



**HAL**  
open science

# Mixing up the Senses: Sensory Substitution Is Not a Form of Artificially Induced Synaesthesia

Louise P Kirsch, Xavier Job, Malika Auvray

► **To cite this version:**

Louise P Kirsch, Xavier Job, Malika Auvray. Mixing up the Senses: Sensory Substitution Is Not a Form of Artificially Induced Synaesthesia. *Multisensory Research*, 2020, pp.1-26. 10.1163/22134808-bja10010 . hal-03087194

**HAL Id: hal-03087194**

**<https://hal.science/hal-03087194v1>**

Submitted on 23 Dec 2020

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Cite as: Kirsch, L., Job, X., & Auvray, M. (2020). Mixing up the senses: Sensory substitution is not a form of artificially induced synaesthesia. *Multisensory Research*. doi:10.1163/22134808-bja10010.

# Mixing up the Senses: Sensory Substitution is Not a Form of Artificially Induced Synaesthesia

Louise P. Kirsch<sup>†,\*</sup>, Xavier Job<sup>†,\*</sup> and Malika Auvray

Institut des Systèmes Intelligents et de Robotique (ISIR), Sorbonne Université, Paris, France

<sup>†</sup> Authors share first authorship

\* To whom correspondence should be addressed. E-mail: [louise.kirsch@sorbonne-universite.fr](mailto:louise.kirsch@sorbonne-universite.fr); [xavier.job@sorbonne-universite.fr](mailto:xavier.job@sorbonne-universite.fr)

## Abstract

Sensory Substitution Devices (SSDs) are typically used to restore functionality of a sensory modality that has been lost, like vision for the blind, by recruiting another sensory modality such as touch or audition. Sensory substitution has given rise to many debates in psychology, neuroscience and philosophy regarding the nature of experience when using SSDs. Questions first arose as to whether the experience of sensory substitution is represented by the substituted information, the substituting information, or a multisensory combination of the two. More recently, parallels have been drawn between sensory substitution and synaesthesia, a rare condition in which individuals involuntarily experience a percept in one sensory or cognitive pathway when another one is stimulated. Here, we explore the efficacy of understanding sensory substitution as a form of ‘artificial synaesthesia’. We identify several problems with previous suggestions for a link between these two phenomena. Furthermore, we find that sensory substitution does not fulfil the essential criteria that characterise synaesthesia. We conclude that sensory substitution and synaesthesia are independent of each other and thus, the ‘artificial synaesthesia’ view of sensory substitution should be rejected.

## Keywords

Sensory substitution, synaesthesia, multisensory perception, senses, brain plasticity

# 1. Sensory Substitution: Theories and Mechanisms

## 1.1. Sensory Substitution Devices

Sensory substitution aims to convey information from one modality (e.g., vision) via another modality (e.g., audition or touch) using a device that converts the information with a predefined transformation code. Sensory Substitution Devices (SSDs) first record information in one modality, typically vision, with a sensor (i.e., a camera), then converts certain features of that information (e.g., luminance and spatial location in the vertical and horizontal planes) into features of another sensory modality (e.g., auditory amplitude and frequency or tactile intensity). Finally the device transmits the newly converted information using an auditory or tactile stimulator. These devices were primarily developed to restore functionality of a sensory modality that has been lost, for example vision in blind people (for reviews see Auvray, 2019; Heimler and Amedi, 2020), but also for perceptual augmentation (e.g., Carton and Dunne, 2013).

Early devices such as the Tactile-Visual Sensory Substitution device (TVSS; Bach-y-Rita *et al.*, 1969) convert visual images obtained from a camera into spatio-temporal patterns of tactile stimuli delivered to the skin on an individual's back. Similarly, the Tongue Display Unit (TDU) converts visual images into electro-tactile pulses delivered to the surface of the tongue (Kaczmarek, 2011). Visual-to-auditory devices convert visual images into patterns of auditory 'soundscapes'. For instance, the vOICe (Meijer, 1992) maps the  $x$ -axis of a visual image into the time domain, the  $y$ -axis into the frequency domain, and visual brightness into auditory amplitude. Numerous studies have shown that in less than 15 hours of training, blind or sighted-blindfolded users of SSDs are able to perform object recognition and discrimination tasks (Auvray *et al.*, 2007; Bermejo *et al.*, 2015; Brown *et al.*, 2011; Kim and Zatorre, 2008; Striem-Amit *et al.*, 2012), visual localisation and reaching tasks (Hanneton *et al.*, 2020; Levy-Tzedek *et al.*, 2012; Proulx *et al.*, 2008) navigation and obstacle avoidance tasks (Chebat *et al.*, 2011, 2015; Kupers *et al.*, 2010) and even, with additional training, face recognition tasks (Striem-Amit *et al.*, 2012). Importantly, recognition has been shown to transfer to novel objects not previously presented during training (Auvray *et al.*, 2007; Kim and Zatorre, 2008; see also Arnold and Auvray, 2014, 2018, for transfer using visual-to-tactile SSDs). Thus, the transfer to novel stimuli demonstrates a generalisable perceptual learning rather than a mere memorisation of stimulus pairings. Many other visual-to-auditory devices were developed varying in their chosen translation codes (e.g., the See ColOr: Bologna *et al.*, 2009; the EyeMusic: Levy-Tzedek *et al.*, 2014; Vibe: Hanneton *et al.*, 2010), allowing a broad range of perceptual abilities (e.g., see Maidenbaum, Abboud, and Amedi, 2014).

## 1.2. Dominance, Deference and Multisensory Views of Sensory Substitution

The mechanisms underlying this remarkable transformation of information from one sensory modality to another has been subject to much debate (Bach-y-Rita and Kerckel, 2003; Keeley, 2002; Ptito *et al.*, 2018). Several theories and models attempt to explain how the brain is able to exploit intact sensory modalities to perceive information that is normally conveyed through another modality. Initially, the debate surrounding sensory substitution concerned in which modality the perception of information is represented. In other words, whether the percept remains within the substituting modality in which the information is presented (i.e., tactile or auditory for the TVSS and vOICe devices, respectively), or whether the percept is represented in the substituted modality (i.e., vision). Early pioneers of sensory substitution claimed that SSDs would allow blind people to "see with their skin" (White *et al.*, 1970) or to "see with their brains" (Bach-y-Rita and Kerckel, 2003). These claims encapsulated the

view that perceptual experience is deferred from one intact modality to another impaired modality, often referred to as ‘cortical deference’ (Hurley and Noë, 2003; O’Regan, 2011). However, others instead proposed that perception remains within the substituting modality, a view referred to as ‘cortical dominance’ (Block, 2003; Keeley, 2002; Prinz, 2006). Although this debate is no longer as prominent in the scientific literature, the cortical deference view still often reappears in articles for the general public, in which SSDs have been advertised as, for instance, “rewiring brains to see with sound” (Trivedi, 2010) or “helping the blind see with their ears” (Jacobson, 2014).

In the last decade, a view has emerged that proficient SSD users acquire a novel way of experiencing the world, the phenomenology of which in part resembles vision and in part resembles the substituting modality (see Deroy and Auvray, 2014; Farina 2013; Kiverstein *et al.*, 2014). This view suggests that sensory substitution goes beyond representation of either the substituting or the substituted modality (Auvray and Myin, 2009; Deroy and Auvray, 2012, 2014; Farina, 2013; Proulx *et al.*, 2014, 2016). Several recent accounts point toward the hypothesis of a novel or multisensory experience. For instance, Humphrey (2006) noted that the majority of subjective reports from expert users of SSDs often reflect a “complicated dual experience”, rather than a ‘visual’ or tactile/auditory experience. Auvray and Myin (2009) also suggest that SSDs may be better compared to ‘mind-enhancing tools’ that expand perceptual experience beyond the existing sensory modalities involved. Following Clark’s (2003) view, such tools provide means to carry out cognitive functions in ways that would have been impossible without them, given the intrinsic properties of the system. Accordingly, SSDs provide cognitive extensions to the existing senses, possibly unmasking a latent potential in the sensory cortex to process stimuli regardless of its sensory modality.

One mechanism thought to support sensory substitution is *crossmodal plasticity*, the notion that the neural resources associated with the substituted modality are recruited to process the same information using input from other sensory modalities (Bach-y-Rita and Kerdel, 2003). In the following section the mechanisms of sensory substitution are examined using key results from neuroimaging and deprivation studies.

### *1.3. Key Results from Neuroimaging and Deprivation Studies*

The advent of neuroimaging methods significantly changed the direction of the debate surrounding sensory substitution. Studies showed that areas of the visual cortex become reliably engaged during the use of auditory (Arno *et al.*, 2001; De Volder *et al.*, 1999; Merabet *et al.*, 2009; Striem-Amit and Amedi, 2014) and tactile (Ptito *et al.*, 2005) SSDs. These remarkable early demonstrations of crossmodal plasticity suggested that a ‘visual’ experience may be evoked when using devices designed to compensate vision. However, activation of occipital areas in response to nonvisual stimuli does not necessarily mean that visual images are formed. For example, Transcranial Magnetic Stimulation (TMS) applied over the occipital cortex of blind individuals resulted in somatotopically organised tactile, rather than visual, sensations in the fingers of braille readers (Ptito *et al.*, 2008) as well as on the tongues of trained users of the TDU (Kupers *et al.*, 2006). Thus, activation of the occipital cortex following tactile stimulation may not necessarily reflect a ‘visual’ experience. Furthermore, the activation of visual areas during auditory/tactile-to-visual sensory substitution could also be due to a top-down influence on visual areas rather than bottom-up information processing (Murphy *et al.*, 2016).

Research on individuals deprived of vision has also been pivotal in changing how the brain’s functional organisation is viewed. Early studies showed that deprived sensory cortices (i.e., the visual cortex of blind people) are activated by input from other sensory channels (Kujala *et al.*, 1992; Sadato *et al.*, 1996). More recently studies have shown that deprived cortical regions such as the visual cortex of the blind can maintain many of their functional

specialisations (e.g., object recognition) using the input from other sensory modalities (for reviews see Dormal and Collignon, 2011; Heimler *et al.*, 2014). Amedi and colleagues (2007) found that following auditory-to-visual sensory substitution training using the vOICE, participants showed greater BOLD signal activation in the lateral occipital complex (LOC), a region thought to be dedicated to visual processing of shape information. However, the LOC has also been shown to process shape information in the tactile domain (Peltier *et al.*, 2007; Pietrini *et al.*, 2004), and increased functional connectivity between the auditory cortex and LOC has been found after training with an auditory-to-visual SSD (Kim and Zatorre, 2008). Thus, the LOC likely processes more abstract object–form information regardless of the sensory modality of the input. This result suggests that the observed crossmodal recruitment of the visual cortex by sensory substitution devices could be due to the unravelling of pre-existing computations through nonvisual inputs, present prior to using the SSD (e.g., Ptito *et al.*, 2005; Striem-Amit *et al.*, 2012; see also Ptito *et al.* 2018, for a review). Beyond the LOC, typically nonauditory areas such as the left precentral sulcus and the right occipital-parietal sulcus also show differential activity following sensory substitution training (Striem-Amit *et al.*, 2011). Further evidence has shown that following sensory substitution training with the vOICE, functional connectivity shifts away from sensory networks towards task-positive networks involved in top-down modulations (Murphy *et al.*, 2016; Deen *et al.*, 2015).

Thus, research is now converging on an understanding of sensory substitution in line with notions that the brain functions in a primarily task-selective and sensory-independent manner (Chan *et al.*, 2018; Heimler and Amedi, 2020; Reich *et al.*, 2011; Striem-Amit *et al.*, 2011). In other words, while certain brain regions show a dominance of one sensory modality, they are able to perform their specific task if they receive relevant input from other sensory channels (Maidenbaum *et al.*, 2014). This provides promise that brain regions are able to maintain or regain functionality in a disrupted modality from the organised input of other sensory channels.

In parallel to this task-selective and sensory-independent view, another account of sensory substitution has drawn parallels with synaesthesia, suggesting that sensory substitution is a form of ‘artificially induced synaesthesia’ (Farina, 2013; Proulx, 2006, 2010; Ward and Wright, 2014). In the next section, we evaluate whether sensory substitution can be understood as a form of artificial synaesthesia. To meet this aim, we first identify and discuss several previous suggestions for a link between synaesthesia and sensory substitution. We then consider each of the established core characteristics of synaesthesia and whether these apply to sensory substitution.

## **2. The Artificial Synaesthesia View of Sensory Substitution**

Synaesthesia is a condition in which people make unusual associations between various sensations. The stimulus triggering the unusual association can be sensory (e.g., the printed letter A, see Grossenbacher and Lovelace, 2001), conceptual (e.g., the result of an arithmetic operation, see Dixon *et al.*, 2000) or emotional (e.g., Ward, 2004). For example, an individual may perceive numerals and letters to be associated with vivid sensations of certain colours, referred to as grapheme–colour synaesthesia — one of the most common and frequently studied forms of synaesthesia (Jäncke *et al.*, 2009). There is now a broad consensus that the condition emerges at an early developmental stage with behavioural markers emerging as young as six years old (Simner *et al.*, 2009) and remaining constant throughout the lifespan (see Auvray and Deroy, 2015, for a review on synaesthesia). The condition also appears to have a genetic basis and runs in families (Asher *et al.*, 2009; Brang and Ramachandran, 2011).

In recent years, the possibility of inducing synaesthetic experiences in nonsynaesthetes, typically referred to as ‘artificial synaesthesia’, has become a topic of

burgeoning interest. Research has sought to demonstrate synaesthesia-like experiences as a result of training (e.g., Bor *et al.*, 2015), post-hypnotic suggestion (e.g., Cohen Kadosh *et al.*, 2009), psychedelic drug use (e.g., Luke and Terhune, 2013), flavour perception (Stevenson and Boakes, 2004; Stevenson and Tomiczek, 2007) and the use of sensory substitution devices (e.g., Farina, 2013; Proulx and Stoerig, 2006; Ward and Meijer, 2010). These phenomena have each been (in)directly linked to synaesthetic experience because they either induce some form of conscious concurrent experience or show patterns of crossmodal interference that characterise canonical cases of synaesthesia (such as the Stroop interference effect, e.g., Mills, 1999; see Eagleman *et al.*, 2007, for a review of the existing tests).

Interest in the possibility of inducing artificial synaesthesia broadly attempts to better understand the mechanisms underlying synaesthesia itself. However, sometimes this endeavour is reversed with research attempting to explain a phenomenon as merely a special, or ‘artificial’, form of synaesthesia. This has been the case particularly for sensory substitution. Indeed, some have proposed that sensory substitution may be a form of artificially induced synaesthesia (Farina, 2013; Proulx, 2006; Proulx, 2010; Ward and Wright, 2014). For example, Ward and Meijer (2010) state that “*Acquired synaesthesia may well be an inevitable consequence of long-term adaptation to a sensory substitution device*”. Since these claims, many studies continue to refer to synaesthesia as among the existing explanations of sensory substitution (e.g., Bermejo *et al.*, 2015; Haigh *et al.*, 2013; Hamilton-Fletcher *et al.*, 2016; Loomis *et al.*, 2013; Renier and De Volder, 2013; Safran and Sanda, 2015). For instance, Hamilton-Fletcher *et al.* (2016) introduce a sensory substitution device called ‘The Syneastheatre’ and state “*SSDs that co-exist with sight give the potential for users to experience colour–sound synaesthesia*”. Similarly, Haigh and colleagues (2013) state that “*Certainly one broad goal for work on sensory substitution is to ultimately provide the phenomenological experience of vision in a form of synthetic synaesthesia*”. However, the purported links between synaesthesia and sensory substitution have not yet undergone enough critical appraisal to justify such an explanation.

## *2.1. Main Claims Made by the Synaesthesia View of Sensory Substitution*

The synaesthesia view of sensory substitution posits that (i) experience with SSDs is akin to the substituted information (i.e., it is visual in nature if using the vOICe for example), and that (ii) both the substituted and substituting information are consciously perceived simultaneously. Next, we assess these claims, with a focus on SSDs that compensate for vision with either auditory or tactile input.

### *2.1.1. Is Experience During SSD Use ‘Visual’?*

The synaesthesia view of sensory substitution assumes that the perceptual experience of trained users is ‘visual’ in nature. This question of whether users’ perceptual experience is ‘visual’ has been a topic of considerable debate within the sensory substitution literature since the very first devices emerged. As was previously mentioned (see above, section 1 *Sensory Substitution: Theories and Mechanisms*), the ‘cortical dominance’ view (e.g., Block, 2003; Keeley, 2002; Prinz, 2006) proposed that after extensive training with an auditory-visual SSD perceptual representation remains within the substituting modality (i.e., auditory) rather than the substituted modality (i.e., ‘visual’). In contrast, the ‘cortical deference’ view (e.g., Hurley and Noë, 2003; Noë, 2004; O’Regan, 2011) proposed that the experience lies in the substituted modality, such that perception can be considered as ‘visual’. These early views often made their case by emphasising the importance of one (or a combination of several) of the criteria traditionally used to distinguish between sensory modalities. This has often led to contradictory conclusions regarding the dominance versus deference debate. For instance, the dedication criterion, i.e., whether or not the sensory organ was evolutionarily

dedicated to process that type of stimulus, is central to Keeley's (2002) case for cortical dominance whereas the sensorimotor equivalence criterion is central to O'Regan's (2011) case for cortical deference. Some authors, reviewing all these criteria, have arrived at different conclusions, either in favour of the cortical deference view (Ward and Wright, 2014) or as an argument to move beyond the dominance vs. deference debate (Auvray and Myin, 2009; see also Pacherie, 1997, for a philosophical discussion of the relevance of these criteria for sensory substitution). In the last decade, a consensus has arisen that SSD use does not constitute a transfer between unisensory modalities (i.e., auditory information is not experienced as visual *per se* in the case of the vOICE), but rather SSD use reflects a complex multisensory experience (e.g., Arnold *et al.*, 2017; Cecchetti *et al.*, 2016; Heimler *et al.*, 2015; Martin and Le Corre, 2015; Proulx *et al.*, 2014, 2016, Stiles and Shimojo, 2015). Thus, the first claim for a synaesthesia view of sensory substitution as being visual in nature is not in line with the most recent theories in the field.

Furthermore, behavioural studies have investigated whether SSD use is 'visual' or not by testing users' sensitivity to illusions that are typically thought to rely on visual mechanisms (Renier *et al.*, 2005, 2006). For example, Renier *et al.* (2005) sought to determine whether users of a visual-auditory SSD would be sensitive to the Ponzo illusion, in which observers perceive two identical horizontal lines as nonidentical when surrounded by two converging lines. The converging lines are thought to act as perspective cues, biasing the observer to believe that one horizontal line is further away than the other. Due to mechanisms of size constancy, the visual system then interprets the 'further away' line as longer. Renier *et al.* (2005) found that sighted-blindfolded individuals using the SSD were susceptible to the illusion, even though the sensory input they received was auditory. However, participants with little to no visual experience (early blind) were not sensitive to the illusion. This suggests that early visual experience is necessary for 'visual-like' experiences during SSD use and is inconsistent with the view that the auditory input is represented in itself as 'visual'. Others have also noted similarly disparate findings when sensory substitution is applied to the blind versus blindfolded-sighted populations (for a review see Poirier *et al.*, 2007), highlighting that activation of occipital areas in users of SSDs may reflect crossmodal plasticity in the blind, but visual imagery in blindfolded-sighted individuals. Together, this suggests that 'visual-like' experiences arising during the use of SSDs cannot so far be disentangled from any additional top-down information arising from pre-existing visual imagery or visual memory.

The need to cautiously differentiate the results obtained by blind and blindfolded-sighted participants applies to many aspects of SSD research. For instance, the translation code used by SSDs is often based on research on sighted adults, where a crossmodal association has been found (for example high pitch can be associated to an elevating line). However, some recent research has not found such crossmodal associations in blind adults (Deroy *et al.*, 2016), a population for whom most SSDs are developed. This creates fundamental but also practical problems, and highlights that caution is required when universally applying translation codes across typical and blind populations.

Moreover, synaesthesia is often linked to sensory substitution because both phenomena involve an atypical perceptual experience elicited by the processing of a qualitatively different stimulus to that which would normally give rise to that experience (Ward and Wright, 2014). For example, alphanumeric letters do not normally give rise to the experience of certain colours for nongrapheme-colour synaesthetes. The synaesthesia view of sensory substitution claims that the same holds for trained users of SSDs, such that an atypical ('visual') perceptual experience, that would not normally occur, is elicited by the processing of a qualitatively different (auditory or tactile) stimulus. Indeed, the substituting information is qualitatively different from any 'visual' experience SSDs users may have, even if this entails visual imagery. However, this does not necessarily support the view that

sensory substitution is a form of artificial synaesthesia. Indeed, the same could be said for the learning and remembering of any relationship between two otherwise unrelated stimuli, yet mechanisms of associative learning and memory are not described as ‘artificial synaesthesia’. Thus, the fact that both phenomena involve relationships between otherwise unrelated percepts is not a strong argument for a synaesthesia view of sensory substitution.

### *2.1.2. Are the Substituted and Substituting Information both Consciously Perceived?*

Synaesthetic experience first requires a pairing between a triggering stimulus, referred to as an ‘inducer’, and a ‘concurrent’, which is the experience of another percept involuntarily triggered by the inducer (Grossenbacher and Lovelace, 2001). Synaesthetes often report conscious access to both the inducer and the concurrent. Indeed, for grapheme–colour synaesthetes, attending to the inducer stimulus (and thus being consciously aware of the stimulus) appears to be necessary in order to experience the concurrent (Mattingley, 2009). The synaesthesia view of sensory substitution argues that the same holds for the substituted and substituting information in trained SSD users. This suggests that the auditory or tactile information provided by the device should not be perceptually lost, yet some authors defend the idea that in trained SSD users, access to the substituting information appears to fade (O’Regan, 2011; O’Regan and Noë, 2001), challenging the view that the substituted and substituting information are both consciously perceived.

Many of the claims equating SSD use and synaesthesia re-occurring in the literature refer to the verbal reports from one of the two participants in Ward and Meijer’s (2010) study who described her experiences as analogous to a form of “*monochrome artificially induced synaesthesia*”. However, while she describes her experience as being akin to synaesthesia, her report also highlights that she switched her attention between the different impressions that the sounds give rise to, which is at odds with synaesthetic experiences. This is problematic for the synaesthesia view of sensory substitution as there is no substantive evidence that both the substituted and substituting information are consciously perceived. Initially, SSD users may be acutely aware of the device and the stimulation it provides. However, with training they begin to ignore the substituting information provided by the device and instead perceive a distal object. This notion of ‘transparency’ describes the assimilation of the sensorimotor contingencies that make using the device ‘second nature’ (Stewart and Khachaturov, 2007) and is at odds with the synaesthetic experience of a consciously accessible inducer *and* concurrent.

Furthermore, concerning the substituted information, SSDs are used in a goal-directed manner such that the user almost always seeks to complete a given task with the device, for example to localise, identify and interact with an object. A user can either rely on the substituting information to complete a task (i.e., actively deduce the required information from the pattern of auditory information) or rely on the substituted information to complete the same task (e.g., see Siegle and Warren, 2010, for a comparison between these two modes with a minimalist SSD). The general understanding is that users transition from the former to the latter with increased training and familiarity with the device. However, in trained users, there is then a certain amount of redundancy in both of these perceptual experiences reaching awareness in order to complete the same task. This may not be the case for synaesthesia, in which the experience is not linked to a goal-directed or task-oriented context in the same sense. Indeed, it is difficult to see how the involuntary experience of a colour elicited by a sound (in sound-to-colour synaesthesia) could aid completion of any task that one is set. Thus, there is no redundancy in the content of the different information (i.e., sounds and colours) in synaesthesia and therefore no reason for only one to reach perceptual awareness. Furthermore, for sensory substitution a redundancy in perceiving both the substituting and the substituted information concurrently questions the assumption that they are qualitatively different from each other.



## 2.2. Does Sensory Substitution Adhere to the Essential Criteria for Synaesthesia?

The former section questioned two claims central to a synaesthesia view of sensory substitution: (i) perception with SSDs is akin to the substituted information (i.e., ‘visual’ in nature) and (ii) both the substituted and substituting information are consciously perceived simultaneously. Considerable caveats to these central claims were identified. The aim in this section is to determine if sensory substitution adheres to the essential criteria that characterises synaesthetic experiences. Four fundamental criteria are used to characterise synaesthesia: (i) an *inducer–concurrent* pairing; (ii) the relative *idiosyncrasy* of the pairings; (iii) the *automaticity* of the process; and (iv) the *consistency* over time. These criteria have been used in the past to evaluate the validity of a synaesthetic view of different processes (see details in Auvray and Farina, 2017<sup>1</sup>; Grossenbacher and Lovelace, 2001; Terhune *et al.*, 2017; see also Deroy and Spence, 2013; Ward, 2013; Ward and Mattingley, 2006). Next, we evaluate whether sensory substitution adheres to each of these criteria in order to establish whether an ‘artificial synaesthesia’ view of sensory substitution is tenable. Results are summarised in Table 1.

**Table 1.**

Summary of the criteria characterising synaesthesia (columns) and the fulfilment of those criteria by various phenomena (rows), including developmental synaesthesia (upper row), the perceptual experience of sensory substitution including the associated phenomenology and additional experiences such as phosphenes (middle row) and the substituted information during sensory substitution (lower row). The terms ‘Yes’ and ‘No’ are used when the claim is not controversial. ‘Debated’ is added when there are existing data, but their interpretation is subject to controversy. ‘Lack of Data’ is used when more empirical data are needed.

Cases	Inducer–concurrent pairing	Idiosyncrasy	Automaticity	Consistency
Developmental synaesthesia	Yes	Yes	Yes	Yes
Sensory substitution: perceptual experience	Debated	Yes (narrow set)	Lack of data	Lack of data
Sensory substitution: substituted information	Lack of data	No	Lack of data	Yes

### 2.2.1. Inducer–Concurrent Pairing

As mentioned in the previous section, synaesthetic experience first requires a pairing between an inducer and a concurrent. The synaesthesia view of sensory substitution suggests that the substituting information — the stimulation provided by the device (e.g., auditory soundscapes for the vOICe) — is akin to the *inducer* in synaesthetic experience (e.g., a sound that induces the vivid sensation of colour in sound-to-colour synaesthesia, i.e., chromaesthesia). The substituted information during SSD use (e.g., ‘visual’ information when using the vOICe) is then considered akin to the conscious *concurrent* in synaesthetic experience (e.g., the vivid experience of a colour induced by sound for sound-to-colour

<sup>1</sup> Note that Auvray and Farina (2017) provide a critique of the research on transient and artificially induced forms of synaesthetic experiences, including but not limited to sensory substitution, in order to determine the boundaries of synaesthesia. Here, we focus on sensory substitution and expand on whether or not it should be considered as a form of ‘artificial synaesthesia’.

synaesthetes). The links between the substituting information and the inducer, as well as the substituted information and the concurrent seem rather intuitive, given that in both cases a stimulus gives rise to a percept not normally experienced.

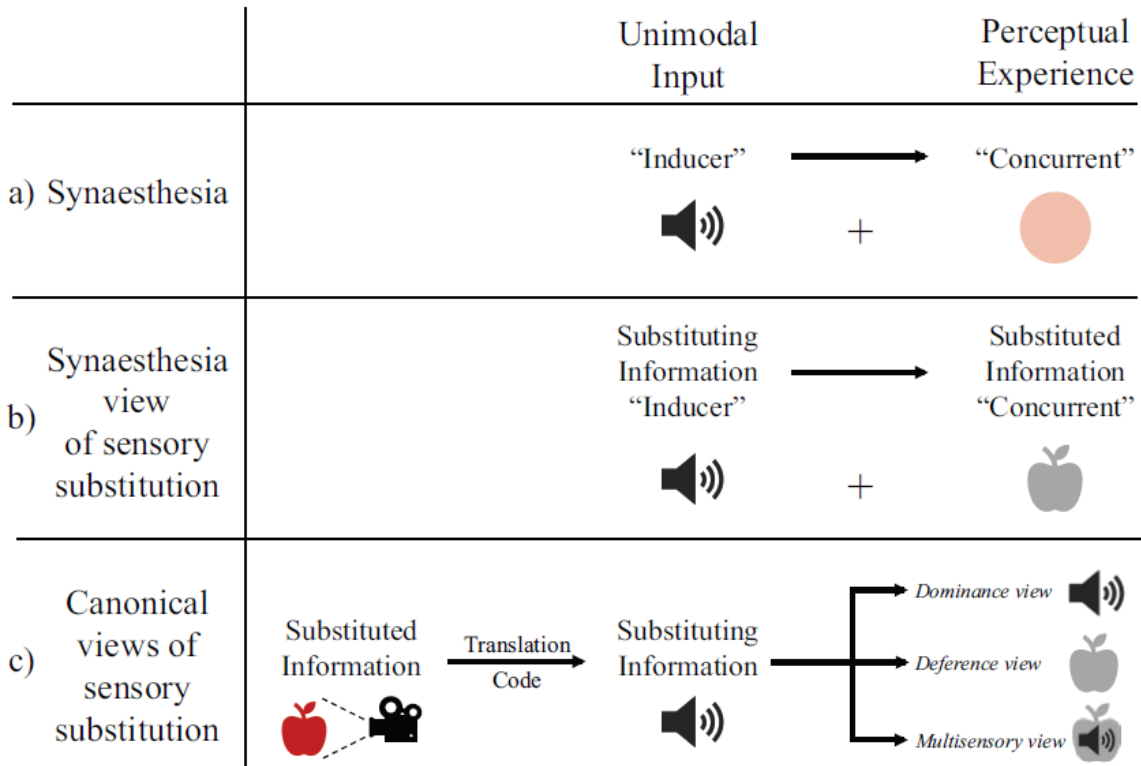
There are some reports suggesting that the associated phenomenology when using a SSD could be considered akin to the concurrent in synaesthetic experience. For example Ward and Meijer (2010) report descriptions from two individuals who became blind later in life and had been using the vOICE for more than 10 years. One of these trained users (PF) describes her experiences as analogous to a form of “*Monochrome artificially induced synaesthesia only in certain frequencies of sound*” (Ward and Meijer, 2010, p. 497). Subjective reports like these may support the idea that the associated phenomenology of using an SSD can be akin to the experience of a concurrent for synaesthetes. However, the same user also suggests that her experience is more complex than usual vision per se:

*“Because my mind automatically records it as a visual sound. It has to be in a certain vOICE frequency. I understand that now. But you can’t use a high car horn and it becomes a vision of a car. But if I hear a car horn, I see it in my mind through the ‘vOICE sight’. I don’t think of it like I used to ‘see sight’. The vOICE sight, I call it The vOICE sight.”* (Ward and Meijer, 2010, p. 498)

Furthermore, the status of these perceptual experiences is rather unclear as they are difficult to disentangle from visual mental imagery, or visual memory. Beyond these subjective reports, there are no quantitative data so far that link the associated phenomenology of SSD use with the experience of a concurrent in synaesthetic experience.

This interpretation also neglects a critical distinction between the *substituted information* and the content of one’s perceptual experience when using an SSD, termed the *associated phenomenology*. First, perception in sensory substitution can be understood at the level of information processing, such that it can be inferred from knowledge of the translational code (e.g., a visual round, small and bright object might be inferred from a soundscape with a particular set of properties). However, perception in sensory substitution can also refer to the associated phenomenology. For example, the associated phenomenology might be the subjective experience that the apple is seen, heard, or an experience that even resembles a sonar-like experience (Auvray *et al.*, 2007). It could also lead to additional experiences such as impressions of light (i.e., phosphenes) elicited by the soundscapes, which may not necessarily relate directly to the translation code but are nonetheless joined to the perceptual experience of using the device. When parallels are drawn between sensory substitution and synaesthesia, it is often unclear whether the substituted information or the associated phenomenology constitutes the perceptual ‘concurrent’ that is elicited. These different views are summarised in Fig. 1, which depicts the synaesthesia view of sensory substitution as well as the canonical views of sensory substitution.

Another important aspect of the inducer–concurrent pairing in synaesthesia is that both are consciously accessible. Indeed, for grapheme–colour synaesthetes attending to the inducer stimulus (and thus being consciously aware of the stimulus) appears to be necessary in order to experience the concurrent (Mattingley, 2009). However, as mentioned earlier, some have suggested that access to the substituting information fades in trained users (O’Regan, 2011; O’Regan and Noë, 2001).



**Figure 1.** Comparison of different views: (a) Synaesthesia, example of sound-to-colour synaesthesia, where the unimodal input, termed the ‘inducer’ (i.e., hearing a sound), elicits an additional experience, termed the ‘concurrent’ (i.e., experiencing red); leading to the percept of a sound and a colour, that are both consciously accessible (denoted by the ‘+’) (b) ‘Synaesthesia view’ of sensory substitution, with the example of an auditory-to-visual Sensory Substitution Device (SSD), such as the vOICE. The substituting modality (e.g., an auditory soundscape), is considered akin to the inducer in synaesthesia, and the substituted modality (i.e., vision) is considered akin to the concurrent, leading to the percept of both a sound and a visual object, that are both consciously accessible (denoted by the ‘+’). It is clear that this view differs considerably from the canonical view of sensory substitution, depicted below. (c) The canonical views of sensory substitution with an auditory-to-visual SSD, such as the vOICE. Substituted information (e.g., an apple) is captured by a camera and converted using a translation code into substituting information (i.e., an auditory soundscape). Depending on the different theories, and likely depending on prior knowledge and training with the device, the resulting perceptual experience can be either (i) a soundscape alone, (ii) a combination of auditory and ‘visual’ information relating to the object (note that the vOICE lacks translation of colour information), or (iii) a ‘visual’ object alone without conscious access to the substituting auditory information.

### 2.2.2. Idiosyncrasy

Synaesthetes experience something additional when perceiving an inducer stimulus that nonsynaesthetes do not. This can also be said for users of SSDs, whose experience is similarly not shared by nonusers. However, synaesthesia is also highly idiosyncratic in the sense that it manifests itself in a personal way for the same inducer stimulus (Grossenbacher and Lovelace, 2001). For example, not all grapheme–colour synaesthetes perceive the same letter as being associated with the same colour, even within the same family or between twins (Barnett *et al.*, 2008). Some evidence has shown broad patterns of associations across sound–colour synaesthetes specifically, for example between treble and brighter colours, bass and darker colours, loud sounds and large shapes and soothing sounds and small shapes (Ward *et al.*, 2006). However, for users of SSDs, the feature pairings are necessarily determined by the translational code inherent to the device. For example, all users of the vOICE must associate the same properties of a soundscape to the same properties of visual objects. Thus, there is no clear idiosyncrasy regarding the processing of the substituted information in sensory substitution. In terms of the associated phenomenology, it is difficult to gauge the

idiosyncrasy of individuals' experiences with SSDs from the data currently available. Indeed, very few instances are reported in which individuals reported experiencing some form of colour or light (Ward and Meijer, 2010). For example, Ward and Meijer (2010) report one SSD user who experiences colour, although these experiences have emerged very slowly over time. The user first described her experiences as

*“black and white and all the little gradients in between”*. Then five years later she stated that *“Before my brain wasn't seeing the finer detail. Over time my brain seems to have developed, and pulled out everything it can from the soundscape and then used my memory to color everything”* (Ward and Meijer, 2010, p. 487). This last example could suggest that SSD users do have relatively idiosyncratic perceptual experiences; however, this is so far the only known report. It is noteworthy that the seemingly vast array of possible pairings experienced by synaesthetes appears to far outweigh the rather limited set of possible idiosyncrasies available for users of SSDs (i.e., colours and light).

### 2.2.3. Automaticity of the Process

Synaesthetic experience is considered automatic such that it does not result from a conscious decision but is triggered by passive exposure to an inducer stimulus (Dixon *et al.*, 2000), although the inducer must be attended to elicit the experience of a concurrent (e.g., Deroy and Spence, 2013; Sagiv *et al.*, 2006). Some have suggested that after training, SSD use becomes automatic (Stiles and Shimojo, 2015) and that from this moment the device and the sensory processing becomes 'transparent'. Similarly, Farina (2013) suggested that *“after extensive practice, the device gets increasingly transparent, its boundaries progressively fade away, and the perception experienced through the coupling with it becomes involuntary.”* (p. 652). However, quantitative data on the automaticity of 'visual' experiences during SSD use are lacking.

Furthermore, if the experience of the substituted information does indeed become automatised, this then becomes difficult to reconcile with the notion that the substituting and substituted information should both be consciously perceived. Before training, the experience may lack automaticity (i.e., the substituted information is cognitively deduced from knowledge of the transformation code), whereas after training the experience may lack conscious access to the substituting information. Users could conceivably regress to the substituting modality, but this may then compromise automaticity. Note that the seemingly difficult reconciliation between automaticity and dual-conscious access remains purely speculative and such claims do require further empirical investigation. To examine the automaticity of sensory substitution, further studies should test for interference effects, for example using adapted Stroop tasks (Stroop, 1935). If large interference effects between incongruent and congruent/neutral stimuli are observed, this would provide evidence for an involuntary and automatic perceptual experience during SSD use.

A first attempt to disentangle these views was conducted in a recent study in our lab. Before and after training with The vOICe (Meijer, 1992), participants were tested to see whether auditory stimuli would spontaneously evoke visual images (Pesnot-Lerousseau, Arnold, and Auvray, *in prep.*), using an adapted version of the Stroop paradigm (Stroop, 1935), consisting of an auditory recognition task combined with the simultaneous presentation of visual distractors. Results revealed a stroop-like interference effect only after training, suggesting that people visualise auditory stimuli. This could support the notion of automaticity following training with an SSD. However, the question of whether the interference appears at the visual or at a supramodal level, as well as the influence of visual imagery in the processes, remains unclear and requires further investigation.

#### 2.2.4. Consistency over Time

Synaesthesia is also characterised by a high degree of consistency, such that the sensations evoked by stimuli do not change over time. Consistency tests are often considered the ‘gold standard’ for establishing genuine cases of synaesthesia (Baron-Cohen *et al.*, 1996; Cytowic, 1989; Rich and Mattingley, 2002). Probable synaesthetes often undergo a surprise re-test approximately six months after an initial test in order to establish consistency over time, with 80% accuracy typically required to be considered a genuine case of synaesthesia.

Users of SSDs are not typically subjected to consistency tests over time, so, to our knowledge, there are no similar quantitative data to confirm or disconfirm the consistency of the perceptual experience with sensory substitution. However, assuming the user is able to effectively complete tasks with SSDs, it can be assumed that the substituted information is consistent. In other words, as the translation code remains the same over time, the same object (substituted information) is likely to be translated with the same substituting information, suggesting a consistency over time of the substituted information, in line with a synaesthesia view. Regarding the associated phenomenology, there is only one verbal report suggesting that the user's experience did not change over time (from PF in Ward and Meijer, 2010). However, even though PF reported consistency over time, she also reported the fact that perception of depth and colour emerged after several years of training. This suggests that while her shape perception remained stable over time (one of the easiest parameters to be trained on), her perceptual experience became richer with time. Thus, more evidence is needed to establish whether the associated phenomenology of sensory substitution is consistent over time. It is also noteworthy that depending on training and individual differences, the perceptual experience while using an SSD may change over time, unlike the experience of the concurrent for synaesthetes.

### 2.3. Conclusions Regarding Sensory Substitution as a Form of Artificial Synaesthesia

First, we have highlighted a number of caveats with the synaesthesia view of sensory substitution, which claims that the perceptual experience of using a sensory substitution device can be considered as a form of ‘artificial synaesthesia’. In particular, we have critically assessed the two underlying assumptions that (i) perceptual experience when using SSDs is ‘visual’ and (ii) that both the substituting and substituted information are consciously accessible, which are far from being granted.

Next, we assessed whether sensory substitution adheres to the four essential criteria that characterise synaesthesia. Regarding the perceptual experience of using SSDs (i.e., the associated phenomenology), there appears to be no clear evidence for an *inducer-concurrent pairing*, *automaticity*, or *consistency over time*. Users’ perceptual experience could be considered somewhat idiosyncratic, but with a far narrower set (e.g., phosphenes or perception of colour) compared to synaesthesia. It should also be noted that the data supporting idiosyncrasy of SSD experience are derived from the subjective reports of only two documented cases, thus further evidence is required. Regarding the substituted information, it does appear to be *consistent over time*, and an *inducer-concurrent pairing* seems tenable, given the translation code. However, the extent to which both the substituted and the substituting information are consciously perceived awaits further empirical data and no idiosyncrasy is observed.

In canonical cases of synaesthesia, only one type of concurrent is elicited by a given inducer. For instance, in grapheme–colour synaesthesia exposure to an alphanumeric letter may elicit the involuntary experience of a colour. In sound–colour synaesthesia, exposure to a sound may similarly elicit the involuntary experience of a colour. For sensory substitution, exposure to the substituting information (i.e., soundscapes or tactile stimulation depending on the device), can elicit the experience of either the substituted information and/or the

associated phenomenology. Thus, a parallel between synaesthesia and SSD use requires specifying the output as either the substituted information or the associated phenomenology. Here, we showed that in either case, sensory substitution only adheres to at most two of the four essential criteria that characterise synaesthesia. Taken together, one should avoid using the analogy between sensory substitution and synaesthesia, as this risks erroneous accounts of sensory substitution mechanisms.

### 3. Beyond the Unisensory Perceptual Assumption: Perspectives and Open Questions

As demonstrated above, synaesthesia may not provide a useful explanatory framework for understanding sensory substitution. Sensory substitution is also not the only phenomenon to recently be linked to synaesthesia. Indeed other phenomena described as forms of ‘artificial synaesthesia’ include experiences elicited from over-training of stimulus pairings (e.g., Bor *et al.*, 2015), the use of psychedelic drugs (e.g., Terhune *et al.*, 2016), post-hypnotic suggestion (e.g., Cohen Kadosh *et al.*, 2009) and sweetness enhancement in flavour perception (Stevenson and Boakes, 2004; Stevenson and Tomiczek, 2007). The extent to which these phenomena can and should be described as ‘artificial synaesthesias’ is also controversial. Indeed, many of these examples do not meet the essential criteria that characterise synaesthesia (for reviews see Auvray and Farina, 2017; Deroy and Spence, 2013; Luke and Terhune, 2013; Terhune *et al.*, 2016, 2017). The over-generalisation of synaesthesia to seemingly related phenomena could risk fundamental misunderstandings of the mechanisms underlying these phenomena. Furthermore, treating such a wide range of phenomena as *genuine* or even *artificial* synaesthetic experiences could undermine the understanding of synaesthesia as a unitary concept. Most importantly here, the analogy with synaesthesia might lead to erroneous interpretations of data gathered on sensory substitution.

The synaesthesia view, as well as the earlier cortical dominance and deference views, remained within a unisensory perceptual interpretation of sensory substitution. This unisensory assumption considers that sensory substitution follows what occurs with canonical cases of perception in which specialized unisensory channels transduce external information. This assumption has led to a confirmation bias in the interpretation of the results (see Deroy and Auvray, 2012). Furthermore, the experimental protocols themselves are built with this unisensory assumption in mind which constrains the kind of data gathered. This occurred in early studies concerning (i) brain activation, where mostly unisensory brain areas were investigated, (ii) phenomenological reports, as SSD users were asked questions assuming their experience would be unisensory, (iii) behavioural measures, as participants underwent unisensory perceptual tasks. Alternative multisensory models have begun to emerge, particularly regarding brain mechanisms; however, multisensory approaches to research on the associated phenomenology and behaviour during SSD use are still lacking.

In line with the view of the functional organisation of the brain as a task-selective and sensory-independent machine (Maidenbaum *et al.*, 2014), we highlight that the brain is not composed of strictly modality-dependent regions, but should be viewed as a collection of densely interconnected networks also comprising many modality-independent regions. Thus, sensory substitution likely arises through the reweighting of functional connectivity between different sensory and sensory-independent networks. In other words, rather than touch being perceived in visual cortical areas, eliciting ‘visual’ percepts, it is more likely that connections between somatosensory, visual and sensory-independent structures are reinforced to support performance on a task while using a sensory substitution device.

However, there are still key unanswered questions regarding such task-selective and sensory-independent functional brain networks. Some researchers have noted a key distinction between what has been referred to as a meta/supramodal account of brain organisation (Kupers and Ptito, 2011; Pascual-Leone and Hamilton, 2001; Ricciardi and

Pietrini, 2011) and a crossmodal plasticity account (for a review see Proulx *et al.*, 2014). Both accounts acknowledge the sensory-independent nature of functional brain organisation, in which brain regions are involved in a given form of information processing (e.g., shape recognition), regardless of the sensory modality of the input. However, they differ in their fundamental assumptions regarding development. While crossmodal plasticity is thought to arise through cortical reorganisation following sensory deprivation (i.e., a response to developmental perceptual experience), meta/supramodal representations are thought to exist independently of developmental experience. These competing accounts may not be mutually exclusive as it is also possible that crossmodal plasticity, following from sensory deprivation, results from an unmasking of existing meta/supramodal organisation (Kupers and Ptito, 2011). Further research on the influence of developmental visual experience could help to disentangle different accounts of the functional organisation of the brain.

#### **4. Conclusions and Future Research**

To summarize, we have emphasized the need to move beyond the synaesthesia analogy and the unisensory perceptual account of sensory substitution. This highlighted the need to gather new data in order to disentangle the remaining views of sensory substitution. In particular, it still remains unknown whether at different timepoints after training with SSDs, both the substituted and the substituting information are consciously perceived. Furthermore, quantitative data on the automaticity of sensory experiences during SSD use are lacking. One way to study this is to use adapted Stroop tasks (Stroop, 1935). As mentioned in section 2.2, *Does Sensory Substitution Adhere to the Essential Criteria for Synaesthesia?*, one recent study made a first attempt (Pesnot-Lerousseau, Arnold and Auvray, in prep); however, from their results, the question of whether the interference appears at the visual or at a supramodal level, as well as the influence of visual imagery, remains unclear and requires further investigation. Moreover, gathering additional subjective reports over time with users of SSDs could reveal whether participants' experience resembles more visual, auditory, or cognitive processes. Further reports of additional experiences such as phosphenes, beyond the two reported so far (Ward and Meijer, 2010), could also shed light on common phenomenological experiences with using SSDs.

In addition, links between the neural mechanisms and the associated phenomenology of sensory substitution are relatively unknown. In tactile training experiments (not to be confused with sensory substitution experiments), some blind participants spontaneously reported experiencing visual qualia and these participants were also found to recruit the occipital cortex more than those who did not report visual qualia (e.g., Ortiz *et al.*, 2011). Furthermore, none of the sighted-blindfolded participants reported visual experiences as a result of training. This approach, of investigating subjective reports alongside neural activity, could prove useful for sensory substitution research in establishing relations between the associated phenomenology and the neural mechanisms underpinning sensory substitution. Furthermore, it highlights the need to consider that those who are more permanently deprived of a sense, such as the blind, may have a considerably different subjective experience while using SSDs to neurotypical individuals, as a function of their developmental visual experience. Thus, the relationship between the neural mechanisms of sensory substitution and the associated phenomenology experienced by the user could be a promising avenue for future research on the nature of sensory substitution.

#### **Acknowledgements**

This work was supported by Agence nationale de la recherche grant ANR-16-CE28-0015 "Developmental Tool Mastery" led by Alessandro Farne and by the Labex SMART (ANR-11-LABX-65).

## References

- Amedi, A., Stern, W. M., Camprodon, J. A., Bermpohl, F., Merabet, L., Rotman, S., Hemond, C., Meijer, P. and Pascual-Leone, A. (2007). Shape conveyed by visual-to-auditory sensory substitution activates the lateral occipital complex, *Nat. Neurosci.*, **10**, 687–689. doi: 10.1038/nm1912
- Arno, P., De Volder, A. G., Vanlierde, A., Wanet-Defalque, M.-C., Streel, E., Robert, A., Sanabria-Bohórquez, S. and Veraart, C. (2001). Occipital activation by pattern recognition in the early blind using auditory substitution for vision, *NeuroImage*, **13**, 632–645. doi: 10.1006/nimg.2000.0731
- Arnold, G., & Auvray, M. (2014). Perceptual learning: Tactile letter recognition transfers across body surfaces. *Multisens. Res.*, **27**, 71–90. doi: 10.1163/22134808-00002443
- Arnold, G., & Auvray, M. (2018). Tactile recognition of visual stimuli: Specificity versus generalization of perceptual learning. *Vision Res.*, **152**, 40–50. doi.org/10.1016/j.visres.2017.11.007
- Arnold, G., Pesnot-Lerousseau, J. and Auvray, M. (2017). Individual differences in sensory substitution, *Multisens. Res.*, **30**, 579–600. doi: 10.1163/22134808-00002561
- Asher, J. E., Lamb, J. A., Brocklebank, D., Cazier, J.-B., Maestrini, E., Addis, L., Sen, M., Baron-Cohen, S. and Monaco, A. P. (2009). A whole-genome scan and fine-mapping linkage study of auditory-visual synesthesia reveals evidence of linkage to chromosomes 2q24, 5q33, 6p12, and 12p12, *Am. J. Hum. Genet.*, **84**, 279–285. doi: 10.1016/j.ajhg.2009.01.012
- Auvray, M. (2019). Multisensory and spatial processes in sensory substitution. *Restor. Neurol. Neurosci.*, **37**, 606-619. doi: 10.3233/RNN-190950
- Auvray, M., and Deroy, O. (2015). How do synesthetes experience the world? In *Oxford Handbook of Philosophy of Perception*, M. Matthen (Ed.), pp. 640–658. Oxford: Oxford University Press. doi: 10.1093/oxfordhb/9780199600472.013.027
- Auvray, M. and Farina, M. (2017). Patrolling the boundaries of synaesthesia: A critical appraisal of transient and artificially induced forms of synaesthetic experiences, in *Sensory Blending: On Synaesthesia and Related Phenomena*, O. Deroy (Ed.), pp. 248–274. Oxford University Press, Oxford, UK.
- Auvray, M. and Myin, E., (2009). Perception with compensatory devices: from sensory substitution to sensorimotor extension, *Cogn. Sci.*, **33**, 1036–1058. doi: 10.1111/j.1551-6709.2009.01040.x
- Auvray, M., Hanneton, S. and O'Regan, J. K. (2007). Learning to perceive with a visuo-auditory substitution system: localisation and object recognition with 'The Voice', *Perception*, **36**, 416–430. doi: 10.1068/p5631
- Bach-y-Rita, P. and Kercel, S. W. (2003). Sensory substitution and the human-machine interface, *Trends Cogn. Sci.*, **7**, 541–646. doi: 10.1016/j.tics.2003.10.013
- Bach-y-Rita, P., Collins, C.C., Saunders, F.A., White, B. and Scadden, L. (1969). Vision substitution by tactile image projection, *Nature*, **221**, 963–964. doi: 10.1038/221963a0
- Barnett, K. J., Foxe, J. J., Molholm, S., Kelly, S. P., Shalgi, S., Mitchell, K. J. and Newell, F. N. (2008). Differences in early sensory-perceptual processing in synesthesia: A visual evoked potential study, *NeuroImage*, **43**, 605–613. doi: 10.1016/j.neuroimage.2008.07.028
- Baron-Cohen, S., Burt, L., Smith-Laittan, F., Harrison, J. and Bolton, P. (1996). Synaesthesia: prevalence and familiarity, *Perception*, **25**, 1073–1079. doi: 10.1068/p251073
- Bermejo, F., Di Paolo, E. A., Hüg, M. X. and Arias, C. (2015). Sensorimotor strategies for recognizing geometrical shapes: a comparative study with different sensory substitution devices, *Front. Psychol.*, **6**, 679. doi: 10.3389/fpsyg.2015.00679
- Block, N. (2003). Tactile sensation via spatial perception, *Trends Cogn. Sci.*, **7**, 285–286. doi: 10.1016/S1364-6613(03)00132-3
- Bologna, G., Deville, B. and Pun, T. (2009). Blind navigation along a sinuous path by means of the See CoLoR interface, in *International Work-Conference on the Interplay Between Natural and Artificial Computation*, J. Mira, J. M. Ferrández, J. R. Álvarez, F. de la Paz, F. J., Toledo (Eds), pp. 235–243. Springer, Berlin, Germany. doi: 10.1007/978-3-642-02267-8\_26
- Bor, D., Rothen, N., Schwartzman, D. J., Clayton, S. and Seth, A. K. (2015). Adults can be trained to acquire synesthetic experiences, *Sci. Rep.*, **4**, 7089. doi: 10.1038/srep07089
- Brang, D. and Ramachandran, V.S. (2011). Survival of the synesthesia gene: why do people hear colors and taste words? *PLoS Biol.*, **9**, e1001205. doi: 10.1371/journal.pbio.1001205
- Brown, D. J., Macpherson, T. and Ward, J. (2011). Seeing with sound? Exploring different characteristics of a visual-to-auditory sensory substitution device, *Perception*, **40**, 1120–1135. doi: 10.1068/p6952
- Carton, A. and Dunne, L.E. (2013). Tactile distance feedback for firefighters: design and preliminary evaluation of a sensory augmentation glove, in *Proceedings of the 4th Augmented Human International Conference*, pp. 58–64. doi: 10.1145/2459236.2459247
- Cecchetti, L., Kupers, R., Ptito, M., Pietrini, P. and Ricciardi, E. (2016). Are supramodality and cross-modal plasticity the yin and yang of brain development? From blindness to rehabilitation, *Front. Syst. Neurosci.*, **10**, 89. doi: 10.3389/fnsys.2016.00089



- Chan, K. C., Murphy, M. C., Bang, J. W., Sims, J., Kashkoush, J. and Nau, A. C. (2018). Functional MRI of sensory substitution in the blind, in *2018 40th Annual International Conference of the IEEE Engineering in Medicine and Biology Society (EMBC)*, pp. 5519–5522, Honolulu, HI, USA. doi: 10.1109/EMBC.2018.8513622
- Chebat, D.-R., Schneider, F. C., Kupers, R. and Ptito, M. (2011). Navigation with a sensory substitution device in congenitally blind individuals, *Neuroreport*, **22**, 342–347. doi: 10.1097/WNR.0b013e3283462def
- Chebat D.-R., Maidenbaum S. and Amedi, A. (2015) Navigation using sensory substitution in real and virtual mazes, *PLoS ONE*, **10**, e0126307. doi: 10.1371/journal.pone.0126307
- Clark, A. (2003). *Natural-Born Cyborgs: Minds, Technologies, and the Future of Human Intelligence*. Oxford University Press, Oxford, UK.
- Cohen Kadosh, R., Henik, A., Catena, A., Walsh, V., and Fuentes, L. J. (2009). Induced cross-modal synaesthetic experience without abnormal neuronal connections, *Psychol. Sci.*, **20**, 258–265. doi: 10.1111/j.1467-9280.2009.02286.x
- Cytowic, R. E., (1989). Synesthesia and mapping of subjective sensory dimensions, *Neurology*, **39**, 849–850. doi: 10.1212/WNL.39.6.849
- Deen, B., Saxe, R. and Bedny, M. (2015). Occipital cortex of blind individuals is functionally coupled with executive control areas of frontal cortex, *J. Cogn. Neurosci.*, **27**, 1633–1647. doi: 10.1162/jocn\_a\_00807
- Deroy, O. and Auvray, M. (2012). Reading the world through the skin and ears: a new perspective on sensory substitution, *Front. Psychol.*, **3**, 457. doi: 10.3389/fpsyg.2012.00457
- Deroy, O. and Auvray, M. (2014). A crossmodal perspective on sensory substitution, in *Perception and Its Modalities*, D. Stokes, M. Matthen and S. Biggs (Eds), pp. 327–349. Oxford University Press, Oxford, UK.
- Deroy, O. and Spence, C. (2013). Why we are not all synesthetes (not even weakly so), *Psychon. Bull. Rev.*, **20**, 643–664. doi: 10.3758/s13423-013-0387-2
- Deroy, O., Fasiello, I., Hayward, V. and Auvray, M. (2016). Differentiated audio-tactile correspondences in sighted and blind individuals, *J. Exp. Psychol. Hum. Percept. Perform.*, **42**, 1204–1214. doi: 10.1037/xhp0000152
- De Volder, A. G., Catalan-Ahumada, M., Robert, A., Bol, A., Labar, D., Coppens, A., Michel, C. and Veraart, C. (1999). Changes in occipital cortex activity in early blind humans using a sensory substitution device, *Brain Res.*, **826**, 128–134. doi: 10.1016/S0006-8993(99)01275-5
- Dixon, M. J., Smilek, D., Cudahy, C. and Merikle, P. M. (2000). Five plus two equals yellow, *Nature*, **406**, 365. doi: 10.1038/35019148
- Dormal, G. and Collignon, O. (2011). Functional selectivity in sensory-deprived cortices, *J. Neurophysiol.*, **105**, 2627–2630. doi: 10.1152/jn.00109.2011
- Eagleman, D. M., Kagan, A. D., Nelson, S. S., Sagaram, D. and Sarma, A. K. (2007). A standardized test battery for the study of synesthesia, *J. Neurosci. Methods*, **159**, 139–145. doi: 10.1016/j.jneumeth.2006.07.012
- Farina, M. (2013). Neither touch nor vision: sensory substitution as artificial synaesthesia? *Biol. Philos.*, **28**, 639–655. doi: 10.1007/s10539-013-9377-z
- Grossenbacher, P. G. and Lovelace, C. T. (2001). Mechanisms of synesthesia: cognitive and physiological constraints, *Trends Cogn. Sci.*, **5**, 36–41. doi: 10.1016/S1364-6613(00)01571-0
- Haigh, A., Brown, D. J., Meijer, P. and Proulx, M. J. (2013). How well do you see what you hear? The acuity of visual-to-auditory sensory substitution, *Front. Psychol.*, **4**, 330. ttps://doi.org/10.3389/fpsyg.2013.00330
- Hamilton-Fletcher, G., Mengucci, M. and Medeiros, F. (2016). Synaesthetre: sonification of coloured objects in space, in *Proceedings of the 2016 International Conference on Live Interfaces*, pp. 252–256, Brighton, UK.
- Hanneton, S., Auvray, M. and Durette, B. (2010). The Vibe: a versatile vision-to-audition sensory substitution device, *Appl. Bionics Biomech.*, **7**, 269–276. doi: 10.1080/11762322.2010.512734
- Hanneton, S., Hoellinger, T., Forma, V., Roby-Brami, A. and Auvray, M. (2020). Ears on the hand: reaching three-dimensional targets with an audio-motor device, *Multisens. Res.*, **33**, 433–455. doi: 10.1163/22134808-20191436
- Heimler, B. and Amedi, A. (2020). Task-selectivity in the sensory deprived brain and sensory substitution approaches for clinical practice: Evidence from blindness, in *Multisensory Perception*, K. Sathian and V. S. Ramachandran (Eds.), pp. 321–342. Academic Press, London, UK. doi: 10.1016/B978-0-12-812492-5.00015-2
- Heimler, B., Weisz, N. and Collignon, O. (2014). Revisiting the adaptive and maladaptive effects of crossmodal plasticity, *Neuroscience*, **283**, 44–63. doi: 10.1016/j.neuroscience.2014.08.003
- Heimler, B., Striem-Amit, E. and Amedi, A. (2015). Origins of task-specific sensory-independent organization in the visual and auditory brain: neuroscience evidence, open questions and clinical implications, *Curr. Opin. Neurobiol.*, **35**, 169–177. doi: 10.1016/j.conb.2015.09.001
- Humphrey, N. (2006). *Seeing Red: A Study in Consciousness*. Harvard University Press, Cambridge, MA, USA.
- Hurley, S. and Noë, A. (2003). Neural plasticity and consciousness, *Biol. Philos.*, **18**, 131–168. doi: 10.1023/A:1023308401356
- Jäncke, L., Beeli, G., Eulig, C. and Hänggi, J. (2009). The neuroanatomy of grapheme–color synesthesia, *Eur. J. Neurosci.*, **29**, 1287–1293. doi: 10.1111/j.1460-9568.2009.06673.x

- Kaczmarek, K. A. (2011). The tongue display unit (TDU) for electrotactile spatiotemporal pattern presentation, *Sci. Iran.*, **18**, 1476–1485. doi: 10.1016/j.scient.2011.08.020
- Keeley, B. L. (2002). Making sense of the senses: Individuating modalities in humans and other animals, *J. Philos.*, **99**, 5–28. doi: 10.5840/jphil20029915
- Kim, J.-K. and Zatorre, R. J. (2008). Generalized learning of visual-to-auditory substitution in sighted individuals, *Brain Res.*, **1242**, 263–275. doi: 10.1016/j.brainres.2008.06.038
- Kiverstein, J., Farina, M. and Clark, A. (2014). Substituting the senses, in *The Oxford Handbook of the Philosophy of Perception*, M. Matthen (Ed.), pp. 659–675. Oxford University Press, Oxford, UK.
- Kujala, T., Alho, K., Paavilainen, P., Summala, H. and Näätänen, R. (1992). Neural plasticity in processing of sound location by the early blind: an event-related potential study, *Electroencephalogr. Clin. Neurophysiol.*, **84**, 469–472. doi: 10.1016/0168-5597(92)90034-9
- Kupers, R. and Ptito, M. (2011). Insights from darkness: what the study of blindness has taught us about brain structure and function, in *Progress in Brain Research*, Vol. 192, A. Green, C. E. Chapman, J. F. Kalaska and F. Lepore (Eds), pp. 17–31. Elsevier, Amsterdam, The Netherlands. doi: 10.1016/B978-0-444-53355-5.00002-6
- Kupers, R., Fumal, A., Maertens de Noordhout, A., Gjedde, A., Schoenen, J. and Ptito, M. (2006). Transcranial magnetic stimulation of the visual cortex induces somatotopically organized qualia in blind subjects, *Proc. Natl Acad. Sci. U.S.A.*, **103**, 13256–13260. doi: 10.1073/pnas.0602925103
- Kupers, R., Chebat, D.R., Madsen, K.H., Paulson, O.B. and Ptito, M. (2010). Neural correlates of virtual route recognition in congenital blindness, *Proc. Natl Acad. Sci. U.S.A.*, **107**, 12716–12721.
- Levy-Tzedek, S., Hanassy, S., Abboud, S., Maidenbaum, S. and Amedi, A. (2012). Fast, accurate reaching movements with a visual-to-auditory sensory substitution device. *Restor. Neurol. Neurosci.*, **30**, 313–323. doi: 10.3233/RNN-2012-110219
- Levy-Tzedek, S., Riemer, D. and Amedi, A. (2014). Color improves “visual” acuity via sound, *Front. Neurosci.*, **8**, 358. doi: 10.3389/fnins.2014.00358
- Loomis, J. M., Klatzky, R. L. and Giudice, N. A. (2013). Sensory substitution of vision: importance of perceptual and cognitive processing, in *Assistive Technology for Blindness and Low Vision*, R. Manduchi and S. Kurniawan (Eds), pp. 161–192. CRC Press, Boca Raton, FL, USA. doi: 10.1201/9781315216935
- Luke, D. P. and Terhune, D. B. (2013). The induction of synaesthesia with chemical agents: a systematic review, *Front. Psychol.*, **4**, 753. doi: 10.3389/fpsyg.2013.00753
- Maidenbaum, S., Abboud, S. and Amedi, A. (2014). Sensory substitution: closing the gap between basic research and widespread practical visual rehabilitation, *Neurosci. Biobehav. Rev.*, **41**, 3–15. doi: 10.1016/j.neubiorev.2013.11.007
- Martin, J.-R. and Le Corre, F. (2015). Sensory substitution *is* substitution, *Mind Lang.*, **30**, 209–233. doi: 10.1111/mila.12078
- Mattingley, J. B. (2009). Attention, automaticity, and awareness in synesthesia, *Ann. N.Y. Acad. Sci.*, **1156**, 141–167. doi: 10.1111/j.1749-6632.2009.04422.x
- Meijer, P. B. L. (1992). An experimental system for auditory image representations, *IEEE Trans. Biomed. Eng.*, **39**, 112–121. doi: 10.1109/10.121642
- Merabet, L. B., Battelli, L., Obretenova, S., Maguire, S., Meijer, P. and Pascual-Leone, A. (2009). Functional recruitment of visual cortex for sound encoded object identification in the blind, *Neuroreport*, **20**, 132–138. doi: 10.1097/WNR.0b013e32832104dc
- Mills, C. B. (1999). Digit synaesthesia: A case study using a Stroop-type test, *Cogn. Neuropsychol.*, **16**, 181–191. doi: 10.1080/026432999380951
- Murphy, M. C., Nau, A. C., Fisher, C., Kim, S.-G., Schuman, J. S. and Chan, K. C. (2016). Top-down influence on the visual cortex of the blind during sensory substitution, *NeuroImage*, **125**, 932–940. doi: 10.1016/j.neuroimage.2015.11.021
- Noë, A. (2004). *Action in Perception*. MIT Press, Boston, MA, USA.
- O’Regan, J. K. (2011). *Why Red Doesn’t Sound Like a Bell: Understanding the Feel of Consciousness*. Oxford University Press, Oxford, UK.
- O’Regan, J. K. and Noë, A. (2001). A sensorimotor account of vision and visual consciousness, *Behav. Brain Sci.*, **24**, 939–973. doi: 10.1017/S0140525X01000115
- Ortiz, T., Poch, J., Santos, J. M., Requena, C., Martinez, A. M., Ortiz-Teran, L., Turrero, A., Barcia, J., Nogales, R., Calvo, A., Martinez, J. M., Cordoba, J. L., Pascual-Leone, A. (2011). Recruitment of occipital cortex during sensory substitution training linked to subjective experience of seeing in people with blindness, *PLoS ONE*, **6**, e23264. doi: 10.1371/journal.pone.0023264
- Pacherie, E. (1997). Du problème de Molyneux au problème de Bach-y-Rita, in *Perception et Intermodalité, Approches Actuelles du Problème de Molyneux*, J. Proust (Ed.), pp. 255–293. Presses Universitaires de France, Paris, France.
- Pascual-Leone, A. and Hamilton, R. (2001). The metamodal organization of the brain, in *Vision: From Neurons to Cognition*, Progress in Brain Research, Vol. 134, C. Casanova and M. Ptito (Eds), pp. 427–446. Elsevier, Amsterdam, The Netherlands. doi: 10.1016/S0079-6123(01)34028-1

- Peltier, S., Stilla, R., Mariola, E., LaConte, S., Hu, X. and Sathian, K. (2007). Activity and effective connectivity of parietal and occipital cortical regions during haptic shape perception, *Neuropsychologia*, **45**, 476–483. doi: 10.1016/j.neuropsychologia.2006.03.003
- Pietrini, P., Furey, M. L., Ricciardi, E., Gobbini, M. I., Wu, W.-H. C., Cohen, L., Guazzelli, M. and Haxby, J. V. (2004). Beyond sensory images: Object-based representation in the human ventral pathway, *Proc. Natl Acad. Sci. U.S.A.*, **101**, 5658–5663. doi: 10.1073/pnas.0400707101
- Poirier, C., De Volder, A. G. and Scheiber, C. (2007). What neuroimaging tells us about sensory substitution, *Neurosci. Biobehav. Rev.*, **31**, 1064–1070. doi: 10.1016/j.neubiorev.2007.05.010
- Prinz, J. (2006). Putting the brakes on enactive perception, *Psyche*, **12**, 1–19.
- Proulx, M. J. (2010). Synthetic synaesthesia and sensory substitution, *Consc. Cogn.*, **19**, 501–503. doi: 10.1016/j.concog.2009.12.005
- Proulx, M. and Stoerig, P. (2006). Seeing sounds and tingling tongues: qualia in synaesthesia and sensory substitution, *Anthropol. Philos.*, **7**, 135–150.
- Proulx, M. J., Stoerig, P., Ludowig, E. and Knoll, I. (2008). Seeing ‘where’ through the ears: effects of learning-by-doing and long-term sensory deprivation on localization based on image-to-sound substitution, *PLoS ONE*, **3**, e1840. doi: 10.1371/journal.pone.0001840
- Proulx, M. J., Brown, D. J., Pasqualotto, A. and Meijer, P. (2014). Multisensory perceptual learning and sensory substitution, *Neurosci. Biobehav. Rev.*, **41**, 16–25. doi: 10.1016/j.neubiorev.2012.11.017
- Proulx, M. J., Gwinnutt, J., Dell’Erba, S., Levy-Tzedek, S., de Sousa, A. A. and Brown, D. J. (2016). Other ways of seeing: From behavior to neural mechanisms in the online “visual” control of action with sensory substitution, *Restor. Neurol. Neurosci.*, **34**, 29–44. doi: 10.3233/rnn-150541
- Ptito, M., Moesgaard, S. M., Gjedde, A. and Kupers, R. (2005). Cross-modal plasticity revealed by electrotactile stimulation of the tongue in the congenitally blind, *Brain*, **128**, 606–614. doi: 10.1093/brain/awh380
- Ptito, M., Fumal, A., Martens De Noordhout, A., Schoenen, J., Gjedde, A. and Kupers, R. (2008). TMS of the occipital cortex induces tactile sensations in the fingers of blind Braille readers, *Exp. Brain Res.*, **184**, 193–200. doi: 10.1007/s00221-007-1091-0
- Ptito, M., Iversen, K., Auvray, M., Deroy, O. and Kupers, R. (2018). Limits of the classical functionalist perspective on sensory substitution, in *Sensory Substitution and Augmentation*, F. Macpherson (Ed.), pp. 130–149. Oxford University Press, Oxford, UK.
- Reich, L., Szwed, M., Cohen, L. and Amedi, A. (2011). A ventral visual stream reading center independent of visual experience, *Curr. Biol.*, **21**, 363–368. doi: 10.1016/j.cub.2011.01.040
- Renier, L. and De Volder, A. (2013). Sensory substitution devices: Creating “artificial synesthesias”, in *The Oxford Handbook of Synaesthesia*, J. Simner and E. Hubbard (Eds), pp. 853–868. Oxford University Press, Oxford, UK.
- Renier, L., Laloyaux, C., Collignon, O., Tranduy, D., Vanlierde, A., Bruyer, R. and De Volder, A. G. (2005). The Ponzo illusion with auditory substitution of vision in sighted and early-blind subjects, *Perception*, **34**, 857–867. doi: 10.1068/p5219
- Renier, L., Bruyer, R. and De Volder, A. G. (2006). Vertical-horizontal illusion present for sighted but not early blind humans using auditory substitution of vision, *Percept. Psychophys.*, **68**, 535–542. doi: 10.3758/BF03208756
- Ricciardi, E. and Pietrini, P. (2011). New light from the dark: what blindness can teach us about brain function, *Curr. Opin. Neurol.*, **24**, 357–363. doi: 10.1097/WCO.0b013e328348bdf
- Rich, A. N. and Mattingley, J. B. (2002). Anomalous perception in synaesthesia: A cognitive neuroscience perspective, *Nat. Rev. Neurosci.*, **3**, 43–52. doi: 10.1038/nrn702
- Sadato, N., Pascual-Leone, A., Grafman, J., Ibañez, V., Deiber, M.-P., Dold, G. and Hallett, M. (1996). Activation of the primary visual cortex by Braille reading in blind subjects, *Nature*, **380**, 526–528. doi: 10.1038/380526a0
- Safran, A. B. and Sanda, N. (2015). Color synesthesia. Insight into perception, emotion, and consciousness, *Curr. Opin. Neurol.*, **28**, 36–44. doi: 10.1097/WCO.0000000000000169
- Sagiv, N., Heer, J. and Robertson, L. (2006). Does binding of synesthetic color to the evoking grapheme require attention? *Cortex*, **42**, 232–242. doi: 10.1016/S0010-9452(08)70348-4
- Siegle, J. H. and Warren, W. H. (2010). Distal attribution and distance perception in sensory substitution, *Perception*, **39**, 208–223. doi: 10.1068/p6366
- Simner, J., Harrold, J., Creed, H., Monro, L. and Foulkes, L. (2009). Early detection of markers for synaesthesia in childhood populations, *Brain*, **132**, 57–64. doi: 10.1093/brain/awn292
- Stevenson, R. J. and Boakes, R. A. (2004). Sweet and sour smells: learned synesthesia between the senses of taste and smell, in *The Handbook of Multisensory Processing*, G. A. Calvert, C. Spence and B. E. Stein (Eds.), pp. 69–83. MIT Press, Cambridge, MA, USA.
- Stevenson, R. J. and Tomiczek, C. (2007). Olfactory-induced synesthesias: A review and model, *Psychol. Bull.*, **133**, 294–309. doi: 10.1037/0033-2909.133.2.294
- Stewart, J. and Khatchatourov, A. (2007). Transparency\_1, in *Enaction and enactive interfaces: a handbook of terms*, A. Luciani and C. Cadoz (Eds), pp. 2990–2991. Enactive Systems Books.

- Stiles, N. R. B. and Shimojo, S. (2015). Auditory sensory substitution is intuitive and automatic with texture stimuli, *Sci. Rep.*, **5**, 15628. doi: 10.1038/srep15628
- Striem-Amit, E. and Amedi, A. (2014). Visual cortex extrastriate body-selective area activation in congenitally blind people “seeing” by using sounds, *Curr. Biol.*, **24**, 687–692. doi: 10.1016/j.cub.2014.02.010
- Striem-Amit, E., Dakwar, O., Hertz, U., Meijer, P., Stern, W., Pascual-Leone, A. and Amedi, A. (2011). The neural network of sensory-substitution object shape recognition, *Funct. Neurol. Rehabil. Ergon.*, **1**, 271–278.
- Striem-Amit, E., Cohen, L., Dehaene, S. and Amedi, A. (2012). Reading with sounds: sensory substitution selectively activates the visual word form area in the blind, *Neuron*, **76**, 640–652. doi: 10.1016/j.neuron.2012.08.026
- Stroop, J. R. (1935). Studies of interference in serial verbal reactions, *J. Exp. Psychol.*, **18**, 643–662.
- Terhune, D.B., Luke, D.P., Kaelen, M., Bolstridge, M., Feilding, A., Nutt, D., Carhart-Harris, R. and Ward, J. (2016). A placebo-controlled investigation of synaesthesia-like experiences under LSD, *Neuropsychologia*, **88**, 28–34. doi: 10.1016/j.neuropsychologia.2016.04.005
- Terhune, D. B., Luke, D. P. and Kadosh, R. C. (2017). The induction of synaesthesia in non-synaesthetes, in *Sensory Blending: On Synaesthesia and Related Phenomena*, O. Deroy (Ed.). pp. 215–247. Oxford University Press, Oxford, UK.
- Trivedi, B. (2010). Sensory hijack: rewiring brains to see with sound, *New Sci. Health*, **2773**, 42–45. Available at <https://www.newscientist.com/article/mg20727731-500-sensory-hijack-rewiring-brains-to-see-with-sound/>
- Ward, J. (2004). Emotionally mediated synaesthesia, *Cogn. Neuropsychol.*, **21**, 761–772. doi: 10.1080/02643290342000393
- Ward, J. (2013). Synesthesia, *Annu. Rev. Psychol.*, **64**, 49–75. doi: 10.1146/annurev-psych-113011-143840
- Ward, J. and Mattingley, J.B. (2006). Synaesthesia: an overview of contemporary findings and controversies, *Cortex*, **42**, 129–136. doi: 10.1016/S0010-9452(08)70336-8
- Ward, J. and Meijer, P. (2010). Visual experiences in the blind induced by an auditory sensory substitution device, *Consc. Cogn.*, **19**, 492–500. doi: 10.1016/j.concog.2009.10.006
- Ward, J. and Wright, T. (2014). Sensory substitution as an artificially acquired synaesthesia, *Neurosci. Biobehav. Rev.*, **41**, 26–35. doi: 10.1016/j.neubiorev.2012.07.007
- Ward, J., Huckstep, B. and Tsakanikos, E. (2006). Sound–colour synaesthesia: to what extent does it use cross-modal mechanisms common to us all? *Cortex*, **42**, 264–280. doi: 10.1016/S0010-9452(08)70352-6
- White, B. W., Saunders, F. A., Scadden, L., Bach-Y-Rita, P. and Collins, C. C. (1970). Seeing with the skin, *Percept. Psychophys.*, **7**, 23–27. doi: 10.3758/BF03210126