



Color synesthesia. Insight into perception, emotion, and consciousness

Avinoam B. Safran^{a,b} and Nicolae Sanda^{a,c}

Purpose of review

Synesthesia is an extraordinary perceptual phenomenon, in which individuals experience unusual percepts elicited by the activation of an unrelated sensory modality or by a cognitive process. Emotional reactions are commonly associated. The condition prompted philosophical debates on the nature of perception and impacted the course of art history. It recently generated a considerable interest among neuroscientists, but its clinical significance apparently remains undervalued. This review focuses on the recent studies regarding variants of color synesthesia, the commonest form of the condition.

Recent findings

Synesthesia is commonly classified as developmental and acquired. Developmental forms predispose to changes in primary sensory processing and cognitive functions, usually with better performances in certain aspects and worse in others, and to heightened creativity. Acquired forms of synesthesia commonly arise from drug ingestion or neurological disorders, including thalamic lesions and sensory deprivation (e.g., blindness). Cerebral exploration using structural and functional imaging has demonstrated distinct patterns in cortical activation and brain connectivity for controls and synesthetes. Artworks of affected painters are most illustrative of the nature of synesthetic experiences.

Summary

Results of the recent investigations on synesthesia offered a remarkable insight into the mechanisms of perception, emotion and consciousness, and deserve attention both from neuroscientists and from clinicians.

Keywords

cerebral disorders, color, consciousness, emotion, perception, synesthesia, vision

INTRODUCTION

Synesthesia is an extraordinary perceptual phenomenon, in which the world is experienced in unusual ways. In this condition, a particular stimulation in a given sensory modality (e.g., touch) or cognitive process (e.g., computing) automatically triggers additional experiences in one or several other unstimulated domains (e.g., vision, emotion) [1]. An illustrative presentation of the condition would be that of a given person in whom hearing the sound of a trumpet consistently elicits the vision of brightly colored triangles dancing in front of his eyes, in association with a sensation of pressure on his arms, letting him feel uncomfortable to sit still. Stimuli generating additional unusual experiences are termed 'inducers', whereas internally produced synesthetic percepts are termed 'concurrents' [2].

Synesthetic experiences have had over the centuries far-reaching sociocultural implications. They prompted philosophical debates on the nature of perception, consciousness and even talent and creativity, and significantly impacted the course

of art history, notably at the turn of the 20th Century [3–6]. Moreover, favored by the emergence of sophisticated tools for functional brain exploration, they have generated a considerable interest among neuroscientists [6,7]. Clinical significance of synesthesia, however, is still largely undervalued.

Although some synesthetic phenomena express the presence of a disease, developmental synesthesia as a rule is considered an individual cognitive

^aSorbonne Universités, UPMC Univ Paris 06, UMR_S 968, Institut de la Vision, INSERM, U968, CNRS, UMR_7210, Paris, France, ^bDepartment of Clinical Neurosciences, Geneva University School of Medicine, Geneva, Switzerland and ^cNeurology Department, Hôpital Foch, Suresnes, Paris, France

Correspondence to Avinoam B. Safran, MD, 17 rue Moreau, Paris, F-75012, France. E-mail: avinoam.safran@unige.ch

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KEY POINTS

- Persons presenting with synesthesia commonly avoid mentioning their unusual percepts and even tend to close on themselves in psychological distress.
- Developmental synesthesia predisposes to changes in primary sensory processing and cognitive functions, and heightened creativity.
- Affected individuals demonstrate distinct patterns in cerebral activation and connectivity, compared with nonsynesthetes.
- Acquired forms of synesthesia are commonly related to drug ingestion or neurological conditions.

variant in the normal population [8]. Unfortunately, the astonishing features of these percepts have too often led the entourage of affected persons, including physicians, to wrongfully consider them as confabulators, drug users, or schizophrenics [7]. In this regard, the following history reported by Vincent Van Gogh is representative. While in 1885 the painter was taking piano lessons, his teacher noticed that he was continually relating the sounds of the piano keys with specific colors; considering then that his pupil was insane, the teacher sent him away [9]. It is therefore understandable that synesthetes (i.e., persons affected by synesthesia) commonly avoid mentioning their percepts and even tend to close on themselves in psychological distress [10–12]. For that very reason, scientific studies probably underestimate synesthesia prevalence in the general population.

SYNESTHESIA VARIANTS

Synesthesia is commonly classified as developmental and acquired. Developmental synesthesia appears to be the most frequent type of this condition, with a 4.4% estimated prevalence rate [13]. It can run in families and demonstrate Mendelian transmission [14]. Different forms of synesthesia can be observed in the same person or in the same family [15]. The condition is occasionally associated with autism spectrum disorders, like Asperger syndrome [16].

The following criteria have been proposed to help establishing a diagnosis of developmental synesthesia: induced percepts should be elicited by a specific stimulus, they should be automatically generated, and typically have percept-like qualities [8,17,18]. Usually, pairings of inducers and concurrents are specific (i.e., a particular stimulus consistently triggers the same synesthetic percept). They

tend to be stable over time in a given individual, although this has recently been challenged by the finding that synesthetic ability can disappear over time [19[■]].

Acquired forms of synesthesia have also been reported, essentially associated with neurologic disorders or following psychotropic drug ingestion [20–23]. In contrast to its developmental counterpart, acquired synesthesia does not demonstrate either idiosyncrasy or automaticity or stability [3,24[■]].

So far, over 60 types of synesthetic phenomena have been described. The apparently most common form (with a 64.4% prevalence among synesthetes) is grapheme–color synesthesia, in which achromatic letters or digits automatically trigger an idiosyncratic color perceptual experience (e.g., the letter ‘m’ induces blue color percepts) [25,26] (Fig. 1 [27]). The second most prevalent form is time unit (e.g., Monday, January)–color synesthesia (22.4%), followed by musical sound–color synesthesia (18.50%) [26,28] (Figs 2 and 3 [29,30]). Inducers and concurrents also include smells, tastes, temperatures, personalities and emotions [26], and can be multiple during a single synesthetic experience. Thus, percepts induced by grapheme–color synesthesia are occasionally accompanied by shape, texture, movement features, and even nonvisual percepts such as smells and tastes, particularly emotions [31,32]. Synesthetic colors generated in grapheme–color synesthesia are determined by systematic rules rather than randomly occurring, and based on the psycholinguistic mechanisms of language processing. The same occurs with both Latin characters and Chinese ideograms [33,34[■]].

An additional type of colored synesthetic experience was recently described and termed ‘swimming-style color synesthesia’. It is characterized by the generation of specific colored percepts upon conceptual representation of swimming in a particular style (i.e., breast, backstroke, crawl, and butterfly) [35,36]. This phenomenon could be triggered by either presenting a picture of a swimming individual or asking the tested individual to think about a given swimming style. It was speculated that this synesthetic type was caused by overactivity in the mirror neuron system responding to the specific representation [37].

Synesthetic experiences are labeled ‘lower’ when triggered by elementary perceptual processes (e.g., texture) or ‘higher’ when involving a higher cognitive process (e.g., semantic, computing) [7,38,39]. Synesthetes who experience the atypical percepts in an internal space (‘in the mind’s eye’, as they sometimes describe it) have been categorized into ‘associators’, whereas those for whom the additional,

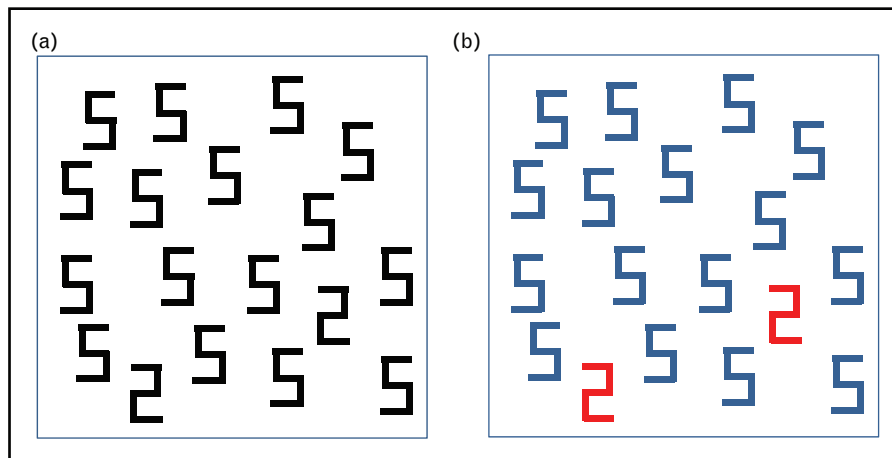


FIGURE 1. Visual segregation test demonstrating improved digit identification performances by grapheme–color synesthetes. (a) Pattern presented to the tested individuals and (b) same pattern as perceived by a grapheme–color synesthete. To identify digits ‘2’, a person with regular visual perception must perform a systematic search; in contrast, for a grapheme–color synesthete, who links a specific color with a given number, digits ‘2’ instantly pop-out. Adapted with permission [27].

atypical percept appears to be ‘out there’, overlaying the actual, external surrounding, are designated as ‘projectors’ [40,41].

PAINTERS’ COMPREHENSION OF SYNESTHESIA

Painters commonly demonstrate unique skills in the observation of visual phenomena, in which

depiction offers an invaluable source of information for neuroscientists investigating visual function in health and disease [42–46]. Regarding our understanding of synesthesia, painters’ contribution is particularly precious. Among this population, the prevalence of synesthesia was found higher than in general population; in addition, their percepts are frequently represented in their artworks [47]. Indeed, synesthete prevalence among fine art students was estimated to be 23% [48]. Among art students, prevalence of grapheme–color synesthesia alone was reported to be 7%, compared to 2% in controls [49].

Interestingly, synesthetes’ personality profile favors their involvement in creative, artistic activities [50]. Recently evaluated by a structured measure of personality (the ‘Big Five Inventory’) and by

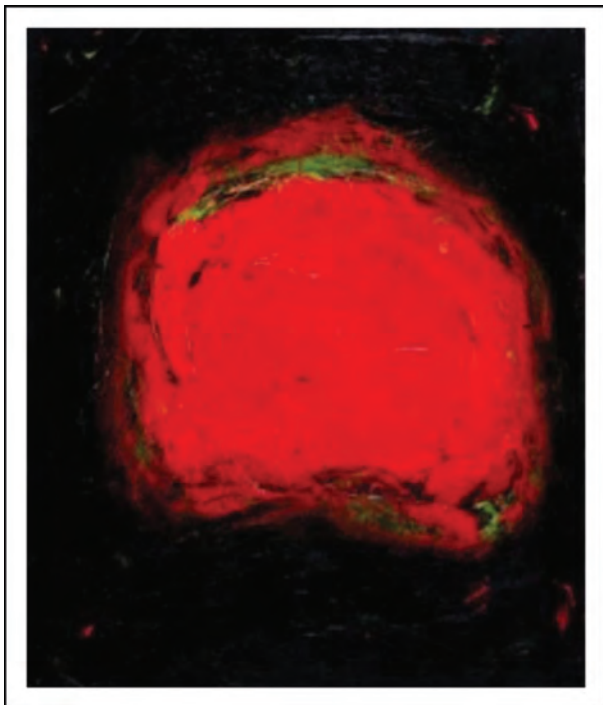


FIGURE 2. ‘Vision’ 1996, by Carol Steen, private collection, represents a synesthetic visual experience elicited in this synesthetic painter by a needle puncture during an acupuncture session [29]. Reproduced with permission.



FIGURE 3. ‘Kondo’s Trumpet’ 2010, by Carol Steen, private collection, depicts the synesthetic visual experience elicited by the timbre of that trumpet [30]. Reproduced with permission.

questionnaires assessing empathy, synesthetes exhibited higher levels of ‘Openness to Experience’, considered to be related to imagination and artistic tendencies, and higher levels of ‘Fantasizing’, conceptually related to ‘Openness’ [51[¶]]. Moreover, grapheme–color synesthetes show a distinct cognitive style, with a preference for processing information in both verbal and vivid imagery styles [52[¶]].

The peculiar world perception decisively impacted the artistic work of numerous ‘synesthetic’ artists. Thus, Kandinsky’s nonfigurative paintings and theory of synesthesia [53], prompted by his experience of extraordinary visions of lines and colors elicited by the sound of musical instruments, paved the way to abstract art and thus marked a turning point in history of art [47]. A recent analysis of Kandinsky’s works using the Implicit Association Test found no implicit association between the original color–form combinations, and authors concluded that these are probably not a universal property of the visual system [44].

Most informative indications on the character of percepts commonly observed by synesthetic painters, as well as on the compulsive manner they depict their visions, were provided by Carol Steen, a remarkable synesthetic painter [54]. She emphasized that synesthetes’ internal world differs tremendously from what is commonly perceived by others. For instance, colors can be perceived intensely bright, ‘similar to sunlight streaming through a stained glass window’. Noteworthy, she felt that the ‘overwhelming beauty of what she has seen’ powerfully compelled her to capture and reproduce her visions, and that ‘urgency to paint needed to be expressed’. To depict the brightness of colors perceived, synesthetic painters reportedly often apply with speed, pure, unmixed oil paint, or watercolor straight from the tube. Faithfully representing their perceptions may require breaking some long-standing rules, a feature that – as underlined by Carol Steen – characterizes modern art. The artist also specified that her visions were never representational nor figurative. This is apparently typical of many synesthetes’ experiences, and probably explains why synesthetic artwork commonly looks abstract, even though it is a ‘realistic’ depiction of the artist’s perceptions [54].

EMOTIONAL DIMENSION OF SYNESTHESIA

Emotional reactions play a prominent role in synesthetic processes. They are commonly experienced in such conditions [32,55], acting as either inducer, concurrent, or modulator [32,56]. A conflict between the actual color of a stimulus and synesthetically induced percepts can generate discomfort, whereas

‘pleasantness’ is experienced when synesthetic and actual stimulus features match. Some synesthetes indicate that all disagreeable events generate same color, specific for the given individual. Saturation of evoked colors is susceptible to be altered by mood [32]. In some personality–color type of synesthesia, viewing known faces elicits emotionally mediated color percepts, presenting either as colored faces or colored auras around heads [1,32,57] (Figs 4 and 5 [58]), conceivably as a result of cross-activation between right, face recognition area and neighboring V4 color cortex [7,59]. In this regard, the following delightful dedication by Julia Simner, a prominent expert in synesthesia, is illustrative: ‘For my two children: the blue one (Indigo) and the brown one (Tommy Bruno)’ [60]. In the so-called ‘ordinal linguistic personification’ synesthesia, letters have emotional valences, as well as a sex and personality [61,62]. Sexual arousal also triggers synesthetic experiences in some 2% of individuals [26]. These perceptual phenomena mainly consist of colored shapes, less commonly of flavors, smells, sounds, or temperatures, and are associated with a higher degree of trance and loss of environmental boundaries [63].

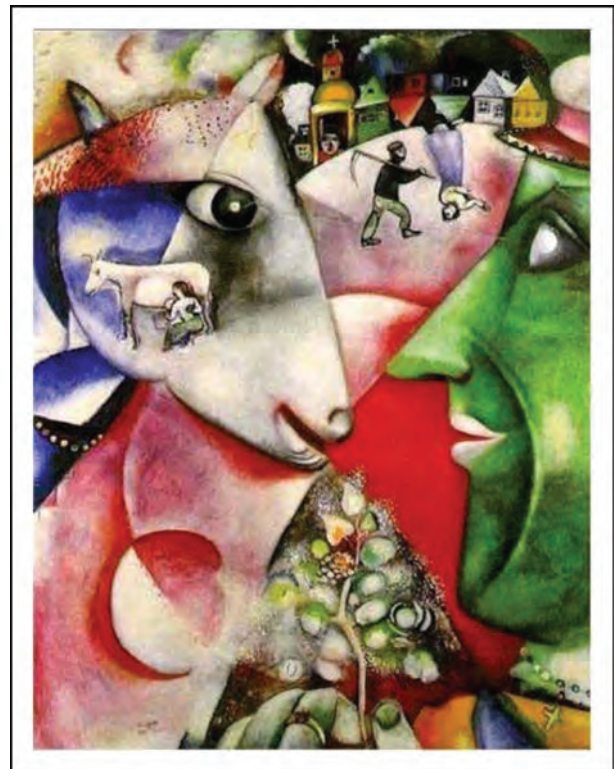


FIGURE 4. ‘I and the Village’ 1911, by Marc Chagall. Museum of Modern Art, New York, USA. Reproduced with permission, © Adagp, Paris 2014. Over decades, Chagall repeatedly depicted using intense green or blue colors, the faces of central characters in his paintings [58]. This most probably reflected a variant of personality–color synesthesia.



FIGURE 5. 'Half-Past Three' ('The Poet') 1911, by Marc Chagall. Philadelphia Museum of Art, The Louise and Walter Arensberg Collection, Philadelphia, PA, USA. Reproduced with permission, © Adagp, Paris 2014. For comments, see the legend of Fig. 4.

Cerebral structures processing emotion are altered in developmental synesthetes. MRI exploration of associator grapheme–color synesthetes recently brought further evidence of structural changes in emotional areas both at cortical and at subcortical levels [64[■]]. Acquired cerebral disorders are also susceptible to cause emotional synesthetic percepts. Thus, a patient who had sustained a post-erolateral thalamus hemorrhage [24[■]] experienced blue photisms, intense extracorporeal sensation, and 'orgasmic' ecstasy when hearing brass instruments, or severe disgust sensations when reading words printed in blue characters. Occurrence, expression, and the underlying mechanisms of affect-related forms of synesthesia have recently been reconsidered [56].

IMPACT OF SYNESTHESIA ON COGNITIVE FUNCTIONS

Synesthetic experiences impact the cognitive functions to a larger extent than believed in the past [65,66[■],67,68]. Constitutional synesthesia

predisposes to better performances in certain aspects and worse in others. Although having better color perception compared with nonsynesthetes [69,70], synesthetes present impaired motion [66[■],67] and speech perception [71]. Speech perception deficit could be a consequence of the impaired motion perception, namely the biological movement of lips or of a much wider deficit in multisensory integration [71]. In grapheme–color and tone–color synesthetes, increased gray matter volume in the left posterior fusiform gyrus and decreased gray matter volume of the anterior part of the same gyrus and in the left MT/V5 support these hypotheses [72]. Improved perception can occur within both inducing stimulus and concurrent domains [68]. Memory was also found enhanced when using synesthetic percepts [25,73].

Improved performances depend partly on preconscious mechanisms, operating early in sensory processing [74]. Thus, a recent investigation using pictures containing hidden letters found that grapheme–color projectors recognized the letters faster than nonsynesthetes; interestingly, tested individuals noted that concurrent colors were generated before conscious letter recognition [75[■]]. Grapheme–color synesthesia even allows computing via synesthetically perceived colors [68] and as expected, emotional experience modulates synesthetes' performances [55].

CEREBRAL DISORDERS CAUSING SYNESTHESIA

Acquired forms of synesthesia have been related to a variety of neurological conditions, including migraine [76,77], multiple sclerosis – radiologically isolated syndrome [34[■]], posthypnotic suggestion [78], and drug ingestion [20,79]. In recent years, secondary synesthesia has been reported following thalamic stroke [24[■],80–83]: two of these affected individuals experienced colored synesthetic percepts [24[■],83]. Thalamic insult may induce large-scale reorganization of the brain, modify the balance between excitatory and inhibitory connections in high-order visual areas, and favor the development of synesthesia [80].

Sensory deprivation favors the occurrence of synesthetic phenomena. With blind people, non-visual stimuli tend to elicit various percepts in the suppressed sensory modality, including colored photisms [84,85] presumably by cross-modal activation of the deafferented cortex [86]. Sound-induced photisms in visually affected people are a well recognized phenomenon [87]. Six late-blind individuals were recently reported experiencing colored phenomena when hearing or thinking

about letters, numbers, and time-related terms [88,89]. In one of these individuals, touching Braille characters induced colored photisms. A patient of ours, blinded by bilateral arteritic anterior ischemic optic neuropathy, reported perceiving colored photisms when brushing his teeth or hearing a hand clap (personal observation). We also recently observed an unusual case of a late-blind individual suffering from retinitis pigmentosa who volunteered consistently 'seeing' his limbs when moving them, a phenomenon presumably related to cross-modal activation of his visual cortex by proprioceptive inputs [90].

Brain lesions disrupting canonical networks and sensory input to associative areas are also susceptible to induce synesthetic-like hallucinatory syndromes. A right monophthalm patient with right parosmia reported intricate visual and olfactory hallucinations following a right occipitotemporal stroke [91]. The patient described seeing people with strong odors. The presumed mechanism of these hallucinations was the disinhibition of the connections from the visual association areas to perirhinal and parahippocampal gyri [92].

ARTIFICIALLY ELICITED SYNESTHESIA

Sensory substitution devices (SSDs) have been developed to provide blind individuals with information on their visual surrounding. They convey visual information through another sensory modality, like audition [93]. Visual-to-auditory SSDs proceed by online translation of camera-captured views into sounds, which represent the visual features of the scene [93,94]. Users of such devices commonly claim to 'see' the objects figured by sounds, and therefore sensory substitution has been considered a kind of synthetic synesthesia [93]. Interestingly, functional magnetic resonance imaging (fMRI) investigations using a visual-to-auditory SSD, both in blindfolded healthy individuals [95] and in congenitally blind individuals [96], showed activation of visual areas. Whether – and to what extent – SSD users also perceive the auditory stimulus as a sound is debated [97,98].

Sensory substitution, however, differs in some respect from the naturally occurring synesthesia. Indeed, intended to reliably figure the visual surrounding, percepts elicited by SSDs are elaborated, whereas regular synesthetic phenomena exhibit essentially idiosyncratic features [8]. Further, in contrast to SSD-provoked synesthetic experiences, in developmental synesthesia, inducers do not conform to sensorimotor contingencies of the concurrent modality [98].

NEURAL FOUNDATIONS OF SYNESTHESIA

Assumptions have been made on the mechanisms underlying synesthesia, including hyperconnectivity between cortical areas [99], reduced level of feedback from inhibitory cerebral structures [2], learned association in early life [100], and a normal perceptual mechanism incompletely suppressed in synesthetes [17]. Neurocognitive models have been elaborated [101–105].

In recent years, brain-imaging studies brought further evidence that synesthetes connect more inside and between sensory regions and less with remote areas, especially the frontal cortex. Indeed, these individuals exhibit increased intranetwork connectivity in medial visual, auditory and intraparietal networks, and internetworks connectivity between the medial and lateral visual networks, the right frontoparietal network and between the lateral visual and auditory networks. In contrast, nonsynesthetes have more intranetwork connections within frontoparietal network [106]. When presented with inducers, synesthetes exhibit a clustering pattern of activated brain areas uniting more visual regions, whereas nonsynesthetes activate particularly frontal and parietal regions [107] (Fig. 6).

Involvement of the bottom-up and top-down mechanisms has further been considered [105,108–111]. The bottom-up model stipulates that the concurrent representation is prompted by the inducer representation via overrepresented and overactive horizontal connections, whereas the top-down model proposes that the inducer stimulates the concurrent percept via an input from a convergent, higher order integrator [2].

Using dynamic causal modeling, Van Leeuwen *et al.* [106] have shown that projectors exhibited effective connectivity patterns involving a bottom-up mechanism, whereas associators used a top-down mechanism. However, a recent electroencephalographic (EEG) study found evidence favoring the top-down disinhibited feedback model as the core of the synesthetic phenomenon [112]. Reduction of long-range couplings in the theta frequency band could facilitate the top-down feedback. An fMRI study demonstrated that, in contrast with projectors, associators' synesthetic experience was related to areas linked to memory processes, including hippocampus and parahippocampal gyrus [113,114].

THALAMUS AND DEVELOPMENTAL SYNESTHESIA

It was suggested that congenital alterations in thalamic circuitry might be responsible for

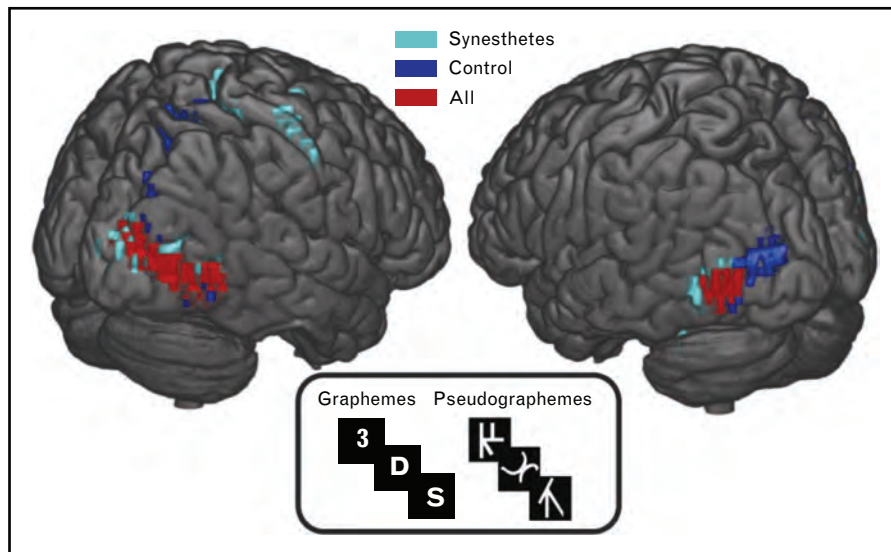


FIGURE 6. Cerebral activation revealing distinct activity patterns for controls and synesthetes during grapheme and pseudo-grapheme presentation. Synesthetes demonstrate the most significant activity in the bilateral posterior inferior temporal gyri. Reproduced with permission [107**].

atypical cortical morphology and connections, found with different synesthetic phenotypes [64**,115]. Cytoarchitectonic maturation of the primary sensory areas and the development of their specific connections are highly dependent on the thalamic input [116]. Enucleation in prenatal macaque drastically alters the equivalents of V1 and V2 visual cortices, and induces rich non-canonical connections with somatosensory, auditory, and frontal areas [117], resembling transient fetal connections [118]. Thus, the visual cortex ends up treating other types of information. Likewise, congenitally blind humans exhibit occipital cortex activation following auditory or somatosensory stimulation [96*]. It is therefore conceivable that in developmental synesthesia, congenitally anomalous sensory input leads to abnormal synaptic pruning and differences in brain connectivity. In grapheme–color synesthetes, low white matter densities in pulvinar, medial and lateral ventral posterior nuclei, and low fractional anisotropy in medial dorsal and ventral anterior nuclei suggest a constitutional disconnection and hypoconnection between thalamus and cerebral cortex [64**]. The concerned white matter tracts project to the left prefrontal cortex and bilateral temporal and posterior parietal cortex, regions that in synesthetes are distinct both in structure and function. Secondary synesthesia after thalamic stroke also support the involvement of thalamic output in synesthetic phenomena [24*,80–83].

CONCLUSION

Over the last few years, substantial advances have been made in the understanding of synesthesia, and hence more globally in the comprehension of perception and consciousness. Fortunately, awareness of this condition in the societal environment also significantly improved, finally allowing synesthetes to feel relieved by the so badly needed recognition of their particular situation. In a near future, in addition to the expected deepening of the explorations undertaken, elaborating a more comprehensive definition of synesthesia would be welcomed. Currently used criteria are rather restrictive for a condition that is quite polymorphic in nature. This process, however, is customary in the history of medicine, which consists of initially establishing a restricted definition to encapsulate the core of the condition and then broadening it, taking into account the numerous subtle presentations encountered.

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Conflicts of interest

There are no conflicts of interest.

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