Colors in the mind's eye

Paolo Bartolomeo[1], Jianghao Liu[1,2], and Alfredo Spagna[3]

1. Sorbonne Université, Institut du Cerveau - Paris Brain Institute - ICM, Inserm, CNRS, AP-HP, Hôpital de la Pitié-Salpêtrière, F-75013 Paris, France
2. Corporate Research, Dassault Systèmes, 78140 Vélizy-Villacoublay, France
3. Department of Psychology, Columbia University in the City of New York, NY, USA, 10027

Keywords

Visual mental imagery; Visual experience; Color imagery; Fusiform gyrus; Single-case studies

Funding

This work is supported by the Agence Nationale de la Recherche through ANR-16-CE37-0005 and ANR-10-IAIHU-06, by the Fondation pour la Recherche sur les AVC through FR-AVC-01, and by funding from Dassault Systèmes.

Abstract

The famous “Piazza del Duomo” paper, published in Cortex in 1978, inspired a considerable amount of research on visual mental imagery in brain-damaged patients. As a consequence, single-case reports featuring dissociations between perceptual and imagery abilities challenged the prevailing model of visual mental imagery. Here we focus on mental imagery for colors. A case study published in Cortex showed perfectly preserved color imagery in a patient with acquired achromatopsia after bilateral lesions at the borders between the occipital and temporal cortex. Subsequent neuroimaging findings in healthy participants extended and specified this result; color imagery elicited activation in both a domain-general region located in the left fusiform gyrus and the anterior color-biased patch within the ventral temporal cortex, but not in more posterior color-biased patches. Detailed studies of individual neurological patients, as those often published in Cortex, are still critical to inspire and constrain neurocognitive research and its theoretical models.

The Piazza del Duomo experiment and imaginal neglect

In 1978, *Cortex* published one of its most celebrated (and cited) articles: “Unilateral neglect of representational space” (Bisiach & Luzzatti, 1978). In this short note, Edoardo Bisiach and Claudio Luzzatti described two Milanese patients with right hemisphere lesions and left spatial neglect who, when asked to describe well-known places from memory, such as the Piazza del Duomo in Milan, systematically “forgot” to mention the details on the left side of their visual mental images. Thus, these patients neglected not only left-sided external stimuli but also the left part of their mental images. Bisiach and Luzzatti’s paper was seminal in initiating research on imaginal neglect (Marshall & Halligan, 2002). It also prompted Guido Gainotti, the mentor of one of the present authors (PB), to assign him and Patrizia D’Erme a similar study, based on asking Roman patients to describe the piazzas of Rome. This study became the main task of PB’s residency in Neurology (Bartolomeo et al., 1994). In 1994, PB moved to Paris, France, carrying a lot of unanswered questions regarding imaginal neglect. For example, one of the lessons he learned in Paris was that drawing from memory is not an appropriate task for imaginal neglect, because as soon as patients put their pencil on the paper, their visual attention is immediately attracted by the right-sided strokes they draw (Chokron et al., 2004; Cristinzio et al., 2009).

With his French co-workers, PB built upon the imaginal test based on the map of France devised in Lyon by Gilles Rode’s team (Rode et al., 2004, 2007), to develop new versions of it using manual and vocal response times (Bartolomeo et al., 2005; Bourlon et al., 2008; Bourlon, Duret, et al., 2011) and eye movements (Bourlon, Oliviero, et al., 2011). A consistent finding that emerged from all these studies is that only a minority of patients with perceptual neglect also exhibited imaginal neglect. The complementary dissociation of imaginal neglect without perceptual neglect, was also reported (Beschin et al., 1997; Guariglia et al., 1993). Even more intriguing, Signor Piazza, another patient described in *Cortex* (Beschin et al., 2000), exhibited right-sided perceptual neglect and left-sided imaginal neglect. Perception and mental imagery of spatial details evidently do not always correspond after brain damage.

Nonspatial mental imagery: the case of color

The impact of the Piazza del Duomo paper extended well beyond imaginal neglect, and sparked interest in the broader subject of visual mental imagery in patients with brain damage (Basso et al., 1980; Farah, 1988; Goldenberg, 1993).

At that time, the dominant neurocognitive model of visual mental imagery was being forcefully articulated by Stephen M. Kosslyn (see, e.g., Kosslyn, 1994) and others. This model stipulated that mental images are projected onto retinotopically mapped regions, including the early visual cortex. Evidence from neurological patients showing an association between perceptual and imagery deficits initially supported the model (Farah, 1988). A few years later, however, detailed case reports emerged describing patients who exhibited perceptual deficits such as cortical blindness (Goldenberg et al., 1995) or visual agnosia (Behrmann et al., 1992; Servos & Goodale, 1995) while maintaining intact visual mental imagery abilities. These case descriptions cast doubts on the hypothesized neural overlap between perceptual and imagery mechanisms. Nevertheless, these dissociations of performance could depend at least in part on the use of strategies different from visualization: for example, to complete the task at hand (e.g., state from memory whether an uppercase A is larger at the top or at the bottom) patients can use spatiomotor, nonvisual strategies (Bartolomeo et al., 2002).

Importantly, however, visual knowledge of colors can hardly benefit from such strategies, as color is a domain that is typically nonspatial. Preserved color imagery in a patient with acquired cerebral achromatopsia would provide compelling evidence against the claim that perception and imagery mechanisms completely overlap in the brain. Patients with cerebral achromatopsia are very rare, but PB encountered one such patient in the neurology ward of the Henri-Mondor hospital on the outskirts of Paris. Madame D, an amateur oil painter, suffered from bilateral hemorrhages in the white matter at the junction between the occipital and temporal lobes (Fig. 1).

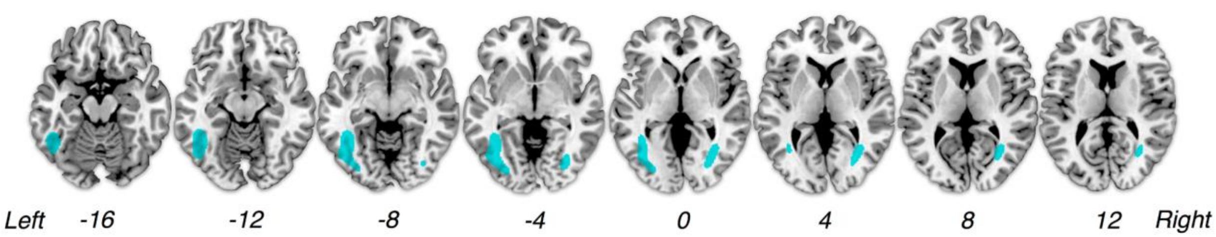

Figure 1. Reconstruction of the lesions of Madame D, who experienced cerebral achromatopsia with perfectly preserved mental imagery for colors. Image modified from Bartolomeo et al. (2014), with permission of Elsevier.

As a consequence, she found herself unable to visually recognize objects, faces, and words. She also discovered that the colors she once enjoyed and used for her painting had vanished from her visual experience, leaving the world appearing as a dull gray to her. PB invited Gianfranco Denes, who was then on sabbatical in Paris, to participate in the evaluation of this patient. It so happened that at the time, Gianfranco was reading Antonio Damasio's book *Descartes' Error* (Damasio, 1994). In that book, Damasio states that "local damage in the early visual cortices causes not only loss of color perception but also loss of color imagery. If you are achromatopsic, you can no longer imagine color in your mind. If I ask you to imagine a banana, you will be able to picture its shape but not its color; you will see it in shades of gray." Thus, Gianfranco Denes started to ask questions to Madame D, asking her to recall the typical colors of objects such as bananas, the sky, the French flag… Contrary to Damasio's claim, Madame D always provided accurate responses to these questions and stated that she could perfectly visualize in her mind the same items she could not visually recognize.

Later on, we learned that people can answer some questions on the visual appearance of objects without actually visualizing them, by using verbal associations (banana/yellow, snow/white, sky/blue, etc.). We thus devised questions that could hardly be answered by relying on non-visual semantic memory, and developed a French-language battery to comprehensively assess visual perception and visual mental imagery, the *Batterie Imagination Perception* (BIP; Bourlon et al., 2009). Madame D was severely impaired on the perceptual part of the battery, yet her performance in the imagery section was flawless, consistent with her subjective experience (Bartolomeo et al., 1998). In particular, the colors that had disappeared from her perception remained perfectly vivid in her mind's eye. For instance, Madame D could effortlessly recall from memory which shade of green is typically darker between spinach and bay leaves, or which shade of red is lighter between cherries and strawberries. After contemplating, and fortunately discarding, the idea of titling our paper *Damasio's Error*, we submitted it as a *Note* to *Cortex*, where it was published under the meticulous and supportive editorship of Ennio De Renzi (Bartolomeo et al., 1997). This case report presented a clear challenge to the model proposing a complete neural overlap between perceptual and imagery mechanisms. In fact, Kosslyn and colleagues later discussed this case, acknowledging that "[t]hese results demonstrate that the two systems are only partially overlapping, which should not be a surprise: imagery is based on stored information that has already been organized, whereas perception requires segregating figure from ground, along with recognizing and identifying a perceived object" (Kosslyn et al., 2006, p. 151f).

Specifying the conclusions through functional neuroimaging

Perusal of the literature revealed that Madame D's pattern of performance was far from being an isolated occurrence. It became evident that several patients exhibited instances of double dissociations between visual perception and visual mental imagery (Bartolomeo, 2002). Importantly, deficits in visual mental imagery typically do not arise as a result of occipital lesions but rather tend to emerge following extensive damage to the temporal lobe of the left hemisphere (Bartolomeo, 2008; Moro et al., 2008), with the possible exception of imagery of faces, where right hemisphere temporal lesions might cause a deficit in some patients (Liu et al., 2022).

However, as often happens in science, this evidence struggled to reach the level of theoretical modeling. Researchers, perhaps not fully recognizing the causal power of evidence from individuals with acquired brain lesions (Bartolomeo et al., 2020), continued to reason within the framework of the traditional perception/imagery equivalence model, with its stress on the role of early visual cortex in mental imagery (Pearson, 2019).

Furthermore, functional neuroimaging findings in healthy participants appeared to be in conflict with evidence from brain-damaged patients, as they indicated activity in V1 during visual mental imagery (see, e.g., Kosslyn et al., 1995). The arrival of Alfredo Spagna as a postdoctoral researcher in PB's lab provided the opportunity to address this puzzle. As a first step, Alfredo proposed to check the neuroimaging literature with an unbiased eye. With the help of Dounia Hajhajate, he collected the 27 fMRI studies of visual mental imagery available at the time and performed a meta-analysis of their results. Despite the wide variety of mental imagery paradigms used in the studies, a clear pattern emerged. The meta-analysis unveiled imagery-related activity, not only in frontoparietal areas, where it had been detected by earlier studies, but also in a previously undescribed functional region of the left Ventral Temporal Cortex (VTC), which we called the Fusiform Imagery Node (FIN). FIN activity was observed across all imagery tests, regardless of the specific domain of imagery (colors, faces, etc.). But what about the early visual cortices? Jianghao Liu, an engineer who had joined the team as a PhD student thanks to the generous support of Dassault Systèmes, conducted a Bayesian analysis on occipital activity and determined that there was no evidence whatsoever of imagery-related activity in the early visual cortices (Spagna et al., 2021). While challenging the prevailing model of visual mental imagery, this pattern of brain activity was clearly consistent with the causal evidence from neuropsychology (Bartolomeo, 2002). Furthermore, it pinpointed the FIN as a plausible critical region within the left temporal lobe, the impairment or disconnection of which could underlie domain-general imagery deficits in neurological patients (Bartolomeo, 2021b).

Knowledge of the color-biased regions on the bottom surface of the brain had also progressed. Using fMRI, Lafer-Sousa, Conway and Kanwisher discovered a longitudinal band of color-biased cortex along the occipito-temporal visual pathway, with three peaks of perceptual activation: a posterior patch, a central patch, and an anterior color-biased patch (Lafer-Sousa et al., 2016). In the framework of Jianghao Liu’s PhD thesis, we used 7T, ultra-high field fMRI (Liu, Zhan, et al., 2023), together with a new, enhanced version of the BIP (Liu & Bartolomeo, 2023), to identify perception- and imagery-related brain circuits in 10 neurotypical participants and 10 healthy individuals who claimed not to experience any visual mental images (so-called aphantasia; Zeman et al., 2015).

Color perception nicely replicated the three color-biased patches identified by Lafer-Sousa et al. Importantly, however, color imagery exclusively engaged the anterior patch among these, in conjunction with the FIN (Liu, Zhan, et al., 2023). Once again, it was demonstrated that visual mental imagery only partially overlaps with visual perception, and this overlap primarily occurs within the high-level visual cortex of the VTC. Interestingly, aphantasic individuals showed a similar pattern of activation, consistent with their ability to answer the BIP questions, albeit with slower response times and less confidence compared to typical imagers (Liu & Bartolomeo, 2023). The main difference between typical imagery and aphantasia was in the pattern of functional connectivity of the FIN: in typical imagery, FIN activity correlated with activity in frontoparietal networks; this correlation was, however, absent in aphantasic individuals. These findings provide strong and converging evidence that visual experience in both perception (Liu, Bayle, et al., 2023; Spagna et al., 2022) and mental imagery relies on the coordinated activity of high-level visual cortex and frontoparietal networks.

Back to patients: what about color agnosia?

Color agnosia is typically considered an impairment in linking color knowledge to objects: patients fail to name and select the canonical color of auditorily presented objects, or to select the correct color for a black-and-white drawing of an object (Bartolomeo, 2021a, 2022; Bartolomeo & Miceli, 2023; Siuda-Krzywicka & Bartolomeo, 2020). Could it be that these patients fail these tasks because they are unable to imagine the objects in color[1]? This may well be the case, especially when considering that lesions in cases of color agnosia often impact the left anterior temporal lobe, encompassing the ventro-rostral regions of the lingual gyrus, the isthmus, and the parahippocampal areas (Luzzatti & Davidoff, 1994; Miceli et al., 2001; Stasenko et al., 2014). Unfortunately, visual mental imagery was not explicitly tested in these rare patients. We can speculate that lesion or disconnection of the circuit including the FIN and the anterior color patch may be a crucial lesional correlate of color imagery deficits. Consistent with this claim, RDS, a patient who experienced color anomia due to extensive damage in the left medial occipito-temporal region (Siuda-Krzywicka et al., 2019, 2020), but with apparent preservation of the FIN and its connections to perisylvian and anterior temporal regions, demonstrated reasonably preserved visual mental imagery abilities for several domains including colors (Hajhajate et al., 2022).

What have we learned from this long journey into visual mental imagery? Perhaps the most important lesson is that causal evidence derived from individual cases of brain-damaged patients, despite its potential shortcomings (Bartolomeo et al., 2017), continues to be a vital element in cognitive neuroscience research. It serves both as inspiration for neuroimaging studies and as a constraint for theoretical modeling. We are indeed lucky that *Cortex* upheld this approach throughout its 60-year history.

[1] We thank an anonymous reviewer for suggesting this possibility

References

Bartolomeo, P. (2002). The relationship between visual perception and visual mental imagery: A reappraisal of the neuropsychological evidence. *Cortex*, *38*(3), 357–378. https://doi.org/10.1016/S0010-9452(08)70665-8

Bartolomeo, P. (2008). The neural correlates of visual mental imagery: An ongoing debate. *Cortex*, *44*(2), 107–108. https://doi.org/10.1016/j.cortex.2006.07.001

Bartolomeo, P. (2021a). Color Vision Deficits. *Current Neurology and Neuroscience Reports*, *21*(10), 58. https://doi.org/10.1007/s11910-021-01137-8

Bartolomeo, P. (2021b). Visual agnosia and imagery after Lissauer. *Brain*, *144*(9), 2557–2559. https://doi.org/10.1093/brain/awab159

Bartolomeo, P. (2022). Visual objects and their colors. In *Handbook of Clinical Neurology* (Vol. 187, pp. 179–189). Elsevier. https://doi.org/10.1016/B978-0-12-823493-8.00022-5

Bartolomeo, P., Bachoud-Levi, A. C., Chokron, S., & Degos, J.-D. (2002). Visually- and motor-based knowledge of letters: Evidence from a pure alexic patient. *Neuropsychologia*, *40*(8), 1363–1371. https://doi.org/10.1016/s0028-3932(01)00209-3

Bartolomeo, P., Bachoud-Lévi, A. C., de Gelder, B., Denes, G., Dalla Barba, G., Brugières, P., & Degos, J. D. (1998). Multiple-domain dissociation between impaired visual perception and preserved mental imagery in a patient with bilateral extrastriate lesions. *Neuropsychologia*, *36*(3), 239–249. https://doi.org/10.1016/s0028-3932(97)00103-6

Bartolomeo, P., Bachoud-Lévi, A. C., & Denes, G. (1997). Preserved imagery for colours in a patient with cerebral achromatopsia. *Cortex*, *33*(2), 369–378. https://doi.org/10.1016/s0010-9452(08)70012-1

Bartolomeo, P., Bachoud-Levi, A.-C., Azouvi, P., & Chokron, S. (2005). Time to imagine space: A chronometric exploration of representational neglect. *Neuropsychologia*, *43*(9), 1249–1257. https://doi.org/10.1016/j.neuropsychologia.2004.12.013

Bartolomeo, P., Bachoud-Lévi, A.-C., & Thiebaut De Schotten, M. (2014). The anatomy of cerebral achromatopsia: A reappraisal and comparison of two case reports. *Cortex*, *56*, 138–144. https://doi.org/10.1016/j.cortex.2013.01.013

Bartolomeo, P., D’Erme, P., & Gainotti, G. (1994). The relationship between visuospatial and representational neglect. *Neurology*, *44*(9), 1710–1714. https://doi.org/10.1212/wnl.44.9.1710

Bartolomeo, P., Hajhajate, D., Liu, J., & Spagna, A. (2020). Assessing the causal role of early visual areas in visual mental imagery. *Nature Reviews Neuroscience*, *21*(9), 517–517. https://doi.org/10.1038/s41583-020-0348-5

Bartolomeo, P., & Miceli, G. (2023). Definition: Object color agnosia. *Cortex*, *167*, 65. https://doi.org/10.1016/j.cortex.2023.07.002

Bartolomeo, P., Seidel Malkinson, T., & de Vito, S. (2017). Botallo’s error, or the quandaries of the universality assumption. *Cortex*, *86*, 176–185. https://doi.org/10.1016/j.cortex.2016.09.026

Basso, A., Bisiach, E., & Luzzatti, C. (1980). Loss of mental imagery: A case study. *Neuropsychologia*, *18*(4–5), 435–442. https://doi.org/10.1016/0028-3932(80)90146-3

Behrmann, M., Winocur, G., & Moscovitch, M. (1992). Dissociation between mental imagery and object recognition in a brain-damaged patient. *Nature*, *359*, 636–637. https://doi.org/10.1038/359636a0

Beschin, N., Basso, A., & Della Sala, S. (2000). Perceiving left and imagining right: Dissociation in neglect. *Cortex*, *36*(3), 401–414. https://doi.org/10.1016/S0010-9452(08)70849-9

Beschin, N., Cocchini, G., Della Sala, S., & Logie, R. (1997). What the eyes perceive, the brain ignores: A case of pure unilateral representational neglect. *Cortex*, *33*, 3–26. https://doi.org/10.1016/S0010-9452(97)80002-0

Bisiach, E., & Luzzatti, C. (1978). Unilateral Neglect of Representational Space. *Cortex*, *14*(1), 129–133. https://doi.org/10.1016/S0010-9452(78)80016-1

Bourlon, C., Chokron, S., Bachoud-Lévi, A.-C., Coubard, O., Bergeras, I., Moulignier, A., Viret, A.-C., & Bartolomeo, P. (2009). [Presentation of an assessment battery for visual mental imagery and visual perception]. *Revue Neurologique*, *165*(12), 1045–1054. https://doi.org/10.1016/j.neurol.2009.04.010

Bourlon, C., Duret, C., Pradat-Diehl, P., Azouvi, P., Loeper-Jény, C., Merat-Blanchard, M., Levy, C., Chokron, S., & Bartolomeo, P. (2011). Vocal response times to real and imagined stimuli in spatial neglect: A group study and single-case report. *Cortex*, *47*(5), 536–546. https://doi.org/10.1016/j.cortex.2010.03.004

Bourlon, C., Oliviero, B., Wattiez, N., Pouget, P., & Bartolomeo, P. (2011). Visual mental imagery: What the head’s eye tells the mind’s eye. *Brain Research*, *1367*, 287–297. https://doi.org/10.1016/j.brainres.2010.10.039

Bourlon, C., Pradat-Diehl, P., Duret, C., Azouvi, P., & Bartolomeo, P. (2008). Seeing and imagining the “same” objects in unilateral neglect. *Neuropsychologia*, *46*(10), 2602–2606. https://doi.org/10.1016/j.neuropsychologia.2008.04.002

Chokron, S., Colliot, P., & Bartolomeo, P. (2004). The role of vision in spatial representation. *Cortex*, *40*(2), 281–290. https://doi.org/10.1016/s0010-9452(08)70123-0

Cristinzio, C., Bourlon, C., Pradat-Diehl, P., Trojano, L., Grossi, D., Chokron, S., & Bartolomeo, P. (2009). Representational neglect in “invisible” drawing from memory. *Cortex*, *45*(3), 313–317. https://doi.org/10.1016/j.cortex.2008.03.013

Damasio, A. R. (1994). *Descartes’ Error: Emotion, Reason, and the Human Brain*. Putnam Publishing.

Farah, M. J. (1988). Is visual imagery really visual? Overlooked evidence from neuropsychology. *Psychol Rev*, *95*(3), 307–317. https://doi.org/10.1037/0033-295x.95.3.307

Goldenberg, G. (1993). The neural basis of mental imagery. *Baillière’s Clinical Neurology*, *2*(2), 265–286.

Goldenberg, G., Mullbacher, W., & Nowak, A. (1995). Imagery without perception—A case study of anosognosia for cortical blindness. *Neuropsychologia*, *33*(11), 1373–1382. https://doi.org/10.1016/0028-3932(95)00070-j

Guariglia, C., Padovani, A., Pantano, P., & Pizzamiglio, L. (1993). Unilateral neglect restricted to visual imagery. *Nature*, *364*, 235–237. https://doi.org/10.1038/364235a0

Hajhajate, D., Kaufmann, B. C., Liu, J., Siuda-Krzywicka, K., & Bartolomeo, P. (2022). The connectional anatomy of visual mental imagery: Evidence from a patient with left occipito-temporal damage. *Brain Structure & Function*, *227*(9), 3075–3083. https://doi.org/10.1007/s00429-022-02505-x

Kosslyn, S. M. (1994). *Image and Brain: The Resolution of the Imagery Debate*. The MIT Press.

Kosslyn, S. M., Thompson, W. L., & Ganis, G. (2006). *The Case for Mental Imagery*. Oxford University Press. http://www.loc.gov/catdir/toc/ecip0513/2005014885.html

Kosslyn, S. M., Thompson, W. L., Kim, I. J., & Alpert, N. M. (1995). Topographical representations of mental images in primary visual cortex. *Nature*, *378*, 496–498. https://doi.org/10.1038/378496a0

Lafer-Sousa, R., Conway, B. R., & Kanwisher, N. G. (2016). Color-Biased Regions of the Ventral Visual Pathway Lie between Face- and Place-Selective Regions in Humans, as in Macaques. *The Journal of Neuroscience*, *36*(5), 1682–1697. https://doi.org/10.1523/jneurosci.3164-15.2016

Liu, J., & Bartolomeo, P. (2023). Probing the unimaginable: The impact of aphantasia on distinct domains of visual mental imagery and visual perception. *Cortex*, *166*, 338–347. https://doi.org/10.1016/j.cortex.2023.06.003

Liu, J., Bayle, D. J., Spagna, A., Sitt, J. D., Bourgeois, A., Lehongre, K., Fernandez-Vidal, S., Adam, C., Lambrecq, V., Navarro, V., Seidel Malkinson, T., & Bartolomeo, P. (2023). Fronto-parietal networks shape human conscious report through attention gain and reorienting. *Communications Biology*, *6*(1), Article 1. https://doi.org/10.1038/s42003-023-05108-2

Liu, J., Spagna, A., & Bartolomeo, P. (2022). Hemispheric asymmetries in visual mental imagery. *Brain Structure & Function*, *227*(2), 697–708. https://doi.org/10.1007/s00429-021-02277-w

Liu, J., Zhan, M., Hajhajate, D., Spagna, A., Dehaene, S., Cohen, L., & Bartolomeo, P. (2023). Ultra-high field fMRI of visual mental imagery in typical imagers and aphantasic individuals. In *bioRxiv* (p. 2023.06.14.544909). https://www.biorxiv.org/content/10.1101/2023.06.14.544909v1

Luzzatti, C., & Davidoff, J. (1994). Impaired retrieval of object-colour knowledge with preserved colour naming. *Neuropsychologia*, *32*(8), 933–950. https://doi.org/10.1016/0028-3932(94)90044-2

Marshall, J., & Halligan, P. W. (2002). Whoever would have imagined it? Bisiach and Luzzatti (1978) on representational neglect in patients IG and NV. In C. Code, C. W. Wallesch, Y. Joanette, & A. Roch Lecours (Eds.), *Classic Cases in Neuropsychology II* (pp. 272–274). Taylor & Francis Books Ltd.

Miceli, G., Fouch, E., Capasso, R., Shelton, J. R., Tomaiuolo, F., & Caramazza, A. (2001). The dissociation of color from form and function knowledge. *Nature Neuroscience*, *4*(6), 662–667. https://doi.org/10.1038/88497

Moro, V., Berlucchi, G., Lerch, J., Tomaiuolo, F., & Aglioti, S. M. (2008). Selective deficit of mental visual imagery with intact primary visual cortex and visual perception. *Cortex*, *44*(2), 109–118. https://doi.org/10.1016/j.cortex.2006.06.004

Pearson, J. (2019). The human imagination: The cognitive neuroscience of visual mental imagery. *Nature Reviews Neuroscience*, *20*(10), 624–634. https://doi.org/10.1038/s41583-019-0202-9

Rode, G., Revol, P., Rossetti, Y., Boisson, D., & Bartolomeo, P. (2007). Looking while imagining: The influence of visual input on representational neglect. *Neurology*, *68*(6), 432–437. https://doi.org/10.1212/01.wnl.0000252936.54063.b0

Rode, G., Rossetti, Y., Perenin, M. T., & Boisson, D. (2004). Geographic information has to be spatialized to be neglected: A representational neglect case. *Cortex*, *40*(2), 391–397. https://doi.org/10.1016/s0010-9452(08)70133-3

Servos, P., & Goodale, M. A. (1995). Preserved visual imagery in visual form agnosia. *Neuropsychologia*, *33*(11), 1383–1394. https://doi.org/10.1016/0028-3932(95)00071-a

Siuda-Krzywicka, K., & Bartolomeo, P. (2020). What Cognitive Neurology Teaches Us about Our Experience of Color. *The Neuroscientist*, *26*(3), 252–265. https://doi.org/10.1177/1073858419882621

Siuda-Krzywicka, K., Witzel, C., Chabani, E., Taga, M., Coste, C., Cools, N., Ferrieux, S., Cohen, L., Seidel Malkinson, T., & Bartolomeo, P. (2019). Color Categorization Independent of Color Naming. *Cell Reports*, *28*(10), 2471-2479.e5. https://doi.org/10.1016/j.celrep.2019.08.003

Siuda-Krzywicka, K., Witzel, C., Taga, M., Delanoe, M., Cohen, L., & Bartolomeo, P. (2020). When colours split from objects: The disconnection of colour perception from colour language and colour knowledge. *Cognitive Neuropsychology*, *37*(5–6), 325–339. https://doi.org/10.1080/02643294.2019.1642861

Spagna, A., Bayle, D. J., Romeo, Z., Seidel-Malkinson, T., Liu, J., Yahia-Cherif, L., Chica, A. B., & Bartolomeo, P. (2022). The cost of attentional reorienting on conscious visual perception: An MEG study. *Cerebral Cortex*, bhac192. https://doi.org/10.1093/cercor/bhac192

Spagna, A., Hajhajate, D., Liu, J., & Bartolomeo, P. (2021). Visual mental imagery engages the left fusiform gyrus, but not the early visual cortex: A meta-analysis of neuroimaging evidence. *Neuroscience & Biobehavioral Reviews*, *122*, 201–217. https://doi.org/10.1016/j.neubiorev.2020.12.029

Stasenko, A., Garcea, F. E., Dombovy, M., & Mahon, B. Z. (2014). When concepts lose their color: A case of object-color knowledge impairment. *Cortex*, *58*, 217–238.

https://doi.org/10.1016/j.cortex.2014.05.013

Zeman, A., Dewar, M., & Della Sala, S. (2015). Lives without imagery – Congenital aphantasia. *Cortex*, *73*, 378–380. https://doi.org/10.1016/j.cortex.2015.05.019