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Review

Sensory substitution as an artificially acquired synaesthesia

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ABSTRACT

In this review we explore the relationship between synaesthesia and sensory substitution and argue that sensory substitution does indeed show properties of synaesthesia. Both are associated with atypical perceptual experiences elicited by the processing of a qualitatively different stimulus to that which normally gives rise to that experience. In the most common forms of sensory substitution, perceptual processing of an auditory or tactile signal (which has been converted from a visual signal) is experienced as visual-like in addition to retaining auditory/tactile characteristics. We consider different lines of evidence that support, to varying degrees, the assumption that sensory substitution is associated with visual-like experiences. We then go on to analyse the key similarities and differences between sensory substitution and synaesthesia. Lastly, we propose two testable predictions: firstly that, in an expert user of a sensory substitution device, the substituting modality should not be lost. Secondly that stimulation within the substituting modality, but by means other than a sensory substitution device, should still produce sensation in the normally substituted modality.

Contents

1. Introduction

In most examples of sensory substitution, visual information is presented to the auditory or tactile modality by systematically converting properties of vision (usually luminance, vertical and horizontal positions) into auditory properties (e.g. amplitude, frequency) or tactile properties (e.g. intensity) by means of a man-made device. It offers a way of restoring some loss of functioning to the blind and visually impaired. Strictly speaking, such devices are not multisensory because the sensory input conveyed to the user is unimodal hearing or unimodal touch. Nevertheless, there is convincing evidence that the use of these devices (at least in experts; typically users who have become proficient over tens of hours) does resemble vision in certain ways. In this review, we summarise and evaluate the various criteria that have been proposed to determine whether sensory substitution resembles the substituting modality (hearing or touch) or the substituted modality (vision). In particular, we consider the following five criteria:

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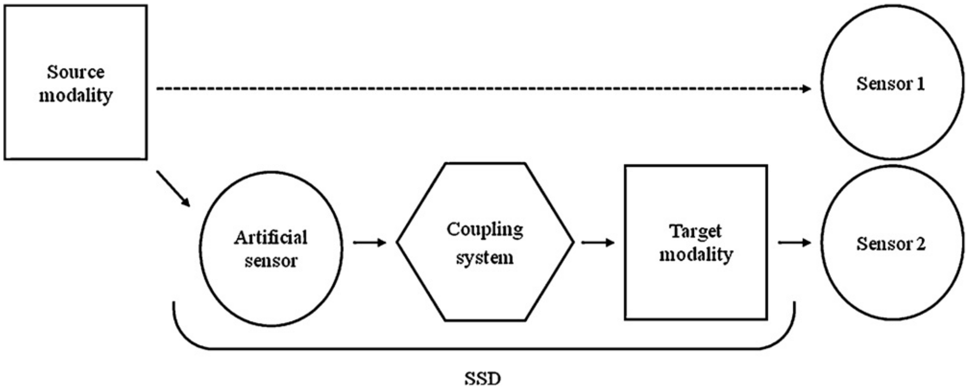

Fig. 1. The basic principles of sensory substitution. In a typical SSD the source modality would be visual information, Sensor 1 would be eyes, and sensor 2 would be the skin or ears. An 'artificial sensor' is typically a camera, the coupling system is the software and the target modality is the hardware relating to the substituting modality (e.g. headphones, vibro-tactile array).

- a behavioural criterion; i.e. the modality is determined by the actions facilitated by use of the device
- a sensory organ criterion; i.e. the modality is determined by the sensory organ that is stimulated and its connections to the brain
- a sensorimotor criterion; i.e. the modality is determined by the way that the sensory signal changes as a result of the users' interactions with the device
- a neurophysiological criterion; i.e. the modality is determined by activity in modality specific neural substrates
- a phenomenological criterion; i.e. the modality is determined by the content of the users' experiences

Whilst we concur with others that sensory substitution has visual-like properties (according to most of the criteria considered), we offer a novel formulation of this. In synaesthesia, a unimodal input (termed the inducer) elicits a percept-like experience (termed the concurrent) that is not normally evoked by that input (this can occur between features of the same sensory modality as well as between modalities). Thus, music may trigger vision (e.g. Goller et al., 2009), sounds may trigger touch (e.g. Beauchamp and Ro, 2008), and touch may trigger vision (Simner and Ludwig, 2012). Similarly, in sensory substitution we suggest that the substituting modality (hearing, touch) is akin to the inducer and the substituted modality (vision) is akin to the concurrent. Importantly though, in synaesthesia the concurrent does not *substitute* for the inducer; for example, music is heard as well as seen. We argue that the same applies to sensory substitution.

Our main position is that sensory substitution shares the characteristics of synaesthesia, but it needs not share the same causal pathways. Certainly the distal (or ultimate) causes of synaesthesia are very different in both cases – developmental synaesthesia is linked to early development and a genetic predisposition (Asher et al., 2009) whereas sensory substitution is linked to experience alone (expertise with the device). It is conceivable however, that they share some of the same proximal causes; for instance, in terms of functional and structural changes to the brain. Whilst others have previously noted a similarity between synaesthesia and sensory substitution (e.g. Cohen Kadosh and Walsh, 2006; Proulx and Stoerig, 2006), in this article we flesh out the similarities in more detail and in the context of the wider literature.

2. Basic principles of sensory substitution

Our working definition of sensory substitution is the artificial conveyance of rich, abstract sensory information of one sense via a different modality. The information is abstract in that it is non-symbolic – that is, the software does not seek to interpret the signal during substitution such as by using object recognition algorithms. The sensory signal is rich in that multiple dimensions within the substituting modality are used to carry visual information.

Sensory substitution is performed by "Sensory Substitution Devices" (SSDs), which are comprised of a sensor, a coupling system and a stimulator. In modern SSDs, the coupling system is typically realised in software. This is illustrated in Fig. 1.

Since the first SSD ("Tactile-Vision Sensory Substitution" or TVSS) was created in the late 1960s (Bach-y-Rita et al., 1969), visual impairment has been the central focus of sensory substitution research. In the original version the information was encoded by touch, but due to the technical difficulties associated with generating tactile stimuli the proliferation of SSDs for the visually impaired have largely targeted audition (Meijer, 1992; Arno et al., 1999; Hanneton et al., 2010). The exception to this trend is the Brainport/TDU (Tongue Display Unit). As a direct descendent of the TVSS, the TDU uses an array of electrodes to deliver electrical stimulation on the tongue (Bach-y-Rita et al., 1998).

All of the aforementioned systems take an image, convert it to greyscale and reduce the resolution. (A notable exception would be the "see ColOr" device, which encodes colour using sounds based on orchestral instruments; Bologna et al., 2009.) Tactile devices map the 2D array of pixels directly onto a 2D array of vibrating points, such that the brightness of each pixel controls the level of vibration (in TVSS) or electrical stimulation (in TDU). Of the auditory systems, it is "The Vibe" that most closely resembles its tactile cousins as it uses the localisation ability of the auditory system to encode the horizontal axis (Hanneton et al., 2010). Due to the relatively poor spatial resolving ability this provides, systems like "The vOICe" encode the horizontal axis in time, so that each image captured by the camera is scanned from left to right over the course of a one-second "soundscape" (Meijer, 1992). Both the vOICe and the Vibe encode the vertical axis using frequency (related to subjective pitch), and encode luminance as intensity (related to subjective loudness). The PSVA functions in a very similar manner to the vOICe, but emulates a human fovea by weighting the centre such that an area one-sixteenth of the total area is responsible for just over half the sounds produced (Arno et al., 1999).

There are certain devices that have a family resemblance to SSDs but would not meet our more restricted definition of sensory substitution. These include white canes and Braille. Both are intended to enable a degree of 'normal' functioning for the blind, and are considered by some as a form of SSD (Bach-y-Rita and Kercel, 2003). Braille systems and Optical Character Recognition (OCR) convert at the symbol-level (letters, words) rather than sensory level. (Embossed letters might be an example of a coupling system at the sensory level.) Language may be better

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understood as being primarily modality-independent (cf. Bellugi et al., 1989).

Canes extend the physical range of our sense of touch, rather than substitute it via a coupling system. In this way they are more like telescopes than sensory substitution devices. Both canes and telescopes are tools that extend and alter perceptual capabilities. Action-based tools have been demonstrated to induce plasticity in the body schema of the user (Cardinali et al., 2009) and plasticity of our visual world may be induced by "tools" such as prisms mounted on to a pair of glasses (Held and Freedman, 1963). Devices which are used instead of canes, but which employ optical or ultrasonic sensors to capture distance information (Farcy and Damaschini, 2001; Froese et al., 2011) more closely resemble our definition of an SSD but lack richness in the type of information that they convey (i.e. a single dimension is converted).

There is no theoretical or practical reason to limit SSDs to the substitution of vision, though non-visual SSDs are less common. A notable example is a tactile-vestibular system which uses electrical stimulation of the tongue to correct posture after the loss of healthy vestibular function (Tyler et al., 2003). A concept related to sensory substitution is sensory augmentation: the addition of a new sensory dimension by presenting it via an existing modality. The best current example of this technique is the "feelSpace" project, which uses a digital compass to control a circular array of vibrating pads worn around the waist. This gives the user access to information about their orientation relative to the earth's magnetic field (Nagel et al., 2005).

3. Is sensory substitution like vision?

In this section we consider how we might know, either from first principles or empirical observation, whether sensory substitution should be categorised as vision (i.e. the substituted modality) or hearing/touch (i.e. the substituting modality). Needless to say, there is likely to be a difference between the novice user and the expert user. How this transition from novice to expert occurs, and how it differs for different devices (e.g. auditory vs. tactile systems), are both important areas for future study. In the early stages of using the vOICe, for instance, auditory working memory ability predicts learning rate with the device but individual differences in visual imagery have little or no impact (Brown et al., 2011).

3.1. A behavioural criterion

A behavioural criterion for seeing is simply that the participant can carry out the functions normally ascribed to vision; i.e. irrespective of sensory input, phenomenology or other considerations. This position is summed up succinctly by Bach-y-Rita (1972): "If a subject without functioning eyes can perceive detailed information in space, correctly localise it subjectively, and respond to it in a manner comparable to the response of a normally sighted person, I feel justified in applying the term 'vision'." (p. ix, Bach-y-Rita, 1972).

The problem with the behavioural criterion is that the accuracy and range of behaviours that can be accomplished with sensory substitution fall far short of that that can be ascribed to vision. To some extent this reflects the limitations of the devices themselves. For instance the TDU and TVSS have array sizes of 20 × 20. This limitation is less severe in auditory devices in which increasing the resolution is done at the level of the software rather than the hardware. Here, the limiting factor in achieving anything approaching visual-like behaviour is the very slow learning rate of the user and their ability to extract the relevant features from the signal (Brown et al., 2011; Kim and Zatorre, 2008). We have recently attempted to modify the image-to-sound conversion algorithm so that it maximises behavioural performance using the process of Interactive Genetic Algorithms in which the parameters determining how vision is converted into sound are optimised iteratively according to the users performance (Wright et al., submitted for publication). However, even so, auditory systems remain slow and difficult to learn.

Although the behaviour when using a SSD is not quantitatively similar to vision, there are some examples in which it is qualitatively similar. One of the most frequently cited examples is of a blind participant wearing the TVSS on their back who lurched backwards when the experimenter increased the magnification on a zoom lens (Bach-y-Rita, 1972). The participant experienced a looming sensation that is more characteristic of vision than touch and, by moving backwards, the implication was that the looming object was in front of the participant rather than behind. In auditory devices, there is evidence that blindfolded-sighted participants (Arno et al., 1999; Cronly-Dillon et al., 1999; Kim and Zatorre, 2008) and blind participants (Cronly-Dillon et al., 2000) can extract shapes from the sounds. This is even true of novice users who can draw simple sonified shapes such as diamonds. Note that shape is normally considered to be a property of visual objects (and haptic ones) but not auditory objects except metaphorically (e.g. sharp tones). However, in this instance, one only needs to rely on certain multisensory 'rules' of association such as the link between frequency, in the auditory domain, and vertical position, in the visuo-spatial domain (such that high pitch denotes high space) to construct shape. Adults show behavioural interference between these dimensions when they are mismatching (Marks, 2004), and even infants show a preference for the matching dimensions (Walker et al., 2010). Similarly, one tends to assume that time also results in extension in horizontal space (Ward et al., 2008b). These innate biases have been likened by some researchers to an implicit or 'weak' form of synaesthesia present in everyone (e.g. Gallace and Spence, 2006; Martino and Marks, 2001). Thus shapes can be constructed intuitively from audition, provided the sensory substitution device exploits naturally occurring multisensory (or 'synaesthetic') associations.

In both the looming anecdote and the shape-from-sound studies, one could argue that the transformation away from the substituting modality is essentially *spatial* rather than visual in nature (Block, 2003). This distinction is, of course, interesting in its own right but the behavioural criterion alone is silent about the phenomenological characteristics. More stringent behavioural tests need to be developed that assess aspects of vision that have less obvious correspondences in other senses such as occlusion, perspective, shadows, or luminance. Visual illusions would be an interesting stimulus material and one study along these lines was carried out by Renier et al. (2005b). The Ponzo illusion is based on perspective and resembles railway tracks converging to a vanishing point. For two horizontal lines of equal length, the line nearer the vanishing point is perceived to be longer. Blindfolded sighted users of an auditory device (PSVA) were susceptible to the illusion when using the sensory substitution device, but only if they focused on the oblique lines before making their judgment about the length of the horizontal lines. Early blind participants, however, failed to show the illusion at all suggesting that interpretation of the auditory representation is mapped to prior visual knowledge but is inconsistent with the idea that the auditory representation is in itself vision-like.

In summary, the behavioural criterion offers some (but only limited) support to the suggestion that sensory substitution is like vision.

3.2. A sensory input criterion

The sensory input criterion is that sensory modalities are determined by the input from the relevant sensory organs (eyes, ears, skin, etc.). The philosophers Keeley (2002) and Grice (1962) are advocates of such a position. In this view, there is an a priori position taken that sensory substitution can never be classed as visual. Keeley (2002) outlines a number of criteria that he considers collectively necessary and sufficient for distinguishing between sensory modalities: these are behaviour; physical stimulation (light, electrical, pressure, etc.); neurobiology (by which he means the sense organ and their connection with the brain); and dedication (by which he means that the organ has been adapted by evolution to respond to certain stimuli; e.g., the eye can produce phosphenes by poking it but it is not dedicated for that kind of stimulation). Thus, whilst humans can detect certain stimuli such as electricity via pain receptors (etc.) they would lack a sense of electroreception. Certain fish, on the other hand, do have dedicated sensory organs for responding to this kind of physical stimulus and would have an electric sensory modality. Keeley (2002) then extends this analogy to sensory substitution and argues that users of such devices can *detect* visual information but that does not constitute vision (just as we can detect electrical information via other senses without having an electrical sense). This logic has more validity for, say, attempts to create a magnetic 'sense' in humans by converting compass points to touch (Nagel et al., 2005) in which there is no pre-existing perceptual qualities or neurophysiology associated with magnetism. However, a reliance solely at the level of sensory organs fails to account for the interesting findings (discussed later) that sensory substitution is linked to visual phenomenology and visual neurophysiology.

One can of course take the sensory input criterion one stage further by considering it at the brain level rather than sensory organ level. One intriguing set of studies along these lines has investigated experimentally 'rewired' ferret brains in which output from the eyes are redirected to the auditory cortex during a critical period. In neonatal ferrets, deafferentation of the pathway from the cochlea to the medial geniculate nucleus results in the development of projections from the retina to the medial geniculate nucleus and thence to the 'auditory' cortex (Sur et al., 1988). By additionally lesioning the lateral geniculate nucleus which projects to the visual cortex the ferrets then develop visual inputs into 'auditory' cortical regions instead of 'visual' cortical regions. Does the auditory cortex take on characteristics normally found in visual cortex? Indeed the neurons in auditory cortex take on visual response properties such as orientation and direction selectivity, and a retinotopic spatial organisation (Sharma et al., 2000). Do the ferrets behaviourally classify retinal input to auditory cortex as vision or sound? The problem with answering this question is that the animal could only do such a task if it had a baseline experience of normal hearing and vision to compare it to. von Melcher et al. (2000) achieved this by performing the rewiring in only one hemisphere, leaving the other hemisphere to perceive sound and light normally. The results are summarised in Fig. 2. When presented with a light to the normal hemisphere the animals were trained to go to spout-V for a reward, and when presented with a sound the animals were trend to go to spout-A (note: the rewired cortex is deaf so performance here depends on the intact hemisphere). The key condition is when light is presented to the rewired hemisphere. In this instance, the animals go to spout-V, consistent with the notion that – in this example – audition has been substituted by the input modality of vision and the sensory modality in the brain derives from the sensory organ.

To translate this research into predictions for human sensory substitution one would be lead to conclude that behaviour defers to the substituting modality; i.e. the use of visual cortex by the blind to process touch and sound should be behaviourally, neurophysiologically and phenomenologically equivalent to touch and sound (not vision). In the sections below, we show that this is not necessarily the case and we argue that these animal studies, intriguing as they are, are not a good analogy for sensory substitution devices.

3.3. Sensorimotor criterion

The sensorimotor criterion for delineating senses (and sensory qualities) states that it does not depend on the physical stimulus, or the brain, or the sensory organs per se but depends crucially on the nature of the *interactions* between the organism and its environment (e.g. Hurley and Noe, 2003; O'Regan and Noe, 2001). In this account the sensory organs are by no means irrelevant and nor is the brain irrelevant (rather it depends on how the brain and environment interact), but neither the sensory organs nor the brain directly determine the content of sensory experience. In fact some go as far as to claim that visual experiences derive from processing in the somatosensory cortex in TVSS (Noe, 2004).

To give some concrete examples, visual objects are affected by occlusion in a different way to auditory objects (such as sound sources). By holding your hands in front of your eyes you can stop seeing someone's face but you will not stop hearing their voice. To give another example, coins can appear elliptical or circular when viewed at different angles and may appear smaller when further away, but a coin manipulated haptically in the hand does not appear to distort in either shape or size. The key point here is that different sensory signals (hearing, vision, touch) change in different – but predictable – ways depending on how one interacts with them.

When visual information is presented in tactile or auditory formats during sensory substitution the substituting modality (audition, touch) takes on the sensorimotor characteristics of the substituted modality (vision) and hence, according to this theory, is constitutive of vision. Thus, an object approaching the body appears to get larger (i.e. occupies more space on the receptive surface) both in vision and when vision is converted to touch, but not in regular tactile perception. Similarly, the sensory signal associated with viewing a plate or coin would change predictably depending on its angle with respect to the receptor surface and this happens in both vision and when vision is converted to sounds, but not during normal auditory perception.

Evidence for the sensorimotor account comes from observations that in order to be able to effectively use a sensory substitution device one needs to 'embody' it; that is, the position of the visual camera (or equivalent) with respect to the body needs to be incorporated into the interpretation of the sensory signal. Bach-y-Rita (1972) noted with TVSS that participants needed to manipulate the camera themselves in order to experience the exteriorised feelings in front of them, and that the same did not occur if the camera was manipulated by the experimenter. In order to localise an object in external space, one needs to compute the position and orientation of the input 'receptor' surface (i.e. the camera in the case of most SSDs). Auvray et al. (2007) trained participants over many hours to locate or recognise objects using the vOICe. Localising, but not recognising, objects was described by participants as resembling vision. The embodiment idea is also supported by behavioural (e.g. Holmes et al., 2007; Serino et al., 2007) and neurophysiological (e.g. Iriki et al., 1996, 2001) studies of active tool use (but not passive holding) in which an external device is incorporated within bodily space (or bodily space is extended/projected into the location of the tool). As noted previously, an SSD is a particular type of tool distinguished only be the fact that it presents information converted from another modality.

Needless to say, not all the sensorimotor aspects of vision are reproduced in sensory substitution devices. Lower level properties, arising at the oculomotor level, do not have a direct parallel in SSDs. However, it would be interesting to know whether, for instance, there are differences in expert users between holding a camera in the hand versus on the head (for behavioural explorations of this with novices see Brown et al., 2011). A head-based location of a sensor may facilitate sensorimotor behaviour that is more comparable to real vision than a hand-held location. One expert user

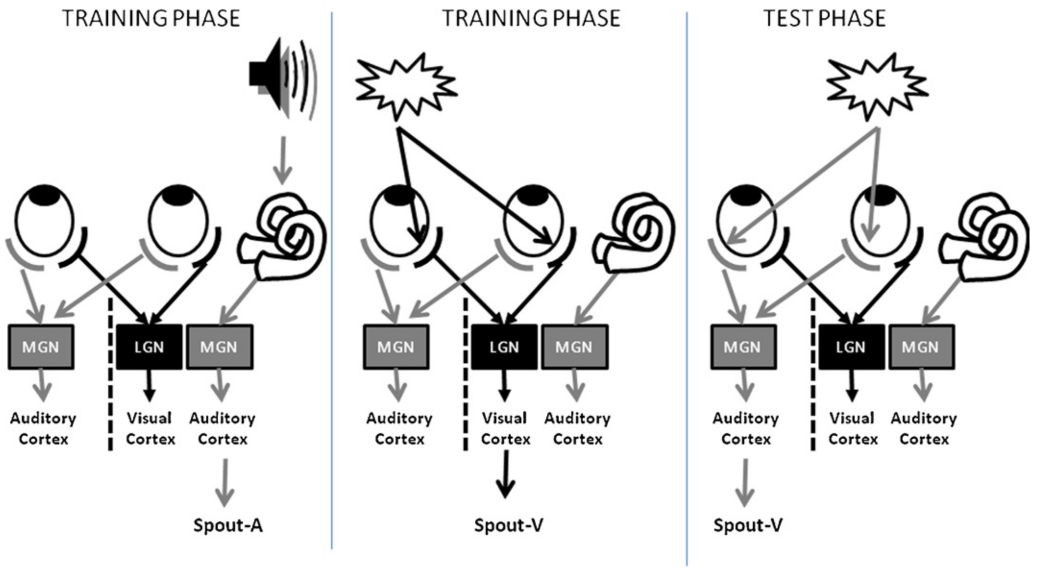

Fig. 2. In the study of von Melcher et al. (2000), ferrets had one intact hemisphere and one 'rewired' hemisphere in which the retina send inputs to the medial geniculate nucleus and thence to the 'auditory' cortex. During training, the ferrets are presented with auditory and visual stimuli to the intact hemisphere (left and middle panels respectively) and trained to go to one of two spouts depending on the stimulus modality. At test (right panel), they were presented with visual stimuli to the rewired hemisphere and the animals spontaneously went to the visual-related spout suggesting that the auditory modality had been substituted by vision.

of the vOICe, PF (discussed in detail below), who users a head-mounted camera is noted to make small continuous movements of her head that resemble saccades, and this may have some similarity to the head-based saccades found in sighted people who have lost the ability to move their eyes (Gilchrist et al., 1998). Not all the sensorimotor aspects of vision are reproduced in sensory substitution devices and, conversely, not all the characteristics of vision may be easy to explain by sensorimotor contingencies. The most obvious property that resembles vision is the spatial 'out there' aspect that is reported. Other aspects of vision such as luminance might be harder to account for in sensorimotor terms, but could be explained by synaesthesia-like multisensory relationships (at least in the late blind) between luminance and loudness (Marks, 2004) and luminance and tactile properties such as smoothness and weight (Martino and Marks, 2000; Ward et al., 2008a).

3.4. *Neurophysiological criterion*

The neurophysiological criterion for establishing whether sensory substitution could be considered a form of seeing is whether it recruits the neural substrates typically used for vision (Poirier et al., 2007a).

One of the first studies to explore this, using PET, was conducted by Arno et al. (2001). Participants were trained and tested on a visual-to-auditory device (PSVA) to recognise patterns and shapes such as a 'T' or 'E' in various rotations and this was done by moving a pen over a graphics tablet which produced a sound when the shape was traversed. Both blindfolded sighted and early blind participants were tested. In both groups, a variety of regions involved in visual and spatial imagery, including the precuneus and the lateral parietal lobes, were activated in this task relative to baselines of auditory detection. Interestingly an extrastriate region of occipital cortex (BA 18) showed a group × task interaction. For the early blind, the region was more active during sensory substitution than rest whereas in the blindfolded group it was more active in rest than during the sensory substitution condition. As such, this study suggests that the use of 'visual' regions during sensory substitution may depend on pre-existing functional reorganisation in the early blind (e.g. Noppeney, 2007) as well as level of expertise with the device. Consistent with this, Collignon et al. (2007) conducted a TMS study on this critical region, in which similar shapes were presented via a camera (rather than graphics tablet) using PSVA to blindfolded-sighted and early-blind participants. Shape recognition was disrupted by TMS but only in the early blind group. The same region was also found to be used by the blind group for spatial localisation of sounds but not for other aspects of auditory processing (loudness, pitch).

A PET study of shape recognition using the TDU (Ptito et al., 2005) is also consistent with the results of Arno et al. (2001) and Collignon et al. (2007). They trained early blind and blindfolded sighted participants to recognise shapes (an 'E' from various orientations). After training the blind participants, but not the sighted, showed evidence of activity in the occipital cortex when performing the task.

Other functional imaging studies have, however, found visual cortical activity from auditory sensory substitution devices using shape recognition (Poirier et al., 2007b) and perception of perspective-based depth cues (Renier et al., 2005a) in *sighted* participants and, in both instances, it was used to endorse the view that "perception through the substitution device could be visual-like" (p. 1108, Poirier et al., 2007b) and "perceptions obtained by sensory substitution of vision are visual in nature" (p. 578, Renier et al., 2005a). The challenge for these studies is to establish whether such activity is functional and how it relates to phenomenology.

Finally, the study of Amedi et al. (2007) differs in that it studied two blind expert users (one late blind, one early blind) who had used an auditory-based device, the vOICe, extensively during daily life rather than having been trained for the purpose of the experiment. A group of sighted controls also received significant training (over 40 h) with the device. The lateral occipital complex, a region known to respond to shapes from touch and vision, was found to be activated by sonified images of objects but not the same sounds scrambled or other control sounds (e.g. "moo", hammering). This activity was found for both sighted experts and blind experts (but not by sighted novices). Moreover, a further study showed that TMS over this region impaired the ability of one of the blind users to recognise objects using the device (Merabet et al., 2009). She also reported that her experiences were 'darker' and 'not as crisp' after occipital stimulation.

In summary, there is evidence that regions of the brain normally dedicated to vision can be used to process visual information presented via touch and sound. This is particularly apparent in the blind, but may also occur in sighted individuals. This may be a more extreme form of the normal tendency for visual cortical involvement in the processing of hearing and touch (Sathian, 2012), which makes it very difficult to equate activity in visual regions with visual experience in a simple manner.

3.5. *Phenomenological criterion*

The phenomenological criterion is that the self-reported experiences when using the device resemble those of the substituted modality (vision) rather than the substituting modality (touch, hearing). This idea has already been encountered, in particular with reference to the observation that TVSS expertise leads to externalised experiences that are more characteristic of vision than touch. The notion that phenomenology resembles vision during sensory substitution is a core part of sensorimotor theories of perception, because these theories assume that sensory phenomenology is essentially nothing more than the mode of interacting with the environment, and the way in which sensory information changes as result of such interactions.

There is not, however, a necessary relationship between using the neural resources of vision and having a visual phenomenology. Both early and late blind people activate the visual cortex when processing touch and sounds (Noppeney, 2007) and such activity appears to be functional, i.e. it contributes to actual performance (e.g. Cohen et al., 1997). However, most blind people do not report “seeing sounds” or “seeing touch” (a few of them do and we regard this is an acquired form of synaesthesia; Afra et al., 2009). There is of course a logical problem here in the case of the early blind, who have no memory of what seeing is like. This leaves the unanswerable possibility that they do experience vision via other senses but are unable to report it as such (because to them vision would be seen as integral to the inducing modality rather than ‘extra’). For proponents of sensorimotor theories of perception, activity in visual regions triggered by *normal* hearing and *normal* touch should not produce experiences of vision (because the sensorimotor contingencies are those of hearing and touch). However, activity in visual regions triggered by tactile devices such as TVSS and auditory devices such as the vOICe should produce experiences of vision (because the sensorimotor contingencies are those of vision despite the input being tactile and visual). Moreover, this would be equally true of early and late blind given that (in this theory) seeing via touch or sound does not require a memory/history of sight, it merely requires sensorimotor interactions that are equivalent to sight. In fact, sensorimotor theories, in their strongest form, predict that visual experiences should arise from visual sensorimotor contingencies irrespective of whether it happens to be supported by the visual cortex, the auditory/somatosensory cortex, or elsewhere.

Although it is meaningless to ask early blind participants whether their sound and touch has visual phenomenology (because they do not know what vision is like), it is possible to train them to use sensory substitution devices and see if their phenomenology changes. Bach-y-Rita presents many anecdotes along these lines. However, the most detailed first person account was given by Guarniero (1974) who did feel that the phenomenology changed as a result of using the device and ascribed words such as ‘seeing’, ‘watching’ and ‘field of view’ to describe it. He notes: “I have used the word ‘see’ for lack of better. The difficulty is not merely one of vocabulary; rather, it is a conceptual one. Very soon after I learned how to scan, the sensations no longer felt as if they were located on my back, and I became less and less aware that vibrating pins were making contact with my skin.” (p. 104). There is, however, little to suggest that Guarniero (1974) had sensations of light and dark and, as such, the new experiences appear primarily to be a remapped spatial representation rather than visual phenomenology.

Moving on to the TDU, what is the phenomenology associated with this device? Kupers et al. (2006) trained sighted and blind participants to detect motion on the tongue using the TDU. They subsequently applied TMS to the occipital cortex to determine whether it elicited visual experiences, tactile experiences, or both. None of the sighted participants reported tactile sensations from TMS over the occipital cortex, whereas four blind participants (3/8 early bind, 1/5 late blind) did report tongue-localised sensations following TMS but only after training with the device. This suggests that, at least in some blind people, the visual cortex gives rise to somatosensory phenomenology. However, the study does not report what phenomenology is experienced when using the TDU itself.

A recent study with a tactile ‘device’ was reported by Ortiz et al. (2011). They used a tactile display in which participants (sighted and blind) were trained over 3 months to discriminate line orientation presented using tactile stimulation of the hand. This is not strictly a SSD (by our definition) because the tactile information delivered to the skin is not derived from another sense. Nor is there an embodiment of the camera or visual-like sensorimotor contingencies. Nonetheless, several of the blind group (both early and late) reported visual experiences as a result of the training such as “I can see a white line . . . Honestly, I can see it but I do not feel it” (p. 3). None of the sighted controls did. EEG recordings were consistent with occipital sources in this blind sub-group. The blind participants who did experience it either had some residual vision (e.g. in the early blind group) and/or lost their sight in adulthood; i.e. sensations of luminance were not experienced for the first time but were, instead, linked to the tactile device. To date, this is the only known reference to luminance perception via a tactile device.

To turn next to the auditory domain, Ward and Meijer (2010) reported detailed descriptions of two long-term users of the vOICe. PF lost her sight in early adulthood as a result of an industrial accident and discovered the vOICe some twenty years later. PF has been the focus of a number of empirical investigations, described above (Amedi et al., 2007; Merabet et al., 2009). CC had progressive visual loss due to rod dystrophy noted in adolescence and was registered blind at the age of 33. She began to use the vOICe around a decade later. The timing here is important because neither participant reported visual experiences from sound in the long period of blindness prior to immersively using the vOICe, despite the likelihood that their brains had undergone neuroplastic changes during this time, and despite the importance of hearing in their daily functioning. However, within only a couple of months of wearing the vOICe both participants reported re-experiencing visual phenomenology. This is broadly consistent with the sensorimotor view that visual experience depends on visual-like modes of exploration (note: PF wears a camera on her head, but CC uses the camera on her mobile phone but typically held on a cord around the neck).

Both PF and CC report luminance perception that is qualitatively different from that experienced in their residual vision. For instance, PF describes it as “There IS true light perception generated by The vOICe. When I am not wearing The vOICe the light I perceive from a small slit in my left eye is a grey fog. When wearing The vOICe the image is light with all the little greys and blacks” (p. 495, Ward and Meijer, 2010) and CC notes that “You can still see blurred things ahead of you [from residual normal vision] but what will occupy your attention is the image of something else” (p. 496, Ward and Meijer, 2010). Depth perception is something that both participants reported as emerging after having a ‘flat’ percept of luminance, shapes, and edges. Depth is not something that is directly represented by the vOICe but is inferred from cues such as perspective and also user-based explorations (e.g. moving the head forwards/backwards and noting how the signal changes).

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Moreover, the vOICe is not well-suited for representing movement (because it takes 1 s to hear a single frame) but both participants report that their experience is continuous rather than a series of snapshots.

Both PF and CC are likely to use their prior experience of vision to augment their phenomenology. For instance, for PF objects such as her computer are seen as box-like and lacking in detail (because she never saw a personal computer before going blind) whereas a Christmas tree can be 'seen' in great detail. This, of course, may make one wonder whether this is just visual imagery rather than vision via sensory substitution. There are two points to note against this. Firstly, visual imagery alone cannot explain the shift in experience before versus after immersion with sensory substitution. Whilst the sound of a car horn could trigger a visual image of a car, this is quite different in nature from the information in a soundscape. The former is a purely symbolic mapping (mediated by the concept of 'car'), whereas the latter could convey the type of vehicle, its perspective, location, and so on (mediated by the algorithm of the device). Secondly, 'normal' vision is itself constrained by top-down knowledge so it would be odd to deny it a role in sensory substitution. As O'Regan (2011) notes: "The only difference is that whereas imagining finds its information in memory, seeing finds it in the environment. One could say that vision is a form of imagining, augmented by the real world." (p. 66). This also seems like an apt description of the visual experiences reported by PF and CC when using the vOICe.

Having outlined the evidence, the next section examines in more detail the hypothesis that sensory substitution is a type of acquired synaesthesia induced by expertise in a SSD.

4. The similarities and differences between sensory substitution and synaesthesia

The section above suggests that, to some extent, sensory substitution is linked to visual-like: behaviour, sensorimotor contingencies, neurophysiology and phenomenology despite not meeting the sensory organ criterion. However, rather than assuming (as others have done) that sensory substitution *is* an example of seeing, our hypothesis is that many of the findings in the sensory substitution literature that have been reviewed above can be best explained by assuming that sensory substitution is, in at least some expert users, akin to synaesthesia. Firstly, we consider synaesthesia in more detail. Then we go on to consider some predictions arising from our hypothesis.

4.1. Synaesthesia: visual-like experiences from non-visual input

In synaesthesia, the phenomenology is often one of visual-like experiences (typically colour, but also luminance, texture and shape) that are triggered by a stimulus that does not typically elicit those experiences. These visual-experiences are linked to functional and structural differences within the visual cortex and fronto-parietal network (Rouw et al., 2011). This 'translation' from one modality to another often happens at the symbolic level. For instance, in the case of 'coloured speech' the colours are often determined by the letters and words themselves rather than the sensory properties of the auditory input (Baron-Cohen et al., 1993). Cases of grapheme-colour synaesthesia are sometimes described as visual-to-visual but the inducer can be more accurately described as symbolic rather than visual given that it is the identity of the letter rather than its perceptual rendering that appears to be crucial (e.g. Myles et al., 2003). However, the translation can also happen at the non-symbolic level such as when voices (Fernay et al., 2012) or music (Ward et al., 2006) trigger vision. In these cases, the translation is sensitive to auditory features such as pitch, loudness and timbre. The same sound played to different synaesthetes tends to result in quite different descriptions. Although the descriptions are heterogeneous they are not random and there is a tendency across synaesthetes to associate high pitch with high vertical space and high luminance, and to experience music as moving from left to right (Ward et al., 2006, 2008b). In the tactile domain, there are reported links between high pressure and high luminance (Ward et al., 2008a). The same 'synaesthetic' mappings have typically been employed in SSDs and affect multisensory judgments in non-synaesthetes (Marks, 2004). As such, it is possible that the choice of mappings employed by SSDs may be conducive to acquiring synaesthetic experience because they are in some sense 'natural' insofar as they reflect the structure and function of the brain rather than contingencies in the environment.

In terms of the causes of synaesthesia, it is generally not considered as something that can be learned via training. Indeed, although training has been shown to facilitate performance on behavioural measures of synaesthesia, it does not appear to cause the development of true synaesthetic associations (Meier and Rothen, 2009; Colizoli et al., 2012) and longer term exposure to colour associations does not result in the same pattern of brain activity as synaesthesia (Elias et al., 2003). Developmental forms of synaesthesia are assumed to have a genetic component (Asher et al., 2009). However, acquired forms do exist and tend to be related to sensory loss, particularly blindness due to damage to the eye or optic nerves (e.g. Jacobs et al., 1981; Rao et al., 2007). However, it can also arise from sensory loss associated with brain damage (Beauchamp and Ro, 2008; Vike et al., 1984). In acquired synaesthesia the cause is considered to be environmental and is attributable to the given pathology or event leading to the damage. In the cases of sensory substitution described above the cause is environmental but is attributed to expertise with the device rather than blindness per se. However, blindness or other forms of sensory deprivation (such as blindfolding) may still be important for acquiring the necessary expertise. Based on the multisensory principle of inverse effectiveness (e.g. Anastasio et al., 2000), mastery of a sensory substitution device is likely to be greater when vision is lost or absent. That is, normal vision is likely to take precedence over visual information translated to sound/touch unless the latter is more informative than the former. At the neural level, one possible mechanism that may account for both acquired synaesthesia after blindness and synaesthesia-like experiences associated with sensory substitution is the 'unmasking' or removal of inhibitory pathways to the occipital cortex from auditory, tactile or multisensory regions. A similar account has been proposed for developmental synaesthesia (Grossenbacher and Lovelace, 2001) but remains controversial (e.g. Hubbard and Ramachandran, 2005).

What is it about expertise with an SSD that can lead to visual-like experiences? We have previously endorsed the sensorimotor view, namely that the auditory/tactile signal obeys the sensorimotor contingencies of vision (Ward and Meijer, 2010). We also suggested that the precise mappings used (e.g. luminance-pressure, pitch-vertical space) may be a second important factor. However, the recent study of Ortiz et al. (2011) is problematic for strict sensorimotor theories of vision (e.g. Hurley and Noe, 2003; O'Regan and Noe, 2001). In that experiment, there was no camera and the tactile signal did not obey the sensorimotor contingencies associated with vision, nevertheless many of the blind experts reported synaesthetic visual phenomenology to the tactile stimuli and showed accompanying visual neurophysiology. This raises the possibility that expertise alone together with an understanding of multisensory principles may be sufficient to induce synaesthetic experiences in the blind.

Sensorimotor theories of vision have difficulty in accounting for the existence of developmental synaesthesia (Hurley and Noe, 2003; Noe and Hurley, 2003). This is because vision triggered by,

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say, music or speech obeys the sensorimotor properties of sound rather than vision. Thus a coloured shape triggered by the sound of a trombone is typically not reported to be sensitive to occlusion, perspective, the position of the eyes (and so on). Thus, sensorimotor accounts may not offer a complete account of either synaesthesia or sensory substitution (Gray, 2003).

4.2. The inducing modality is not lost in sensory substitution

We disagree with the view presented elsewhere that sensory substitution entails losing the properties of the inducing modality. For instance, O'Regan (2011) states that "He rapidly came to feel the stimulation he was receiving on the skin of his back as not being on the skin, but 'out there' in front of him" (p. 137). However, there is no evidence that suggests that normal tactile or auditory processing is lost (or even disrupted) by sensory substitution – but that is exactly what is predicted by proponents of the sensorimotor view.

Our account is similar to that offered by others. For example, Humphrey (2006) describes reports of sensory substitution as a "complicated *dual* experience" (p. 58, emphasis in original). Bach-y-Rita (1996), whilst proposing that TVSS can be classed as vision, also maintains that touch is not lost: "even during task performance... the subject can perceive purely tactile sensations when he is asked to concentrate on those sensations". Auvray and Myin (2009) also argue that sensory substitution could be considered a novel form of perception that is neither visual nor auditory/tactile but that contains elements of them both. However, none of these previous researchers made an explicit comparison with synaesthesia.

It is not difficult to account for why the inducing modality may *appear* to be diminished. Namely, that expertise reduces the need to attend to the inducing modality and thereby reduces awareness of it. Whether or not participants can allocate attention to the concurrent modality independently of the inducing one is an open one that would be interesting to explore. Moreover, it would be interesting to compare to the literature on multisensory attention (Koelewijn et al., 2010) and synaesthesia (Mattingley, 2009). In grapheme-colour synaesthesia, attention to (and awareness of) the inducing stimulus appears to be an important factor for the concurrent to be experienced at all (Mattingley, 2009).

There could be various reasons why the substituting modality is not lost. For instance, this could happen if the sensory organs (or the modality-specific cortices) themselves provide constraints or biases on what is experienced (Hurley and Noe, 2003). Perhaps more importantly the blind user continues to have 'normal' auditory and tactile stimulation in addition to those coupled to the substituting device and this may be sufficient to prevent them being truly substituted. In this key respect it differs from the rewired ferrets in which normal sensory functioning is lost (through lesioning) in addition to new pathways being formed (von Melcher et al., 2000). As such, this example should not be considered an animal analogue of synaesthesia and, by extension, nor does it bear close resemblance to sensory substitution.

4.3. The inducing stimuli should not be limited to the device itself

The idea that sensory substitution resembles an acquired synaesthesia makes further predictions. Namely, that auditory stimuli that resemble those linked to the SSD should also generate visual phenomenology (and be linked to visual neurophysiology in the brain). This is indeed the case for the vOICe users PF and CC (Ward and Meijer, 2010). When the device is not worn, similar sounds do indeed trigger visual experiences (e.g. the sound of a reversing lorry may elicit a streak of light), but they did not do so before acquiring expertise with the device. As such, their brains have internalised the 'rules' by which the device converts vision into sound and these rules are automatically applied to convert sounds into vision irrespective of whether the sounds have a real world correspondence to vision (in terms of meaningful input from an SSD) or not. Again, this automaticity and inevitability is strongly characteristic of synaesthesia in general.

We predict that the same should be true for touch. We predict that, after sufficient learning of the TVSS, appropriate stimulation of the back should elicit visual-like experiences irrespective of whether the stimulation is delivered by the device or by other means. However, contrary to our prediction, Bach-y-Rita and Kercel (2003) note that "when he/she scratches his/her back under the [TVSS] matrix nothing is 'seen'". We suggest that it is possible that users of the TVSS/TDU do have such experiences but have not been tested or questioned thoroughly enough about it. There is also the possibility that what counts as 'appropriate stimulation' is narrowly defined. We know that not all sounds elicit vision in users of the vOICe (it may depend on how similar the sounds are to the vOICe; Ward and Meijer, 2010) and the same is likely to be true in the tactile domain (e.g. food on the tongue is likely to be treated differently to electrical stimulation of the tongue). However, our explanation makes the testable prediction that visual-like experiences should not be limited to use of the device itself in expert users and should generalise to at least *some* comparable inducing stimuli.

5. Summary, challenges and further questions

We have shown that sensory substitution devices meet (with varying success) the behavioural, sensorimotor, neurophysiological and phenomenological criteria for being categorised as the sense that they substitute. Consequently, sensory substitution matches the schema for synaesthesia, with the substituting sense acting as the synaesthetic inducer and the substituted sense as the resulting synaesthetic concurrent. An important distinction between sensory substitution and developmental synaesthesia, however, is the nature of acquisition. In the case of the latter, the inducer does not obey the sensorimotor contingencies of the modality of the concurrent, so the origin of these links cannot be explained by sensorimotor accounts. We have also suggested that sensorimotor theories may not be able to offer a complete account of sensory substitution too. It remains an open question as to whether sensory substitution, acquired synaesthesia, and developmental synaesthesia share similar neural mechanisms (despite having different distal causes).

By associating sensory substitution with synaesthesia, we have been able to make some testable predictions. Firstly, we claim that in sensory substitution the substituting/inducing modality is not lost. It is possible that the existing evidence which seems to contradict this view can be explained in terms of a shift of salience, rather than the loss of a sensory event. A second hypothesis arising from this classification of sensory substitution is that it should be possible to induce phenomena in expert users using stimuli in the substituting modality even when that stimuli is not produced by an SSD. The reverse, that developmental synaesthesia might eventually be better understood as a result of this comparison, is at present less obvious. Nevertheless, by exploring how two fascinating behaviours of the brain are related, we are sure to further our understanding of these, and related, processes.

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