

SYNAESTHESIA: CROSS ACTIVATIONS, HIGH INTERCONNECTIVITY, AND A PARIETAL HUB

Abstract

This review summarizes the most recent studies on synaesthesia, particularly studies on grapheme-colour synaesthesia, time-space synaesthesia, and coloured-hearing synaesthesia. Based on behavioural as well as neuroimaging studies, there is emerging evidence that synaesthesia is not only caused by the cross activation of two sensory areas but that it may require additional binding processes, which are assumed to take place in the parietal lobe. However, divergent results exist with respect to the lateralization of this effect, i.e. whether it is the left or right parietal lobe most responsible. Studies also indicate that attention modulates the synaesthetic experience. Furthermore, it has been shown that synaesthetes demonstrate a higher level of connectivity, thus supporting the view of a genetic pre-disposition of synaesthesia.

Keywords

• Synaesthesia • Grapheme-colour synaesthesia • Time-space synaesthesia • Coloured-hearing synaesthesia
• Cross-activation theory • Two-stage model • Functional imaging

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What is synaesthesia?

Synaesthesia describes a rare condition in which a particular sensory stimulus involuntarily evokes an additional, concurrent sensation, which may or may not be in the same sensory modality. The term "synaesthesia" is a combination of the Greek words οὐν (syn) = together/ joined, and of the Greek word αἴσθησις (aisthēsis), which means perceptions. In other words, a synaesthete perceives two joint and concurrent perceptions, where only one is caused by a real, external stimulus, while the other is an internally-evoked synaesthetic experience without any direct external cause. The cross-link between the real stimulus and the synaesthetic experience is always the same, for example: seeing the letter A always evokes the synaesthetic experience of seeing the letter in yellow, independent of the real printed colour. In order to understand the processes behind synaesthesia, one has to bear in mind that perception goes beyond the simple processing of sensory information. In general, other cognitive processes involving

experience and expectancy, and additionally, conflicting and interfering information, always influence perception. This is the same for synaesthetes and non-synaesthetes. However, the important difference between synaesthesia and, for example, a learned association is that a synaesthetic experience cannot be trained and thus the concurrent synaesthetic experience is involuntary and automatically generated. This cross-sensational perception is highly consistent throughout the lifespan, as it remains unchanged from early childhood. It is also important to note that synaesthesia is by no means a psychological, psychiatric, or neurological 'illness' [1,2]. The origin of synaesthesia is still unknown and the prevalence of synaesthesia within the normal population is estimated to be around 4% [3]. Furthermore, synaesthesia is not confined to just one form or type [4]. It comes in many different and unique forms, with only a very small overlap in its appearance from one individual to another. This may also help to explain why, only recently, a more standardized test battery for synaesthesia has been developed [5]. There are some types

of synaesthesia that are reported to be more frequent than others, such as grapheme-colour, time-space, and coloured-hearing synaesthesia. Furthermore, there is evidence that synaesthesia runs in families, although this does not necessarily imply the exact same form of synaesthesia between relatives [6], and it may also skip one generation [7]. This points towards a genetic pre-disposition to synaesthesia [8], although the mechanisms are not yet fully understood. Also, there are cases of monozygotic twins, where only one twin is became a synaesthet [9,10].

The following section of this review is divided into two parts. The first part will summarize the most recent research on synaesthesia by focusing on the three most frequent types of synaesthesia; namely, grapheme-colour synaesthesia, time-space synaesthesia, and coloured-hearing synaesthesia. The second part will discuss the most recent theories and models of synaesthesia, derived in particular from neuroimaging studies, which point to some commonality across individuals and even across different types of synaesthesia. With

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the use of advanced neuroscience methods, like functional magnetic resonance imaging (fMRI) and transcranial magnetic stimulation (TMS), it has become possible to investigate not only neuronal responses, but also neural networks and to perturb these networks with TMS. Combined with other methods, such as behavioural data, eye-tracking data, and diffusion tensor imaging (DTI, for investigating fiber connections), the number of publications focusing on synesthesia has seen a remarkable increase over the last few years, and a more consistent picture of the neuronal and neurobiological mechanisms of synesthesia has emerged.

Grapheme-colour synesthesia

One of the most studied phenomena, out of the pool of different types of synesthesia is the grapheme-colour synesthesia [7,11-17]. In this form of synesthesia, a synesthete perceives every single letter in a different colour (i.e. the letter A as always perceived in yellow) (see Figure 1).

This colour association is very consistent and reliable, even when repeatedly tested after long intervals [7]. Among these synesthetes, it is also a common observation that entire words tend to generate a colour experience when read. However, where it was first assumed that this word colouring is dominated by the first letter of the word, for example, all words starting with 'A' are yellow, there is some evidence that – at least for real words – the first stressed syllable dominates the colour of the word [18]. Although there is significant inter-individual variability in which

colour synesthetes perceive different letters and words, there is, however, a reasonably high probability that a synesthete sees the letter 'D' in brown, the letter 'R' in red, or the letter 'Y' in yellow [2]. Furthermore, Brang and colleagues have shown that similarly shaped letters also induce similar colours [19]. This is seen as evidence for the cascaded cross-tuning (CCT) model of synesthesia [20], which suggests an interaction between colour and form at an early perceptual stage. However, there is on-going discussion on how a synesthete experiences the colour. There appears to be a differentiation into synesthetes who project the synesthetic colour onto the letter (*projectors*), i.e. they see the colour in the external space, and others that associate the letter with a colour by seeing the colour with their "mind's eye" (*associators*) [21, 22].

In recent years, several studies have attempted to investigate whether synesthesia is primarily a perceptual or conceptual phenomenon. In these studies, grapheme-colour synesthetes were tested with a variety of different cognitive tasks, probing particular aspects of visual attention. These tests were especially designed to generate either an advantage for synesthetes against control subject (through a 'synesthetic pop-out' effect), or interference conditions that generate conflict in synesthetes only. In the first type of study, synesthetes performed detection tasks, where target letters have to be detected among distractors, e.g. a "2" among "5"s [23], or shapes composed of certain letters embedded in a background of distracting letters [7]. Overall, all studies revealed better performances of synesthetes, with faster reactions and fewer errors, thus performing like in a "pop-out" search. However, synesthetes perform worse than controls when control subjects perform the tasks with differentially coloured targets, such like a synesthete is supposed to perceive the task, or when the background is coloured in the same colour as the synesthetic colour of the target [17]. Another aspect to consider is visual attention. Palmeri observed that the perceived synesthetic colour changes, when synesthetes are changing their focus of attention in a local-global task, for example, when looking at a "5", composed

out of "2"s [23]. Laeng has shown that when a synesthete performs a target detection task, the performance is only superior over non-synesthetes for targets within an visual angle of about 10 degrees from fixation, thus indicating that the observed pop-out effect is restricted to the attentional focus [24].

In other studies, Stroop-like interference effects were investigated where only synesthetes experienced conflicting perceptions. In the classical Stroop task, words for colours are written either in a congruent colour, such as the word 'blue' written in blue ink, or in an incongruent colour, like the word 'blue' written in green ink. The typical finding is that when subjects are asked to report the ink colour and not to read the word, a conflicting situation occurs when the ink colour is different from the meaning of the word and thus creates a delayed response and higher error rates. In this respect, synesthetes experience the same conflicting situation when presented with single letters. Therefore, a single-letter Stroop task is an often-used task for investigating different effects between synesthetes and non-synesthetes. One question that has often been addressed in recent research was the perceptual nature of synesthesia. To try to answer this question studies used interference tasks in combination with direct or indirect measures of brain responses. Paulsen and Laeng directly assessed visual experiences by measuring the pupillary response to Stroop-like stimuli [14]. They found that when synesthetes saw incongruently coloured single-letters, this caused an automatic response of the pupils to dilate more than when they viewed congruently coloured single-letters, which could be taken as direct evidence of the perceptual nature of synesthesia.

A different approach was used by Meier and Rothen (2007). They developed a startle response paradigm, where participants were conditioned to a specific colour. However, while non-synesthetes demonstrated a startle response only for the conditioned colour, synesthetes also developed the same startle response to the graphemes, inducing the conditioned colour. This was taken as evidence that the

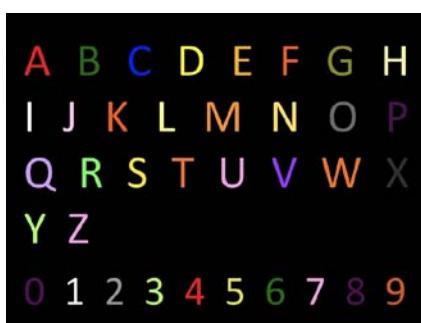


Figure 1. Alphanumeric symbols as coloured by grapheme-colour synesthete.

conditioned response was also generalized to the synaesthetic colour [25].

Using neuroimaging, such as fMRI or magneto-encephalography (MEG), recent studies have consistently confirmed the view of the perceptual nature of synaesthesia by showing differential effects between synaesthetes and non-synaesthetes, particularly in colour processing areas, such as V4 [13,15,20,26,27]. These results are further supported by reports, demonstrating increased grey-matter volume in the right fusiform gyrus and left intraparietal sulcus [28]. In order to investigate the perceptual nature of synaesthesia, Specht and Laeng (2011) used an independent component analysis (ICA) approach in order to separate the networks for visual perception from higher cognitive processes. Comparing non-synaesthetes and synaesthetes, performing an ordinary Stroop task and a single-letter Stroop-like task, revealed an interaction within V4 only for the component that reflected the perceptual network. Thus, it was concluded that the often observed increased V4 involvement in synaesthetes reflects differential perceptual processing [15]. This perceptual nature of synaesthesia was confirmed in an fMRI study using colour distance as the varying parameter [13]. The colour distance measures the Euclidian distance in the RGB colour space between the synaesthetic experienced colour and the ink colour. The authors demonstrated that the activation within colour processing areas, such as V4, varied with the colour distance (i.e. the neuronal activation increased as the displayed colour became dissimilar to the synaesthetic one). However, this occurred only when the synaesthetes focused their attention onto the synaesthetic colour [13]. Additionally, measures of structural connectivity revealed an increased connectivity, as measured with DTI in the superior frontal, and, again, left parietal and right temporal lobes [16]. Furthermore, the same authors also demonstrated that there were differences in the connectivity, grey matter density, as well as activation pattern between associator synaesthetes and projector synaesthetes [16,22]. While sharing some common mechanisms in the parietal lobe, projector synaesthetes showed particularly stronger activations, increased connectivity, and grey matter density, in sensory areas as well

as in the frontal lobe. Associator synaesthetes activated more medial temporal areas, i.e. hippocampus and the parahippocampal gyrus, where increased grey matter was also found [22].

Time-space synaesthesia

A time-space synaesthesia is another frequent form of synaesthesia. These synaesthetes perceive time units as spatial forms (i.e. the days of the week arranged on a circle, years as columns, etc.) with specific localisation of the respective subunits (i.e. a Monday is always on a circle at the bottom to the left) (see Figure 2). However, in contrast to all other cases of synaesthesia, this is a form of synaesthesia not triggered by an external sensory stimulation but rather by some semantic information, usually a unit of time, for example, as a day of the week, a specific year, or a month of the year, etc. [29-35]. Similarly to the case of grapheme-colour synaesthesia, there are two forms of synaesthesia described, where a synaesthete perceives the time information as spatial forms, either in the external space or by seeing it with the "mind's eye" [32]. The

interesting aspect of this type of synaesthesia is that these synaesthetes are clearly benefiting from this gift, as they perform superiorly in temporal and visuo-spatial tests [31,32]. The self reported day-by-day advantage is that these synaesthetes organise and memorise schedules, and appointments, both as semantic as well as spatial information.

One way of investigating the nature of time-space synaesthesia is by using spatial cueing paradigms, where a month of the year directs attention to a specific location, which might be the valid or invalid location for the following target [33]. A recent event-related potential (ERP) study, using a similar cueing paradigm, demonstrated not only an effect in particular on the P3b component, but also that names of months were more efficient for directing spatial attention than arrows or direction words, such as "left" [36].

A different way of investigating time-space synaesthesia is by the use of the SNARC effect (Spatial Numerical Association of Response Codes). The SNARC effect was originally investigated with respect to number processing, where it is a common finding that

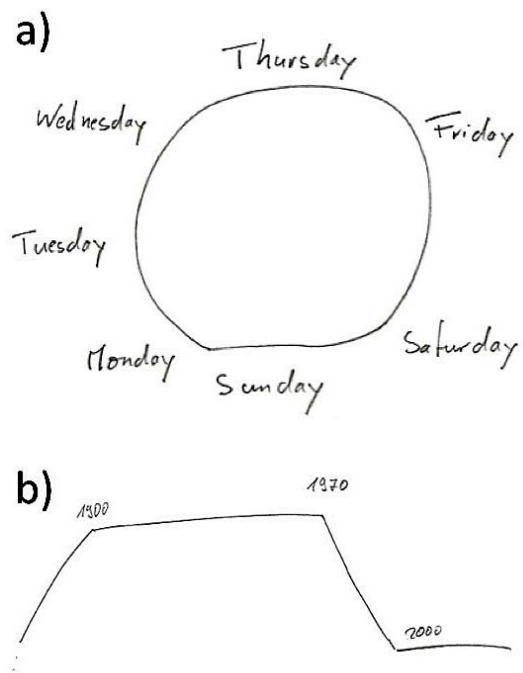


Figure 2. (a) Time-space configuration for days of the week and (b) time-line of the years as drawn by a time-space synaesthete.

subjects respond faster to lower numbers with their left hand, and faster to higher numbers with their right hand. This is often taken as support for the notion that number magnitudes are represented along a mental number line [37,38]. However, the same effect can be reproduced in synaesthetes by using the months of the year instead, which are perceived to be either to the left or to the right, thus showing the same hand preference (i.e. shorter response times with the left hand, to those months which are “seen” to the left, and the same for the right hand, respectively) [35,39]. However, it remains an open question as to whether this spatial representation of numbers, assumed to be present also in non-synaesthetes, and the time-space synaesthesia share the same neuronal origin [39].

Coloured-hearing synaesthesia

Another frequent type of synaesthesia is coloured-hearing synaesthesia, which may also be the most common form of synaesthesia [40]. While current research predominantly focuses on grapheme-colour synaesthesia, coloured-hearing synaesthesia is a type of synaesthesia that attracted the interest of researchers first, with reports dating back more than 200 years [41]. A coloured-hearing synaesthete perceives either tones and/or tone-intervals as being in a specific colour [42], or a spoken utterance causes a colour percept [43, 44]. Similar to grapheme-colour synaesthetes, coloured-hearing synaesthesia activates brain areas for visual processing, such as V4, immediately after the auditory perception, indicating an automatic linking of sounds and colours [43]. Based on this, Paulesu, as well as Nunn, suggested that such cross-modal activation occurs for sensory areas that are anatomically close to each other (see also [50]), and that a visual percept could also be generated by higher-visual areas alone, without the involvement of the primary visual cortex [44, 45]. In accordance are the observations of coloured synaesthesia in the blind, triggered through heard words, touching Braille characters, or thinking about letters [46]. However, Steven studied only late-blind subjects who had retained such synaesthetic colour perceptions.

Besides an involvement of higher visual areas during the auditory perception of tones, vowels, or words, imaging studies consistently report a contribution from parietal areas, although the localisation varies between studies [43-45,47]. Jancke and Langer have made a strong argument about the parietal involvement through their network analysis, which revealed that the left parietal lobe acts as a hub with strong interconnections with other brain areas, in particular areas for processing sensory information; meanwhile, this degree of interconnection is absent in non-synaesthetes.

Neurobiology of Synaesthesia

In recent years, research has focused predominantly on grapheme-colour synaesthesia. Based on these results, several models were developed in attempts to explain the observed effects. There is now converging evidence from many studies, on a variety of synaesthesia, that the involved sensory areas for processing the real and synaesthetic information are adjacent to each other. This is particularly striking for grapheme-colour synaesthesia, since the areas relevant for colour-processing (V4/V8), and the visual word form area [48] relevant for reading, are side-by-side [27,49,50]. Based on this evidence, Ramachandran and Hubbard formulated their cross-activation theory [50,51]. The reason for this cross activation, however, remains unclear. One assumption is that there is a higher level of connectivity between these adjacent areas, due to a perturbed pruning of neuronal connections during childhood, which leaves a higher degree of inter-regional connectivity in synaesthetes compared with non-synaesthetes [52]. It is assumed that infants are initially synaesthetes [53], but lose this condition through refinement of neuronal connections, i.e. pruning, and thus reduce the degree of connectivity. Support for this notion of an altered developmental aspect comes from the observation that synaesthesia runs in families, which points towards a genetic pre-disposition to synaesthesia [8]. Interestingly, there is also a higher incidence of “*Mitempfindung*” in synaesthetes (40% synaesthetes, 10% non-synaesthetes). This is a condition where a

tactile stimulation of one part of the body causes a simultaneous sensation at another location, which could be taken as further evidence for a higher degree of intra-regional connectivity [54]. However, although there is strong and increasing evidence for such a higher degree of connectivity, the causality for this still remains unclear (i.e. whether a higher degree of connectivity causes synaesthesia, or whether it emerges as a consequence of synaesthesia). Therefore, current research is increasingly focusing on aspects of inter-regional connectivity. Several methods are being utilised for this research and include: DTI for detecting anatomical connections; network model approaches such as dynamic causal modelling (DCM) [55] or graph-theoretical approaches [56]; multi-modal integration, such as combined EEG and functional imaging; and measures of neurotransmitter concentrations through MR spectroscopy (MRS). The latter technique is especially of interest as MRS allows the measurement of the concentration of the excitatory neurotransmitter, glutamate, and the inhibitory neurotransmitter, GABA, in a predefined area. This may help identify an inhibitory mechanism, which is the key mechanism in the disinhibited-feedback model. This model, which provides an alternative to the cross-activation theory, assumes that the degree of connectivity is not different in synaesthetes and non-synaesthetes, but that they differ in the level of inhibition, thus causing cross regional activation [57].

Besides the evidence for a higher level of connectivity between (adjacent) sensory areas, there is also increasing evidence for the involvement of the inferior parietal lobe. It has been suggested that the involvement of this area reflects a “hyperbinding” process that combines the real and synaesthetic sensory experiences into one common percept (see Figure 3). Therefore, the original formulation of the cross-activation theory has recently been extended to a two-stage model, which includes the binding process through the parietal areas [49,50]. Evidence for a central role of the parietal lobe in synaesthesia comes not only from functional imaging studies but also from structural imaging and TMS studies. However, there is an unresolved inconsistency

across studies with respect to lateralization, as some studies are indicating a left parietal involvement, while other studies point more to right parietal areas [50]. Weiss and Fink (2009) [28] found increased grey-matter in the left inferior-parietal area of grapheme-colour synaesthetes. The same area was identified as a hub in a network analysis in coloured-hearing synaesthetes [47]. However, while Rothen and co-workers found in their TMS study a significant contribution from the parietal lobe of both hemispheres in their synaesthetic conditioning experiment [58], Esterman and co-workers demonstrated that rapid TMS stimulation over the right (but not left) parietal lobe causes the disruption of an interference effect in a Stroop-like single letter task in grapheme-colour synaesthetes [59]. Similarly, Laeng et al. (2011) found right inferior parietal lobe involvement only when synaesthetes had to name the synaesthetic colour, but not when naming the ink-colour or when performing an ordinary Stroop task [13]. In other words, the right inferior parietal lobe was activated only when attention was directed towards the synaesthetic experience. This emphasizes the notion that attention and stimulus awareness play an important

role in modulating synaesthetic experiences [24,60,61].

Another often-discussed question is whether it is possible to train synaesthesia. Recently, Meier and Rothen demonstrated that they were able to induce a synaesthetic Stroop effect in non-synaesthetes after one week of training. However, in contrast to real synaesthetes, their trained subjects did not show a conditioned response [25, 62]. They also conclude that parietal mechanisms are involved in this neuronal “backfiring” in synaesthetes [25], and that synaesthetes actually activate a bi-directional association (i.e. graphemes trigger colours and colours trigger graphemes), but that the subjective experience is only unidirectional [62].

One remaining question is, whether synaesthetes benefit from their “gift”. There are different reports that actually support this view. However, there is no clear evidence for an evolutionary selection preference that could explain why some humans develop synaesthesia and others do not. Nevertheless, it has been shown that grapheme-colour synaesthetes are, for example, better at recalling names [63]. Rothen and Meier found that grapheme-colour synaesthetes

performed better in episodic memory tests but not in short-term memory tests, thus indicating that memory performance is not generally improved but rather is task specific [64]. The reason may be that synaesthetes can use additional cues for recalling information through verbal encoding, since grapheme-colour synaesthetes often encode entire words in specific colours, based on the colour of the first stressed syllable [18]. Another example of a benefit from this “gift” is time-space synaesthetes, who perform superiorly in temporal and visuospatial tests [31,32]. Finally, there is some evidence that the proportion of synaesthetes among artists is as high as 7% (as based on a recent sample of art students), which is slightly higher than in the normal population, where it is assumed to be 2-4% [65]. Artists that are synaesthetes typically choose an art-form where they benefit from the synaesthesia, for example, a coloured-hearing synaesthete is more likely to play an instrument [66]. Ward and co-workers found a tendency towards higher creativity, and an elevated preference to engaging in art, in some of the used measures [66]. However, it might be wrong to claim that synaesthetes are, in general, more creative.

Cumulatively, all the studies presented in this review demonstrate the increasing evidence that synaesthesia does not occur only through cross-activation of different sensory areas (irrespective whether they are adjacent or not), but that parietal areas contribute significantly to forming a common percept out of the concurrent stimulations. However, many questions still remain unsolved. One central question targets the mechanisms that are driving the cross activation. So far, it is unclear whether this occurs through increased connectivity or through a lack of inhibition. Furthermore, it has been shown that attention modulates the effect of synaesthesia. Finally, and perhaps related to the aspect of attention, the contribution of the parietal areas are not yet fully explained, the question involving the contribution of the parietal areas has not been solved yet. Future studies need to assess the involvement of the left or right parietal cortex by applying modern imaging methods and network modelling approaches.

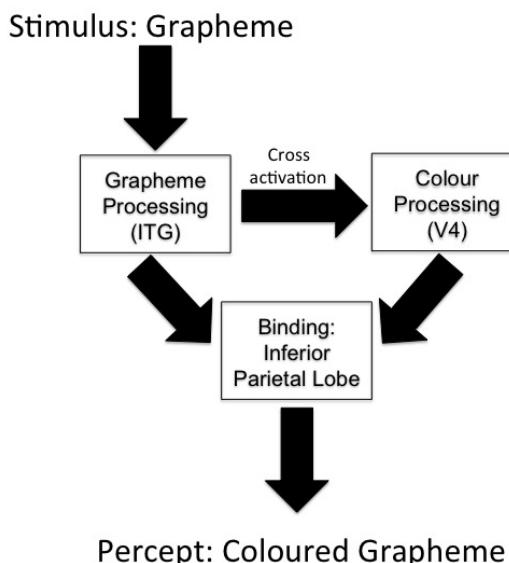


Figure 3. Adapted cross-activation and two-stage model of grapheme-colour synaesthesia: A grapheme trigger activation of grapheme sensitive areas in the inferior temporal gyrus (ITG), which causes cross activation of the colour processing area V4. Finally, the inferior parietal lobe creates a common percept out of the simultaneously generated percept of a letter and a colour.

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