

The biological bases of colour categorisation: from goldfish to the human brain

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Abstract

We review research on the neural correlates of colour categories, and categorical responses in preverbal infants and animals. Our aim was to address the question of the functional segregation of colour categories from colour perception and colour language, i.e. whether or not colour categorisation shares processing resources with language and perception. Together, the reviewed findings suggest that colour categorisation often involves automatic language processing, but it can also occur in the absence of language or colour naming, as suggested by research on brain-damaged patients, preverbal infants, and non-human animals. Furthermore, there is no compelling evidence coming from human neuroimaging and neuropsychological studies, or from animal studies, that categorisation is inherent to colour perception. Instead, colour categorisation might simply build upon the continuous perception of colour and may interact with perception through the direction of attention to colour differences that are relevant to categorisation. Altogether, the reviewed evidence does not seem to offer a straightforward account of the origin of lexical colour categories. We suggest that future research in all areas (1) requires methodological improvements, in particular in stimulus control, (2) should overcome the universalist-realist debate and go beyond a simple contrast between perception and language, and (3) should consider the link between object colours and colour categories to establish both evolutionary and developmental continuity between categorical responses in animals, infants and adult humans.

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1. Introduction

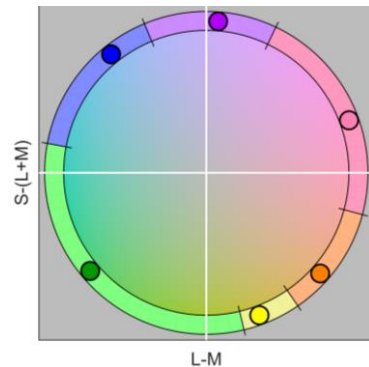
An evolutionary sequence marked the beginning of empirical research on colour categorisation. Colour categories are the ensembles of colours that we identify with a colour term, such as red, yellow, and brown. The categorization of colour through linguistic colour terms contrasts our ability to perceive colours continuously in terms of hue, saturation, and lightness. This contrast between perception and categorisation made colour a prime example to investigate the Sapir-Whorf hypothesis, that is the idea that language determines the concepts we use to understand and think about the world (Brown & Lenneberg, 1954). A seminal study (Berlin & Kay, 1969) compared colour naming in speakers of different languages. The authors found similarities across languages, and developed a universal scheme of colour term evolution. They suggested that languages evolve from a set of only two colour categories towards a full set of eleven categories along a fixed sequence that holds for all languages.

A debate developed between proponents of the Sapir-Whorf hypothesis (linguistic relativists) and proponents of the universal scheme (universalist): linguistic relativists insisted that colour categories are shaped by language and culture, while universalists claimed that colour categories originate from perceptual mechanisms that are innate and independent of language and culture. Colour terms are thus merely associated with those pre-existing categories during language acquisition (for review, see Kay & Regier, 2006; Witzel, 2018). This debate motivated a new research program, using different approaches to address the question about the origin of colour categories.

Across the years, cross-cultural studies showed evidence for both, significant variability of colour terms across cultures and languages (e.g. Berlin & Kay, 1969; Roberson, Davidoff, Davies, & Shapiro, 2005; Roberson & Hanley, 2007) and for universal, statistical patterns (or *motifs*) that transcend cultural and linguistic boundaries (e.g. Berlin & Kay, 1969; Gibson et al., 2017; Kay & Regier, 2003; Lindsey & Brown, 2006; Lindsey & Brown, 2009; Lindsey, Brown, Brainard, & Apicella, 2015; Regier, Kay, & Cook, 2005). At the same time, psychophysical research showed that colour categories cannot be explained by the sensory stages of colour processing in the retinogeniculate pathway (see box 1). As a result, the evolutionary scheme itself evolved and the newest version of the scheme allows for considerable cross-cultural variation (Kay, 2015). More details on cultural variants and on psychophysical studies about the relationship between categorization and perception may be found in recent reviews (Kay & Regier, 2006; Regier & Kay, 2009; Witzel, 2018; Witzel & Gegenfurtner, 2018b).

Box 1| Colour categorization and sensory stages of colour processing

Colour perception starts in the retina, where the photoreceptors - the S, M and L cones – differentially absorb wavelengths of light. This stage is referred to as the **first stage mechanisms** of colour perception. **Second stage mechanisms** constitute of the cone-opponent channels in the retinal ganglion cells and the lateral geniculate nucleus in the thalamus (reviewed in Gegenfurtner & Kiper, 2003; Conway *et al.*, 2010). The three kinds of cones are often called blue, green, and red, and the cone-opponent channels red-green and blue-yellow. Note that these labels are simplifications to facilitate communication: neither the peak sensitivities of the cones nor those of the cone-opponent channels align with the most typical red, yellow, green, and blue (cf. Figure box 1). **First and second stage mechanisms also do not coincide with the boundaries between most linguistic categories. The full set of eleven basic colour terms can neither all be mapped onto first nor onto second stage mechanisms** (fig 1 in Malkoc *et al.*, 2005; Wuerger *et al.*, 2005; fig 9 in Witzel & Gegenfurtner, 2013 ; Emery *et al.*, 2017; fig 2 in Witzel & Gegenfurtner, 2018a). **Exceptions are the green-blue and yellow-green boundaries**, which happen to



Colour categories and second-stage mechanisms. Colour categories from Witzel and Gegenfurtner (2013, cf. figure 9.a) are represented in DKL-space, a model of the second-stage mechanisms. X- and y-axis (in white) correspond to the L-M (“green-red”) and S-(L+M)-mechanism (“yellow-blue”), respectively. Coloured segments represent categories, black lines are category boundaries, and circles are category prototypes. Note that neither all category boundaries nor all prototypes are located at the poles of the axes.

be close to the cone-opponent channels when colours have the same lightness as the background. For this reason, any “category effects” obtained at those boundaries could possibly be explained by high sensitivity along the second stage mechanisms.

Apart from cross-cultural research and psychophysics, three fundamental approaches have been taken to single out the role of perception and language in colour categorisation. A developmental approach investigated colour categorization in infants who do not yet have language (Bornstein *et al.*, 1976). If infants showed signs of colour categorization, categorization should be considered to be independent of language. Following a similar logic, a second approach investigated categorization in non-human animals that do not possess language. These two approaches go beyond the cross-cultural and psychophysical work in that they allow establishing when colour categories emerge in the course of the ontogenetic development and the phylogenetic evolution, respectively. Third, a growing line of research investigates whether human colour categorization is due to neural processes that are related to either perception or language. This approach aims at unravelling how colour categorization is implemented in the human brain.

Box 2 | Stimulus control in colour categorisation research.

In most of the studies reviewed here, colour categories are measured indirectly. Experiments test for discontinuities along a continuous measure that can be attributed to colour categories (*category effects*). Such continuous measures are for example BOLD signals in fMRI, ERP components in EEG recordings, eye movements in infants, or the frequency of learned responses in animals (see main sections). For all these approaches, stimulus control is crucial (for review see Witzel, 2018; Witzel & Gegenfurtner, 2018b).

A first major issue is the control of differences between the colours in a stimulus set according to some reference metric. The physical reference are differences in wavelength. However, the responses of the photoreceptors (cone sensitivities) are not constant but change abruptly (non-linearly) across wavelengths (see e.g. Figure 2 in Gegenfurtner & Kiper 2003). Therefore, wavelengths cannot provide a reference for assessing category effects in colour perception because abrupt changes could simply be due to cone sensitivities rather than colour categories (see box 1). For this reason, category research has adopted a perceptual reference metric that controls stimulus differences so that they are perceptually uniform. In most cases, “perceptually uniform” meant that adjacent stimuli can be discriminated equally well. For this, differences in the Munsell system, CIELAB and CIELUV colour space have typically been used. Unfortunately, the available approaches are only very roughly approximate and fail to control for fine-grained colour differences (Kuehni, 2003; Hunt & Pointer, 2011; Fairchild, 2013). Spurious effects and methodological artefacts may still result from those sampling methods. In particular, such effects could be shown for colours around the green-blue boundary and may be explained by the role of the second-stage mechanisms in colour discrimination (cf. box 1; see e.g. Lindsey *et al.*, 2010; Witzel & Gegenfurtner, 2011; Brown *et al.*, 2011; Witzel & Gegenfurtner, 2013).

A second issue concerns perceptual salience. A colour is salient when it strongly contrasts with its background and “jumps out to the eye”. For example, on a grey background, salience is determined by the lightness and chroma of a colour. Salience is known to automatically (*exogenously*) attract attention and gaze. To avoid confounds when testing for category effects, salience must also be controlled in a stimulus set.

The third issue is adaptation. Single colours are always perceived relative to the temporal and spatial context, i.e. preceding stimulation and surround (e.g. Hansen *et al.*, 2007; Fairchild, 2013). A large part of adaptation is achieved within only 10ms, but full adaptation requires 20-30s (Rinner & Gegenfurtner, 2000). In paradigms that use computer screens with a black background, or changing backgrounds, the observer’s adaptation is not controlled and the stimulus colours are ill-defined (for a thorough discussion see Witzel & Gegenfurtner, 2011). When colours are presented as coloured surfaces (e.g. Munsell chips), the spectrum of the illumination is fundamental. Not only does the colour of the illumination control the state of adaptation; the spectra also affect differences between colours.

Over decades of research, these three approaches provided a huge range of diverse and divergent findings. Currently, no review is available with a synthesis of the state-of-the-art. One review concerns neural processing (Regier & Kay, 2009), but given the recent advances in the field it requires an update. To fill this gap, we review recent evidence on these three important approaches to colour categorisation. The first part presents the state-of-the-art on colour categories in the absence of language. It includes both research in infants and research in non-human animals, because those two approaches follow a similar logic and meet similar methodological challenges. The second part reviews studies on the neural substrate of colour categories. A synthesis at the end of each main section highlights the insights across all reviewed areas. In the fourth, concluding part we summarize the commonalities across these different areas of investigation and make suggestions for future research.

2. Colour categorisation without language

The investigation of colour categorization across species allows for examining evidence for categories in the absence of language. Colour has multiple functions in the animal kingdom (Cuthill *et*

al., 2017), and many of those functions could potentially be understood through the idea of categorisation. Evidence towards category effects in non-lexical animals would strongly support the claim that colour categorization appears at early stages of brain evolution and/or development and as such does not necessitate human-specific cognitive functions. In addition, studying young infants provides the unique opportunity to investigate colour categorisation in human observers that do not yet possess language. Evidence for colour categories in preverbal infants supports the idea that colour categorisation does not depend on language.

However, research on non-linguistic colour categories faces important methodological challenges. In adult humans, the number and range of colour categories can be directly assessed with the use of verbal labels. In individuals without language evidence for colour categorization cannot be accessed directly - we cannot ask animals or infants about colour categories. Colour categories are thus inferred from indirect category probing measures (discrimination, generalisation, novelty preference etc.) in comparison to a perceptual reference metric that defines the stimuli (see box 2).

In particular, the sensitivities of human cones and of the photoreceptors in many species vary as a function of wavelength; this results in abrupt changes in perceived colour differences across the spectrum (for an example in the bumble bee, see Figure 2.c in Gumbert, 2000). It is likely that the nonlinear sensitivity of the photoreceptors is an adaptation to functional requirements and ecological constraints (Osorio & Vorobyev, 2008; Cuthill *et al.*, 2017). According to some definitions of categorical perception, this non-linear relationship between receptor sensitivity and physical measures might be taken as a kind of categorical perception (reviewed in Witzel, 2018). However, the sensitivities of the photoreceptors do not predict linguistic colour categorisation in humans (boxes 1 and 2). For this reason, we do not consider the non-linear responses due to the sensitivities of photoreceptors to be an interesting case of categorisation for this review.

In the following part, we will look for traces of colour categories across different examples of non-lexical cognition. We will go through evidence for categorical colour responses in animals, for the capacities of learning colour names in chimpanzees under language training, for the neural substrates of colour categories in the primate brain, and finally, for categorical responses in human infants before language acquisition.

2.1. Categorical responses in non-human species

In most of the studies on categorical responses in animals, animals are trained through operant conditioning to act upon colours in order to obtain a reward. Then, it is examined how responses associated to a trained colour are generalised to other, novel colours (Shepard 1987). The rationale behind the generalisation approach is to control colour similarities between different colour pairs of

conditioned and novel colours, and to test how responses generalise across colour pairs that supposedly have the same colour difference (see box 2). If a colour pair does not yield generalisation of responses even though other colour pairs with the same colour differences do, these responses are taken as evidence for a category boundary between the colours in the respective stimulus pair. In the simplest version of this method, the association between a specific colour and a response behaviour is learned in a training phase. In a test phase, the transfer of the response behaviour to another colour is tested. In a more elaborate approach, the animal is not trained to respond to a specific colour, but to indicate whether a colour is the same as a test colour. In this *matching-to-sample* task, the animal is presented a test colour and has to choose which of two comparison colours corresponds to the test colour. During the training, the animal is rewarded when it correctly indicates the comparison colour that is the same as the test colour. During a test phase, none of the comparison colours is the same as the test, and the question arises of whether the animal would pick more often one than the other colour, even when they have the same difference to the test colour. Note that in the simple generalisation task the animal is trained to respond to a particular colour while in the matching-to-sample task the animal is trained to respond to the relationship between two colour probes.

Pioneering studies showed seemingly categorical responses in different species such as pigeons (*Columba livia domestica*, Wright & Cumming, 1971), or goldfish (*Carassius auratus*, Goldman *et al.*, 1991). However, due to the use of wavelengths as reference metric (box 2) it is uncertain to what extent these responses reflect colour categories or higher sensitivities to some wavelength differences due to cone sensitivities (Vorobyev *et al.*, 1998; Jacobs, 2018).

A study in macaque monkeys (*Macaca fascicularis*) found reduced generalisation to colours at the blue-green, green-yellow and yellow-red boundary of human observers (Sandell *et al.*, 1979). These results have been replicated in electrophysiological and lesion research on the macaque visual cortex (Walsh *et al.*, 1992; Yoshioka *et al.*, 1996). However, the areas between categories span large ranges of hues (Munsell 2.5BG6/8 to 2.5B6/8; 2.5Y7/10 to 5GY7/10; and 5R6/10 to 10YR6/10), which include not only human category boundaries, but also category prototypes (red, orange, yellow) and even complete categories (orange; e.g. Figure 8 in Olkkonen *et al.*, 2010; for other examples see Berlin & Kay, 1969; Sturges & Whitfield, 1995). In addition, the Munsell chips used in the study (Sandell *et al.*, 1979) were controlled in terms of physical distances based on dominant wavelength. Hence, the observed categorical responses in macaques are confounded with sensory mechanisms of colour perception (box 2).

When using a perceptual rather than a physical reference metric, evidence on categorical responses to colour in non-human species is mixed. On the one hand, several studies showed

categorical responses to colours when using discrimination thresholds as a perceptual reference for controlling colour differences. Goldfish and poultry chick responses to colours followed a categorical pattern (Jones *et al.*, 2001; Poralla & Neumeyer, 2006). Chicks trained to respond to two colours, generalised their responses to colours that spanned training colours, but did not extrapolate to colours beyond the trained boundaries (Jones *et al.*, 2001). More importantly, in both goldfish and chicks, there were regions in the continuum of colours across which the animals have never generalized. This observation could be taken as evidence for category boundaries. In addition, goldfish also showed preferences for some spectral lights (i.e. wavelengths) over others (see fig. 6 in Poralla & Neumeyer, 2006). These preferences could not be explained by discrimination thresholds and peak sensitivities of the goldfish cones, and might be considered as category prototypes.

On the other hand, baboons (*Papio papio*) did not show categorical responses to colours probed from the Munsell system, neither in generalisation nor matching-to-sample tasks (Fagot *et al.*, 2006; Davidoff & Fagot, 2010). However, it cannot be guaranteed that colour discrimination for those stimuli is comparable between baboons and humans since baboon responses (58%) were overall much lower than those of humans (80%; cf. Davidoff and Fagot, (2010).

The above studies used “decontextualized colours”, such as coloured patches or lights, that are meaningless and uninteresting to most animals. For that reason, animals required extensive training in order to elicit systematic behaviour towards those colours. In contrast, two recent studies (Hanley *et al.*, 2017; Caves *et al.*, 2018) investigated colours that are ecologically relevant. By ecologically relevant, we mean colours of objects that are important for the animal’s behaviour in their natural environment because they are desirable (food, water, mates), or important to avoid (predators).

The first of these studies (Hanley *et al.*, 2017) examined the decision criterion according to which blackbirds (*Turdus merula*) and American robins (*T. migratorius*) rejected foreign eggs put in their nests by avian brood parasites, such as cuckoos. Rejection depends on the eggs’ colour. The researchers placed artificially coloured eggs in birds’ nests and recorded how often eggs were rejected by the hosts. They manipulated egg coloration along two continuous colour dimensions, while controlling the similarity to the birds’ own eggs through discrimination thresholds. If rejection only depends on colour similarity, it should occur in the same way in all directions of the continuous dimensions (grey curve in fig 1.A). However, rejection almost exclusively occurred when colour differences straddled a sharp boundary between the colour of their own eggs and the brown colour of the eggs of brood parasites (brown bar in fig 1.A). In the second study (Caves *et al.*, 2018) female zebra finches (*Taeniopygia guttata*) were trained to respond to colour pairs varying continuously from orange to red. Female zebra finches have a mating preference for males with red vs. orange beaks. Accordingly, they did not respond similarly across the whole range of orange-red colours, even though

colour differences were roughly equal according to estimated discrimination thresholds. Instead, they showed particularly high responses when colours straddle a specific point on the continuum, suggesting that this point constitutes a category boundary.

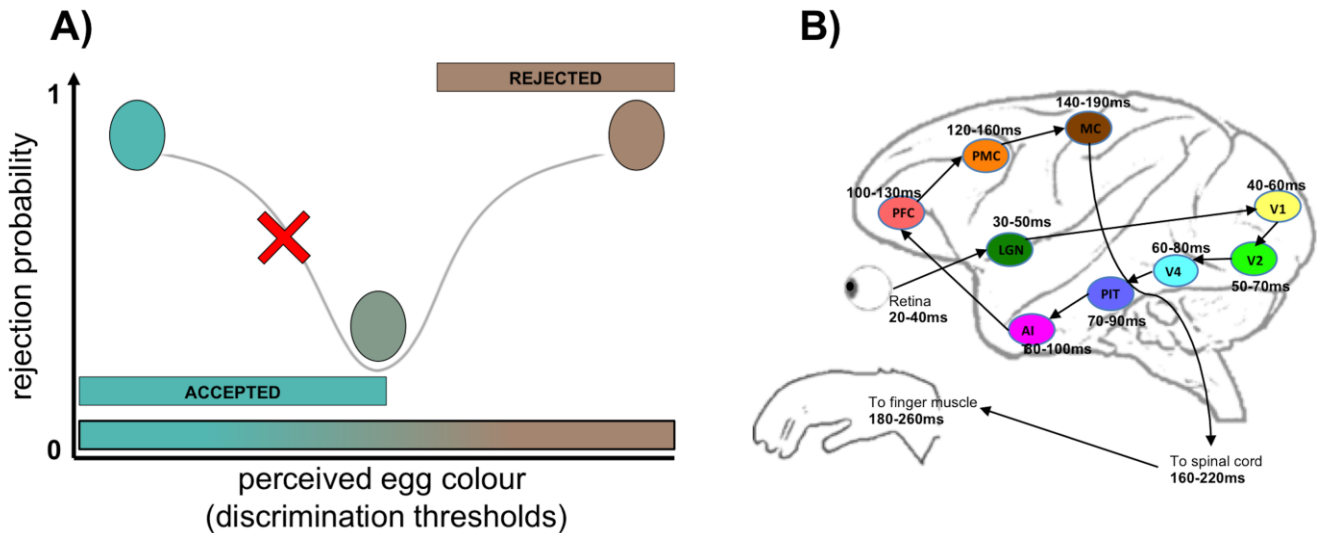


Figure 1. (A) Robins' probability of rejecting a coloured foreign egg relative to the position of hosts' own egg colour along the blue-green to brown colour gradient. The birds rejected brown eggs only. No rejection occurred in the blue-green direction (red X). Adapted from: Hanley *et al.*, 2017. (B) The schematic drawing of the hierarchy and timing of visual processing in the macaque (adapted from: Thorpe & Fabre-Thorpe, 2001).

It is surprising that evidence for categorical responses was found in goldfish and birds, but not in primates. There are substantial differences between goldfish, bird and human colour vision (Kitschmann & Neumeyer, 2005; Osorio & Vorobyev, 2008), while primate colour vision shares close resemblance with humans (Bowmaker *et al.*, 1991). Moreover, baboons and other primates can succeed in categorization tasks (Bovet & Vauclair, 2001; Freedman *et al.*, 2001; Fagot & Maugard, 2013) and seem to have visual categories similar to humans, such as categories for animals, trees, and faces (Sigala *et al.*, 2002; Fabre-Thorpe, 2003; Fize *et al.*, 2011), processed along a neural hierarchy similar to the one known from humans (cf. Figure 1B). Why would their categorisation abilities exclude the colour domain?

One problem with the primate studies might be the choice of reference metric. Munsell chips might not be optimal to control colour discrimination in baboons. They only roughly approximate discriminable differences in humans (see box 2). For baboons this approximation may be even worse. Although low-level mechanisms might be comparable between human and primates to some extent (Bowmaker *et al.*, 1991; Lindbloom-Brown *et al.*, 2014), colour discrimination is also shaped by cortical processing (Krauskopf & Gegenfurtner, 1992; Witzel & Gegenfurtner, 2013), about which

little is known in humans and even less so in baboons (see Colour categories in the human brain, and Gegenfurtner & Kiper, 2003; Conway *et al.*, 2010; Conway, 2018 for review). Hence, the assumption that small colour-differences designed for humans should be equally discriminable by the baboons might be wrong. In contrast, the studies on goldfish and birds used discrimination thresholds that are specific to their species.

Another important difference across studies is the ecological relevance of the colours used as stimuli. The two studies (Hanley *et al.*, 2017; Caves *et al.*, 2018) that used ecologically relevant colours were successful in showing categorical responses. This makes us wonder how important ecological relevance is for animal categorisation.

2.2. Colour term learning in chimpanzees

Another line of research on colour categorization in primates relies on the attempt to demonstrate human-like colour categories in language-trained chimpanzees. In this approach, apes are trained to associate lexigrams (i.e. symbols corresponding to objects or ideas) to the prototype colours of the lexical colour categories. Then, chimpanzees are presented with colour patches they have not seen during training and are prompted to choose one of the learned lexigrams. If chimpanzees generalise the lexigram associations across colours similar to human categories, this is taken as evidence for the existence of colour categorization in this species.

After massive training, chimpanzees generalised lexigram-associations according to human-like categories (Essock, 1977; Matsuzawa, 1984). Chimpanzees consistently chose lexigrams across hues, regardless of changes in brightness or saturation (Essock, 1977). When having trouble with hues at category boundaries, only two lexigrams competed as a response, which corresponded to adjacent hue categories (Essock, 1977; Matsuzawa, 1984). Chimpanzees' generalisation was similar to human categories and the category prototypes of the basic colour names of various languages were almost always included in the colour categories of the chimpanzees (Matsuzawa, 1984).

However, language-like learning is limited in apes (Gardner & Gardner, 1969; Patterson, 1978; Savage-Rumbaugh, 1987). Once learned, language-like skills are used to intentionally communicate with human caretakers (Pika, 2012), but seems to have little or no value in communication with conspecifics (Gardner & Gardner, 1969; Savage-Rumbaugh *et al.*, 1978). The low ecological relevance of lexigrams for chimpanzees requires an extensive amount of training. It is thus unclear to what extent the colour categories reported in the above studies reflect a stage of chimpanzee's colour processing, or a spurious manifestation of long-lasting training. Answering this question would require measuring categorical colour responses in lexigram-naïve apes.

If chimpanzees have stable, human-like colour categories, they do not need to learn associations between lexigrams and single colours through intensive training. Instead, they should generalize responses to category prototypes to other colours of the respective categories without large-scale learning. This has been tested with a generalization paradigm (similar to the logic of studies with goldfish, birds and macaques), which compared a “lexigram-expert” chimpanzee that had had long-term lexigram training, with an “lexigram-naïve” chimpanzee with little such training (Matsuno *et al.*, 2004). Although both chimpanzees had almost perfect responses to category prototypes after a training phase, the lexigram-naïve chimpanzee showed substantially less generalisation of responses across colours. This observation suggests that, unless massively trained, chimpanzees do not present stable, human-like colour categories. The study raises an interesting question of whether generalisation in apes depends on the amount of training or on a sensitive period, similar to the one known from human language development.

In sum, these studies show high amounts of generalisation across colours after massive training. However, they do not allow for concluding that apes have non-lexical colour categories.

2.3. Colour categories in the primate brain

The studies on the neural basis of colour categories in primates were motivated by two main reasons. First, colour vision in both species seems to be guided by roughly similar subcortical and primary cortical mechanisms, thus enabling translation of the results to humans (see Conway *et al.*, 2010 for review; Bohon *et al.*, 2016). Second, studies on non-human primates allow for the use of more invasive techniques, such as experimental lesioning or intracranial recordings, that grant more precise measurement of brain activity and allows for causal inferences.

Several pioneering studies showed signs of categorical processing in primates, both at the behavioural and at the neural level (Walsh *et al.*, 1992; Yoshioka *et al.*, 1996). However, the use of wavelengths as perceptual reference metric in these studies makes it impossible to disentangle categorical responses from non-linearities in colour perception (that are uninformative about categories; see box 2 and the subsection on Categorical responses in non-human species). A more recent study attempted to demonstrate categorical coding in the macaque inferior temporal cortex (IT, Stoughton & Conway, 2008, for the schema of anatomical location see fig 1B); but results were inconclusive due to insufficient stimulus control (Mollon, 2009). Instead, a recent study (Bohon *et al.*, 2016) found that colour representation in the monkey’s inferior temporal cortex is uniformly distributed across the perceptual colour space, and shows no specific preferences for human-like categories.

At the same time, one study showed that the responses of macaque (*macaca fuscata*) IT can be categorical, but the response mode strongly depends on task demands (Koida & Komatsu, 2007). In a categorisation task, monkeys were trained to respond categorically to colours. In single cell recordings, their IT neurons responded more strongly and more categorically in the categorisation task as compared to a colour discrimination task. So, IT can respond categorically as well as non-categorically. This depends on task demands, which might be mediated through top-down connections from prefrontal cortex.

2.4. Infant colour categories

A major approach to probe the presence of categorisation in infants involves category effects on *novelty preferences*. This paradigm is based on the fact that infants tend to look at new stimuli and to look away from stimuli they have been prolongedly exposed to (Fantz, 1964; Fagan, 1970; reviewed in: Aslin, 2007). When the infant looks away from the stimulus, this is taken as a sign that the child is familiar with the stimulus. When presenting a novel stimulus after familiarisation with another stimulus, the infant will look at the novel stimulus. This response to novel stimuli, or novelty preference, can be used to identify when a difference between a familiar colour and a novel colour is large enough to produce a novelty preference. A category effect on novelty preference implies that novelty preferences occur when familiar and novel colours belong to different categories, but do not occur, or are weaker, when they belong to the same category. This can be tested by simply comparing the looking times towards the novel colours between across- and within-category novel colours (e.g. Bornstein *et al.*, 1976). In a more elaborate version, the *paired-comparison novelty preference paradigm*, after the familiarisation phase, the novel colour is shown side by side with the familiar colour. It is tested whether the infant looks significantly longer at the novel than at the familiar colour (e.g. Catherwood *et al.*, 1990). Table 1 provides an overview of studies on infant categories.

Category effects in 4-5 months old infants have originally been shown with the simple novelty preference paradigm and with monochromatic stimuli with equal wavelength differences (Bornstein *et al.*, 1976). Then, evidence for category effects has also been provided with the paired comparison novelty preference paradigm and Munsell chips with equal distances in the Munsell system (Catherwood *et al.*, 1990; Franklin & Davies, 2004; Skelton *et al.*, 2017). With the exception of Catherwood *et al.* (1990), these studies found no significant novelty preferences for colours within a category, no matter how different they were. This suggested that novelty preferences are not only enhanced when colours belong to different categories, but they are completely categorical.

Other paradigms have also been used to reveal category effects. In a colour detection task, a coloured disk (*target*) is presented on a coloured background. If visible, the infant will look at the target. The time the infants take to fixate the target is measured. Category effects have been shown with this paradigm: latencies were shorter when target and background colours belonged to different categories than when they belonged to the same category (Franklin *et al.*, 2005; Franklin *et al.*, 2008a; Ozturk *et al.*, 2013).

Another approach aims at testing category effects on pop-out, i.e. the detection of a different colour among an ensemble of stimuli with the same colour (Gerhardstein *et al.*, 1999). The authors trained infants to give a motor response to a particular colour, and tested whether a new colour presented among the trained colours would interrupt the motor response. They found that the motor response depended on the differences between the colours, but not on category membership.

Categorical effects in infants have also been investigated at the neural level. In an oddball task performed in EEG, the oddball colour that crossed a category boundary was associated with greater amplitude of event related potentials Nc and *negative slow wave*, reflecting attentional load and novelty effect, respectively (Clifford *et al.*, 2009). Functional near infra-red spectroscopy (fNIRS) showed that in infants (and in adults), the sensitivity to categorical differences between colours occurs in bilateral occipito-temporal areas (Yang *et al.*, 2016). These regions are known to be associated with higher-level perception and perceptual categories.

In some of those studies (cf. Table 1), the control of colours might not fully disentangle genuine category effects from spurious effects due to the colour sampling method (e.g. wavelengths in Bornstein *et al.*, 1976; green/blue boundary in Franklin *et al.*, 2005; Franklin *et al.*, 2008a; Clifford *et al.*, 2009; Ozturk *et al.*, 2013; Yang *et al.*, 2016). See also boxes 1 and 2. or non-standard illumination (Catherwood *et al.*, 1990; Gerhardstein *et al.*, 1999; see discussion in Franklin & Davies, 2004).¹ In addition, the colour detection task does not sufficiently control for the state of adaptation (Franklin *et al.*, 2005; Franklin *et al.*, 2008a; Clifford *et al.*, 2009; Ozturk *et al.*, 2013). See also boxes 1 and 2.

Nevertheless, there is convincing evidence. Franklin & Davies (2004) tested category effects at several category boundaries with Munsell chips under controlled lighting and adaptation. It is unlikely that potential failures in stimulus control occur by accident at several category boundaries. The study of Skelton *et al.* (2017) is by far the most thorough study on infant colour categories, involving a huge sample of overall 179 infants and 14 different colours. Although this study used

¹ Some of the colour samples used in these studies (Franklin *et al.*, 2008; blue-purple set of Ozturk *et al.*, 2013) seem to be biased towards spurious category effects when calculating the differences between the colours in CIELUV and CIELAB: Colour differences tend to be larger for differences of stimuli between than within categories (e.g. Clifford *et al.* 2009; blue-purple set in Ozturk *et al.*, 2013).

maximally saturated Munsell chips that do not control for salience and colour differences, the results were unrelated to the variation of saturation and colour differences. Overall, three studies did not find significant novelty preferences when increasing colour differences for colours within categories, implying that the variation of colour differences is irrelevant for the observed category effects (Bornstein *et al.*, 1976; Franklin & Davies, 2004; Skelton *et al.*, 2017). A potential problem with this approach is that it relies on the absence of significant effects to prove the categorical character of novelty preferences. However, this criticism is weakened by the observation that the infant categories found across the three studies seem to be similar, and are hence replicable with different colour samples.

The most recent study of Skelton *et al.* (2017) raised important questions about the nature and origin of infant colour categories. We reproduce Skelton *et al.*'s (2017) results in Figure 2. For this purpose, we prefer using DKL-space over the Macleod-Boynton space used by Skelton *et al.* (2017), because DKL-space was precisely developed to model second-stage, rather than cone-isolating mechanisms (cf. box 1). Since colours are darker than the background, results differ across the two spaces (stretched along second diagonal and slightly shifted with respect to background grey), but the main observations hold.

First, previous studies had assumed that infant categories correspond to the lexical colour categories of adults, and they had chosen their stimuli and tested hypothesis accordingly (see in particular Franklin & Davies, 2004). Skelton *et al.* (2017) showed that categories of English infants do not fully correspond to the lexical categories of English adults (see Figure 2.b; see also figure 5 in Lindsey & Brown, 2014; Figure 1 in Skelton *et al.*, 2017). Instead, Skelton *et al.* (2017) found similarities between infant categories and cross-cultural patterns of adult colour categorisation in non-industrialised cultures, such as the category centroids across cultures (as in Figure 4 of Kay & Regier, 2003). This raises the question of why infant categorical responses bear similarities to categorical patterns of languages other than their own.

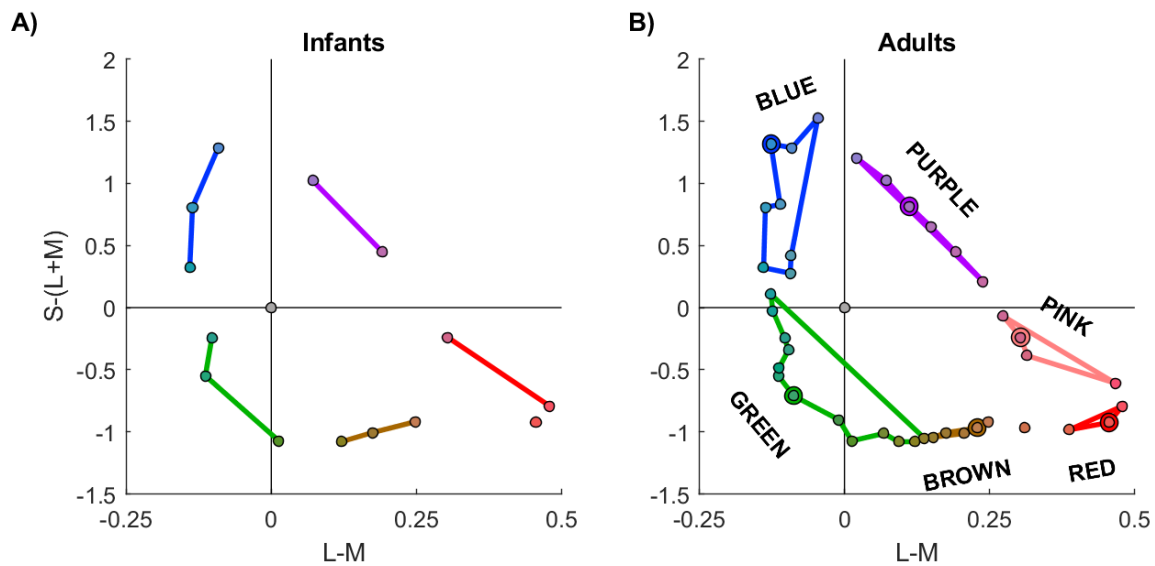


Figure 2. Infant and adult colour categories. Panel a represents categorical responses in infants from Skelton et al. (2017) in DKL-space; panel b indicates membership of colours to linguistic colour categories in English adults as measured by Witzel et al., (2013). The x-axis represents the L-M cone-opponent channel (“green-red”), the y-axis the (L+M)-S cone-opponent channel (“blue-yellow”). Each symbol corresponds to a Munsell chip and is coloured accordingly. Category prototypes are highlighted by a coloured border. The grey disk corresponds to the neutral background. Lines connect chips within each category. Cone sensitivities (Stockman & Sharpe, 2000), illuminant (D65), grey background (Munsell N5), and spectra (Joensuu Color Group database) are the same as in Skelton et al. (2017). DKL-space is calculated following Brainard (1996) with L and M weighted according to the luminosity efficiency function. Note that the distribution of colour categories in cone-opponent space differs for these dark colours from the distribution known for isoluminant colours (cf. box 1).

Second, Skelton et al. (2017; see their Figure 2) observed that infant category boundaries coincide with or are close to the cone-opponent dimensions that result from the subcortical second-stage mechanisms (Fig 2B). This feature of infant categories is in stark contrast to the fact that adult colour categories do not align with those sensory mechanisms. Although Figure 2B indicates that, at the lightness level of the colours used by Skelton *et al.* (2017), adult blue-purple and purple-pink boundaries coincide with the cone-opponent dimensions, this is not the case for other lightness levels, as shown by numerous studies (cf. box 1; Fig. 2 in Bosten & Lawrance-Owen, 2014; figure 2 in Emery *et al.*, 2017; Figure 4 in Webster *et al.*, 2000; Witzel & Gegenfurtner, 2013; 2015). Second-stage mechanisms are known to provide the basic dimensions for low-level colour processing, such as the sensitivity to colour (Krauskopf & Gegenfurtner, 1992; Hansen *et al.*, 2008; Giesel *et al.*, 2009; Witzel & Gegenfurtner, 2013). These cone-opponent dimensions do not represent high-level colour processing, including supra-threshold colour discrimination (e.g. Wuerger *et al.*, 1995), subjective colour appearance (Abramov & Gordon, 1994; Fig. 2 in Bosten & Lawrance-Owen, 2014; Krauskopf *et al.*, 1982; De Valois *et al.*, 1997; Malkoc *et al.*, 2005; Wuerger *et al.*, 2005; Witzel & Gegenfurtner, 2018a) and colour categories (for reviews see: Witzel, 2018; Witzel & Gegenfurtner, 2018b). In

addition, a relationship has been found between cone-opponent mechanisms and simple preferential looking in infants, that is without any familiarization as in the novelty preference paradigm (Franklin *et al.*, 2010; Brown & Lindsey, 2013). These observations in infants can be explained by the importance of second-stage mechanisms for discriminability and salience. However, categorical novelty preferences seem not to be related to the sensitivity to colour. Skelton *et al.* (2017) showed that infants responded to within-category colours when shown as background and target in the colour detection task, even though the same colours did not yield significant novelty preferences. The aforementioned caveats about this task (problem of adaptation) notwithstanding, these observations suggest a dissociation between novelty preferences and the sensitivity to colour. This makes us wonder how infant categories can be related to second-stage mechanisms, if they are unrelated to the functions (such as sensitivity to colour) that are typically attributed to the second-stage mechanisms.

To answer these questions, Skelton *et al.* (2017) speculated that human colour categories are determined by innate second-stage mechanisms and are then changed through culture during development. This idea assumes that infant categorical responses are equivalent to adult categories. However, a direct comparison between infant responses and adult categories is complicated by the fact that the measurements with infants require colour samples with much larger colour differences than comparable measurements with adults (cf. fig 2). As a result, the gap between infant categories may include an adult category boundary (e.g. red-orange) and prototype (typical red), and two different adult boundaries (e.g. red-orange, orange-brown). The comparison is further complicated by the fact that the relationships between infant categories, cone-opponent dimensions and adult categories are only partial and approximate. Not all infant categories align with those mechanisms (Figure 2A and Figure 2 in Skelton *et al.*, 2017), and not all adult category boundaries differ from the poles of the categories (Figure 2B). Further experiments are needed, that are designed to specifically test the relationship between infant categories and second-stage mechanisms.

Since it is uncertain to what extent infant categorical responses and adult categories overlap, the theoretical link between infant novelty responses and adult categories becomes crucial. Here, the biggest challenge is the interpretation of infant responses, even in the elaborate paired-comparison novelty preference paradigm (Aslin, 2007). Clearly, a response to a novel colour shows that infants can see the difference between familiar and novel colours. It also shows that infants remember the familiar colour, because novelty preferences require visual memory of the familiarised stimulus to allow a response to a novel stimulus. However, novelty preferences may be affected by still other factors. It is possible that infants' gaze reflects an exogenous allocation of attention. New stimuli are salient because they indicate a change, and this might automatically attract the infants' attention. As still another factor, infant looking behaviour might also be influenced by pleasantness, that is by what

the infant likes to look at. Infants might thus direct their gaze towards novel colours because they like seeing novel colours, and get bored by repetitions of familiarised colours (Kidd *et al.*, 2012). As a consequence, little can be inferred from the absence of a response. In that case, it is difficult to establish whether infants did not see, did not remember, did not pay attention to, or simply did not like to look at a novel stimulus. For these reasons, it is not yet clear whether infant categorical responses may inform us about the adult colour categories that correspond to colour terms.

Table 1. Studies on infant colour categories. Categ: (relevant) colour categories, G = Green, B = Blue, Y=yellow, O=orange, Pu=Purple, Pi=Pink; # number of colours, Ref metric: Reference metric used to control stimuli, wl=wavelengths, sim Mun = simulated Munsell chips; N number of participants (\ excluded).

Study	Categ	#	Reference metric	Measure	N	Age
Bornstein et al. (1976)	RYGB	15	wl	NovPref	80	4mo
Gerhardstein et al. (1999)	~RO	5	~Mun*	Pop-out	24 (\7)	3mo
Franklin & Davies (2004)	GB BPu PiR	10 4 4	Mun	NovPref	54 (\22)	4mo (16-20we)
Franklin et al. (2005)	GB	4	~SimMun**	Chromatic detection	21(\6)	5mo
Franklin et al. (2008)	GB	3	~SimMun**	Chromatic detection	26 (\13)	4-5mo (20 we)
Clifford et al. (2009)	GB	3	~SimMun***	ERP	39 (\20)	7mo
Ozturk et al. (2013)	GB PB	4 4	~SimMun***	Chromatic detection	38 (\5)	8mo
Yang et al. (2016)	GB	4 3	~Lab****	NovPref NIRS	36 (\18) 36 (\18)	5-7mo
Skelton et al. (2017)	R Br G B Pu Pi	14	SimMun	NovPref	295 (\112)	4-6 mo

* Munsell distances are uncertain because incandescent light was used instead of standard illuminant C; category membership of stimuli is also uncertain.

** Uncontrolled adaptation due to task design (chromatic detection)

*** Uncontrolled adaptation due to black background.

**** Stimuli were specified in CIELAB, but differences varied across stimulus pairs; assumed WP differed from adapting background.

2.5.Synthesis

Both in infants and in animals, there is evidence for some sort of categorical responses to colours. The potential role of macaque IT in categorisation matches the evidence for categorical responses in the infants' occipito-temporal areas, because IT may be considered an evolutionary predecessor of the human occipito-temporal cortex.

However, the extent to which those responses can be related to lexical colour categories in adult humans remains an open question. Colour categories are inferred from indirect category probing measures (discrimination, generalisation, novelty preference etc.), leaving us with two main problems. First, it is particularly difficult to define a perceptual reference metric in infants and animals. In infants,

colour discrimination differs from that of adults (Knoblauch et al., 2001). Although second stage mechanisms are assumed to be the same, this is still debated (Brown & Lindsey, 2013). In non-human animals, the receptor noise limited model (Vorobyev & Osorio, 1998) can give an approximation of continuous colour discrimination, but its accuracy for fine colour differences is uncertain for many species. Hence, we cannot be sure that some categorical responses are not due to insufficiencies of that metric. Second, a theory is needed that links the observed category effects to underlying cognitive processes, and hence justifies why category effects occur given the control with the selected reference metric. Given the uncertainties about the perceptual metric, a linking theory (cf. “linking hypothesis” in (Teller, 1984; Aslin, 2007) seems to be crucial to relate the measures of categorization without language to lexical categories. Optimally, such theory would allow for establishing both evolutionary and developmental continuity between categorical responses in animals, infants and adult humans.

Non-human animals cannot manipulate colours independent of objects, and only see colours as an integral part of objects. Yet, few of the reviewed studies took the link between colours and objects into account. We believe that looking at ecologically relevant objects is a promising step towards developing a linking theory. In the animal kingdom, colour signals are relevant for foraging, reproduction, warning and repelling predators (*aposematic signals*, Mollon, 1989; Regan *et al.*, 2001; Osorio & Vorobyev, 2008; Cuthill *et al.*, 2017). The ecologically relevant objects may play the role of reinforcement stimuli in the process of learning associations between colours and rewards (food, mates, avoiding danger). Colour categories would then result from a generalisation of those associations to other colour shades. Which objects are important and what range of colours they imply depends on the type of animal (human, primate, bird), and on its visual system; however, the underlying generalisation mechanism might still be the same. In this view, colour categorisation would partition the colour space in categories centred around the relevant colour shades, facilitating responses to important visual stimuli.

While this account could potentially explain categorical colour responses in adult non-human animals, its generalization to human infants is more debatable, because of their limited experience with objects and their colours during development. The extent to which infants have object colour knowledge remains unclear; some found evidence for object colour knowledge as early as 6 months after birth (Kimura *et al.*, 2010); others claim that object-colour knowledge develops at later stages (Davidoff & Mitchell, 1993; Gleason *et al.*, 2004). Another mechanism that could possibly explain categorical responses in infants is joint attention (Moore & Durham, 1995). Being adults, infants’ caregivers have an explicit knowledge of colour categories, and may selectively attend to them. Thus, infants might simply follow the caregivers’ attention to colours, and develop some preference for certain colours over others.

As a more general approach, it might be possible to model categorical responses through Bayesian models (Tenenbaum & Griffiths, 2001). The key idea is that categorical responses to perceptually continuous colours result from prior probabilities (see, e.g., Cibelli *et al.*, 2016). Priors are categorical rather than continuous because colours vary in their ecological relevance. The priors could be acquired through associative learning. In experiments with laboratory training, animals may learn prior probabilities for particular colours because these colours imply rewards. Such a Bayesian model would describe a general fashion according to which colour categories may be acquired through experience with a few examples that are relevant to the subject, no matter whether the subject is a human adult, an infant, or a non-human animal.

3. Colour categories in the human brain

The low-level mechanisms of colour perception in the retina and the thalamus are known to a large extent; we also know that colour categories cannot be explained by these low-level mechanisms (see box 1). Much less is known about colour processing in the neocortex (reviewed in Gegenfurtner & Kiper, 2003; Gegenfurtner, 2003; Conway *et al.*, 2010). Consider Figure 3. In the visual cortex, colour representation is distributed: colour selective neurons can be found in the primary and secondary visual cortex (V1, V2), as well as in the ventral extrastriate regions. The mosaic of category-selective regions in the ventral extrastriate cortex (Grill-Spector & Weiner, 2014) contains distinct, highly colour-selective regions: the human V4, or hV4 (Zeki & Marini, 1998; Wade *et al.*, 2002), ventral-occipital cortex VO (Brewer *et al.*, 2005) and the anterior colour complex (Lafer-Sousa *et al.*, 2016; Fig 3). There is evidence that these regions are important for colour discrimination and cognition (e.g., colour memory, Zeki & Marini, 1998; reviewed in Conway *et al.*, 2010). However, the exact colour-related computations performed in these regions remain unclear, and even the basic cortical mechanisms underlying colour discrimination are still debated (Eskew, 2009; Hansen & Gegenfurtner, 2013; Shepard *et al.*, 2017).

Several approaches have been developed to investigate colour categorisation in the cortex. All these approaches involve indirect measures of categories: they test whether continuous measures of neural activity are related to the behaviourally observed categories. Category effects have been detected in the temporal dynamics of colour processing by using the divided visual field paradigm, electroencephalography (EEG), magnetic resonance imaging (fMRI), and lesion studies.

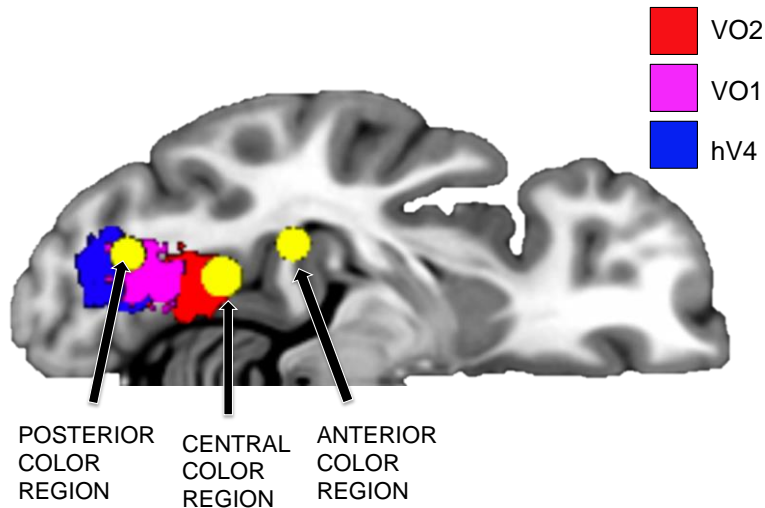


Figure 3. Colour-biased extrastriate regions in the left hemisphere of the human brain. In yellow, 5-mm spheres centred on the peaks of the posterior, central and anterior colour regions identified by Lafer-Sousa *et al.* (2016). In the background, colour-selective extrastriate regions defined by retinotopy by Wang *et al.* (2015), including the human V4, VO1 and VO2

3.1. Brain dynamics: event-related brain potentials

EEG studies on colour categorization have focused on the event related potentials (ERP) approach using an oddball task (Thierry *et al.*, 2009; Clifford *et al.*, 2012; He *et al.*, 2014; Forder *et al.*, 2017b). Consider Figure 4. A given colour shade (*standard*) is presented on the majority of the trials. On infrequent trials, a different colour shade (*deviant*) appears and it either crosses or does not cross the categorical boundary. Amplitude or latency changes in ERPs in response to a cross-category deviant presentation are assumed to reflect the effects of colour categories (*category effects*). In the active version of the oddball task (*active oddball*, Figure 4A), participants react when they detect a colour change, whereas in the passive version (*passive oddball*) they are asked to perform a colour-unrelated task, for instance to respond to a change in stimulus shape (Figure 4B).

If colour categories affect early components, this suggests that category effects result from perceptual stages of processing. Early components include the first positive (N1) and negative (P1) component and the visual mismatch negativity (vMMN, for details see Kimura *et al.*, 2011). If, however, colour categories affect later components, they should be associated with post-perceptual, higher-level cognition such as memory and language. Post-perceptual components include the second and third positive (P2, P3) and negative deflections (N2, N3).

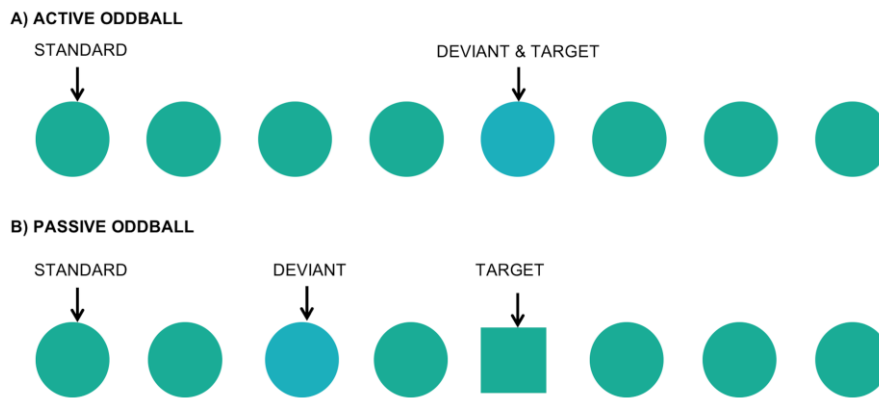


Figure 4. (A) In an active oddball task, the infrequent colour (deviant) is also a target to which subject is responding. In a passive oddball task (B), subjects respond to colour-unrelated targets while passively viewing standard and deviant colours.

Table 2 gives an overview of relevant ERP studies. Results are inconsistent with respect to the components involved in category effects. On the one hand, several studies showed that colour categories affect early components, most notably P1 (Fonteneau & Davidoff, 2007; Holmes *et al.*, 2009) and vMMN (Thierry *et al.*, 2009; Athanasopoulos *et al.*, 2010; Clifford *et al.*, 2010; Mo *et al.*, 2011; Zhong *et al.*, 2015). On the other hand, other studies reported categorical effects only on later, post-perceptual stages (Clifford *et al.*, 2012; He *et al.*, 2014; Forder *et al.*, 2017a), and in some studies, categorical effects occurred on both components (Fonteneau & Davidoff, 2007; Holmes *et al.*, 2009).

Some of the category effects on early ERPs may depend on insufficient stimulus control, in particular because most studies used the notorious set of green-blue Munsell chips (cf. Table 2, box 2). However, contradictory results emerged even when colour differences are controlled through empirically measured discrimination thresholds; some found category effects on early components (Forder *et al.*, 2017b) others only on later components (He *et al.*, 2014). Similar inconsistencies occurred in studies that compared individuals who partition the colour continuum into different categories, due to differences in languages (Thierry *et al.*, 2009; Maier & Rahman, 2018), to learning novel categories (Clifford *et al.*, 2012; Zhong *et al.*, 2015), or to small individual differences in colour naming (Forder *et al.*, 2017b). Some of these studies observed effects on early components (Thierry *et al.*, 2009; Forder *et al.*, 2017b; Maier & Rahman, 2018); others on later components (Clifford 2012; Forder 2014; 2015). The category effects observed in these studies cannot be simply explained through stimulus biases.

Task differences do not seem to account for the discrepant results across studies, either (cf. Table 2). The passive oddball task led the observers' attention away from colours, toward an unrelated cover task. Some of the studies using this kind of task found category effects on early components (Thierry *et al.*, 2009; Forder *et al.*, 2017b), while others did not (Clifford *et al.*, 2009). In contrast, the

active oddball task and the attentional blink task (Maier & Rahman, 2018) required observers to focus on the colours. Again, some studies using these sorts of task observed category effects on early ERPs (Maier & Rahman, 2018), but others did not (Clifford *et al.*, 2012; He *et al.*, 2014).

It is possible that stimulus control and task characteristics interact in more complex ways. For example, attention to colours might be more important for colours that are difficult to discriminate than for easy ones. Other methodological characteristics, such as the stimulus display (one vs. two colours, e.g. Mo *et al.*, 2011), and the precise timing of task and stimulus presentation may also play a role in these discrepancies.

However, the most important challenge might well reside in the experimental logic of the studies. If the reference metrics (Munsell chips, discrimination thresholds) control for colour discriminability, no category effects should be expected on early ERPs, precisely because early ERPs are assumed to reflect colour discrimination. Thus, ERPs evoked by equidistant colours should not vary as a function of colour changes in the stimulus set. The observation of category effects on early ERPs raises the question of whether those early components reflect perceptual stages of processing exclusively, or also involve higher-level, cognitive processing. A growing body of evidence shows that the processes underlying the ERP components are far more complex than what can be accounted for by the early/perceptual vs. late/cognitive interpretation. First, the assumption that modulations of P1 and vMMN are purely perceptual is now debated, because it has been shown that attention may well affect even early ERPs. For example, the P1 and N1 amplitudes are enhanced by spatial attention - stimuli that fall into an attended location elicit larger P1 and N1 amplitudes at posterior scalp sites than do stimuli falling into the same location when this location is not attended to (Hillyard & Anllo-Vento, 1998; Luck & Ford, 1998; Chica *et al.*, 2010; Chica *et al.*, 2012). Intracranial recordings in primates show that attentional modulation in the visual cortex can occur as early as 70ms after stimulus onset (Martínez *et al.*, 1999; Pooresmaeili *et al.*, 2014). Similarly, the MMN can also rely on attentional load (Erlbeck *et al.*, 2014; Hedge *et al.*, 2015), even in passive oddball tasks (Hedge *et al.*, 2015). Those results question the conclusions from studies interpreting the vMMN as a perceptual, pre-attentive component (e.g. Thierry *et al.*, 2009).

Table 2. Overview of EEG studies. Categ: (relevant) colour categories, G = Green, B = Blue, B1 = Blue1, B2 = Blue2; # no. of colours; Ref metric: Reference metric used to control stimuli, simMun simulated Munsell chips, JNDs (just noticeable difference) empirically measured discrimination thresholds; Interaction: Interaction effects. Cross-language comparisons: G = Greek, R = Russian, E = English, GE = Greek-English bilinguals. Latcat lateralised category effect (see section 3.2 below), learn pre and post learning; Indiv Comparison between individuals with slightly different category boundaries.

Study	Categ	#	Reference metric	Inter-action	Task	Measure	Component
Fonteneau & Davidoff (2007)	GB	3	simMun	-	Passive Oddball	Amp	P2, P3
						Lat	P1, N1, N2,
Thierry et al. (2009) Athanasopoulos et al. (2010)	GB1B2	4	simMun	G-E GE	Passive Oddball	Amp	P1, vMMN
						Lat	P1
Mo et al. (2011)	GB	4	simMun	Latcat	Passive Oddball	Amp	vMMN
Liu et al. (2009)	GB	3	simMun	Latcat	Visual Search	Amp	N2pc
Holmes et al. (2009)	GB	8	simMun	-	Active Oddball	Amp	P2 & P3
						Lat	P1, N1,N2
Clifford et al. (2009)	GB	3	simMun	-	Passive Oddball	Amp	Nc, NSW
Clifford et al. (2010)	GB	3	simMun	Lower/Upper VF	Passive Oddball	Amp	vMMN
Clifford et al. (2012)	GB	8	simMun	Learn	Active oddball	Amp	P3
He et al. (2014)	GB	4	JNDs	-	Active Oddball	Amp	N2, P3, Frontal Positivity
Forder et al. (2015)	GB1B2	3	JNDs	G-R	Active Oddball	Amp	P2/N2
Forder et al. (2017)	GB	3	JNDs	Indiv	Passive oddball	Amp	P1, Frontal Positivity
Zhong et al. (2015)	B	6	simMun	Learn	Passive oddball	Amp	vMMN
Maier & Rahman (2018)	GB1B2	3	simMun	G-R-E	Attentional blink	Amp	P1, N2

3.2.Lateralized Category Effect

A second neurocognitive approach aims at probing the involvement of language in category effects based on the hemispheric lateralisation of language processing and early visual processing. This approach has three core assumptions (Fig. 5A). First, in the majority of people (about 90-92%) language is predominantly processed in the left hemisphere (reviewed in: Corballis, 2012; Ocklenburg & Güntürkün, 2018). Second, visual information coming from one visual hemifield is projected to the contralateral hemisphere (reviewed in Bourne, 2006). Visual information travels across the hemispheres through the splenium of the corpus callosum, a white matter structure that connects the two occipital lobes. This callosal transfer takes time. As a result, information from the left visual field/right hemisphere reaches the language areas in the left hemisphere slightly later than visual information from the right visual field/left hemisphere (Hunter & Brysbaert, 2008). Third, the time for callosal transfer modulates category effects on speeded colour discrimination, i.e. colour discrimination under time pressure. A category effect implies faster response times for discriminating two colours when they belong to different categories as compared with discrimination between same-category colours (Bornstein & Korda, 1984). If colour categories depend on language, category effects should occur in the right visual field, but not, or less, in the left visual field, because of the time-consuming callosal transfer (Gilbert *et al.*, 2006; Gilbert *et al.*, 2008; Kay *et al.*, 2009). Such lateralised category effects have been investigated in speeded visual search tasks, involving lateralized stimulus presentation (cf. fig. 5B). Observers have to indicate as fast as possible which side of the screen contains a different colour (Gilbert *et al.*, 2006).

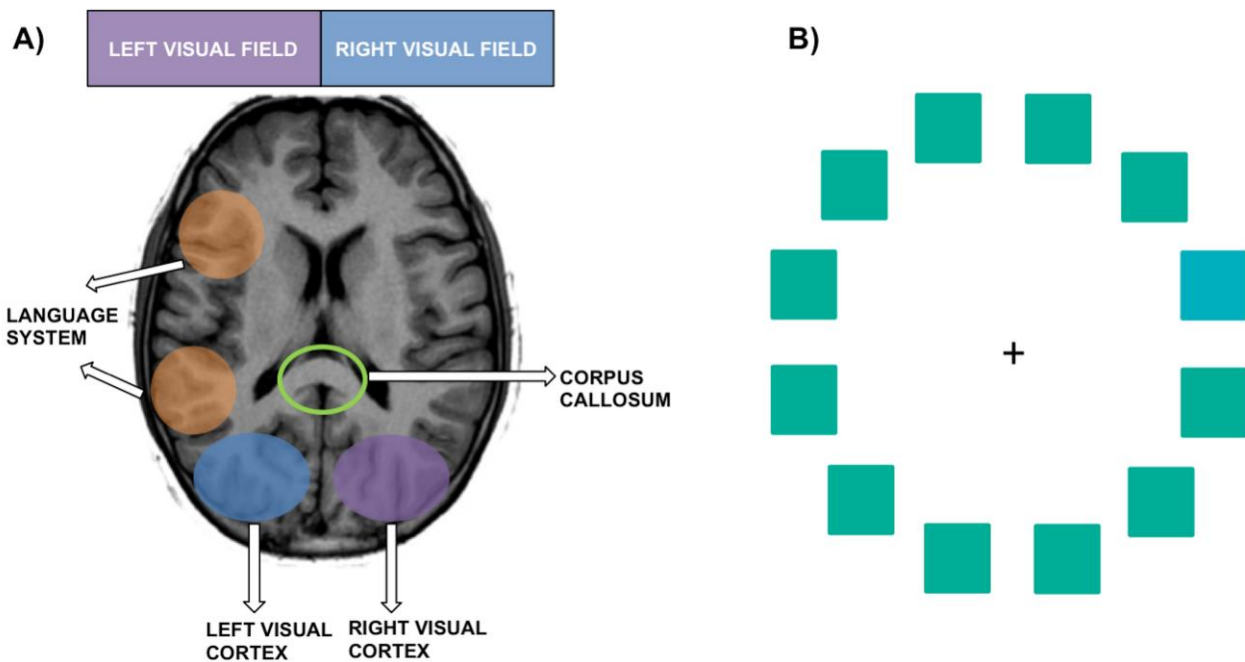


Figure 5. The lateralized category effects. (A) Lateralisation of language and early visual processing. Information from the right visual field (in blue) directly reaches the left hemisphere (in blue), where language is also processed for most people (see orange dots). If speeded response times do not allow for interhemispheric transfer (through corpus callosum, green) of visual information, and if language is necessary for categorisation, then category effects can only occur for stimuli presented in the right visual field and processed by the left hemisphere. (B) Display of a visual search task commonly used to demonstrate lateralized category effects. The subjects are asked to detect the side (left/right) of target presentation.

Table 3 gives an overview of behavioural studies on the lateralised category effect. Several behavioural experiments provided evidence for a lateralized category effect (Drivonikou *et al.*, 2007; Franklin *et al.*, 2008a; Roberson *et al.*, 2008; Franklin *et al.*, 2008b; Roberson *et al.*, 2009; Zhou *et al.*, 2010; Paluy *et al.*, 2011; Al-rasheed *et al.*, 2014), including a study that used cat and dog images as stimuli instead of colour patches (Gilbert *et al.*, 2008).

Still other studies dealt with the neural correlates of the lateralised category effects. In some studies, lateralised category effects occurred on the second negative ERP component of the posterior electrodes contralateral to the visual field of the target (N2pc, ~220–320 ms post-stimulus; and N2, 260-310ms, Liu *et al.*, 2009; Liu *et al.*, 2010). In other studies (Mo *et al.*, 2011; Zhong *et al.*, 2015), lateralised category effects were found on visual mismatch negativity (vMNN, ~130-190 ms). An fMRI study reported increased activity in the left language areas, i.e. the inferior frontal gyrus (BA 47), the middle temporal gyrus (BA21) and the supramarginal gyrus (BA 40) when subjects discriminated cross-category colours presented in the right visual field (Ting Siok *et al.*, 2009). A split-brain patient with callosal lesion presented category effects only in the right visual field (left

hemisphere), as if his right hemisphere, deprived of left-hemispheric input, were blind to colour categories (Gilbert *et al.*, 2006). Additional studies suggested that there is a second kind of non-lexical category effect that occurs in the absence of language and is lateralized to the right hemisphere (for review see Regier & Kay, 2009). Such opposite lateralised category effects have been observed in pre-verbal infants (Franklin *et al.*, 2008a; Franklin *et al.*, 2008b) and in aphasic patients (Paluy *et al.*, 2011).

In stark contrast to these studies supporting the presence of lateralised category effects, there have also been thorough but unsuccessful attempts to replicate them. Some studies did not find any category effects when using different sets of colour pairs (Brown *et al.*, 2011; Webster & Kay, 2012; Brederoo *et al.*, 2019); others reported category effects of similar magnitude in either visual field (Liu *et al.*, 2008; Witzel & Gegenfurtner, 2011; 2015; 2016, behavioural results in Liu *et al.*, 2009 and in Siok *et al.*, 2009; behavioural results in Siok *et al.*, 2009); still others found category effects in the left visual field (Suegami *et al.*, 2014). Furthermore, putative category effects on ERPs (Fonteneau & Davidoff, 2007; Holmes *et al.*, 2009) were not lateralised.

If colour categorization were directly related to language processing in the left hemisphere, response times for colour naming, rather than category effects, should be faster in the right visual field. However, evidence for this hypothesis is mixed (Bornstein & Monroe, 1980; Wuerger *et al.*, 2012; Lu *et al.*, 2012). Furthermore, there is evidence for lateralised category effects that seem unrelated to language. Lateralised category effects with stimuli other than colour can occur independent of verbal labelling and language (Holmes & Wolff, 2012; Suegami & Laeng, 2013; Holmes *et al.*, 2017). Category effects lateralised to the left hemisphere for cool and warm colour categories do not correspond to basic colour terms (Holmes & Regier, 2017).

A fundamental problem for the replication of lateralised category effects is the fact that none of the studies in support of lateralised category effects provided exact colour specifications that would allow for reproducing the original stimuli (cf. footnotes in Table 3). It seems unlikely that the failure to reproduce the original lateralised category effects in follow-up studies is due to differences in colour sampling. Those critical studies included a large range of carefully controlled stimulus samples, including thorough attempts to reproduce the colours of the seminal studies based on personal communication with the respective authors (Witzel & Gegenfurtner, 2011; Brederoo *et al.*, 2019). In addition, evidence for and against lateralised category effects was found independent of the control of eye movements. Hence, the contradictory findings may not be explained by insufficient control of the separation between visual fields. Two studies suggested that lateralisation is modulated by response speed (Roberson *et al.*, 2008; Constable & Becker, 2017), which depends on task difficulty (Constable

& Becker, 2017). This idea is in line with the original assumption that lateralised category effects are due to the effects of callosal transfer on response speed.

However, it is possible that the original explanations of the observed effects might not hold because the core assumptions underlying the lateralized category effect are not safe. First, the response speed observed in studies on the lateralised category effect cannot exclude callosal transfer. Figure 1B illustrates the speed of processing visual scenes in monkeys. Even though the processing speed in monkeys is known to be a bit faster than in humans, this scheme provides a rough approximation of the processing speed in humans. In humans, inter-hemispheric transfer takes about 4-40ms (Marzi, 2010; Nowicka & Tacikowski, 2011; Phillips et al., 2015); visual processing time can be as fast as 150ms when categorizing natural scenes (Thorpe et al., 1996; van Rullen & Thorpe, 2001; Fabre-Thorpe, 2011). In this context, it seems hardly probable that the fastest response times in visual search tasks (~400ms, see Gilbert et al., 2006; Drivonikou et al., 2007; Liu et al., 2008; Liu et al., 2009; Ting Siok et al., 2009; Zhou et al., 2010) would be fast enough to prevent the callosal transfer of linguistic information from the left to the right hemisphere.

Second, left lateralisation does not guarantee linguistic processing. The left hemisphere seems to be involved in categorical processing both in humans (Kosslyn *et al.*, 1989). Some even claim that this left-lateralised categorical processing could be a precursor to the specialisation for language rather than the other way around (see section 5.4 in Rogers *et al.*, 2013). Moreover, evidence from brain-damaged patients (De Renzi & Spinnler, 1967; Damasio & Damasio, 1983; Miceli *et al.*, 2001; Stassenko *et al.*, 2014) and fMRI studies (Simmons *et al.*, 2007) suggests that higher-level colour processing may be lateralized to the left hemisphere, without necessarily involving language processing. For instance, patients with colour agnosia due to left occipito-temporal damage fail to associate objects with their typical colours, while having no trouble in naming colours (Luzzatti & Davidoff, 1994; Miceli *et al.*, 2001; Stassenko *et al.*, 2014)

Third, the response time pattern that is taken as evidence for category effects is not specific to language. Opposite lateralised category effects in the left visual field occurred in observers who, presumably, lack language processing (Franklin *et al.*, 2008a; Paluy *et al.*, 2011). Studies that tested lateralised category effects with stimuli other than colour found that these effects can be produced independent of verbal labelling and language (Holmes & Wolff, 2012; Suegami & Laeng, 2013; Holmes *et al.*, 2017). Hence, the observation of category effects cannot be taken as evidence for the involvement of language, either.

Fourth, the stimulus control in many of the studies does not guarantee that the observed effects are genuine category effects. Problems of stimulus control in studies on the lateralised category effects have previously been discussed in great detail (Witzel & Gegenfurtner, 2011). Most studies supporting

the lateralised category effect used colours at the green-blue boundary, which risk producing spurious category effects (see boxes 1 and 2). Consequently, the effects taken to be lateralised category effects might not even be specific to colour categories. Taken together, the theory and empirical evidence on the lateralized category effect are inconclusive.

Table 3. Overview of behavioural experiments on the lateralised category effect. If studies included both, behavioural and other (e.g. neuroimaging) experiments, this table exclusively refers to the behavioural experiments of those studies. ERP and fMRI experiments are included in Tables 2 and 4, respectively. The column Effect reports the size of the lateralized category effect. It is calculated as the difference between within and across category colours in the right and left visual fields.

Study	Categ	#	Reference metric	Task	N	Effect
Gilbert et al. (2006)	GB	4	SimMun*	Left-right Discrimination	27	~24ms
Drivonikou et al. (2007)	GB	4	SimMun**	Chromatic detection	24	30 & 60ms
	BP	4			34	
Franklin (2008)	GB	4	SimMun**	Chromatic detection	18	~40ms
Roberson et al. (2008)	YG	9	SimMun*	Left-right Discrimination	22	~100ms
Roberson et al. (2009)	YG	9	SimMun*	Left-right Discrimination	14	~50ms
					14	(when fixating)
Siok et al. (2009)	GB	4	SimMun*	Left-right discrimination	14	12ms n.s.
Zhou et al. (2010)	GB	4	SimMun*	Left-right discrimination	18 (31)	20ms
Paluy et al. (2011)	GB	4	SimMun*	Left-right discrimination	11	~20ms
Liu et al. (2008)	GB	4	SimMun*	Chromatic detection	18	5ms n.s.
Liu et al. (2009)	GB	4	SimMun*	Left-right discrimination	12	-12ms
Brown et al. (2011)	GB		CIELAB + MDS	Left-right discrimination	39	n.s.
Suegami (2014)	GB	4	SimMun**	Colour naming	30	n.s.
Witzel et al. (2011)	GB	4	SimMun	Discrimination & detection	230	-19:18ms n.s.
	BP	4				
Witzel et al. (2015)	Pi O Y G B Pu	40	JNDs	4 AFC Discrimination	12	n.s.
Witzel et al. (2016)	RBr	4	JNDs	4 AFC Discrimination	15	n.s.
Constable & Becker (2017)	GB	4	CIE 1931*	Left-right Discrimination	16	n.s.
Zhong et al. (2017)	GB	4	SimMun	Left-right Discrimination	33	0-9ms

* Irreproducible colour specification (e.g. device-specific RGB values, lack of specification of adapting background) and/or imprecise calibration (e.g. easyrgb.com).

** Uncontrolled adaptation due to task design (chromatic detection)

3.3. Neuroimaging

Functional magnetic resonance imaging (fMRI) has been used to identify brain structures involved in colour categorization. Knowledge about the functions of those brain structures allows clarifying which perceptual or cognitive functions are involved in colour categorization.

fMRI studies in colour categorization have produced mixed results (see Table 4). Several studies found evidence for category-specific processing in the visual cortex, including V2/3 (Ting Siok *et al.*, 2009; Kwok *et al.*, 2011) and hV4/VO (Brouwer & Heeger, 2013). Some reported category-specific effects in regions typically associated with language, such as the left frontal, temporal and

parietal regions (Ikeda & Osaka, 2007; Tan *et al.*, 2008; Ting Siok *et al.*, 2009). Still others found evidence for domain-general categorization in prefrontal and frontal areas, such as the bilateral inferior frontal gyri, the superior frontal sulci and the middle frontal gyri (Bird *et al.*, 2014; Persichetti *et al.*, 2015). Some studies also found evidence for the involvement of the left cerebellum (Kwok *et al.*, 2011; Bird *et al.*, 2014); however the exact reasons for cerebellar contribution to colour categorization remains unclear.

One possible reason for these discrepancies could be the stimulus sampling. Some studies (Ikeda & Osaka, 2007; Tan *et al.*, 2008; Brouwer & Heeger, 2013) assessed colour categorization using very different colours, making it impossible to directly compare how their colour sampling methods affected the results. Four studies (Ting Siok *et al.*, 2009; Kwok *et al.*, 2011; Bird *et al.*, 2014; Persichetti *et al.*, 2015) assessed colour categorization with similar colours around the problematic green-blue boundary (see box 2). However, even these studies reported different brain regions, implying that stimulus sampling alone cannot explain the variability of results. Among all these studies, Brouwer and Heeger (2013) were the only ones who thoroughly investigated more than one category boundary (12 colours).

The tasks used to explore colour categorization also varied substantially across different studies, including passive colour viewing (Brouwer & Heeger, 2013; Bird *et al.*, 2014; Persichetti *et al.*, 2015), colour discrimination (Tan *et al.*, 2008; Ting Siok *et al.*, 2009), colour naming (Tan *et al.*, 2008; Brouwer & Heeger, 2013; Persichetti *et al.*, 2015), or a two-back memory task (Ikeda & Osaka, 2007). Each of those tasks require different sets of cognitive functions, and it is unclear to what extent these abilities interacted with colour categorization. For instance, the activity of language regions in short-term memory tasks (Ikeda & Osaka, 2007) could suggest the engagement of verbal labelling as a memorization strategy, rather than an inherent component of colour categorization.

It is also important to distinguish between studies focusing on colour categorisation and studies showing category effects on perception (categorical perception). Category-specific modulation of the visual cortex was reported only when subjects engaged in colour-related tasks, such as colour discrimination (Ting Siok *et al.*, 2009), colour naming (Brouwer & Heeger, 2013; Persichetti *et al.*, 2015), or colour memory (Ikeda & Osaka, 2007). Studies that systematically compared occipital activity in colour naming and colour-unrelated tasks (Brouwer & Heeger, 2013; Persichetti *et al.*, 2015) did not find anything specific for colour categories in the latter. This result contradicts the idea that colours are processed categorically in the visual cortex in a bottom-up manner, and contrasts with ERP results demonstrating category effects on early components in a passive oddball task (Thierry *et al.*, 2009; Forder *et al.*, 2017b). However, the category-sensitive regions revealed with the naming task also differed across the two studies, and none reported regions commonly associated with language

(Brouwer & Heeger, 2013; Persichetti *et al.*, 2015). It is thus unclear how the results observed with active colour naming relate to categorical perception effects observed during colour discrimination (Tan *et al.*, 2008; Ting Siok *et al.*, 2009). Hence, it is impossible to draw conclusions about areas involved in colour categorization as a function of differences among the tasks used to reveal them.

Furthermore, the above studies used three different kinds of fMRI analysis. First, the *activation-based* approach compares the averaged BOLD signal in each volume unit (voxel) between experimental conditions, e.g. between performing a task on the same category colours versus different-category colours (Ikeda & Osaka, 2007; Tan *et al.*, 2008; Ting Siok *et al.*, 2009). Second, *fMRI adaptation* exploits the fact that fMRI signals decrease when two successive stimuli activate the same neural population (Grill-Spector *et al.*, 2006; Barron *et al.*, 2016). Thus, when a given area is sensitive to a particular colour category, it should show a decrease in BOLD response to a colour preceded by a different exemplar of that same category (Bird *et al.*, 2014; Persichetti *et al.*, 2015). Third, multi-voxel pattern analysis (*MVPA*) focuses on local, multi-voxel patterns of BOLD responses to single stimuli and the relationship between those patterns (for review, see Norman *et al.*, 2006; Kriegeskorte & Bandettini, 2007). In colour category research, it has been tested whether pattern similarities between colours are higher within than across categories. Researchers investigated this hypothesis using Representational similarity analyses, RSA (Bird *et al.*, 2014), and forward models (Brouwer & Heeger, 2013). A problem with comparing the results across the different studies is that those different types of analysis have different sensitivities, i.e. they involve different signal-to-noise ratios. For instance, fMRI adaptation was shown to be less sensitive than the MVPA approaches in detecting small differences between visual stimuli (Sapountzis *et al.*, 2010). This fact could explain why a study using the adaptation method did not find category effects in the occipital regions (Persichetti *et al.*, 2015), while another study did find such effects using MVPA (Brouwer & Heeger, 2013).

While activation-based, fMRI adaptation and MVPA results are usually consistent (Kriegeskorte *et al.*, 2006; Jimura & Poldrack, 2012; Barron *et al.*, 2016), this seems not to be the case for colour categorization. Particularly, studies using the activation-based technique showed some evidence for a contribution of language-related areas to colour categorisation (Ikeda & Osaka, 2007; Tan *et al.*, 2008; Ting Siok *et al.*, 2009). In contrast, studies using adaptation or MVPA neither found left-lateralized effects, nor involvement of language areas in the whole-brain analysis (Brouwer & Heeger, 2013; Bird *et al.*, 2014; Persichetti *et al.*, 2015). Thus, different analysis strategies may reveal different aspects of the cognitive architecture of colour categories. In particular, Jimura and Poldrack (2012) suggested that activation-based analyses reveal areas that are sensitive to global cognitive processes which are engaged in a given task, while MVPA is sensitive to fine-grained differences between the processed patterns of content.

In sum, given the small numbers of neuroimaging studies, it seems difficult to establish how stimulus selection, behavioural tasks, and the type of analysis could explain the very different results across studies. Each study seems to provide a different speculative explanation of why the particular brain areas they identified might be involved (or not) in colour categorisation. Some claim that there is a top-down influence of language (Ting Siok *et al.*, 2009; Kwok *et al.*, 2011; Brouwer & Heeger, 2013); others that there is a top-down influence of non-verbal categorization (Bird *et al.*, 2014). We suggest that it is important to integrate these ideas in coherent, testable models, and to compare them in studies that are designed to systematically test the predictions derived from the different models.

Table 4. Overview of MRI studies. Categ: (relevant) colour categories, G = Green, B = Blue, Y=yellow, O=orange, Pu=Purple, Pi=Pink; # number of colours; Ref metric: Reference metric used to control stimuli

Study	Categ	#	Reference metric	Task	Measure	Area
Ikeda & Osaka (2007)	-	-	-*	Two-back	activation	left inferior frontal gyrus left inferior parietal lobule
Tan et al. (2008)	3	3	RGB*	Colour discrimination (same/different)	activation	left posterior superior temporal gyrus left inferior parietal lobule
Siok et al. (2009)	GB	4	SimMun*	Visual search	activation	left inferior frontal gyrus middle temporal gyrus supramarginal gyrus V2/3
Kwok et al. (2012)	GB	4	SimMun*	Cat. training	Pre-post VBM	V2/3 Left cerebellum
Brouwer & Heeger (2013)	GBPuPiO	12	DKL*	Color naming	MVPA	hV4 / VO
Bird et al. (2014)	GB	4	Sim Munsell	cover	Adaptation, MVPA	Middle frontal gyrus Left cerebellum
Persichetti et al. (2015)	GB	10	Sim Munsell	colour naming	Adaptation	precentral sulcus, pars triangularis of inferior frontal gyrus, posterior part of the superior frontal sulcus [all bilateral]]

* Irreproducible colour specification (e.g. device-specific RGB values, lack of specification of adapting background and/or axis scaling) and/or imprecise calibration (e.g. easyrgb.com).

3.4. Lesion neuropsychology

Studies on patients with brain damage provided strong evidence that cortical colour processing in the human brain is highly modular, with separate modules for conscious colour experience (Bouvier & Engel, 2006; Bartolomeo *et al.*, 2014), colour naming (Geschwind & Fusillo, 1966; Oxbury *et al.*, 1969; Damasio & Damasio, 1983), and object-colour knowledge - the association between objects and their typical colours (Beauvois & Saillant, 1985; Luzzatti & Davidoff, 1994; Miceli *et al.*, 2001; Zandvoort *et al.*, 2007; Stassenko *et al.*, 2014). Rare patients with left occipito-temporal lesions, spanning from primary visual cortex to the parahippocampal regions, show selective deficits in naming colours with spared colour perception and general language functioning (Oxbury *et al.*, 1969; Damasio & Damasio, 1983). Neuropsychological investigations of colour categories focused mainly on patients with language impairment, and in particular with an inability to name colours (*colour anomia*).

Evidence that such patients are able to categorize visually presented colours suggests that colour categorization does not depend on naming, and that the involvement of language areas is not crucial for colour categorization.

Classic neuropsychological models of colour cognition assumed that colour categorization is processed at a stage prior to colour naming (e.g. Davidoff, 1991 p. 217). However, the classical studies in the domain (Kinsbourne & Warrington, 1964; Geschwind & Fusillo, 1966; Stachowiak & Poeck, 1976; Beauvois & Saillant, 1985) tested colour categorisation without any control measures to disentangle colour categorization from colour discrimination or colour naming. More recent investigations specifically tested the relationship between colour naming and colour categorization. Some showed that patients can sort colours into consistent categories despite severe language deterioration in semantic dementia (Haslam *et al.*, 2007; but see Rogers *et al.*, 2015) or colour-specific naming deficits (Fukuzawa *et al.*, 1988; but see Roberson *et al.*, 1999). Others showed category effects on perceptual tasks in patients with selective naming deficits (Roberson *et al.*, 1999) or more general aphasias (Paluy *et al.*, 2011). Together, these studies suggest that colour categorization can endure language deterioration, and can be independent from colour naming.

However, definite conclusions are complicated by the fact that those studies often used different stimulus sets to assess categorisation and naming. Categorisation and naming consistency strongly vary across colours (see Fig 8 in Olkkonen *et al.*, 2010). Moreover, clinical cases are hardly ever clear-cut, and patients with language impairments often have some residual naming competences (e.g. Fukuzawa *et al.*, 1988; Woodward *et al.*, 1999). To control for variation due to different stimulus sets, we suggest measuring colour categorisation and naming with the same colours. In addition, it seems crucial to ensure that the pattern of performance obtained in the categorisation tasks cannot be explained by perceptual properties of the stimulus samples, such as colour differences and salience (see box 2). Otherwise, putative categorisation performance might well be due to intact colour perception.

3.5. Synthesis

The reviewed evidence for neural correlates of colour categorisation is contradictory: Some findings suggest a perceptual, others a linguistic origin of colour categorization, and still others associate it with areas involved in domain-general categorization. We identify three core challenges for future research.

First, a recurrent issue with almost all reviewed studies (except Brouwer & Heeger, 2013) is the limited sample of stimuli and categories. This makes it difficult to disentangle the observed effects

from factors related to the specific stimulus sample, in particular at the green-blue boundary. It would be advisable to use a large range of colours spanning through different colour categories, or to cross-validate the results obtained at one category boundary with results for other boundaries.

Second, behavioural tasks used to elicit colour categorisation and category effects varied significantly, ranging from visual detection, colour discrimination, short-term memory to colour naming. It is also important to clearly separate between categorisation proper, understood as grouping different colours into distinct categories, and top-down category effects, i.e. how those groupings affect continuous, non-categorical measures, such as response times. Within-subject comparisons of different tasks are needed to disentangle candidate cognitive functions involved in colour categorisation. For example, approaches comparing neural activity during colour naming and during nonverbal, colour-related tasks seem promising to us (Brouwer & Heeger, 2013; Bird *et al.*, 2014; Persichetti *et al.*, 2015).

Third, much of the research on neural correlates is motivated by the universalism-realism debate, focussing on a dichotomous contrast between perception and language (e.g. perceptual ERP-components, lateralised category effects). At the same time, neuropsychological lesion studies provide an alternative approach according to which colour categorisation is considered to be distinct from both perception and language. Similarly, recent fMRI studies suggest a role of domain-general categorization regions in the prefrontal cortex rather than the visual cortex or language areas (Bird *et al.*, 2014; Persichetti *et al.*, 2015). If we look beyond the classical perception-language dichotomy, still other cognitive processes and related cortical areas could play a role in colour categorisation, such as the following.

Colour categorisation could be related to the processes of semantic categorisation in the anterior temporal lobes (Ralph *et al.*, 2017). Though, it might be difficult to detect category effects in these areas, because temporal regions are prone to susceptibility artefacts due to magnetic field inhomogeneities close to air-tissue boundaries (Embleton *et al.*, 2010).

Attention might play a role in colour categorisation (Brouwer & Heeger, 2009; Persichetti *et al.*, 2015) and in category effects on colour discrimination (cf. “categorical facilitation” in Witzel & Gegenfurtner, 2015; Witzel, 2018; Witzel & Gegenfurtner, 2018). Attention may explain differences across tasks and experimental conditions for equivalent stimuli. Discrimination performance with stimuli in the focus of attention is higher than for stimuli that are not attended, even if the stimuli are equivalent in sensitivity and discriminability (Carrasco *et al.*, 2004; Chica *et al.*, 2011). If observers pay attention to differences between colour categories, this would result in better discrimination performance for colours across than within categories. Attentional biases towards the right hemisphere could account for some of the reported lateralized category effects (Chen & Spence, 2017). Exogenous

and endogenous allocation of attention might also differentially affect ERP components. Exogenous attention is attracted by stimulus properties, such as contrast and salience; while endogenous attention is controlled by the observers' intentions and aims (Chica *et al.*, 2013). Instructions and task requirements may modulate the allocation of attention, and hence contribute to different results across ERP studies. Finally, attention may interact with language: language could modify attentional filters and make individuals attend to items that are relevant to their culture, such as the distinctions between language-specific colour names (Thierry *et al.*, 2009; Maier & Rahman, 2018). Language would then serve as an indicator, rather than a generator, of colour categories. The role of attention might also explain the involvement of different frontal regions (see Table 3) in colour categorisation, as suggested by exploratory whole-brain analyses (Bird *et al.*, 2014; Persichetti *et al.*, 2015). In particular, the dorsolateral prefrontal cortex might play a role for colour categorisation because it is part of the fronto-parietal attention system (Corbetta & Shulman, 2002; Bartolomeo & Seidel Malkinson, 2019).

Recent hypotheses on colour perception and neural colour processing suggest that the main function of colour is to provide information about the behavioural relevance of objects in the natural environment (Conway, 2018; Witzel & Gegenfurtner, 2018b). The link between objects and colours has also been implicated in some neuroimaging studies. For instance, the anterior colour region identified by Lafer-Sousa and colleagues (2016, see Fig. 3) is sensitive to both colour and shape, suggesting possible integration of the two types of information. Colour tuning of colour selective regions in the macaque IT (see fig 1B) are biased towards colours that are most likely to be present on objects (Rosenthal *et al.*, 2018). These general ideas on colour processing might also extend to colour categories. We suggest that colour categories should be regarded in relation to objects and object features. Colour categories may result from an interaction between high-level regions processing object identity in the temporal lobes and visual regions sensitive to colour.

Finally, it is important to consider that cognitive abilities are based on the concerted activity of highly distributed, large-scale networks of brain areas (Mesulam, 1990). One study indicated that the neural representation of colour interacts with the representation of other object features in a network of different brain areas to establish object identity (Coutanche & Thompson-Schill, 2015). Analogously, the neural basis of colour categories does not necessarily identify with one single region but most probably depends on a network of areas, including colour-biased, language-related, and object-selective regions. This view also accounts for task-dependent responses in the occipito-temporal cortex of both humans (Brouwer & Heeger, 2013; see also Yang *et al.*, 2016 for infants) and primates (Koida & Komatsu, 2007). The task-dependency may result from top-down input from the prefrontal cortex (see Koida & Komatsu, 2007 for primates and Bird *et al.*, 2014; Persichetti *et al.*, 2015 for

humans) and possibly language-regions (Ikeda & Osaka, 2007; Ting Siok *et al.*, 2009, see also Lateralized category Effects).

4. Conclusions

Research into the biological basis of colour categorisation provided mixed, and often contradictory results. Although the areas of research reviewed above differ fundamentally from one another, there are also important common challenges across these areas. To conclude, we summarize the three challenges that we consider as crucial for the success of future advances in the interdisciplinary research on colour categorisation.

First, many ambiguities across studies are due to methodological concerns, in particular stimulus control. Research on colour categories in all reviewed areas involve category effects on indirect measures that do not directly assess colour categorisation through colour naming. These measures include EEG and BOLD signals, infant and animal responses and responses in neurological patients that are unable to name colours. It is crucial that the observed effects can be related to colour categories. A perceptual reference metric is needed that controls nonlinearities in colour perception that are unrelated to lexical colour categories (box 2). This includes in particular the control of colour differences and saliency. None of the available colour spaces satisfactorily achieves such a control. In some cases, a colour space is not even known. This is the case for infants, for whom we do not know the resolution along the colour dimensions, and for non-human animals, for which we often do not even know the dimensions. As a general rule, it seems inappropriate to investigate only one exemplary boundary, and in particular the green-blue one. Instead, we suggest examining several categories across colour space to make sure that putative category effects are not due to other factors, and can be unambiguously related to colour categories.

Second, much of previous research has been grounded on the universalist-relativist debate. This debate focuses on a contrast between innate perception and learned language. This simple dichotomy is clearly inconsistent with the empirical evidence reviewed above. Colour categorisation research needs to go beyond the gross distinction between language and perception. For example, research on neurological patients suggested that neural processes responsible for categorisation might be functionally segregated from those related to perception or to language. Research on non-human animals highlighted the potential role of associative learning in colour categorisation. Research focusing on the neural origins of colour categories, or on psychophysical evidence indicated that attention might play an important role in colour categorisation. Attention might not only explain category effects on perception. Colour naming and categories may also direct the observer's attention towards particular colours and colour differences. The direction of attention during communication

might be an important function of colour categories. The function of highlighting particular colours might explain why we categorise colours when communicating.

Third, all areas of research have neglected the link between colours and objects and focused instead on colours independent of objects. However, colour names and categories serve a purpose in communication: They are used to describe colours as a feature of objects and scenes (Gibson *et al.*, 2017; Kemp *et al.*, 2018; Witzel, 2018; Zaslavsky *et al.*, 2018; Witzel & Gegenfurtner, 2018b). Colours are strongly associated with objects, such as green with plants, blue with sky and sea, and red with blood (Levinson, 2000; Palmer & Schloss, 2010; Wierzbicka, 2015). In non-human animals, colour is an inherent, indissociable property of an object. The link between colours and objects might reveal the ecological origin of colour categories, and allow researchers to establish an evolutionary framework of how colour categories develop across species.

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