Hearing Research 343 (2017) 50–63

Contents lists available at ScienceDirect

Hearing Research

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

Higher-order auditory areas in congenital deafness: Top-down interactions and corticocortical decoupling

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ARTICLE INFO

Article history:
Received 26 April 2016
Received in revised form
25 July 2016
Accepted 29 August 2016
Available online 13 September 2016

Keywords:
Deafness
Sensory deprivation
Top-down
Predictive coding
Prediction error
Cross-modal plasticity

ABSTRACT

The theory of predictive coding assumes that higher-order representations influence lower-order representations by generating predictions about sensory input. In congenital deafness, one identified dysfunction is a reduced activation of deep layers in the auditory cortex. Since these layers play a central role for processing top-down influences, congenital deafness might interfere with the integration of top-down and bottom-up information flow. Studies in humans suggest more deficits in higher-order than in primary cortical areas in congenital deafness. That opens up the question how well neurons in higher-order areas can be activated by the input through the deprived auditory pathway after restoration of hearing with cochlear implants. Further it is unclear whether their interconnections to lower order areas are impaired by absence of hearing. Corticocortical anatomical fiber tracts and general auditory responsiveness in both primary and higher-order areas are generally preserved in absence of auditory experience. However, the existing data suggest a dichotomy between preservation of anatomical cortical connectivity in congenital deafness and functional deficits in corticocortical coupling. Further, cross-modal reorganization observed in congenital deafness in specific cortical areas appears to be established by functional synaptic changes and rests on anatomically preserved, genetically-predetermined and molecularly patterned circuitry connecting the sensory systems. Current data indicate a reduced corticocortical functional coupling between cortical auditory areas in congenital deafness, both in bottom-up and top-down information stream. Consequently, congenital deafness is likely to result in a deficit in predictive coding that affects learning ability after late cochlear implantation.

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http://dx.doi.org/10.1016/j.heares.2016.08.017
0378-5955/

1. Introduction

The brain continuously generates predictions about the environment that shape perception. While a city dweller visiting the rain forest perceives an irritating complex mixture of unfamiliar sounds coming from the nature, the native person can easily disentangle the mixture of acoustic features and instead perceives the presence of the animals generating these sounds. In familiar soundscapes the individual sensory features of sounds step into background and the sensory objects step forward (Ahissar et al., 2009; Hochstein and Ahissar, 2002).

The brain, based on experience and active interaction with the environment, groups individual sensory features into meaningful sensory objects. A sensory object is here understood as a neuronal representation of a delimited pattern of features that is subject to a figure-background distinction. In this sense, sensory objects are the result of grouping features into stable perceptual units (Bizley and Cohen, 2013). They are the result of abstraction of the sensory input into the essential, distinctive features defining the object. The object, once created, is consequently invariant to non-distinctive features. Many features are required to be able to safely discriminate between individual objects, but once the objects have been defined by experience as a perceptual category, already few, and even downgraded features in the sensory stimulus can be used to perceive the corresponding object. This greatly facilitates the identification of sensory objects even in noisy backgrounds.

Adult, experienced subject‘s cognition is not a passive blank slate that is bottom-up written by the sensory systems. Cognitive structures formed by experience are constantly active, forming a “framework” for perception. The cognitive framework is defined at any given moment by the active objects and the sensory input is fed into this active framework. This framework, given by the behavioral context, can significantly affect perception. Consequently, we have expectations on the type of sensory input we are likely to receive in the given situation, shaping the perception.

Indeed, cortical responses to sensory stimuli measured by imaging methods were suggested to reflect the difference between the expectation and the actual stimulus (Arnal et al., 2011; den Ouden et al., 2010; Friston, 2010; Sedley et al., 2016). Learning itself, e.g. learning of a sensory skill, is possibly initiated by a difference between prediction and actual input, and the goal of learning is to minimize this difference, the “prediction error” (Rescorla and Solomon, 1967; Sevenster et al., 2013; Sohoglu and Davis, 2016). The error signal resulting from the comparison between expectation and actual sensory input is the driving signal for learning (Rescorla and Solomon, 1967).

The computation of the prediction error requires a circuitry that compares what has been learned previously and what enters the brain through the sensory systems (Bastos et al., 2012; Friston, 2010). This postulates a cortical circuitry capable of performing a comparison between bottom-up information, reflecting the sensory stimulus, and top-down information, reflecting the information on sensory objects. Cortical columns represent a candidate for such function (Kral and Eggermont, 2007; Raizada and Grossberg, 2003; Bastos et al., 2012).

Here we review evidence that congenitally deaf show deficits in this circuitry indicating that top-down information cannot be integrated in the processing of sensory input when sensory restoration is performed late. We suggest that such functional deficits in the columnar microcircuitry contribute to deficits in auditory perception and closure of sensitive periods in congenitally deaf subjects after late cochlear implantation.

2. Congenital deafness and the representation of sensory features and objects

The effects of sensory loss can be differentiated into deficits in the ability to discriminate stimuli (i.e. perceive their difference) and deficits in the ability to identify auditory objects (i.e. to abstract from the features and to identify the same stimulus as the same one). The restoration of hearing with cochlear implants allows investigating the deficits that were caused by development in absence of hearing with regard to feature sensitivity and the ability to form auditory objects. There is a remarkable difference in auditory performance between subjects that lost hearing in adult age and those that lost hearing in early childhood, if both groups receive cochlear implants in adulthood (reviewed in Kral and O'Donoghue, 2010; Kral, 2013). It is important to note that when stimulated with a cochlear implant, both groups of subjects “hear” a sound. However, after receiving the cochlear implant, the adult deafened subjects tune-in to the new auditory input and can learn to discriminate and categorize the electrical stimuli even after decades of complete deafness. Within three months after implantation such late-deafened subjects as a rule reach a reasonable hearing performance and start to understand spoken sentences in a natural environment. In contrast, early-deafened subjects who are implanted late in life show persisting deficits in discrimination and identification of sounds and in speech understanding (Busby et al., 1992). Despite some improvement in auditory performance with time (Busby et al., 1992; Schorr et al., 2005), they do not reach performance comparable to late-deafened subjects. Implantation has to take place during first years of life to allow development of auditory performance and speech understanding (Fryauf-Bertschy et al., 1997; Kral and O'Donoghue, 2010; McConkey Robbins et al., 2004; Niparko et al., 2010; Schorr et al., 2005; Waltzman et al., 1992). It is one major task of auditory neuroscience to understand the reasons behind these differences between early- and late-implanted congenitally deaf individuals.

Historically, auditory neuroscience has mostly concentrated on easily observable feature sensitivity like tonotopic/cochleotopic organization in primary auditory areas. In contrast, higher-order areas have been so far less in the focus of research. Because of this, more knowledge is required about interareal interactions and the function of categorization in auditory processing. As suggested previously (Kral, 2013), however, feature sensitivity and categorization are interdependent: feature representation is a prerequisite for categorization, and the framework of active objects can influence feature representation. In natural conditions, lower order and higher-order representations continuously interact. As we will show below, the precondition for this interaction, the cortical microcircuitry, requires hearing experience to develop and become functional.

3. Models of auditory deprivation

The role of experience on interactions between higher and lower order cortical areas can be ideally investigated in an animal model that is congenitally deprived of sensory experience. This