimilar (e.g., red versus green) might be more decodable than colours that are more similar (e.g., orange versus yellow, see Figure 2A). To test this, we trained a classifier to distinguish between the coloured shapes of two different colours, for each of the possible pairs in turn. To illustrate, for red versus green, we trained the classifier on trials with all red and green shapes except one shape of each colour. We then tested the classifier on trials containing this left-out pair. This process was repeated until all matched shapes had been left out once (5-fold cross validation). This method ensured that the colour classifier always had to generalise to different object forms. We conducted this classification analysis for each of the six possible colour pairs (i.e., red-green, red-orange, red-yellow, green-orange, green-yellow, yellow-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

(e.g., yellow strawberry). Any differential response that depends on whether a colour is typical or atypical for an object (a congruency effect) requires binding the perceived shape and colour and comparing this input with a conceptual object representation activated from memory. To assess whether there is a congruency effect, we ran a decoding analysis to test for reliable differentiation of congruent and incongruent trials. We trained the classifier on all congruent and incongruent trials *except* for trials in which one pair of matched exemplars was shown (e.g., all instances of congruent and incongruent strawberries and congruent and incongruent bananas). To test the classifier, we only used the left-out exemplar pair. This process was then repeated such that each matched exemplar pair had been left out (used as test data) once. Leaving an exemplar pair out ensures that there are identical shapes and colours for both classes (congruent and incongruent) in both the training and the testing set, and that the stimuli of the test set have different shape characteristics than any of the training objects. That means the only distinguishing feature between the conditions is the conjunction of shape and colour features, which defines congruency. This allows us to compare directly whether (and at which timepoint) object-colour knowledge interacts with object representations.

Second, we examined whether the conjunction of object and colour influenced colour perception. It is likely that over the course of our lives we have learned statistical regularities regarding common shape-colour pairings. Perceiving a certain shape might thus lead to a stable colour representation early in the signal. For example, if we see a yellow banana, it is possible that the shape leads to a stable colour representation of yellow earlier than if we see a yellow strawberry. To assess this possibility, we trained the classifier to distinguish between the surface colours of the abstract shapes (i.e., red, orange, yellow, green, chance: 25%). We then tested how well the classifier could predict the colour of the congruent and the incongruent objects. Training the classifier on the same shapes across colour categories makes it unlikely that a certain shape-colour combination drives an effect. Instead, the only

distinguishing feature is colour. This analysis allows us to compare whether the typicality of colour-form combinations has an effect on colour processing.

Third, we tested whether the conjunction of object and colour had an effect on object decoding. If object-colour influences early perceptual processes, we might see a facilitation for decoding objects when they are coloured congruently or interference when the objects are coloured incongruently. We used the greyscale object trials to train the classifier to distinguish between all of the objects. The stimulus set contained two exemplars of each item (e.g., strawberry 1 and strawberry 2). We used different exemplars for the training and testing set to minimise the effects of low-level visual features. The classifier was trained on one exemplar of all of the greyscale trials. We then tested the classifier's performance on the congruent and incongruent object trials using the exemplars the classifier did not train on. We then swapped the exemplars used for training and testing set until every combination had been used in the testing set. Essentially, this classifier is trained to predict which object was presented to the participant (e.g., was it a strawberry or a frog?).

Statistical Tests. In all our analyses, we used random effects Monte-Carlo cluster statistic using Threshold Free Cluster Enhancement (TFCE, Smith & Nichols, 2009) as implemented in the CosmoMVPA toolbox to see whether the classifier could predict the decisions above chance. The TFCE statistic represents the support from neighbouring time points, thus allowing for detection of sharp peaks and sustained weaker effects over time. We used a permutation test, swapping labels of complete trials, and re-ran the decoding analysis on the data with the shuffled labels 100 times per participant to create subject-level null-distributions. We then used Monte-Carlo sampling to create a group-level null-distribution consisting of 10,000 shuffled label permutations for the time-resolved decoding, and 1000 for the time-generalisation analyses (to limit computation time). The null distributions were then transformed into TFCE statistics. To correct for multiple comparisons, the *maximum* TFCE

values across time in each of the null distributions was selected. We then transformed the true decoding values to TFCE statistics. To assess whether the true TFCE value at each timepoint is significantly above chance, we compared it to the 95th percentile of the corrected null distribution. Selecting the maximum TFCE value provides a conservative threshold for determining whether the observed decoding accuracy is above chance, corrected for multiple comparisons.

Results

We first present the behavioural data to confirm that our stimuli induce a congruency effect on object naming times. All incorrect responses and microphone errors were excluded from analysis. We then calculated the median reaction time for naming each stimulus. If a participant named a specific stimulus incorrectly across trials (e.g., incongruently coloured strawberry was always named incorrectly), we removed this stimulus completely to ensure that the reaction times in one condition were not skewed. For example, if it took longer to name one stimulus (e.g., “frog”) in comparison to the other stimuli and that stimulus was only ever named correctly in one of the conditions, this condition would overall have longer reaction times; hence we would exclude this stimulus from both congruent and incongruent conditions (on average this occurred in 5.4% of cases). At the group level, participants were faster to name the congruently coloured (702ms, 95% CI [663.8 740.2]) than incongruently coloured (750ms, 95% CI [698.5, 801.5]) objects ($t(17) = 4.06$, $p < .001$). This suggests that the objects we used here do indeed have associations with specific canonical colours, and we replicate the effect of colour congruency on recognition of these objects (Bannert & Bartels, 2013; Joseph, 1997; Lloyd-Jones et al., 2012; Naor-Raz et al., 2003; Tanaka & Presnell, 1999; Therriault et al., 2009).

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

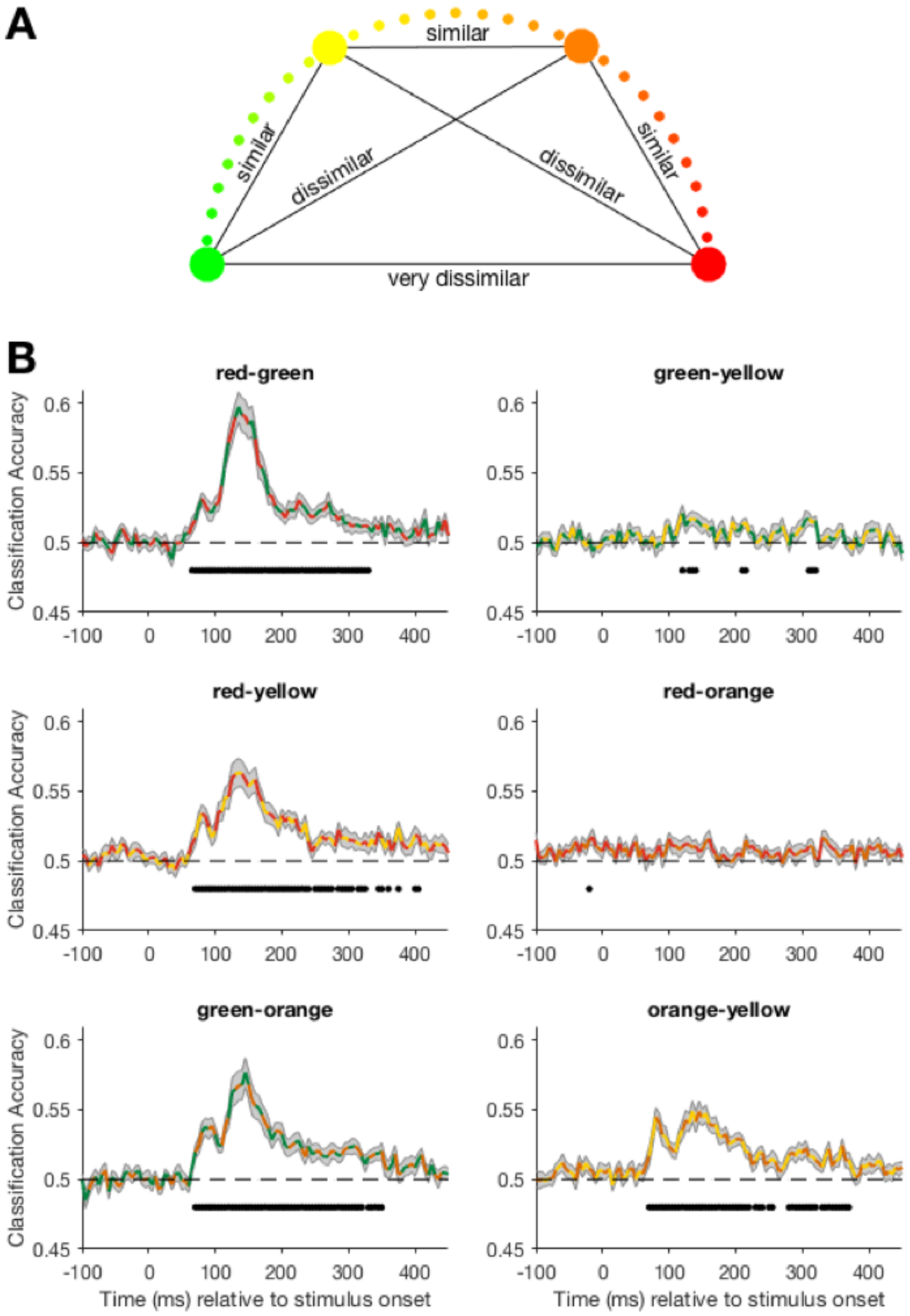

Figure 2. (A) shows the similarity between colour categories based on colour distance. (B) shows the results of the real colour decoding analysis for all colour pairs. The classifier was trained on the abstract shape trials to distinguish between two colours at a time. Each colour category contained 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.

The classification accuracy over time for the real colour decoding analysis for each colour pair is plotted above. Shading represents the standard error. Black dashed line represents chance level (50% - pairwise comparison). Black dots highlight significant timepoints for each pairwise comparison ($p<0.05$), corrected for multiple comparisons.

A controlled approach of testing whether there is any representational overlap between real and implied colours is training a classifier on real colour and testing on implied colour trials. Successful cross-generalisation implies that the brain representation of colour accessed via colour perception and implied colour activation share characteristics. To see whether this is the case we trained a classifier to distinguish between patterns evoked by pairs of our coloured abstract shapes, as in our first analysis. We then tested the classifier on distinguishing between the grey-scale objects that are associated with those colours. Consistent with previous work (Teichmann et al., 2018, *Preprint*), the representational overlap for real and implied colours dynamically evolves over time. We therefore ran this analysis as a time-generalisation analysis, training and testing the classifier at every timepoint combination (Carlson et al., 2011; King & Dehaene, 2014). We ran the analysis separately for each of the colour pairs as the real colour decoding results showed that the classifier cannot reliably distinguish all colour pairs (Figure 2). Across the time-time decoding matrices (Figure 3), we can see that the classifier can cross-generalise best between real and implied colours when the colours are most dissimilar (i.e., red and green). Accessing colour via real colour perception and implied colour activation occurred at the same time, around 150ms. For red versus green, there was additional significant decoding off the diagonal, which indicates a temporal difference in the instantiation of a similar pattern. Colour information evoked by real colours from ~150ms-450ms resembles colour information evoked by greyscale objects in a timewindow from ~150-170ms after stimulus onset. This indicates that colour information evoked by association is only briefly in the signal. There also is a reactivation of colour information for the red-green comparison at ~400ms after stimulus onset. For the red versus yellow and green versus orange contrast there is cross-generalisation in a timewindow around

~150ms after stimulus onset. In contrast, we did not observe successful cross-generalisation when training and testing on colours that are similar. This is not surprising given that we did not have a reliable model to distinguish between these real colours (i.e., red versus orange, Figure 2).

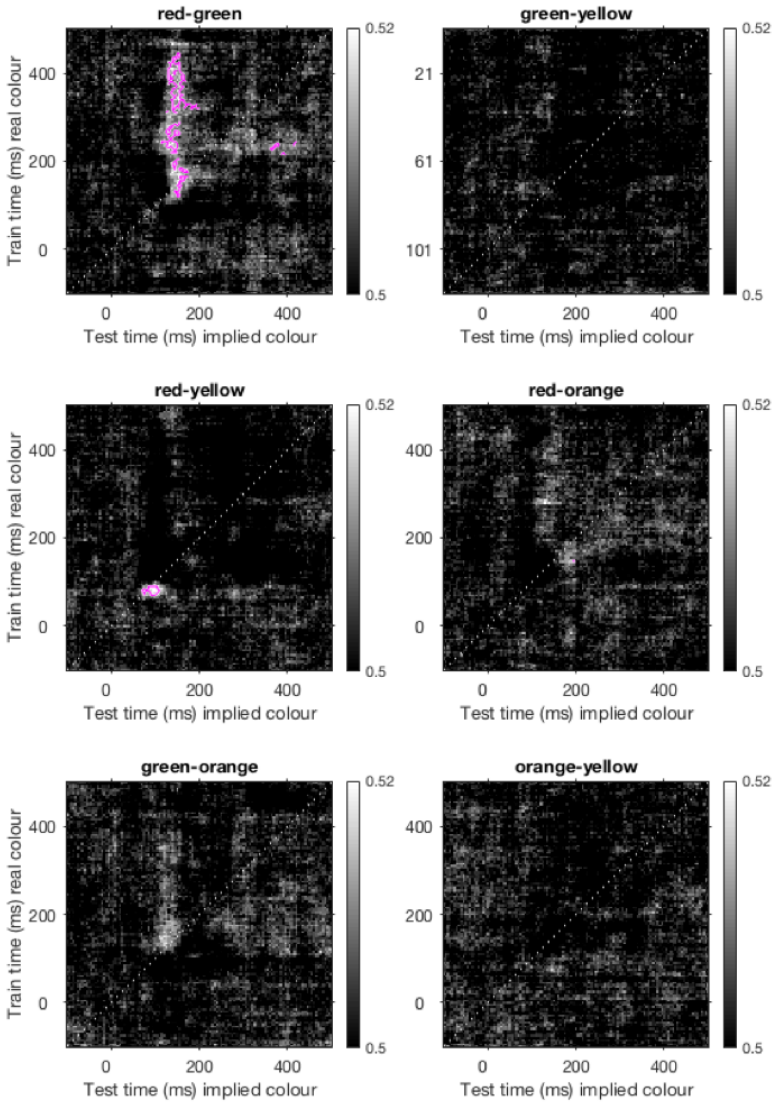

Figure 3. Time-generalisation for cross-decoding, training the classifier on real colour trials and testing on grey-scale object trials. The analysis was done separately for each pairwise colour comparison. The plots in show the decoding accuracies for every timepoint combination when training on real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

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.

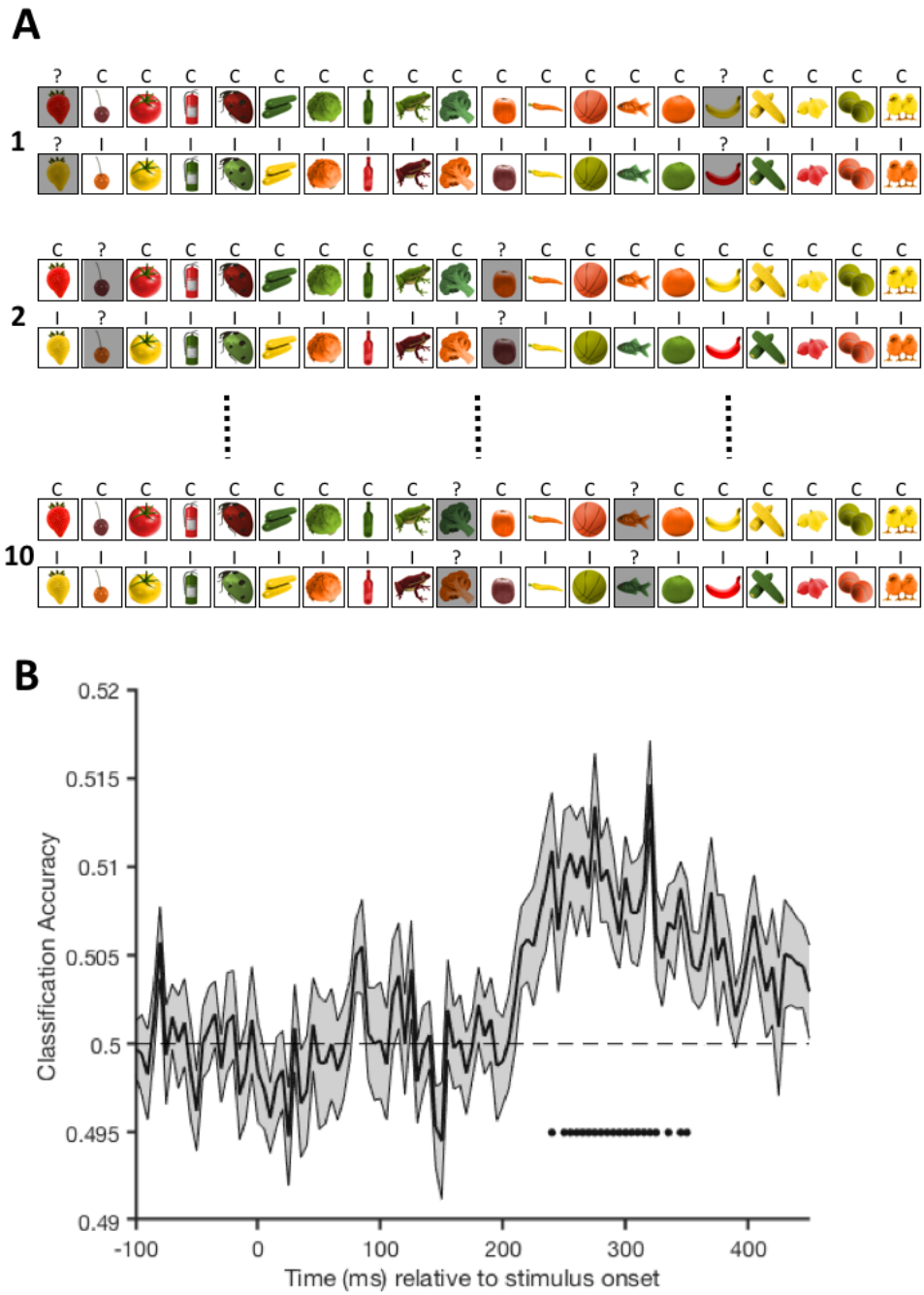

Figure 4. Cross-validation and results of the congruency analysis. We are here contrasting trials from the congruent and incongruent conditions. (A) shows the leave-one-matched-exemplar-out cross validation approach used for the congruency decoding analysis. The classifier was trained on all “clear” 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.

To assess whether the typicality of object-colour combinations influences colour perception, we trained a classifier to distinguish between the colours in the abstract shape condition and then tested it on the congruent and incongruent trials separately. The data show that colour can be successfully classified in a cluster stretching from 75 to 125ms for the congruent and in a cluster stretching from 75 to 185ms for the incongruent trials (Figure 5A). Looking at these results it seems like there is a qualitative difference between the colour information in the congruent and the incongruent trials. To assess how the signal in these two conditions evolved over time, we also looked at the time-generalisation matrices for these analyses (Figure 5B and 5C). Colour category was decodable form both conditions early on (~70ms) but the activation associated with colour seems to be sustained longer for the incongruent (Figure 5C) than for the congruent condition (Figure 5B). This suggests that colour signals are prolonged when object-colour combinations are atypical in comparison to when they are typical.

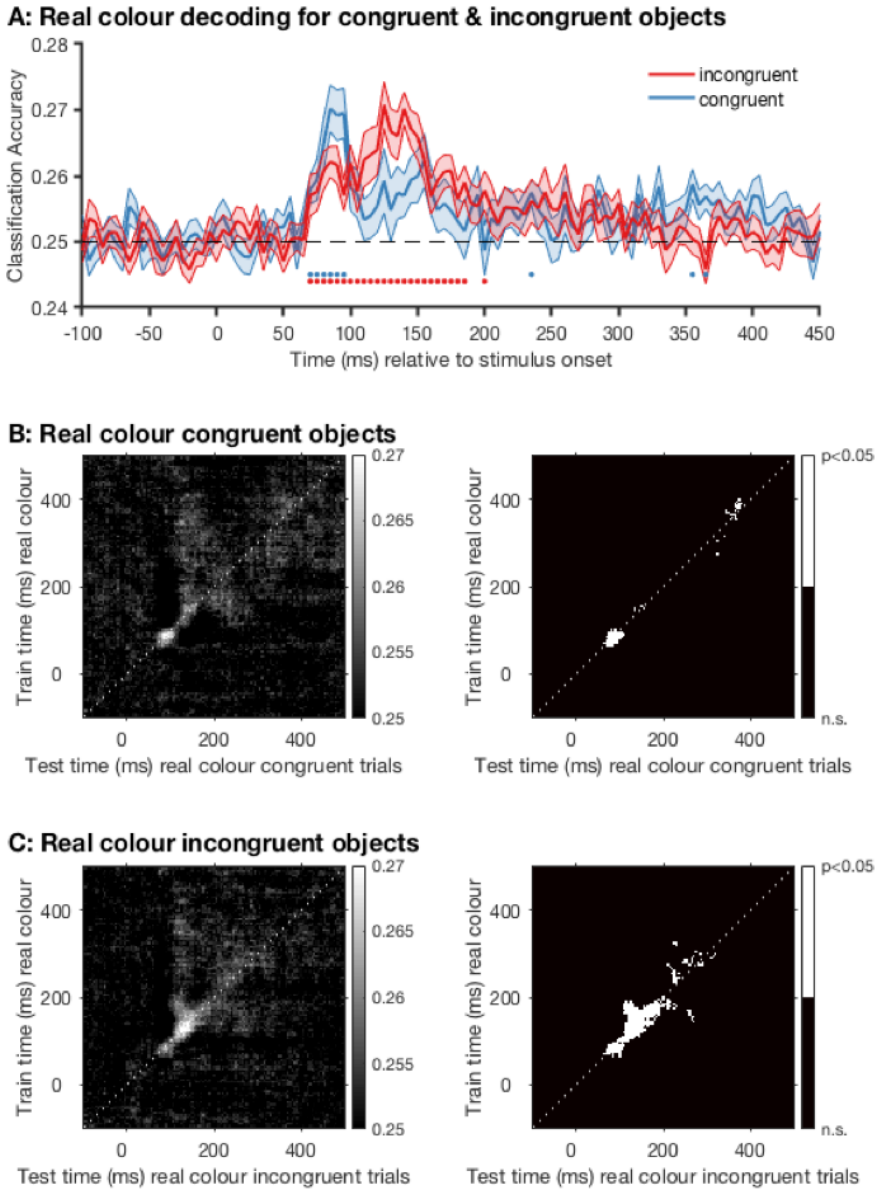

Figure 5. Results of the colour decoding analysis for the congruent and incongruent trials. Here, the classifier was trained to distinguish the colour of all abstract shape trials and tested on the congruent and incongruent trials separately. (A) shows the classification accuracy over time for this analysis.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

The goal of the third analysis was to examine whether shape representations are affected by colour congruency. We trained a classifier to distinguish between trials in which the participant saw one of the exemplars of each of the twenty objects in greyscale (e.g., greyscale strawberry 1, greyscale cherry 1…). We then tested at which timepoint the classifier could successfully cross-generalise to the other exemplar of that object in the congruent and incongruent condition separately. Note that although the exact images are unique, there are shared shape characteristics between exemplars (e.g., frog exemplars share some similar shape aspects despite being different postures). The results show that the classifier can generalise to the other exemplar in a cluster stretching from 80 to 450ms for the congruent test set and from 90 to 450ms for the incongruent test set (Figure 6A). The decoding performance over time for congruently coloured and incongruently coloured exemplars follows a highly similar pattern. These results show that we can decode the object category early on, suggesting that the classifier is driven by low-level visual features such as shape or texture. The timecourses for congruent and incongruent exemplar decoding are very similar, suggesting that colour might not affect the initial processing that contributes to object identification. To test whether the classifier makes the same mistakes when decoding from the congruent and incongruent trials, we looked at the confusion matrices averaged across timepoints where decoding was significant (Figure 6B). To assess the similarity of the confusion matrices over time, we correlated the average matrix across participants at each timepoint (Figure 6C). The high correlation between the matrices suggests that the object representations for the congruent and incongruent condition were similar. Thus, we have no evidence that shape representations are affected by colour congruency.

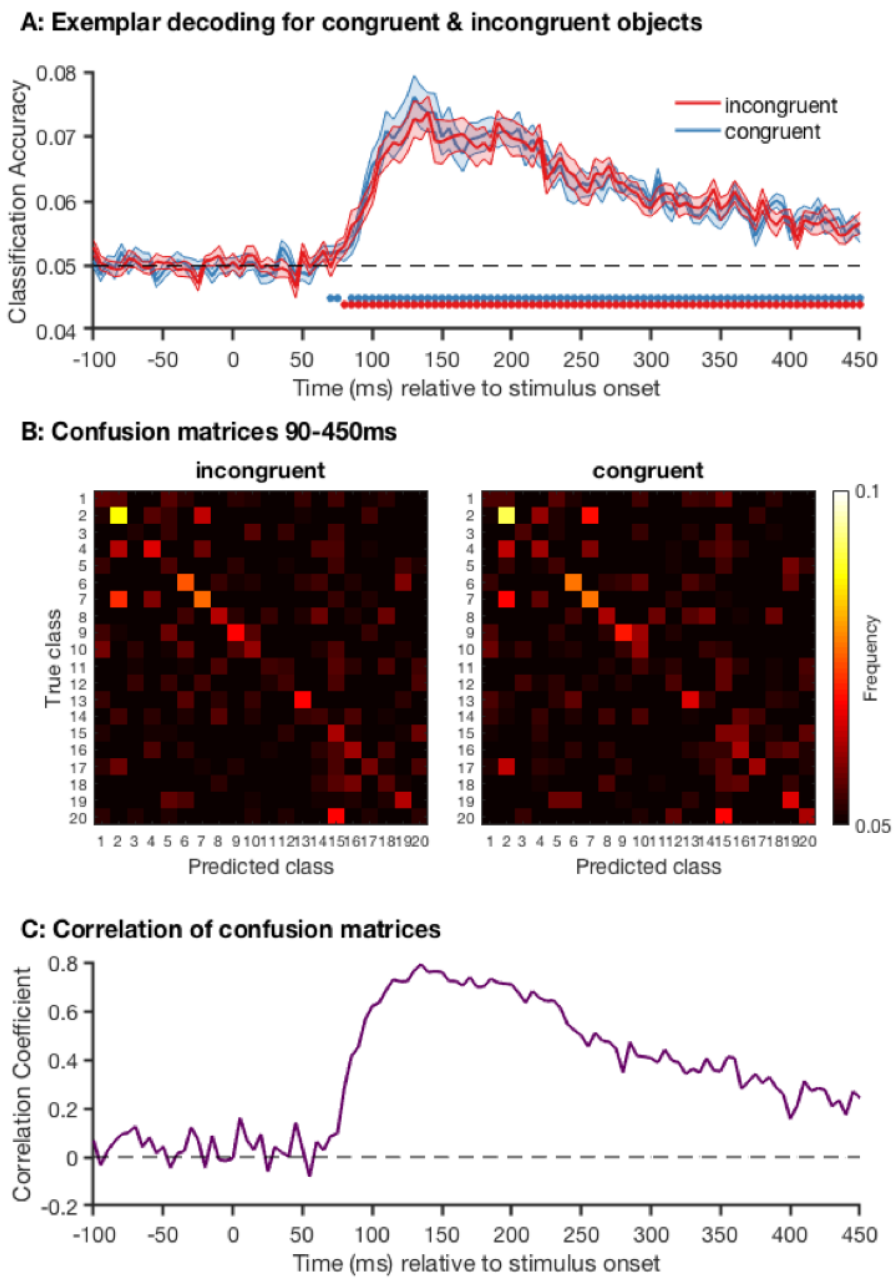

Figure 6. Results of the object exemplar decoding analysis. The classifier was trained on distinguishing between all object classes in the greyscale object condition. We used one exemplar of each class for the training and the other exemplar for testing the classifier. Testing was done for the congruent 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

activated along with other low-level features which are dominant earlier in the signal. Further work is needed to test this idea.

The timecourse of exemplar decoding we present is consistent with previous studies on object recognition. Here, we found that exemplar identity could be decoded at ~90ms (Figure 6A). Similar latencies have been found in other M/EEG decoding studies (Carlson et al., 2013; Cichy et al., 2014; Contini, Wardle, & Carlson, 2017; Grootswagers, Robinson, & Carlson, 2018; Isik, Meyers, Leibo, & Poggio, 2013) and single unit recordings (e.g., Hung, Kreiman, Poggio, & DiCarlo, 2005). Behavioural data, including the reaction times collected here in our participants, show that colour influences object identification speed (e.g., Bramão, Faísca, Petersson, & Reis, 2010). The neural data, however, did not show an effect of object colour on the classifier's performance when distinguishing the neural activation patterns evoked by different objects. For example, the brain activation patterns in response to a strawberry could be differentiated from patterns evoked by a lemon, regardless of the congruency of their colours. This suggests that colour and shape processing affect each other in an asymmetric way: colour representations are influenced by object shape but that shape representations are not influenced by colour. This findings is consistent with previous results (Proverbio et al., 2004) but might seem puzzling because colour congruency has been shown to have a strong effect on object naming (e.g., Chiou et al., 2014; Nagai & Yokosawa, 2003; Tanaka & Presnell, 1999). One possible interpretation of this finding is that the typicality between object and colour combination does not affect early stages of processing but that it has an effect on later stages of processing. For example, it is possible that the source of behavioural congruency effects is at the stage of response selection, which would not show up in these early neural signals. More evidence is needed for this interpretation, but the current data suggest that colour congruency does not have an impact on early stages of shape processing.

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.

Our data speak to the debate of whether specific object-features activated from memory share similarities with perceiving these object-features. Bannert and Bartels (2013) previously showed that there is an overlapping brain activation pattern in early visual cortex when colour is activated via colour perception and implied colour activation. This finding shows that a similar neural representation is activated via implied colour activation and real colour perception, even in the total absence of real colour in the stimulus. The data here are consistent with this finding but with regard to temporal dynamics rather than brain regions. In line with one of our previous MEG studies (Teichmann et al., 2018, *Preprint*), we showed that the colour representations for red and green accessed via perception and implied colour activation are similar enough to allow for cross-generalisation at ~150-200ms. The data suggest that colour representations accessed via real colour perception and implied colour activation shared similar patterns at the same time (~150-200ms) and that cross-decoding remained stable across a narrow testing time window (~150-450ms). For colour pairs that were more similar (e.g., red versus yellow), decoding was not as stable as for the red-green pair, however, a classifier trained on the brain activation patterns distinguishing between other colours such as red and yellow can still cross-generalise to patterns evoked by grey-scale objects that are associated with these colours. There were not as many timepoints in which cross-generalisation worked in comparison to the red-green distinction and the cross-generalisation is limited to the same time window (~160ms after stimulus onset) rather than being sustained (as it is for red vs green). This difference is partially accounted for by the strength of decoding of the real colour pairs in the first place: real colours that are more similar in colour space are also more similar in neural space and are therefore more difficult to decode. This points to a limitation in the sensitivity of our current methods, such that the subtle differences in patterns for similar colours are beyond our reach at this point. Another potential reason for unsuccessful decoding of similar implied colour is that object representations must 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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