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The modularity of high-level colour processing: evidence from brain damage

La modularité du traitement de haut-niveau des couleurs: l'apport de la neuropsychologie

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Abstract

We examined the effects of brain lesions in humans on the interdependences between three modules of cortical colour processing, namely colour perception, naming and object-colour knowledge. We first focused on colour categorisation - a case-in-point of the interplay between perception and language. Reviewed evidence from cognitive development, comparative psychology and cognitive neuroscience hints that colour categorisation originates from neither perception nor language, as assumed by the Nature-Nurture debate. Instead, colour categories may reflect relevant objects in the environment. To assess the causal link between categorization and naming, we investigated a stroke patient, RDS. Despite severe difficulties in naming chromatic colours, due to a left occipito-temporal lesion, RDS's colour categorisation was relatively spared. Multimodal MRI experiments revealed that the language-perception connectivity is essential for efficient colour naming but not for categorisation. Investigation of object-colour knowledge in the context of RDS's colour-naming impairment showed that RDS could not link colour perception to neither language nor semantic knowledge. He could not associate a visual colour to a colour name or to the shape of its typical object. Overall, we demonstrated three functional segregations in colour processing: between (1) colour categorisation and colour naming, (2) naming of chromatic and achromatic colours and (3) knowing about coloured objects and knowing about abstract colours. The main purpose of high-level cortical colour mechanisms could be providing sensory and semantic information to guide object-related behaviour, by achieving (1) stable colour perception, (2) relevant colour categories, and (3) joint mental representations of shapes and colours. These neural computations may have been recycled in cultural evolution to isolate colours from objects and label them with names.

Résumé

Nous avons examiné l’effet des lésions cérébrales chez l'homme sur les interdépendances entre trois modules de traitement cortical de la couleur: la perception, la dénomination et la connaissance de la couleur de l'objet. Nous avons étudié la catégorisation des couleurs - un exemple de l'interaction entre la perception et le langage. La littérature suggère que cette catégorisation ne provient ni de la perception ni du langage, mais pourrait plutôt refléter la pertinence des objets dans leur environnement. Pour évaluer la causalité entre la catégorisation et la dénomination, nous avons étudié un patient victime d’un AVC, RDS. Malgré des difficultés pour nommer les couleurs chromatiques, sa catégorisation des couleurs est relativement épargnée. Des expériences d'IRM multimodale ont révélé que la connectivité perception-langage est essentielle pour un nommage efficace des couleurs, mais pas pour leur catégorisation. Nous démontrons trois ségrégations fonctionnelles dans le traitement cortical des couleurs: (1) la catégorisation et la dénomination des couleurs, (2) la dénomination des couleurs chromatiques et achromatiques et (3) la connaissance des objets colorés et celle des couleurs abstraites. Les mécanismes corticaux du traitement des couleurs pourraient avoir pour objectif de lier des informations sensorielles et sémantiques afin de guider le comportement lié aux objets, en réalisant (1) une perception des couleurs stable, (2) des catégories de couleurs pertinentes et (3) des représentations mentales communes des formes et des couleurs. L'évolution culturelle peut avoir recyclé les circuits neuronaux concernés pour isoler la couleur de l'objet et l'étiqueter avec des noms de couleur.

LIST OF PUBLICATIONS

1. Siuda-Krzywicka, K., Boros, M., Bartolomeo, P., and Witzel, C. (2019). The biological bases of colour categories: from goldfish to the human brain. Cortex.
2. Siuda-Krzywicka, K., Witzel, C., Taga, M., Delanoe, M., Cohen, L., and Bartolomeo, P. When Colours split from Objects: The Disconnection of Colour Perception from Colour Language and Colour Knowledge. (*Accepted*) Cogn. Neuropsychol.
3. Siuda-Krzywicka, K., Witzel, C., Chabani, E., Seidel Malkinson, T., Taga, M., Coste, C., Cools, N., Ferrieux, S., Cohen, L., and Bartolomeo, P. Colour categorisation independent of colour naming. (*Accepted*) Cell Reports
4. Siuda-Krzywicka, K. & Bartolomeo, P. What cognitive neurology teaches us about our experience of color. (*Accepted*) the Neuroscientist

LIST OF SCIENTIFIC COMMUNICATIONS

1. Siuda-Krzywicka, K., Witzel, C., Chabani, E., Taga, M., Cohen, L., & Bartolomeo, P. (2018). *Colour categorization without colour naming: Neuropsychological evidence*. Paper presented at the Cognitive Neuroscience Society 25th Annual Meeting Boston, MA.
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Colour is my day-long obsession, joy and torment.
Claude Monet

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Antoś, Mila, this work was done with you, thanks to you and for you. Your mom.

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1 General introduction

Everything that you can see in the world around you presents itself to your eyes only as an arrangement of patches of different colours.
John Ruskin

Humans and other trichromats are lucky to live in a world enriched with myriads of colours. Apart from the indisputable aesthetic value, colours convey crucial information about the state and function of objects that surround us (Cuthill et al., 2017; Mollon, 1989). Colour differentiates edible from poisonous foods, indicates potential mating candidates, aids in recognition of predators and hiding from them (camouflage). Despite the tremendous ecological relevance of colour, seminal psychophysical and neuroimaging studies on object recognition and categorization ignored, to a large extend, the role of colour (e.g. Biederman & Ju, 1988; Grill-Spector & Weiner, 2014), leaving the field of high-level visual cognition basically colour-blind. As a result, while the low level mechanisms of colour perception have been thoroughly investigated (reviewed in Gegenfurtner & Kiper, 2003), the cortical pathways processing colours remain poorly understood (Conway, 2018; Gegenfurtner, 2003).

Low level mechanisms of colour perception occur in the retina and thalamus. Light that arrives to our eyes differentially excites three types of retinal photoreceptors, the S (from short wavelength sensitive), M (medium wavelength sensitive) and L (long wavelength sensitive) cones. This differential cone excitation is called a *first-stage mechanism* of colour perception. At the next stage, the cone signals are compared in the retinal ganglion cells and the lateral geniculate nucleus (LGN) of the thalamus (De Valois, Abramov, & Jacobs, 1966). This comparison, called *cone opponency*, translates cone excitations into three information channels: the luminance channel that summarizes the signals from L and M cones (L+M), the red-green channel consisting of the difference between L and M cones (L-M), and the blue-green channel, the sum of the L- and M-cone signals subtracted from the S-cone (S-(L+M)). These three channels are commonly referred to as *the cardinal directions of colour space* (Krauskopf, Williams, & Heeley, 1982), and the computation of the cone-opponent channels is referred to as *the second stage mechanism* of colour perception (Derrington, Krauskopf, & Lennie, 1984).

Each colour can be quantified as the amount of differential excitation of at least two types of cones. Yet, the transition between cone excitation and apparent object colour is not straightforward. Two identical objects give rise to a very different colour experience depending on the spatial and temporal context (Conway, 2009; Conway et al., 2010; Witzel & Gegenfurtner, 2018). Consider Figure 1A: patches A and B appear to have different colours, and patch B lays in the shade of the green cylinder. Yet, when we disregard the context of shade, the two patches are identical (Figure 1B). The way individuals interpret a given context also seems to matter. Consider figure 1C. This seemingly ordinary image of a dress took the Internet by the storm in 2015. Some observers reported seeing the dress as white and gold, while others saw it in blue and black. These striking individual differences in colour perception were attributed to the assumptions about illumination, e.g. whether observers reported to see the dress in the sunlight, artificial light or in a shadow (Lafer-Sousa, Hermann, & Conway, 2015; Witzel, Racey, & O'Regan, 2017). The dress is only one example of numerous environmental, psychological and cultural factors that modulate colour appearance (reviewed in: Witzel & Gegenfurtner, 2018). These top-down effects are the basis of the dissociation between the cardinal directions of colour space and the *perceptual colour space,* i.e. the organisation of colours that reflects how colours appear to the observer. Cone-opponent signals are transformed into the perceptual colour space through the *high-level mechanisms of colour vision* computed in the visual cortex (Eskew, 2009; Shepard, Lahlaf, & Eskew, 2017). This transformation can be understood in terms of an interaction between the bottom up input from photoreceptors and the top-down influence of knowledge and expectations about the world. Understanding the cortical mechanisms of colour processing would allow not only to understand how colour perception comes about, but also how the priors coming from life experience, education and culture can interact with visual perception in a more general way.

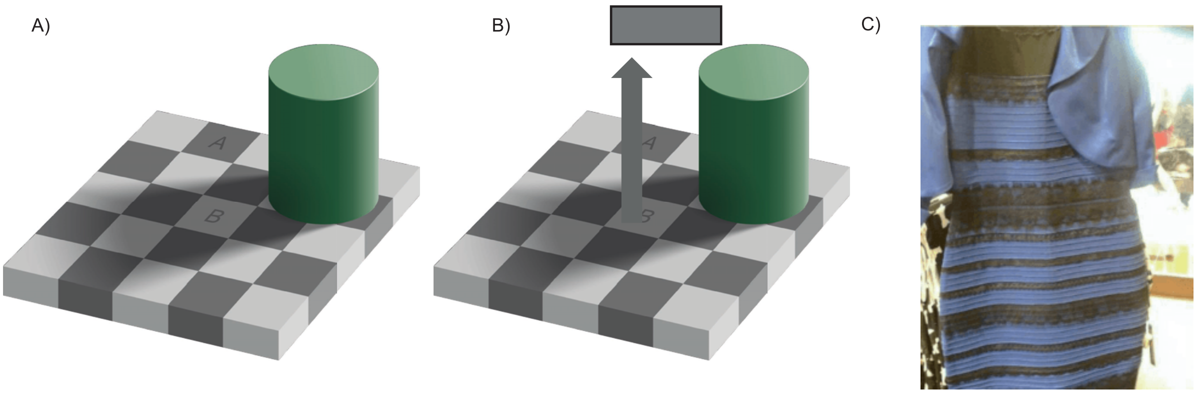

Figure 1. Examples of how our knowledge and expectations affect color perception. Color constancy allows for a stable object color representation over space and time. The patches A and B are identical (B), however the spatial context of the cylinder's shade makes them appear different (A). The viral Internet image of #theDress (C) revealed striking individual differences in color perception depending on individual assumptions about the object context. Sources: A and B "Checker shadow illusion" by Edward H. Adelson licensed under CC BY-SA 4.0. C Photograph of the dress by Cecilia Bleasdale licensed under WP: NFCC.

This thesis concerns the organisation of high-level colour cognition computed in the cortex. In this introduction, I review the state-of-the-art evidence on colour processing in the cortex coming from neuroimaging and neurophysiological investigations in human participants and electrophysiology and lesion studies in non-human primates. Then, I introduce the idea of modularity of cortical colour processing based on the reports of how brain damage affects colour processing in neurological patients. Finally, I discuss the theoretical and methodological aspects of single case studies and the extent to which they allow drawing inference about healthy cognitive architectures and their neural implementation.

1.1 Cortical colour processing

Colour inputs from the LGN reach the visual cortex through anatomically distinct, retino-geniculo-cortical pathways: the magnocellular pathway consisting mostly of luminance (L+M) sensitive cells; the parvocellular pathway transmitting the red-green (L-M) information; and the koniocellular pathway transmitting the yellow-blue information (S-(L+M) (e.g. Gegenfurtner & Kiper, 2003). In the visual cortex, colour representation is largely distributed: colour selective neurons can be found in the early visual cortex and in the ventral extra-striate regions (Brouwer & Heeger, 2009; Gegenfurtner, 2003), although there seems to be a qualitative difference between colour representation in the early and high-level visual cortices. While the colour representation in the early visual cortices resembles the cardinal directions of colour space, the representation in the extrastriate regions is tuned towards the perceptual colour space (e.g. Brouwer & Heeger, 2009).

1.1.1 Early visual cortex

The relationship between colour representation in V1 and colour perception is debated. Some demonstrated that colour-selective cells in V1, organised in a form of blobs, are tuned to the cardinal directions of colour space, showing similar tuning patterns to the LGN cells (Horwitz & Hass, 2012). Others showed that those cells show preference to colours associated with daylight suggesting a relationship with colour appearance (Conway, 2001; Lafer-Sousa, Liu, Lafer-Sousa, Wiest, & Conway, 2012). Colour-selective neurons in V1 may thus serve as an intermediate point between the low-level colour representation coming from the LGN and colour perception (Brouwer & Heeger, 2009). Neurons in V2, organised in a form of stripes, present tuning properties similar to V1 (Burkhalter & Van Essen, 1986; Kiper, Fenstemaker, & Gegenfurtner, 1997; Moutoussis & Zeki, 2002) and the correspondence between their tuning patterns and perceptual colour space is debated (Lim, Wang, Xiao, Hu, & Felleman, 2009; Xiao, Wang, & Felleman, 2003). The engagement of V3 in colour processing is less clear (Baizer, 1982; Brouwer & Heeger, 2009; Gegenfurtner, Kiper, & Levitt, 1997; Wade, Brewer, Rieger, & Wandell, 2002).

1.1.2 Extrastriate cortex

There are distinct, highly colour-biased regions within the mosaic of the category-selective regions in the ventral extra-striate cortex of both human (Grill-Spector & Weiner, 2014) and non-human primates (Lafer-Sousa & Conway, 2013). In non-human primates the areas are referred to as V4 and PIT (Conway, Moeller, & Tsao, 2007). V4 and PIT contain colour-biased subregions dubbed *globs* that are separated by regions showing lower colour bias, called the *interglobs* (Conway et al., 2007). Glob cells show narrow colour tuning and the organisation of colours they represent share similarities with colour spaces modelling perceptual colour space. Glob cells retain their hue tuning across luminance levels, showing some levels of hue-invariance. Interglob cells, on the other hand, show broader colour tuning and preference for changes in luminance levels, what implicates their engagement in cognitive functions coupling colour and luminance information such as e.g. detection of colour boundaries in object recognition (Bohon, Hermann, Hansen, & Conway, 2016). Colour-biased cells in PIT were shown to prefer colours that are more often present on objects rather than scenes (Rosenthal, Ratnasingam, Haile, Eastman, Fuller-Deets, & Conway, 2018).

This suggests that those regions are involved in high-level colour mechanisms giving rise to colour appearance and the computation of object colours.

In humans, colour-biased regions were demonstrated in fMRI using retinotopic mapping and task-fMRI. Retinotopic mapping (Figure 2A) identified two extrastriate clusters showing colour bias: a ventral area adjacent to V3 dubbed hV4 (human equivalent of the area V4, Wade et al., 2002); and VO, anterior to the hV4 and divided into two subsections VO1 and VO2 (Brewer, Liu, Wade, & Wandell, 2005). hV4 and VO show distinct retinotopic maps covering the entire contralateral hemifield and the fovea. hV4 was shown to be strictly colour selective, while VO showed both colour and object selectivity. Interestingly, regions lateral to VO1 showed lateralization in colour responsiveness, the regions located in the right hemisphere responded more strongly to colours (Brewer et al., 2005).

Task fMRI demonstrated three distinct, colour selective regions dubbed the posterior, central and anterior colour regions (Figure 2A; Lafer-Sousa, Conway, & Kanwisher, 2016). The posterior and central colour regions, mentioned also in earlier neuroimaging studies (McKeefry & Zeki, 1997; Simmons, Ramjee, Beauchamp, McRae, Martin, & Barsalou, 2007; Zeki & Marini, 1998) correspond to the locations of hV4 and VO1 retinotopic regions, respectively, and respond selectively to colour, with little or no sensitivity to other visual categories (such as faces and objects). The anterior colour region (reported also in Simmons et al., 2007) lies more anterior to the VO complex and responds to both colours and objects. Importantly, other category-biased regions such as the face of object-biased areas show little sensitivity to colour, relying primarily on luminance information (Lafer-Sousa et al., 2016). This suggests that form and colour are processed by separate neural pathways in the posterior portions of the ventral visual stream (Conway, 2018). Task fMRI did not confirm the right-sided lateralization of colour response in the ventral visual stream suggested with retinotopy. The causal role of the extrastriate visual regions in colour perception was confirmed by electrical stimulations experiments in epileptic patients (Murphey, Yoshor, & Beauchamp, 2008; Schalk et al., 2017) and by detailed studies on neurological patients reviewed below.

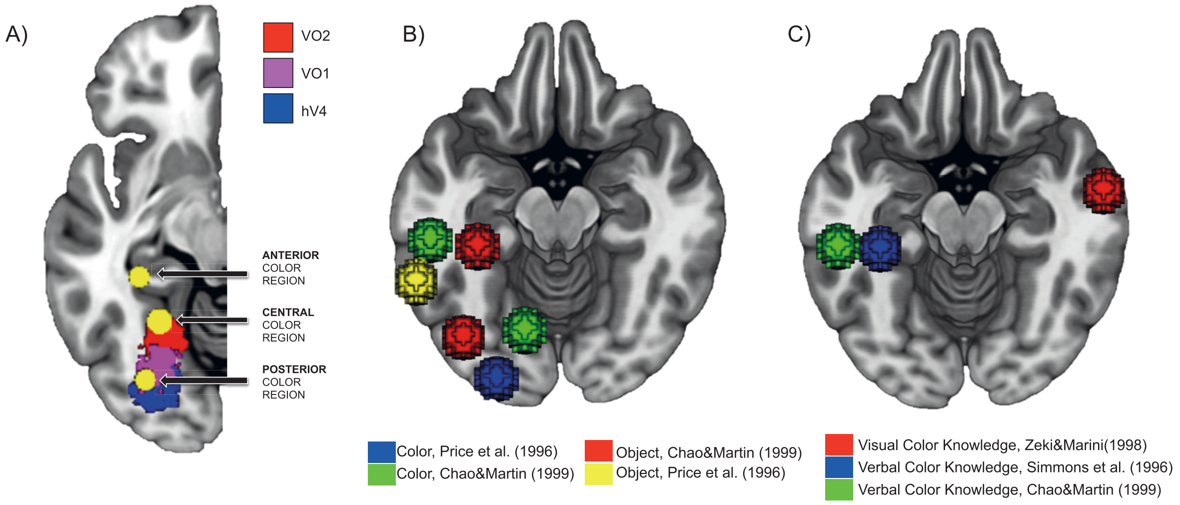

Figure 2. Cortical color processing. Cortical color-biased regions were demonstrated with retinotopy (blue, violet and red patches, Wang et al., 2015) and task-fMRI (yellow 5mm spheres centered on peak activities reported in Lafer-Sousa et al., 2016). High-level color-related functions selectively activate different, non-overlapping regions in the occipito-temporal cortex. 5 mm. spheres are centered on the fMRI activation peaks for color naming (B) and color knowledge (C).

1.1.3 The model of organisation of colour processing in the ventral visual stream.

It was recently suggested that cortical colour processing is organised in a hierarchy (Conway, 2018), similar to the idea of the hierarchical processing of faces (Freiwald & Tsao, 2010). In such a hierarchy, posterior colour-biased regions encode single hues and compute the perceptual colour space. The perceptual colour space is the basic input of high-level cognitive functions processing colour information. Then, the central colour-biased regions group colours, varying continuously in hue, lightness and saturation, into behaviourally relevant ensembles, i.e. *colour categories* that in humans are associated with specific colour names (green, yellow etc). Finally, the anterior colour-regions represent the memory of colours typical for given objects, i.e. object-colour knowledge (Conway, 2018).

Several neuroimaging and neurophysiological studies provide some support to the idea of a hierarchical processing of colour in the ventral visual stream. fMRI activation patterns analysis revealed that colour representation in V4 and VO encoded colours organised around perceptual similarity, suggesting the existence of perceptual colour space in those regions (Brouwer & Heeger, 2009). The evidence towards the engagement of the central colour regions in colour naming and categorisation is mixed. In pioneering fMRI investigations, colour naming was associated with selective activity in the central portions of the lingual and fusiform gyri (Figure 2B; Chao & Martin, 1999; Price, Moore, Humphreys, Frackowiak, & Friston, 1996). One more recent study demonstrated categorical clustering of neural patterns evoked by naming visually presented colours (Brouwer & Heeger, 2013), but others did not (Persichetti, Thompson-Schill, Butt, Brainard, & Aguirre, 2015, discussed in detail in Chapter 2).

Anterior colour regions were activated in tasks requiring the retrieval of object colour knowledge (Figure 2 C; Chao & Martin, 1999; Simmons et al., 2007; Zeki & Marini, 1998). Retrieving object-colour knowledge verbally was associated with activity in the left inferior temporal cortex (in naming typical colours of achromatic objects, Chao & Martin, 1999), left mid-fusiform gyrus (in verbally associating object and colour names, Simmons et al., 2007). Object-colour knowledge retrieved visually was associated with activity in bilateral areas anterior to VO (during viewing of typically vs. atypically coloured objects, Zeki & Marini, 1998). Recent fMRI studies suggested that regions encoding object-colour knowledge send top-down signals to the early visual cortex (Bannert & Bartels, 2013; Vandenbroucke, Fahrenfort, Meuwese, Scholte, & Lamme, 2014). This result corroborates behavioral studies showing that memory-colour affects the perception of colour-diagnostic objects (Hansen, Olkkonen, Walter, & Gegenfurtner, 2006; Witzel, Valkova, Hansen, & Gegenfurtner, 2011); and with neurophysiological data suggesting that the early visual cortex may receive top-down inputs and constitutes an intermediate step between cardinal and perceptual colour space (Brouwer & Heeger, 2009; Conway, 2001; Lafer-Sousa et al., 2012).

In sum, the fMRI results hint a possible hierarchy of colour processing. Colour categorization could involve bilateral, central colour-biased regions, colour naming - the left central colour-biased regions, and colour knowledge - the anterior colour-biased regions, with verbal colour knowledge lateralized to the left. However, given the correlational character of fMRI measurements, it is unclear to what extent these different areas are specific to a given function. Also, the hierarchical model (Conway, 2018) assumes some level of functional segregation between different high-level colour processing functions which cannot be stated with fMRI. These questions can be answered by looking at studies of neurological patients with acquired brain damage.

1.2 The modules of cortical colour processing

The question regarding the functional segregation between different colour-processing functions has been addressed in studies on colour-related cognitive impairments resulting from brain damage. These studies demonstrated at least three functionally segregated modules of colour processing: conscious colour perception, colour naming and colour knowledge.

1.2.1 Conscious Colour Perception

Lesions to the ventral occipito-temporal regions can lead to the loss of conscious colour experience, a symptom dubbed *achromatopsia* (Bartolomeo, Bachoud-Lévi, & Thiebaut de Schotten, 2014; Bouvier & Engel, 2006; Short & Graff-Radford, 2001). Such patients report seeing the world in shades of black, white or brown (sepia). I define achromatopsia as a deficit in conscious colour experience, because subjective reports of colour vision loss are often associated with normal or close-to-normal performance on colour vision tests. The most extensive meta-nalysis of patients with achromatopsia (Bouvier & Engel, 2006) reported that 29% of achromatic patients tested with the Ishihiara plates read them normally; a majority of those tested with the Fansworth Munsell 100 Hue test performed better than chance (some even performed normally); and, strikingly, 49% of the patients who were asked to name colours succeeded in the task. One case report of achromatopsia demonstrated that patient's response certainty correlated with colour recognition scores (Carota & Calabrese, 2013). Given these observations it seems inappropriate to define achromatopsia as an objective colour vision loss. Achromatopsia oftentimes co-occur with prosopagnosia (Bouvier & Engel, 2006), most likely due to the close proximity of the cortical face and colour-biased regions (Lafer-Sousa et al., 2016). The cooccurrence of achromatopsia and alexia or object agnosia is less prevalent (Bouvier & Engel, 2006).

Lesions that lead to achromatopsia coincide with the location of the posterior colour centres reported in fMRI (Bouvier & Engel, 2006; Lafer-Sousa et al., 2016; Zeki & Marini, 1998). Unilateral lesions can lead to achromatopsia restricted to contralateral visual hemifield, consistent with the reports of retinotopic organisation of colour-biased regions (Brewer et al., 2005; Wade et al., 2002). Achromatopsia is more prevalent in right-hemispheric lesions and in rare cases achromatopsia encompassing the entire visual field can occur after a right-sided lesion (e.g. Bartolomeo, Bachoud-Lévi, & Thiebaut de Schotten, 2014). These observations are consistent with the reports of lateralization in colour selectivity (Brewer et al., 2005), but in some cases could also be explained by white matter disconnection. However, white-matter connectivity analysis is seldom performed in achromatopsic patients (Bartolomeo et al., 2014).

Reports of achromatopsic patients suggest that posterior colour-biased regions may serve as the cortical centre of conscious colour experience. Such a centre may integrate inputs from the earlier stages of colour perception and high-level cortical networks responsible for conscious experience (Dehaene & Changeux, 2011).

1.2.2 Colour naming

Lesions located in the left occipito-temporal cortex can cause selective deficits is colour naming. Such patients present selective difficulties in naming visually presented colours with spared colour perception and object-colour knowledge. First report of such a patient by Wilbrand (1887) was followed by numerous similar case-reports summarized in Table 1. In this thesis I will divide patients with colour naming deficits into two subtypes (as proposed by De Vreese, 1988; Oxbury, Oxbury, & Humphrey, 1969): (1) *colour-name anomia* where patients cannot name visually presented colours, retrieve colour names from memory and verbally associate objects with their typical colour (e.g. banana-yellow); and (2) *visuo-verbal disconnection of colours* or *optic aphasia for colours,* where patients are able to recall colour names or verbally associate colours with objects, but they cannot name visually presented colours nor point to colours on verbal cues. It is noteworthy that this classification is very coarse, and that patients with colour-naming deficits present heterogenous symptomatology (Table 1). It might be that the deficits of colour naming, or more broadly colour language, are better depicted as a spectrum rather than discrete subtypes. However, the sparsity of reports dominated by case studies examined with different tests and experiments makes it impossible to reliably reconstruct such a spectrum. It is also important to mention that in this classification patients are diagnosed with selective colour naming deficits when their symptoms are limited to language functions. Patients showing impairments in purely visual tasks, such as differentiating between typically from atypically coloured objects, are classified as *colour agnosic* (De Vreese, 1988)[1]. Colour agnosia is discussed in the next section.

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[1] Note that some use the term colour agnosia when referring to colour naming deficits (e.g. Mohr, Leicester, Stoddard, & Sidman, 1971).

Table 1. Summary of case reports presenting colour-naming deficits. Colour naming=naming of visually presented colours; object-colour naming=naming of colours of typically coloured objects; colour-name matching=associating visually presented colours with colour names presented auditorily, includes colour pointing; verbal colour-objects association=ability of saying a typical colour of a cited objects or vice versa; object naming=naming of visually presented objects. Imp=impaired; Norm=normal; NA=not assessed.

ARTICLE	COLOUR NAMING	OBJECT-COLOUR NAMING	COLOUR-NAME MATCHING	VERBAL COLOUR-OBJECT ASSOCIATIONS	OBJECT NAMING
STENGEL ET AL. (1947) CASE 1	Imp	Imp	NA	Imp	Norm
STENGEL ET AL. (1947) CASE 2	Imp	Imp	NA	Imp	Norm
KINSBOURNE AND WARRINGTON (1964)	Imp	Imp[a]	Imp	Imp	Imp
GESCHWIND AND FUSILLO (1966)	Imp	Imp	Imp	Norm	Norm
OXBURY ET AL. (1969) CASE 1	Imp	NA	Imp	Norm	Imp
OXBURY ET AL. (1969) CASE 2	Imp	NA	Imp	Imp	Imp
MOHR ET AL. (1971)	Imp	NA	Norm[b]	Norm	Norm
STACHOWIAK & POECK (1976)	Imp	NA	Imp	Norm	Imp
DAVIDOFF & OSTERGAARD (1984)	Imp	NA	Norm[b]	NA	Norm
BEAUVOIS AND SAILLANT (1985) CASE MP	Imp	Imp	Imp	Norm	Imp[d]
FUKUZAWA ET AL. (1988) CASE 1	Imp	NA	Imp	Norm	Imp
DE VREESE 1991 CASE 1	Imp	Norm	NA	Norm[c]	Imp
DE VREESE 1991 CASE 2	Imp	Norm	NA	Norm[c]	Imp

Note: [a] except for black and white objects; [b] with no delay; when a delay between colour and name presentation was introduced, the accuracy dropped. [c] for highly colour-diagnostic objects (e.g. banana, strawberry), [d] severe naming impairment.

To the best of my knowledge, all colour-naming deficits reported in the literature are associated with reading deficits (pure alexia) and right homonymous hemianopia (see also: Damasio & Damasio, 1983). Oftentimes they co-occur with global naming impairment - in these cases colour-naming deficits are diagnosed when colour deficits are more pronounced than deficits for other visual categories such as objects or faces (Beauvois & Saillant, 1985; De Vreese, 1991; Fukuzawa, Itoh, Sasanuma, Suzuki, Fukusako, & Masui, 1988; Kinsbourne & Warrington, 1964; Oxbury et al., 1969; Stachowiak & Poeck, 1976).

Lesions that cause colour naming deficits are usually located in the left mesial occipito-temporal areas, comprising the lingual, fusiform and parahippocampal gyri (A. Damasio & Damasio, 1983). They usually comprise the callosal splenium, but not always (Mohr, Leicester, Stoddard, & Sidman, 1971). There are several neuro-cognitive hypotheses of the origin of colour specific naming deficits. Some say that colour anomia is a symptom of general naming deficits, and more impaired colour naming is simply due to the fact that colour naming is more difficult than naming other categories (discussed in De Vreese, 1988, but see Goodglass *et al.*, 1966). The dissociation between colour naming and colour name matching (Davidoff & Ostergaard, 1984; Mohr et al., 1971) is explained in terms of colour-selective short-term memory deficit. The visual memory trace of colours is unstable, causing difficulties in associating colour names to colours (Davidoff & Ostergaard, 1984; see also learning experiments in Oxbury et al., 1969). Some argue that naming colours may depend on a separate neuro-cognitive system that naming objects, and that colour naming deficits result from a deficit to this system (Bornstein, 1985; A. Damasio & Damasio, 1983). Colour anomia could occur due to a lesion to the left-sided language areas, in regions specifically involved in storing colour lexicon (De Vreese, 1988; Kinsbourne & Warrington, 1964; Oxbury et al., 1969). This would imply that there is a high degree of differentiation within the cortex underpinning lexicon storage.

There are two main hypotheses explaining the neuro-cognitive underpinnings of optic aphasia for colour. According to the first one, visual color information cannot reach the language system because the left visual cortex is damaged and interhemispheric transfer from the right visual cortex is prevented by a caudal callosal lesion (Geschwind & Fusillo, 1966). Naming of other visual categories is spared because their representations activate tactile associations that can reach the left hemisphere via more anterior portions of corpus callosum. The second hypothesis stipulates that color information can reach the left hemisphere through the anterior corpus callosum, but it cannot reach the language system because of damage to a cortical color-naming hub, linking colors to their names (A. Damasio & Damasio, 1983).

The existence of colour-specific naming deficits demonstrates that there is a separate module in the hierarchy of colour processing that is specifically engaged in linking perceived colours with their names and in storing colour-related language (colour lexicon). This module is functionally segregated from colour perception and colour knowledge.

1.2.3 Object-colour knowledge

Rarely, lesions in left ventral visual stream cause selective loss of associations between objects and their typical colours, a symptom dubbed *colour agnosia* (Luzzatti and Davidoff, 1994; Davidoff, 1996; Woodward *et al.*, 1999; Miceli *et al.*, 2001; Stasenko *et al.*, 2014; note a case of developmental colour agnosia: Zandvoort, Nijboer and Haan, 2007). Colour agnosia is understood as a selective deficit of object-colour knowledge, and it can affect the visual colour knowledge, i.e. the ability to visually differentiate between typical and atypical colours of objects, or verbal colour knowledge, i.e. the ability to associate colour names with object names (reviewed in: Tanaka, Weiskopf, & Williams, 2001).

Table 2 Summary of case reports presenting colour agnosia. Colour verification=differentiating between typically and atypically coloured objects; object-colour matching=matching black-and-white object drawings/pictures to colour patches/crayons; verbal colour knowledge=verbal associations between object and colour names; object property knowledge=knowledge about non-colour features of objects (parts, size, weight etc.) All other abbreviations are as in Table 1.

ARTICLE	COLOUR VERIFICATION	OBJECT-COLOUR MATCHING	VERBAL COLOUR KNOWLEDGE	COLOUR NAMING	OBJECT NAMING	OBJECT PROPERTY KNOWLEDGE
LEWANDOWSKY (1908)	Imp	Imp	Imp	Imp	Norm	NA
BEAUVOIS AND SAILLANT (1985) CASE R.V.	Imp[a]	Imp[a]	Norm[a]	Imp*	Imp[b]	NA
FUKUZAWA ET AL. (1988) CASE 2	Imp	NA	Imp	Imp	Imp	NA
LUZZATTI AND DAVIDOFF (1994) CASE G.G.	Imp*	Imp*	Imp*	Norm	Imp[c]	Imp
LUZZATTI AND DAVIDOFF (1994) CASE A.V.	Imp*	Imp*	Imp*	Norm[d]	Norm	Imp
MICELI ET AL. (2001) CASE P.C.O.	Imp	Imp[c]	Imp[c]	Norm	Imp	Imp[c]
MICELI ET AL. (2001) CASE I.O.C.	Imp	Imp	Imp	Norm	Imp	Norm
STASENKO ET AL.(2015)	Imp	Imp	Imp	Norm	Imp[c]	Norm

Note: [a]when relying on verbal mediations; [b]agnosic rather than aphasic errors; [c]more impaired for animate than inanimate objects; [d]accurate but slow

Similar to colour-naming deficits, symptoms associated with colour agnosia are heterogenous (Table 2). The majority of cases present a global deficit in colour knowledge, comprising both visual and verbal modalities (Luzzatti & Davidoff, 1994; Miceli et al., 2001; Stasenko et al., 2014; Woodward et al., 1999), however dissociations between verbal and visual colour knowledge also occur (Beauvois & Saillant, 1985). Most cases of colour agnosia present spared or only slightly impaired colour-naming (Luzzatti & Davidoff, 1994; Miceli et al., 2001; Stasenko et al., 2014), but there are patients that show a deep disturbance in high-level colour processing, involving both colour naming and colour knowledge (Fukuzawa et al., 1988; Woodward et al., 1999). Colour agnosia can be associated with impairment in more general object knowledge (Luzzatti & Davidoff, 1994), but in some cases a selective deficit in object-colour knowledge can occur (Miceli et al., 2001; Stasenko et al., 2014). In the majority of cases, object naming is impaired (Beauvois & Saillant, 1985; Luzzatti & Davidoff, 1994; Miceli et al., 2001; Stasenko et al., 2014; Woodward et al., 1999), and in some cases colour knowledge is harder to retrieve for objects whose naming is impaired (but see IOC in Miceli et al., 2001 and AC in Stasenko et al., 2014). The co-occurrence with reading disorder is frequent, but colour agnosia can appear with spared reading (case GG in Luzzatti & Davidoff, 1994). Also, hemianopia does not necessarily occur (see case AV in Luzzatti & Davidoff, 1994).

Lesions causing colour agnosia are usually located in the left occipito-temporal cortex. Case reports specifically mention damage to the left anterior temporal lobe (Case GG in Luzzatti & Davidoff, 1994 and IOC in Miceli et al., 2001), the ventro-rostral portions of the lingual gyrus (Stasenko et al., 2014, AV in Luzzatti & Davidoff, 1994, IOC in Miceli et al., 2001), medial fusiform gyrus (IOC in Miceli et al., 2001; Stasenko et al., 2014), the isthmus (I.O.C. in Miceli et al., 2001; Stasenko et al., 2014), and the parahippocampal areas (I.O.C. in Miceli et al., 2001). Parietal damage was also reported (Case A.V. in Luzzatti & Davidoff, 1994; Stasenko et al., 2014).

The existence of colour agnosia supports the idea that different, non-overlapping neural modules process colour perception, naming and knowledge. The exact organization of object-colour knowledge is still debated, with two competing models. The first, stemming from the edge-based theories of object recognition, states that object-colour knowledge is organized around the associations between the achromatic representation of shape and a representation of memory colour (e.g. Biederman & Ju, 1988). Alternative theories suggest that colour knowledge is stored as a set of coloured templates, joint representations of both shape and colour (reviewed in: Tanaka, Weiskopf, & Williams, 2001). This issue is discussed in detail in chapter 4.

1.2.4 Summary

Detailed studies of colour processing in neurological patients support the existence of a hierarchy of high-level colour processing and suggest the following principles of its organisation.

First, high-level, cortical colour processing is divided into separate modules that can be independent from each other. Conscious colour perception can dissociate from colour knowledge, colour imagery or even colour naming. Also colour naming and colour knowledge can be independent from each other.

Second, colours seem to be processed by neural modules that are separate from form-processing modules. This conclusion is congruent with fMRI evidence showing differential pathways processing form, colour and texture (Cavina-Pratesi, Kentridge, Heywood, & Milner, 2010; Lafer-Sousa et al., 2016). The dissociation between colour and form processing occurred at every level considered in the present chapter, namely: conscious perception, naming and knowledge.

Third, this modular hierarchy may be implemented in the brain in the occipito-temporal regions along the anterior-posterior axis. Lesions overlapping with posterior colour-biased regions cause impairments in conscious colour processing. Lesions coinciding with anterior colour-biased regions in the left hemisphere cause impairments in object colour knowledge. Finally, left-sided lesions to mesial portions of the ventral visual stream cause impairments in colour naming. The effects of lesions lateralisation implicate that the right hemisphere may be more engaged in conscious colour perception, while the left hemisphere may subserve colour naming and object colour knowledge.

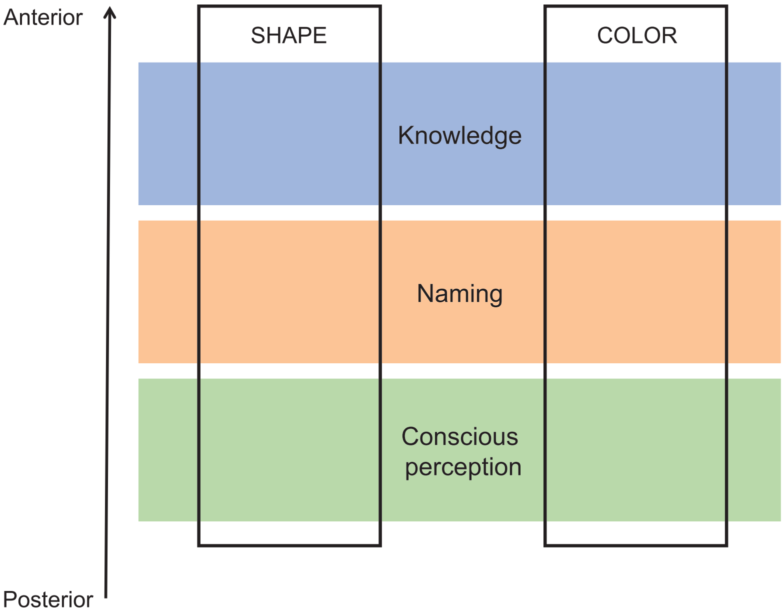

Figure 3. A schematic drawing of a hierarchy of cortical colour processing. Colour is processed in a separate pathways from shape at the three identified levels of processing: conscious perception, naming and knowledge. The arrow indicates a possible organization on the posterior/anterior axis of the occipito-temporal cortex.

1.3 Theoretical and methodological issues in single-case approach

The above-mentioned principles on the organisation of colour processing in the ventral visual stream are based on studies on single neurological patients. Reports of surprising patterns of behaviour in patients with brain lesions are considered by some as the origin of cognitive neuroscience (e.g. Geschwind, 1997). Yet, it is debated to what extent it is legitimate to draw inference about the structure of normal cognitive systems from patterns of impaired performance in single patients (Adolphs, 2016; Bartolomeo, Seidel Malkinson, & de Vito, 2016; Coltheart, 2017; Fischer-Baum & Campana, 2017; Medina & Fischer-Baum, 2017; Patterson & Plaut, 2009; Rorden & Karnath, 2004). Below, I review this debate.

1.3.1 The theory behind single-case studies

The validity of the single-case approach is predicated on four basic assumptions (Caramazza, 1984, 1986). *The assumption of universality* stipulates that the architecture of the cognitive system follows the same principles in all neurologically intact individuals. According to this assumption, any individual differences should be considered noise that cancels out in the averaging of response patterns. Second, *the assumption of transparency* states that the cognitive system of a brain-damaged patient is fundamentally the same as that of a normal subject except for a “local” modification of the system caused by the brain lesion. This assumption rejects the possibility that brain damage creates a novel cognitive architecture in the place of the damaged ones. Third, *the modularity assumption* states that complex cognitive functions can be broken into more basic components, or modules. Fourth, *the fractionation assumption* states that brain damage can result in selective impairments of those components, in the sense that for any particular patient some components of cognition are impaired while others are preserved. When these assumptions are not met, drawing inference on a normal cognitive system from abnormal behaviors caused by brain lesion is considered logically flawed.

The existence of selective, cognitive impairments in patients with circumscribed brain lesions validates the fractionation assumption; thus, this assumption will not be discussed further. The other three assumptions have been widely criticized in the face of recent methodological and theoretical developments in cognitive neuroimaging (Adolphs, 2016; Coltheart, 2017; Rorden & Karnath, 2004). Regarding the universality assumption, recent findings in neuroimaging demonstrated that significant interpersonal variation in brain anatomy, connectivity and function can be correlated with human behaviour (reviewed in Bartolomeo, Seidel Malkinson, & de Vito, 2016). These observations implicate that individual differences, neglected by the universality assumption as non-informative noise, may actually be informative about cognition and behaviour. Findings on cortical plasticity undermined the transparency assumption. Even short-term training can induce chances in the brain structure and function (e.g. Bola et al., 2017; Siuda-Krzywicka et al., 2016; Striem-Amit, Cohen, Dehaene, & Amedi, 2012), not to mention the massive cortical reorganisation that can appear after stroke (reviewed in: Fischer-Baum & Campana, 2017). Therefore, it is unlikely that changes caused by brain damage are limited only to the localized areas. Finally, complex cognitive functions seem to be supported by distributed brain networks (Behrmann & Plaut, 2013; Freud, Plaut, & Behrmann, 2016; Mesulam, 1990), rather than localized modules. For instance, the activity patterns of colour-biased cortical regions depends on top-down signals from distant cortical areas (Brouwer & Heeger, 2013; Koida & Komatsu, 2007). This was taken as a criticism of the modularity assumption.

Did the development of neuroimaging make single case reports obsolete? Novel neuroimaging and neurophysiological techniques keeps challenging our understanding or brain's structural and functional organization (Bedny, 2017; Mur, Bandettini, & Kriegeskorte, 2009; Pascual-Leone & Hamilton, 2001; Tal Yarkoni & Westfall, 2017). However, neuroimaging techniques also have limitations. Statistically complex, they are prone to errors and misuse (e.g. Kriegeskorte, Simmons, Bellgowan, & Baker, 2009; Vul, Harris, Winkielman, & Pashler, 2009; Yarkoni, 2009). More importantly, functional neuroimaging techniques are based on the correlations between brain signals and behavior, and thus does not allow for causal inferences. The extent to which neuroimaging can theoretically advance our view on the organisation of the cognitive architectures is debated (Coltheart, 2006). Au contraire, studying brain-lesioned patients can drive radical changes of models of cognitive architectures because some patients demonstrate dissociations in cognition that could never be observed in the healthy individuals (reviewed in: McCloskey & Chaisilprungraung, 2017).

Theorizing about cognitive processes can be divided in two separate strands. One strand regards the organization of cognitive architectures; the second concerns its neural implementation (Shallice, 2009). Although related, these two strands can be considered orthogonal (Coltheart, 2017; Fischer-Baum & Campana, 2017; Medina & Fischer-Baum, 2017; Shallice, 2009). When we do so, it can be easily stated that the main criticism of the single-case approach considers the second strand, i.e. drawing inference about the neural substrates of cognition in neurotypical individuals. The four core assumptions of cognitive neuropsychology remain robust when only the first, cognitive strand is considered.

Consider the assumption of transparency. Even though brain plasticity can lead to reorganisation of the neural implementation of cognitive functions, the cognitive functions themselves remain qualitatively unchanged - until now no-one reported the emergence of a completely new cognitive function as a result of brain damage. In this sense, the assumption of transparency is robust against plastic changes in the brain, provided that the inference made is limited to the organisation of cognitive architecture, excluding its neural implementation (Fischer-Baum & Campana, 2017).

Similar arguments apply to modularity. The fact that complex psychological functions are implemented in the brain as networks rather than circumscribed centres does not imply that cognitive processes by themselves are not modular (Coltheart, 2017). Moreover, the assumption of modularity does not exclude the possibility that the modules themselves are interactive (see Coltheart, 2017 in response to Patterson & Plaut, 2009; and p. 1 in ; Fodor, 1983). The recent advances in neuroimaging allow relating symptoms of single patients not only the lesion locations but also to entire brain networks (Thiebaut de Schotten & Foulon, 2018), conciliating the assumption of cognitive modularity with the connectionist view of brain organisation.

Regarding the universality assumption, the inter-subject variability limits the extent to which we can generalise observations from a single-patient to the entire population on both cognitive and neural level (it is however noteworthy that individual differences and replicability of psychological research is a more general issue not restricted to the field of single-case studies, e.g. Shrout & Rodgers, 2018). Yet, this assumption can be met provided an appropriate study design (Bartolomeo et al., 2016; Coltheart, 2017). First, referring a single patient to a demographically matched control group allows to approximate the patient's premorbid cognitive state. Age and education are obvious examples of variables on which patients and controls should be matched. On top of that, they should be matched on variables important for a given study (Caramazza, 1986; Coltheart, 2017). For instance, if one wants to study spatial memory in a single patient that used to be a taxi driver, it could be noteworthy to recruit neurotypical taxi drivers as a control group. Second, to control for idiosyncratic patterns of behaviour, single patients should be tested on several occasions. This allows controlling for confounds such as malingering, cognitive fatigue or stroke-induced performance variability (e.g. Corballis, Corballis, Fabri, Paggi, & Manzoni, 2005). Finally, the best source of evidence for meeting the universality assumption is to replicate findings in other patients presenting similar symptoms (Bartolomeo et al., 2016).

Finally, the seminal theoretical papers regarding single-case approach in cognitive neuropsychology clearly state that this approach allows to test specific, a priori models of cognitive architectures (Caramazza, 1986). Single-case reports need to be built on a strong theoretical background to allow drawing inference about healthy cognition. Exploratory single-case studies, while interesting and potentially informative, do not allow to conclude anything regarding healthy cognitive architectures.

In sum, the objections that have been raised against the assumptions of the single-case approach do not seem to pose insurmountable problems provided that one limits the conclusions to the level of cognitive architectures. It is however tempting to draw inferences about the neural substrates of cognitive architectures, especially in the case of well-defined lesions and highly selective impairments. Keeping in mind that single case reports provide substantially weaker evidence regarding neural substrates than regarding cognitive architectures (Fischer-Baum & Campana, 2017; Rorden & Karnath, 2004), inferences about the latter can be drawn thanks to the increasing availability of MRI machines and open-access

MRI big data repositories. fMRI experiments in single patients can demonstrate the neural substrates of patient's cognitive architectures and rule out (or confirm) any brain plasticity that could yield patient's brain different from the demographically-matched controls. Open-access big-data repositories allow to refer one single patient to big control groups without the hassle of subject recruitment and testing. Finally, novel tools allow to refer lesion locations to atlases of functional brain regions, and structural and functional connectivity (e.g. Foulon et al., 2018). These advances make detailed and multimodal neuroimaging assessment of single subjects feasible. In that sense, advances in neuroimaging and increasing accessibility of MRI techniques can strengthen the conclusions regarding neural substrates based on single subjects

1.3.2 Methodological challenges in the single-case approach

The methodology behind the single-case approach is built around the idea of a dissociation, i.e. a differential performance on two tasks measuring different aspects of a cognitive model of interest (see e.g. Caramazza, 1984; Shallice, 1988) For instance, a deficit in reading with spared visual object identification in a neurological patient can be taken as evidence for the independence between the visual processing of objects and orthographic material.

Stating the existence of a dissociation requires a set of statistical operationalisations. It is needed to define precisely a) what is understood as a deficit or a performance within a normal range; b) when the difference between the two tasks is big enough to state the dissociation. Such operationalisations were provided by Crawford and colleagues (Crawford, Garthwaite, & Gray, 2003; Crawford, Garthwaite, & Porter, 2010; Crawford & Howell, 1998).

The Crawford methods are developed around a modification of a two-samples t-test that allows to compare a single subject's performance with a group of controls' (Crawford & Howell, 1998). This test (hereafter referred to as Crawford and Howell t-test, or CH t-test) is a modification of the independent samples t-test, where the patient is treated as a group with n = 1, and consequently does not participate in the calculation of the variance (see Equation1).

$$t = \frac{x - \bar{x}}{s\sqrt{(n+1)/n}}$$

Equation 1. Modified two-samples t-test, comparing single case results to a group of healthy controls. x is the patient's score, x̄ and s are the mean and standard deviation of scores in the control sample respectively, and n is the size of the control sample.

CH t-test assesses whether the patient's score is sufficiently below those of the controls to reject the null hypothesis that the patient's performance is an observation from the control population. Importantly, the one-tailed p value of this test also provides an estimated percentile of the population with a score lower than that of the patient (Crawford et al., 2010). For instance, p=0.05 means that 5% of healthy population are expected to obtain a score lower that the patient.

The Revised Standardized Difference Test (RSDT, Crawford & Garthwaite, 2005b) allows to assess the dissociations. It compares the difference between a single patient's performance in tasks X and Y, relative to the corresponding difference in performance in the healthy control group. Its logic follows a slight modification of a paired t-test presented in Equation 3:

$$t = \frac{(x - \bar{x}) - (y - \bar{y})}{\sqrt{\left(s_x^2 + s_y^2 - 2 \ \ s_x s_y r_{xy}\ \right) * \left(\frac{n+1}{n}\right)}}$$

Equation 2 The Revised Standardized Difference Test (RSDT): a modified paired t-test, comparing results in two tasks in a single case and a group of healthy controls. x and y are the scores of the patient on tasks x and y, respectively, and $\bar{x}$ and $\bar{y}$ are the corresponding control means. The first bracketed term under the radical sign is the variance of the difference for controls, and it is obtained from the variance of tasks x and y in the controls (s_x and s_y) and the covariance of x and y ($s_X s_Y r_{xy}$) in controls; the p value of this test statistic can be derived from a t distribution on $n_{controls}$-1 degrees of freedom.

Garthwaite & Crawford (2004) proposed a modification of Equation 2 to allow for the standardization of a case's score while controlling for Type I error rate. They used asymptotic expansions to obtain a test statistic that closely approximates a t distribution when the patient's score has been standardized. This modification is what constitutes the RSDT. The derivation of this modification is long and technical, and beyond the scope of this thesis, thus I will not discuss it in detail (see Garthwaite & Crawford, 2004 for derivation and in depth explanations). Still, the overall logic of the RSDT can be readily appreciated by looking at Eq 2 .

Based on these two statistical operationalizations, Crawford and colleagues proposed the following definitions of deficit and dissociation (Crawford et al., 2003): a *deficit* occurs when a patient's score is significantly lower than controls when tested with the CH t-test. Conversely, if the patient's score doesn't differ significantly from controls', it can be concluded that he/she performs *within normal limits*. A *classical dissociation* occurs when a patient presents a deficit on a task A, performs within normal limits on task B and the difference between tasks A and B is significantly more pronounced than in the control group, as measured with RSDT. A *strong dissociation* occurs when a patient is impaired on both tasks A and B, but still the difference in his performance in the two tasks is significantly greater than in controls.

The Crawford methods have their limitations. For instance, the diagnosis of a performance within normal limits is based on the lack of significant difference, while it is widely known that absence of evidence is not evidence of absence (see e.g. Dienes, 2014). Still, a single deficit has a limited inferential power and more reliable conclusions regarding the cognitive architectures can be drawn from the analysis of dissociations, which can be readily assessed without necessarily diagnosing performance within normal limits. Extensive tests using Monte Carlo simulations demonstrated that the Crawford methods provide a decent control over type I error rate in smaller group sizes (Crawford & Garthwaite, 2005), and can achieve 80% of statistical power provided that the patient's deficit is strong (at least 2.5 standard deviations different from the controls' mean, Crawford & Garthwaite, 2006). Crawford methods are not the only existing methods available to assess the performance of single patients, but they seem to be the best option available (reviewed in: Crawford & Garthwaite, 2006). For this reason they are commonly used to compare a single subject's performance with that of a group of healthy controls, and have been widely accepted in high-impact journals (e.g.: Thiebaut de Schotten et al., 2005; Konen, Behrmann, Nishimura, & Kastner, 2011; Striem-Amit, Vannuscorps, & Caramazza, 2017). These methods can be also used in the settings of neuroimaging, when one wants to test for differences in brain structure or function between a single patient and a healthy control group (see e.g. Striem-Amit, Vannuscorps, & Caramazza, 2017).

The Crawford methods are applied to averaged scores obtained in the patient and in healthy controls. In some cases, however, one may be willing to assess more fine-grained relationships between the two tasks or control for possible trial-by-trial confounds of the task such as the visual complexity of images or the frequency of presented words. To do so, the experimenter can explore the test structure using binary regression models (Smithson, Davies, & Davies, 2011) with the response in each trial coded as a binary dependent variable. This methods allow for more nuanced statistical analyses and may increase the statistical power.

1.3.3 Summary: a recipe for a compelling single-case study

In the sections above I reviewed the theoretical and methodological concerns in single-case research. To summarize them, below I present a point-by-point recipe of how to perform a case study that would allow for drawing inference on the healthy cognitive architecture.

1. Provide a strong theoretical background: pick a model to test and see if your case present novel findings regarding this model: does it solve an established debate

concerning the model or does it completely negate the model and propose a new one.

2. Design a test that allows to measure not only a deficit but also a dissociation.
3. Test your patient using multiple repetitions and preferably on multiple testing sessions to avoid the risk of malingering or other sources of idiosyncrasy.
4. Compare your patient to a group healthy controls matched for age, education, gender but also other variables that may be relevant to the study (occupation, special skills etc.) using the established statistical methods that allow for single case-controls comparisons.
5. If possible, test other patients presenting the symptom of interest. If not, relate your findings to other findings on brain-damaged patients.
6. Limit your conclusions to the structure of a cognitive system in question. Any discussion regarding the neural substrates of the cognitive system should be presented as hypothetical.

If, however, assessing the patient's brain function and structure with MRI is possible, drawing inferences regarding the neural substrates of a given cognitive model could be allowed by following the additional steps below:

7. Design a case-control experiment that elucidate the neural substrate of the cognitive function in question and/or allow for controlling for stroke-related brain plasticity and functional reorganization; alternatively test the patient using standard protocols included in big data MRI repositories and refer your results to the results of those repositories.
8. Refer the patient's lesion location to available atlases of brain's structural and functional connectivity, to reveal not only the local but also the distal effects of the lesion.

Fulfilling the aforementioned steps require an extensive and risky research program (discussed in: Medina & Fischer-Baum, 2017). The challenges of single-case research occur at every level of an academic project. First, finding an appropriate patient to study is like finding a *perle rare*. Patients with selective deficits are rare, and to reach them one needs to work in collaboration with clinicians, which is not always feasible. When a potentially interesting patient is found, he or she needs to be capable and willing to engage in substantial amounts of testing. This is not obvious in elderly population, often with pre-existing cardiovascular problems.

A detailed single case study requires to design and run multiple experiments in order to isolate a deficit of a specific function. The preparation of such experiments and data analysis can take months or even years if one wants to include neuroimaging.

Finally, the publication of single-case reports in the scientific literature is a further challenge, with some journals that previously published case-reports now refusing to do so, or doing so only in the case of very rare and surprising patterns of performance. On top of it, the most popular preprint server in biological sciences, biorXiv, refuses a priori to publish single cases, making it difficult to share the results before publication.

Given the pressure to publish and the competitive grant seeking climate, single-cases are risky, especially for early career researchers. Still, when a *perle rare* is found, I feel that it is a moral obligation of a researcher in cognitive neuroscience to dive for it, as it may provide evidence that can change our understanding of the organisation of the mind and, potentially, of the brain.

1.4 Summary and outline of the thesis

In this introduction I reviewed the evidence showing that high-level colour processing may be divided into at least three functionally segregated modules, namely conscious colour perception, colour naming and colour knowledge. Building upon the evidence that the modules of high-level colour processing are functionally segregated, in the second and third chapter of this thesis I focus on colour categorisation as a case-in-point of studying the interplay between colour perception and naming. In **Chapter 2** I present the theoretical debate regarding the origins of colour categorisation and review evidence on the functional segregation between colour perception, categorisation and language in human and non-human animals. In Chapters 3 and 4 I apply the reviewed guidelines for single case studies to examine how colour language interacts with colour categorisation and colour knowledge in a single patient, RDS, who presented colour naming deficits due to a left, ventral occipitotemporal lesion. In **Chapter 3**, I provide empirical evidence for the independence of colour categorisation and colour language and examine what RDS's brain function and structure can tell us about the neural substrates of colour naming. In **Chapter 4** I test alternative models of colour knowledge organisation, by examining the interplay between RDS's colour language and colour knowledge. Overall, this thesis demonstrates three novel functional segregations in cortical colour processing: (1) between colour categorisation and colour naming, (2) between the naming of chromatic and achromatic colours and (3) between the processing of coloured objects and the processing of abstract colours, i.e. colours detached from objects.

2 The biological bases of colour categorisation.

The fact that the colors in the flower have evolved in order to attract insects to pollinate it is interesting; that means insects can see the colors. That adds a question: does this aesthetic sense we have also exist in lower forms of life?

Richard P. Feynmann

In this chapter, we reviewed state-of-the-art research concerning the biological bases of colour categorisation. In doing so, we were particularly interested in functional segregation between colour categorisation, perception and language. We searched for traces of colour categories in animal cognition and in infants before language acquisition. The existence of colour categories in these populations would indicate that colour categories can occur without language. Then, we explored the interplay between colour categorisation, perception and language in studies concerning adult human cognition and its neural substrates. Altogether, the reviewed evidence show that colour categorisation can appear in individuals without language; and may not require automatic language activation in the adult human brain. At the same time, we found no compelling evidence that colour categorisation originates from low level stages of colour perception. We suggest that colour categories may build upon continuous colour perception through a top-down modulation from high-level cognitive systems such as attention or semantic knowledge. We propose that colour categories may emerge from colours of objects that are ecologically relevant in the environment. Such ecological perspective on colour categorisation can provide a common explanation of categorical responses in non-human animals and adult humans.

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

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ABSTRACT

How are colour categories related to perception and language? To answer this question, we review research on the neural correlates of colour categories, and categorical responses in preverbal infants and non-human animals. With respect to language, the reviewed findings suggest that colour categorisation often involves automatic language processing. At the same time, evidence from non-human animals, infants, and patients with brain lesions indicates that colour categorisation may also occur in the absence of language. Concerning perception, there is little convincing evidence that the bottom-up processes of colour perception are the origin of colour categories. Instead, colour categorisation might simply build upon the continuous colour perception and interact with perception through the direction of attention to colour differences that are relevant to categorisation. We make three suggestions for future research. First, future research in all areas requires methodological improvements, in particular in stimulus control. Second, future research should overcome the universalist-realist debate and go beyond a simple contrast between perception and language. Third, the link between object colours and colour categories provides an alternative approach that might reveal the ecological origin of colour categories. The ecological approach promises establishing evolutionary and developmental continuity between categorical responses in non-human 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 associate 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 (universalists): linguistic relativists insisted that colour categories are shaped by language and culture. In contrast, 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).

Across the years, cross-cultural studies provided 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, 2014; Lindsey & Brown, 2009; Lindsey, Brown, Brainard, & Apicella, 2016; 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). A detailed discussion of findings from cross-cultural and 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).

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, Kessen, & Weiskopf, 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 aim at establishing when colour categories emerge in the course of the ontogenetic development and the phylogenetic evolution, respectively. Third, a growing line of research has been investigating 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.

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 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 substrates 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 summarise 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 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 require 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 simply ask animals or infants to categorise colours. 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 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 (Cuthill

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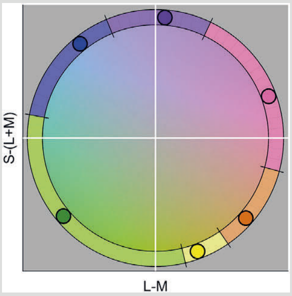
Box 1
Colour categorization and sensory stages of colour processing.

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 (Figure 1 in Malkoc, Kay, & Webster, 2005; Wuerger, Atkinson, & Cropper, 2005; Figure 9 in Witzel & Gegenfurtner, 2013; Emery, Volbrecht, Peterzell, & Webster, 2017; Figure 2 in Witzel & Gegenfurtner, 2018a). Exceptions are the green-blue and yellow-green boundaries, which happen to 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.



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.*

et al., 2017; Osorio & Vorobyev, 2008). 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 (discussed 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 responses in animals, for the capacities of learning colour categories 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, Lanson, & Rivera, 1991). However, due to the use of wavelengths as reference metric (box 2) it is unclear to what extend these responses reflect colour categories or higher cone sensitivities to some wavelength differences (Jacobs, 2018; Vorobyev, Osorio, Bennett, Marshall, & Cuthill, 1998).

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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 (Fairchild, 2013; Hunt & Pointer, 2011; Kuehni, 2003). 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, Lindsey, & Guckes, 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., Fairchild, 2013; Hansen, Walter, & Gegenfurtner, 2007). A large part of adaptation is achieved within only 10 msec, 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.

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, Gross, & Bornstein, 1979). These results have been replicated in electrophysiological and lesion research on the macaque visual cortex (Walsh, Kulikowski, Butler, & Carden, 1992; Yoshioka, Dow, & Vautin, 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, Witzel, Hansen, & Gegenfurtner, 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 inconsistent. 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, Osorio, & Baddeley, 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 generalised. 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 Figure 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 (Davidoff & Fagot, 2010; Fagot, Goldstein, Davidoff, & Pickering, 2006). 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 "decontextualised colours", such as coloured patches or lights, that are meaningless and

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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 (Caves, Green, Zipple, Peters, & Nowicki, 2018; Hanley et al., 2017) 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. 1A). 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. 1A). 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 versus 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.

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, Astell, Hunt, & Mollon, 1991). Moreover, baboons and other primates can succeed in categorization tasks (Bovet & Vauclair, 2001; Fagot & Maugard, 2013; Freedman, Riesenhuber, Poggio, & Miller, 2001). They seem to have visual categories similar to humans, such as categories for animals, trees, and faces, processed along a neural hierarchy similar to the one known from humans (cf. Fig. 1B; Fabre-Thorpe, 2003; Fize, Cauchoix, & Fabre-Thorpe, 2011; Sigala, Gabbiani, & Logothetis, 2002). 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. Low-level mechanisms might be comparable between humans and non-human primates to some extent (Bowmaker et al., 1991; Lindbloom-Brown, Tait, & Horwitz, 2014); but it is uncertain how colour discrimination corresponds between humans and primates (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 (Caves et al., 2018; Hanley et al., 2017) 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

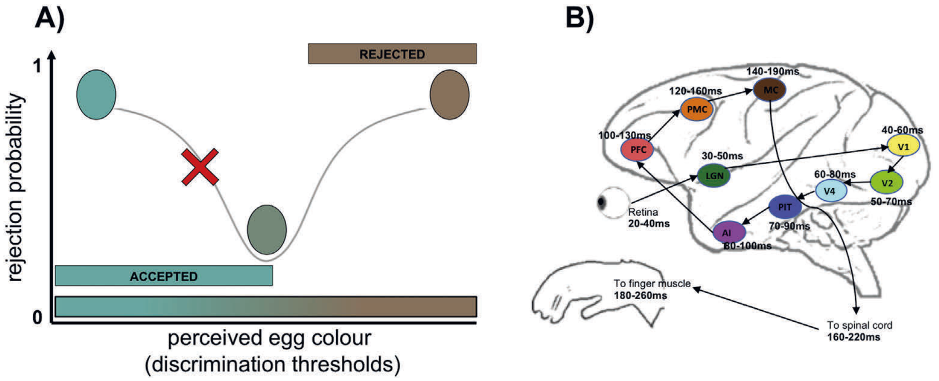

Fig. 1 — (A) Robins' probability of rejecting a coloured foreign egg relative to the position of hosts' own egg colour along the blue-green to brown colour gradient. The birds rejected brown eggs only. No rejection occurred in the blue-green direction (red X). Simplified illustration adapted from: Hanley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

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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 chimpanzee colour categories almost always corresponded to the category prototypes of the basic colour terms of various languages (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 seem to have little or no value in communication with conspecifics (Gardner & Gardner, 1969; Savage-Rumbaugh, Rumbaugh, & Boysen, 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 generalise 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, Kawai, & Matsuzawa, 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, Hermann, Hansen, & Conway, 2016). Second, studies on non-human primates allow for the use of invasive techniques, such as experimental lesioning or intracranial recordings. These techniques grant more direct measurement of brain activity and allow 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 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 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, Crassini, & Freiberg, 1990). Table 1 provides an overview of studies on infant categories.

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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, Catchpole, Abbott, Bosten, & Franklin, 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, 2008a; Ozturk, Shayan, Liszkowski, & Majid, 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, Renner, & Rovee-Collier, 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.

Category 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, Franklin, Davies, & Holmes, 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, Kanazawa, Yamaguchi, & Kuriki, 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) or non-standard illumination (Catherwood et al., 1990; Gerhardstein et al., 1999; see discussion in Franklin & Davies, 2004).[2] In addition, the colour detection task does not sufficiently control for the state of adaptation (Clifford et al., 2009; Franklin et al., 2005, 2008a; Ozturk et al., 2013). See also boxes 1 and 2.

Nevertheless, there is convincing evidence. Franklin and 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 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 Fig. 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 Fig. 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.

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. 2A). This feature of infant categories is in stark contrast to the fact that adult colour categories do not align with those sensory mechanisms. Although Fig. 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; Figure 2 in Bosten & Lawrance-Owen, 2014;

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[2] Some of the colour samples used in these studies 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., Franklin et al., 2008; Clifford et al., 2009; Ozturk et al., 2013).

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Table 1 – Studies on infant colour categories. Categ: Colour categories, R = Red, O = Orange, Y = Yellow, G = Green, B = Blue, Pu=Purple, Pi = Pink, Br = Brown; # number of colours, Ref metric: Reference metric used to control stimuli, wl = wavelengths, Mun = Munsell chips, SimMun = simulated Munsell chips; ~ = approximate; NovPref = Novelty preference; N number of participants (\ excluded).

Study	Categ	#	Ref metric	Measure	N	Age
Bornstein et al. (1976)	R Y G B	15	wl	NovPref	80	4mo
Gerhardstein et al. (1999)	~R O	5	~Mun[a]	Pop-out	24 (\7)	3mo
Franklin and Davies (2004)	G B	10	Mun	NovPref	54 (\22)	4mo (16-20we)
	B Pu	4				
	Pi R	4				
Franklin et al. (2005)	G B	4	~SimMun[b]	Chromatic detection	21 (\6)	5mo
Franklin et al. (2008)	G B	3	~SimMun[b]	Chromatic detection	26 (\13)	4–5mo (20 we)
Clifford et al. (2009)	G B	3	~SimMun[c]	ERP	39 (\20)	7mo
Ozturk et al. (2013)	G B	4	~SimMun[c]	Chromatic detection	38 (\5)	8mo
	P B	4				
Yang et al. (2016)	G B	4	~CIELAB[d]	NovPref	36 (\18)	5–7mo
		3		NIRS	36 (\18)	
Skelton et al. (2017)	R Br G B Pu Pi	14	SimMun	NovPref	295 (\112)	4–6 mo

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

[b] Uncontrolled adaptation due to task design (chromatic detection).

[c] Uncontrolled adaptation due to black background.

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

Figure 2 in Emery et al., 2017; Figure 4 in Webster, Miyahara, Malkoc, & Raker, 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, Giesel, & Gegenfurtner, 2008; Giesel, Hansen, & Gegenfurtner, 2009; Witzel & Gegenfurtner, 2013). These cone-opponent dimensions do not represent high-level colour processing, including supra-threshold colour discrimination (e.g., Wuerger, Maloney, & Krauskopf, 1995), subjective colour appearance (Abramov & Gordon, 1994; Figure 2 in Bosten & Lawrance-Owen, 2014; Krauskopf, Williams, & Heeley, 1982; De Valois, De Valois, Switkes, & Mahon, 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

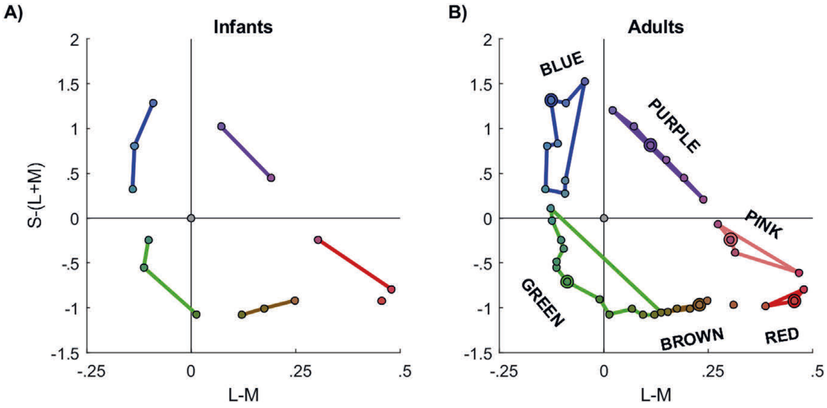

Fig. 2 – Infant and adult colour categories. Panel a represents categorical responses in infants from Skelton et al. (2017) in DKL-space; panel b indicates membership of colours to linguistic colour categories in English adults as measured by Witzel, Sanchez-Walker, and Franklin (2013). The x-axis represents the L-M cone-opponent channel ("green-red"), the y-axis the S-(L+M) cone-opponent channel ("yellow-blue"). Each symbol corresponds to a Munsell chip and is coloured accordingly. Category prototypes are highlighted by a ring. 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).

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(Brown & Lindsey, 2013; Franklin, Catherwood, Alvarez, & Axelsson, 2010). 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 (Fig. 2A and Figure 2 in Skelton et al., 2017), and not all adult category boundaries differ from those mechanisms (Fig. 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, Piantadosi, & Aslin, 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.

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, Vital-Durand, & Barbur, 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 Aslin, 2007; Teller, 1984) 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.

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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, Fiske, & Chan, 2004). Another mechanism that could possibly explain categorical responses in infants is joint attention (Moore & Durham, 1995). Being adults, infants' caregivers have 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, Xu, Austerweil, Griffiths, & Regier, 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 observer, no matter whether the observer 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 Fig. 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, Brewer, Rieger, & Wandell, 2002), ventral-occipital cortex VO (Brewer, Liu, Wade, & Wandell, 2005) and the anterior colour complex (Lafer-Sousa, Conway, & Kanwisher, 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, Lahlaf, & Eskew, 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 found in the temporal dynamics of colour processing using electroencephalography (EEG); and in brain function and structure using the divided visual field paradigm, magnetic resonance imaging (fMRI), and lesion studies.

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 (Clifford et al., 2012; Forder, He, & Franklin, 2017b; He, Witzel, Forder, Clifford, & Franklin, 2014; Thierry, Athanasopoulos, Wiggett, Dering, & Kuipers, 2009). Consider Fig. 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*, Fig. 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 (Fig. 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, Schröger, & Czigler, 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).

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, Franklin, Clifford, & Davies, 2009) and vMMN (Athanasopoulos, Dering, Wiggett,

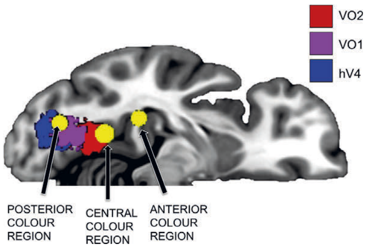

Fig. 3 — Colour-biased extrastriate regions in the left hemisphere of the human brain. In yellow, 5-mm spheres centred on the peaks of the posterior, central and anterior colour regions identified by Lafer-Sousa et al. (2016). In the background, colour-selective extrastriate regions defined by retinotopy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

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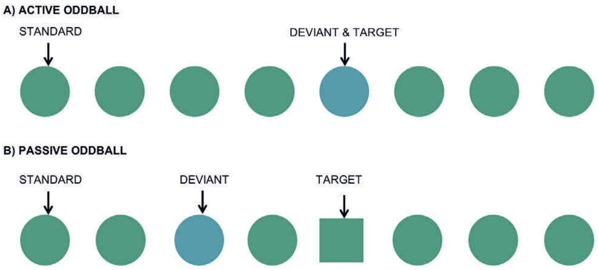

Fig. 4 – (A) In an active oddball task, the infrequent colour (deviant) is also a target to which observers is responding. In a passive oddball task (B), observers respond to colour-unrelated targets while passively viewing standard and deviant colours.

Kuipers, & Thierry, 2010; Clifford, Holmes, Davies, & Franklin, 2010; Mo et al., 2011; Thierry et al., 2009; Zhong, Li, Li, Xu, & Mo, 2015). On the other hand, other studies reported category effects only on later, post-perceptual stages (Clifford et al., 2012; Forder, Bosten, He, & Franklin, 2017a; He et al., 2014), and in some studies, category effects occurred for both components (Fonteneau & Davidoff, 2007; Holmes et al., 2009).

Some of the putative category effects on early ERPs may be due to 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 were 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 (Maier & Rahman, 2018; Thierry et al., 2009), 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 (Forder et al., 2017b; Maier & Rahman, 2018; Thierry et al., 2009); others on later components (Clifford et al., 2012; see also Forder et al., 2014 and for details Forder, 2015 pp. 80–115). 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 (Clifford et al., 2010; Forder et al., 2017b; Thierry et al., 2009), while others did not, at least not in infants (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; Liu et al., 2009).

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

Table 2 – Overview of EEG studies. Categories: B1 = Blue1, B2 = Blue2. JNDs (just noticeable differences) 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); Learn = pre and post learning; Indiv = Comparison between individuals with slightly different category boundaries. Amp = Amplitude; Lat = Latency.

Study	Categ	#	Ref metric	Interaction	Task	Measure	Component
Fonteneau and Davidoff (2007)	G B	3	~SimMun[a]	–	Passive Oddball	Amp	P2, P3
						Lat	P1, N1, N2,
Thierry et al. (2009)	G B1 B2	4	~SimMun[a]	G-E	Passive Oddball	Amp	P1, vMMN
Athanasopoulos et al. (2010)				GE		Lat	P1
Mo et al. (2011)	G B	4	~SimMun[a]	Latcat	Passive Oddball	Amp	vMMN
Liu et al. (2009)	G B	3	~SimMun[a,b]	Latcat	Visual Search	Amp	N2pc
Holmes et al. (2009)	G B	8	~SimMun[a]	–	Active Oddball	Amp	P2 & P3
						Lat	P1, N1,N2
Clifford et al. (2009)	G B	3	~SimMun[a,c]	–	Passive Oddball	Amp	Nc, NSW
Clifford et al. (2010)	G B	3	SimMun[d]	Lower/Upper VF	Passive Oddball	Amp	vMMN
Clifford et al. (2012)	G B	8	~SimMun[a]	Learn	Active oddball	Amp	P3
He et al. (2014)	G B	4	JNDs	–	Active Oddball	Amp	N2, P3, Frontal Positivity
Forder (2015)	G B1 B2	3	JNDs	G-R	Active Oddball	Amp	P2/N2
Forder et al. (2017)	G B	3	JNDs	Indiv	Passive oddball	Amp	P1, Frontal Positivity
Zhong et al. (2015)	B	6	~CIELUV[a,b]	Learn	Passive oddball	Amp	vMMN
Maier and Rahman (2018)	G B1 B2	3	SimMun[d]	G-R-E	Attentional blink	Amp	P1, N2

All other abbreviations as in Table 1.

[a] Munsell distances are uncertain because adaptating background and illuminant are either unspecified or do not correpond to N5 and standard illuminant C.

[b] Imprecise calibration based on easyrgb.com.

[c] Uncontrolled adaptation due to black background.

[d] Backgroud was close to N5 under illuminant C, and Euclidean distances in CIELAB and CIELUV were roughly equal.

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characteristics, such as the stimulus display (one versus two colours, e.g., Mo et al., 2011), and the precise timing of task and stimulus presentation may also contribute to the discrepant findings.

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 versus late/cognitive interpretation. First, the assumption that modulations of early components (P1, N1, 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 (Chica et al., 2010, 2012; Hillyard & Anllo-Vento, 1998; Luck & Ford, 1998). Intracranial recordings in primates show that attentional modulation in the visual cortex can occur as early as 70 msec after stimulus onset (Martínez et al., 1999; Pooresmaeili, Poort, & Roelfsema, 2014). Similarly, mismatch negativity can also rely on attentional load (Erlbeck, Kubler, Kotchoubey, & Veser, 2014; Hedge et al., 2015), even in passive oddball tasks (Hedge et al., 2015). Those results question the conclusions from studies interpreting mismatch negativity (vMMN) as a perceptual, pre-attentive component (e.g., Thierry et al., 2009).

3.2. *Lateralised category effect*

A second 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, 2008; Kay, Regier, Gilbert, & Ivry, 2009). Such lateralised category effects have been investigated in speeded visual search tasks, involving lateralised 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).

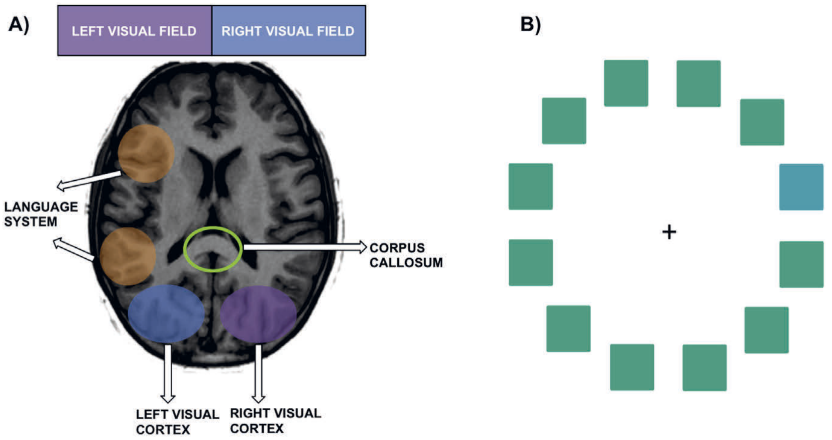

Fig. 5 – The lateralised category effect. (A) Lateralisation of language and early visual processing. Information from the right visual field (in blue) directly reaches the left hemisphere (in blue) where language is also processed for most people (see orange dots). If speeded response times do not allow 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 lateralised category effects. The observers are asked to detect the side (left/right) of target presentation.

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Table 3 gives an overview of behavioural studies on the lateralised category effect. Several behavioural experiments provided evidence for a lateralised category effect (Al-rasheed, Franklin, Drivonikou, & Davies, 2014; Drivonikou et al., 2007; Franklin et al., 2008a; Franklin et al., 2008b; Paluy, Gilbert, Baldo, Dronkers, & Ivry, 2011; Roberson, Pak, & Hanley, 2008; Roberson, Hanley, & Pak, 2009; Zhou et al., 2010), 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 msec post-stimulus; and N2, 260–310 msec, 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 msec). 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 observers discriminated across-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 category effect that occurs in the absence of language and is lateralised to the right hemisphere (for review see Regier & Kay, 2009). Such opposite, non-lexical lateralised category effects have been observed in pre-verbal infants (Franklin et al., 2008a, 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 (Brederoo, Nieuwenstein, Cornelissen, & Lorist, 2019; Brown et al., 2011; Webster & Kay, 2012); others reported category effects of similar magnitude in either visual field (Liu, Chen, Wang, Zhou, & Sun, 2008; Witzel & Gegenfurtner, 2011; 2015; 2016, behavioural results in Liu et al., 2009 and in Ting Siok et al., 2009; behavioural results in Ting Siok et al., 2009); still others found category effects in the left visual field (Suegami et al., 2014; Suegami, Aminihajibashi, & Laeng, 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 should also be faster in the right visual field when observers complete a simple colour naming task. However, evidence for this hypothesis is mixed (Bornstein & Monroe, 1980; Lu, Zhang, & Wang, 2012; Wuerger 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, Moty, & Regier, 2017; Holmes & Wolff, 2012; Suegami & Laeng, 2013). 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 (Brederoo et al., 2019; Witzel & Gegenfurtner, 2011). In addition, evidence for and against lateralised category effects was found independent of the control of eye movements (e.g. Witzel & Gegenfurtner, 2011). 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 (Constable & Becker, 2017; Roberson et al., 2008), 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 lateralised category effect are not safe. First, the response speed observed in studies on the lateralised category effect cannot exclude callosal transfer. Fig. 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 4–40 msec (Marzi, 2010; Nowicka & Tacikowski, 2011; Phillips et al., 2015); visual processing time can be as fast as 150 msec when categorizing natural scenes (Fabre-Thorpe, 2011; Thorpe, Fize, & Marlot, 1996; van Rullen & Thorpe, 2001). In this context, it seems hardly probable that the fastest response times in visual search tasks (~400 msec, 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 without necessarily involving language processing (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, Vallortigara, & Andrew, 2013). Moreover, evidence from brain-damaged patients (Damasio & Damasio, 1983; De Renzi & Spinnler, 1967; Miceli et al., 2001; Stasenko, Garcea, Dombovy, & Mahon, 2014) and fMRI studies (Simmons et al., 2007) suggests that higher-level colour processing may be lateralised 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; Stasenko et al., 2014).

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Table 3 – Overview of behavioural experiments on the lateralised category effect. When 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 on the lateralised category effect are included in Tables 2 and 4, respectively. The column Effect reports the size of the lateralised category effect. It is calculated as the difference between within and across category colours in the right and left visual fields.

Study	Categ	#	Ref metric	Task	N	Effect
Gilbert et al. (2006)	G B	4	~SimMun[a]	Left-right Discrimination	27	~24 msec
Drivonikou et al. (2007)	G B B P	4 4	~SimMun[b]	Chromatic detection	24 34	30 & 60 msec
Franklin (2008)	G B	4	~SimMun[b]	Chromatic detection	18	~40 msec
Roberson et al. (2008)	Y G	9	~SimMun[a]	Left-right Discrimination	22 20	~100 msec (fast responders)
Roberson et al. (2009)	Y G	9	~SimMun[a]	Left-right Discrimination	14 14	~50 msec (when fixating)
Ting Siok et al. (2009)	G B	4	~SimMun[a]	Left-right discrimination	14	12 msec n.s.
Zhou et al. (2010)	G B	4	~SimMun[a]	Left-right discrimination	18 (31[c])	20 msec
Paluy et al. (2011)	G B	4	~SimMun[a]	Left-right discrimination	11	~20 msec
Liu et al. (2008)	G B	4	~SimMun[a]	Chromatic detection	18	5 msec n.s.
Liu et al. (2009)	G B	4	~SimMun[a]	Left-right discrimination	12	−12 msec
Brown et al. (2011)	G B		CIELAB + MDS	Left-right discrimination	39	n.s.
Suegami (2014)	G B	4	~SimMun[b]	Colour naming	30	n.s.
Witzel et al. (2011)	G B B P	4 4	SimMun	Discrimination & detection	230	−19:18 msec n.s.
Witzel et al. (2015)	Pi O Y G B Pu	40	JNDs	4 AFC Discrimination	12	n.s.
Witzel et al. (2016)	R Br	4	JNDs	4 AFC Discrimination	15	n.s.
Constable and Becker (2017)	G B	4	CIE 1931[a]	Left-right Discrimination	16	n.s.
Zhong et al. (2015)	G B	4	~CIELUV[a]	Left-right Discrimination	33	0–9 msec

All other abbreviations are as in Table 1.

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

[b] Uncontrolled adaptation due to task design (chromatic detection).

[c] Including control group.

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 et al., 2017; Holmes & Wolff, 2012; Suegami & Laeng, 2013). 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 lateralised category effect are inconclusive.

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 on colour categorization have produced mixed results (see Table 4). Several studies found evidence for category-specific processing in the visual cortex, including V2/V3 (Kwok et al., 2011; Ting Siok et al., 2009) 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, Berens, Horner, & Franklin, 2014; Persichetti, Thompson-Schill, Butt, Brainard, & Aguirre, 2015). Some studies also found evidence for the involvement of the left cerebellum (Bird et al., 2014; Kwok et al., 2011); however the exact reasons for cerebellar contribution to colour categorization remains unclear.

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Table 4 — Overview of MRI studies.

Study	Categ	#	Ref metric	Task	Measure	Area
Ikeda and Osaka (2007)	unspecified	—	unspecified[a]	Two-back	activation	left inferior frontal gyrus left inferior parietal lobule
Tan et al. (2008)	R G B	3	RGB[a]	Colour discrimination (same/different)	activation	left posterior superior temporal gyrus left inferior parietal lobule
Ting Siok et al. (2009)	G B	4	~SimMun[a]	Visual search	activation	left inferior frontal gyrus middle temporal gyrus supramarginal gyrus V2/3
Kwok et al. (2011)	G B	4	~SimMun[a]	Category training	Pre-post VBM	V2/3 Left cerebellum
Brouwer and Heeger (2013)	G B Pu Pi O	12	DKL[a]	Colour naming	MVPA	hV4/VO
Bird et al. (2014)	G B	4	CIELUV hue	Cover task	Adaptation, MVPA	Middle frontal gyrus Left cerebellum
Persichetti et al. (2015)	G B	10	SimMun	Colour naming	Adaptation	precentral sulcus, pars triangularis of inferior frontal gyrus,posterior part of the superior frontal sulcus [all bilateral]]

Abbreviations are as in Table 1.

[a] 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).

One possible reason for these discrepancies could be the stimulus sampling. Some studies (Brouwer & Heeger, 2013; Ikeda & Osaka, 2007; Tan et al., 2008) assessed colour categorization using very different stimulus samples. In those cases, it is difficult to assess how the colour sampling methods explain the discrepant findings. Four studies (Bird et al., 2014; Kwok et al., 2011; Persichetti et al., 2015; Ting Siok et al., 2009) assessed colour categorization with a similar set of colours around the problematic green-blue boundary (see box 2). However, even those studies reported different brain regions, implying that stimulus sampling alone cannot explain the variability of results. Among all those 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 (Bird et al., 2014; Brouwer & Heeger, 2013; Persichetti et al., 2015), colour discrimination (Tan et al., 2008; Ting Siok et al., 2009), colour naming (Brouwer & Heeger, 2013; Persichetti et al., 2015; Tan et al., 2008), 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. In the visual cortex, category effects were only reported when observers 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 passive viewing (Brouwer & Heeger, 2013; Persichetti et al., 2015) did not find anything specific for colour categories during passive viewing. This result contradicts the idea that colours are processed categorically in the visual cortex in a bottom-up manner. This contrasts with ERP results demonstrating category effects on early components in a passive oddball task (Forder et al., 2017b; Thierry et al., 2009). 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). Overall, 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 (Barron, Garvert, & Behrens, 2016; Grill-Spector, Henson, & Martin, 2006). 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, Polyn, Detre, & Haxby, 2006; Kriegeskorte & Bandettini, 2007). In colour category research, it has been tested whether pattern similarities between colours are higher within than across

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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, Schluppeck, Bowtell, & Peirce, 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 (Barron et al., 2016; Jimura & Poldrack, 2012; Kriegeskorte, Goebel, & Bandettinia, 2006), 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-lateralised effects, nor involvement of language areas in the whole-brain analysis (Bird et al., 2014; Brouwer & Heeger, 2013; 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 (Brouwer & Heeger, 2013; Kwok et al., 2011; Ting Siok et al., 2009); 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.

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 (Bartolomeo, Bachoud-Lévi, & Thiebaut de Schotten, 2014; Bouvier & Engel, 2006), colour naming (Damasio & Damasio, 1983; Geschwind & Fusillo, 1966; Oxbury, Oxbury, & Humphrey, 1969), and object-colour knowledge - the association between objects and their typical colours (Beauvois & Saillant, 1985; Luzzatti & Davidoff, 1994; Miceli et al., 2001; Stasenko et al., 2014; Zandvoort, Nijboer, & Haan, 2007). 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 (Damasio & Damasio, 1983; Oxbury et al., 1969). 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 categorise visually presented colours suggests that colour categorization does not dependent 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 (Beauvois & Saillant, 1985; Geschwind & Fusillo, 1966; Kinsbourne & Warrington, 1964; Stachowiak & Poeck, 1976) 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, Graham, & Patterson, 2015) or colour-specific naming deficits (Fukuzawa et al., 1988; but see Roberson, Davidoff, & Braisby, 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 Figure 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, Dixon, Mullen, Christensen, & Bub, 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

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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 (cf. categorical perception). 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 (Bird et al., 2014; Brouwer & Heeger, 2013; 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, Jefferies, Patterson, & Rogers, 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, Haroon, Morris, Ralph, & Parker, 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, 2018b). 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, Ling, & Read, 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 hemispace could account for some of the reported lateralised 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, Bartolomeo, & Lupiáñez, 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 4) 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 (Bartolomeo & Seidel Malkinson, 2019; Corbetta & Shulman, 2002).

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 et al. (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 Lateralised category Effects).

4. Conclusions

Research into the biological basis of colour categorisation provided mixed, and often contradictory results. Although the areas

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of research reviewed above differ fundamentally from one another, there are also important common challenges across these areas. To conclude, we summarise 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 non-human 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, with a few exceptions all areas of research have largely neglected the link between colours and objects and focused instead on colours independent of objects. However, in non-human animals colour is an inherent, indissociable property of objects. In humans, 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). We propose the idea of an ecological origin of colour categories as an alternative to the perception-language-dichotomy. According to this approach, the purpose of colour categories consists of identifying objects and scenes, and colour terms allow for communicating them across observers (Gibson et al., 2017; Kemp, Xu, & Regier, 2018; Witzel, 2018; Witzel & Gegenfurtner, 2018b; Zaslavsky, Kemp, Regier, & Tishby, 2018). In non-human animals, the relationship between objects and colour categories could be learned through experience with the visual environment. In humans, the acquisition of colour categories might also be culturally reinforced through the child's interaction with their caregivers during development. A link between objects and colour categories would thus explain how categories develop in children prior to language acquisition and how they evolve across species.

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3 Colour categorisation independent of colour naming.

Color! What a deep and mysterious language, the language of dreams.
Paul Gauguin

In this chapter we investigated if automatic language activation is a *sine equa non* condition of colour categorisation in adult humans. To do so, we tested colour categorisation in a neurological patient, RDS, who lost the ability to efficiently name visually presented colours due to the left occipito-temporal stroke. We tested RDS's colour categorisation and naming on the same set of colour stimuli and demonstrated that there was a dissociation between his colour categorisation and naming, and that the two functions were independent: RDS did not use his residual colour naming to perform in colour categorisation and vice-versa.

On top of the thorough behavioural testing, RDS underwent multimodal neuroimaging experiments including task and resting-state fMRI as well as structural MRI. Neuroimaging measures demonstrated that the left occipito-temporal lesion destroyed the left-sided colour biased regions and disconnected their right-hemispheric equivalents from the left anterior temporal lobe. Based on these findings, we suggest that RDS's visuo-verbal disconnection stems from the lack of communication between sensory regions processing colour signals, and verbal semantics represented in the left anterior temporal lobe. We also speculate that the left colour-biased regions may be particularly engaged in colour naming by linking colour perception with colour lexicon. Noteworthy, this anatomical and functional disconnection had disproportionality greater effect on RDS's colour naming than on colour categorisation implying that non-overlapping neural systems support the two functions, and that accessing to language regions, while essential for colour naming, is not crucial for colour categorisation.

Color categorization independent of color naming.

Paper under review.

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3.1 Summary

Color is continuous, yet we group colors into discrete categories associated with color names (e.g. yellow, blue). Color categorization is a case in point in the debate on how language shapes human cognition. Evidence suggests that color categorization depends on top-down input from the language system to the visual cortex. We directly tested this hypothesis by assessing color categorization in a stroke patient, RDS, with a rare, selective deficit in naming visually presented chromatic colors, and relatively preserved achromatic color naming. Multimodal MRI revealed a left occipito-temporal lesion that directly damaged left color-biased regions, and functionally disconnected their right-hemisphere homologs from the language system. The lesion had a greater effect on RDS's chromatic color naming than on color categorization, which was relatively preserved on a nonverbal task. Color categorization and naming can thus be independent in the human brain, challenging the mandatory involvement of language in adult human cognition.

3.2 Introduction

Does language shape human cognition? Color categories and their relationship to language are a case in point of this theory, sometimes referred to as the Sapir-Whorf hypothesis (Deutscher, 2010). Colors vary continuously in hue, lightness, and saturation, but we group them into discrete categories with specific names (green, yellow, etc.). The origin of color categories is intensely debated, and some suggest that color categories derive from language and depend on culture-specific sets of color names (Regier and Kay, 2009; Gibson *et al.*, 2017; Witzel, 2018; Witzel and Gegenfurtner, 2018; Siuda-Krzywicka *et al.*, 2019). Despite evidence that infants process colors categorically before language acquisition (Yang *et al.*, 2016; Skelton *et al.*, 2017), neuroimaging results strongly suggest a top-down influence of language on visual processing in adult color categorization (Ikeda and Osaka, 2007; Thierry *et al.*, 2009; Ting Siok *et al.*, 2009; Brouwer and Heeger, 2013). Thus, language acquisition may reorganize the cognitive and neural representation of infant preverbal color categories and make it language-dependent (Franklin *et al.*, 2008; Regier and Kay, 2009; Skelton *et al.*, 2017). However, given the correlational nature of neuroimaging results, it remains unclear whether or not language abilities are causally related to color categorization.

In rare cases, damage to occipito-temporal regions in the left hemisphere can impair the ability to name visually presented colors (Oxbury, Oxbury and Humphrey, 1969; De Vreese, 1988), relatively sparing naming of other visual stimuli such as objects, animals, plants or people. Here, we probed the causal relationship between color naming and color categorization by gathering extensive behavioral and neuroimaging evidence from one such patient, who developed a naming deficit selective to visually presented chromatic colors as a consequence of a stroke. Our multifaceted evidence indicates the independence of color naming and color categorization, and provides a neural basis for color naming.

3.3 Results

3.3.1 Case history

RDS, a right-handed 54-year-old man, suffered an ischemic stroke in the territory of the left posterior cerebral artery in February 2014. He is of Portuguese origin, but completed his education in France and has been living in France most of his life. After the stroke, RDS found himself unable to read words and numbers, and struggled to find the names of visually presented colors. These deficits obliged him to retire from work. Since his stroke, RDS has shown a dense right-sided homonymous hemianopia on confrontation test. Goldmann perimetry performed 26 months post-stroke confirmed a complete hemianopia without macular sparing.

3.3.2 Color perception

Six months post-stroke, RDS performed at ceiling on the Ishihara plates test (Ishihara, 1974). His error score on the Fansworth-Munsell 100 Hue test was only slightly above the typical cut-off score for his age (187 vs. 161, according to (Verriest, Van Laethem and Uvijls, 1982). We also tested RDS's color perception using the Colour Assessment and Diagnosis (CAD) test, a very sensitive chromatic detection test (Rodriguez-Carmona, O'Neill-Biba and Barbur, 2012). The testing took place 55 months post-stroke. On the CAD, RDS had a normal red-green color vision (r-g threshold of 2.38 SNU), however his yellow-blue color vision showed some deficiency (y-b threshold of 6.97 SNU). Importantly, RDS reported no color vision problems and no subjective change in his color perception after the stroke. This suggests that his y-b dyschromatopsia did not result from the extremely rare genetic form of tritanomaly, or from stroke-induced change in perception. It might instead be of degenerative origin, perhaps linked to his long-standing type II diabetes (Ayed, Jeddi and Kallal, 1990). In any case, all the chromatic colors stimuli used in this study were well above RDS's chromatic detection thresholds (see Fig. 1B), and he was always able to distinguish those colors from the grey background.

3.3.3 Color naming

We asked RDS to name 34 color patches presented on a computer screen (13°18'x18°55' visual angle, see Methods for display details). Eight of the patches were achromatic (white, black and grey) and 26 patches were chromatic. The patches were chosen on the basis of being named with at least 90% accuracy by healthy controls in a separate experiment, where subjects attributed color patches to one of 11 color categories (see Supplemental Information 1). The same colors were used to probe color categorization. RDS was asked to name each patch three times, performing 102 trials in total. There was no time limit for response.

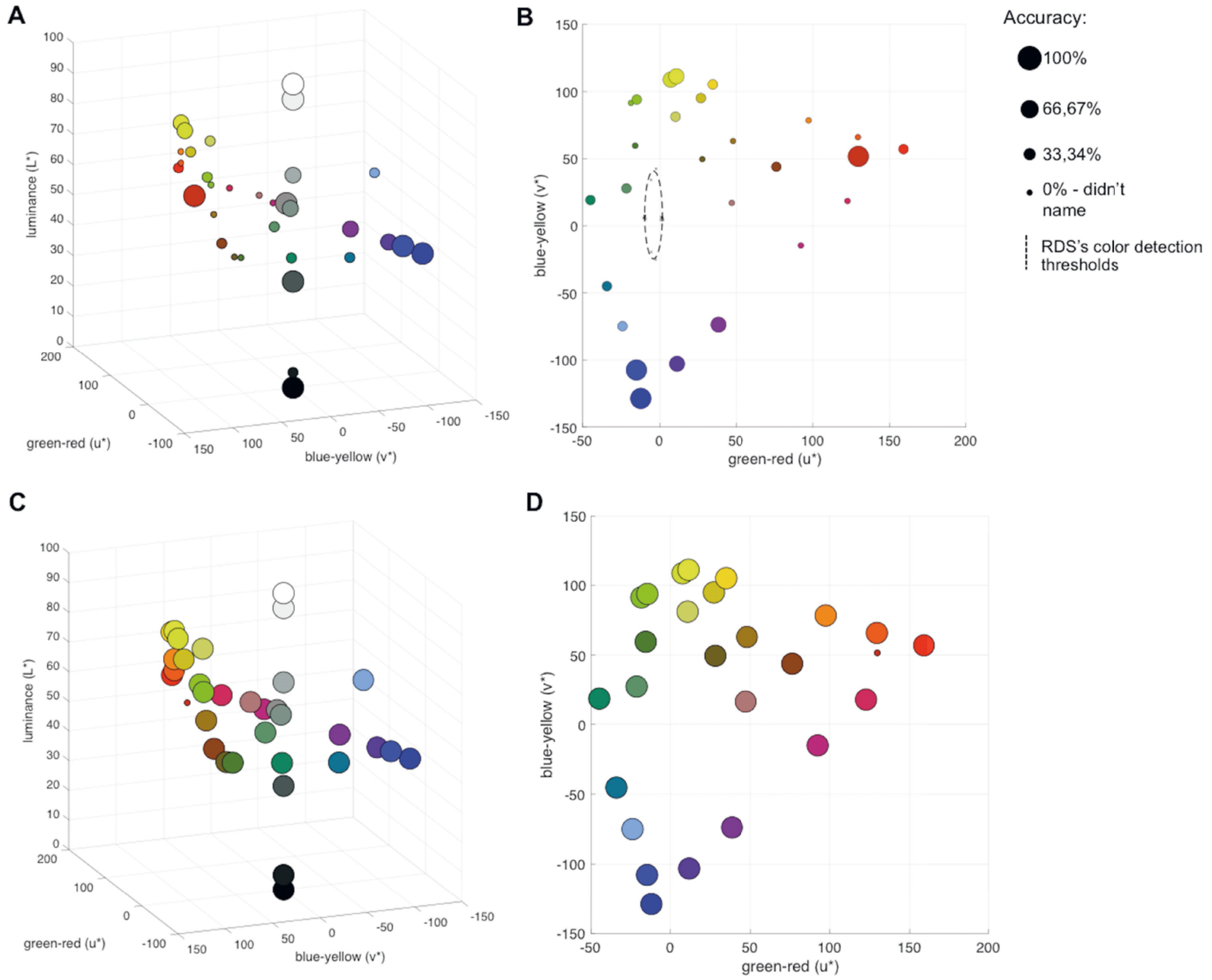

Figure 4. RDS's color naming performance (A) RDS's color naming accuracy projected on the 3D CIELUV color space. Dot colors represent the color RDS was asked to name, and dot sizes designate naming accuracy (% of correct color identification). (B) RDS's color naming accuracy (corresponding to dot sizes) projected on the CIELUV chromatic (u*v*) axes. RDS's chromatic detection thresholds as measured with the CAD are depicted as black crosses. An ellipse fitted to the discrimination thresholds corresponds to the region in which RDS had troubles in color detection. The colors used in our task are well outside this region. (C, D) Color naming results of a demographically matched control subject. See also Fig S1.

Overall, RDS was 83% correct when naming achromatic colors (vs. 98±4% in 12 demographically-matched controls, t(11)=-2.31, p=0.021), but only 34% correct when naming chromatic colors (vs. 93±4%, t(11)=-17.38, p<0.001). Naming performance was thus dramatically different for chromatic and achromatic colors (p<0.001, see (Crawford and Garthwaite, 2005) and Methods). When attempting to name colors, RDS typically hesitated, and often used the strategy of associating a color patch with a color-diagnostic object: for example, he said “this is the color of blood; it must be red”, or “this is the color of the sky; it must be blue". He never made such comments when naming achromatic patches. Fig. 1 displays RDS's color-naming accuracy ranging from 0 (when a given color was never accurately named) to 3 (when a color was named correctly 3 out of 3 times) projected on the CIELUV color space. Colors along the luminance (L*) axis were all named with high accuracy (see Fig. 1A), while the blobs of the most consistently named colors along the chromatic axes (u* and v*) were located on extreme values on the axes, corresponding to the highest color saturation. The overall average accuracy was 2.50 for achromatic colors and 1.04 for chromatic colors (Fig. 1B; for more details on RDS's naming errors see Supplemental Information 2 and Fig. S1). Figure 1 A and B also demonstrate that RDS achieved better performance when naming colors of high saturation (see the "blobs" of high naming accuracy at the extreme values of u' and v' axes). Indeed, stimulus saturation correlated positively with RDS's naming accuracy ($r_{(24)}=0.43$, $p=0.026$). Importantly, all the colors used to assess RDS's color naming were well above his color detection thresholds, depicted by the ellipse in Fig. 1B. Thus, RDS's color naming disorder cannot be accounted for by perceptual difficulties.

3.3.4 Color categorization vs. color-name comprehension

We assessed RDS's color categorization by developing a non-verbal color categorization task, and compared his performance with his ability to access color names from visually presented colors (color-name comprehension task; Fig. 2A-B, Table S1). In the color categorization task, two vertically arranged, bipartite discs were presented on each trial. Each disk contained two colors, either from the same color category (e.g. two blue shades) or from different categories (e.g. brown and red). Participants had to indicate the disc containing the same-category colors. The same displays were used for the color-name comprehension task. Participants heard a color name and had to indicate the disc containing the corresponding color (see Table S1 for design details). For the analysis, the stimuli pairs were divided into two conditions: the chromatic condition (Fig. 2A,B upper), whereby both discs contained at least one chromatic color; and the achromatic condition (Fig. 2A,B lower), whereby at least one disc contained only achromatic colors (black, white or grey). The categorical membership of the colors was carefully controlled in a separate, color-name matching experiment (Supplemental Information 1). Additionally, to check if the color categorization task was robust against individual differences in color categorization (Wright, 2011), before testing RDS we validated it in 39 healthy, non-age-matched controls (Supplemental Information 3).

Afterwards, RDS and 17 demographically-matched controls performed both the color categorization and name-comprehension tasks (see Methods).

RDS's performance on both tasks did not differ from age-matched controls' for achromatic stimuli (Fig. 2D), but showed a different pattern for chromatic stimuli ($p<0.001$, Fig. 2E). For chromatic colors, RDS was severely impaired on the color-name comprehension task, which the age-matched controls performed at ceiling (76% correct in RDS vs. 99% in age-matched controls; $t_{(16)}=-15.22$, $p<0.001$). In contrast, RDS's performance on a more difficult color-categorization task was only slightly worse than age-matched controls' (80% vs. 90%, $t_{(16)}=-2.71$, $p=0.047$, Fig. 2 D-E); and was comparable to the performance of the aforementioned sample of 39 younger controls (Supplemental Information 3, Fig. 2C), who scored on average 89.83% (±6.73, range 70.97 – 100, $t_{(38)}=-1.51$, $p=0.07$).

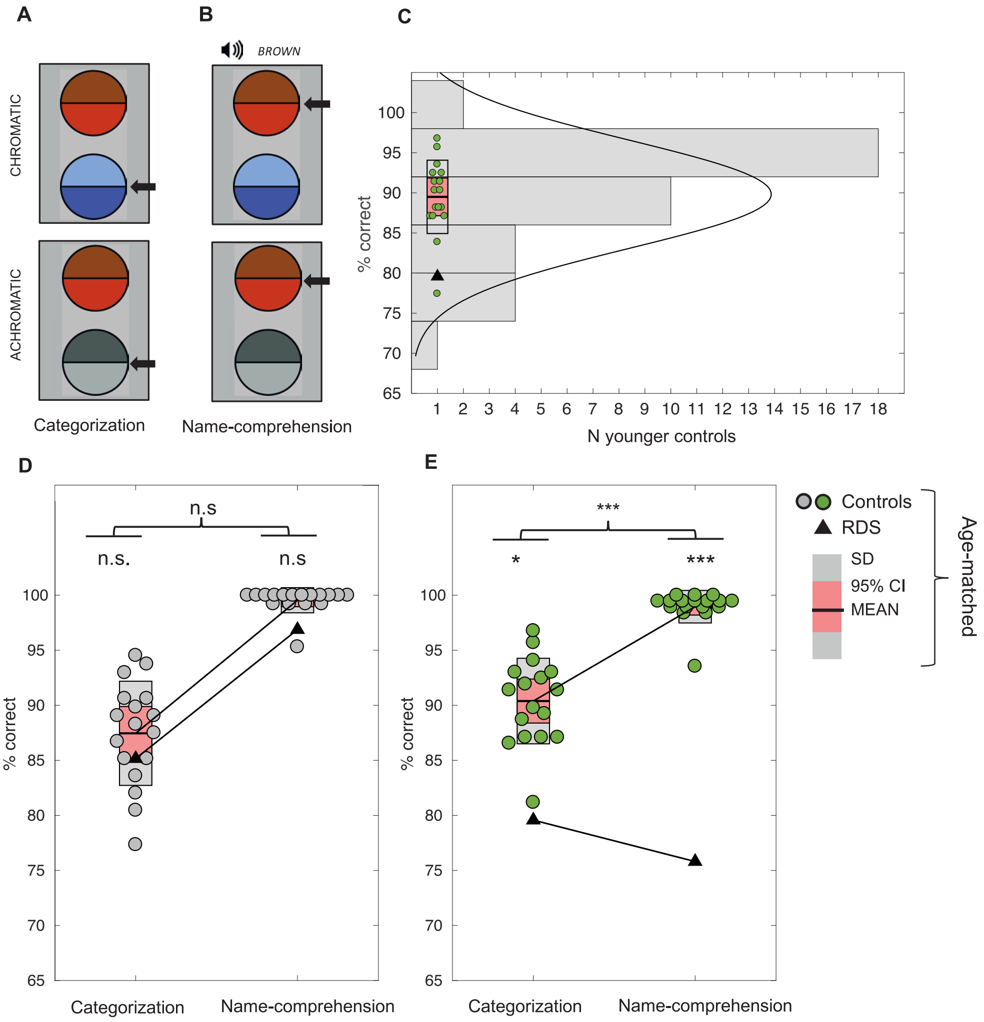

Figure 2. RDS's color categorization vs. color-name comprehension. Examples of displays used for the tasks of color categorization (A) and of color-name comprehension (B). Arrows indicate correct responses. (C) Color categorization accuracy in the chromatic condition (one block only, see Methods and Supplemental Information) for RDS (triangle), age-matched controls (green dots, boxplot) and the younger group of 39 controls (histogram). The black line

indicates the normal distribution fit on the younger controls' data. The x-axis represents the number of younger controls (the boxplot is arbitrarily positioned at x=1). RDS's responses were within the range of the younger controls. (C) With achromatic colors, RDS's performance did not differ from age-matched controls on both color categorization and name-comprehension tasks. (D) With chromatic colors, RDS's performance for color comprehension was significantly more impaired than for color categorization. ***p<0.001 **p<0.01 *p<0.05

Even though RDS was severely impaired on the chromatic color-name comprehension task, he performed above chance level. Could his color-categorization rely on his residual color-name comprehension abilities? If so, then (1) his correct responses on the color name-comprehension task should predict his correct responses on the color categorization task; and (2) the presence of an achromatic stimulus in a trial would be associated with more correct responses on both tasks. To test these predictions, we set up a logistic regression model with RDS's color-categorization accuracy for each trial as a binary dependent variable (0 for incorrect and 1 for correct answers), and two independent variables: (1) RDS's accuracy in color-name comprehension for each trial; and (2) whether or not a given trial contained an achromatic stimulus (see Table S2 and S3). The model showed that neither RDS's color-name comprehension, nor the presence of an achromatic stimulus, were significant predictors of his performance on color categorization (respectively, B=-0.13±0.42, p=0.749; B=0.41±0.32, p=0.194, Table S2). There was a significant effect of the constant (B=1.46±0.37, p<0.001)**, i.e.** the overall probability of RDS giving a correct response, independent of his performance on the color-name comprehension task, and of the presence/absence of an achromatic stimulus. Overall, RDS was 4.31 times more likely to give a correct response than an incorrect response on the color categorization task. We then repeated this analysis with the color-comprehension accuracy as a dependent variable and the accuracy in color categorization as a predictor (see Table S2). The only significant predictor of RDS's color-name comprehension performance was the presence of an achromatic stimulus in the stimulus pair (B=2.3±0.53, p<0.001, Odds Ratio=9.97). RDS was thus about 10 times more likely to give a correct response on the color-name comprehension task, when at least one achromatic stimulus was present in the display. His color-name comprehension performance was not significantly modulated by his accuracy on the color categorization task (B=-0.13±0.42, p=0.748). These analyses show that RDS's patterns of performance on color categorization and on color-name comprehension were independent, and that the presentation of an achromatic stimulus was a strong facilitating factor for his performance only in the color name comprehension task. Thus, it is unlikely that RDS's color categorization relied on his color naming.

3.3.5 Structural and functional neuroanatomy of selective visuo-verbal disconnection for colors

Multimodal imaging revealed the likely neural origin of RDS's color naming deficit. Structural MRI showed that the ischemic lesion encompassed the calcarine sulcus, the lingual, fusiform and parahippocampal gyri in the left hemisphere, as well as the callosal splenium (Fig. 3A). Overlapping the lesion with an atlas of the visual cortex (Wang *et al.*, 2015), and relating it to extra-striate color-biased regions reported in the literature (Simmons *et al.*, 2007; Lafer-Sousa, Conway and Kanwisher, 2016), showed that the lesion damaged the left color-biased extra-striate regions (Fig. 3B). Analysis of the structural connectivity demonstrated a damage to the splenium of the corpus callosum and a resulting disconnection between the left and right occipital lobes (Fig. 3C, Supplemental Information). The lesion also deafferented portions of the ventral occipito-temporal network: it affected 9% of the inferior fronto-occipital fascicle (IFOF), 18% of the inferior longitudinal fascicle (ILF), and 30.2% of the optic radiations (see Methods and Foulon et al. 2018). White matter tractography confirmed the splenial and ventral occipito-temporal damage (Fig. 3D, STAR Methods).

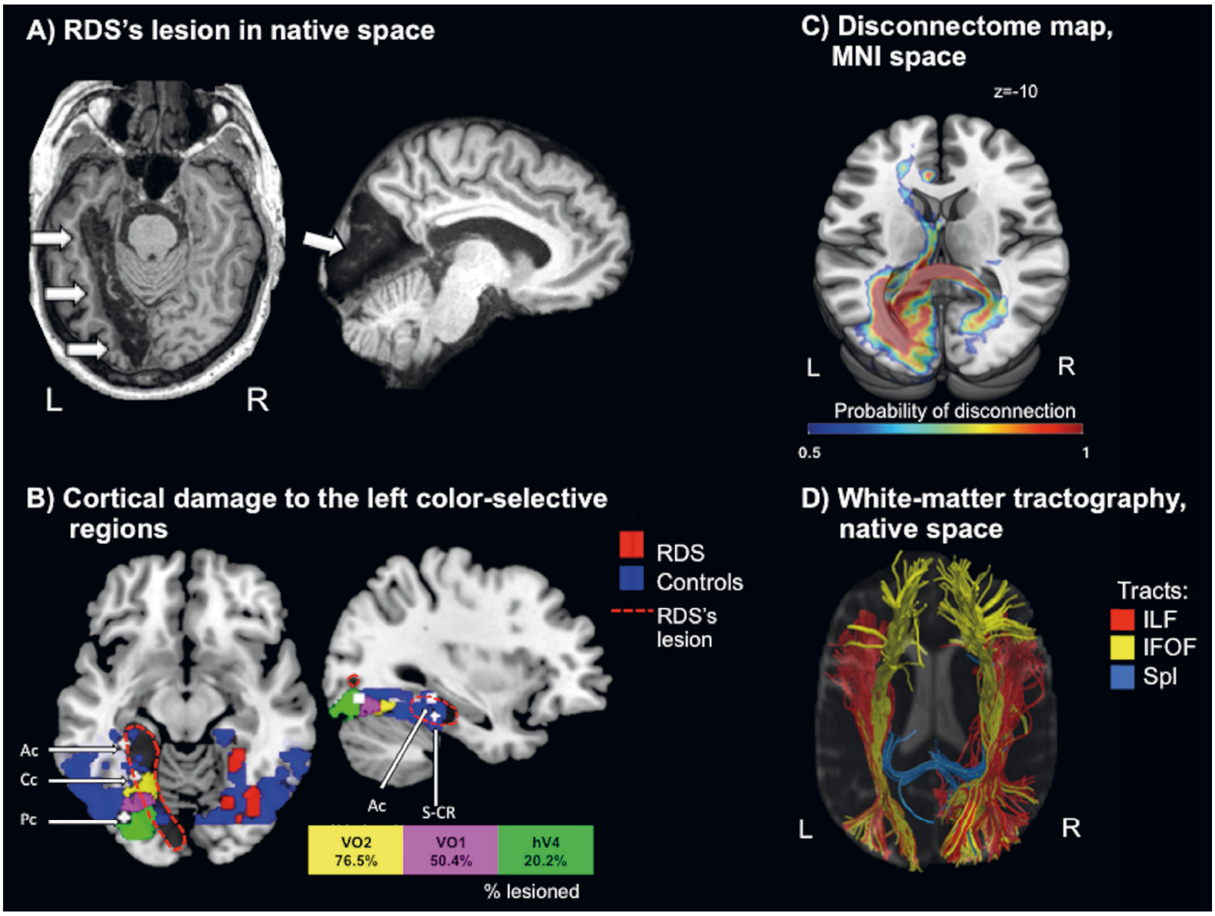

Figure 3 | Structural MRI (A) T1-weighted MRI showing RDS's lesion (arrows) in native space. (B) Lesion overlap with the color-biased regions. The lesion (in black, outlined by a red dashed line) damaged the anterior (Ac) and central (Cc) color-biased regions reported by Lafer-Sousa et al. (2016), as well as the region reported by Simmons et al. (2007) (S-CR: Simmons Color, the white points represent 3mm spheres centered on the activity peaks for each region). The lesion also affected three retinotopically-defined color-biased ventral regions in the left hemisphere (Wang *et al.*, 2015) : hV4 (green cluster), VO1 (pink cluster) and VO2 (yellow cluster). In blue, the controls' probability map for fMRI contrast of Color>Grey-scale; in red, the binarized activity map for RDS for the same contrast. (C) Disconnectome map depicting white-matter tracts passing through the lesion. (D) Diffusion-based white matter tractography confirmed the disruption of the splenium and of the caudal portions of the ILF and IFOF.

We conducted two fMRI experiments to study the architecture of the cortical ventral stream in RDS and 14 age-matched controls (see Methods). In the first experiment, participants saw colored and grey-scale Mondrians and images of objects. In the second, they viewed black-and-white drawings of houses, faces and tools. In RDS, the contrast of colored minus grey-scale images revealed color-biased activations in right-hemisphere structures (Fig. 4A): middle occipital (peak-coordinates (MNI)=[36;-76;-2], cluster-size=205), fusiform (peak=[38;-62;-14], cluster-size=205), lingual (peak=[20;-68;-10], cluster-size=70), and parahippocampal gyri (peak=[28;-42;-12], cluster-size=124). Thus, color-information was exclusively processed in the right-hemisphere ventral stream (such unilateral activity was also present for house-selective regions, see Fig. 4A). In contrast, domains with preserved naming (faces and objects) activated RDS's ventral visual regions bilaterally (Fig. 4A), despite the damage to the left primary visual cortex and the callosal splenium. RDS's activity in the intact occipitotemporal cortex overlapped with healthy controls', indicating no major post-lesional reorganization in these circuits.

We used resting-state fMRI to explore RDS's whole-brain functional connectivity, using his right-hemisphere color- and domain-selective areas as seeds (see Fig. 4A, red). Because RDS's naming disorder was color-specific, we analyzed the unique connectivity of the color-biased regions in the right hemisphere, regressing out the influence of the seeds corresponding to unaffected domains (right-hemisphere face-, place- and tool-selective areas, see Methods, for bivariate correlations see Fig. S2A). Compared to controls, RDS showed reduced color-unique connectivity to the left anterior middle temporal gyrus (peak=[-64;-10;-22], cluster-size=141) and the left temporal pole (peak=[-42;16;-32], cluster-size=132, Figure 4C). In controls, these left anterior temporal lobe (l-ATL) regions were connected to the language network (Fig. S2B), consistent with evidence for l-ATL engagement in naming (Rice *et al.*, 2018).

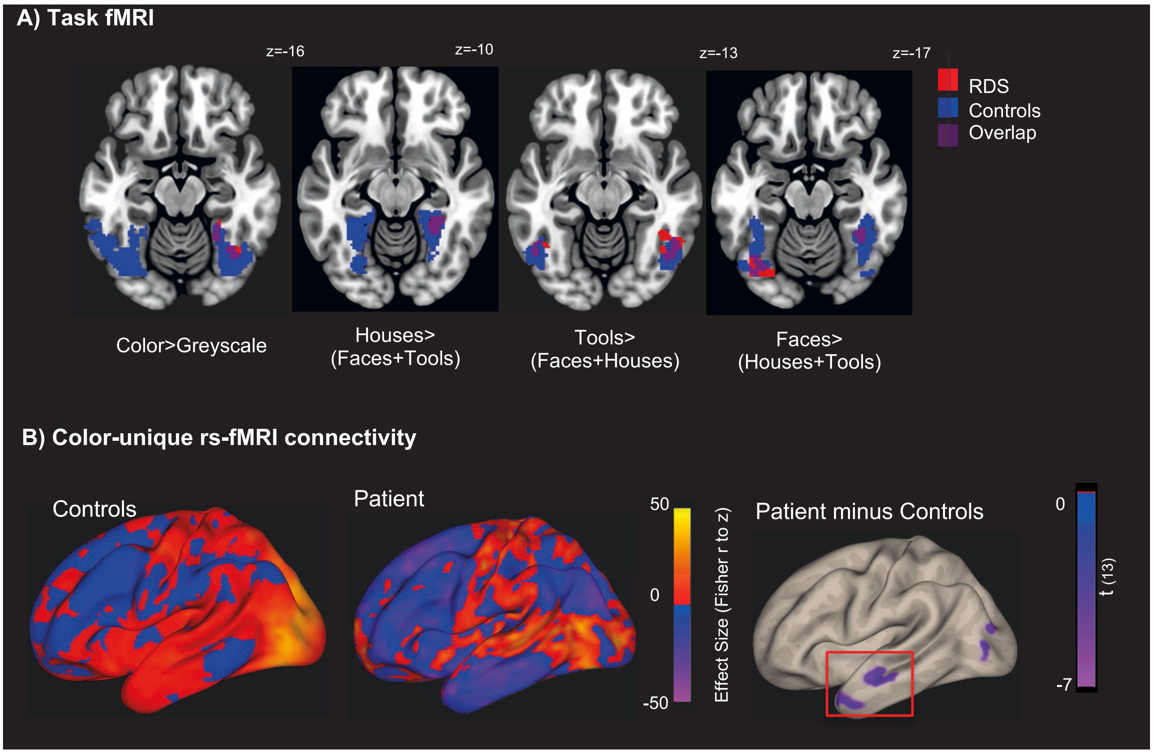

Figure 4. Functional MRI (A) Task fMRI: RDS's color-selective activity was only present in the right cortical ventral stream, whereas activity to tools and faces was bilateral. RDS's and controls' activation patterns largely overlapped. (B) Resting-state color-unique connectivity. Compared with controls (left panel, averaged first level effect size maps, unthresholded), RDS (middle panel, first level unthresholded effect size map) showed decreased color-unique connectivity to the right frontal and occipito-parietal regions, and to the left anterior temporal lobe (right panel) Voxel-wise thresholds: (A) Color vs. grey-scale, $p<0.05$; remaining contrasts, $p<0.005$ (B) left and middle panels uncorrected; right panel, Crawford & Howell modified t-test comparing the patient to the healthy controls, $p=0.005$ one-way. Cluster-wise thresholds (A) color vs. grey-scale $p<0.05$; remaining contrasts, clusters containing the strongest peaks (see Methods), (B) left and middle panels uncorrected; right panel, $p=0.05$ FDR-corrected. See also Fig. S2.

3.4 Discussion

Our study demonstrates the segregation of color categorization and color naming in patient RDS, with acquired brain-damage and a selective naming deficit for visually presented chromatic colors. RDS performed significantly better in a color categorization task than in a task requiring the matching of visual colors to their names. His performance on color naming could not predict his pattern of performance on color categorization. The dissociation we observed, between clearly impaired color-name comprehension and performance close to the normal range on color categorization, qualifies as a "strong" dissociation according to Shallice (1988, see his Fig. 10.3), and challenges the hypothesis that adult color categorization and color naming depend on the same set of neural processes (Thierry *et al.*, 2009; Ting Siok *et al.*, 2009; Athanasopoulos *et al.*, 2010; Brouwer and Heeger, 2013). Thus, the present evidence supports the view that color-categorization can be independent from color-naming in the adult human brain.

3.4.1 The neural bases of color categorization

There is no consensus on the neural locus of color categorization (Siuda-Krzywicka *et al.*, 2019). The present results challenge the hypothesis that adult color categories are lateralized to the left hemisphere and depend on the activity of the language network (Regier and Kay, 2009). Instead, our findings dovetail with more recent neuroimaging studies suggesting that color categorization is distributed bilaterally in the human brain (Brouwer and Heeger, 2013; Bird *et al.*, 2014; Persichetti *et al.*, 2015), with bilateral occipital (Brouwer and Heeger, 2013) or frontal areas (Bird *et al.*, 2014; Persichetti *et al.*, 2015) as possible candidates. We show that the integrity of the left ventral visual stream, including the color-biased regions, is not essential for color categorization, contrary to some neuroimaging results (Ting Siok *et al.*, 2009; Kwok *et al.*, 2011).

3.4.2 The neural bases of color naming

The underlying neural mechanisms of color naming and its deficits are also unclear. Brain lesions can disconnect color names from color percepts. There are two main hypotheses accounting for this visuo-verbal disconnection. (1) Visual color information cannot reach the language system because the left visual cortex is damaged, and interhemispheric transfer from the right visual cortex is prevented by a caudal callosal lesion (Geschwind and Fusillo, 1966). Naming of other visual categories is spared because their representations activate tactile associations that can reach the left hemisphere via more anterior portions of corpus callosum. (2) Color information can reach the left hemisphere through the anterior corpus callosum, but it cannot reach the language system because of damage to a cortical color-naming hub, linking colors to their names (Damasio and Damasio, 1983). The present multimodal imaging data support the color-naming hub hypothesis. Despite extensive damage to the left primary visual cortex and the callosal splenium (see Fig. 3), there was bilateral occipital activity for tools and faces in RDS's ventral cortical visual stream (see Fig. 4A), implicating cross-callosal transfer of visual information. This interhemispheric transfer most likely exploited more anterior callosal and fronto-temporal pathways (both spared in RDS, see Fig. 3D; see also (Tomita *et al.*, 1999) for supporting evidence in non-human primates). No such bilateral activity was present for colors (Fig. 4A). At the same time, RDS's right hemisphere color regions showed unique connectivity with large portions of the left hemisphere (see Fig. 4B and Fig. S2A). Thus, despite evidence for inter-hemispheric connectivity selective to colors, there was no remaining left ventral occipital module to process colors (as opposed to object- and face-related information). This pattern of results is consistent with the hypothesis stating that the integrity of the left mesial ventral visual stream, rather than the callosal splenium, is crucial for color naming (Damasio and Damasio, 1983). Thus, our evidence indicates that the left color-biased regions may serve as color-naming hubs, linking visual color percepts with their verbal labels. This conclusion is also consistent with the report of a case of color anomia without splenial damage (Mohr *et al.*, 1971).

As a consequence of the lesion, RDS's right hemispheric color-biased regions showed reduced functional connectivity to the left anterior temporal lobe (ATL). This selectively reduced connectivity between right-sided color areas (in the absence of their left homologs) and language-related regions is likely the basis of RDS's color-biased naming deficit. There is abundant evidence for the involvement of the left ATL in naming and speech production. Left-hemisphere ATL lesions, compared with their right-hemisphere homologs, are more likely to cause anomia and language deficits, as shown by lesion overlap studies (Damasio *et al.*, 1996, 2004; Belfi *et al.*, 2018; Rice *et al.*, 2018), and by intraoperative electrical stimulation (Mandonnet *et al.*, 2007). The absence of a left hemisphere color module could have deprived the left ATL of chromatic information, leading to a naming disorder selective for chromatic colors. Information related to other visual domains, as well as to achromatic colors, could reach the language system through the unaffected functional visual modules in the left hemisphere.

3.4.3 Naming chromatic and achromatic colors

We report the detailed description of a dissociation between chromatic and achromatic color-naming in a patient with impaired color-naming. A previous case study on a patient with visual agnosia briefly mentioned better performance with achromatic than with chromatic colors for real objects (Kinsbourne and Warrington, 1964), but achromatic color patches were not tested. Preserved linguistic processing of achromatic colors in RDS might rely on spared visual dorsal pathways (see Mullen et al. 2015; Conway 2014) for evidence of achromatic contrast processing in the dorsal cortical visual streams).

In order to name a chromatic color, RDS was referring to objects that are usually linked with a given color (e.g. red-blood, blue-sky). This strategy seems consistent with the view that color name lexicons are built upon the colors of objects that are functionally relevant to the observers (Levinson, 2000; Gibson *et al.*, 2017; Witzel, 2018; Zaslavsky *et al.*, 2018), and suggests the importance of object color for high level color cognition (Conway, 2018; Witzel and Gegenfurtner, 2018).

3.4.4 Validity of single-case studies

Our conclusions are based on behavioral and neuroimaging results of a single patient. To assess whether RDS's responses reflect idiosyncratic patterns of performance or abnormal pre-lesional brain organization (Bartolomeo, Seidel Malkinson and de Vito, 2017), we compared his behavioral and neuroimaging results to that of controls matched for age, gender and education; as well as to findings reported in the literature (Simmons *et al.*, 2007; Wang *et al.*, 2015; Lafer-Sousa, Conway and Kanwisher, 2016; Foulon *et al.*, 2018). Our results strongly suggest that RDS's premorbid neurocognitive profile was representative of the general population. Note that other single-case reports of acquired brain lesions have provided critical evidence on normal color perception (Bouvier and Engel, 2006; Bartolomeo, Bachoud-Lévi and Thiebaut de Schotten, 2014) and color knowledge (Luzzatti and Davidoff, 1994; Miceli *et al.*, 2001; Stasenko *et al.*, 2014).

3.5 Conclusions

The present detailed evidence for the segregation of color categorization and color naming in the adult brain corroborates recent reports of categorical responses to color in preverbal infants (Skelton *et al.*, 2017), reappraises a long-standing neuropsychological debate (Roberson, Davidoff and Braisby, 1999; Haslam *et al.*, 2007), and defines a specific mechanism for visuo-verbal disconnection (Geschwind and Fusillo, 1966). Our study stresses the role of detailed descriptions of neurological patients in constraining hypotheses on the involvement of language in human cognition.

3.6 STAR METHODS

3.6.1 LEAD CONTACT AND MATERIALS AVAILABILITY

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Paolo Bartolomeo (paolo.bartolomeo@gmail.com).
This study did not generate new unique reagents.

3.6.2 EXPERIMENTAL MODEL AND SUBJECT DETAILS

RDS (54-year-old male) and seventy-three healthy participants participated in the study. Seventeen healthy subjects aged 21-40 years (mean 25.12 ± 4.40, 11 females) took part in the first experiment aiming in establishing categorical membership of color stimuli. Seventeen healthy participants served as “demographically-matched controls” for RDS’s performance in color categorization and name-comprehension tasks. They were males, matched for age and education with RDS (age 49-59 years, mean 53.41±3.73; all worked as office workers). Additionally, thirty-nine “young controls” aged 19-44 (mean 26.25 ± 6.85, 19 females) performed the color categorization task All participants were right-handed according to the Edinburgh Inventory (Oldfield, 1971), had normal or corrected-to-normal vision, and showed normal color vision on the Ishihara Color plates test. The present research was promoted by the Inserm (CPP C13-14) and approved by the Ile-de-France I ethical committee. Before participating in this research, all participants signed an informed consent form. The form was read to RDS because of his reading disorder.

3.6.3 METHOD DETAILS

3.6.3.1 Categorical membership of colors: color-name matching experiment

To ensure that the colors used in the color categorization task were not ambiguous in terms of categorical membership in native French speakers, we ran a color-name matching experiment.

Visual display. In all behavioral experiments outside the scanner the stimuli were displayed on a CRT monitor, driven by a NVIDIA Ge Force GT640 graphics card with a spatial resolution of 1024x758 pixels, a refresh rate of 60 Hz, and a color resolution of 8 bits per channel. Color rendering was calibrated, and gamma corrected. The CIE 1931 chromaticity coordinates and luminance for the monitor primaries were R = (0.614, 0.356, 27.3), G = (0.286, 0.600 60.1), and B = (0.146, 0.070, 9.4); and the CIE 1931 xyY of the white-point were 0.3055 0.3091 99.45]. The viewing distance was 60 cm. The experiments were designed using PsychToolbox 3 (Brainard, 1997), MATLAB 2011b. In all experiments, the stimuli were presented on a uniform grey background (L*=77.54, u*=4.48, v*=4.48)

Stimuli. We produced 13 sets of colors. The colors were defined by a line between the (approximate) prototypes of: (1) red (L*u*v*=[58.22 157.12 55.52]) and orange [69.11 106.44 74.51], (2) orange and yellow ([92.56 14.80 113.54]), (3) yellow and green ([50.13 -53.06 68.06]), (4) green and blue([39.92 -18.78 -136.33]), (5) blue and red, (6) red and brown ([38.87 61.93 41.68]), (7) brown and yellow, (8) brown and green, (9) grey ([60 0 0]) and red, (10) grey and yellow, (11) grey and green, (12) grey and blue, (13) black ([0 0 0]) and white ([100 0 0]).

The prototypes were chosen in such a way that all colors along the line connecting them lay in the monitor gamut. In this way, for each line the colors crossed (at least) one category boundary. Colors were probed with a resolution of 5 ΔELUV (adjacent colors differed from each other with the distance of 5 ΔELUV). Overall, these 13 sets involved 320 different colors. Colors were presented as disks subtending 1.9° of visual angle.

Procedure. Each trial consisted of a single-color patch presented at the center of the screen on a grey background. There were 3 blocks of the experiment; each block contained 320 trials, one per each unique color. In total, each subject completed 960 trials. On each trial, subjects had to match a color label (black, blue, brown, green, grey, orange, pink, purple, red, yellow or white) with the patch presented. To do so, they had to press a key corresponding to one of the eleven color names in French. The labels with color names were glued to a numerical keyboard (keys 1:9, "+" and Backspace) in an alphabetical order. Time to answer was not limited. After response, the chosen color name appeared centrally on the screen for 500ms, and the next trial started.

Results. We selected the colors that were matched with a given color label with at least 90% consistency to be used for the color categorization task. This was possible for all color categories except red. In case of this category, we chose color probes with the highest consistency.

3.6.3.2 Color categorization and color-name comprehension experiments

Stimuli. Each stimulus consisted of two colors. In order to ensure that color-categorization was not confounded with judgments of perceptual distances, we chose the two colors that were furthest apart but still unambiguously within the same category (color-name matching accuracy > 90% in another color-naming experiment, see Supplemental Information) as the within stimulus pair. Cross-category pairs were chosen as the closest stimuli that were unambiguously in two different categories (accuracy > 90% in either category). Because of this approach, there were within category stimuli (e.g. green, ΔE_{LUV} = 80.86) that were perceptually much more different from corresponding across-category stimuli (e.g. green-yellow, ΔE_{LUV} = 35). Overall, there were 15 within-category and 13 cross-category stimuli. They represented 11 color categories (black, blue, brown, green, grey, orange, pink, purple, red, yellow and white). In order to obtain a closer number of within and cross-category stimuli, we added 3 colors for which the color-name matching accuracy data were not acquired (blue $L^*=70.32$ $u^*=-23.94$ $v^*=-74.99$; red $L^*=59.39$ $u^*=159.23$ $v^*=56.96$; and brown $L^*=54.77$ $u^*=47.98$ $v^*=62.96$). Cross- and within-category stimuli did not differ significantly, either in luminance (ΔL, mean within-category $\Delta L=10.58$, mean cross-category $\Delta L=11.77$, $t=-0.3$, $p=0.76$, ns.), or in hue (Δuv, mean within-category $\Delta uv=32.16$, mean across-category $\Delta uv=40.75$, $t=-0.9$, $p=0.37$, ns.). Additional Bayesian analysis revealed strong evidence towards the null hypothesis (lack of difference) for both ΔL^* (BF=0.35) and Δu^*v^* (BF=0.47). Color pairs were presented as bipartite discs with a diameter subtending 8° of visual angle (Fig. 2A-B).

Procedure. Each trial started with the presentation of a central, black fixation cross (1° visual angle) for 500-ms. Then two bipartite discs appeared, one above the other, aligned with the central meridian of the screen. The distance between the two discs was 4° 45' visual angle. In the color-categorization task subjects had to identify the disc containing colors from the same category. In the color-name comprehension task, the trial started with the auditory presentation of a pre-recorded color-name and the subjects' task was to indicate the bipartite disc containing the named color. Subjects responded by pressing the upper arrow key with their right hand to indicate the upper disc, or the lower key for the lower disc. There was no time limit for responses. There were 157 trials in each experimental block. Within one trial, cross-category and within-category stimuli never contained the same color categories (e.g. a blue/green cross-category stimulus was never presented with a green within-category stimulus). RDS and demographically matched control subjects performed 2 experimental blocks of color-categorization and 2 blocks of color-name comprehension tasks.

The younger controls were recruited to validate the color categorization task. The range of the presented colors can considerably influence color naming and categorization. Results from a larger group of controls allowed us to ensure that our newly developed task was robust against this factor. The younger controls were tested prior to RDS and demographically matched controls, and performed only one block of the color-categorization task. For that reason, Figure 2C contains data from the first block of the color categorization task in RDS and the age-matched controls. Also, only the data from the first block were used to compare RDS to the younger controls.

3.6.3.3 Neuroimaging experiments

Participants. RDS and 14 of the 17 demographically-matched controls who participated in the behavioral experiment took part in an MRI session (mean age: 53.8±3.8), in a 3T Siemens Verio MRI scanner with a 32-channel head coil.

Task fMRI stimuli. For the domain-localizer, the procedure was adapted from a previous study (Mongelli *et al.*, 2016). We used six categories of achromatic pictures: faces, tools, houses, pairs of words, pairs of numbers and body parts. Each category contained 38 pictures. Faces, houses and tools were black line drawings on a white background derived from highly contrasted gray-level photographs matched for size and overall luminance. Faces (17 females, 21 men) were front or slightly lateral views of non-famous people. Houses comprised outside pictures of houses and buildings. Tools were common hand-held household objects (e.g., knife, hair-dryer) presented in a standard orientation. Brain responses to words, numbers, and body-parts weren't further analyzed in this study.

In the color localizer, the stimulus set comprised five categories of pictures: chromatic and achromatic Mondrians, highly color diagnostic objects in congruent color, incongruent color and grey scale. Note that incongruently colored images were not analyzed further in this study. Chromatic Mondrians were 200 x 200 pixel images, comprising color patches of 50 pixels mean edge length and the following colors (RGB): yellow (255,255,0), red (255,0,0), green (0,200,0), purple (220,0,255), pink (255,120,150), blue (0,70,255), brown (127,66,0), grey (127,127,127), orange (255,127,0). Assuming the white-point of the monitor of the fMRI set-up (xyY = [0.3114 0.3624 243.9]), those RGB-defined colors correspond to the following CIELUV coordinates: yellow [L* = 98.2, u* = 3.5, v* = 107.8], red [50.4 234.8 19.3], green [75.2, -93.8, 97.5], purple [50.3, 92.6 -132.2], pink [68.9 105.1 -14.5], blue [40.2, -16.4 -135.2], brown [39.4 61.8 34.0], grey = [58.9, -2.1, -5.2], and orange [69.1 120.6 57.6]. Colored elements within Mondrians were assembled in such a way as to provide an abstract scene with no recognizable objects. The color diagnostic stimuli were images (200x200 pixels), depicting 13 man-made objects (wooden furniture, highly frequent grocery products, street signs, cartoon characters), 25 natural objects (animals, plants, fruits and vegetables, geographic elements such as the sun or water), all on white background. There were 8 drawings and 30 photographs. To obtain grey-scale images, we represented the colors of the images in CIELUV space (using monitor white as white-point) and set chromatic coordinates (u*, v*) to zero.

Task fMRI procedure. The color and domain localizer experiments shared the same design. They were programmed using E-Prime 2.0 software (Psychology Software Tools, Pittsburgh, PA). Subjects were presented with an alternation of blocks of pictures (8,000 ms per block) and blocks of rest (7,800 ms per block). Each stimulation block included eight pictures from one category of stimuli. Each picture was displayed for 600 ms and followed by a 400 ms blank screen. During rest and inter-trials intervals, a black central fixation cross was presented to minimize eye-movements. The experiment included 10 s of initial rest, followed by 30 blocks of pictures (six for each category) and 30 blocks of rest. Blocks were presented in pseudorandom order to maximize the variety of transitions between conditions while avoiding repetition of the same condition in successive blocks. Participants were asked to press a button with their right thumb whenever a picture was identical to the previous one, which was the case for 20% of stimuli (1-3 repetitions/block). Subjects first underwent the domain-localizer, and afterwards the color-localizer.

Task fMRI image acquisition and preprocessing. We used a multiband echo-planar imaging sequence sensitive to brain oxygen-level-dependent (BOLD) contrast (45 contiguous axial slices, 2.5 mm isotropic voxels, in-plane matrix ¼ 80 80; TR ¼ 1022 ms; angle ¼ 62, TE ¼ 25 ms). 482 volumes were acquired. Five additional BOLD volumes with reverse phase encoding direction were also acquired. Functional images were realigned, treated with the FSL "Topup" toolbox in order to correct EPI distortions due to B0 field inhomogeneity (Andersson, Skare and Ashburner, 2003), normalized to the standard MNI brain space and spatially smoothed with an isotropic Gaussian filter (6 mm full width at half-maximum, FWHM). Deformations were applied to the whole brain except for the voxels contained in the lesion mask to avoid deformation of the lesioned tissue.

Resting-state fMRI image acquisition and preprocessing. We acquired 10-minute series of whole-brain resting-state BOLD sensitive images (gradient-echo (GE) echo planar imaging (EPI) sequence, 45 slices, slice thickness = 3mm, FOV 220 x 220mm, A>>P phase encoding direction, TR=2990ms, TE=26ms, flip angle=90°). Data preprocessing and statistical analysis was performed with the CONN v.17 functional connectivity toolbox (Whitfield-Gabrieli and Nieto-Castanon, 2012) (www.nitrc.org/projects/conn). We used standard preprocessing steps including: slice-time correction, realignment, segmentation of structural data, normalization into standard stereotactic MNI space (in RDS, deformations were applied to the whole brain except for the voxels contained in the lesion mask to avoid deformation of the lesioned tissue) and spatial smoothing using a Gaussian kernel of 6 mm FWHM.

To account for the fMRI signal attenuation, after slice-time correction, realignment, motion-correction and normalization, functional scans were subjected to intensity based masking (Peer *et al.*, 2016). In this method, a histogram of maximum BOLD intensity values per voxel for each fMRI acquisition is generated for each subject. Such histogram can be modeled as a sum of two Gaussian distributions, where the first Gaussian includes low-intensity voxels reflecting signal attenuation or no-brain signal, and the second includes high intensity voxels (white or grey matter). Then, a linear function is used to model the transition zone between the two Gaussians. The intensity threshold used for masking reflects the lowest intensity value in the transition zone between the Gaussians. Voxels with below-threshold intensity were masked-out from the functional scans, and are thus excluded from further analysis (for details of this method, see Peer *et al.*, 2016).

We then used the Artifact Detection Tool (ART; http://www.nitrc.org/projects/artifact_detect/) to identify scans exceeding 3 SD in mean global intensity, and scan-to-scan motion that exceeded 0.5 mm. We regressed out those scans as nuisance covariates in the first-level analysis, together with the head motion parameters (three rotation and three translation parameters). Physiological and other spurious sources of noise were estimated with the aCompCor method (Behzadi *et al.*, 2007; Whitfield-Gabrieli *et al.*, 2009; Chai *et al.*, 2012); they were then removed together with the movement- and artifact-related covariates mentioned above. A temporal band-pass filter of 0.008–0.09 Hz was applied.

Structural MRI image acquisition and preprocessing. Participants underwent a high-resolution T1 sequence (repetition time: 2300 ms; echo time: 2980 ms; inversion time: 900 ms; flip angle: 9; acquisition matrix: 256x240; voxel resolution: 1x1x1 mm3) and a diffusion tensor sequence using echo-planar imaging (repetition time: 690ms, echo time: 85 ms; flip angle: 90; acquisition matrix: 110x110; percent phase field of view = 100; slice thickness = 2mm; no gap; voxel resolution = 2, 2, 2 mm^3). Sixty diffusion images weighted with a b-value of 1500s/mm2 and six volumes with no diffusion gradient were acquired.

T1 image was segmented and normalized to the MNI space with SPM12. Diffusion images were treated with the FSL “Topup” toolbox to correct EPI distortions due to B0 field inhomogeneity (Andersson, Skare and Ashburner, 2003). Topup parameters were then implemented in FSL “Eddy”, a tool to correct for eddy current-induced distortions and subject movements. Damped Richardson Lucy Spherical Deconvolution (Dell'Acqua *et al.*, 2010) was computed to estimate multiple orientations in voxels containing different populations of crossing fibers (Tournier *et al.*, 2004; Anderson, 2005; Alexander, 2006). Algorithm parameters were chosen as previously described (Dell'Acqua *et al.*, 2013). A fixed-fiber response corresponding to a shape factor of α = 2 × 10–3 mm2/s was chosen (Dell'Acqua *et al.*, 2013). Whole brain tractography was performed by selecting every brain voxel with at least one fiber orientation as a seed voxel. From these voxels, and for each fibre orientation, streamlines were propagated using Euler integration with a step size of 1 mm, as described in (Dell'Acqua *et al.*, 2013). When entering a region with crossing white matter bundles, the algorithm followed the orientation vector of least curvature, as described in (Schmahmann and Pandya, 2007). Streamlines were halted when a voxel without fiber orientation was reached, or when the curvature between two steps exceeded a threshold of 35°. Spherical deconvolution, fiber orientation vector estimations and tractography were performed in Startrack (http://www.natbrainlab.co.uk).

3.6.4 QUANTIFICATION AND STATISTICAL ANALYSIS

3.6.4.1 Behavioral experiments

We compared the patient's performance with controls' performance using a t-test modified in order to compare a single subject's performance with a group of controls' (Crawford and Howell, 1998). This test (hereafter referred to briefly as t-test) is a modification of the independent samples t-test, where the patient is treated as a group with n = 1, and consequently does not participate in the calculation of the variance.

To compare RDS's performance between the two tasks, we applied the Revised Standardized Difference Test (RSDT) (Crawford and Garthwaite, 2005), with a threshold of $p<0.05$, two-tailed. The RSDT compares the difference between a patient's performance in tasks X and Y, relative to the corresponding difference in performance in the healthy control group.

In total, we performed six statistical tests (2 RSDT for dissociations in color-name comprehension and categorization in achromatic and chromatic conditions, and 4 t-tests for simple effects), with Bonferroni correction for multiple comparisons (alpha = 0.008 for each test). The main text reports the Bonferroni-corrected p-values.

3.6.4.2 Task-fMRI

For RDS and each healthy control, first-level analysis was implemented. in SPM12 software (http://www.fil.ion.ucl.ac.uk/spm/software/spm12/). Data were high-pass filtered and modeled by regressors obtained by convoluting the experimental conditions and the button presses with the canonical SPM hemodynamic response function (a combination of 2 gamma functions, with a rise peaking around 6 sec followed by a longer undershoot).

We used four contrasts to explore RDS's ventral visual stream architecture. For the domain localizer, we used contrasts of tools vs (faces+houses), faces vs. (houses+tools), and houses vs. (tools+faces). For the color localizer, we used contrast of (colored images+ colored Mondrians) vs. (grey-scale images + grey-scale mondrians) (referred henceforth as color vs. grey-scale). To take into account the inter-subject variability, RDS's activations were compared to probability maps derived from healthy controls. For each healthy control, we masked each contrast of interest's first-level t-map with an anatomical mask of the ventral visual stream. The mask included the inferior occipital, inferior temporal, fusiform, lingual and parahippocampal gyri of both hemispheres from the AAL atlas (Tzourio-Mazoyer *et al.*, 2002). The mask was truncated to keep only regions extending roughly between MNI $y=-70$ and $y=-35$, encompassing most of group-level activations to houses, music, words, and faces (see Fig. 1 in Bouhali, Mongelli and Cohen, 2017). Then, within each masked image we identified the biggest cluster of voxels surpassing a voxel-wise threshold of $p=0.005$ for contrasts of tools, faces and houses vs. the remaining categories. As color-biased activations are usually weaker than other domain-selective activations and are distributed across the ventral stream (Lafer-Sousa, Conway and Kanwisher, 2016), for the contrast of colored images vs. grey-scale we applied a liberal threshold of $p=0.05$, with clusters bigger than 50 voxels. Thresholded images from each participant were subsequently binarized. We created probability maps for each contrast of interest by summing individual binarized images, dividing them by the number of participants and multiplying by 100. Hence, the value in each voxel of the probabilistic map corresponded to a percentage of participants showing activity in this voxel. In figure 3, the maps were thresholded at the level of 10% probability. RDS's first level maps underwent the same procedure as each individual control's maps.

3.6.4.3 Resting-state fMRI

Seed-to-voxel whole brain connectivity first level maps were created for each participant. The average BOLD time course was extracted from four ROIs corresponding to the ventral activation maps of RDS for the following contrasts: tools vs. (faces+houses), faces vs.

(houses+tools), houses vs. (tools+faces) and colors vs. grey-scale (see task-fMRI, section 3.3.4, the same ROIs were used for the patient and each of the control participants). A whole-brain connectivity map was computed, and correlation values were Fisher r-to-Z transformed to Z-values.

The individual Z-maps were entered to a second-level group analysis. To generate functional connectivity maps representing the color-unique connectivity, we used semi-partial correlation coefficients. We calculated the connectivity values from the color seed, regressing-out the time courses of all other seeds (tools, faces and houses) included in the first level analysis. Thus, the color-unique connectivity reflected only the variance specific to connectivity patterns encompassing the color-biased ventral ROI. We then applied the modified t-test (Crawford and Howell, 1998) to compare RDS's color-unique connectivity map to the averaged color-unique connectivity map of the control subjects. Unless stated otherwise, results were thresholded at two-way, p=0.01, cluster-size p=0.05 FDR corrected.

3.6.4.4 *Structural MRI*

Lesion masking and normalization. The lesion mask of the patient was first drawn on a native 3D T1 image using the MRIcron software (Rorden, Karnath and Bonilha, 2007). Then, the T1 image was normalized to a standard brain template (MNI 152) using affine and diffeomorphic deformations implemented in the BCB Toolkit (Klein *et al.*, 2009; Avants *et al.*, 2011; Foulon *et al.*, 2018). In order to avoid lesion effects on the spatial normalization, we used an enantiomorphic transformation (Nachev *et al.*, 2008), where the lesion or signal abnormalities due to the lesion is replaced symmetrically by the healthy tissue of the contralateral hemisphere. Finally, the patient's lesion was manually segmented a second time on the normalized images by a neuropsychologist trained in lesion analysis (K.S-K) and reviewed by an expert anatomist (Michel Thiebaut de Schotten).

Lesion overlap with an atlas of visual cortical topography. To explore the severity of the damage to the left color-biased regions in RDS, we overlapped his normalized lesion mask with the probabilistic atlas of visual topography (Wang *et al.*, 2015). For each region of interest (ROI) included in the atlas, we calculated the percentage of overlap with the lesion according to the following equation:

$$\frac{nVoxels(ROI) \cap nVoxels(Lesion)}{nVoxels(ROI)} \times 100\%$$

This percentage of lesion overlap was calculated for probability maps thresholded at 75% probability (overlapping the lesion with full probability maps yielded similar results).

Lesion overlap with white matter tracts. We mapped the normalized lesion mask onto tractography reconstructions of white matter pathways obtained from a group of healthy controls (Rojkova *et al.*, 2016). We quantified the extent of the disconnection by assessing the probability of the tract to be disconnected (Thiebaut De Schotten *et al.*, 2015; Foulon *et al.*, 2018, see http://www.toolkit.bcblab.com). The normalized lesion was used to produce disconnectome maps. This approach uses a diffusion weighted imaging dataset obtained in 10 healthy controls (Rojkova *et al.*, 2016) to track fibers passing through the lesion. For each participant, tractography was estimated as indicated in (Thiebaut de Schotten *et al.*, 2011). The patient's lesion in the MNI152 space was registered to the native space of each control, by using affine and diffeomorphic deformations (Klein *et al.*, 2009; Avants *et al.*, 2011), and subsequently used as seed for the tractography in Trackvis (Wang *et al.*, 2007). Tractographies from the lesion were transformed into visitation maps (Thiebaut de Schotten *et al.*, 2011), binarized and brought to the MNI152 using the inverse of precedent deformations. Finally, we produced a percentage overlap map by summing at each point the normalized visitation map of each healthy subject in MNI space. Hence, in the resulting disconnectome map, the value in each voxel takes into account the inter-individual variability of tract reconstructions in controls, and indicates a probability of disconnection from 0 to 100% for a given lesion (Thiebaut De Schotten *et al.*, 2015).

White-matter tractography. We explored the integrity of the ventral cortical visual network in the each hemisphere, by using the regions of interest (ROIs): whole occipital lobe, temporal pole (anterior 4th of the temporal lobe), and external capsule. An additional ROI explored the splenium of the corpus callosum. All ROIs were defined anatomically in the patient's MRI on the b0 image in native space. Their anatomical location was revised by an expert anatomist, Michel Thiebaut de Schotten.

3.6.5 DATA AND SOFTWARE AVAILABILITY

The data of the behavioral experiment are available on the OwnCloud Repository under: https://owncloud.icm-institute.org/index.php/s/aMhiBhqloSbGKIL. The neuroimaging data supporting the current study have not been deposited in a public repository because of the restrictions to the availability of the patient's neuroimaging data in order to protect confidentiality. The data can be made available from the corresponding author on request.

3.7 References

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4 When Colours split from Objects: The Disconnection of Colour Perception from Colour Language and Colour Knowledge

“Colour… thinks by itself, independently of the object it clothes.”
Charles Baudelaire

In this chapter, we investigated if RDS’s colour naming deficit was associated with impairments of visual colour knowledge, i.e. visual representations of objects in their typical colours. We hypothesised that difficulties in visual colour knowledge could occur because previous studies on young children and patients with aphasia demonstrated that some aspects of visual colour knowledge could be linked with language processing. We demonstrated that RDS has spared visual and verbal colour knowledge: he was able to differentiate between typically and atypically coloured images; and to associate colour names with object names. However, he could not match colour names to colour patches and to typically coloured objects, neither could he match a colour patch to an achromatic object image. We concluded that RDS’s disconnection goes beyond colour naming: in RDS perceived colours were disconnected from colour knowledge. These results bring novel insights into the cognitive and neural architecture of colour knowledge.

When Colours split from Objects: The Disconnection of Colour Perception from Colour Language and Colour Knowledge

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When Colours split from Objects: The Disconnection of Colour Perception from Colour Language and Colour Knowledge

4.1 Abstract

We investigated object-colour knowledge in RDS, a patient with impaired colour naming after a left occipito-temporal stroke. RDS's colour perception, object naming and verbal colour-knowledge (the ability to verbally say the typical colour of an object) were relatively spared. RDS was also able to state if an object was appropriately coloured or not. However, he could neither match colour names to coloured objects, nor match colour patches to grey-scale objects. Thus, RDS's colour-naming deficit was associated with an impaired ability to conceptually relate visually presented object shapes and colours. These results suggest that objects in their typical colour are processed holistically in the visual modality, and that abilities important for colour naming may also be involved in abstracting colours from visual objects. We discuss these findings in the context of developmental psychology and linguistic anthropology, and propose a model of neuro-functional organization of object-colour knowledge.

4.2 Keywords

colour knowledge; colour naming; language; concepts; visuo-verbal disconnection; inferior temporal cortex; ventral cortical visual stream

4.3 Introduction

Colour cognition has often served as a probe to investigate the extent to which language can interact with perception and other cognitive systems. In particular, it has been debated weather colour naming and categorisation can influence colour perception (reviewed in: Davidoff, 2001; Regier & Kay, 2009; Siuda-Krzywicka, Boros, Bartolomeo, & Witzel, 2019; Witzel, 2018; Witzel & Gegenfurtner, 2018). Here, we investigated how language interacts with knowledge about the colours of objects.

Some objects, such as animals, plants and fruits, are typically associated with a specific colour. Such objects are dubbed *colour-diagnostic* and the associated colours is their *memory colour* (Witzel & Gegenfurtner, 2014). Neuropsychological evidence shows that knowledge of memory colours can be stored in verbal and visual formats (reviewed in: Tanaka, Weiskopf, & Williams, 2001). Verbal colour knowledge refers to purely verbal associations between colour names and object names (e.g. strawberry - red, or banana - yellow). Visual colour knowledge refers to visual representations of memory colours. There are two competing views on the organization of visual colour knowledge. According to the *edge-based theories* of visual recognition (Biederman & Ju, 1988), visual colour knowledge could be organized as a system of associations between non-coloured representations of object shapes (edges) and the representations of colours. Alternatively, the *Shape + Surface model* claims that, at least for colour-diagnostic objects, colour is an integral part of object representation, and that visual colour knowledge stores colour and shape of an object in an integrated way (Figure 1; see Tanaka et al., 2001 for review).

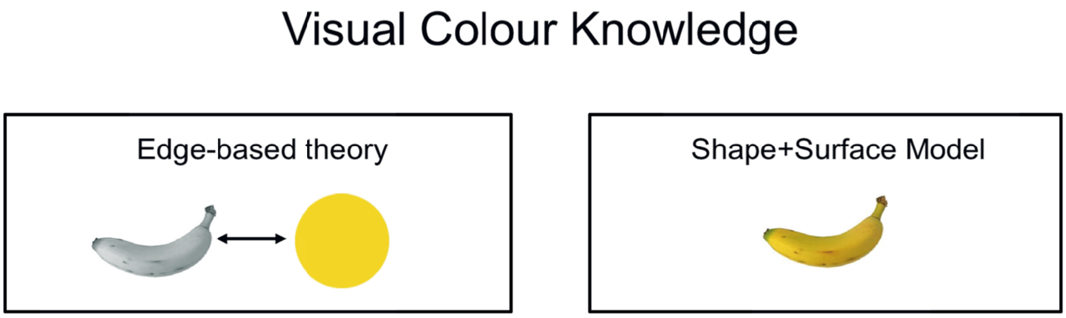

Figure 1. Models of the organisation of visual colour knowledge. Edge-based theory states that knowledge about typical object colours is stored as associations between separate representations of object shapes and colours. Alternative, Shape+Surface model proposes that visual colour knowledge consists of sets of coloured templates, joint representations of colour and shape.

Visual colour knowledge is assumed to be acquired through frequent visual experience with colour diagnostic objects (Bartleson, 1960; Witzel & Gegenfurtner, 2014; Witzel & Hansen, 2015). However, evidence from young children and neurological patients suggests that language could play a role in its acquisition and retrieval. Young children (2-5 years old) and aphasic patients have difficulties when differentiating between congruently and incongruently coloured line-drawings of colour diagnostic objects and when colouring line drawings of colour-diagnostic objects (Basso, Capitani, Luzzatti, Spinnler, & Zanobio, 1985; Basso, Faglioni, & Spinnler, 1976; Cohen & Kelter, 1979; Davidoff & Mitchell, 1993; De Renzi & Spinnler, 1967; Gleason, Fiske, & Chan, 2004). The connection between objects and their typical colours could thus be at least partially mediated by language.

Here, we assessed the two rival models of visual colour knowledge, as well as the role of language in its formation and maintenance, in a stroke patient, RDS. As a consequence of a left occipito-temporal lesion, RDS presented a right homonymous hemianopia and a selective inability to name visually presented colours and orthographic material. Neuropsychological assessment showed that RDS's naming impairment was colour-specific, with spared naming of objects and faces. RDS's lesion did not cause dramatic impairments in colour-vision, neither did it affect his colour lexicon. RDS was able to freely recall colour names in a colour-fluency test and associate colour names with object names, showing spared verbal colour knowledge. Thus, in RDS perceived colours were disconnected from colour names (Geschwind & Fusillo, 1966).

We investigated how RDS's visuo-verbal disconnection interacts with his colour knowledge in three experiments. In experiment 1, we assessed RDS's visual recall of memory colours under two conditions: when colours were presented on objects, or when colours were presented as colour patches next to achromatic object shapes. If visual colour knowledge is stored as associations between separate representations of object shapes and colours, RDS's performance should be comparable on both conditions. A dissociation between the two conditions would suggest the functional segregation between processing of coloured objects and linking object's shapes and colours. In the second experiment we assessed RDS's general abilities to simultaneously process multiple visual stimuli, by asking him to judge the congruency of simultaneously presented object shapes and textures, and different object parts.In the third experiment (colour-name matching), we assessed whether or not RDS can use his spared object identification and verbal colour knowledge to facilitate colour naming. We asked RDS to match colour names to colour patches, typically coloured objects and typical colours of objects presented in grey scale.

Our results show that RDS had spared knowledge of typically coloured objects, which he was not able to break down to separate features of colour and shape. Our findings support the Shape+Surface model of the object-colour knowledge organisation; and imply that language contributes to breaking down object representation to separate features of colour and shape.

4.4 Case Report

RDS, a right-handed 54-year-old man, had an ischemic stroke in the territory of the left posterior cerebral artery in February 2014. Before the stroke, he had worked with colours daily as a manager and car paint expert in an insurance company. After the stroke, RDS presented with right homonymous hemianopia, alexia without agraphia and difficulties in naming visually presented colours. When tested, he was well oriented in time and space, fully cooperative, and had preserved general intellectual abilities. The testing took place between 5 and 55 months post-stroke.

4.4.1 Lesion Location

RDS's lesion was situated in the left mesial occipito-temporal cortex. It encompassed the calcarine sulcus, the lingual, fusiform and parahippocampal gyri in the left hemisphere, as well as the splenium of corpus callosum (Figure 2). The lesion damaged the left primary and secondary visual cortices, causing complete hemianopia without macular sparing.

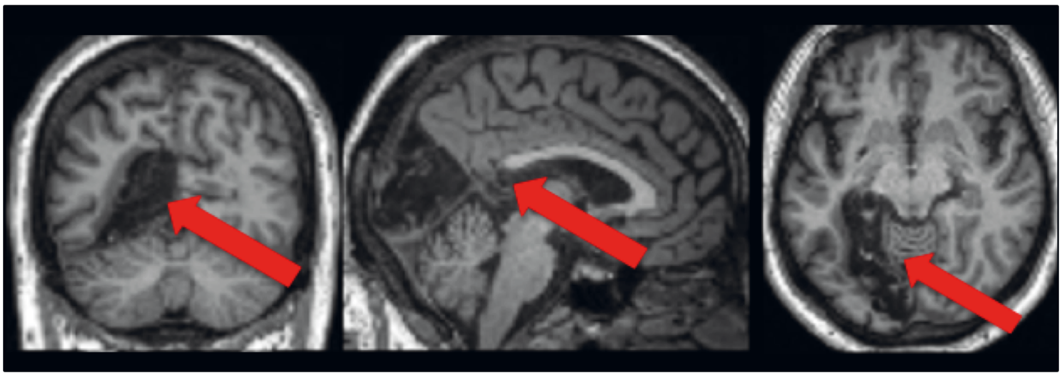

Figure 2. T1-weighted images of RDS's brain. Arrows indicate the lesion.

4.4.2 General Intellectual Abilities

RDS performed the Wechsler Adult Intelligence Scale, fourth edition (WAIS-IV) 46 months post-stroke. He exhibited normal performance on the subscales measuring verbal comprehension (score 94, 88-101 95% CI, 34th percentile), and working memory (score 91, 84-99 95%CI, 27th percentile). His perceptual reasoning skills were within the low average (score: 86, 80-93 95%CI, 18th percentile). His performance was impaired on the Visual Puzzles (7/26, standard score 5), and on the Block Design tasks (32/66, standard score 7). This suggests some difficulties in assessing the relationships between parts, simultaneously processing multiple visual stimuli and visualizing spatial conformations. RDS's relatively high score in Matrix Reasoning task (20/26, standard score 11) indicates normal non-verbal concept formation. Finally, RDS was severely impaired in the processing speed subscale (score 61, 57-71 95%CI, 0.5th percentile), likely because of his reading disorder.

4.4.3 Colour Perception and Naming

Details on RDS's colour perception and naming can be found in Siuda-Krzywicka et al (submitted). Briefly, RDS showed signs of a yellow-blue dyschromatopsia, likely associated with his type II diabetes (O'Neill-Biba, Sivaprasad, Rodriguez-Carmona, Wolf, & Barbur, 2010). His red-green colour perception was normal. Fifty-two months post-stroke, RDS was able to name only 34% of visually presented, chromatic colours.

4.4.4 Colour-name Fluency

RDS was asked to freely recall as many colour names as possible in one minute. He provided 13 different colour names in the following order: white, black, blue, red, green, yellow, purple, indigo, violet, grey, anthracite, pink, orange. The published controls' mean score on such colour fluency task is 10.41 ± 2.15 (De Vreese, 1991). This result indicates that RDS had preserved to colour lexicon.

4.4.5 Verbal Colour Knowledge

To assess RDS's verbal colour-knowledge, we asked him to say the appropriate colour of 20 objects named by the examiner. We used the list of 20 objects published by Bartolomeo et al. (1997, see Bourlon et al. 2009, for normative data). RDS responded correctly on 16 out of 20 trials. For instance, he was able to say that a cotton wool is typically white, a flamingo is pink, or that a tree's trunk is brown. His errors concerned the following objects: tarantula (he couldn't recall what the animal looked like), pumpkin ("brown"), strawberry ("pink") and dolphin ("white", the correct response being grey). Although not dramatically impaired, RDS's overall performance was lower than the published norm (19.13±0.8; (Bourlon et al., 2009), $t(24)=-3.83$, $p<0.001$, $z=-3.91$).

4.4.6 Object Naming

Six months post-stroke, RDS presented signs of optic aphasia, a naming impairment specific to visually presented objects (Rodrigues, Adda, Cristina, Lucia, Scaff, & Miotto, 2008). For example, when shown a black-and-white image of a sled, he said: "Something to protect yourself, something you give to the kids when they go to the pool, a bathrobe, to protect themselves from the snow, the cold, to slide on the snow, to go sledding... a sled". At this time, he correctly named 16 out of 24 (66%) images of animals, fruits and vegetables, and man-made objects from the Snodgrass and Vanderwart pictorial set (Snodgrass & Vanderwart, 1980). We tested his object naming again 38 months post-stroke. RDS was asked to name a set of 80 black-and-white images and grey-scale photographs of objects, including natural and man-made items. Note that the same set of object images was used in experiments 1 and 3. RDS named correctly all the objects, thus showing full recovery from the optic aphasia he had presented in the subacute stage.

4.4.7 Face Naming

We examined RDS's face identification 11 months post-stroke. We asked him to identify a set of 20 coloured photographs of famous people and compared his naming accuracy to the normative data collected by Bourlon et al. (2009). RDS correctly identified all the presented faces (healthy subjects ages 31-60 identified 19±1 images, see Bourlon et al, 2009).

4.5 General experimental methods

4.5.1 Participants

RDS and several groups of healthy controls participated in the different measurements reported below. In total, these groups included sixteen males aged 49-59 years (mean 53.41±3.73), working as office workers, like RDS used to. All controls were right-handed according to the Edinburgh Inventory (Oldfield, 1971), had normal or corrected-to-normal vision, and showed normal red-green colour vision with the Ishihara Colour plates test (Ishihara, 1974). The present research was promoted by the Inserm (CPP C13-41) and approved by the Ile-de-France I ethical committee. Before participating in this research, all participants signed an informed consent form. The form was read to RDS because of his reading disorder.

4.5.2 Materials

The computerized tests were designed in Eprime 2 (Psychology Software Tools, Inc.) and OpenSesame (Mathôt, Schreij, & Theeuwes, 2012) software. In all the computerized tests, the trial duration was not limited, and a subsequent trial appeared after key press. Unless stated otherwise, the stimuli were displayed on a CRT monitor, driven by a NVIDIA Ge Force GT640 graphics card with a spatial resolution of 1024x758 pixels, a refresh rate of 60 Hz, and a colour resolution of 8 bits per channel. The viewing distance was 60 cm. In the experiments assessing colour cognition colour rendering was calibrated, and gamma corrected. The CIE 1931 chromaticity coordinates and luminance for the monitor primaries were R = (0.614, 0.356, 27.3), G = (0.286, 0.600 60.1), and B = (0.146, 0.070, 9.4).

4.5.3 Quantification and statistical analysis

Experiments 1-3 consisted of yes/no tasks, involving congruent (signal) trials for which the correct response was “yes”, and incongruent (noise) trials for which the correct response was “no”. We quantified separately participants’ accuracy (% of correct responses) on congruent trials and on incongruent trails. Additionally, we applied Signal Detection Theory to analyse participants’ performance in terms of sensitivity (d’, describing subjects’ ability to distinguish between signal and noise) and bias (c, reflecting subjects’ general tendency to respond yes or no). High c values indicate a conservative bias, i.e. overall tendency to respond “no”, while low c values indicate a liberal bias, with a tendency to respond “yes” (Stanislaw & Todorov, 1999).

We performed case-control comparisons with the Crawford modified t-test (Crawford & Howell, 1998). This test calculates the probability that the case comes from the distribution of a control sample. To test for a dissociation between two tasks or conditions, we used the Revised Standardized Difference Test (RSDT, Crawford & Garthwaite, 2005). RSDT is a modification of a paired t-test that compares the difference between case scores on two tasks with the analogous difference in the control sample.

4.6 Experiment 1: Colour congruency judgment

4.6.1 Methods

4.6.1.1 Participants

RDS and 11 age-, gender- and education-matched healthy controls took part in the study.

4.6.1.2 Design

Participants were asked to decide whether a visually presented colour was congruent with the memory colour of a visually presented objects shape. There were two experimental conditions. In the *colour-on-object* condition, RDS was presented with congruently and incongruently coloured images of objects. In the *colour-split* condition, the same colour-diagnostic objects were presented in grey scale, together with a separate colour patch containing either a congruent or an incongruent colour (see Figure 3).

4.6.1.3 Materials

We used a selection of 80 pictures of objects taken from the image sets used in Naor-Raz, Tarr, & Kersten, 2003; Rossion & Pourtois, 2004; Witzel, Valkova, Hansen, & Gegenfurtner, 2011. The objects' typical colours comprised 4 categories: brown, green, yellow and red. At the time of the test, RDS identified correctly all of the visually presented objects (see Case Description: Object naming). To obtain grey-scale images, we represented the colours of the images in the CIELUV space (using monitor white as white-point) and set chromatic coordinates (u*, v*) to zero. For the atypically coloured images, we rotated the chromatic distributions of the colour-diagnostic features of an object (e.g. the red fruit but not the green tail of a strawberry) to the opponent areas in the CIELUV colour space to ensure that their colour could not be considered typical for a given object.

4.6.1.4 Procedure

Each trial started with a 500-ms fixation point. Then, in the colour-on-object condition, an image was presented at the monitor centre. In the colour-split condition, a grey-scale object and a colour patch were presented, one under another, on the vertical meridian of the screen. Subjects responded with their right hand as to whether the object was typically coloured by pressing upper arrow for yes and lower arrow for no. Each object was presented in the colour-on-object and the colour-split condition, in a congruent and incongruent colour, resulting in 320 trials and a 50% chance level. The two conditions were interleaved.

4.6.2 Results

Figure 3 summarizes the results. In the colour-on-object condition, on both congruent and incongruent trials, RDS's performance was above 90% correct. Still, he was impaired as compared with controls' (congruent trials accuracy, 91% for RDS vs. 98±2% for controls, $t(10)=-3.73$, $p=0.002$, $z=-3.9$; incongruent trials accuracy, 92% vs. 97±2%, $t(10)=-2.47$, $p=0.016$, $z=-2.58$). RDS did not show dissociation in performance between incongruent and congruent trials: the difference between RDS's scores in the two conditions was not significantly larger than the analogous difference in the control group (RSDT p=0.341). STD analysis revealed that RDS's sensitivity was impaired (d'=2.72 vs 4.07±0.5%, t(10)=-2.41, p=0.018); and his response bias did not differ significantly from controls' (t(10)=0.21, p=0.418).

In contrast, in the colour-split condition RDS was much less accurate on the congruent (31% vs. 86±8% correct, t(10)=-6.73, p<0.001, z=-7.02) than on the incongruent trials (where his performance did not differ significantly from controls', p=0.207), showing a dissociation (RSDT p=0.004). His sensitivity was impaired (d'=0.92 vs, 2.7±0.35, t(10)=-5.02, p<0.001), and he presented a conservative bias (c=0.96 vs c=0.21±0.19, t(10)=3.67, p=0.002, z=3.84).

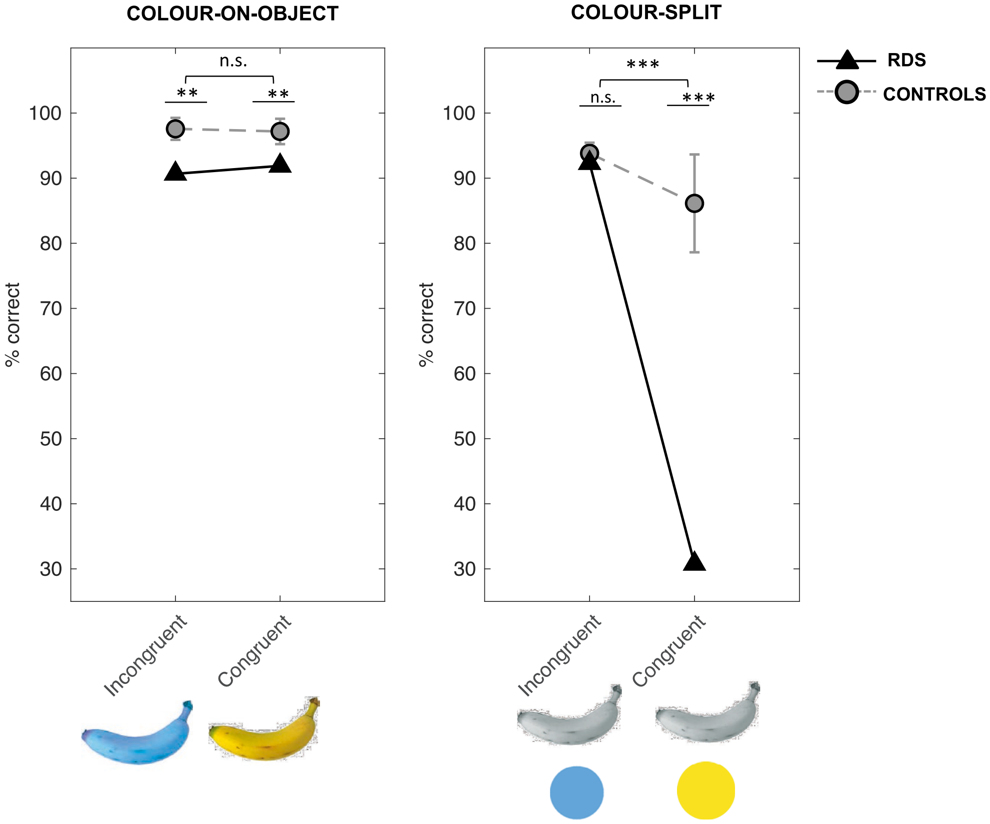

Figure 3. Experiment 1: Colour Congruency Judging. RDS's (black triangle) relatively good performance in the colour-on-object condition contrasted with impairment in the colour-split condition, where he showed strong conservative response bias. Error bars depict ± 1 standard deviation in the control group (n=11). Images below the x axis show examples of trials for each condition. *p<0.05, **p<0.01, ***p<0.001.

4.6.3 Discussion

The results of experiment 1 show that RDS had a relatively spared ability to distinguish between congruently and incongruently coloured images of objects. However, he was severely impaired in judging whether colour patches depicted a memory colour of a simultaneously presented grey-scale object.

To judge if a given colour is typical for object shape, one can possibly use two strategies. According to the first strategy, consistent with edge-based theories of visual recognition (Figure 1A), a shape representation is first activated, then it is associated with a memory colour, and finally compared to the visual input (see Davidoff & Mitchell, 1993, p 134, for discussion). In this case, we would not expect a difference in performance in the colour-on-object and colour-split conditions, because the same mental operation (matching a colour to an achromatic shape) would underlie both conditions. According to the alternative strategy, the object's image could be directly compared to a coloured template, a joint representation object and colour, in agreement with the Shape+Surface models (Figure 1B; Tanaka et al., 2001). If so, resolving the colour-on-object condition would be easier because the task would come down to comparing a mental template to a perceptual object. The colour-split condition would be more difficult because it would require two comparisons; one between the template and the achromatic object; and second between the template and the colour patch. Our results are consistent with the second scenario, and thus support the Shape+Surface model of visual cognition.

An alternative explanation of our results could be that the patches we created did not reliably reflect the typical colour of the grey scale objects. This however is unlikely because control subjects performed at ceiling on this task. RDS could also be impaired in the colour-split condition because of a colour-unrelated difficulty in simultaneously assessing multiple visual stimuli, such as in simultagnosia. Such impairment would also be consistent with his results on the WAIS-IV scale (see Case Report). We ran Experiment 2 to control for this possibility.

4.7 Experiment 2: Property verification

4.7.1 Methods

4.7.1.1 Participants

RDS and 5 demographically-matched control subjects took part in the study. The 5 control subjects were different from those who participated in experiment 1.

4.7.1.2 Design

Participants had to judge the congruency between a visually presented object form and a texture patch (*texture verification condition*), or between visually presented object parts (*shape verification condition*). We initially aimed at testing if colour information would modulate RDS's performance in the texture-verification condition, so for each object form we created coloured and grey-scale texture patches. The results showed that colour did not significantly affect RDS's performance (see Supplementary Materials), thus we combined coloured and grey-scale textures and analysed them as a single texture-verification condition.

4.7.1.3 Materials

All images used in this experiment were downloaded from Wikimedia Commons (https://commons.wikimedia.org). In the texture-verification condition, we used a set of 21 photographs depicting animals, fruits and vegetables, and manmade objects. To obtain images including only object shape information without any surface information, for each photograph we created an object mask. For each object, we downloaded an image depicting a corresponding texture patch (e.g. bear-fur, snake-snake skin etc.). In the shape-verification condition, we used 40 photographs of animals, fruits and vegetables and manmade objects and turned them to grey-scale with MATLAB rgb2grey function. Subsequently, the object parts images were cut out by hand.

4.7.1.4 Procedure

On each trial, two images were presented. In the texture verification condition, the image of object form and the texture patch were aligned on the central vertical meridian of the screen (like in the colour-split condition of Experiment 1). In the shape-verification condition, most of the stimuli were created by cutting the images into two parts on the vertical axis. To prevent RDS from resolving this task by making a judgment based on the perceptual Gestalt, we aligned the object parts horizontally (see Figure 4). To facilitate RDS's performance in view of his right homonymous hemianopia, in this condition the images were presented on the left side of the screen. Participants responded with their right hand as to whether the texture patch corresponded to object form by pressing the upper arrow key for yes and the lower arrow key for no. In each condition a stimulus was presented on both congruent and incongruent trials, resulting in 84 trials in the texture-verification condition (note the presentation of coloured and grey-scale textures, see Experiment 2: Design and Supplementary Materials), 80 trials in the shape verification condition, and 50% chance level. The conditions were blocked, and the texture-verification condition was always administered first.

4.7.2 Results

Figure 4 reports the results. In the texture-verification condition, RDS did not differ significantly from the controls on any of the performance measures (congruent trials accuracy, incongruent trials accuracy, d' or c). In the shape-verification condition, the only performance measure in which RDS differed significantly from the controls was sensitivity (d'), which was higher in RDS than in controls (d'=4.2 vs. 3.4±0.33, t(4)=2.21, p=0.045, z=2.42).

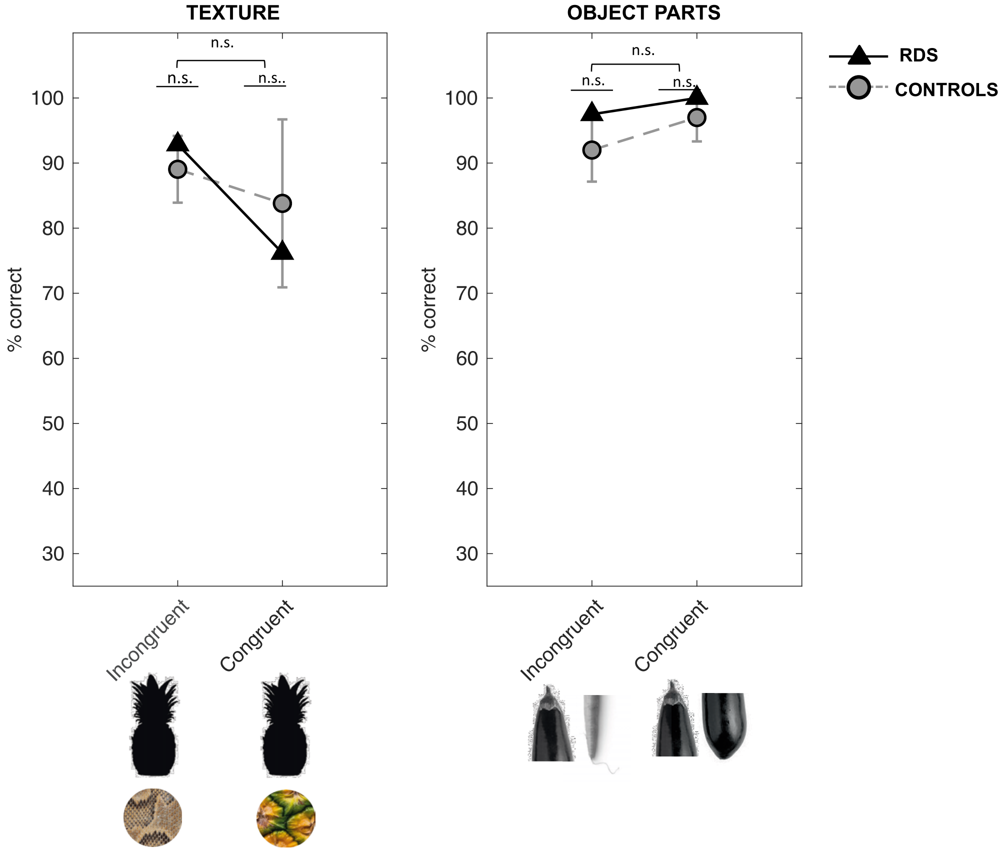

Figure 4. Experiment 2: Property Verification Task. RDS's was not impaired in colour unrelated tasks requiring simultaneous processing of two stimuli. Error bars depict ± 1 standard deviation in the control group (n=5). Images below the x axis show examples of trials for each condition. *p<0.05, **p<0.01, ***p<0.001.

4.7.3 Discussion

Experiment 2 results did not evidence any obvious problems in simultaneous processing of two visual stimuli in RDS. Thus, RDS's failure in the colour-split condition of experiment 1 is unlikely to be explained by simultagnosia. Experiment 2 also suggests that RDS's inability to match object's features may be colour-specific, as he was not significantly impaired on the texture-verification condition. This is consistent with reports showing different processing streams for colour and texture information (Cavina-Pratesi et al., 2010). However, caution is needed when interpreting the results because our study might be underpowered to show a deficit, especially in the congruent trials of the texture-verification task.

4.8 Experiment 3: Colour-name matching

4.8.1 Methods

4.8.1.1 Participants

RDS and the same control participants as in experiment 1.

4.8.1.2 Design

There were 3 experimental conditions. Participants matched pre-recorded, auditorily presented colour-names to visually presented colour patches *(colour-patch condition)*, to typically coloured objects *(typical object-colour condition)* and to typical colours of grey-scale objects *(achromatic object condition)*.

4.8.1.3 Materials

For the colour-patch condition, we used 50 colour patches, 10 for each of the following categories: blue, brown, green, pink and yellow. Patches were chosen on the basis of being named with at least 90% consistency by healthy native French speakers in another, colour-naming experiment (see Supplemental Information to Siuda-Krzywicka et al., submitted). The stimuli did not include red colours because the control, colour-naming experiment did not result in 10 colour probes that would be named with high consistency as red. In the conditions involving objects we used the same stimuli as in experiment 1.

4.8.1.4 Procedure

Each trial started with a 500-ms fixation point, followed by the simultaneous presentation of a spoken colour name and a visual stimulus (colour patch or object), located centrally on the monitor screen (see Figure 5). Participants had to judge whether the colour name matched the colour patch, the colour of the typically coloured object, or the typical colour of a grey-scale object. Participants pressed the upper arrow key of the computer keyboard for yes, and the lower arrow key for no. For each condition, the auditorily presented colour name was congruent with the visual stimulus in half of the trials (50% chance level). Overall, participants completed 420 trials, that is 100 in the colour patch condition and 160 in the two object conditions. Each participant was presented with identical colour-name - colour combinations. The conditions were blocked. To avoid interference between object-colour and achromatic conditions, all participants performed first the colour patch condition, then the typical colour of greyscale object condition, and finally the typically coloured objects condition.

4.8.2 Results

When matching colour names to colour patches and typically coloured objects, RDS answered “no” more often than “yes”, showing a pathologically conservative response bias (c=1.08 vs. -0.43±0.22 in the control group for colour patches, t(10)=6.6, p<0.001; and c =1.04 vs. 0.38±0.22 for typically coloured objects, t(10)=2.85, p=0.009, z=2.98). His performance was significantly more impaired in congruent trials, i.e. the trials where the visual colour matched the colour name (42% vs. 99±1% correct in the colour-patches condition, t(10)=-52.17, p<0.001, effect size z=-54.48; and 39% vs. 97±2% in the object-colour, t(10)=-26.55, p<0.001, z=-27.76), than in incongruent trials (98 vs. 94±2% correct in the colour-patches condition, t(10)=1.70, p=0.06, z=1.77; and 96% vs 99±2% in the typically coloured objects condition, t(10)=-1.53, p=0.077, z=-1.61). There was a significant dissociation between congruent and incongruent trails in both conditions (RSDT p<0.001).

RDS presented a different pattern of performance in matching colour names to typical colours of grey-scale objects. Despite performing well above chance level, compared with controls RDS was impaired on both congruent and incongruent trials (incongruent trials accuracy, 86% vs. 97±3%, t(10)=-3.18, p=0.005, z=-3.32; congruent trials accuracy, 76% vs. 95±5%, t(10)=-3.93, p=0.002, z=-4.10). The difference between RDS’s accuracy between congruent and incongruent trials was not significantly greater than in controls (RSDT p=0.360), neither was his response bias (0.19 vs. 0.11±0.18, p=0.349). Importantly, on congruent trials RDS performed significantly better when matching colour names to grey-scale objects than to typically coloured objects (76 vs. 39% correct, RSDT p<0.001).

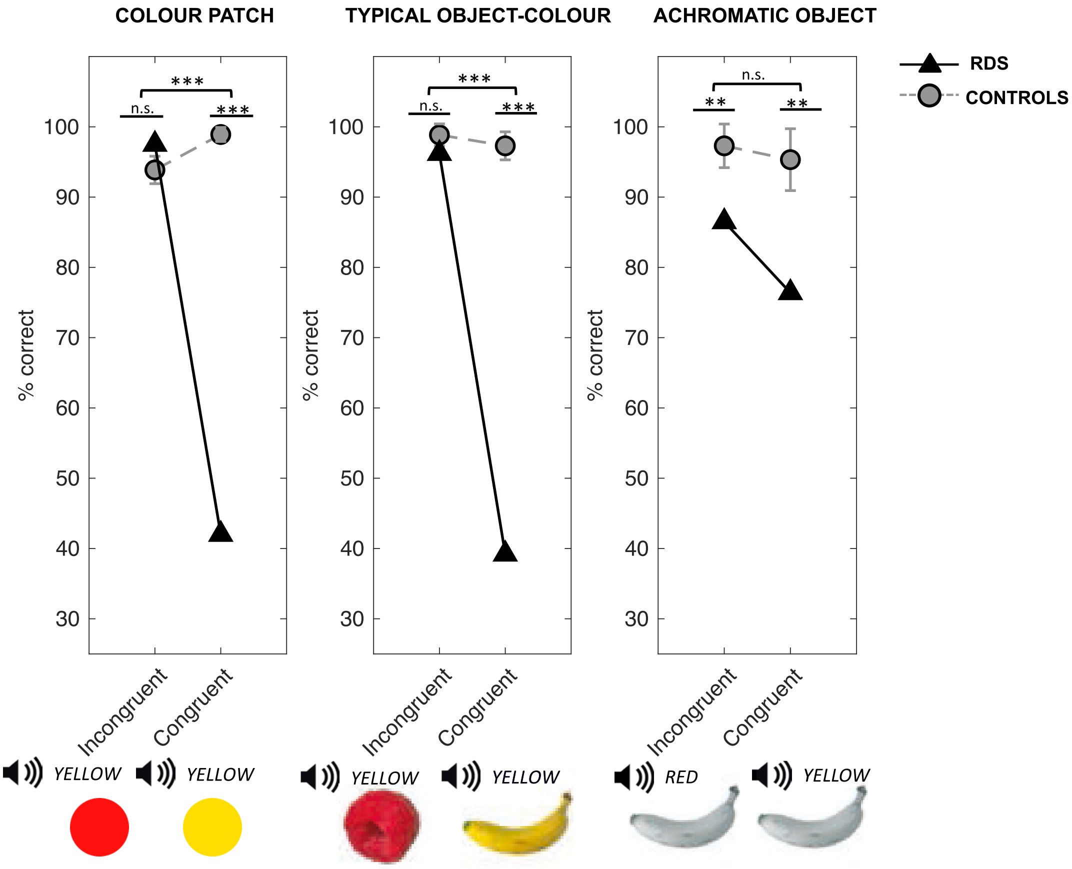

Figure 5. Experiment 3: Colour-Name Matching. RDS could not match colour names to colour patches and typically coloured objects and showed a pathologically conservative response bias. At the same time, his performance pattern was different and overall better when matching colour names to colours retrieved from verbal colour knowledge. Error bars depict ± 1 standard deviation in the control group (n=11). Images below the x axis show examples of trials for each condition. *p<0.05, **p<0.01, ***p<0.001.

4.8.3 Discussion

RDS performed better in the achromatic than in the two chromatic conditions, in particular since he did not show a conservative bias. This suggests that RDS could use his verbal colour knowledge to name the memory colour of grey-scale objects, but could not name the visually presented colours. It is particularly interesting that he did not recur to verbal colour knowledge in the object-colour condition, where the name of memory colour could be retrieved from both, visual and semantic information.

It might be that in the object-colour condition the task instructions drove RDS's attention away from the object's shape and focused it on the colour. However, attention is not likely to divide between two features when those features are part of a single object (Blaser, Pylyshyn, & Holcombe, 2000). It is thus unlikely that attending to object colour would compete with attending to object shape. A more plausible scenario is that RDS's default strategy was to encode the coloured object as a single entity, rather than in separate channels of colour and shape. After the encoding phase, RDS attempted to match the heard colour name to the visual stimulus, but failed, just like he failed in the colour-patch condition. This finding suggest that RDS was more likely to encode typically coloured objects as coloured templates, joint representations of colour and shape, rather than associations between separate representations of shapes and colours. This would support the Surface+Shape model of visual cognition (Tanaka et al., 2001).

4.9 General discussion

We tested rival models of the organisation of visual colour knowledge in a stroke patient, RDS, who showed impaired naming of visually presented colours with spared object identification and verbal colour knowledge (e.g., the ability to state that bananas are typically yellow). RDS was able to distinguish between typically and atypically coloured objects, presenting intact visual colour knowledge. However, he could not match colour names to colour patches and to typically coloured objects; neither could he match a colour patch to a memory colour of a grey-scale object. To the best of our knowledge, this is the first case of functional segregation between spared processing of coloured objects and impaired linking of object's shapes and colours. Our results bring insights into the organization of visual colour knowledge, and its relationship with language.

4.9.1 The cognitive organization of visual colour knowledge

RDS's pattern of performance supports the organization of visual colour knowledge proposed in the Shape+Surface model of visual recognition (Tanaka et al., 2001). According this model, visual colour knowledge is stored as a set of coloured templates, rather than in a system of associations between separate representations of achromatic shapes and abstract colours. Our results are consistent with psychophysical and fMRI findings. The information about colour is automatically retrieved when observers view achromatic object shapes (Bannert & Bartels, 2013; Hansen et al., 2006; Vandenbroucke et al., 2014; Witzel & Hansen, 2015). Grey-scale versions of colour diagnostic objects are recognized slower than their coloured equivalents (review in Bramão *et al.*, 2011); and colours of atypically coloured objects (e.g. a purple banana) are harder to identify than colours of typically coloured objects (e.g. yellow banana, Naor-Raz et al., 2003). The visual representation of colour-diagnostic objects may thus form a Gestalt made of joint representations of shape and colour. Considering that object recognition is driven predominantly by shape, in such Gestalt the weight of shape and colour features are not equal, with shape being more functionally diagnostic than colour.

4.9.2 The relationship between colour knowledge and colour naming

RDS's impaired performance in linking colour patches to grey-scale objects, and in matching colour names to colour patches and typically coloured objects shared striking similarities. In the three cases, RDS was impaired on congruent trials, i.e. when a colour name matched a visual stimulus; and presented a pathological, conservative bias (Figure 6). Could breaking down the shape+colour Gestalts into separate features of colour and shape involve colour language?

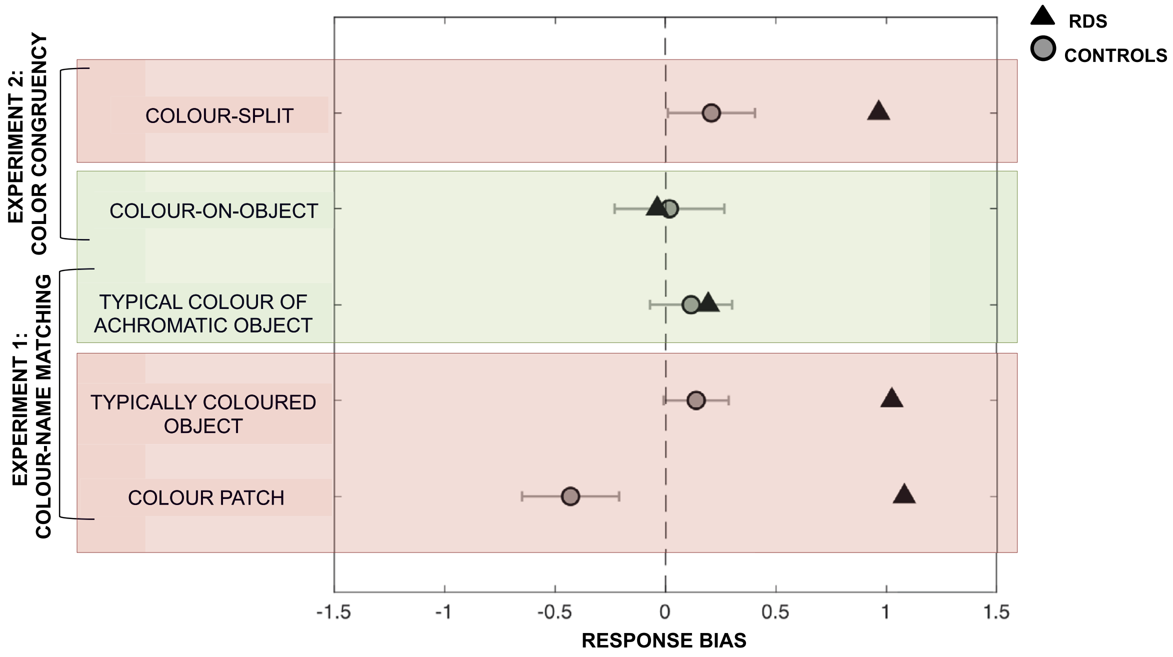

Figure 6. Response bias in experiments 1 and 3. The red rectangle contains the tasks where RDS (black triangles) presented a significantly more conservative bias that the healthy controls (grey dots). The green rectangle contains the tasks where RDS's bias did not differ significantly from controls'. Error bars depict ± 1 standard deviation in the control group.

Studies in cognitive development and cultural anthropology imply that processing colour-diagnostic objects in separate channels of colour and shape might not be the default way in which humans conceptualize their environment. Studies on cognitive development showed that young children struggle when asked to sort or match objects according to their colours (Kowalski & Zimiles, 2006; Sandhofer & Smith, 1999; Smith, 1984), as if colour was not easily accessible to judge object similarity. A child starts to understand that colour can be independent from particular objects at the same time when he or she acquires their first colour names (Baldwin, 1989; Kowalski & Zimiles, 2006; O'Hanlon & Roberson, 2006; Soja, 1994). Children might not attend to colours as interesting object properties unless their attention is explicitly drawn to it with the use of colour names, because colours, contrary to shape, are relatively uninformative about object's function (Baldwin, 1989; O'Hanlon & Roberson, 2006; Sandhofer & Smith, 1999). Colours might also be especially difficult to conceptualize. The same colours can characterize objects from completely different object classes, such as apples and fire engines. Finding common traits between these objects, such as a similar colour, requires relational thinking about them while disregarding the vast differences in their shape and function. Explicit verbal cues, such as colour names, may facilitate this process (Kowalski & Zimiles, 2006; see also Pitchford & Mullen, 2001 for the discussion of color as a special case of conceptualization).

Similar suggestions were made based on research in linguistic anthropology. In some remote cultures inhabitants rarely use colours to identify objects or differentiate between objects (Kuschel & Monberg, 1974; Levinson, 2000). Using colour names and detaching colour from object shape seem to be related. Levinson (2000) suggested that "it is only when colour is detachable from objects with inherent colours that a colour terminology has any real communicational function" (p. 41), and pointed to the discovery of paints and dyes as a possible reason underlying the development of colour names. Consistent with this hypothesis, Gibson and colleagues (2017) showed that Tsimane, an indigenous Amazonian tribe, were more prone to use colour names when identifying non colour-diagnostic, artificial objects, such as cups or ropes, rather than natural objects (e.g. bananas or leaves, see their figure 6).

The conceptualization of colour as an abstract property, detachable from object, may depend on the use of colour names. Our results, together with the reports on aphasic patients (Basso et al., 1985; De Renzi & Spinnler, 1967), provide evidence for this account on a neurobiological level. RDS, whose lesion prevented him from retrieving names of visually presented colours, was also impaired in linking colours and shapes of colour diagnostic objects. Consistent with this association, some aphasic patients have difficulties in picking up the correct crayon to colour line drawings of objects (Basso et al., 1985, 1976; Cohen & Kelter, 1979; De Renzi & Spinnler, 1967; Varney, 1982).

There are multiple ways in which language can interact with perception and thought (reviewed in Wolff & Holmes, 2011). Concerning the relation between object colour and object shape, language could act as an augmenter (Christie & Gentner, 2012; Wolff &

Holmes, 2011). In this view, language (colour names) could introduce the idea of colour as a separate, object-independent entity, thus “augmenting” thought by offering a new equivalence class to organise knowledge about the environment. Evidence from young children and remote cultures suggest that such equivalence class is not available unless developed by the acquisition of colour names. However, such an equivalence class could in principle become internalised and language-independent in development (e.g. Loewenstein & Gentner, 2005). Observations that neurological patients with language impairments struggle in relating abstract colour to object shapes suggest otherwise, showing that language is operative in detaching colour from object representation even in the adult cognitive system.

4.9.3 The neuro-functional organization of visual colour knowledge

It was recently suggested that cortical colour processing in the ventral occipito-temporal cortex is organised in a hierarchy (Conway, 2018), similar to the idea of the hierarchical processing of faces (Freiwald & Tsao, 2010). In such a hierarchy, posterior colour-biased regions encode single hues; the central colour-biased regions group the hues into behaviourally relevant ensembles, i.e. colour categories*;* and the anterior colour-regions represent the memory of colours typical for given objects, i.e. object-colour knowledge (Conway, 2018).

Our results further extend this analogy (see Figure 7). The content of object-colour knowledge - coloured templates, or joint representations of shape and colour - could constitute a visual Gestalt, similar to the idea of holistic processing of faces (for review see Maurer, Grand, & Mondloch, 2002). The coloured templates could be processed in the anterior colour region, selective to both shape and colour (Lafer-Sousa et al., 2016) and built upon inputs from the shape-selective patches in the lateral parts of the inferior temporal cortex (Grill-Spector & Weiner, 2014), and the central colour regions, located in its more mesial portions (Lafer-Sousa et al., 2016; Rosenthal et al., 2018; Zeki & Marini, 1998). In this view, colour agnosia could be understood as a deficit in object-colour knowledge (Miceli et al., 2001; Stasenko et al., 2014), and would be caused by brain damage affecting the neural substrates of the colour and shape Gestalts.

We also speculate that the cultural invention of paints and dyes that might have led to the formation of colour as an abstract (object-independent) semantic category, could have also led to the neural reorganization of cortical circuits that process colours, similar to the reorganization of object-selective structures with the development of writing systems (Dehaene & Cohen, 2007). As a result, the left colour-selective regions, thanks to their proximity to language regions, could support the ability to detach colours from objects, and to link these abstract colour concepts to their names. Colour naming deficits typically occur after damage to the left mesial occipito-temporal cortex, including the lingual gyrus and the parahippocampal areas (A. Damasio & Damasio, 1983). Lesions causing colour-naming deficits frequently overlap with the described locations of the ventral colour-selective regions (Lafer-Sousa et al., 2016). The left colour-selective regions could therefore connect visually presented colours with colour names (Siuda-Krzywicka et al., submitted) .

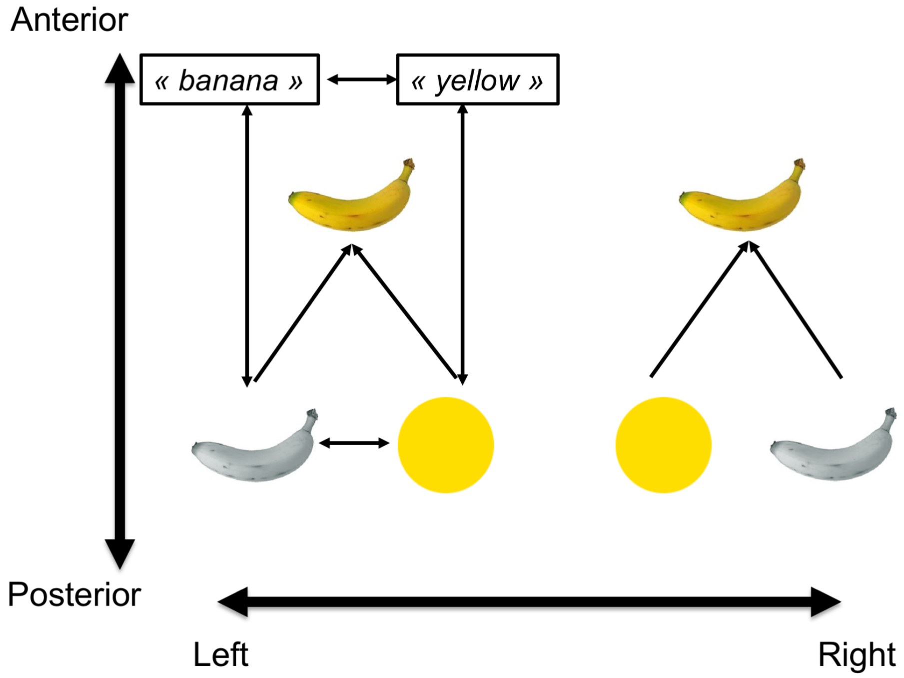

Figure 7. A proposed model of the neuro-functional organization of object-colour knowledge along the posterior/anterior and left/right axis of the inferior occipito-temporal cortex. Most posterior parts of the occipito-temporal cortex, not illustrated here, encode single hues and line-junctions, the basic building blocks of more complex shape and colour representations (reviewed in Conway, 2018; Conway et al., 2010; Gegenfurtner & Kiper, 2003; Grill-Spector & Weiner, 2014). Colour and shape selective regions in the central parts of the occipito-temporal cortex compute object colours (Lafer-Sousa et al., 2016; Rosenthal et al., 2018) and object shapes (Grill-Spector & Weiner, 2014) respectively; and send it to the most anterior, colour- and shape-selective patches (Lafer-Sousa et al., 2016) that compute the joint representation of objects in their typical colour, constituting the visual colour knowledge. The intermediate stage of this model is lateralized, with left colour and shape patches being preferentially connected to language regions, enabling the associations between visually presented colours and shapes, and their names. The associations between colour and shape names constitute the verbal colour knowledge. This left lateralized system could also support abstracting colours from objects and conceptually relating visually presented abstract colours to object shapes.

Does the ability to abstract colours from objects rely on the same cortical circuits as colour naming? RDS's lesion is well-delimited but quite extensive. This leaves open the possibility that the cortical maps of conceptual colour processing and of colour naming are distinct but closely neighbouring. Previous reports on impaired colour-object matching in aphasic patients did not include the lesion locations, thus it is unclear what are the exact lesion sites that cause impairments in colour conceptualization (Basso et al., 1985, 1976; Cohen & Kelter, 1979; De Renzi & Spinnler, 1967). However, Varney (1982) reported that in his study all of the aphasic patients showing deficits on the colour-object matching task were also alexic, which suggests that colour abstraction is computed within the left ventral visual stream. The fact that colour naming and colour conceptualization may be dissociated comes from a seminal case report of visuo-verbal disconnection specific to colours (Geschwind & Fusillo, 1966). The patient reported by Geschwind and Fusillo (1966) was able to pick a typical colour for grey-scale objects, while not being able to name visually presented colours. The exact relationship between abstracting colour from objects and colour naming remains to be established.

4.10 Conclusions

Across the three experiments, patients RDS presented an association between colour-selective naming deficits and impaired matching of colour patches to visually presented object shapes. Thus, in RDS the bottom-up visual colour information was disconnected from the top-down colour language and colour knowledge. Based on RDS's performance patterns and lesion location, and further examples from the literature, we suggest that (1) visual colour knowledge is organized as a set of coloured templates rather than associations between separate representations of achromatic shapes and colours; (2) language is involved in abstracting colours from their objects; and (3) the neural hierarchy of colour processing in occipito-temporal cortex is lateralized, with left-hemisphere colour patches engaged in abstracting colours from objects and linking them to colour names.

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5 General Discussion

Colour is only beautiful if it means something.
Robert Henri

In the introduction I discussed the idea of modularity of high-level colour processing, and proposed the existence of three functional modules, on the basis of evidence provided by the study of patients with brain damage: colour perception, colour naming and colour knowledge. The aim of this thesis was to investigate the possible existence of additional, functionally segregated modules, with a specific focus on colour categorisation and colour knowledge. In **Chapter 2** my colleagues and I proposed that colour categorisation does not originate from either perception or language, as assumed by the traditional nature-nurture debate. Instead, it may result from the interaction of continuous colour perception and high-level cognition; and serve the aim to aid recognition of important objects in the environment. As such, human colour categorisation might be independent of language. In **Chapter 3**, I described an empirical study that we conducted to verify the causal relationship between colour categorization and naming. In-depth investigation of RDS, a patient with a left occipito-temporal damage, demonstrated that colour categorisation and language can be independent in the adult human brain, which runs against the prevalent hypothesis that automatic language activation is required for colour categorisation. Additional MRI experiments revealed a possible neural underpinning of colour naming, and the neuroanatomical features of his optic aphasia for colours. Then, in **Chapter 4** my colleagues and I investigated the interplay between colour language and colour knowledge in RDS. We showed that, in RDS, disconnection was not specific to colour names, but it affected also the semantic representation of colour: RDS was not able to associate a visually presented colour to the object that typically wears it. Together, these results suggest the possibility of three novel modules of colour processing, namely: colour categorisation independent from language, naming achromatic and chromatic colours, and knowing about coloured objects as opposed to knowing about abstract colours. Below, I discuss each of these dissociations in more detail.

5.1 Colour categorisation / colour naming

In the healthy, fully developed human brain, colour categorisation and naming are closely related, and thus difficult to disentangle (some even use the terms colour categorisation and naming interchangeably, see e.g. Brouwer & Heeger, 2013). We had the unique opportunity to assess this issue in RDS, a patient who presented with colour naming deficits due to the left occipito-temporal lesion. By doing so, we provided detailed behavioural and neural evidence for a dissociation between colour categorisation and naming. It is, however, important to note that several previous studies tackled this issue in neurological patients.

In pioneering neuropsychological studies researchers assessed colour categorization with standardised sorting tasks that do not provide reliable control of perceptual distance between colours (see e.g. Beauvois & Saillant, 1985; Geschwind & Fusillo, 1966; Kinsbourne & Warrington, 1964; Stachowiak & Poeck, 1976). While I acknowledge the attempts made in these studies, below I focus only on experiments that provided at least a coarse control over the perceptual differences between colours in their stimulus sets.

Patient LEW described by Roberson and colleagues (1999) suffered from severe naming difficulties not restricted to, but including colour names. He was impaired when asked to group a large set of colours in discrete categories. However, his impairment in colour sorting contrasted with a relatively unimpaired performance on a forced-choice task where he had to identify the odd colour among three colours, two of which belonged to the same category. This striking dissociation between colour sorting and a forced-choice tasks led the authors to conclude that LEW had impaired *explicit* colour categorization, with spared *implicit* categorisation. In other words, LEW's knowledge of categorical boundaries was intact, but he could not access it explicitly, when asked to put arbitrary boundaries between colours that varied continuously in hue. Interestingly, this pattern of performance was not colour-specific; he behaved similarly when asked to categorize facial expressions ranging continuously from one emotional expression to another.

However, this interpretation was criticized in a subsequent study (Haslam et al., 2007). The main source of critique was the qualitative rather than quantitative approach in the analysis of the free-sorting performance of LEW, compared with the performance of a limited group of three healthy controls. Haslam and colleagues used the same colour probes and the same task instructions as Roberson et al. (1999), to examine a larger control group and a patient (JB), who showed progressive language deterioration resulting from semantic dementia. Haslam et al. (2007) quantified the coherence and consistency of groupings with measures commonly employed in categorization research. They showed that (1) healthy participants varied substantially in terms of number and content of final categories in the free-sorting task; (2) longitudinal examination of colour sorting in JB showed that his categorisation performance remained relatively stable in terms of coherence and consistency, despite a profound and progressive loss of colour language and (3) categories generated by JB were more self-consistent, and more consistent with the categories of healthy controls, than would be expected if he were creating coherent categories “by chance”. These results question the dissociation between implicit and explicit colour categorization proposed by Roberson and colleagues (1999), and speak for the independence of colour categorization from language processing.

Similar conclusions come from Case I reported by Fukuzawa and colleagues (1988). This patient suffered from selective naming deficit associated with pure alexia after a left parieto-occipital lesion, with involvement of the splenium of the corpus callosum. Her colour categorization was spared in both colour-sorting and forced choice tasks, in which she was asked to classify a given colour to one of two categories represented by category prototypes. One has to note, however, that her colour naming deficits were relatively mild; thus, it remains unclear whether her residual colour naming could explain her correct performance in the categorization tasks.

Thus, the idea of the independence between colour categorisation and colour language has been emerging in the field of neuropsychology. Our study on patient RDS provided it with conclusive evidence by:

(1) Investigating a patient presenting a selective deficit in colour naming, with spared other language functions, relatively good overall cognitive functioning, and a neurotypical organization of the remaining ventral visual stream architecture. These three factors allowed us to measure precisely the effects of colour anomia on colour categorization, controlling for potential idiosyncrasies stemming from deeper issues in semantic categorization or plastic brain reorganization;

(2) Probing colour categorization on a stimulus set that was carefully controlled for categorical membership (through additional colour naming tests in the healthy) and perceptual distances between colours (by controlling the Euclidean distances in the CIELAB space), and which comprised multiple colour categories. These measures ensured that the colour categories used in the study stemmed from a consensus among French speakers and could not be formed based solely on perceptual similarity of colours. The stimulus design also allowed us to avoid measuring effects that would be specific only to a given category boundary (see Boxes 1 and 2 in Chapter 2);

(3) Comparing RDS’s categorization and naming abilities using the same colours presented in the same context and in the same experiential session. This allowed us to directly tackle the interdependence of colour categorization and naming with within-subject design. Colour categorisation and naming can be affected by the number and

range of colours used in a study (see e.g. Wright, 2011). The use of exactly the same colours provided a control over that factor as well.

Our results challenge the hypothesis that communication between language and vision is crucial for colour categorization, as suggested by previous evidence for lateralised category effects (Gilbert, Regier, Kay, & Ivry, 2006; Ting Siok et al., 2009), and by some of the EEG studies (Thierry et al., 2009) and fMRI studies (Brouwer & Heeger, 2013).

5.1.1 The ecological perspective on the origin of colour categorisation

If colour categorisation does not stem from language, what could be its possible origin? The origin of colour categorisation *has long been caught in the cross-fire between universality and cultural relativism* (Gibson et al., 2017 pp. 10785). Based on the research reviewed in Chapter 1, my colleagues and I suggested that the framework of the relativist-universalist debate, although historically relevant, is not likely to account for the complex picture that emerges from the multidisciplinary research on colour categorisation. Consistent with new perspectives on psychophysical studies (Witzel, 2018; Witzel & Gegenfurtner, 2018), we suggested a new, ecological perspective on the biological bases of colour categorisation (Figure 7). One of the fundamental mysteries of colour categorisation is why colour categories have different sizes and are irregularly distributed in the perceptual colour space (reviewed in Witzel, 2018). We hypothesised that this may happen because different colours may provide information on different aspects of the environment. Some objects in the environment are more relevant than others, since they may be desirable (food, water, mates), or important to avoid (predators). These objects may play the role of reinforcement stimuli in the process of learning associations between colours and rewards. 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, non-human primate, bird), and on its visual system; however, the underlying generalisation mechanism might still be similar. In this view, colour categorisation would group the relevant colour shades into categories, allowing for faster reactions to ecologically important visual stimuli.

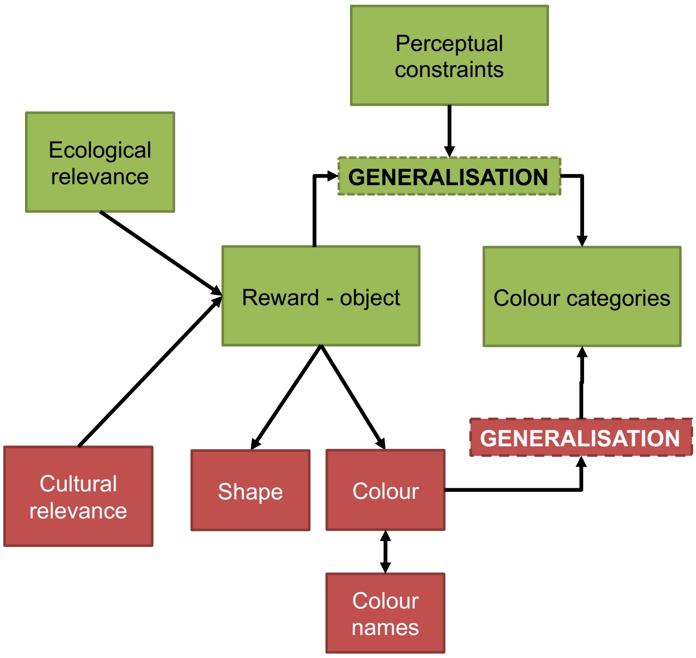

Figure 5 An ecological perspective of colour categorisation. The ecological model of colour categorisation assumes that colour categories result from a generalisation of associations between relevant objects and their colour, to other colour shades. The relevance of objects results from ecological and, in humans, cultural factors. The generalisation is constrained by perceptual qualities of animal or human visual system. For non-human animals, colour is an intrinsic property of the object, so the only purpose of colour categories would be object identification. In humans, cultural evolution led to the abstraction of colours from objects and to the emergence of colour terms. As such, colour became a concept by itself, and colour categories could organise the internal structure of this concept. Human colour categories are thus shaped by both ecological and cultural factors. Green boxes correspond to universal processes that could be identified across species. Red boxes depict human-specific, cultural factors.

Establishing the link between relevant objects in the environment and colour categories is a difficult task in humans, whose relationship to objects is strongly shaped by culture. However, evidence that colours of objects may be relevant in the formation of colour categories was put forward in a cross-cultural studies (discussed in Witzel, 2018 section 3.2.1). Non-industrialized cultures often use object-names to refer to colours (Levinson, 2000; Brown, Isse and Lindsey, 2016; Groh, 2016; Haynie and Bowern, 2016; Gibson *et al.*, 2017). Also, and the origin of many Indo-European colour names can be traced back to object names (e.g. Biggam, 2010).

In Chapter 4, we discussed the idea that detaching colour from object and processing it as an independent concept may have been driven by the cultural evolution, and the discovery of dyes and paints in particular (Levinson, 2000). Colour concept may have determined the emergence of human-specific colour categories, stemming from the generalisation around artificial colours. This idea could explain the cross cultural differences in colour categorisation (Roberson, Davidoff, Davies, & Shapiro, 2004; Roberson, Davies, & Davidoff, 2000), and the fact that the number of colour categories in industrialised societies is changing with time, and seem to be increasing (e.g. Lindsey & Brown, 2014). The universalities in colour categorisation across cultures [2], would be explained by ecologically relevant objects that are common for our species, and the perceptual constraints of human colour vision.

5.1.2 Neural substrates

Neural basis of colour categorization

My colleagues and I demonstrated that RDS's colour categorisation is relatively spared. Therefore, RDS's lesion location does not provide crucial insights into the neural substrates of colour categorisation, except for the fact that intact connectivity between language and sensory regions is not a *sine qua non* condition of adult colour categorisation. One could however speculate about the possible regions involved in colour categorisation based on the ecological perspective introduced above.

The ecological perspective on colour categorisation calls for a shift in the search for the neural underpinnings of colour categories in humans to previously unexplored brain areas. To date, studies on neural substrates of colour categories have focussed on areas known to be involved in colour perception or in language. However, if we expect that colour categories are linked to information about visual objects, we should also explore regions involved in object recognition and classification. It has been shown that colour selective areas lie close to areas important for the identification of objects, faces and places (Lafer-Sousa et al., 2016). Even though the exact computations and connectivity patterns of colour selective areas remain unknown, evidence suggests important interactions between object and colour processing. The anterior colour regions are sensitive to both colour and shape (Brewer et al., 2005; Lafer-Sousa et al., 2016). These regions could possibly integrate the two types of information. Furthermore, psychophysical evidence indicate that colour appearance is modulated by colour memory (Hansen et al., 2006; Witzel, Olkkonen, & Gegenfurtner, 2018). Information-based imaging techniques confirmed this modulation by revealing that the information about objects' typical colour could be decoded from the activity pattern in the early visual areas

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[2] Colour categories could also be universal across species. Similar objects may be of importance for humans and non-human primates. For instance, trichromatic colour vision in primates could have evolved to allow detecting fruit from foliage (Regan et al., 2001). Colour categorisation could exploit similarities in perceptual categorisation in humans and non-human primates (Fize, Cauchoix, & Fabre-Thorpe, 2011) and build upon trichromatic colour vision to render object detection more efficient.

when subjects viewed grey-scale or ambiguously coloured images of highly colour-diagnostic objects (Bannert & Bartels, 2013; Vandenbroucke et al., 2014). Thus, even the early stages of cortical colour processing are tightly linked to object recognition and classification. This could well be also the case for the high-level processes of colour categorisation.

If colour categories are linked to object colours, one could predict that patients with colour agnosia would present deficits of colour categorisation. Colour categorization has not yet been thoroughly examined in patients with colour-memory issues. A pioneering case of a colour agnostic patient, reported by Lewandowsky (Jules Davidoff & Fodor, 1989), presented signs of impaired colour categorisation. When presented with a number of different colour shades (Holmgren Wool test) and asked to pick the colours that were most "similar" to a colour chosen by the experimenter, the patient was unable to understand the task. At the same time, he matched identical colours flawlessly. Interestingly, the patient used exclusively terms depicting brightness (DARK, LIGHT) when talking about colour, as if the terms depicting hues or saturation were unavailable for him. It is however important to note that problems in such sorting tasks may not necessarily reflect a complete categorisation impairment (discussed in detail in section 5.3). Slightly impaired performance in colour categorization tasks was reported in Case II described by Fukuzawa et al. (1988). Case II suffered from a lesion in the medial occipito-temporal cortex and subcortical structures and presented a profound, global impairment in high-level colour processing, involving both colour naming and colour memory. His colour categorization impairment (measured with both colour sorting and forced-choice tasks) was restricted to colours ranging between yellow and green. He performed normally for the remaining colour categories. The specificity of the impairment to only come categories makes the data difficult to interpret. It may suggest that each categorical boundary is encoded separately in the human brain, a hypothesis hitherto unsupported by any neurocognitive evidence. Alternatively, the patient's premorbid colour categorization at that boundary could have been different from the majority of the population. In this case his presumably impaired performance may simply reflect this idiosyncratic profile. More research on brain-damaged patients is needed to establish the relationship between colour categorization and colour memory impairments.

Colour-naming hubs in the left ventral visual stream

The areas in left ventral visual stream seem to be specifically engaged in linking perception to language and semantic systems (the exact mechanisms of this engagement is debated, see e.g.

McCandliss, Cohen, & Dehaene, 2003; Price & Devlin, 2003, 2011). For instance, the Visual Word Form Area, a region showed to respond preferentially to orthographic material (Dehaene & Cohen, 2011; but see Price & Devlin, 2011), has distinct connectivity patterns that allow it to integrate the information about low-level features of letter strings, such as edges and line junctions, with the high-level semantic system (Bouhali et al., 2014). Results described in Chapter 3 demonstrated that RDS's damage of the left colour-biased regions resulted in colour-selective dysconnectivity between the intact right-sided colour-biased regions and the left anterior temporal lobe engaged in verbal semantics (Ralph, Jefferies, Patterson, & Rogers, 2017; Rice, Caswell, Moore, Hoffman, & Ralph, 2018; Rice, Hoffman, & Lambon Ralph, 2015). These patterns of results indirectly suggest that the left colour-biased regions may serve as a Colour-Naming Hubs connecting lower-level, sensory colour representation with the language/semantic system; damage to those hubs could result in optic aphasia for colours. Let me discuss the possible characteristics of the Colour-Naming Hub through an analogy with the Visual Word Form Area (VWFA).

Perceptual invariance

The VWFA is a neural implementation of the theoretical model of the Visual Word Form proposed by Warrington and Shallice (1980):

We would define a visual word-form system as follows: that which parses (multiply and in parallel) letter strings into ordered familiar units and categorizes these units visually. The components can range in size from graphemes, syllables, morphemes to whole words.

As a result of such parsing and categorisation, the orthographic representation in the Visual Word Form Area is perceptually invariant. VWFA responds to specific words independently of the words' location in space, changes in case, size or font, and even for printed vs. handwritten words (reviewed in: Dehaene & Cohen, 2011).

Through analogy, the Colour Naming Hubs could link colour names with colour representations that are invariant to the changes in spatiotemporal context (colour constancy) and to particular hues (colour categorization, Figure 8). This is not to say that the Colour Naming Hubs compute colour categories and constancy, thus the term *hub* rather than *area* or *region*. As relay regions, Colour Naming Hubs would receive categorical input that, according to the the research reviewed in this thesis, results from the interaction between the perceptual colour space computed in the cortical areas hV4 and VO (Brouwer & Heeger, 2009, 2013), task demands (Brouwer & Heeger, 2013; Koida & Komatsu, 2007; Persichetti et al., 2015) and object-colour knowledge (Bannert & Bartels, 2013; Rosenthal et al., 2018) and probably other factors (see section 5.1.2). Colour Naming Hubs would then transmit this categorical input to a verbal semantic system depending on the left anterior temporal lobe (Ralph et al., 2017; Rice et al., 2018, 2015).

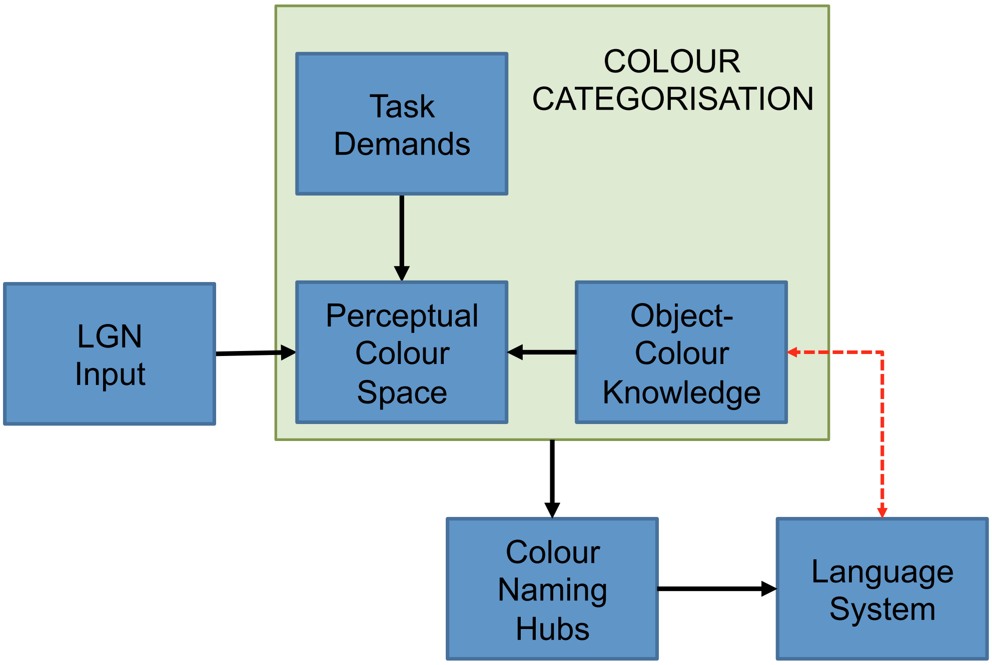

Figure 8 The Colour-Naming Hubs Model. Colour Naming Hubs are cortical relay regions that connect the categorical colour representation with corresponding colour names. Colour categories result from the modulation of the perceptual colour space (hV4/VO) by top-down inputs from task demands (prefrontal cortex) and object-colour knowledge (anterior occipito-temporal regions, temporal poles). Colour Naming Hubs transmit the results of categorical colour computing to the left anterior temporal lobe, a part of a language system engaged in verbal semantics and naming in particular. RDS's performance in the naming task suggests that when Colour Naming Hubs are impaired, the access to colour names can be reached indirectly through object-colour knowledge (red arrow). Please note that colour representation received by the Colour Naming Hubs is also luminance invariant, but the details of neural processing of colour constancy are beyond the scope of this thesis and are thus not represented in the model.

Reproducible anatomical location

The location of the VWFA (around the -42,-57,-12 MNI coordinates) is surprisingly reproducible across individuals, even when they come from cultures that vary in reading direction or type of script (Bolger, Perfetti, & Schneider, 2005; Rueckl et al., 2015), or even when they read in different sensory modalities (Reich, Szwed, Cohen, & Amedi, 2011; Siuda-Krzywicka et al., 2016; Striem-Amit et al., 2012). Colour naming deficits appear as a consequence of lesions with reproducible spatial distribution (reviewed in: A. Damasio & Damasio, 1983), even in patients from non-western cultures (Fukuzawa et al., 1988), which suggests a similar location reproducibility for the Colour-Naming Hub.

Cultural Recycling of cortical maps

It has been proposed that the VWFA emerges by recycling cortical areas that support fine-grained object processing (Dehaene & Cohen, 2007; Dehaene et al., 2010). With the acquisition of reading, those cortical areas become preferentially connected to the language system (Bouhali et al., 2014; Thiebaut De Schotten, Cohen, Amemiya, Braga, & Dehaene, 2014). It has been hypothesised that colour names emerged as a result of the discovery of paints and dyes (Levinson, 2000). As such, the emergence of colour names could have reorganized the neural architecture of colour-biased regions. Left sided colour-biased regions, thanks to their proximity to language system, may have become specialised with linking visual colours with the names.

Biases towards the "known"

The VWFA is sensitive to bigram and word frequency and it responds strongly to orthographic regularity (Binder, Medler, Westbury, Liebenthal, & Buchanan, 2006; Vinckier, Dehaene, Jobert, Dubus, Sigman, & Cohen, 2007). Similarly, Colour-Naming Hubs could be specifically tuned towards the colour of external environment that we want to communicate most, with colours of graspable objects being a possible candidate (see e.g. Gibson et al., 2017; Rosenthal et al., 2018).

Testing the above-mentioned hypotheses calls for a research program using task-fMRI, functional and structural connectivity to study participants from different cultures and different age groups. It is important to reiterate here that we are not the first to make the theoretical proposal of the existence of a left-hemispheric colour centre relying visual and semantic information. Similar notions were proposed earlier by Damasio and Damasio (1983) in the context of colour naming deficits, and by Lewandowsky (Jules Davidoff & Fodor, 1989) in the context of colour agnosia. The latter author explained the neural basis of colour agnosia as following:

> *I am sure that this lesion had destroyed what one might call the colour centre in the left hemisphere. The colour centre in the right hemisphere has been preserved. However, the association of the colour sense*[3]*, not only of the left but also of the still functioning right half of the retina, with the other visual elements, took place in the man only from or through the colour centre in the left hemisphere. With its destruction this association was lost. Colour*

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[3] By colour sense, Lewandowsky meant the semantic representation of colours as in both colour naming and object-colour knowledge. Footnote added by the author of the present thesis.

perception in the ordinary sense remained intact since this was still present in the right hemisphere.(pp. 171, Davidoff and Fodor, 1989).

To the best of my knowledge, the neurofunctional results described in Chapter 3 provide the first neuroimaging proof of the neural mechanism proposed by Lewandowsky over a century ago.

5.2 Naming chromatic colours / naming achromatic colours

RDS's striking pattern of performance demonstrates that within the colour naming module, achromatic and chromatic colours can dissociate. Naming black, white and grey colours may therefore involve different neural mechanisms than naming chromatic colours.

Chromatic contrast is distributed differently than luminance contrast in natural scenes (Hansen & Gegenfurtner, 2009). Chromatic contrast corresponds to low spatial frequency and its distribution is patchy, especially in scenes containing objects in grasping distance (Párraga, Troscianko, & Tolhurst, 2002; Yoonessi, Kingdom, & Alqawlaq, 2008). Within an object, chromaticity and luminance are similar, while boundaries between objects are associated with abrupt hue changes independent on lightness (Kingdom, Beauce, & Hunter, 2004). These findings imply that chromaticity and luminance convey different information about the environment, with chromaticity being especially indicative of objects (Witzel & Gegenfurtner, 2018).

According to some theories, the organization of the ventral visual stream follows the low-level image properties that co-occur in natural stimuli (see e.g. Andrews, Watson, Rice, & Hartley, 2015). In light of this theory, different spatial distribution of chromatic and luminance contrast may be reflected by different ventral visual pathways for achromatic and chromatic signals. Indeed, these findings are supported by fMRI studies. In the extrastriate cortex, chromaticity and luminance signals diverge, with chromaticity being processed in the ventro-mesial portions and luminance processed in the dorso-lateral portions (Conway, 2014; Mullen et al., 2015; Mullen, Dumoulin, McMahon, De Zubicaray, & Hess, 2007). Our results suggest that the luminance and chromaticity information may reach the language system separately. The ventral pathway conveying chromaticity would be impaired in RDS, while the dorso-lateral luminance pathway would be spared, consistent with the fact that RDS's lesion did not affect the dorso-lateral parts of the left ventral visual cortex.

5.3 Knowing about object colours / knowing about abstract colours

RDS's pattern of performance on colour knowledge tasks (Chapter 4) implicates that colours of objects and abstract colours may be processed independently in high-level cognition.

Surprising at first sight, such dissociation makes sense in the context of the functional aspects of colour vision (Witzel & Gegenfurtner, 2018). Context is a key factor to interpret colour information. Colours in forms of abstract patches do not exist in the environment; they are always assigned to an object or to a scene. Animal studies reviewed in Chapter 2 illustrate this point by demonstrating that animals require long-lasting training to evoke the response to colour patches or coloured light. Abstract, unnatural colours may constitute an unprecedented stimulus that non-human animals simply do not know how to process. Similar evidence for difficult conceptualization of colour comes from young children (reviewed in the discussion of Chapter 4). Moreover, the colours of natural objects are never uniform. They vary as a function of lighting and shading, external factors (such as black stains on the banana that reflect points of pressure), and nonrepresentative object parts (e.g., the leaves of a strawberry).

Yet, there is a large consensus that when humans perform tasks requiring picking a representative colour for a given object (see the results of healthy controls in Chapter 4 experiment 1 and behavioural measures in X. Wang, Han, He, Caramazza, Song, & Bi, 2013). How do we reach such consensus is yet unknown (Witzel & Gegenfurtner, 2018). To estimate the lightness of objects, observers fixate at the brightest parts of the objects and then use that image region as the estimate. This strategy seems adaptive because the brightest parts of an object are often directly illuminated and least affected by shading – they thus contain thus the most object-specific information (Giesel & Gegenfurtner 2010, Toscani et al. 2013). How would that work for other colour dimensions such as hue and saturation is still being investigated and mean hue was proposed as a possible estimate (Milojevic, Ennis, Toscani, & Gegenfurtner, 2018).

Our results suggest that language may be operative in deciding if a given colour is representative for a given object. In order to decide if a given colour is typical for a given object, one needs to understand that such colour should represent all the colours that can possibly be indicative of a banana. Such conceptualization may be mediated by language: linking abstract colours and colour knowledge could pass through colour names.

The idea that abstraction is a process mediated by language was introduced in the seminal works by Kurt Goldstein (Goldstein, 1946 in: Noppeney and Wallesch, 2000).

Goldstein understood the *abstract attitude* as the ability to extract main features of a stimulus that would be independent of a particular context (e.g. the colour of a banana, independent of brown stains or tail), combine and integrate these features to form a concept: a mental representation of a stimulus class (e.g. the concept of yellowness). The concrete attitude, contrary to the abstract one, is based on a specific context and is anchored in the "here and now". According to Goldstein, the abstract attitude links language and thought. Verbal labels allow transforming concrete concepts to abstract ones, and the act of naming is an act of conceptualisation by itself:

It [NAMING –note by the author of the present thesis] *is not based on a simple association between an object and a sound, but presupposes a special attitude toward the object. The name is an expression of the conceptual. Words used as names are not simply tools which may be handled like concrete, but a means to detach man from an external world.* (Goldstein, 1946 pp. 404 in: Noppeney and Wallesch, 2000 pp. 377).

RDS's inability to detach colours from objects could be understood as a loss of Goldstein's abstract attitude in the domain of colour, and linked to his colour-specific inability to name. RDS is able to access his colour-knowledge from visual stimulation when colour is presented in a particular context (on object), but fails to do so when colour is decontextualized (colour patch). Thus, following Goldstein's terminology, RDS's visual colour cognition could be classified as "concrete" (note that RDS's colour knowledge is significantly better when accessed through verbal cues).

Goldstein measured abstract attitude in neurological patients by asking them to sort coloured wools. He noted that aphasic patients showed difficulties in this task (Jules Davidoff & Roberson, 2004; Noppeney & Wallesch, 2000). However, sorting tasks can be resolved using multiple strategies and even healthy subject vary in their results (Jules Davidoff & Roberson, 2004; Haslam et al., 2007). Performance on free sorting can dissociate from other categorisation tasks suggesting that inability to sort might not be a specific sign of category loss (see patient LEW in Roberson, Davidoff and Braisby, 1999). Also, the relationship between sorting performance and language is complex (Haslam et al., 2007; Malt, Sloman, Gennari, Shi, & Wang, 1999). Thus, while the Goldstein's work on colour provides a valuable theoretical framework for a relationship between language and other cognitive systems, it does not to allow us to address the question of colour categorisation and language.

5.4 Conclusions

Research on brain-damaged patients, including the findings of this thesis, demonstrated that high-level colour processing in the cerebral cortex is highly modular. What is the purpose of such modularity?

The way we see colour cannot be simply predicted by how retinal cones respond to isolated sources of light. However, the dissociation between colour appearance and the low-level mechanisms of colour vision is not random and seems to serve a purpose: to normalise and stabilize the perception of objects and scenes as they naturally occur in our environment (Conway, 2018; Witzel & Gegenfurtner, 2018). In this perspective, the stabilization and normalization of object colour would be the final output of the modules of high-level colour processing in the cerebral cortex. Thus, the context of an object seems to be crucial for understanding the high-level mechanisms of colour vision.

In this thesis I argued that the context of object could explain the origin of colour categorisation. Patient RDS had spared visual colour knowledge: he knew how typically coloured objects look like and had no problems in differentiating them from the atypically coloured ones. His colour categorization was also relatively spared when measured on a non-verbal task. This association speak towards the hypothesis that colour categories could be linked to object colours. At the same time, RDS could not name all the colours, could not match colour patches to colour names and could not state if a colour patch is representative of a given object. These finding suggest that dissociating colours from objects and treating them as independent concepts could be a human-specific cognitive function and may depend on the presence of colour names.

The division into universal and human-specific high-level colour functions could be reflected in the functional lateralization of colour-biased regions in the ventral occipito-temporal cortex. Universal colour processing functions, such as colour perception, categorization and visual colour knowledge could be computed in the right-sided or bilateral ventral visual stream: RDS, in whom these functions were relatively spared, had an intact right hemisphere. Posterior colour-biased regions could compute the perceptual colour space and provide illumination-invariant representations of object colours; central colour-biased regions could gather those colours into categories that reflect colours usually represented by relevant objects; and finally anterior colour-biased regions would provide a joint representation of behaviourally relevant combinations of shape and colours. The human-specific colour functions such as colour conceptualisation and colour naming could be lateralized to the left hemisphere; these functions were affected in RDS, concomitantly to damage to his left colour-biased regions. Left colour-biased regions could be specifically connected to the language system, thus enabling the connection between perceptual colours and language, and possibly breaking down the joint representation of colour and shape into independent shape and colour channels.

Evidence from neuroimaging and brain damage shows that processing of colour and shape is segregated (e.g. Lafer-Sousa et al., 2016). Similarly, the achromatic and chromatic contrasts in natural scenes were shown to be independent (Hansen & Gegenfurtner, 2009). However, these observations should not be taken as evidence that shape and colour information are unrelated. Instead, shape and colour could jointly contribute to the formation of the final object representation, though providing different types of information (Conway, 2018; Lafer-Sousa et al., 2016; Rosenthal et al., 2018). Shape representation is relatively invariant in time and space and could thus provide information important to object identification. Colour, on the other side, could provide information about the behavioural relevance of an object in a given moment of time: e.g. the ripeness of the fruit or the emotional state of the face (Conway, 2018; Witzel & Gegenfurtner, 2018). To put it simply, shape would tell us what the object is, while colour could tell us if and how we would want to act upon it. Computation of these two types of information could require neural assemblies of non-overlapping properties, explaining the neural segregation of colour and shape in the ventral visual stream. At some point of the processing hierarchy the results of these neural computation are integrated to guide object-directed behaviour.

The potential contribution of colour to the functional organisation of object representation in the ventral visual stream might have been overlooked because many studies focused on achromatic images. This research practice lead some to believe that colour is not important for object recognition (Biederman & Ju, 1988; Riesenhuber & Poggio, 1999). Yet, colour seems to be an integral part of object representation, an important signal to guide object-related behaviour. Incorporating colour into the research on neural substrates of object recognition could provide an important dimension in the representational organization of objects in the ventral visual stream (Conway, 2018). Conversely, incorporating information about shape in the research on colour perception could elucidate the neural substrates that give rise to colour appearance (Witzel & Gegenfurtner, 2018).

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7 Supplementary materials

7.1 Supplemental Information to Chapter 3

7.1.1 RDS's color naming errors

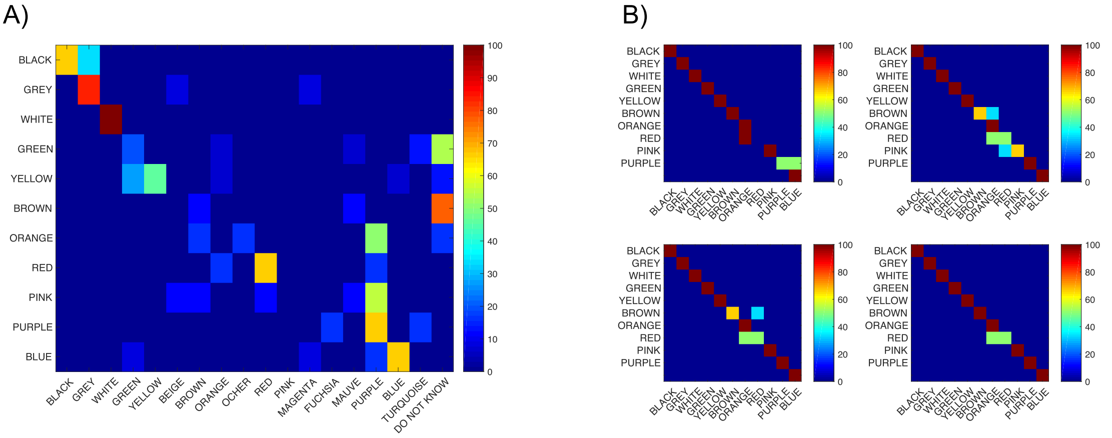

Figure S6. RDS's color naming errors, related to Fig. 1. To allow the reader to appreciate not only the level of naming consistency for each color, but also the types of errors that RDS made, we present RDS's color naming data as a category-wise confusion matrix **(A).** The rows of the matrix correspond to color categories presented to the patient (defined by the naming consistency of healthy participants, see Method's Details: Categorical membership of colors: color-name matching experiment); the columns correspond to labels given by RDS. The cells of this matrix reflect the percentage (%) of category-label combinations per each row (e.g., percentage of black patches labeled as black, grey, white, green etc.), such that the values of the cells in a row sum to 100%. Note that RDS also produced non-basic color terms such as magenta, fuchsia or turquoise when labeling colors. For some colors he was not able to produce a label – these instances are reflected in the last column of the matrix (UNKNOWN). The rows and columns of the confusion matrix reflect the order of colors in the hue circle (separately for achromatic - the first 3 rows - and chromatic colors; sorting individual colors according to lowest pairwise distances in the CIELUV space resulted in a similar arrangement). The additional, non-basic color labels were introduced in their likely positions among the basic color labels.

In the confusion matrix, the correct responses are located along the diagonal line, and the errors are consequently represented as a dispersion of responses from the diagonal. Close misses (naming a given color using an adjacent category) are located in the proximity to the diagonal. The errors produced by RDS were often placed far from the diagonal of the matrix. This suggests that RDS's naming errors neither were always close misses, nor were they completely random. Only achromatic labeling (first 3 columns) shows high specificity. Additionally, there is variability among different chromatic labels. Some labels (such as purple) are used more often than others. **(B)** Confusion matrices based on the data of four age- and education- matched control subjects.

7.1.2 Supplemental resting-state results

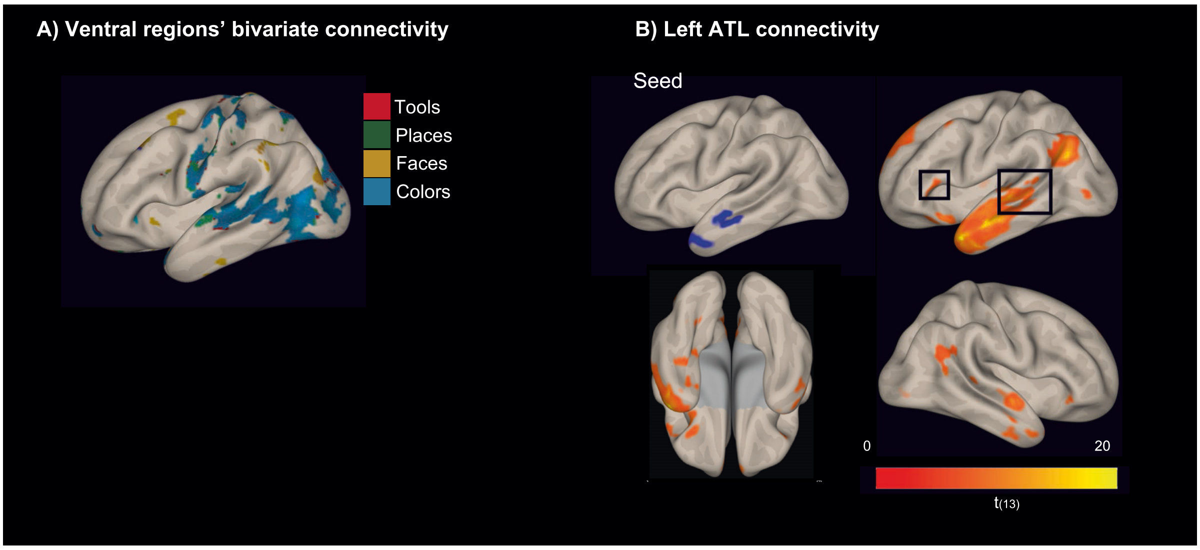

Figure S2. Resting-state MRI, related to Fig 4. (A) Left-hemispheric connectivity patterns (bivariate correlations) encompassing category-selective ventral regions in RDS (for seeds see Fig. 4A). **(B)**The resting-state connectivity patterns (bivariate correlations) encompassing the seed located in the left ATL cluster (Fig. 4C) in the 14 healthy controls included in the study. The left anterior temporal lobe (ATL) is highly connected to the left language network: the left inferior frontal gyrus (BA 44/45) and the left middle and superior temporal gyri (BA 21/22). Thresholds **(A)** voxel-wise $p<0.001$, cluster-wise $p<0.05$FDR-corrected; **(B)**Voxel-wise and cluster-wise $p<0.05$ FDR corrected.

7.1.3 Supplemental Tables

Table S2. Logistic regression results for RDS's color-categorization and name-comprehension. Related to Fig. 2.

	Parameter	*B (SE)*	*Odds ratio*
Color-categorization	Constant	1.46 (0.37)***	4.31
	Color-comprehension	-0.13 (0.42)	
	Achromatic stimulus	-0.64 (0.54)	
Color comprehension	Constant	1.25 (0.38)	3.49
	Color-categorization	-0.13 (0.42)	
	Achromatic stimulus	2.3 (0.53)***	9.97

Note. For the color-categorization model: **R2 = 0.009 (Nagelkerke), Model $\chi^2(2)$= 1.72, p=0.422; for the color-comprehension model: R2 = 0.16 (Nagelkerke), Model $\chi^2(2)$= 30.64, p<0.001; ***p<0.001**

Table S3. Logistic regression model of the color categorization accuracy including the Euclidean distances between colors of within (e.g. Fig 2 A, discs with two blue shades) and across-category stimuli (e.g. Fig 2 A, discs with a brow and a red shade) as independent variables; related to Fig. 2. The distances were calculated separately for the luminance axis (ΔL) and the chromaticity axis (Δuv, see Fig 1 A). The perceptual differences between colors (in both luminance and chromaticity, and in both within- and cross-category stimuli) were significant predictors of RDS's categorization accuracy. However, their effects were relatively small. For instance, with one unit increase of within – category Δuv, RDS was only slightly (Odds ratio=0.96) less likely to give a correct response in the task. This implicates that RDS did not strongly rely on the perceptual differences between colors to perform the color categorization task.

	Parameter	*B (SE)*	*Odds ratio*
Color-categorization	*Constant*	1.83 (0.76)*	6.26
	Δuv *within*	-0.04 (0.01)***	0.96
	ΔL *within*	-0.07 (0.02)***	0.94
	Δuv *cross*	0.02 (0.01)*	1.02
	ΔL *cross*	0.10 (0.03)***	1.10
	Color-comprehension	0.06 (0.46)	
	Achromatic stimulus	-0.64 (0.54)	

Note. R2 = 0.26 (Nagelkerke), Model $\chi^2(6)$= 54.43, p<0.001, mean VIF=1.75,*p<0.05, ***p<0.001

Supplementary Materials

When Colours split from Objects: The Disconnection of Colour Perception from Colour Language and Colour Knowledge

Supplementary materials

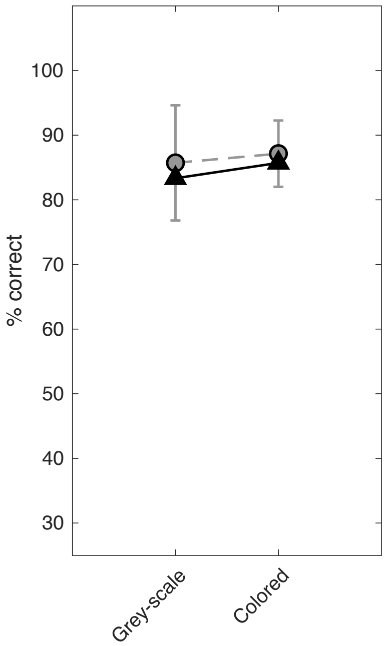

Figure S1. Performance in the texture-verification task for colored and grey-scale textures. We created grey-scale texture patches by transforming the colored texture to grey-scale using matlab rgb2grey function.RDS's performance did not differ significantly from the controls in either condition. Grey dots and dashed line represent results in the healthy control group (n=5), while black triangle and solid black line represents the patient. Error bars depicts ± 1 standard deviation in the control group.