Neuroscience and Biobehavioral Reviews xxx (2015) xxx–xxx

Contents lists available at ScienceDirect

Neuroscience and Biobehavioral Reviews

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

Review

Perceptual inference

Nikolaos C. Aggelopoulos*

Leibniz Institute for Neurobiology, Brenneckestr. 6, 39118 Magdeburg, Germany

ARTICLE INFO

Article history:
Received 10 December 2014
Received in revised form 30 April 2015
Accepted 2 May 2015
Available online xxx

Keywords:
Perception
Inference
Vision
Sensorimotor
Reflex
Active inference
Bayesian inference

ABSTRACT

Perceptual inference refers to the ability to infer sensory stimuli from predictions that result from internal neural representations built through prior experience. Methods of Bayesian statistical inference and decision theory model cognition adequately by using error sensing either in guiding action or in "generative" models that predict the sensory information. In this framework, perception can be seen as a process qualitatively distinct from sensation, a process of information evaluation using previously acquired and stored representations (memories) that is guided by sensory feedback. The stored representations can be utilised as internal models of sensory stimuli enabling long term associations, for example in operant conditioning. Evidence for perceptual inference is contributed by such phenomena as the cortical co-localisation of object perception with object memory, the response invariance in the responses of some neurons to variations in the stimulus, as well as from situations in which perception can be dissociated from sensation. In the context of perceptual inference, sensory areas of the cerebral cortex that have been facilitated by a priming signal may be regarded as comparators in a closed feedback loop, similar to the better known motor reflexes in the sensorimotor system. The adult cerebral cortex can be regarded as similar to a servomechanism, in using sensory feedback to correct internal models, producing predictions of the outside world on the basis of past experience.

Contents

* Tel.: +49 391 6263 94511; fax: +49 391 6263 95489.
E-mail address: nikolaos.aggelopoulos@lin-magdeburg.de

http://dx.doi.org/10.1016/j.neubiorev.2015.05.001
0149-7634/© 2015 Published by Elsevier Ltd.

1. Introduction

Subsequent to Barlow's proposal that perceptual awareness is linked to the firing of individual neurons (Barlow, 1961, 1972), visual perception had been regarded as the ultimate outcome of sensory input through a feedforward process arising in the retina. The simplest impression of such a process came from the pioneering description of simple, complex and hypercomplex cells in areas 17, 18 and 19 of the cat neocortex (Hubel and Wiesel, 1962, 1965) indicating a progressive feedforward increase in the complexity of physiological receptive field properties with successive hierarchical stages (Felleman and van Essen, 1991). Nevertheless in a different context, when behaviour is also under consideration, the input from sensory organs has been traditionally seen not as feedforward but as a feedback input (e.g. Eldred and Buchwald, 1967; af Klint et al., 2010).

An approach to visual perception that bridges this apparent divide, proposed indeed more than a century ago by Helmut von Helmholtz (1910), puts an emphasis on the formation of a percept within a process of evaluation. On Helmholtz's suggestion, the evaluation involves a test of a hypothesis about what is being seen based on "inductive inferences" gained from "sensations". By inductive inference Helmholtz meant that perceptions are conclusions based not only on present sensations but also with reference to past sensations of the objects perceived. Latent within this conceptualisation is the idea that the perceived image is at least partly the outcome of stored information – a stored representation, that is a memory – of that object or of similar objects in similar contexts. This was potentially the first proposal of a top-down influence in perception. It regard perception not primarily as a sensory phenomenon but as perceptual inference relying on internal models built through past experience. Helmholtz's idea of perceptual inference has been revived by computational models of perception relying on statistical inference (Hinton and Sejnowski, 1983; Dayan et al., 1995).

1.1. Alternative theories of visual perception

Between Helmholtz's proposal and its recent revival, several other theories of perception were advanced. Most of these proposals were based on the hierarchical organisation of the visual system and the increasing complexity of visual fields in occipital cortex in particular, and were influenced by the binding theory.

1.2. The binding problem

The binding theory in linguistics is a theory of syntax and phrase structure grammar, given that the same words in a sentence when rearranged can have different meanings (e.g. "Mark said he was present" vs "He said Mark was present"). The idea was subsequently applied to visual perception as a model solution to the "binding problem". The binding problem considers that features of an object need to be bound together by some neuronal mechanism across a population of neurons, so that the object can be perceived as a whole. It rather assumes that representations of that object are not possible unless a bottom-up binding of its features can bring it into consciousness and make it a subject of attention.

A further idea proposes that the mechanism by which the features of objects are bound together is spike-correlations (von der Malsburg, 1981). This idea assumes that neuronal responses to features of an object need to be bound to a single entity, which is ultimately achieved through spike synchrony. Certain predictions from this theory have not found experimental support (Golledge et al., 2003; Thiele and Stoner, 2003; Rolls et al., 2003a,b; Dong et al., 2008). One difficult problem arising, if objects had no permanent representation in the brain but had to be bound anew every time, from scratch so to speak, through an essentially bottom-up binding of their features, would be how would then an object be associated through experience with another object, or with a place or with an action or conditioned response.

Two alternative theories, those of feature integration and the structural description theories, place a greater emphasis on lateral or top-down influences.

1.3. Feature-integration theory

The feature integration theory, developed by Treisman and Gelade (1980) proposes that different attentional mechanisms are responsible for binding different features into consciously experienced wholes. The theory has been one of the most influential psychological models of human visual attention.

According to Treisman, in a first step to visual processing, several primary visual features are processed and represented with separate feature maps that are later integrated into a "saliency map" that can be accessed in order to direct attention to the most conspicuous areas. Although this model does not preclude and is not aimed at precluding top-down influences, the modularity of this system based on "features" and its ability to function at the pre-attentive state, puts an emphasis on the ability to perceive objects on the basis of a bottom-up mechanism arriving stepwise at higher-order features, albeit stored (i.e. already represented internally) in saliency maps. It has been argued, moreover, that bottom-up salience-driven mechanisms can draw attentional selection only in as much as there exist learned associations between the relevant stimuli and rewards (Anderson, 2013).

1.4. Structural description theories

The structural description theories generally propose that complex shapes are built up of more elementary features or primitives. In these sets of theories (reviewed by Peissig and Tarr, 2007), an actual object is thought to be represented in the brain by a structural description of its parts, in other words by its features and a syntax that describes how these features are combined. The features can be elementary 3-D primitives as in the theory of Marr

Please cite this article in press as: Aggelopoulos, N.C., Perceptual inference. Neurosci. Biobehav. Rev. (2015), http://dx.doi.org/10.1016/j.neubiorev.2015.05.001