

# Influence of Language on Colour Perception: A Simulationist Explanation

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“How can perception be altered by language?” is the fundamental question of this article. Indeed, various studies have pointed out the influence of colour-related knowledge on object and colour perception, evoked by linguistic stimuli. Here the relevance of the simulationist approach is assumed in order to explain this influence, where the understanding of colour-related words or sentences involves a process of colour simulation that is supported by a neuronal network partially similar to the network involved in colour perception. Consequently, colour-related knowledge and colour perception can interact through a process of pattern interference. In support of this idea, studies are discussed showing priming effects between colour simulation and colour perception, but two limitations are also raised. Firstly, these works all used between-category colour discrimination tasks that allow the intervention of lexical processes that can also explain priming. Secondly, these works control the congruency link between prime and target at the level of ‘colour category’, and no demonstration is made of an influence at the level of specific hues. Consequently, the simulationist view of language/perception interactions seems an interesting way to thinking but more experiments are needed in order to overcome some limitations.

*Keywords:* colour perception; colour simulation; interaction; knowledge; language; priming

## 1. Introduction

For many years, perception was considered to be a process extracting information from the environment (Pylyshyn 1981; Fodor 1983). In parallel to this classic cognitivist approach, many researchers have developed the idea that perception is a process of construction of information that can integrate various influences (e.g., Neisser 1967; Stein & Meredith 1995). Firstly, bottom-up signals that come from all senses, for example judgments about taste and smell can be altered by colour perception (Spence *et al.* 2010). Secondly, perception may be constrained by the carrying out of actions (Gibson 1979). Thirdly, emotion conjured up by a stimulus or by mood can disrupt or facilitate the perception of



emotional stimuli (Bocanegra & Zeelenberg 2009). Finally, a lot of studies have shown an influence of memory and knowledge on perception, mainly *via* language (e.g., label effect; see Pohl 2004 for a review).

The aim of this article is to suggest a possible explanation of language/perception interaction based on simulationist approach of memory retrieval. We specifically focus our attention on the influence of colour-related words (e.g., banana, tomato) on colour perception because this case of language/perception interaction is strongly supported empirically. More specifically, we discuss two lines of research: (i) research on object recognition and (ii) on colour perception (section 2). In a third section, we present core ideas of sensorimotor models of memory including the simulationist conception of memory retrieval. Based on this approach, we develop the possibility that colour-related words can influence colour perception because each recruits common neuronal substrate. Indeed, in a sensorimotor model of memory colour simulation (i.e. a specific form of retrieval) would recruit sensory areas of the brain in order to represent sensory attributes of knowledge. In the fourth section, we discuss recent neuro-imaging evidences supporting this major assumption. However, based on these studies, we specified this basic idea. More precisely, we suggest that the neuronal substrate of colour simulation and colour perception would be best conceived as two partially overlapping neuronal networks that can interact only partially. This particular extension led us to expect two forms of priming: (i) from colour simulation to colour perception and (ii) from colour perception to colour simulation. In line with these predictions, we report a few studies demonstrating these possibilities (section 5). In a sixth section, we suggest that these studies have, at least, two limitations. We develop these limitations and try to propose possible experiments in order to overcome them in further research. Finally, in the last section (section 7), we sum up the potential simulationist explanation of language/perception interactions and develop two empirical ideas in order to best support this approach.

## 2. Influences of Colour Related Knowledge

Researchers working on knowledge organization and memory have been interested in 'sensori-knowledge' that we define as the knowledge of objects that are strongly associated with specific sensory attributes, such as their shape, their colour, their location, their sound, their movement, and so on (e.g., Pulvermüller 2003; Martin 2007; Barsalou 2008). In this flow of research, colour is a feature that has received much attention. This section develops studies suggesting the storage of colour in knowledge (section 2.1) and the influence of this knowledge (activated by processing linguistic stimuli) on perception (sections 2.2 and 2.3).

### 2.1. Colour Associations: A Stored Information

The memory of colour was first studied by pre-cognitivist researchers. For instance, Bruner & Postman (1949) studied colour associated with playing cards. Authors presented cards with congruent or incongruent colours: A red clover or

a black clover, a red heart or a black heart. The participant's task was to judge the colour of the cards. Results indicated that in the incongruent condition, participants perceived a colour between red and black, suggesting an influence of the colour stored in memory (i.e. colour associated with the card) and thus the colour storage (see also Duncker 1939; Bruner & Postman 1949; Bruner *et al.* 1951; Harper 1953; Delk & Fillenbaum 1965). More recently, Reilhac & Jimenez (2006) brought to light the memory of colour by using black-and-white line drawings of objects strongly associated with yellow (e.g., banana) or green colours (e.g., artichoke). In this experiment, authors asked participants to categorize a drawing target presented subsequently to a drawing prime. Primes and targets either belonged to the same category or to a different one (i.e. animals or vegetables) and/or were of the same typical colour or of a different one (e.g., prime: *Frog* or *lettuce*, target: *Crocodile*). Only drawings with an important degree of colour agreement were used (estimated in a pilot study). Results showed priming when the drawings (i) belonged to the same category and (ii) more importantly when they were associated with the same typical colour. This last result suggests that colour association is stored in memory, more precisely in semantic memory. The study of Nijboer *et al.* (2007) focusing on scene recognition reinforces this conclusion. Generally, the results in the recognition of visual scenes show a facilitation effect for the recognition of natural scenes (e.g., beach *vs.* town) when they are presented in their usual colours; thus suggesting the part played by colour in the recognition of visual scenes (Oliva & Schyns 2000). Nijboer *et al.* (2007) found that this facilitation effect is absent in a subject suffering from a developmental colour agnosia. According to Nijboer *et al.* (2007), this participant would have a specific impairment of colour association stored at a semantic level. Consequently, the facilitation observed in healthy participants' results would be due to the retrieval of colour representations stored at a semantic level (absent in the agnosic patient).

To resume, colour seems to be a sensory feature of particular concepts or knowledge (i.e. that represent objects strongly associated with a colour) that can be available and automatically activated when participants have access to these concepts. In the next two subsections we discuss experiments reporting influence of these concepts on perception and we will concentrate on experiments using linguistic stimuli.

## 2.2. *Influence on Perception of Coloured Objects*

In the field of the perception of objects, various studies have indirectly tested the possible influence of colour on perception. Indeed, there are two theories that oppose each other concerning the part played by colour in the recognition of objects. On the one hand, the 'edge-based theory' assumes that recognition is mainly or only based on the shape of the object (Biederman 1987), whereas on the other hand the 'surface-plus-edge-based theory' defends that colour is an important cue for the recognition of objects. To settle between these two theories, different studies have measured the time taken to recognize objects presented in colour in comparison with objects presented in their greyscale version (i.e. without colour). The results obtained were recently synthesized by Bramão *et al.* (2011). Their review suggests that colour is an important cue only for the recogni-

tion of objects that are strongly associated with a particular colour (e.g., banana). These objects have been named 'high diagnostic colour' objects (i.e. HDC objects).

In one of their experiments, Tanaka & Presnell (1999, experiment 2) first presented two words each denoting an object, one appeared on the left-hand side of the screen and the other one on the right-hand side. In the second step, a drawing of an object was presented at the centre of the screen, in a coloured or greyscale version. Participants had to decide whether the object corresponded to the word presented earlier on the right or on the left-hand side (i.e. recognition task). Results showed that the decision time was faster when objects were HDC and appeared in colour compared with the conditions in which (i) the same objects were presented in greyscale and (ii) compared with the coloured or greyscale version of 'low diagnostic colour' objects (i.e. non HDC objects such as a chair). This result is important because it suggests that the recognition of objects involves information about colour and this supports the 'surface-plus-edge-based' theory. This result is also important because it suggests that reading words denoting objects strongly associated with a colour facilitates perception of congruent coloured objects.

Therriault *et al.* (2009) extended this previous research. In their second experiment, they asked participants to read a word that represented either an HDC object (e.g., pumpkin) or a non-HDC object (e.g., chair, car). Then participants had to judge whether the subsequently presented drawing represented the same object or a different one (i.e. verification task). The latter drawing appeared in a congruent colour (e.g., an orange pumpkin), in an incongruent colour (e.g., a blue pumpkin), or in greyscale (i.e. control condition). Results demonstrated that response times in the congruent condition were faster than in the greyscale condition, and the latter were faster than in the incongruent condition. In other words, the activation of colour when participants read words can either facilitate or disrupt the recognition of objects. In a third experiment, Therriault *et al.* (2009) obtained similar results when attention wasn't directly focused on colour.

In short, these various experiments and also others (see Bramão *et al.* 2011 for a review) suggest that colours stored in memory can facilitate or disrupt perception of objects presented in colour. Moreover, they demonstrate that this influence is produced by reading the linguistic stimuli that denotes colour-related objects, suggesting an interaction between memory, language, and object perception.

### 2.3. Influence on Colour Perception

The retrieval of colour-related objects influences not only the perception of objects but also the perception of colours. For instance, Mitterer & de Ruiter (2008) conducted an experiment in which participants had to discriminate the colour of an object. Participants saw three black-and-white line drawings: A carrot (i.e. a prototypically orange object), a banana (i.e. prototypically yellow), and a sock (i.e. without a particular colour association). These specific drawings appeared in various hues from a 'good orange' to a 'good yellow'. The results obtained with an ambiguous hue (i.e. between yellow and orange) were very

informative. When a banana drawing was in this ambiguous hue, it was more often seen yellow, whereas when the drawing represented a carrot, the ambiguous hue was more often seen orange (compared with the sock condition). This result demonstrates convincingly that knowledge can influence colour perception.

Olkkonen *et al.* (2008) reach the same conclusion with a very different method. In their experiments, participants were presented with two types of stimuli: (i) fruit and vegetables with a typical colour (e.g., lemon, cucumber) and (ii) disks (i.e. control condition). Participants had to adjust the colour of the objects in order to make them appear in grey. Participants had four keys allowing them to add a bit of blue, yellow, green or red. Results showed that for fruit and vegetables that possess a typical colour, participants added more of the colour opposed to the typical colour than in the control condition (to perceive in grey). In practical terms, when participants perceived a yellow banana and that they had to colour it in grey, they added more blue (i.e. the opposite colour to yellow in the colorimetric model used) in comparison to a yellow disk that they had to colour in grey (see also Hansen *et al.* 2006; Nijboer *et al.* 2011; Witze *et al.* 2011 for similar results).

Another work conducted by Naor-Raz *et al.* (2003) also shows an influence of colour knowledge on colour perception but by using linguistic stimuli. In their second experiment, Naor-Raz *et al.* (2003) used a Stroop-like procedure in which participants had to name the colour in which the words were printed. Words used represented objects strongly associated with a colour (e.g., banana) and could appear written in the congruent colour (e.g., banana written in yellow) or in an incongruent colour (e.g., banana written in purple). Results show that colour-naming times were faster for the incongruent conditions compared with the congruent ones. Despite a slowdown of response times opposed to previous data, these results also demonstrated the possibility that colour-related knowledge can influence colour perception (see also Klein 1964; Yee *et al.* 2012).

Consequently, studies presented here give evidence that retrieval of knowledge can influence colour perception and not only object perception. We report studies using pictures but also words that suggest, once again, that this influence may be mediated by reading linguistic stimuli (also Kubat *et al.* 2009).

The aim of this first section was to develop studies indicating an influence of colour-related knowledge on colour perception. To sum up, results reported here suggest that the retrieval of colour-related knowledge while words are processed can influence both recognition of coloured objects and perception of colours. More precisely, colour or colour association seems to be a component of some knowledge able to interact with the processing of perceived colour. This influence can be found when participants have to implicitly process colour such as for objects or scene recognition or explicitly when participants have to discriminate colour of target stimuli. Nevertheless, the underlying process that allows this interaction remains largely unexplored. One possible candidate lies in the retrieval process assumed by the sensorimotor models of memory. In the next section, we develop the core ideas of these models as well as the specific retrieval process that it assumes.

### 3. Simulationist Approach of Cognition and Memory

Experiments presented above show an influence of colour-related knowledge elicited by language on perception (both object and colour perception); but why such an influence? Here, we will develop on the idea that a possible answer can be found in a recent approach of cognition that assumes both a distributed memory across the entire brain and a particular form of retrieval that can be called 'simulation'. More precisely, it is possible to postulate that the interaction may be explained by the nature of the format in which colour knowledge is stored and retrieved from memory. In this section, we will first develop the core ideas of the sensorimotor models of memory. Then, we explain the specificity of the simulation process by which knowledge is retrieved. Accordingly, we develop a simulationist explanation of memory/perception interaction based on the use of the same neuronal substrate.

#### 3.1. *Sensorimotor Models of Memory*

The organization and format of knowledge that the sensorimotor models stand for is a key specificity of the models in comparison to other memory models developed until now. We will mainly develop on the originator model of Allport (1985); all the other sensorimotor models of memory are strongly similar to this one (e.g., Schacter *et al.* 1998; Martin & Chao 2001; Pulvermüller 2001; Barsalou *et al.* 2003; Versace *et al.* 2009). Allport (1985) explains that there are two ways of conceiving the implementation of knowledge (or concepts) in the brain. The first considers that knowledge corresponds to a precise physical unit (e.g., neuron or a group of neurons). Thus, a physical unit would be dedicated to the implementation of only one concept. The second considers that knowledge corresponds to a specific pattern of activity of a group of neurons. Thus, a same group of neurons can support different concepts as long as different patterns of activity are involved (i.e. distributed knowledge). On the basis of the work of Hebb (1949), he explains that such patterns would form and reinforce themselves as long as co-occurrent activations (pre- and post-synaptic) occur between neurons. More precisely, a neuronal pattern would constitute itself step by step *via* the alteration of synaptic weights (i.e. the correlation learning rule; Hebb 1949). This leads Allport to talk about 'auto-associated patterns' to support the idea that a pattern is a stable unit with specific properties. Nevertheless, until then Allport (1985) only details a model of knowledge already developed by the connectionists (e.g., Hinton 1981, Farah & McClelland 1991, McClelland & Rumelhart 1985).

Allport's main contribution that will characterize the sensorimotor models of memory is the way he considers the implementation of knowledge at the level of the brain. According to him, the auto-associated patterns representing objects in memory would be composed of auto-associated sub-patterns distributed across all the sensory and motor domains. He takes for example a 'telephone' and explains that the pattern representing this object is distributed at a visual, tactile, auditory and motor level coded in the form of visual (e.g., format, size), tactile (e.g., texture), auditory (e.g., ringing) and motor (i.e. motor routine carried out with the object: to pick it up, to hold it, etc.) attributes. He also explains that the

attributes associated with the verbal interaction regarding the telephone, such as the phonological, spelling and written attributes of the referent word can be respectively stored at an auditory, visual and motor level. Thus, the encoding process is above all an associative process implying that the different sensory and motor attributes, supported by brain structures all across the brain, have to constitute themselves in a unit (i.e. binding). Moreover, Allport (1985) explains that the auto-associated sub-patterns can also be embedded in other patterns as long as they represent the objects sharing similar attributes. For example, the auto-associated sub-pattern of the 'yellow' attribute can be part of the pattern representing not only a 'banana' but also a 'lemon' or a 'chick', etc. In the wake of Allport (1985), different authors have added various ideas in order to precise this model. First, Pulvermüller (2003) adds the idea of functional units of the patterns. According to this author, the different areas composing the network would work as a unit. The functioning of this unit would depend on the integrity of each part of the unit. If one part of the cortex happens to be damaged, the networks based on this area would consequently be more or less affected. Secondly, Barsalou (2009) suggests that the neuronal patterns representing knowledge would not only be composed of sensory and motor attributes but also of emotional attributes.

### 3.2. *Simulation Process of Retrieval*

Given the way with which knowledge is encoded and organized, the different sensorimotor models of memory agree on the nature of the retrieval process. These models assume that retrieval implies reactivation of neuronal networks representing knowledge, a process named 'simulation' (Barsalou 1999). Simulation has at least two main characteristics. Firstly, partial activation of a knowledge tends to reactivate all aspects of this knowledge, including all sensory attributes. This feature is due to the 'process of pattern completion' whereby an input that stimulated only a small number of neurons, composing a pattern, tends to reactivate the entire pattern. For instance, the reading of a word (e.g., banana) only involves the activation of the orthographic and phonological attributes of this knowledge. However, through the 'pattern completion process' all components of the network are rapidly active including the associated colour yellow (Pulvermüller 2003). This process occurs because every part of the pattern is strongly connected with each other through a Hebbian principle of reinforcement (Hebb 1949). Barsalou *et al.* (2003) underlined the fact that a simulation is never complete and involves bias compared with the original sensory experience. Secondly, and more importantly, activation of various sensory attributes of knowledge seems to involve the use of common neuronal structures with on-line perception, more precisely structures involved in low-level perceptual processing. This specificity is due to the fact that sensory attributes would be stored in areas of the brain also involved in perception. In the case of the word 'banana', the knowledge retrieved involves a specific network distributed in part on the neuronal substrate involved in colour perception. Accordingly, it is possible to assume that perception of colour and language can interact because language processing involves a simulation process in order to reactivate colour-related

knowledge. The use of such a process involves the use of common neuronal structures or the sharing of the same processes or same resources by language processing and perception. In other words, the format in which colour information is stored (connection between neurons of the visual area) and retrieved (by reactivation of the visual area) implies its automatic interaction with colour perception that uses the same visual areas.

To conclude, remember that the purpose of this section was to develop a process that would explain the influence of colour-related words on colour perception. We suggest that one possible candidate is the specific retrieval process assumed in sensorimotor models of memory usually called 'simulation'. Indeed, sensorimotor models of memory explain that memory would be a property of the entire brain including sensorimotor areas and retrieval of knowledge would occur *via* reactivation of neuronal patterns distributed over the brain. In the case of colour-related words, reading would involve activation of the entire patterns representing referents of words including in the visual area (specifically the colour perception area) supporting the colour attributes of knowledge. The recruitment of the same neuronal structures in order to simulate and perceive colour involves a meeting point for these two functions that can explain how colour-related knowledge can influence low-level colour perception. In the next section and in support of this simulationist explanation, we discuss studies showing the involvement of the same neuronal structures for colour simulation and colour perception (i.e. gyri lingual and fusiform). Moreover, based on these works we also specify more this possible explanation.

#### **4. Colour Perception and Colour Simulation: Similar Neuronal Patterns**

In this section, we will first review neuro-imaging studies having looked for the 'colour perception centre' within the visual cortex. Then, we will review neuro-imaging studies that have tried to point out the use of the same neuronal structures to retrieve colour-related knowledge. In a third sub-section, we discuss the implications of a neuropsychological dissociation in which participants have preserved mental colour imagery whereas colour perception is impaired (i.e. achromatopsia). We finally explain that colour perception and colour simulation seem to recruit partially overlapping neuronal networks.

##### **4.1. Cortical Structures Involved in Colour Perception**

Various experiments trying to situate the 'cortical colour centre' and conducted on healthy participants suggest different results. First, Zeki *et al.* (1991) situated this centre in the lingual gyrus in the occipital cortex. Its activation was found when participants passively viewed basic coloured stimuli (i.e. Mondrian). Authors have named this structure the hV4 area, human equivalent of the monkey V4 area (Zeki 1983a, 1983b, 1983c). Other studies have found a more extensive activation around the lingual gyrus when participants had to actively discriminate the colour of the stimuli, which suggests that there is a part played by the task applied to coloured stimuli (Corbetta *et al.* 1991; Guylás & Roland



1994). In order to clarify the structures involved in colour perception taking into account the potential role of tasks, Beauchamp *et al.* (1999) carried out an experiment where they compared activations in function of the task. They adapted the Farnsworth-Munsell Test (Farnsworth 1957) usually used to detect achromats (i.e. people with a specific loss of colour vision). The procedure used involved perception of various hues of the same colour presented in a linear gradient from light hue to dark hue or presented in a disorderly manner. Two tasks were used: (i) A passive viewing condition of stimuli and (ii) an active condition where participants had to discriminate ordered stimuli and disorderly ones. When participants passively viewed coloured stimuli, results showed the same activation that Zeki *et al.* (1991) found and also an extended activation in the anterior portion of the fusiform gyrus. When participants carried out a judgment on the stimuli, three major results are founded. Firstly, ventro-occipito-temporal activations both in lingual and fusiform gyri were observed as in the passive condition. Secondly, the activation of the fusiform gyrus is more important. Thirdly, they also observed distributed activations over the cortex, such as activations of V1 and V2 areas (i.e. within the visual cortex) and activations of the left frontal cortex, dorso-lateral part of the occipital cortex and superior parietal lobe in a majority of participants (see also Engel *et al.* 1997 for a similar result; see Gegenfurtner & Kiper 2003 for a review).

Based on these results, Beauchamp *et al.* (1999) explained that the carrying out of a task involving judgment about colour involves the activation of more colour selective regions compared with the passive condition. Consequently, they assumed a 'decentralized view' of colour perception in which there is no specific colour centre. The colour perception results from the activation of a complex distributed network across the cortex mainly concentrated around the lingual and fusiform gyri. Results of Corbetta *et al.* (1991) and Guylás et Roland (1994) that used a discrimination task as well as results of Zeki & Marini (1998) that used coloured photos of objects support this view. Indeed, Zeki & Marini (1998) made an experiment with complex colour pictures of objects and scenes rather than abstract coloured stimuli (i.e. Mondrian). In this experiment, results show that perception of these more complex stimuli also involves an activation of the lingual and fusiform gyri compared with the perception of the same objects in greyscale (see also Bramão *et al.* 2010 for similar results). Moreover, this 'decentralized view' of colour perception is in accordance with results showing that a lesion of the V4 area in a monkey involves only a small disturbance of colour perception suggesting the implication of other structures (Gegenfurtner 2003). This view is also in accordance with complementary results showing the impairment of many areas in 'cerebral achromates', and not only of the fusiform and lingual gyri (Bouvier & Engel 2006).

In short, the 'cortical colour centre' should rather be seen as a distributed network, concentrated around the lingual and fusiform gyri, that can be differentially activated according to the perceptual task and the coloured stimuli used.

#### **4.2. Cortical Structures Involved in Colour Simulation**

Various experiments have sought to bring to light that retrieving coloured-

related knowledge or low-level colour perception call on to the same structures. The first experiments were conducted by Martin *et al.* (1995). They compared brain activations in two conditions; participants either had to name colour-related objects represented by black-and-white line drawings (e.g., banana) or produce the colour associated with the objects (i.e. yellow). The underlying idea is that a production task would involve the retrieving of colour information while the naming task would not. Results showed an activation of the fusiform gyrus in the production task compared with the naming task. Moreover, they found the same results in a second experiment where drawings were replaced by words denoting the same objects. These results are congruent with neuro-imaging studies on colour perception that have showed the main role of the fusiform gyrus in colour perception (e.g., Beauchamp *et al.* 1999). Wiggs *et al.* (1999) carried out a similar experiment and obtained the same results. Moreover, they showed that the naming task also involved the activation of the fusiform gyrus compared with the control condition where participants viewed a visual noise. This last result suggests that simply naming an object strongly associated with a colour seems to involve the colour perception network. In another study, Chao & Martin (1999) directly compared, for the same participants, activations when (i) they perceived abstract coloured stimuli (i.e. Mondrian), (ii) named black-and-white line drawings, and (iii) produced the associated colour. Results showed that perception and production did not activate the same neuronal structure, but very close structures 2 centimetres (cm) away from one another. Based on this result, Chao & Martin (1999) concluded that perception of colour and retrieval of coloured-related knowledge do not require the same neuronal structure. Nevertheless, Martin (2009) explains that they failed to find the use of exactly the same neuronal structure in this previous study, simply because they used a passive perception task: a passive-viewing Mondrian task which activated only the lingual gyrus (Zeki *et al.* 1991). It is possible that by using more complex stimuli or a more active-viewing condition (Beauchamp *et al.* 1999), perception would be more complex and an activation of the fusiform gyrus would be found in both tasks. Simmons *et al.* (2007) directly tested this hypothesis. In their experiment, authors compared, for the same participants, activations that occurred when they (i) carried out the same 'colour-perception-task' used by Beauchamp *et al.* (1999) and (ii) carried out a retrieval task where participants had to judge the veracity of sentences involving a concept and a colour (e.g., a banana is yellow?). The results showed an activation of a common neuronal substrate in the two tasks: The left fusiform gyrus. Moreover, activations that occurred in the retrieval task were consistent with activations found in previous studies (Chao & Martin 1999; Martin *et al.* 1995; Wiggs *et al.* 1999). This study shows that the retrieval of colour-related knowledge involves the recruitment of the same neuronal structures that are used to perceive colour and more precisely involved in low-level colour perception (i.e. that does not involve object identification or object recognition). Nevertheless, these structures only overlap when the task and the stimuli are relatively complex.

Moreover, consistent with the second experiment of Martin *et al.* (1995), the work of Simmons *et al.* (2007) suggests an activation of the fusiform gyrus when participants process linguistic inputs (i.e. short sentences, see also Goldberg *et al.*

2006 for a similar procedure and results). This idea of an activation of the fusiform gyrus when participants read colour-related words is also reinforced by studies conducted by Kellenbach *et al.* (2001) and Oliver & Thompson-Schill (2003). In their experiments, authors used the same procedure: They asked participants to judge if a word was associated or not with a colour (e.g., banana *vs.* snow). Black, white, and grey hues were defined as non-colours. Results showed an activation of part of the fusiform gyrus close to the active part found in the previous studies ( $\approx 1\text{cm}$ ).

Recently two other studies extended these results. Firstly, Hsu *et al.* (2011) made an experiment in order to understand why the lingual gyrus activated in colour perception is not found to be activated in retrieval of colour-related knowledge. In order to best understand this absence of activation, Hsu *et al.* (2011) manipulated two variables: (i) level of detail of the colour simulation and (ii) the cognitive style of participants. In their experiment, participants had to carry out a judgment on luminance in the same way as in the work of Simmons *et al.* (2007) and also carry out a conceptual task involving colour simulation. More precisely, participants first saw two words representing two colour-related objects. Then, a third word would appear on the screen and participants had to select which of the two words represented the object associated with the closest colour. In one bloc, the three words belonged to the same colour category and similarities occurred at a specific hue level (e.g., 'SCHOOL BUS' compared with 'BUTTER' and 'EGG YOLK'). Whereas in another bloc, the three words belonged to different colour categories (e.g., 'BEETLE' compared with 'PAPRIKA' or 'BANANA'). The first bloc involved a colour simulation level deeper than the second bloc. Moreover, participants were divided in two groups based on their score to the VVQ (i.e. *Verbal and Visual Questionnaire*; Kirby *et al.* 1988). In one group, participants had a visual cognitive style whereas in the other, participants had a verbal cognitive style. Results show an activation of the left lingual and fusiform gyri during the conceptual task. The activation of the fusiform gyrus is more important when the level of simulation is deeper and the activation of the lingual gyrus is more important for participants with a visual cognitive style. Moreover, Hsu *et al.* (2011) observed an overlap of structures activated in the colour perception task and in the conceptual task both at the level of the lingual and fusiform gyri.

In other recent work, Hsu *et al.* (2012) extended their previous results. In this experiment, Hsu *et al.* (2012) compared the activation found when participants have to compare colours associated with two words. In one condition, words denote colour objects with the same or a different colour (e.g., 'BANANA' *vs.* 'BUTTER'). In a second condition, words denote achromatic objects identical or different on the level of grey (e.g., 'SNOW' *vs.* 'COAL'). The goal is to compare the activation of the cortex in the 'conceptual colour condition' with the 'conceptual achromatic condition' in order to know which cortex areas are specifically activated when a 'chromatic condition' is compared with an 'achromatic condition'. Indeed, comparing a 'chromatic condition' with an 'achromatic condition' is the usual way to determine which cortex areas are specifically activated in colour perception (i.e. chromaticity effect; e.g., Beauchamp *et al.* 1999; Chao & Martin 1999; Simmons *et al.* 2007). In previous experiments, activation in the

conceptual task is obtained by comparing retrieval of colour-related knowledge with retrieval of non colour-related knowledge, like action concepts (e.g., Simmons *et al.* 2007) and not 'achromatic conditions'. The major result is the overlap of colour perception and colour simulation at the lingual gyrus level.

In short, all these studies converge on the evidence that retrieval of colour-related knowledge, through the processing of linguistic stimuli, involves the activation of the same neuronal structures: the lingual and fusiform gyri also used when participants perceive colours or coloured objects (Zeki & Marini 1998, Beauchamp *et al.* 1999). Nevertheless, the implication of the same neuronal structures seems to depend on many variables such as the type of stimuli, cognitive style, type of conditions compared in order to define the neuronal structures activated. Moreover, it is important to note that colour conceptual tasks, as used in previous presented experiments, leave the possibility that participants used mental imagery of colour in order to complete the tasks. For instance, the conceptual task used by Hsu *et al.* (2012) is also used by researchers wanting to measure mental imagery of colour (e.g., De Vreese 1991; Bartolomeo *et al.* 1997; van Zandvoort *et al.* 2007). Consequently, it seems a risk to extend this similarity in brain structures to all tasks involving an access to colour-related knowledge, especially given the current state of knowledge on the question.

#### **4.3. *Achromatopsia with Preserved Colour Mental Imagery?***

If the same structures are used to perceive and retrieve colour, it would not be possible to find people with impairment in colour perception (i.e. achromatopsia) and a preserved ability to retrieve colour (e.g., colour mental imagery). However, Shuren *et al.* (1996) and Bartolomeo *et al.* (1997) report two cases of patients who were impaired on tasks involving colour perception: the Ishihara test (Ishihara 1974) and the Farnsworth-Munsell test (Farnsworth 1957). However, these patients accurately carried out tasks involving the imagination of colours: naming the colour of objects from memory, mentally comparing hues (De Vreese 1991), and giving the most objects as possible associated with a given colour. This dissociation is an issue. Nevertheless, as Simmons *et al.* (2007) explain, the neuropsychological evidence of the dissociation between the access to colour-related knowledge and the perception of colour does not necessarily imply that these two abilities are completely independent from one another. It is possible that the perception of colour and the access to the knowledge related to colour involve brain structures only partly identical.

#### **4.4. *Overlap of Neural Networks***

Studies on colour perception suggest that a neuronal substrate must be conceived as a neuronal network distributed across the brain (i.e. 'decentralized view'; cf. Bouvier & Engel 1997; Beauchamp *et al.* 1999). More precisely, this network seems to be mainly concentrated around the lingual and fusiform gyri, but its distribution is relative to various factors, such as a perceptual task and the type of stimuli perceived (Zeki & Marini 1998; Beauchamp *et al.* 1999; Bramão *et al.* 2010). On the other hand, studies focusing on the neuronal bases of the retrieval of

colour-related knowledge, in other words 'colour simulation', point out the involvement of the same neuronal structures. Nevertheless, it is also possible to assume a 'decentralized view' in this case. Indeed, colour simulation seems to be supported by a distributed neuronal network also concentrated around the lingual and fusiform gyri ( Martin *et al.* 1995; Chao & Martin 1999; Wiggs *et al.* 1999; Kellenbach *et al.* 2001; Oliver & Thompson-Schill 2003; Goldberg *et al.* 2006; Simmons *et al.* 2007; Hsu *et al.* 2011, 2012), but the distribution of the network changes depending on various factors such as a conceptual task, the type of stimuli, the type of cognitive style, etc. Moreover, results agree with the possibility that these two networks partially overlap each other at the level of the lingual and fusiform gyri because these structures are active in conceptual and perceptual tasks. This overlap also depends on the combination of various factors affecting independently colour perception and colour simulation (i.e. type of coloured stimuli, type of perceptual and conceptual task, etc.). Note that this distributed approach is more consistent with studies demonstrating a dissociation between central colour blindness (i.e. achromatopsia) and colour imagery ( Shuren *et al.* 1996; Bartolomeo *et al.* 1997). Indeed, this dissociation implies that it seems exaggerated to consider the perception and simulation of colour as fully supported by well-defined structures, such as the lingual and fusiform gyri, which once damaged must affect both functions simultaneously. In contrast, a design in terms of overlap of distributed networks allows the possibility of relatively independent processing.

Consequently, this conception helps explain the influence of colour simulation on colour perception through a process of 'neuronal pattern interference'. Indeed, colour simulation can affect colour perception because colour simulation recruits a neuronal network similar, in particular points, to the network used when colours are perceived. The idea of pattern interference can already be found in the work of Masson (1995) who tries to explain the semantic priming from a connectionist point of view. The idea of Masson (1995) is that we observe semantic priming because the neuronal pattern involved in the representation of the prime can be, at least, partially similar to the neuronal pattern representing the target. Accordingly, priming emerges from the pre-activation of parts of the neuronal network representing the target that are common with the neuronal network representing the prime. The same idea can be assumed for the case of the influence of colour simulation on colour perception. Indeed, colour simulation induces a pre-activation of certain parts of the neuronal network (i.e. lingual and fusiform gyri) that will be re-used for perception.

In others words, retrieval of colour-related knowledge involves the activation of parts of a neuronal network also involved in low-level colour perception. More importantly, this approach of interference between retrieval of colour-related knowledge and colour perception allows specific predictions about this interaction. Firstly, it is possible to expect a form of priming of colour perception whereas the prime involves only colour simulation. Indeed, until now all the works that show an influence of knowledge on colour perception use procedures in which stimuli simultaneously involve access to knowledge and perception of colour (e.g., coloured drawings and coloured words). These two activities are not separated in time. But the idea that this interference arises from

the overlap of network parts also predicts the possibility of interference even when the simulation is not performed at the same time as perception. Consequently, colour simulation can affect colour perception in a priming procedure. Moreover, the direction of influence is not restricted, and colour perception could also influence colour simulation. In the next section, we report experiments that support the possibility to observe an influence even when simulation and perception of colour are supported by temporally separate stimuli (i.e. a form of perceptual priming). Moreover, we also report evidence showing reversed priming because the direction of the influence is not restricted.

## 5. Bidirectional Priming between Colour Simulation and Colour Perception

The simulationist view of cognition emphasizes that colour-related knowledge can influence colour perception because the retrieval of this type of knowledge involves a simulation process using a neuronal network partially similar to the network involved in colour perception. This conception leads to the idea that colour simulation can affect colour perception even if these two processes are temporally separated. In this fifth section we will subsequently report two lines of evidence supporting this possibility. Firstly, we discuss results showing the possibility to prime colour perception *via* colour simulation and in a second subsection we discuss works showing the possibility to prime colour simulation *via* colour perception.

### 5.1. Priming of Colour Perception by Colour Simulation

The first interesting work showing a priming of colour perception *via* colour simulation is the work of Richter & Zwaan (2009). Authors conducted an experiment where participants saw a coloured square, immediately followed by a word and followed itself by a second coloured square, in each trial. Participants had to perform two different tasks successively: They (i) had to carry out a lexical decision on the word and (ii) decide if the second square appeared in the same or in a different colour as the first one. In target trials, words were nouns that denoted a colour (e.g., yellow, blue) that corresponded or not to the colour of the last square. Results showed that response times were shorter when the colour of the word was congruent with the colour of the last square in comparison with the condition where the colours were different. This result suggests that colour perception involving low-level processes can be influenced by linguistic stimuli even when simulation is carried out just before colour perception. Nevertheless, this study has a limitation. Indeed, in order to compare the two coloured targets, participants have to store, in short-term memory, the colour of the first square in order to compare it with the second square. Consequently, the influence of words can be situated at a perceptual level (i.e. affects the perception of the second square) or at a memory level (i.e. affects the remembering of the first square). This second possibility is supported by various works showing an influence of colour-related knowledge on the remembering of colour (Duncker 1939; Loftus 1977).

In order to overcome this limitation, we have recently conducted experiments using a perceptual task that precludes the conservation of colour in memory. Moreover, we used words denoting objects associated with a colour and not directly a colour label in order to extend the results of Richter & Zwaan (2009). In the first experiment (Heurley *et al.* 2012), participants saw words presented very briefly and immediately followed by a green or yellow circle. Participants had to discriminate only the colour of the circle (i.e. chromatic discrimination task). Prime words denoted natural things strongly associated with a green or yellow colour (e.g., chick, artichoke). This strong association was controlled in a pilot study where participants had to give the first colour that came to mind when they read colour-related words. Only words with a colour consensus higher than 70% were used. Results showed facilitation when the colour elicited by the words matched the perceived colour compared with the condition where the colours were different. We replicated this facilitation in a second experiment where the participant's task did not explicitly focus attention on colour or involve a colour label answer. Indeed, lexical priming of colour name could explain the facilitation effect in this experiment. In other words, perception of the word 'banana' elicits spontaneously the word 'yellow' facilitating the 'yellow response'. In the second experiment (Heurley *et al.* in press), participants saw two circles in the target's display. These two circles were presented in the same colour or in a different one. In the case where the circles appeared in the same colour, they could either appear in yellow or in green. Participants had to detect whether target circles were presented in the same colour or in different colours. When circles appeared in the same colour, results showed facilitation when the colour of the two circles was congruent with the colour elicited by the prime (e.g., two yellow circles preceded by the word 'BANANA') compared with the condition in which the colour elicited by the prime was different (e.g., 'ARTICHOKE'). In this last experiment, the effect observed can not be explained in terms of lexical priming because response labels were not colour labels. Moreover, the use of a mental imagery strategy, that could explain our results, seems precluded because words were only presented during 150 ms (with a 350 ms SOA) and participants only had to read the words as fast as possible.

Taken together, these studies support the possibility of obtaining perceptual colour priming whereas priming occurs *via* colour simulation. In these experiments, primes involve a colour simulation activating a neuronal network composed of parts that are also used by the neuronal network used in order to perform the perceptual task on the target. Moreover, primes are always words (colour words or words denoting colour-related objects) showing that this effect can be mediated by language comprehension as is assumed by various researchers (Pulvermüller 2001, 2003; Barsalou *et al.* 2003; Zwaan & Kaschak 2009).

## 5.2. *Priming of Colour Simulation by Colour Perception*

If language influences colour perception through the use of partial overlapping of close neuronal networks, it is also plausible to expect a reverse influence: of perception on language. Indeed, colour perception may pre-activate part of the

network that could be used to process linguistic stimuli. The first evidence of this opposite influence is found in a study by Richter & Zwaan (2009) already reported. In their study, participants first saw a coloured square followed by a word denoting the same or a different colour (or a non word), followed itself by a second coloured square (in the same colour as the first square or in a different one). Results showed that lexical decision times for words were influenced by the colour of the first square: response times were faster when the same colour was perceived and simulated compared with the condition where they were different. Thus, Richter & Zwaan (2009) showed an influence of colour perception on language processing. This result seems to suggest that language processing can be influenced by perception. However, in this work, words used denoted directly a colour, thus this can give place to another explanation in lexical terms. For instance, perception of a colour can automatically activate the associated word that facilitates subsequent language processing of a congruent word (i.e. colour labels). In consequence, the facilitation observed can be explained by lexical priming.

Nijboer *et al.* (2006) conducted an experiment where the same reverse influence was found. But in this experiment, authors used colour-related words (e.g., tomato) thus this prevents an explanation in terms of lexical priming. In this experiment, participants had to decide whether a target word was an existing word or a pseudo-word (i.e. lexical decision task). In each trial, participants saw a coloured prime followed by a target word or a pseudo-word. Fifty six colour-related words were mixed with non-related colour words (i.e. 168) and pseudo-words. Primes used could occur in seven prototypical colours (i.e. red, blue, green, yellow, pink, orange, and brown). In target trials, a colour-related word could be preceded by a congruent colour patch (e.g., red patch – TOMATO) or an incongruent colour patch (bleu patch – TOMATO). Results showed that lexical decision times for colour-related words were shorter in the congruent condition than in the incongruent condition. Moreover, Nijboer *et al.* (2006) added a control condition where the colour patch was multicoloured. Lexical decision times in this condition differed from the congruent condition but not from the incongruent condition. These results strongly support the possibility that language processing can be facilitated by an earlier low-level colour perception.

Recently, Gebuis *et al.* (2009) investigated bidirectional influence between perception and language in colour-grapheme synesthetes. In colour-grapheme synesthesia, letter or number leads to a vivid and robust experience of a colour. Accordingly, this effect is interesting for our purpose because this effect can be seen as a particular case of language/perception influence. Gebuis *et al.* (2009) explained that it is well established that in participants with colour-grapheme synesthesia, colour perception can be affected by the perception of numbers. For instance, naming the colour of the ink in which a number is written can be facilitated if the colour associated with the number in the memory of the synesthetes is congruent. However, if the colour associated with the number is different, a slowdown is observed: this is a type of Stroop effect. Accordingly, the access to colour information when numbers are processed seems to be strongly supported. The reverse access: the access to number information when colours are processed also seems possible. In their experiment, Gebuis *et al.* (2009) try to



demonstrate this bidirectional link between number and grapheme in synesthesia. Participants saw a number coloured in the colour associated with this number in their memory (congruent condition) or coloured in a different colour (incongruent condition). Then participants had to do two different tasks. In the first one, they had to name aloud the number in order to investigate the influence of colour on number processes. In the second task, they had to name aloud the colour of the ink in order to investigate the influence of number on colour processes. Gebuis *et al.* (2009) observed a priming effect in both tasks showing the bidirectional influence between number and colour in synesthetes. More precisely, perception of a number involved access to colour information (i.e. that can be named in the context of our article: colour simulation) that influenced colour perception, and perception of colour involved access to numerical information that influenced number processing. This last influence suggests that colour perception could automatically reactivate the link in memory between the colour and the number (as a particular colour/object association) influencing number processing.

To sum up, in this fifth section, we reported works suggesting the possible priming of colour simulation on colour perception as well as the reverse priming. These works support the idea that colour-related knowledge and colour perception interact in a bidirectional way *via* the reciprocal influence of underlying neuronal networks (i.e. pattern interference process). Indeed, as predicted by this approach it is possible to find an influence even when colour simulation and colour perception are performed separately in time. More precisely, it is possible to observe a form of colour priming when prime only involves a simulation of colour, not real perception and it is also possible to find semantic priming when prime involves real perception, not semantic processing. However, in the next section, we develop two limitations of these various studies that challenge the simulationist approach.

## 6. Two Problems for the Simulationist Approach

In the previous sections, we assumed the possibility that colour-related knowledge could influence colour perception through a colour simulation process. Studies supporting this hypothesis show an influence of colour-related knowledge on colour perception in a priming paradigm (Heurley *et al.* 2012, in press, Nijboer *et al.* 2006, Richter & Zwaan 2009). However, we suggest that these works have two limitations. First, recent studies suggest the possibility that specific colour perception tasks can not only involve perceptual processes but also lexical processes. Accordingly, it is possible that the influence of colour-related knowledge on colour perception occurs at a lexical level and not at a perceptual level in previously reported experiments. Secondly, various experiments, discussed in the previous sections, manipulate the congruence link between knowledge and coloured target at a 'colour category' level and not at the level of specific hues. However, it is possible that colour simulation involves simulation of specific hues (e.g., dark green, light green) rather than the general 'colour category' (e.g., green). We develop these two problems in the two

following sub-sections and based on the literature, we try to put forward ideas in order to overcome these limitations.

### 6.1. *Lexical Influence?*

Studies on categorical perception of colour have shown that response times to discriminate two hues belonging to two different colour categories (e.g., green hue *vs.* yellow hue) are shorter than response times to discriminate two hues belonging to the same colour category (e.g., dark green *vs.* light green; see Goldstone & Hendrickson 2009 for a review). Bornstein & Korda (1984) have developed the idea that this difference could be due to the intervention of two cues in order to discriminate two hues from two different categories (i.e. between-category discrimination): a perceptive cue and a lexical cue. However, only the perceptive cue would be used to discriminate two hues from the same category (i.e. within-category discrimination). This idea is similar to the 'Whorf hypothesis' according to which colour perception could be influenced by language (i.e. colour labels; see Kay & Kempton 1984).

Recently, a number of works have confirmed this hypothesis. For example, Roberson and Davidoff (2000) carried out an experiment where every trial started with the brief appearance of a coloured target on the screen. This was followed by a 5 second delay. Then two colours appeared. Participants had to choose which of the two colours corresponded to the first coloured target (i.e. 'two Alternative-Forced Choice' task). The two coloured choices either belonged to the same category (i.e. within-category discrimination) or to two different categories (i.e. between-category discrimination). During the five second delay, participants either (i) faced a white screen (i.e. control condition), either (ii) had to follow a curved line with the eyes (i.e. visual interference), either (iii) read a list of words (i.e. verbal interference). Results show a classic effect in the control condition: participants are faster to discriminate the target colour when the two colours belong to two different categories. This effect persists even with a visual interference. However, the effect disappears when the interference is of a verbal nature. Roberson & Davidoff (2000) explain that the verbal task disrupts the retention of the label of the colour of the target. This disruption cancels the lexical cue supposed to create an advantage in the between-category discrimination task, which induces a disappearance effect. This result thus confirms the involvement of a lexical cue in a between-category discrimination task (see Pilling *et al.* 2003 for identical results).

Gilbert *et al.* (2006) carried out another experiment confirming this conclusion. Participants had to discriminate two targets which appeared simultaneously on the screen. At each trial, twelve coloured squares were presented in a circle. One square among the twelve was presented in a different hue. The participants' task was to detect as fast as possible if this different square had appeared on the left or right side of the circle. The hue of the target square could either belong to the same category as the other squares or to a different category. Gilbert *et al.* (2006) observe a 'categorical perception effect' only when the targets were presented on the right side of the circle. Authors explain these results by the fact that the right part of the circle is situated in the right visual

field which is linked to the left hemisphere dedicated to language processing. Consequently, this result would confirm the involvement of linguistic processing during colour perception, at least during a between category discrimination task (see also Drivonikou *et al.* 2007).

Recently, Siok *et al.* (2009) carried out an experiment in which they directly focused on the cortical structures activated during a between- and a within-category discrimination task. For this, Siok *et al.* (2009) used the same procedure as Gilbert *et al.* (2006); however, this time participants' cortical activity was recorded by fMRI. The results highlight an activation of the areas involved in the processing of language when participants have to discriminate a square target coloured in a hue belonging to a category different to the other squares (i.e. between-category discrimination task). This last study reinforces, in the same way as the two previous ones, Bornstein & Korda (1984)'s hypothesis according to which between-category discrimination involves two cues: a perceptive and a lexical cue.

Taken together, these results confirm the possibility that colour perception involves lexical processes, at least in a between-category discrimination task. Previous results demonstrating that colour-related knowledge influences colour perception all used between-category discrimination tasks. For instance, in one of our experiments (Heurley *et al.* 2012), the perceptual targets were composed of two coloured circles that appeared in the same colour (i.e. they belonged to the same colour category) or in a different colour (i.e. they belonged to two different colour categories). In the work of Nijboer *et al.* (2006), various primes were used that belonged to different categories, the authors never used different hues of a same colour category. Richter & Zwaan (2008) tried to control the link between the two different colour targets that participants had to compare in order to obtain colours that belonged to the same lexical category. They did a pre-test where participants had to name the colour of various targets used. It seems that, at least for various couples of colours used, a colour would imply different colour labels. Accordingly, it is possible that in these various experiments, the colour perception task used implied lexical processes. This is an issue because lexical cues used in order to perceive colour could be influenced by colour labels associated with colour-related knowledge. Consequently, the influence observed could be the result of a form of lexical priming of the label rather than perceptual priming. In order to ensure this possibility, further experiments would need to be developed in which participants would have to carry out a within-category discrimination task on coloured targets primed by congruent or incongruent colour-related words. Indeed, this type of task only seems recruit low-level perceptual processes. Accordingly, if retrieval of colour-related knowledge involves a colour simulation process that influences colour perception *via* neuronal pattern interference, we would always observe perceptual priming.

## 6.2. *Simulation of Hues?*

The second problem concerns what is simulating in colour simulation? All the experiments reported here agree, implicitly, on the idea that colour simulation is the simulation of 'colour categories' and not specific hues. Indeed, all studies

control the link of congruence between prime and target at a level of colour category. For instance, Richter & Zwaan (2009) used names of colour categories (e.g., BLUE, YELLOW, GREEN) that matched or mismatched with coloured targets at a level of colour categories (e.g., blue, yellow, or green patches). In Heurley *et al.* (in press) or in Nijboer *et al.* (2006), words used represented objects associated with a colour (e.g., BANANA, TOMATO, ARTICHOKE), that matched or mismatched with coloured patches also at a level of colour categories (e.g., yellow, red or green patches). More precisely, in Heurley *et al.* (2012, in press), we used for instance the word 'LETTUCE' and the word 'ARTICHOKE' presented just before two simultaneous green patches in each trials (i.e. congruent trials) or two simultaneous yellow patches (i.e. incongruent trials). In the congruent trials, there was congruence because the labels of the colour associated with the words and with the patches were similar (i.e. label 'green'). Indeed, the difference of hues associated with the object was not taken into account. For instance, the fact that the hue of green associated with the word 'LETTUCE' is lighter than the hue of green associated with 'ARTICHOKE' was not taken into account because the same green colour was used as target each time. Consequently, the link of congruence between words and patches was controlled at the level of colour category and not at a level of specific hue.

At the perceptual level, discrimination of specific hues of a 'colour category' seems natural. For instance, in Beauchamp *et al.* (1999), participants were able to discriminate various hues of a same colour category in order to discriminate if the various patches were arranged from a dark hue to a light hue or were arranged in a disorderly manner (see also Simmons *et al.* 2007; Hsu *et al.* 2011, 2012). Results of studies on categorical perception of colour also support this capacity. Indeed, participants are able to discriminate various hues of a same colour category in within-category discrimination tasks (Roberson & Davidoff 2000; Pilling *et al.* 2003; Gilbert *et al.* 2006; Drivonikou *et al.* 2007; Siok *et al.* 2009). Finally, a recent study on colour memory also reinforces this possibility. In the experiment of Allen *et al.* (2011) participants had to adjust a test patch in order to look like the patch seen just before. Each trial was divided in three phases. In the 'learning phase', participants saw a coloured circle during 60s and were instructed to memorize the colour. Then in a retention phase, participants had to count during 120s. More precisely, beeps indicated to participants to say out loud a number from 0 to 9 in a random order. The goal of this task was to prevent verbal rehearsal of the colour test. In a test phase, participants had to set the new central patch to look like the test colour they remembered seeing previously. Moreover in order to test the role of working memory, participants were divided in two groups: one group with high working memory capacity and the other with low capacity, tested *via* the 'Reading Span' and the 'Operation Span' tests (Daneman & Carpenter 1980; Unsworth *et al.* 2005). Results showed that the differences between coordinates of the selected colour and colour learning, in the specific colourimetric model used, were relatively low suggesting that participants had a good capacity to remember specific hues of learning colour (see also Olkkonen *et al.* 2008; Witze *et al.* 2012). Let us note that this result was found for the two groups of participants showing the independence of working memory capacity. Taken together, these results support the idea that participants are able to

discriminate different hues. Consequently, if colour simulation is really a neuronal simulation of colour perception, colour simulation can involve simulation of hues, not just 'colour categories'.

One result of Hsu *et al.* (2011), already presented, partially supports the possibility to simulate specific hues in word reading. Indeed, in their experiments, participants first saw two words on the screen representing two colour-related objects. Then, a third word would appear on the screen and participants had to choose the object that was associated with the most similar colour. In one of the two blocs, the three words belonged to the same colour category and similarity occurred at a level of specific hue. For instance, participants had to compare the target word 'SCHOOL BUS' with two words also associated with the colour yellow: 'BUTTER' and 'EGG YOLK'. In this case, the answer was 'EGG YOLK' because its yellow hue is closest to the yellow hue of a school bus than to the yellow hue of butter. In this condition, Hsu *et al.* (2011) observed an activation of the fusiform and lingual gyri that are also involved in colour perception. Accordingly, this result seems to suggest the possibility to simulate specific hues in word reading. Nevertheless, a major question remains open: can hue simulation influence hue perception? Indeed, no work seems designed to test this hypothesis whereas it is a possible prediction of the simulationist approach of knowledge/perception interaction. In order to test this new prediction, further experiments would need to control the link of congruence between colour-related knowledge and coloured targets at the level of specific hues.

In this section, we developed two limits of current works supporting the simulationist approach of knowledge/perception interaction in colour perception. Firstly, we developed the idea that perceptual tasks generally used could involve lexical processes that could explain the observed priming without the use of a simulation process. To overcome this possibility, we propose to use within-category colour discrimination tasks in order to ensure the recruitment of lexical processes. Secondly, we developed the possibility that colour simulation could involve simulation of specific hues. Indeed, up to now, experiments have only controlled the congruency link at the level of colour category and absolutely not at the level of specific hues. Consequently, it is not possible to know if colour simulation can influence perception at a hue level. To overcome this limitation, new experiments must be carried out controlling the link of congruency at the level of specific hues.

## 7. Conclusion

"How can perception be altered by language?" was the fundamental question of this article. Indeed, various studies have pointed out the influence of colour-related knowledge on object and colour perception (Tanaka & Presnell 1999; Naor-Raz *et al.* 2006; Mitterer et De Ruitter 2008; Theurriault *et al.* 2009). Thus, the article does not focus directly on the language function but more precisely on how language can interact with perception, specifically with colour perception. We assumed the relevance of the simulationist approach which defends a specific form of retrieval using the same neuronal substrate than low-level perception.

We developed the hypothesis that the use of a common structure creates a meeting point for language and perception by coordinating the two through the neural bases of a distributed memory. Results from neuroimaging studies studying neuronal bases of colour perception and colour simulation allow us to conclude that these two functions are supported by two distributed neuronal networks (Shuren *et al.* 1997; Bartolomeo *et al.* 1998; Simmons *et al.* 2007; Hsu *et al.* 2011, 2012). These two networks can interact at particular point and also seem independent. Consequently, we develop the idea that colour-related knowledge and colour perception can interact through a process of pattern interference (Masson 1995). Based on this idea, we suggest the possibility that colour simulation and colour perception can interact in a bi-directional way even when colour simulation and colour perception are slightly separated in time. In other words, we expected the possibility to obtain a priming effect between colour simulation and colour perception. In support of this hypothesis, we discussed results showing (i) an influence of words denoting colour or colour-related objects on a subsequent low-level colour processing (Heurley *et al.* 2012, in press, Richter & Zwaan 2009), and (ii) results that suggest a reverse influence, from perception to language processing (Nijboer *et al.* 2006; Gebuis *et al.* 2009; Richter & Zwaan 2009). These various works are in accordance with the simulationist view; nevertheless we also develop two limitations of these studies. Indeed, these works all used between-category colour discrimination tasks that allow the intervention of lexical processes in colour perception, not only perceptual processes (Bornstein & Korda 1984; Pilling *et al.* 2003; Roberson & Davidoff 2003; Gilbert *et al.* 2006; Drivonikou *et al.* 2007). This limitation is important because the priming effect observed can be potentially explained in terms of lexical priming rather than perceptual priming. The second limitation is that these works control the congruency link between prime and target at the level of 'colour category' rather than at a level of specific hue. But, if colour simulation is a neuronal simulation of colour perception, hue simulation can be expected because hue perception is possible (e.g., Beauchamp *et al.* 1999; Simmons *et al.* 2007; Allen *et al.* 2011; Hsu *et al.* 2011, 2012). In order to overcome these two limitations and to support and extend the simulationist explanation, we propose new experimental controls.

To conclude, we would like develop two other untested predictions of the simulationist view. First, it is possible to expect an effect of delay that separates colour simulation and colour perception. Indeed, activation of a neuronal pattern can imply a refractory period of their constitutive neurons that preclude their immediate re-use. Consequently, it is possible that with a short SOA, the influence would not be obtained or a slowdown could appear. A slowdown of response times when the previous simulation is congruent with the actual perception has been obtained in two studies. For instance, in the experiment of Estes *et al.* (2008), a slowdown of response times was observed when prime words were associated with a spatial location identical to the location where subsequent perceptual targets appeared (e.g., the word ATTIC followed by a perceptual target on the top of the screen). Meteyard *et al.* (2007) studied the impact sentence implying a lateral movement towards the right or the left-hand side on the perception of a moving stimulus. Once again, when the simulated and perceived movements were identical, response times were longer. These

works allow the possibility to observe the same slowdown for a particular SOA in the case of colour perception.

A second possible prediction concerns the neuronal process underlying the influence of colour simulation on colour perception. Possible insight comes from the work of Kristjánsson *et al.* (2007) who focused on the neuronal correlates of the perceptual priming of colour. Kristjánsson *et al.* (2007) replicated the experiment of Maljkovic & Nakayama (1994) while cortical activity was recorded by fMRI. Three coloured diamond shapes placed as a triangle were presented to the participants. The right or left diamond shape placed at the base of the triangle was presented in a different colour. Participants simply had to say in what form appeared the target coloured differently from the others. Kristjánsson *et al.* (2007), in the same way as Maljkovic & Nakayama (1994), observed a priming effect when the colour of the target was the same during two consecutive trials in comparison to when the colour of the target changed from one trial to another. Moreover, Kristjánsson *et al.* (2007) observed a decrease of the BOLD signal (*Blood Oxygen Level Dependent*) in the visual areas involved in the perception of colour. This 'suppression effect' is often observed in perceptual priming tasks and is seen to be the neuronal correlate to perceptual priming (for a review see Wiggs & Martin 1998). In the case where the priming effect observed when colour simulation precedes colour perception results from perceptual priming, it is possible to expect the same decrease of the BOLD signal in the visual areas involved in the perception of colour. Such a result could bring to light the fact that colour simulation and colour perception recruit the same neuronal substrate as well as the fact that the influence of colour simulation on colour perception is supported by the same neuronal process as colour priming.

Finally, in this article, we developed a functional consequence of grounded and embodied language on the sensorimotor areas of the brain: the possibility that language can influence perception through a simulation process (and also the reverse influence). Not only did we focus our attention on how cognition and language are embodied or grounded but we also focused our attention on the functional consequence of embodying cognition for the cognitive system. In line with recent work of the embodied and grounded approach (Wu & Barsalou 2009; Barsalou 2003; Pulvermüller 2010), we tried to build explanations for cognitive functioning without a symbolic and amodal architecture. According to this approach, memory, knowledge, language and perception function in a coordinated way which can either alter or facilitate perception. We agree that this view needs more work in order to overcome various limitations and to test other possible predictions. However, it seems an interesting way to conceive the language/perception interaction while including the constraints of the neuronal substrate underlying cognitive functioning.

## References

Allen, Elizabeth C., Sian L. Beilock & Steven K. Shevell. 2011. Working memory is

- related to perceptual processing: A case from color perception. *Journal of Experimental Psychology: Learning, Memory, and Cognition* 37(4), 1014–1021.
- Allport, D. A. 1985. Distributed memory, modular subsystems and dysphasia. In S. K. Newman & R. Epstein (eds.), *Current Perspectives in Dysphasia*, 32–60. Edinburgh: Churchill Livingstone.
- Barsalou, Lawrence W. 1999. Perceptual symbol systems. *Behavioral and Brain Sciences* 22, 577–660.
- Barsalou, Lawrence W. 2008. Grounded cognition. *Annual Review of Psychology* 59, 617–645.
- Barsalou, Lawrence W. 2009. Simulation, situated conceptualization, and prediction. *Philosophical Transactions of the Royal Society of London: Biological Science* 364, 1281–1289.
- Barsalou, Lawrence W., W. Kyle Simmons, Aron K. Barbey & Christine D. Wilson. 2003. Grounding conceptual knowledge in modality-specific systems. *Trends in Cognitive Sciences* 7(2), 84–91.
- Bartolomeo, Paolo, Anne-Catherine Bachoud-Lévi & Gianfranco Denes. 1997. Preserved imagery for colours in a patient with cerebral achromatopsia. *Cortex* 33, 369–378.
- Beauchamp, Michael S., James V. Haxby, Jonathan E. Jennings & Edgar A. de Yoe. 1999. An fMRI version of the Farnsworth-Munsell 100-hue test reveals multiple colour-selective areas in human ventral occipitotemporal cortex. *Cerebral Cortex* 9, 257–263.
- Biederman, Irvin. 1987. Recognition-by-components: A theory of human image understanding. *Psychological Review* 94(2), 115–147.
- Bocanegra, Bruno R. & René Zeelenberg. 2009. Emotion improves and impairs early vision. *Psychological Science* 20(6), 707–713.
- Bornstein, Marc H. & Nancy O. Korda. 1984. Discrimination and matching within and between hues measured by reaction times: Some implications for categorical perception and levels of information processing. *Psychological Research* 46, 207–222.
- Bouvier, Seth E. & Stephen A. Engel. 2006. Behavioral deficits and cortical damage loci in cerebral achromatopsia. *Cerebral Cortex* 16, 183–191.
- Bramão, Ignês, Luis Faísca, Christian Forkstam, Alexandra Reis & Karl M. Petersson. 2010. Cortical brain regions associated with colour processing: An fMRI study. *The Open Neuroimaging Journal* 4, 164–173.
- Bramão, Ignês, Alexandra Reis, Karl M. Petersson & Luis Faísca. 2011. The role of colour information on object recognition: A review and meta-analysis. *Acta Psychologica* 138(1), 244–253.
- Bruner, Jerome S. & Leo Postman. 1949. On the perception of incongruity: A paradigm. *Journal of Personality* 18, 108–143.
- Bruner, Jerome S., Leo Postman & John Rodrigues. 1951. Expectation and the perception of colour. *American Journal of Psychology* 64, 216–227.
- Chao, Linda L. & Alex Martin. 1999. Cortical regions associated with perceiving, naming, and knowing about colours. *Journal of Cognitive Neuroscience* 11(1), 25–35.
- Corbetta, Maurizio, Francis M. Miezin, Suzan Dohmeyer, Gordon L. Shulman & Steve E. Petersen. 1991. Shape, colour, and speed: Functional anatomy by



- positron emission tomography. *The Journal of Neuroscience* 11(8), 2393–2402.
- Daneman, Meredyth & Patricia Carpenter. 1980. Individual differences in working memory and reading. *Journal of Verbal Learning and Verbal Behavior* 19, 450–466.
- De Vreese, Luc P. 1991. Two systems for colour-naming defects: Verbal disconnection vs colour imagery disorder. *Neuropsychologia* 29, 1–18.
- Delk, John L. & Samuel Fillenbaum. 1965. Differences in perceived colour as a function of characteristic colour. *American Journal of Psychology* 78, 290–293.
- Drivonikou, Gilda V., Paul Kay, Terry Regier, Richard B. Ivry, Aubrey L. Gilbert, Anna Franklin *et al.* 2007. Further evidence that Whorfian effects are stronger in the right visual field than the left. *Proceedings of the National Academy of Sciences of the United States of America* 104, 1097–1102.
- Duncker, Karl. 1939. The influence of past experience upon perceptual properties. *American Journal of Psychology* 52, 255–265.
- Engel, Stephen, Xuemei Zhang & Brian Wandell. 1997. Colour tuning in human visual cortex measured with functional magnetic resonance imaging. *Nature* 388, 68–71.
- Estes, Zachari, Michelle Verges & Lawrence W. Barsalou. 2008. Head up, foot down: Object words orient attention to the objects' typical location. *Psychological Science* 19(2), 93–97.
- Farah, Martha J. & James L. McClelland. 1991. A computational model of semantic memory impairment: Modality-specificity and emergent category-specificity. *Journal of Experimental Psychology: General* 120, 339–357.
- Farnsworth, Dean. 1957. *The Farnsworth-Munsell 100-hue for the examination of the colour vision*. Baltimore, MD: Munsell Colour Compagny.
- Fodor, Jerry. A. 1983. *The Modularity of Mind: An Essay on Faculty Psychology*. Cambridge, MA: MIT Press.
- Gebuis, Titia, Tanja. C. W. Nijboer & Maarten J. van der Smagt. 2009. Of colored numbers and numbered colors: Interactive processes in grapheme-color synesthesia. *Experimental Psychology* 56(3), 180–187.
- Gegenfurtner, Karl R. 2003. Cortical mechanisms of colour vision. *Natural Review: Neuroscience* 4, 563–572.
- Gegenfurtner, Karl R. & Daniel C. Kiper. 2003. Color vision. *Annual Review of Neuroscience* 26, 181–206.
- Gibson, James J. 1979. *The Ecological Approach to Visual Perception*. New York: Psychology Press.
- Gilbert, Aubrey. L., Terry Regier, Paul Kay & Richard B. Ivry. 2006. Whorf hypothesis is supported in the right visual field but not the left. *Proceedings of the National Academy of Sciences of the United States of America* 103, 489–494.
- Goldberg, Robert E., Charles A. Perfetti & Walter Schneider. 2006. Perceptual knowledge retrieval activates sensory brain regions. *Journal of Neuroscience* 26, 4917–4921.
- Goldstone, Robert L. & Andrew T. Hendrickson. 2009. Categorical perception. *Interdisciplinary Reviews: Cognitive Science* 1, 69–78.
- Guyllás, Balázs & Per E. Roland. 1994. Processing and analysis of form, colour and binocular disparity in the brain: Functional anatomy by positron emission tomography. *European Journal of Neuroscience* 6, 1811–1828.

- Hansen, Thorsten, Maria Olkkonen, Sebastian Walter & Karl R. Gegenfurtner. 2006. Memory modulates colour appearance. *Nature Neuroscience* 9(11), 1367–1368.
- Harper, Robert S. 1953. The perceptual modifications of coloured figures. *American Journal of Psychology* 66, 86–89.
- Hebb, Donald O. 1949. *The Organization of Behavior: A Neuropsychological Theory*. New York: John Wiley & Sons.
- Heurley, Loïc P., Thibaut Brouillet, Gabrielle Chesnoy & Denis Brouillet. 2012. Color perception involves color representations firstly at a semantic level and then at a lexical level. *Cognitive Processing*. doi: 10.1007/s10339-012-0527-z.
- Heurley, Loïc P., Elisabeth Rolland-Thiers, Laurent P. Ferrier & Denis Brouillet. In press. Influence des connaissances associées à une couleur dans une tâche de discrimination chromatique. *L'Année Psychologique*.
- Hinton, Geoffrey. 1981. Implementing semantic networks in parallel hardware. In G. Hinton & J. A. Anderson (eds.), *Parallel Model of Associative Memory*, 191–217. Hillsdale, NJ: Lawrence Erlbaum Associates.
- Hsu, Nina S., Steven M. Frankland & Sharon L. Thompson-Schill. 2012. Chromaticity of color perception and object color knowledge. *Neuropsychologia* 50, 327–333.
- Hsu, Nina S., David J. M. Kraemer, Robyn T. Oliver, Margaret L. Schlichting & Sharon L. Thompson-Schill. 2011. Color, context, and cognitive style: Variations in color knowledge retrieval as a function of task and subject variables. *Journal of Cognitive Neuroscience* 23(9), 2544–2557.
- Ishihara, Shinobu. 1974. *Tests for Colour-Blindness*. Tokyo: Kanehara Shup.
- Kay, Paul & Willet Kempton. 1984. What is the Sapir-Whorf Hypothesis? *American Anthropologist* 86(1), 65–79.
- Kellenbach, Marion L., Matthew Brett & Karalyn Patterson. 2001. Large, colourful, or noisy? Attribute- and modality-specific activations during retrieval of perceptual attribute knowledge. *Cognitive, Affective, & Behavioral Neuroscience* 1(3), 207–221.
- Kirby, John, Phillip Moore & Neville Schofield. 1988. Verbal and visual learning styles. *Contemporary Educational Psychology* 13, 169–184.
- Klein, George S. 1964. Semantic power measured through the interference of words with color-naming. *American Journal of Psychology* 77, 576–588.
- Kristjánsson, Árni, Patrik Vuilleumier, Sophie Schwartz, Emiliano Macaluso & Jon Driver. 2007. Neural basis for priming of pop-out during visual search revealed with fMRI. *Cerebral Cortex* 17, 1612–1624.
- Kubat, Rony, Daniel Mirman & Deb Roy. 2009. Semantic context effects on colour categorization. In Niels A. Taatgen & Hedderik van Rijn (eds.), *Proceedings of the 31st Annual Conference of the Cognitive Science Society*, 491–495. Austin, TX: Cognitive Science Society.
- Loftus, Elizabeth F. 1977. Shifting human color memory. *Memory & Cognition* 5(6), 696–699.
- Maljkovic, Vera & Ken Nakayama. 1994. Priming of pop-out: I. Role of features. *Memory & Cognition* 22, 657–672.
- Martin, Alex. 2007. The representation of object concepts in the brain. *Annual*

- Review of Psychology* 58, 25–45.
- Martin, Alex. 2009. Circuits in mind: The neural foundations for object concepts. In Michael S. Gazzaniga (ed.), *The Cognitive Neurosciences*, 4th edn., 1031–1045. Cambridge, MA: MIT Press.
- Martin, Alex & Linda L. Chao. 2001. Semantic memory and the brain: Structure and process. *Current Opinion in Neurobiology* 11, 194–201.
- Martin, Alex, James V. Haxby, Francois M. Lalonde, Cheri L. Wiggs & Leslie G. Ungerleider. 1995. Discrete cortical regions associated with knowledge of colour and knowledge of action. *Science* 270, 102–105.
- Masson, Michael E. J. 1995. A distributed memory model of semantic priming. *Journal of Experimental Psychology: Learning, Memory and Cognition* 21(1), 3–23.
- McClelland, James L. & David E. Rumelhart. 1985. Distributed memory and the representation of general and specific information. *Journal of Experimental Psychology: General* 114, 159–197.
- Meteyard, Lotte, Behador Bahrami & Gabriella Vigliocco. 2007. Motion detection and motion verbs: Language affects low-level visual perception. *Psychological Science* 18(11), 1007–1013.
- Mitterer, Holger & Jan Peter de Ruiter. 2008. Recalibrating colour categories using world knowledge. *Psychological Science* 19(7), 629–634.
- Naor-Raz, Gallit, Michael J. Tarr & Daniel Kersten. 2003. Is colour an intrinsic property of object representation? *Perception* 32, 667–680.
- Neisser, Ulric. 1967. *Cognitive Psychology*. New York: Appleton-Century-Crofts.
- Nijboer, Tanja C. W., Titia Gebuis, Susan F. te Pas & Maarten J. van der Smagt. 2011. Interactions between colour and synaesthetic colour: An effect of simultaneous colour contrast on synaesthetic colours. *Vision Research* 51, 43–47.
- Nijboer, Tanja C. W., Maarten J. van der Smagt, Martine J. E. Van Zandvoort & Edward H. F. De Haan. 2007. Colour agnosia impairs the recognition of natural but not of non-natural scenes. *Cognitive Neuropsychology* 24(2), 152–161.
- Nijboer, Tanja C. W., Martine J. E. van Zandvoort & Edward H. F. de Haan. 2006. Seeing red primes tomato: Evidence for comparable priming from colour and colour name primes to semantically related word targets. *Cognitive Processes* 7, 269–274.
- Oliva, Aude & Philippe G. Schyns. 2000. Diagnostic colors mediate scene recognition. *Cognitive Psychology* 41, 176–210.
- Oliver, Robyn T. & Sharon L. Thompson-Shill. 2003. Dorsal stream activation during retrieval of object size and shape. *Cognitive, Affective, & Behavioral Neuroscience* 3(4), 309–322.
- Olkkonen, Maria, Thorsten Hansen & Karl R. Gegenfurtner. 2008. Color appearance of familiar objects: Effects of object shape, texture, and illumination changes. *Journal of Vision* 8(5), 1–16.
- Pilling, Michael, Alison Wiggett, Emre Özgen & Ian R. L. Davies. 2003. Is colour ‘categorical perception’ really perceptual? *Cognition* 31, 538–551.
- Pohl, Rüdiger. F. 2004. Effects of labelling. In Rüdiger F. Pohl (ed.), *A Handbook of Fallacies and Biases in Thinking, Judgment and Memory*, 327–344. New York:

- Psychology Press.
- Pulvermüller, Friedmann. 2001. Brain reflections of words and their meaning. *Trends in Cognitive Sciences* 5(12), 517–524.
- Pulvermüller, Friedmann. 2003. *The Neuroscience of Language*. Cambridge: Cambridge University Press.
- Pulvermüller, Friedmann. 2010. Brain-language research: Where is the progress? *Biolinguistics* 4(2–3), 255–288.
- Pylyshyn, Zenon W. 1984. *Computation and Cognition*. Cambridge, MA: MIT Press.
- Reilhac, Gilles & Manuel Jiménez. 2006. Amorçage de la couleur typique d'un objet lors d'une tâche de catégorisation. *Canadian Journal of Experimental Psychology* 60(4), 285–293.
- Richter, Tobias & Rolf A. Zwaan. 2009. Processing of colour words activates colour representations. *Cognition* 111(3), 383–389.
- Roberson, Debi & Jules Davidoff. 2000. The categorical perception of colors and facial expressions: The effect of verbal interference. *Memory & Cognition* 28, 977–986.
- Schacter, Daniel L., Kenneth A. Norman & Wilma Koutstaal. 1998. The cognitive neuroscience of constructive memory. *Annual Review of Psychology* 49, 289–318.
- Shuren, Jeffrey E., Thomas G. Brott, Bruce K. Schefft & Wes Houston. 1996. Preserved color imagery in an achromatopsic. *Neuropsychologia* 34, 485–489.
- Simmons, W. Kyle, Vimal Ramjee, Michael S. Beauchamp, Ken McRae, Alex Martin & Lawrence W. Barsalou. 2007. A common neural substrate for perceiving and knowing about colour. *Neuropsychologia* 45, 2802–2810.
- Siok, Wai Ting, Paul Kay, William S. Y. Wang, Alice H. D. Chan, Lin Chen, Kang Kwong Luke *et al.* 2009. Language regions of brain are operative in color perception. *Proceedings of the National Academy of Sciences of the United States of America* 106(20), 8140–8145.
- Spence, Charles, Carmel A. Levitan, Maya U. Shankar & Massimiliano Zampini. 2010. Does food colour influence taste and flavor perception in humans? *Chemosensory Perception* 3, 68–84.
- Stein, Barry E. & Alex M. Meredith. 1993. *The Merging of the Senses*. Cambridge, MA: MIT Press.
- Tanaka, James W. & Lynn M. Presnell. 1999. Colour diagnosticity in object recognition. *Perception & Psychophysics* 61(6), 1140–1153.
- Therriault, David J., Richard H. Yaxley & Rolf A. Zwaan. 2009. The role of colour diagnosticity in object recognition and representation. *Cognitive Processes* 10(4), 335–342.
- Unsworth, Nash, Richard P. Heitz, Josef C. Schrock & Randall W. Engle. 2005. An automated version of the operation span task. *Behavior Research Methods* 37, 498–505.
- Van Zandvoort, Martine J. E., Tanja C. W. Nijboer & Edward de Haan. 2007. Developmental colour agnosia. *Cortex* 43, 750–757.
- Versace, Rémy, Elodie Labeye, Guillemette Badard & Marylène Rose. 2009. The contents of long-term memory and the emergence of knowledge. *European Journal of Cognitive Psychology* 21(4), 522–560.
- Wiggs, Cheri L. & Alex Martin. 1998. Properties and mechanisms of perceptual

- priming. *Current Opinion in Neurobiology* 8, 227–233.
- Wiggs, Cheri L., Jil Weisberg & Alex Martin. 1999. Neural correlates of semantic and episodic memory retrieval. *Neuropsychologia* 37, 103–118.
- Witze, Christoph, Hanna Valkova, Thorsten Hansen & Karl R. Gegenfurtner. 2011. Object knowledge modulates colour appearance. *i-Perception* 2, 13–49.
- Wu, Ling-ling, & Lawrence W. Barsalou. 2009. Perceptual simulation in conceptual combination: Evidence from property generation. *Acta Psychologica* 132, 173–189.
- Yee, Eiling, Sarah. Z. Ahmed & Sharon L. Thompson-Schill. 2012. Colorless green ideas (can) prime furiously. *Psychological Science* 23, 364–369.
- Zeki, Semir. 1983a. Colour coding in the cerebral cortex: The reaction of cells in monkey visual cortex to wavelengths and colours. *Neuroscience* 9, 741–765.
- Zeki, Semir. 1983b. Colour coding in the cerebral cortex: The responses of the wavelength-selective and colour-coded cells in monkey visual cortex to changes in wavelength composition. *Neuroscience* 9, 767–781.
- Zeki, Semir. 1983c. The distribution of wavelength and orientation selective cells in different areas of the monkey visual cortex. *Proceedings of the Royal Society B: Biological Sciences* 217, 449–470.
- Zeki, Semir & Ludovica Marini. 1998. Three cortical stages of colour processing in the human brain. *Brain* 121, 1669–1685.
- Zeki, Semir, James D. G. Watson, C. J. Lueck, K. J. Friston, C. Kennard & R. S. J. Frackowiak. 1991. A direct demonstration of functional specialization in human visual cortex. *The Journal of Neuroscience* 17(3), 641–649.
- Zwaan, Rolf A. & Michael P. Kaschak. 2009. Language in the brain, body and world. In Philip Robbins & Murat Aydede (eds.), *The Cambridge Handbook of Situated Cognition*, 368–381. Cambridge: Cambridge University Press.

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