



Review article

Adaptive and maladaptive neural compensatory consequences of sensory deprivation—From a phantom percept perspective



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ABSTRACT

It is suggested that the brain undergoes plastic changes in order to adapt to changing environmental needs. Sensory deprivation results in decreased input to the brain leading to adaptive or maladaptive changes. Although several theories hypothesize the mechanism of these adaptive and maladaptive changes, the course of action taken by the brain heavily depends on the age of incidence of damage. The growing body of literature on the topic proposes that maladaptive changes in the brain are instrumental in creating phantom percepts, defined as the perception of a sensory experience in the absence of a physical stimulus. The current article reviews the mechanisms of adaptive and maladaptive plasticity in the brain in congenital, early, and late-onset sensory deprivation in conjunction with the phantom percepts in the different sensory domains. We propose that the mechanisms of adaptive and maladaptive plasticity fall under a universal construct of updating hierarchical Bayesian prediction errors. This theory of the Bayesian brain hypothesizes that the brain constantly compares its internal milieu with changing environmental cues and either adjusts its predictions or discards the change, depending on the novelty or salience of the external stimulus. We propose that adaptive plasticity reflects both successful bottom-up compensation and top-down updating of the model while maladaptive plasticity reflects failure in one or both mechanisms, resulting in a constant prediction-error. Finally, we hypothesize that phantom percepts are generated by the brain as a solution to this prediction error and are thus a manifestation of unsuccessful adaptation to sensory deprivation.

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Abbreviations: EEG, electroencephalography; fMRI, functional magnetic resonance imaging; PET, positron emission tomography; GABA, gamma amino butyric acid; HAROLD, hemispheric asymmetric reduction in older adults; CRUNCH, compensatory-related utilization of neural circuits.

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1. Introduction

It is generally agreed that the brain creates an internal representation of the environment that it is exposed to (Friston, 2012; Friston et al., 2006). Bottom-up sensory information received by the brain is constantly compared with this internal representation, leading to predictions about the causes of changes in sensory information (Friston, 2005). This process takes place in a hierarchical fashion, such that the beliefs of each level of bottom-up information are estimated by top-down predictions from the succeeding levels (Penny, 2012). Changes in environmental stimuli result in prediction errors (Arnal and Giraud, 2012) between the bottom-up information and top-down predictions (De Ridder et al., 2014b; Friston, 2009; Friston et al., 2006). These changes can be due to an enrichment or impoverishment in environmental stimuli. Damage to peripheral sensory structures or central processing centers leads to sensory deprivation, exposing the brain to decreased sensory input which results in sensory uncertainty. This uncertainty may be minimized by either (a) active sampling of the new environment providing corresponding bottom-up cues and/or (b) appropriate updating of top-down beliefs by the successive levels of the hierarchy (De Ridder et al., 2014b; Friston, 2012; Friston et al., 2006).

In general terms, compensation may be defined as the process of overcoming losses and deficits through one of several neural mechanisms (Dixon and Bäckman, 1999). Evidence for the brain’s bottom-up compensatory ability is provided in both neural and cognitive domains. Examples of the brain’s bottom-up compensatory techniques include increased activity in sensory and non-sensory regions of the brain (Vanneste and De Ridder, 2012), reorganization of cortical maps following amputation of an extremity (Knecht et al., 1996), extensive cross-modal plasticity of neurons in early loss of a sensory domain (Bavelier and Neville, 2002b; Cohen et al., 1997), and recruitment of bilateral neural resources with aging in cognitively normal adults (Cabeza et al., 2002). Conversely, a top-down compensation mechanism for sensory deafferentation is the successful adjustment of the prediction model at different levels of the hierarchy by learning the changes in bottom-up input (De Ridder et al., 2014b). Updating the prediction model at different hierarchical levels follows a Bayesian statistical approach (Friston, 2005). Empirical Bayes is a method of arriving at statistical inferences by setting prior beliefs based on existing data and updating these beliefs based on new data. This involuntary bottom-up sampling of the environment and top-down updating of prior beliefs is popularly known as the Bayesian brain theory (Friston, 2012), which may be used as a universal construct to explain how the brain adapts to new environments by successfully minimizing sensory uncertainty. Although the brain is very resilient to local and global damages

(Alstott et al., 2009; David and Aguayo, 1981; Kaas et al., 1983; Kaiser et al., 2007), the success of both bottom-up and top-down compensatory techniques heavily depends on the time of incidence of the damage. The sensitive or critical period is the time frame in the lifespan of the brain within which it is most susceptible to changes in behavioral and biological development (Kral, 2013). Since the brain is most plastic in the early years of life, compensatory mechanisms for sensory deprivation seem to differ depending on congenital, early, or late-onset of sensory damage.

Adaptive compensation could be achieved through changes in the bottom-up mechanism or top-down updating of a prediction error. However, if these adaptive mechanisms fail, irrespective of the time of incidence of sensory damage, the system needs to compensate for the prevailing uncertainty in alternative ways. This is engineered through maladaptive compensation—by the generation of a phantom percept (De Ridder et al., 2014b). Phantom perception is the experience of a sensory representation (vision, audition, touch, olfaction, gustation, balance, or proprioception) in the absence of an external sensory stimulus (Jastreboff, 1990; Ramachandran and Rogers-Ramachandran, 1996; Schultz and Melzack, 1991; Yanagisawa et al., 1998). The pathways of the different sensory domains from the peripheral receptors to their primary sensory cortices are illustrated in Fig. 1. In general, phantom percepts seem to occur in response to sensory deprivation, specifically damage to peripheral structures such as receptors (Grouios, 2002; Jastreboff, 1990), nerves (Eggermont, 2005; Wrobel and Leopold, 2004), or damage to early stages of sensory processing in the brainstem and cortex (Ramachandran, 1993). They have also been observed as a common after-effect of surgeries such as cataract surgery (Schultz and Melzack, 1991), tonsillectomy (Tomofuji et al., 2005), etc. Although there are ongoing debates about phantom percepts in congenital and early sensory deprivation, their relation to late sensory deprivation is universally accepted.

The aim of this article is to review the literature on bottom-up and top-down adaptive compensatory techniques in congenital, early and late sensory deprivation and phantom percepts in all sensory domains, proposing a universal construct for adaptive and maladaptive compensation of sensory deafferentation. In this article, we will first review different bottom-up and top-down adaptive compensatory techniques employed by the brain in response to congenital, early, and late-onset sensory deprivation. We will then review the phantom percepts in different sensory domains and detail the maladaptive compensatory mechanisms behind their generation. In doing so, we suggest that phantom percepts may be a maladaptive compensatory manifestation to offset the inability of the brain to adapt to decreased sensory input independent of the sensory domain and the time of incidence of deprivation.

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