

# The Process of Distal Attribution Illuminated Through Studies of Sensory Substitution

Jess Hartcher-O'Brien<sup>1,2,\*</sup> and Malika Auvray<sup>1,2</sup>

<sup>1</sup> Institut Jean Nicod, CNRS UMR 8129, Département d'Etudes Cognitives, Institut d'Etude de la Cognition, Ecole Normale Supérieure, Paris, France

<sup>2</sup> LIMSI CNRS, B.P. 133, Orsay-Cedex, 91400 France

Received 31 December 2013; accepted 30 June 2014

---

## Abstract

When we interact with objects in our environment, as a general rule we are not aware of the proximal stimulation they provide, but we directly experience the external object. This process of assigning an external cause is known as distal attribution. It is extremely difficult to measure how distal attribution emerges because it arises so early in life and appears to be automatic. Sensory substitution systems give us the possibility to measure the process as it occurs online. With these devices, objects in our environment produce novel proximal stimulation patterns and individuals have to establish the link between the proximal stimulation and the distal object. This review disentangles the contributing factors that allow the nervous system to assign a distal cause, thereby creating the experience of an external world. In particular, it highlights the role of the assumption of a stable world, the role of movement, and finally that of calibration. From the existing sensory substitution literature it appears that distal attribution breaks down when one of these principles is violated and as such the review provides an important piece to the puzzle of distal attribution.

## Keywords

Sensory substitution, distal attribution, prior of a stable world, movement, calibration, externalisation

## 1. Distal Attribution

As we move through the world, we are directly aware of external objects not the proximal stimulation they provide at our receptors (Crick and Koch, 1995; O'Regan, 1992). For instance, changes in air pressure or vibrations arriving at our cochlea are perceived as arising from an object in the environment (such as a moving car) rather than from the cochlea itself. In this instance, proxi-

---

\* To whom correspondence should be addressed. E-mail: jesshartcher@gmail.com

mal patterns of stimulation (e.g., vibrations in the cochlea) are perceived as having an external cause (e.g., the car). What are the cues necessary for this assignment to emerge?

### 1.1. Definition

Distal attribution, also known as externalisation, occurs when we experience a pattern of stimulation and assign the cause of this stimulation to an object, stimulus, or event located in external three-dimensional space. This process allows us to make sense of the world around us. When proximal stimulation (i.e., stimulation received at the receptor surface) is not assigned an external cause, it gives rise to a mere sensation, not the perception of an object located at a distance. Therefore understanding how distal attribution emerges is key to understanding the distinction between sensation and perception.

### 1.2. The Problems in Investigating Distal Attribution

The process of distal attribution is so automatic and present so early in life that it is extremely difficult to investigate it objectively or even to understand how it emerges (Bach-y-Rita, 2002; Loomis, 1992). Studies attempting to understand the phenomenon of distal attribution have therefore relied upon instances where distal objects give rise to novel proximal stimulation patterns, as happens with the use of sensory substitution devices (SSDs from now on) (Auvray *et al.*, 2005; Bach-y-Rita, 1972; Bach-y-Rita *et al.*, 1969; Epstein *et al.*, 1986; Loomis, 1992; von Békésy, 1955; White *et al.*, 1970).

To introduce them, SSDs were initially designed to assist or replace specific functions of a deficient sensory modality by providing corresponding information to an alternative sensory modality. This can be achieved by converting the stimuli normally sensed through the deficient modality (e.g., light for SSDs compensating for vision) into stimuli accessible to another sensory modality (e.g., tactile vibrations or sounds). Since their inception in the sixties various kinds of devices have been developed, tested, and shown to allow their users to behave to some degree as if they possessed the substituted sensory organ (see Auvray and Myin, 2009; Bubic *et al.*, 2010; Deroy and Auvray, 2012, for reviews). For instance, thanks to visual-to-auditory and visual-to-tactile conversion systems, blind individuals report being able to localize and recognize objects in three-dimensional space (e.g., Auvray *et al.*, 2007; Bach-y-Rita *et al.*, 1969; Levy-Tzedek *et al.*, 2012). Sensory substitution offers a novel way to investigate how distal attribution emerges because with sensory substitution devices the boundary between proximal- and distal-attribution is blurred. Such devices provide the unusual circumstance in which the perceiver initially experiences a proximal pattern of stimulation and, after training, perceives this same pattern as a distal event (Bach-y-Rita, 2002).

### *1.3. Review Objectives*

With SSDs, it is possible to observe how users transform the proximal stimulation rendered by the device into an experience of external objects. In such mediated perception (similar to the non-mediated kind), if we fail to assign a distal cause, we would no longer have a perceptual space corresponding to physical space, but we would be left with the sensation only. Therefore, as was mentioned above, understanding how distal attribution emerges, in both instances, is crucial to understanding perception itself. When distal attribution fails to emerge with SSDs, the users do not establish the corresponding hypothesis of a distal cause of the sensation (e.g., Bach-y-Rita, 1972; Epstein *et al.*, 1986). The literature to date has not directly addressed the link between prior beliefs of an external stable world and the process of distal attribution. Here we will explore the role of such assumptions in the emergence of distal attribution using SSDs. Furthermore we will identify three components essential for distal attribution to emerge: movement with its consequent feedback about the world, calibration of space, and the prior of a stable world. In turn this will allow us to reconcile how the use of distance perception as synonymous with distal attribution has changed our approach to testing distal attribution with SSDs. We would suggest that distance perception is a bi-product of the distal attribution process and that both phenomena depend on a prior of a stable world (e.g., Glennerster *et al.*, 2006; Knill, 2007).

## **2. Establishing External Space**

### *2.1. Problems of Establishing External Space with SSDs*

As was noted above, SSDs allow us to sense distal objects by providing novel proximal stimulation that corresponds to the external object at an alternative receptor surface. As such, the novel perceptual space that emerges is not necessarily a function of the same assumptions, regularities or spatial maps as those underpinning non-mediated perception. Through the SSD interface, observers have to re-learn the relationships between the experienced pattern of stimulation and the properties of the external objects. When distal attribution of proximal stimulation does not occur in SSD space, it is possible to see how prior beliefs fail to transfer and how the process of distal attribution breaks down. For example, if a proximal pattern of stimulation is experienced on the skin and is derived from interacting with a teacup 0.5 meters away, then the observer needs to re-establish the relationship that links the received proximal patterns to the teacup. If only the proximal pattern is experienced, i.e., without its link to the external object, then the perceiver does not experience external space and as a consequence no distance estimate can be derived.

On the other hand, if the observer has no reason to assume that the experienced pattern represents an object 0.5 meters away, then the mere experience of tactile vibrations, i.e., the lack of distal attribution, is the most parsimonious interpretation of the incoming stimulation. In a recent study, Siegle and Warren (2010) investigated the perceived distance of objects experienced through a minimalistic SSD. Participants were divided into two groups and performed the task under two different conditions: observers were asked either to focus their attention on the proximal stimulation on the body surface or, in the second condition, they were asked to focus their attention on the distal source. Blindfolded participants observed a target light using a device consisting of a single finger-mounted photodiode that drives tactile vibration on the back whenever the finger points at the target. After active exploration of their environment, participants had to move a reference object (experienced without the SSD) to match the perceived egocentric distance of the target. The participant group who were instructed to focus their attention on the distal object had higher performance than the group who focused their attention on the proximal stimulation during the task. However, while Siegle and Warren's study clearly showed a difference in performance between the two groups, this difference could be the result of attention rather than distal attribution per se. In non-mediated perception both externalisation and distance estimation depend upon the prior of an external world. Although the two can be conflated, as in Siegle and Warren's study, it is important to understand their relative contributions to our construction of an external space. In the following sections we will discuss what is known about the emergence of the concept of space in non-mediated perception and then turn to the role of such processes in SSD space.

### *2.1.1. The Emergence of Space During Non-Mediated Perceptual Processing*

We do not have direct access to the physical world. When we move our nervous system is provided with feedback about its current environment. Thus what we have access to are the relative changes in position of our sensory organs (e.g., our eyes or hand), and the consequent changes in sensory input. The consequence of movement is that our senses acquire a sequence of stimulation patterns. The information from this sequence is sufficient to determine the structure of 3D space (e.g., Glennerster *et al.*, 2006; Graham, 1989). Therefore we can experience space through the simple relationship between, for example, the distance the eyes have moved and concurrent changes in sensory stimulation. Thus our experience of an external world depends upon our ability to account for the effects of self-generated movement on changes in proximal stimulation. When the two are correlated in time, the sensory input can be experienced as objects in external space. In a Bayesian sense, the nervous system has a remarkable ability to detect statistical correlations between

sensory inputs and receptor states and it can use this information to form perceptual representations of the external world.

To minimise the cost of keeping track of the changes, the nervous system can establish the likelihood that a given sensorimotor relationship indicates a particular physical object and thus predict the influence of other exploration patterns. Previous research suggests that the cost of keeping track of the changes can also be minimised by integrating prior knowledge we have about the world and the physical laws that constrain objects therein (e.g., Glennerster *et al.*, 2006; Hayward, 2011; Loomis, 1992). To map proximal stimulation to objects in external space, the nervous system has to have an assumption that there is an external world. Inherent in this is the belief that the world is stable and that any physical object can only change its position (according physical laws) or its state (according to the laws of nature).

When space emerges from our interactions with the environment, the number of spatial dimensions that we perceive depends upon the sensor we use to detect the incoming information: perception of objects in depth is most easily accessed through vision, audition and haptics/kinaesthetic. In his seminal work, “The World of Touch”, Katz (1925) suggested that touch has many of the capabilities of a distal or ‘far’ sense, such as vision and audition (see also Krueger, 1970 for a summary of Katz’s work). However, spatial properties of objects, such as their distance from the observer, are readily available through the ‘far senses’ but not to the other senses and in this way our experience of space depend on the sensory receptor stimulated. For tactile perception, attribution to a distal source or to the body surface can differ depending on the circumstances: Active exploration via touch tends to promote distal attribution, whereas passively received tactile input to the skin are more likely to be experienced as coming from the body itself (Gibson, 1962; Katz, 1925). If visual information is converted into a tactile code then the ability to passively experience depth depends on remapping this property into a property accessible to the skin. Therefore, it is important to consider how the perception of external objects changes when we use a SSD. One issue is that in non-mediated perception, experience consolidates the mapping between the proximal stimulation and its distal object over time. In SSD space novel mappings emerge and need to be consolidated over time. Moreover, the information experienced via the device needs to be aligned with information coming from other sensory modalities.

### *2.1.2. Maintaining Spatial Relations when Going from Physical to Perceptual Space*

In order to survive, organisms need to correctly locate objects in space, orient to them, or flee from them. To aid in this response optimisation, humans and other animals have evolved spatial maps or fields that organise the incoming

information according to the spatial relations among physical objects. Each sensory modality has its own map and set of coordinates. The nervous system establishes spatial maps at low-level processing sites and all perceptual information is segregated according to these maps throughout the processing hierarchy. To be beneficial to behaviour, information from the different maps needs to be aligned such that a coherent object localisation emerges despite different sensory co-ordinates. Animal research indicates that neurons at multisensory sites such as the SC and the VPM cortex code the object location relative to the receptor used and furthermore that different sensory maps are aligned (e.g., Graziano *et al.*, 1999; Lee and Groh, 2009). When an auditory signal is moved in depth, neurons in the monkey's ventral premotor cortex are selectively tuned to respond maximally to specific locations in physical space (Graziano *et al.*, 1999). Through the selective responses a neural spatial map is established in the premotor cortex. Critically, these neurons, unlike those in A1 or visual areas, also respond to visual stimuli located in the same external co-ordinates. Animal and human research alike suggests that these maps are critical to our perceptual representation of space and spatial relations (Graziano *et al.*, 1999; King *et al.*, 2001; Moore and King, 1999; Poggio and Fisher, 1977).

We acquire information about the world from all of our senses. Our ears detect air pressure changes, our eyes monitor light patterns, our skin reports the pressure of objects impinging on it, and our nose and mouth measure the chemical content of our current environment. Despite the variety of routes that sensory information can take to get to our brains, we tend to experience the world as a unified entity. We are also capable of recruiting different types of sensory information for the same purpose, irrespective of which sensor was initially responsible for detecting the information. Given this, proximal stimulation through a SSD should potentially correspond to the experience of an object located in external space. Although distal attribution through SSDs has been the subject of many studies, most research has focused on the behavioural changes and therefore there is no information relating spatial map organisation to perception of spatial properties of the world during SSD use. It remains to be seen which maps will be recruited for coding the incoming information and how the interactions with the objects in 3D space are altered. One possibility is that perception mediated by a SSD, produces similar neural changes as those occurring in sensory deprivation (see Knudsen, 1999) and the consequent recruitment of a different sensory pathway to process incoming information. That is, the maps recruited to organise the proximal stimulation would correspond to those of the functional modality. In any case, for distal attribution to emerge the nervous system needs to adapt to the novel sensorimotor mappings and thus re-establish external space. Whether and how this changes the neural processing is not yet completely understood. The interesting aspect for the

current review is how the possible changes in sensory information would be organised to maintain spatial relations.

### **3. The Process of Distal Attribution**

The distinction between proximal stimulation and attribution of this stimulation to an external object requires the assumption of an external world (e.g., Epstein *et al.*, 1986). This may seem an obvious statement. Indeed it is. However, not addressing such assumptions alters how we define the key principles or mechanisms underlying distal attribution. Many studies have explored the question of how distal attribution arises during SSD-use. Early studies were based on qualitative reports (e.g., Bach-y-Rita *et al.*, 1969) whereas later studies used different measurement techniques, differing not only in their objectivity, but also in whether participants had direct knowledge of external space or only the sensory substitution space (e.g., Epstein *et al.*, 1986; White *et al.*, 1970). Each measurement technique has advantages and disadvantages. But here we focus on how embedding the assumption of an external world in the task itself, as opposed to defining space as purely an internal entity, alters the attribution process. We will address how valid the SSD data are in informing us about the process of distal attribution itself. We will then define the essential components influencing distal attribution. The factors involved in this process are: (1) the prior of a stable world; (2) the link between self-generated movement and the resulting sensory stimulation patterns and the additional laws of movement necessary for spatialisation (i.e., reversibility and interposition); and (3) the role of calibration in establishing and maintaining an experience of external space.

#### *3.1. The Problematic Aspects of SSD Measures for Understanding the Process of Distal Attribution*

There are numerous verbal reports from participants in SSD studies that detail the emergence of distal attribution after prolonged SSD-mediated experience (Bach-y-Rita *et al.*, 1969). That is, SSD-users report experiencing objects in the environment and this tends to dominate the proximal stimulation afforded by the device (Bach-y-Rita, 1972; Lenay *et al.*, 2003; Segond *et al.*, 2005). More particularly, SSD-users have indicated that, as a consequence of training, they no longer feel the tactile stimuli on their skin, where they occur, but interpret them directly as an object located in external space (see Bach-y-Rita, 2002). One well-cited verbal report comes from Guarniero, a blind philosophy student, after training with the TVSS: "... very soon after I had learned how to scan, the sensations no longer felt as if they were on my back, and I became less and less aware that vibrating pins were making contact with my skin. By this time objects had come to have a top and a bottom; a right side and a left;

but no depth — they existed in an ordered two dimensional space.” (Guarniero, 1974, p. 104).

One issue with verbal reports is that they cannot be verified in the way an objective measure can (e.g., a left–right judgment). Although these verbal reports indicated that distal attribution emerges in SSD space after training, there was no additional measure to specify how it emerged. That is, it remains unclear whether these reports reflect a genuine perceptual experience of distal objects or a cognitive inference based on perceived patterns in the proximal stimulation. The techniques used to address the question of distal attribution via SSDs have improved since the inception of the devices. In the following sections we will highlight the assumptions and cues to distal attribution that have emerged from the existing studies.

### *3.2. The Role of the Prior of a Stable External World*

To externalize proximal stimulation we need to assume the existence of an external world. Without this prior belief (or assumption) that the external world is a stable entity, neither distal attribution nor the explicit distance estimates of the distal object would be possible. As mentioned above, when we explore the world, we do not have direct access to the objects in space. What we have access to are the proximal patterns of activation and our own movements (Merleau-Ponty, 1945). The nervous system compensates for the distortions in incoming stimulation, due to movement, and manages to maintain the experience of a stable world and of the objects therein. The prior of an external, stable world is essential to this process. This prior posits that objects are stable. Inherent in this is that if an object changes it can only change its state (according to the laws of nature) or its position (according to the laws of physics). When a change is inconsistent with either positional or state changes in the object itself, the parsimonious assumption is that observer-generated movement must have caused the change in incoming information. These kind of changes can easily be correlated with the efference copy of the observer’s movement and therefore compensated for. The compensation phenomenon is known as perceptual constancy (e.g., Gregory, 1963). This mechanism suggests how the distal object is maintained, not how it emerges. Below we consider the relative contribution of this prior compared to that of the signal-receptor interaction to shaping the experience of an external world.

One way to explore this is to look at the modality specific constraints to distal attribution and measure their influence. If modality specific constraints prevent attribution to a distal source then it is reasonable to assume that the process is not amodal in nature but depends on cues that are modality specific. For example, visual-to-tactile SSDs may provide inputs that obey visual laws or principles. Yet, it is also possible that such constraints do not apply to the tactilely sensed information. There is a vibrant discussion addressing this is-

sue of whether the novel emergent perceptual space is defined by either the substituting or substituted modality, or something else altogether (Auvray and Myin, 2009; Deroy and Auvray, 2012; Loomis *et al.*, 2012).

Feedback about the world (the result of an action/perception loop) makes it possible to establish the mapping between self-generated movement and changes in the proximal stimulation. One question is what is altered in our representation of space when information is remapped from one sensory modality to another with SSDs? Using a visual-to-tactile SSD, Epstein *et al.* (1986) delivered patterns of vibrotactile stimulation to the participants' index fingertip. They assessed how the participants attributed the transformations of vibrotactile stimulation as a consequence of self-generated movement. Attribution was measured through asking participants to rate how well a variety of scenarios matched what they experienced. Analysis of the ratings from these scenarios revealed that although the participants became aware of the relationship between self-generated movement and stimulation transformations, they never chose the scenario that corresponded to the real set-up, i.e., the SSD set up. The authors concluded that their participants had not developed the hypothesis of distal sources, that is, the hypothesis that the ultimate cause of their vibrotactile experience was an encounter with an object in an external world. Here we see an example in which no distal cause is assigned probably because participants do not have an assumption that the stimulation is part of an external world.

However, a second study by Auvray *et al.* (2005), using a visual-to-auditory sensory substitution device (the Vibe, see Hanneton *et al.*, 2010) and a similar method to that of Epstein *et al.* (1986) demonstrated that people appeared to be able, under certain conditions, to attribute stimulation to a distal object. In this study, the scenarios were re-written in order to determine which component of distal attribution the participants reached: the existence of a correlation between their movements and the resulting sensory stimulation (coupling), the existence of an object that caused their sensations (object), and the existence of external space produced by this coupling (space). In the conditions in which there were no additional cues to that provided in Epstein *et al.*'s study, participants in Auvray *et al.*'s study similarly failed to reach the hypothesis of a distal cause although participants indicated that they experienced a sensorimotor coupling between their own actions and the sensed information.

In this case, the device rendered the objects in such a way that they could plausibly exist independently of the existence of external space. However, in a second condition Auvray *et al.* gave their participants a cardboard sheet that they could use as an occluder. The cardboard served as an occluder because by moving the sheet vertically participants could interrupt the source of stimulation. As such intermittent calibration of external space occurred because, if the cardboard could interrupt the source of stimulation, it must therefore be

located *behind* the cardboard, i.e., in external space. These two studies demonstrate the importance of (a) the assumption of an external stable world and (b) the ability to interact with that world and account for the perturbations caused by the interactions.

Other studies used both 2D and 3D spatial estimates (White *et al.*, 1970) and egocentric distance estimates (Siegle and Warren, 2010) to specify the external world. As such they invoked the stable world prior, which informed the way users made sense of the SSD input. White *et al.* (1970) observed that SSD users were able to estimate the slant of a tactually sensed visual object. That is, they had access to the third dimension of external space in their novel perceptual space. Siegle and Warren tested whether observers were more veridical in distance estimates when they focused on the proximal patterns of stimulation or on the distal object. Both the study by White *et al.* (1970) and Siegle and Warren (2010) demonstrated improvements in performance when observers assumed an external 3D world. From the work mentioned so far it is possible to see that SSDs offer a unique opportunity to study distal attribution as it emerges. However, as discussed here, the SSD studies also have their limitations.

### 3.3. *The Role of Movement*

What are the cues necessary for the nervous system to assign a distal cause to the proximal stimulation at a receptor surface? Many studies note the importance of movement (e.g., Bach-y-Rita *et al.*, 1969; Haynes *et al.*, 1965; White, 1970): In all SSD studies, active exploration of the environment is necessary to establish the existence of external space. During exploration the organism can determine the mapping between changes in the incoming stimulation and its self-generated movements (Auvray *et al.*, 2005; Bach-y-Rita *et al.*, 1969; Hurley and Noë, 2003; Loomis, 1992; O'Regan and Noë, 2001; von Békésy, 1955; White *et al.*, 1970). Movement also allows us to account for deformations that are derived from self-generated movement or physical displacement. For example, spatial position of physical objects is mapped onto retinal location when objects are sensed visually. If an external object caused the stimulation pattern then eye movements should alter the retinal location of the object; whereas if the input is not linked to a position in external space, then eye-movements should have no impact on the perceived location of the stimulation. For proximal attribution on the other hand, incoming sensory information and your efference information should not be correlated. For example, the locus of pain in your fingertip remains at your fingertip even if you move your finger relative to the rest of your body. Therefore being able to account for changes in feedback about the environment as a consequence of exploring it is essential for externalisation of the proximal stimulation.

### *3.3.1. Space from Eye Movements*

If we take the example of visual processing, the retinotopic coding of the eye might suggest that the location can be read off from the receptor array, yet the retinal image is not the only source of spatial information. Important contributions to the updating of spatial representations come from efferent oculomotor signals (von Helmholtz, 1925), as revealed by experiments in which stimuli are displayed immediately before or during saccades (Hallett and Lighthstone, 1976; Wurtz, 2008). The role of local movement patterns coupled to afferent information could also be derived from the extra-ocular muscle proprioception as was suggested by Sherrington (1918). However, experimental evidence on the function of eye proprioception has remained controversial (Donaldson, 2000), leading to the idea that this signal is primarily used for oculomotor calibration and learning rather than for spatial representation (Lewis and Maler, 2001; Poletti *et al.*, 2013). However, in a first instance the correlation can be used to define stimulation in external co-ordinates. Extra-retinal signals can consequently calibrate this space. Whether the correlation between the extra-ocular muscle movement and the retinal image combined is sufficient to experience 3D space without early calibration from touch is still a contentious issue (e.g., Gori *et al.*, 2010).

When we consider space perception, we usually refer to the process through which humans and other organisms become aware of the relative positions of their own bodies and objects around them. Space perception provides cues, such as depth and distance, which are important for movement and orientation in the environment. At a functional level if we consider that space emerges in the interaction between the organism and its environment (e.g., Terekhov and O'Regan, 2013) then spatial perception is derived from the organism establishing the relationship between action and the resulting stimulation patterns. Furthermore, the ability to perceive different spatial dimensions depends upon the constraints of each sensory modality to move within two or three dimensions. In the case of the latter, what assumptions constrain the space that emerges through SSD-information? How do these assumptions differ from those derived by exploration and perception during unmediated circumstances? To tentatively address these questions let's consider the experience of three-dimensional space during normal development. In a series of intriguing studies into spatial constancy, Bower (1964, 1965, 1966a, b) explored whether infants perceive only the retinal projection or the external object. Using generalization of operant responding to assess discrimination, Bower demonstrated that two-month-old infants see the constant real size and shape of an unfamiliar object despite variation in its projective size and shape produced by altering distance and slant. In addition, consistent with processing of visual objects in adult humans, these infants detect variation in the object's physical size and shape when its angular projection remains constant. This evidence for object

representation in such a young developing nervous system suggests that attribution of the proximal stimulation to a coherent external object is present in pre-crawl infants. Thus, simple eye and head movement appear to be sufficient to establish an external cause of the proximal stimulation patterns.

Similar findings (e.g., Caron *et al.*, 1978; Shuwairi *et al.*, 2007) also highlight some of the behavioural changes (and the corresponding evoked potential changes) that allow somatosensory externalization (Rigato *et al.*, 2014). Rigato *et al.* (2014) provided recent insights into how the developing nervous system establishes the external location of visual and somatosensory objects and re-maps the proximal stimulation (in receptor coordinates) into external coordinates. These authors demonstrated that making the transformation from proximal stimulation to an external source occurs slowly during the first year of life, and involves not only neural response changes but the ability to update for postural changes in the infant's own body representation. Therefore infants require knowledge about effector position changes in order for them to be able to externalise incoming patterns of stimulation.

The knowledge derived from movement, both for distance perception and distal attribution is the corner stone of the sensorimotor tradition (e.g., O'Regan and Noë, 2001). From a more traditional viewpoint, von Helmholtz (1909) also observed its importance: "It is only by voluntarily bringing our organs of sense in various relations to the objects that we learn to be sure as to our judgments of the causes of our sensations. We explain the table as having existence independent of our observation because, at any moment we like, simply by assuming the proper position with respect to it, we can observe it." It should be mentioned that this necessity of a structured correlation between actions and sensations in order to allow distal attribution was nicely anticipated by Condillac (1754). If we were only able to passively receive sensations, we would not understand that these sensations refer to objects that exist in an external world. Indeed, if all our knowledge about the world came from our sensations, and if sensations were just passive modifications of our minds, how could we infer the existence of an external world? For Condillac, our exploratory movements allow us to extract the spatial organisation present in our sensations; it is this spatial organisation of the objects in the world that allows us to consider them as external. In other words, spatialisation and object-hood emerge simultaneously.

It should be noted that the movement necessary to reach distal attribution goes beyond a mere coupling between sensation and actions; it must also reflect a group structure. In other words, the experience of external space cannot be reduced to correctly extracting the existence of a coupling between action and sensation. Indeed, understanding a correlation between self-generated movements and their resulting stimulation involves understanding that *different* actions give rise to *different* sensations. There is a space of displacements

when the *same* actions can give rise to *different* sensations, and when *different* actions can give rise to the *same* sensation. For instance, von Helmholtz (1909) highlighted that actions that can cancel each other from the viewpoint of sensory inputs determine a mathematical group structure, and properties of such a group characterize displacements within a geometrical space. The same sensation obtained by different actions can then be understood as “position” of an object. This was concisely explained by Poincaré (1905) according to who reversibility is the only way to differentiate a change in state from a change in position.

Movement along multiple axes is useful for establishing the existence of external objects. With SSD study results, it is tempting to try to disentangle which movement trajectories are most useful in this process, e.g., translation (changing the position of an object), or rotation (circular movement around a centre point). Comparing the movement type (translation and rotation) across studies demonstrating either distal attribution or a lack thereof, however does not lead to a definitive picture. Both Siegle and Warren (2010) and Epstein *et al.* (1986) allowed observers to translate the sensor through space. In one case the consequent vibrotactile pattern was attributed to an external object (Siegle and Warren, 2010) while in the other, no distal attribution emerged (Epstein *et al.*, 1986). As such we can simply conclude that correlated changes between self-generated movement (even with a camera end-point) and sensory feedback are necessary, without being able to classify the optimal motion type. However, the essential difference between the two studies for this review is that Siegle and Warren’s study involved the prior of an external world whereas Epstein *et al.*’s study did not, suggesting this prior to be an important factor for distal attribution.

### 3.4. *Calibrating and Maintaining External Space*

We have discussed the importance of a prior of a stable world and the role of movement in the emergence of distal attribution. In the following sections we address how our experience of external space is maintained via sensory calibration and spatial maps in non-mediated perception. Although a lot is known about the role of calibration of space for information that is conveyed by functional sensory modalities (e.g., King *et al.*, 1988; Knudsen, 1999; Lee and Groh, 2009), the role that calibration plays in maintaining an experience of external space in SSD environments has been rather neglected. In the following two sections we discuss how calibration operates for perception in non-mediated conditions and then postulate its possible role in SSD-mediated external space.

#### 3.4.1. *The Potential Role of Calibration*

All measurement systems require calibration to become and remain accurate. Our perceptual system is no different. Calibration, in the case of our senses,

usually refers to the process of adaptation as a way of producing environmentally geared behaviour (Mon-Williams and Bingham, 2007). While this is particularly critical in vision given that our visual system has no direct access to attributes such as distance, solidity, and size (Ho *et al.*, 2009), cross-sensory calibration occurs for most senses at one time or another: Visual object attributes must be calibrated, that is, verified through touch; auditory position must be calibrated by vision (e.g., King *et al.*, 2001). In each instance the sense with the least error calibrates its co-occurring counterpart. Indeed, since vision is often distorted (see Gori *et al.*, 2010) haptic feedback may be fundamental in improving visual perception through calibration. Calibration has been recognized as essential for maintaining a coherent representation across the senses (e.g., Wallace *et al.*, 1998). In calibration it is important that the system receives feedback (traditionally an error signal) in order to be able to adapt to the conditions it currently experiences: changes in object information occur as we move through the world, calibration is necessary to link the consequent changes in stimulation patterns to the experienced objects (e.g., Ernst, 2008).

However, calibration may also be fundamental to more gradual processes occurring during development, in which a sensory modality calibrates (or teaches) the others about some properties of the world. For instance, recent studies reinforce the suggestion that the haptic system has a role in calibration of the visual system in judgments of position and size. Both animal and human studies have highlighted the role of cross-sensory calibration in the development of spatial processing (Bergan and Knudsen, 2009; Gori *et al.*, 2011; Zwiers *et al.*, 2001, 2003).

If the nervous system is to make full use of the spatial relations among objects and use these relationships to interact with the environment, then online (re)calibration is essential. Experiments in which animals have been reared with modified auditory or visual inputs have revealed substantial plasticity in the animal's spatial representations (e.g., Knudsen, 1999). If animals are raised with distorted binaural cues (used for sound localisation) locating auditory objects in external space produces compensatory changes that can be induced in the auditory space map (e.g., in ferrets, see King and Parsons, 1999; and barn owls, Gold and Knudsen, 2000). These adjustments in auditory spatial tuning tend to preserve the alignment with the visual representation. In owls, they are brought about by frequency-specific shifts in neuronal tuning to interaural time differences (ITDs) and interaural level differences (ILDs) (Gold and Knudsen, 2000), although, as discussed below, the basis for this adaptive plasticity in humans may be different. It is also important that information coming in from completely different co-ordinate systems can be integrated if co-occurring and segregated if not. Spatial maps are one way to achieve this (see Lee and Groh, 2009).

The human (and other animal) nervous system clearly establishes spatial maps to enable efficient processing of incoming information and allow the stimulation to be mapped from receptor to external space. As such there is a need for calibration across the sensors to verify object positions in external coordinates (for example, see Lee and Groh, 2009; Mancini and Haggard, 2014). From the studies exploring space perception via SSDs, there is almost no consideration given to the role of such calibration in learning to perceive the proximal stimulation as distal and maintain this experience over time (e.g., Auvray *et al.*, 2005; Bach-y-Rita, 1972; Bubic *et al.*, 2010; Epstein *et al.*, 1986; Hanneton *et al.*, 2010; Siegle and Warren, 2010). One could speculate that the SSD experiments require such a long training phase not only due to learning the translation code between substituted and substituting modality but also as they may involve a calibration phase. In such an interpretation the nervous system would calibrate the space by feedback derived from self-generated movement.

When we experience visual or tactile objects, they are generally coded within a specific set of coordinates that allows the nervous system to extract the relative position of the object in space. The nervous system establishes spatial maps at low-level processing sites and the perceptual information is segregated according to these maps throughout the processing hierarchy. Sensorimotor acts involve multiple transformations: When we point to an object, a chain of nested coordinate transformations occurs. These include the retinal map itself (target-to-eye), eye-to-head, head-to-body, and body-to-arm mappings. The complexity of coordinating such simple actions is aided by spatial map alignment. However, in exploring the relationship between distance perception and distal attribution, the role of spatial maps and calibration for updating the perceptual space need to be considered separately.

### *3.4.2. Spatial Maps and the Calibration of External Space*

Before crossmodal spatial calibration can effectively guide interactions in the world the incoming information needs to be organised in a spatial field in which coordinate systems can be compared and integrated. Not only are signals in the environment organised in a spatial pattern but this pattern is mirrored at a neural level for vision, audition, and touch (see King and Moore, 1991). In fact the amount of plasticity evident at the level of the superior colliculus in many animals is a clear indicator that the sensory maps are used to coordinate action and integrate information across the different coordinate systems. The assumed functional use of spatial maps in the superior colliculus is that they are for optimising orientation responses to incoming information. Detecting and orienting to objects in external space is already one step up from the simple process of using online feedback (from movement) to establish the existence of an external space. The question posed here is whether

the documented training required for SSD-users to experience proximal stimulation as distal is required because training and movement allow the user to 're-establish' or recalibrate existing maps. These maps definitely play a role in non-mediated perception with neurophysiological evidence for the existence of spatial maps both in the superior colliculus and ascending to higher cortical regions like A1 (King *et al.*, 1988; Zwiers *et al.*, 2003). Moreover, for estimates of distance there is evidence that calibration is essential (see Smets *et al.*, 1987) for the percept to emerge. We therefore suggest that whether the spatial maps emerge within the interaction or are established at a neural level, they appear to play a role in maintaining the experience of an external 3D world.

### 3.4.3. Calibration and Distance

As was discussed in Section 3.4.1, calibration is important in maintaining the veridical perception of external space and it therefore plays an important role in distal attribution. The process is also important for distance estimates using 2D surfaces. Smets *et al.* (1987) suggested that distance perception (on a 2D surface) relies upon a focus point; i.e., a reference against which to calibrate the estimate. Calibration of space increases the veridicality of the judgment. This is also true for the auditory space where relative distance estimates are more accurate than those derived from absolute cues (Shinn-Cunningham, 2001). In distal attribution, a focus point (also achieved through an interposition of two objects) is important for calibrating external space. Establishing spatial relations among objects and perceivers allows us to extract the different reference frames that can be used to describe external space (see, e.g., Knapen *et al.*, 2010; Poletti *et al.*, 2013).

If we take the example of visual perception, the distance of a visual object cannot be directly sensed (Koenderink *et al.*, 2001). However, perception does not only depend on currently sensed information and sensor position. Experience is also shaped by our previous interactions with the world through which we move, our assumptions about the physical world and underlying principles. For example, the emergence of depth is possible due to the priors we have about the world and the physical laws that constrain the (visually) sensed objects and events therein. We assume the world is stable (Glennerster *et al.*, 2006). One piece of evidence for the strength of our stable world prior is the ability to compensate for changes in an object's size and shape. Perceptual constancies of shape and size are used to compensate for distance in vision are effective because of our prior of a stable world (Glennerster *et al.*, 2006). If we assumed that objects could change their shape or form, then these cues to distance would no longer be valid. There is no origin for depth per se in physical terms although a metric of length is valid. However, a ruler for visual depth, for example, is an internal scale, a compromise between priors about object

constancy and a stable world, likelihood given the retinal projection and the compensation mechanisms provided by our nervous system.

The existence of a distal visual object, as opposed to the proximal pattern of stimulation it affords, can be verified via touch. As such it could be suggested that crossmodal calibration gives the nervous system a direct access to the distal form of objects. To reiterate, distance is an estimate that defines an external world that exists independently of the perceptual processing of the information. Organisms perceive objects in space. Such perception represents the response of the organism to a complex pattern of stimulation, integrated with the remaining effects of past experience with similar objects.

#### **4. Summary**

To highlight what has been learnt about distal attribution through the prism of SSDs, let's explore the factors that appear to be essential to its emergence. First distal attribution depends upon the assumption (or prior) of an external world. Non-separable from this belief of an external world, is the coupling between self-generated movements and the resulting changes in stimulation. This factor is crucial given that if there is no correlation between changes in motor output and changes in proximal patterns of stimulation, then the stimulation will be experienced solely as sensation, not perception (as was made evident in relation to the example of pain). The coupling emerges due to an organism's ability to move and explore the physical world. From the movement patterns the organism can learn about the constraints on external objects such that they can change only in two ways: their position according to the laws of physics or their state according to the laws of nature. In Bayesian terms this second level is the likelihood or currently available stimulation. Using both prior and likelihood the nervous system can then assign a cause, distal or receptor based, given the proximal pattern and its coupling to sensor movement. In this context, distance perception can be seen as a bi-product of the distal attribution process with both phenomena depending on the prior of a stable world (e.g., Glennerster *et al.*, 2006; Knill, 2007). Finally, calibration also plays an important role in maintaining the experience of a stable external world. The ability to assign co-ordinates to the object position in space is possible due to sensory maps which help translate and maintain the input from external world co-ordinates into perceptual co-ordinates.

To summarize, distal attribution of incoming sensory information is influenced by three main parameters: the prior of an external world, the coupling between movements and the resulting changes in stimulation, and calibration. Furthermore, distal attribution has proved crucial for distance perception, in that estimating the co-ordinates of an object in external space requires the object to be perceived as distal, rather than as a proximal pattern of stimulation.

Thus, without the process of distal attribution, perceived distance would not be possible.

### *Acknowledgements*

We would like to thank Irene Fasiello for the invigorating discussions regarding the nature of distal attribution. We would also like to thank Verena Conrad for her input on earlier drafts of this manuscript. Jess Hartcher-O'Brien is supported by a two-year post-doctoral fellowship from the Foundation Fyssen. Malika Auvray was funded by a grant from the Agence Nationale de la Recherche (ANR-11-JSH2-003-1). The DEC supported via ANR-10-LABX-0087 IEC and ANR-10-IDEX-0001-02 PSL.

### **References**

- Auvray, M., Hanne-ton, S., Lenay, C. and O'Regan, J. K. (2005). There is something out there: distal attribution in sensory substitution twenty years later, *J. Integr. Neurosci.* **4**, 505–521.
- Auvray, M., Hanne-ton, 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.
- Auvray, M. and Myin, E. (2009). Perception with compensatory devices: from sensory substitution to sensory motor extension, *Cogn. Sci.* **33**, 1036–1958.
- Bach-y-Rita, P. (1972). *Brain Mechanisms in Sensory Substitution*. Academic Press, London, UK, and New York, NY, USA.
- Bach-y-Rita, P. (2002). Sensory substitution and qualia, in: *Vision and Mind*, A. Noë and E. Thompson (Eds), pp. 497–514. MIT Press, Cambridge, MA, USA.
- Bach-y-Rita, P., Collins, C. C., Saunders, F., White, B. and Scadden, L. (1969). Vision substitution by tactile image projection, *Nature* **221**, 963–964.
- Bergan, J. F. and Knudsen, E. I. (2009). Visual modulation of auditory responses in the owl inferior colliculus, *J. Neurophysiol.* **101**, 2924–2933.
- Bower, T. G. R. (1964). Discrimination of depth in premotor infants, *Psychonom. Sci.* **1**, 368.
- Bower, T. G. R. (1965). Stimulus variables determining space perception in infants, *Science* **149**, 88–89.
- Bower, T. G. R. (1966a). Slant perception and shape constancy in infants, *Science* **151**, 832–834.
- Bower, T. G. R. (1966b). The visual world of infants, *Sci. Am.* **215**, 80–92.
- Bubic, A., Striem-Amit, E. and Amedi, A. (2010). Large-scale brain plasticity following blindness and the use of sensory substitution devices, in: *Multisensory Object Perception in the Primate Brain*, M. J. Naumer and J. Kaiser (Eds), pp. 351–380. Springer, New York, NY, USA.
- Caron, A. J., Caron, R. F. and Carlson, V. R. (1978). Do infants see objects or retinal images? Shape constancy revisited, *Infant Behavior and Development* **1**, 229–243.
- Condillac, E. B. (1754). *Traité des Sensations [Treatise of Sensations]*. Reissued in the series *Corpus des Œuvres de Philosophie en Langue Francaise*. Fayard, Paris, France, 1984.

- Crick, F. and Koch, C. (1995). Are we aware of neural activity in primary visual cortex? *Nature* **375**, 121–123.
- Deroy, O. and Auvray, M. (2012). Reading the world through the skin and ears: a new perspective on sensory substitution, *Front. Theor. Phil. Psychol.* **3**, 457.
- Donaldson, I. (2000). The functions of the proprioceptors of the eye muscles, *Phil. Trans. R. Soc. B Biol. Sci.* **335**, 1685–1754.
- Epstein, W., Hughes, B., Schneider, S. and Bach-y-Rita, P. (1986). Is there anything out there? A study of distal attribution in response to vibrotactile stimulation, *Perception* **15**, 275–284.
- Ernst, M. O. (2008). Multisensory integration: a late bloomer, *Curr. Biol.* **18**, R519–R521.
- Gibson, J. J. (1962). Observations on active touch, *Psychol. Rev.* **69**, 477–490.
- Glennester, A., Tcheang, L., Gilson, S. J., Fitzgibbon, A. W. and Parker, A. J. (2006). Humans ignore motion and stereo cues in favor of a fictional stable world, *Curr. Biol.* **16**, 428–432.
- Gold, J. I. and Knudsen, E. I. (2000). Abnormal auditory experience induces frequency-specific adjustments in unit tuning for binaural localization cues in the optic tectum of juvenile owls, *J. Neurosci.* **20**, 862–877.
- Gori, M., Sandini, G., Martinoli, C. and Burr, D. (2010). Poor haptic orientation discrimination in nonsighted children may reflect disruption of cross-sensory calibration, *Curr. Biol.* **20**, 223–225.
- Gori, M., Sciutti, A., Burr, D. and Sandini, G. (2011). Direct and indirect haptic calibration of visual size judgments, *PLoS ONE* **6**, e25599.
- Graham, N. (1989). *Visual Pattern Analyzers*. Oxford University Press, New York, NY, USA.
- Graziano, M. S., Reiss, L. A. and Gross, C. G. (1999). A neuronal representation of the location of nearby sounds, *Nature* **397**, 428–430.
- Gregory, R. L. (1963). Distortions of visual space as inappropriate constancy scaling, *Nature* **199**, 678–680.
- Guarniero, G. (1974). Experience of tactile vision, *Perception* **3**, 101–104.
- Hallett, P. E. and Lightstone, A. D. (1976). Saccadic eye movements towards stimuli triggered by prior saccades, *Vis. Res.* **16**, 99–106.
- Hanneton, S., Auvray, M. and Durette, B. (2010). The Vibe: a versatile vision-to-audition sensory substitution device, *Appl. Bionics Biomech.* **7**, 269–276.
- Haynes, H., White, B. L. and Held, R. (1965). Visual accommodation in human infants, *Science* **148**, 528–530.
- Hayward, V. (2011). Is there a ‘plenhaptic’ function? *Phil. Trans. R. Soc. B Biol. Sci.* **366**, 3115–3122.
- Ho, Y. X., Serwe, S., Trommershauser, J., Maloney, L. T. and Landy, M. S. (2009). The role of visuohaptic experience in visually perceived depth, *J. Neurophysiol.* **101**, 2789–2801.
- Hurley, S. and Noë, A. (2003). Neural plasticity and consciousness, *Biol. Philos.* **18**, 131–168.
- Katz, D. (1925). *The World of Touch*. Erlbaum, Hillsdale, NJ, USA (translation published 1989, translated by L. E. Kmegeer).
- King, A. J., Hutchings, M. E., Moore, D. R. and Blakemore, C. (1988). Developmental plasticity in the visual and auditory representations in the mammalian superior colliculus, *Nature* **332**, 73–76.
- King, A. J. and Moore, D. R. (1991). Plasticity of auditory maps in the brain, *Trends Neurosci.* **14**, 31–37.
- King, A. J. and Parsons, C. H. (1999). Improved auditory spatial acuity in visually deprived ferrets, *Eur. J. Neurosci.* **11**, 3945–3956.

- King, A. J., Schnupp, J. W. and Doubell, T. P. (2001). The shape of ears to come: dynamic coding of auditory space, *Trends Cogn. Sci.* **5**, 261–270.
- Knapen, T., Rolfs, M., Wexler, M. and Cavanagh, P. (2010). The reference frame of the tilt aftereffect, *J. Vis.* **10**, 1–13.
- Knill, D. C. (2007). Learning Bayesian priors for depth perception, *J. Vis.* **7**, 1–20.
- Knudsen, E. I. (1999). Mechanisms of experience-dependent plasticity in the auditory localization pathway of the barn owl, *J. Comp. Physiol.* **185**, 305–321.
- Koenderink, J. J., van Doorn, A. J., Kappers, A. M. L. and Todd, J. T. (2001). Ambiguity and the “mental eye” in pictorial relief, *Perception* **30**, 431–448.
- Krueger, L. E. (1970). David Katz's *Der Aufbau der Tastwelt* (The World of Touch): a synopsis, *Atten. Percept. Psychophys.* **7**, 337–341.
- Lee, J. and Groh, J. M. (2009). Auditory signals evolve from hybrid- to eye-centered coordinates in the primate superior colliculus, *J. Neurophysiol.* **108**, 227–242.
- Lenay, C., Gapenne, O., Hanneton, S., Marque, C. and Genouëlle, C. (2003). Sensory substitution: limits and perspectives, in: *Touching for Knowing*, Y. Hatwell, A. Streri and E. Gentaz (Eds), pp. 275–292. John Benjamins, Amsterdam, The Netherlands.
- 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.
- Lewis, J. E. and Maler, L. (2001). Neuronal population codes and the perception of object distance in weakly electric fish, *J. Neurosci.* **21**, 2842–2850.
- Loomis, J. M. (1992). Distal attribution and presence, *Presence* **1**, 113–119.
- Loomis, J. M., Klatzky, R. L. and Giudice, N. A. (2012). 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. 162–191. CRC Press, Boca Raton, FL, USA.
- Mancini, F. and Haggard, P. (2014). Perception: a motion after-effect for voluntary actions, *Curr. Biol.* **24**, R70–R72.
- Merleau-Ponty, M. (1945). *Phénoménologie de la Perception*. Gallimard, Paris, France.
- Mon-Williams, M. and Bingham, G. P. (2007). Calibrating reach distance to visual targets, *J. Exp. Psychol. Hum. Percept. Perform.* **33**, 645–656.
- Moore, D. R. and King, A. J. (1999). Auditory perception: the near and far of sound localization, *Curr. Biol.* **9**, R361–R363.
- O'Regan, J. K. (1992). Solving the “real” mysteries of visual perception: the world as an outside memory, *Can. J. Psychol.* **46**, 461–488.
- O'Regan, J. K. and Noë, A. (2001). A sensorimotor account of vision and visual consciousness, *Behav. Brain Sci.* **24**, 939–973.
- Poggio, G. F. and Fisher, B. (1977). Binocular interaction and depth sensitivity in striate and prestriate cortex of behaving rhesus monkeys, *J. Neurophysiol.* **40**, 1392–1405.
- Poincaré, H. (1905). *La Valeur de la Science [The Value of Science]*. Flammarion, Paris, France.
- Poletti, M., Burr, D. C. and Rucci, M. (2013). Optimal multimodal integration in spatial localization, *J. Neurosci.* **33**, 14259–14268.
- Rigato, S., Begum Ali, J., van Velzen, J. and Bremner, A. J. (2014). The neural basis of somatosensory remapping develops in human infancy, *Curr. Biol.* **24**, 1222–1226.
- Segond, H., Weiss, D. and Sampaio, E. (2005). Human spatial navigation via a visuo-tactile sensory substitution system, *Perception* **34**, 1231–1249.

- Sherrington, C. S. (1918). Observation on the sensual role of the proprioceptive nerve supply of the extrinsic ocular muscles, *Brain* **41**, 332–343.
- Shinn-Cunningham, B. G. (2001). Localizing sound in rooms, in: *Proceedings of the ACM/SIGGRAPH and Eurographics Campfire: Acoustic Rendering for Virtual Environments*. Snowbird, UT, USA.
- Shuwairi, S. M., Albert, M. K. and Johnson, S. P. (2007). Discrimination of possible and impossible objects in infancy, *Psychol. Sci.* **18**, 303–307.
- Siegle, J. H. and Warren, W. (2010). Distal attribution and distance perception in sensory substitution, *Perception* **39**, 208–223.
- Smets, G. J. F., Overbeeke, C. J. and Strathman, M. H. (1987). Depth on a flat screen, *Percept. Mot. Skills* **64**, 1023–1034.
- Terekhov, A. and O'Regan, J. K. (2013). Space as an invention of biological organisms. <http://arxiv.org/abs/1308.2124>
- von Békésy, G. (1955). Human skin perception of traveling waves similar to those on the cochlea, *J. Acoust. Soc. Am.* **27**, 830–841. [Reprinted in: G. von Békésy (1960). *Experiments in Hearing*, E. G. Wever (Ed. and Trans.), pp. 547–634. McGraw-Hill, New York, NY, USA.]
- von Helmholtz, H. (1909). *Physiological Optics*. Optical Society of America, Rochester, NY, USA.
- von Helmholtz, H. (1925). *Treatise on Physiological Optics*. Dover, New York, NY, USA.
- Wallace, M. T., Meredith, M. A. and Stein, B. E. (1998). Multisensory integration in the superior colliculus of the alert cat, *J. Neurophysiol.* **80**, 1006–1010.
- White, B. W. (1970). Perceptual findings with the vision-substitution system, *IEEE Trans. Man-Mach. Syst.* **11**, 54–58.
- 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.
- Wurtz, R. H. (2008). Neuronal mechanisms of visual stability, *Vis. Res.* **48**, 2070–2089.
- Zwiers, M. P., Van Opstal, A. J. and Cruysberg, J. R. M. (2001). Two-dimensional sound-localization behavior of early-blind humans, *Exp. Brain Res.* **140**, 206–222.
- Zwiers, M. P., Van Opstal, A. J. and Paige, G. D. (2003). Plasticity in human sound localization induced by compressed spatial vision, *Nat. Neurosci.* **6**, 175–181.