Neuroscience and Biobehavioral Reviews xxx (2012) xxx–xxx

Contents lists available at SciVerse ScienceDirect

Neuroscience and Biobehavioral Reviews

journal homepage: www.elsevier.com/locate/neubiorev

Review

The Bayesian brain: Phantom percepts resolve sensory uncertainty

Dirk De Ridder[a,*], Sven Vanneste[a,b], Walter Freeman[c]

[a] Brai²n, TRI & Department of Neurosurgery, University Hospital Antwerp, Belgium
[b] Department of Translational Neuroscience, Faculty of Medicine, University of Antwerp, Belgium
[c] Department of Molecular & Cell Biology, University of California at Berkeley, USA

ARTICLE INFO

Article history:
Received 16 January 2012
Received in revised form 13 March 2012
Accepted 1 April 2012

Keywords:
Neuropathic
Pain
Tinnitus
Uncertainty
Cingulate
Insula
Information
Free energy
Bayes

ABSTRACT

Phantom perceptions arise almost universally in people who sustain sensory deafferentation, and in multiple sensory domains. The question arises 'why' the brain creates these false percepts in the absence of an external stimulus? The model proposed answers this question by stating that our brain works in a Bayesian way, and that its main function is to reduce environmental uncertainty, based on the free-energy principle, which has been proposed as a universal principle governing adaptive brain function and structure. The Bayesian brain can be conceptualized as a probability machine that constantly makes predictions about the world and then updates them based on what it receives from the senses. The free-energy principle states that the brain must minimize its Shannonian free-energy, i.e. must reduce by the process of perception its uncertainty (its prediction errors) about its environment. As completely predictable stimuli do not reduce uncertainty, they are not worthwhile of conscious processing. Unpredictable things on the other hand are not to be ignored, because it is crucial to experience them to update our understanding of the environment. Deafferentation leads to topographically restricted prediction errors based on temporal or spatial incongruity. This leads to an increase in topographically restricted uncertainty, which should be adaptively addressed by plastic repair mechanisms in the respective sensory cortex or via (para)hippocampal involvement. Neuroanatomically, filling in as a compensation for missing information also activates the anterior cingulate and insula, areas also involved in salience, stress and essential for stimulus detection. Associated with sensory cortex hyperactivity and decreased inhibition or map plasticity this will result in the perception of the false information created by the deafferented sensory areas, as a way to reduce increased topographically restricted uncertainty associated with the deafferentation. In conclusion, the Bayesian updating of knowledge via active sensory exploration of the environment, driven by the Shannonian free-energy principle, provides an explanation for the generation of phantom percepts, as a way to reduce uncertainty, to make sense of the world.

Contents

* Corresponding author at: Brai²n, University Hospital Antwerp, Wilrijkstraat 10, 2650 Edegem, Belgium. Tel.: +32 821 33 36.
E-mail address: dirk.de.ridder@uza.be (D. De Ridder).
URL: http://www.brai2n.org (D. De Ridder).

0149-7634/$ – see front matter © 2012 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.neubiorev.2012.04.001

1. Introduction

In 1551, exactly 300 years before Herman Melville described phantom pain in Captain Ahab's missing leg in the book Moby Dick (1851), Ambroise Paré, a French military surgeon described the first phantom pain, and he believed it to be originating in the brain (Bittar et al., 2005).

Somatosensory deprivation leads to phantom perception in 90–98% of limb amputees (Ramachandran and Hirstein, 1998): immediately after the amputation in 75% of the patients and in a delayed fashion, after two to three weeks, in the remaining 25% (Ramachandran and Hirstein, 1998). Phantom pain, a specific kind of phantom perception, is present in 70% of limb amputees (Sherman et al., 1984). Even though in 14% the pain decreases in time (Sherman et al., 1984) it is generally accepted that once the pain continues for more than 6 months it becomes difficult to treat (Ramachandran and Hirstein, 1998).

Similarly, deprivation of auditory input can result in an auditory phantom phenomenon, also known as tinnitus. In sudden deafness 67% of patients present with tinnitus (Graham et al., 1978). In patients presenting with a vestibular schwannoma 70–80% of patients have tinnitus referred to the ipsilateral ear to the schwannoma (Moffat et al., 1998) and between 8.5% (Kameda et al., 2010) and 39.8% (Levo et al., 2000) of those who have no tinnitus develop it after tumor and cochlear nerve resection.

Both phantom perceptions occur in the deafferented area. For phantom sound the frequency spectrum of the tinnitus reflects the individual's hearing loss (Norena et al., 2002). Neuropathic pain is felt as coming from the area that was initially innervated by the injured neural structure (Flor et al., 2006) and phantom pain is perceived in the missing body part (Flor et al., 2006; Ramachandran and Hirstein, 1998). Phantom pain has to be differentiated from residual limb (or stump) pain in the still-present body part, adjacent to the amputation or deafferentation line (Flor et al., 2006).

Tinnitus and phantom pain can thus be defined as an involuntary simple auditory or somatosensory conscious percept in the absence of an external stimulus. In this sense it can be regarded as a simple form of hallucinations. The involuntary aspect differentiates it from imagery, and the absence of an external stimulus excludes it to be considered as an illusion, a distorted percept of a sensory stimulus. It is a symptom that can develop in virtually all diseases and disorders associated with a lesion in any part of the auditory or somatosensory pathway leading to partial or complete sensory deafferentation. Furthermore it is not limited to the auditory and somatosensory domain. Some cases of phantom percepts have also been described for the visual (Ffytche et al., 1998), olfactory and gustatory systems (Henkin et al., 2000). So, the question is why does this almost universally occur? Why does the brain, as Ambroise Paré already suggested 500 years ago, generate phantoms for missing sensory input? The answer to this question might be simple: this is the way brains operate normally on sensory input, constructing orderly perceptions from chaotic sensations. Why do brains do this? It is to reduce uncertainty and why phantom phenomena?

2. Two models of perception

Perception is different from sensation. Whereas sensation can be defined as the detection and processing of sensory information, perception is the act of interpreting and organizing this sensory information to produce a meaningful experience of the world and of oneself (De Ridder et al., 2011a; Freeman, 1999).

Historically two different models of perception have been developed (see Fig. 1), one which assumes that the brain passively absorbs sensory input, processes this information, and reacts with a motor and autonomic response to these passively obtained sensory stimuli (Freeman, 2003). This concept is based on Plato, later Christianized via Saint Augustine and has become mainstream thinking in sensory neuroscience through Descartes' influence (Freeman, 2003). However, a second model of perception posits that the brain actively looks for the information it predicts to be present in the environment, based on an intention or goal. This goal or intention can drive action which will influence perception. According to David Hume the motivation for action is desire, with reason being a slave, steering emotionally motivated action in a certain direction (Hume, 1740). This active form of perception is based on Aristotle, Christianized via Thomas Aquinas (Aquinas, 1268; Freeman, 2003) and evolved in constructivist or representational perception (Norman, 2002). Aristotle used Plato's concept of 'forms', which were abstract ideals and made it into something practical. According to Aristotle, in his book 'On the Soul' the 'form' is the sum of essential properties of a thing, which is stored in the soul, and used as a reference to look for as a recognizable pattern in the environment (Aristotle, 1986). In-form-ation is then imposing a 'form' on something (von Baeyer, 2003).

Constructivist perception is a top down indirect information creation, depending on what is expected in the sensory environment, relying on what is stored in memory ('form'). This goes back to the philosophy of Hume (1740) and Merleau-Ponty (1945), according to whom perception is always directed 'towards something': "to move one's body is to aim at things through it" (Merleau-Ponty, 1945).

Active touch perception has the advantage of being a better discriminator of the sensory environment than passive perception (Gibson, 1962). Active touch is an exploratory rather than a merely receptive sense. In fact, active touch can be termed tactile scanning, by analogy with ocular scanning (Gibson, 1962). When people are given six different equally large forms (cookie cutters) such as a triangle, a star, and teardrop, the accuracy of recognition can be compared when the form is pressed into the palm of the hand (passive touch) and when it is held above the palm and explored by the fingertips (active touch). A chance level of judgments would be 1/6 or 16.7%. For passive touch the mean frequency of correct matches was 49%. For active touch the mean frequency was 95%, significantly different (Gibson, 1962). This is similar to the visual system. During natural, active vision, we move our eyes to gather task-relevant information from the visual scene: objects and subjects are actively scanned (Yarbus, 1967). Thus seeing is similar to exploratory touch.

The major difference between passive perception and active constructive perception is that active perception critically depends on predictions of what is likely to occur in the environment, based on intentions or goals arising from experience, in contrast to passive perception.

3. The Bayesian brain

Humans and other animals operate in a changing environment (Knill and Pouget, 2004). In phenomenological terms, uncertainty