EMBJ.ORG FOR YOUNG DOCTORS

EUROMEDITERRANEAN BIOMEDICAL JOURNAL
2018,13 (33) 145-149
(*FORMERLY: CAPSULA EBURNEA*)

Review

CHANGING PERSPECTIVE ON PERCEPTION PHYSIOLOGY: CAN YOU REALLY SEE WHAT IS HAPPENING?

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ARTICLE INFO

Article history:
Received 25 August 2018
Revised 24 September 2018
Accepted 06 November 2018

Keywords:
perception, cognition, models, neurological.

ABSTRACT

Perception is a complex, neural mechanism that requires organization and interpretation of input meaning and it has been a key topic in medicine, neuroscience and philosophy for centuries. Gestalt psychology proposed that the underlying mechanism is a constructive process that depends on both input of stimuli and the sensory-motor state of the agent. The Bayesian Brain hypothesis reframed it as probabilistic inference of previous beliefs, which are revised to accommodate new information. The Predictive Coding Theory proposes that this process is implemented through a top-down cascade of cortical predictions of lower level input and the concurrent propagation of a bottom-up prediction error aimed at revising higher level expectations. The 'Active Inference' theory explains both perception and action, generalising the prediction error minimisation process. In this focused-review we provide a historical overview of the topic and an intuitive approach to the new computational models.

1. Introduction: the history of perception

"*Nihil est in intellectu quod prius non fuerit in sensu*" (De Anima, 388-322 a.C.) [Nothing is in the intellect which before was not in the senses]. This sentence, by the philosopher Aristotle, is perhaps the first attempt to describe the Perception mechanisms.

Later, in the Middle Ages, this same hypothesis constituted the foundation of the Scholasticism philosophy by Thomas Aquinas (1225-1274). In the modern age, Empiricists John Locke, George Berkeley, and David Hume believed that the mind is a blank slate ("tabula rasa") that is able to be imprinted by perceptual objects.

According to this view, perception is a mere collection of data from the external world, and no active processes are required from the agent. It is worth noticing that the word perception comes from the Latin word *precipere*, to collect; however, Helmholtz (1860)[1] distinguished *sensation*, that can be reduced to sensory input, from *perception* that requires computations of the input in order to give them a meaning (or recognizing the causes of sensory input).

Another philosophical current, Transcendental Idealism, first hypothesized the opposite thesis that the mind creates perceptions for itself by means of "innate categories" as exemplified by Kant, ",… if I remove the thinking subject, the whole material world must at once vanish because it is nothing but a phenomenal appearance in the sensibility of ourselves as a subject, and a manner or species of representation" (Immanuel Kant, Critique of Pure Reason, 1787). However, all the hypotheses on perception were still lacking empirical evidence until the birth of Fechner's pioneering studies in the field of psychophysics (1889) [2]. The goal of this new empirical science was to investigate the relationship between stimulation and sensation, specifically the scaling of sensory magnitude (outer psychophysics). In the first half of the 20th century, the German school of Gestaltism joined these empirical methods with the idea that the brain itself has a generative role in perception. Gestalt Psychology (Gestalt, German: configuration, form) stated that perception is a constructive process. Based on experimental psychology of vision, and especially visual illusions, Gestalt psychologists hypothesized that while sensation is made up of every single low level object element, the percept, as a whole, depends on the interpretation of input meaning in light of previous experiences, emotions, and rewards.

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DOI: 10.3269/1970-5492.2018.13.33

An effective, if not overused, example to explain the concept can be found in the Kanizsa's illusory figures [3], in which distant elements induce the emergence of a perceived surface, when no true, luminance difference exists to form a complete shape (see figure 1). The neural mechanisms underlying this phenomenon is the so-called "intermediate vision" [4] in which an effortless and automatic organization of the visual field occurs to generate the perception of a shape.

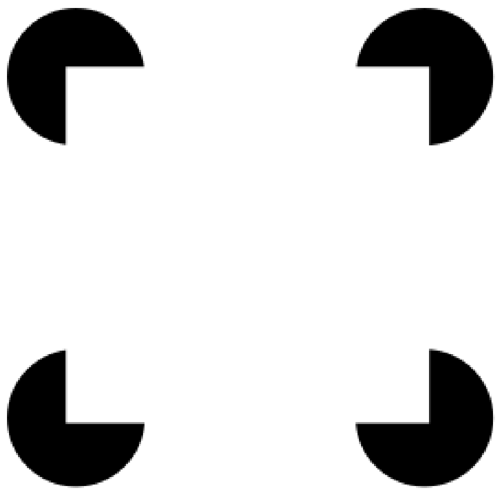

Figure 1 - Kanizsa square

2. The uncertainty boundary

Even if Gestalt psychology is able to narratively explain why we actively construct the perception of a triangle when only three pac-men appear in front of our eyes, where the triangle category is 'pre-built' in our brains, it cannot explain how we are able to perceive a stable, three dimensional reality in a world where objects are constantly overlapped, thus limiting us to detect only a small portion of any object. Crucially, this stable perception is only gained when a bi-dimensional bitmap is captured in the retina, which is limited by the small size of the fovea, thus, unable to acquire the whole scene in having to select which information to process. Moreover, execution of human action is not always precise as long eye movement often presents a successive, corrective saccade. In this condition of missing information and uncertain outcome, the brain is constantly asked to find the distal cause, the real state of the world, underlying its limited perceptions as well as defining and solving the problem of selecting the correct corresponding behavioural response.

This problem can be mathematically modeled as a Markov Decision Problem (MDP) with partially observable input (POMDP), in which states are not directly observable but have to be inferred from observation [5]

As it can be easily understood, a neural process disregarding the probabilistic nature of interaction can't be the basis of perception, whose input are stochastic variables (i.e. neural noise in the detection system, noticeable in conditions with too much or too little light or distant objects).

3. The bayesan brain hypothesis

The basis of the Bayesian Brain Hypothesis [6] is the idea of perception as a process of unconscious probabilistic inference about the cause of the incoming neural signals. For example, when we see a movement in a wood with our peripheral vision, our Bayesian Brain behaves as a probabilistic *Inference Machine* that represents and updates the spatial location not as a set of three coordinates, but as a *conditional probability density function* of the coordinates[*]. In other words, our perceptual system will infer the probability $P(m=(x,y,z)|s)$ that the movement took place at different positions m=(x,y,z), considering the observed sensory signal s coming from the receptors. It will also represent other variables of interest as part of a more complex distribution e.g. if the cause c of the movement was the wind w or a boar b e.g. $P(p=(x,y,z),c=w|s)$. A similar probabilistic inference can take place even if we were to observe somebody starting to move his hand toward two nearby glasses, in which case the brain would infer the probability distribution of position h and direction d of the hand as well as identity g of the glass to be grasped (e.g left glass l) $P(h=(x,y,z), d=(u,v,w),g=l|s)$ [7]. Note that in all these cases the distribution on different variables are connected, e.g. if the left glass is full and the right one is empty, the hand is more likely to be approaching the left one:

$$P(h=(x,y,z),d=(u,v,w),g=l|s,l=full,r=empty)/P(p=(x,y,z),d=(u,v,w),c=r|s,l=full,r=empty)>>P(h=(x,y,z),d=(u,v,w),g=l|s)/P(p=(x,y,z),d=(u,v,w),c=r|s)$$

Once additional sensing signals e.g s_1 are received, our Bayesian Brain uses its probabilistic model of the world to update its estimation on the state of the world w or movement position m and to generate predictions. This inference will follow the Bayes rule $P(m|s_1)$~$P(m)P(s_1|m)$. In this case, $P(m)$ would represent the distribution on the position of the movement, *the belief*, before observing s_1. Accordingly, P(p) is named *prior*. The model in this equation is represented by the other factor $P(s_1|p)$, *which is* named *likelihood*, the probability of sensory signals given their causes. It intrinsically represents a (probabilistic) prediction of the sensory input s_1 when it is known that the real position is p.

This update process can be seen as a an hypotheses comparison process [8] . Two hypotheses or values of p_1 and p_2 will respectively generate different predictions or more exactly induce different distributions for s_1 $P(s_1|p_1)$ and $P(s_1|p_2)$. The prediction nearer to the observed sensory input s_0, i.e. has higher value $P(s_1=s_0|p)$, will favour the corresponding hypothesis. Thus, perception can be seen under the metaphor of hypothesis comparison, in which the previous likelihood model is inverted to infer the posterior probability of the causes, given the sensory data.

[*] ***This means that for each object and position in space and orientation we assign a weight, or probability, that is the real configuration of the object given what has been sensed. Also, the probabilities may be connected, e.g the probability of the position of a book is connected to the probability of the position of the shelves containing it.***

4. Why Does Perception Avoid Prediction Errors?: The Free Energy Principle and the Active Inference Theory

An intuitive manner in which to evaluate the performance of perception is by measuring the (relevant) mismatch between expected and actual results of an interaction. This obviously also covers the simple case of passive observation, interaction with ‘no-action’, with the mismatch between predicted and actual evolution of the environment without the agent intervention. When this intuition is followed, the aforementioned way of updating hypotheses and changing beliefs is optimal. Perception also requires adaptation and the same approach is at the base of different mechanisms of self-organization which can be seen as improvement of performance in changing and diverse environments.

This intuition is at the base of many formal measures of (perception) performance adopted across different fields that can be intuitively described in terms of (weighted) *prediction error, which can be formalized as the difference between a sensory input and a prediction* [9] . Why does the prediction error need to be weighted?

Remembering the condition of uncertainty in which the brain operates, the formally correct way of evaluating the prediction error should consider how confident the agent was in its predictions both in taking action and when updating its beliefs.

Let’s consider the condition when an agent is betting with an unfair coin where tails appears 90% of the time. He could bet a different amount of money on both sides. The optimal strategy would be to bet on the option in proportion to the related confidence. If the confidence reflects the environment statistics (coin), on average the agent will not lose any money. In this case, the losing option prediction, having only 10% of confidence in the wrong result, should produce a minimal update of its beliefs, and believe that the tail is slightly more probable than 90%. However, with 10% probability that heads will be tossed and a prediction error with high confidence will be processed and reduce the confidence in the tail result. However, when initial beliefs are wrong the average prediction error will be high till when the predictions confidence matches with the actual environment statistics after multiple updates. Minimization of prediction error translates in *estimation of the posterior distribution in Bayesian statistics.*

However, estimation of the posterior distribution easily becomes intractable and any physical system must adopt an approximation. *Variational Bayes* is an approximation adopted in Statistical Physics, Machine Learning, Artificial Intelligence and recently in Computational Neuroscience which selects the approximating ‘variational’ posterior from a limited family of distributions, i.e. the recognition density, that has the minimum distance from the actual posterior.

To compute this distance, it relies on a function named ‘*variational free energy*[†]’ that is a non negative quantity easier to compute and provides an upper bound (is always greater than) to the distance between a target and a proposal distribution [‡]. Another important feature of variational free energy is that it is an upper bound of the surprise of sensory input. Minimising free energy can thus be connected to minising, or better bounding, entropy of the input signal, which under some assumptions is the average of the surprise.

This point is particularly interesting. In fact, the relationship between entropy and organism behaviour goes back to Shoeringer [11], who wrote in his book ‘ What Is Life? The Physical Aspect of the Living Cell’ observing that living creatures are not only extremely complex and organised, but also spontaneously spread and that they replicate these conditions generating a continuous minimisation of entropy [§]. Also, evolution has been seen as a mechanism of complexity increase and entropy decrease. Apart from the connection between entropy and organisms, as extremely complex and self-organising systems, a more important point may be that the connection comes from the homeostatic imperative for living organisms to resist external perturbations and keep their state within a limited set of desired conditions (e.g. body temperature). In statistical terms this means that organisms aim at keeping their own state predictable or, in other words, with limited entropy (e.g. the set of body temperature allowed is limited, thus limiting entropy). These connections lead to the basic intuition of *Active Inference*, that not only perception and learning are aimed at minimizing free-energy, but the same is also true for action. According to Active Inference, or the minimum free energy principle, *actions are realised to keep the organism in a predictable condition given its priors*. This is connected to the recent development in Artificial Intelligence and Machine Learning showing the equivalence between planning and inference problems [13],[14]. This unifies perception and the control process under the same variational inference formulation which can then rely on the same neural machinery for implementation.

Under this assumption, understanding the brain becomes understanding the form of the hierarchical priors involved in the definition of the system. These are now particularly important. These priors not only encode the objective structure of the world, as it is often assumed in robotics, they

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[†] *The name free energy come from the origin of the variational methods in statistical physics where the distribution of interest had form for which the expression of the variational free energy was similar to that of thermodynamics with an energy minus entropy [10] .*

[‡] *Note that while the Active Inference proposal initially suggested the explicit use of variational bayes inference and proposed that the cortex, and the brain in general, is performing it through a specific type of variational bayes message passing, any bayesian inference (approximation) can be seen as minimising variational free energy.*

[§] *This idea may seem to contradict the second principle of thermodynamics, stating that entropy in isolated systems always increases, however organisms are open systems continuously exchanging energy and mass with the surrounding environment. Decrease of entropy in an organism takes place at the cost of energy (e.g. sunlight) and external entropy. While entropy decreases in other non isolated systems, such as crystals, the idea of characterising life as a process that minimises entropy and obtains higher levels of complexity was also at the base for NASA projects aimed at detecting life in outside Earth. [12]*

now include beliefs *on the states that the agent is supposed to stay in*, e.g. staying at the right temperature, not being hungry or bleeding, etc. Under this assumption, the brain has to maximize only one common currency, *variational free-energy*, with which it can evaluate, compare and choose between all the different possible drives (sex, fear, hanger, etc). To understand the importance of using a free-energy formulation and discovering the actual form of the priors, a specific example can be of interest: the Dark Room - a condition where the agent may forever observe the same input. This would reduce entropy to zero. However, if the priors of the agent do not represent this condition, if his generative model does not cover it, the surprise will still be high and the free energy will not be minimized. On the other hand, reaching a position with high probability according to the agent model, where the variational approximation is close to the posterior, would decrease free-energy.

How can our Bayesian Brain avoid these surprising states considering that information comes from the outside world?

The Free Energy crucially depends on both sensory states (which are related to external world) and the *recognition density* (i.e. internal Bayesian models, which is determined by the internal representation capability of the agent and his sensorimotor trajectory). So the brain must manipulate both, by acting on sensory states, for example by selectively sampling only data that are predicted (and maximizing the probability of desired observations), and on recognition density by changing conditional expectations about what is sampled. See figure 2 for a mathematical explanation.

However, it must be considered that any behaviour must be optimized in order to be efficient. Optimization can be performed by both reducing expected costs or maximizing expected reward.

Coming back to the view of Perception as POMDP, it should be noticed that different approaches to the latter have been proposed in the field of Game theory, Machine learning, and Economics, as an 'optimal control' problem (i.e. the mathematical treatment of acting to minimise expected costs).

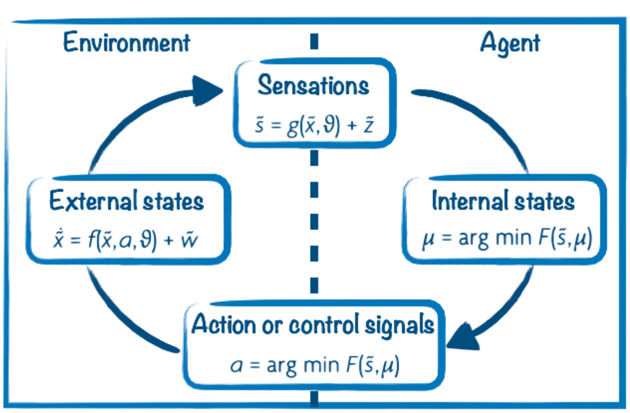

Figure 2 - diagram explaining the free energy principle (Modified from Friston K, 2010)[26]

5. The Neurobiological Implementation and Predictive Coding

Models have proposed that this idea can be at the base of neural response as well as connectivity adaptation. A relevant example of the power of prediction error minimization in explaining both perception and its adaptation in the brain was presented by Rao and Ballard in 1999 [15] as a *predictive coding* neural architecture. Using minimization of prediction error to define *both* neural connectivity and dynamics, they were able to simulate several features of 'extra classical' (see Rao and Ballard 1999 for details) response in the visual cortex. This was achieved using a hierarchical neural architecture where, consistently with neuroanatomy, top-down connections come from high order extrastriate cortex trying to predict neural activity in lower order areas, while bottom-up stream codes for prediction errors (unpredictable and thus salient information). These prediction errors lead to modify expectations in higher levels in order to generate better explanations for lower levels. Other similar examples, based on information theory and machine learning, comprise the work of Mumford [16] and that of Dayan and colleagues [17]. It is also worth noting that animal learning theory points to a similar mechanism, while viewing dopamine neurons as coders of reward prediction error [18]. Moreover the same mechanism has been proposed as the basis of addiction behaviour [19]. Friston instead suggests that dopamine encodes how important the observed prediction error signal is [20]. Going back to the example of the bet, the dopamine signal would be higher when the confidence in the observation reward, or punishment, was high, but the outcome falsifies the expectation. In this theory the final cost, which also refers to actions, is absorbed into prior beliefs about future states that inform posterior beliefs about future control.

An interesting application of this approach in Neuroscience selects the variational density from the family of *hierarchical gaussian distributions.* This family has strong representational power, i.e. can describe many phenomena, and has several analytical properties that made it useful in other fields (as an example, brain imaging [21]). Like in Rao and Ballard's work (1999), they also have a neural implementation which is quite intuitive. The Gaussian family can be described with two quantities: the mean and variance. Thus, these are the two top-down signals that must be encoded in the neural architecture.

Consistently with anatomical and functional evidences that show extensive bidirectional (top-down and bottom-up) connections among cortical nodes [22], on this basis, the *Hierarchical*** *Bayesian Network (HBN)* hypothesis [23] states that in order to *minimize prediction error* each node can modify the state of the generative model (i.e. updates it) until the sampled input match the model and the most likely causes of sensory input have been identified. These quantities are putatively embodied by neural network as associative plasticity. Moreover, the system must also encode another quantity, the uncertainty itself (for example, the amplitude of random noise in the acquiring system) which at neural level could be encoded as post-synaptic gain [24].

***** In hierarchical form, the output of one level acts as an input to the next.***

The HBN model has been proven to fit in with many neurophysiological data, such as associative plasticity, mismatch negativity, P300 in EEG and behavioural data like priming [21]. Moreover, it has been used as a model for illusory phenomena, like mirror-touch synaesthesia [25].

6. Acknowledgements

The authors would like to thank Dr. Viviana Santoro, latinist, for her excellent help with Latin quotations.

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