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Exploring Dopamine-Mediated Reward Processing through the Analysis of EEG-Measured Gamma-Band Brain Oscillations

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Abstract

The central role of the dopamine system on reward brain processing is now quite well delimited. Its influence on other brain areas for learning and decision-making is still a matter of intense research. Most of this is based on fMRI imaging methods, which excel in terms of spatial resolution for source localization but lack the ability to trace the time-course of the signals. Incipient efforts have been made to address this issue from the point of view of EEG-measured brain oscillation theories. We review recent advances in this area and propose a broad framework for EEG-based reward processing analysis.

Introduction

Extensive research has now laid the foundations to describe the involvement of the brain dopamine system in the processing of rewards and reward-predicting stimuli. Dopamine neurons are mostly located in the substantia nigra and ventral tegmental area of the brain. They broadcast a somehow homogeneous signal as a parallel wave of activation capable of influencing "upstream" postsynaptic brain areas (Schultz, 2002).

It is now quite well established that the dopamine signal itself does not differentiate between different types and sensory modalities of reward, but is sensitive to the non-occurrence of reward. It is also agreed that its functionality is more sophisticated than that of a simple attentional signal. Thus, the dopamine system must interact with other dopaminoceptive regions of the brain for its signals to become operative in real-time decision-making.

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In fact, the dopamine signal seems to code a reward prediction error that entails ongoing comparisons between actual rewards and the predictions made about the future occurrence of such rewards (Barto, 1995; Montague *et al.*, 1996; Hollerman and Schultz, 1998). This feature of the system leads to several considerations on its functionality:

The dopamine signal might be considered as a teaching signal for reinforcement learning processes: The existence of reward prediction errors leads to neuronal adaptation as a result of neuronal plasticity capabilities. This process has quite successfully been simulated by the Temporal-Differences (TD) model (Montague *et al.*, 1996). Recently, O'Doherty *et al.* (2003) corroborated that, according to their experimental results, computations described by the TD learning theory have a neurophysiologic counterpart in the human brain. According to learning theory, a prediction error signal, before learning actually occurs, should respond at the time of presentation of reward but, after learning, it should shift its response to the time of onset of any learned conditioned stimulus. fMRI was used by O'Doherty and colleagues (2003) to reveal that responses in ventral striatum and orbitofrontal cortex were significantly correlated with this error signal.

Learning through reward could be seen as an adaptive search for accurate reward predictors, in such a way that the concept of predictability comes to play a mayor role in the processing of rewards. As part of the learning process, the dopamine activity has been shown to transfer from the occurrence of reward itself to the occurrence of the predictors of reward. Unpredicted events may lead to major shifts in learning, whereas learning does not happen by occurrence of fully predicted events.

Fiorillo *et al.* (2003) examined the influence of reward probability and uncertainty on the activity of primate dopamine neurons. In a reward task, dopamine neurons showed little or no response to fully predicted reward (reward with probability of occurrence $P = 1.0$), but phasic activation was elicited for reward delivered with $P < 1.0$. Phasic activations varied with inverse proportionality to reward probability, supporting the nature of the dopamine signal as a carrier of prediction error information. Most interestingly, a novel type of concurrent signal, part of the activation of dopamine neurons, was also found. An increase in activity, from the onset of a conditioned stimulus to the expected time of reward, was demonstrated. For the neuron population response, the activation peaked at reward probability $P = 0.5$, and decreased at lower and higher probabilities, being almost negligible at probabilities $P = 0.0$ and 1.0. This led the authors to suggest that such activity actually codes the level of the uncertainty related to the predicted reward.

The functional form for this uncertainty coding remains to be described. Montague and Berns (2002) did provide a formulation for the influence of uncertainty in the value of a future

reward (a calculation that can be seen as a top-down brain process), but no claim was made about the uncertainty coding functional form itself (although the signal described in Fiorillo *et al.*, 2003, increases monotonically with time, in agreement with the proposals in Montague and Berns, 2002).

As previously said, the dopaminergic system appears to have a rather well-defined but limited functionality. Nevertheless, is densely connected to several dopaminoceptive brain regions. The aim of the following sections is to review the workings of the dopamine system as an element of broader reward-processing schemes. In particular, the focus will be placed on the study of reward processing from the point of view of brain oscillatory behaviour as measures by means of EEG recordings. Most research in this field has resorted to fMRI and related non-invasive methods. These are most suited to achieve spatial resolution and signal source localization, but they are limited when it comes to explore the signal time-course. Some first attempts have been made to explore dopamine activity and reward processing through EEG measurements (Arthurs *et al.*, 2004; Gehring and Willoughby, 2002). We aim here to outline a more general an inclusive theoretic framework that allows for a broader scope to approach this problem.

From reward to its value

Montague and Berns (2002) inscribe the workings of the dopamine system, summarized in the previous section, within a broader scheme. The central idea of their hypothesis is the concept of economic evaluation, worded as the "need for an internal currency that can be used as a common scale to value diverse behavioral acts and sensory stimuli".

Dopaminoceptive regions like the orbitofrontal cortex and striatum (OFS circuits) appear to be involved in valuation processes meeting the need described above, which might be thought of as top-down brain activity. A real-world sensory cue that predicts the future time and magnitude of a reward through estimation must have a level of uncertainty associated to it, with a corresponding cost attached. Experiments on reward uncertainty, and risk-taking behaviour in potentially rewarding tasks (e.g., Egelman *et al.*, 1998) led Montague and Berns to propose that the OFS circuit "computes an ongoing valuation of rewards, punishments, and their predictors. By providing a common valuation scale for diverse stimuli, this system emits a signal useful for comparing and contrasting the value of future events that have not yet happened: a signal required for decision-making algorithms that assign attention, plan actions, and compare disparate stimuli".

The idea of a common value scale can be valid for both rewards and their predictors. A neural system must have a way to compute the predictors' value before the corresponding reward

actually arrives and, therefore, neural signals that encode ongoing valuations must exist. These authors hypothesize that such feature might be represented, at single cell level, as changes in spike production occurring prior to the arrival of a predicted reward.

This proposed valuation scheme for reward predictors is grounded in two main principles: First, the fact that a dynamical estimate of future events cannot be exact and, as a result, the uncertainty in the estimate should accumulate. Second, the value of a potential reward should diminish with time to the actual reward arrival. The authors choose a simple diffusion approach to describe the accumulation of uncertainty in a future reward, and justify an exponential decrease of the value of a reward predictor with time. The scheme that combines these two principles is called the predictor-valuation model. This model results in a procedure for continuously deciding whether the current estimated value of a predictor justifies either continuing its processing, or switching to a better valued alternative. It is hypothesized that the orbitofrontal cortex and striatum are the likely sites to participate in such a valuation function.

The concept of a "valuation system" is also the subject of current research by Holroyd and Coles (2002). On the basis of the study of electrical activity data and, particularly, Event–Related Potentials (ERP), these authors argue that the so called Error-Related Negativity (ERN) component represents the activity of a system concerned with monitoring the value of stimuli. The anterior cingulate cortex (ACC) is seen as a decision-making actor that takes account of the dopamine reward prediction-error signal.

O'Doherty *et al.* (2002) found that the expectation of a reward produced activation in midbrain dopamine system, posterior dorsal amygdala, striatum, and orbitofrontal cortex. But apart from the orbitofrontal cortex, these regions were not activated by the reward receipt itself. This indicates that when rewards are predictable, brain regions recruited during expectation are, in part, dissociable from areas responding to reward receipt. Such dichotomy might well be consistent with the valuation model described in this section, as the orbitofrontal cortex rather be involved in the prediction of the reward, the valuation associated to the reward, reward discrimination, and the subsequent behavioural performance.

It could also be hypothesized that the uncertainty signal, produced by dopamine cells, proposed by Fiorillo *et al.* (2003) feeds the orbitofrontal cortex through thalamo-cortical loops, where a valuation, that also took on board memory processes, would happen as a top-down process that might provide feedback to the error processing system (i.e., produce a prediction error signal on arrival of reward) Some orbitofrontal areas have been shown to discriminate between rewards according to subjective preferences, generating signals that could serve for the valuation of competing rewards (Tremblay and Schultz, 1999).

Reward processing: beyond the dopamine system

The dopamine system has a very well defined anatomical structure. For it to be relevant, beyond basic task processing, in real-world, real-time complex tasks, its influence upon post-synaptic brain structures must be defined.

It has been proposed that the dopamine signal can have a selective influence on postsynaptic structures through coincidence with activity in the cortical inputs linked to the same postsynaptic neuron spines (Smith *et al.*, 1994). In that way, the dopamine activity could work out as an "instruction, biasing, gating or enabling signal" and "it could produce a rapid switch of attentional and behavioural processing to reward-predicting, error-generating external events" (Schultz, 2002), effectively filtering uninteresting bottom-up information.

This is not the only theory attempting to explain what happens at the link between the dopamine system and other top-down-acting post-synaptic structures: Engel *et al.* (2001) put forward a theory based on the time-course of brain oscillatory behaviour that will be described in subsequent sections.

The interactions of the systems involved might benefit from the use of model simulations, as for instance in Cohen *et al.* (2002) who have reviewed the important interactions between the dopamine system and the prefrontal cortex from a connectionist point of view.

Brain oscillations and reward processing

Different techniques are used to gauge brain activity. These might be roughly classified into two groups: invasive (intracranial recordings, mostly used in non-human brains) and non-invasive techniques. Amongst the latter, for instance fMRI and PET, and also EEG, to which special attention will now be paid as it provides the means to explore brain dynamics with high time-resolution. Traditionally, the study of brain electrical activity, as measured from electrodes placed in the scalp, has focused on Event-Related Potentials (ERPs), averages of electric potentials over different trials of the same task as expressed through time. This is the source of a major limitation of ERP studies: any response which is precisely time-locked to stimulus will occur at the same time over trials, but any induced response generated by internal, top-down processes, will be averaged out. The importance of single-trial analysis, and some very interesting examples of how the basic ERP study can sometimes be misleading, can be found in Jung *et al.* (2001).

The time resolution of EEG recordings allows for the analysis of a broad frequency range of the signal. Different frequency bands have been proposed, which are not neatly separated but each of which has been shown to correspond to specific functionalities. High-level cognitive functions have been associated to electric activity at high frequencies, in what is known as gamma band, from around 20Hz upwards (Pulvermuller *et al.*, 1997). There is a well-known evoked, stimulus time-locked, response in the gamma band in the vicinity of 40Hz frequency. This activity would be picked-up by ERP calculations. Instead, a later induced gamma response with slightly changing latency would not be registered using this approach. This induced response bears special significance because it is the one related to high-level functions such as perceptual binding, object representation, and visual information processing, amongst others. Gamma-band can globally be seen as an integrative mechanism that may bring a widely distributed set of neurons together into a coherent ensemble that underlies a cognitive act. Examples and descriptions of the functionality of gamma-band activity can be found, for instance, in Karakaş *et al.*, 2001; Tallon-Baudry and Bertrand, 1999; and Gruber *et al.*, 2002.

Accepted that electric activity in different frequency bands and, very specifically, in the high-frequency gamma-band, in terms of magnitude and synchrony, is linked to high-level cognitive processes, the next step is finding out to what extent could reward processing, as described in previous sections, be linked to brain oscillatory activity. Some cues on this issue can be found in the work by Engel *et al.* (2001). Bottom-up stimuli's (including reward) processing is related to higher-level brain processes expressed as top-down influences, generating, as a whole, the dynamics of thalamo-cortical circuits which involve diverse and well-delimited brain areas. As mentioned in previous sections, the brain must generate ongoing predictions about forthcoming sensory events, such as rewards and reward predicting cues. Such predictions, according to Engel and colleagues, might be embodied in the temporal structure of stimuli-evoked and induced activity. Synchronous oscillations are particularly important in this process. Filtering of meaningful inputs can only happen if the brain uses top-down resources, allowing it to create predictions about future events. Engel and colleagues propose that this prediction might be encoded in the temporal structure of neural activity patterns: in this way "spatio-temporal patterns of ongoing activity" mediate to generate "dynamic systems of anticipation" from the functional architecture of neural systems and the pre-stimulation history.

One "early" theory that assumes that prediction signals travel along feedback connections from "higher to lower" areas of processing is known as ART, by Grossberg (1980, 1999). In this theory, a match between prediction and stimuli leads to the amplification of the signal. Engel *et al.* (2001) put forward an alternative proposition based on *temporal binding*, in

which synchrony in neural oscillatory activity is seen as crucial for object representation, response selection, and other functions such as those listed in previous paragraphs. Neural synchrony, as an *enhancer of response saliency* might select and link subsets of individual neuronal responses for further joint processing. The coherent activity that might then be generated via large-scale interactions would induce the synchronization of diverse input signals, leading to a selective enhancement of temporal correlations in subsets of activated populations, and resulting in a competitive advantage for that neural population.

This proposition has to be compared to that in Smith *et al.* (1994), reviewed in Schultz (2002), and described in the introduction, which puts forward the dopamine signal as a selective influence on postsynaptic structures through coincidence with activity in the cortical inputs linked to the same postsynaptic neuron spines. Top-down influences that originate in the prefrontal and parietal areas of the cortex, where assemblies of neurons represent action goals, would provide modulatory bias signals to sensory-motor circuits, whereas dopamine-related reward signals would gate learning processes that optimize functional connections between prefrontal and lower-order sensorimotor assemblies.

The proposition should also be compared to the model recently put forward by Holroyd and Coles (2002), suggesting that the ACC, which receives signals from several high-level cognitive and executive areas such as the amygdala, dorsolateral prefrontal cortex, orbitofrontal cortex, etc., and also from the dopamine system itself, acts as a "control filter", deciding which of these "command centers" actually take executive control.

Can the proposals of Engel *et al.* (2001) and Holroyd and Coles fit within a single framework? Top-down factors can lead to states of expectancy or anticipation, expressed in temporal structures of brain activity even previous to stimuli. If latency shifting can be controlled by top–down processes, then the saliency of neuronal responses coding for an expected stimulus could be enhanced efficiently. Engel *et al.* (2001) propose that top–down influences can enhance the coherence of ongoing oscillations selectively for neuron assemblies. Neurons participating in coherently oscillating assemblies would, when stimulated, show well-synchronized responses that are transmitted faster and more reliably than non-synchronized responses. So, stimuli that meet the 'expectancies' expressed by coherent states of the network generate more salient responses than non-attended or unexpected stimuli. It must be noted though that this mechanism is, in principle, not restricted to a particular brain processing area.

There is evidence that the influence of top-down processes on the temporal structure of neural responses, manifests mostly in the gamma-band (Pulvermuller *et al.*, 1997; Tallon-Baudry and Bertrand, 1999; Karakas *et al.*, 2001). Synchronization in this band is enhanced by

attentional selection (Fries *et al.*, 2001; Steinmetz *et al.*, 2000). Gamma synchronization has been shown between sensory and motor areas and between motor and parietal areas. Most importantly, signal synchronization is also enhanced by expectancy (Roelfsema *et al.*, 1997), and the ACC has been shown to generate precisely a signal describing the level of reward expectancy (Shidara and Richmond, 2002). Therefore, the ACC, a "controller" that receives input from the dopamine system, would also influence the synchrony of the temporal patterns of neural assemblies' oscillatory behaviour, leading to the priming of certain responses.

Other studies (Bernasconi *et al.*, 2000) show that synchrony in the gamma band occurs mostly for novel (i.e. unexpected) stimuli and, corroborating this, Von Stein *et al.* (2000) show that high-frequency interactions in the 20-100Hz (gamma) band reflect the processing of novel unexpected stimuli. Also, as indicated in Von Stein *et al.* (2000) and Burguess and Ali (2002), the frequency of synchronization is likely to be related to "locality", with high-frequency gamma synchronization functionally bounding nearby areas in short-range interactions, and lower-frequency synchronization bounding distant areas in long-range interactions.

Can reward processing be visualized via EEG?

As stated in the introduction, we attempt to clarify how the processing of reward, which involves diverse brain areas, manifests itself as scalp electric potential activity recorded by EEG. Recently, Gehring and Willoughby (2002) studied reward processing in humans engaged in a monetary gambling task. The focus was on the study of reward outcome (as opposed to reward anticipation –see, for instance Knutson *et al.*, 2001a, 2001b-), using event-related potential (ERP) from EEG measurements. A medial-frontal negativity (MFN) potential was found, larger on gamble loss trials than in gain trials. The source of this activity was located in the medial frontal cortex, in the vicinity of the ACC, and the authors inferred that activity in this area contributes to high-level decision-making. The responsibility of the ACC in decision-making tasks has also been reported elsewhere (Bush *et al.*, 2002; van Veen *et al.*, 2001), as well as its role, described in the previous section, as the generator of a signal describing the level of reward expectancy (Shidara and Richmond, 2002). This last function has also been suggested as one that can actually underlie others attributed to the ACC. The ACC has even been linked to a function as neural marker for positive affective reaction (Berridge, 2003).

The ACC activity has also been reported to be the source of an error-related negativity (ERN) in Coles *et al.*, 2001, and Gehring and Fencsic, 2001. This activity would be related to prediction error signals. Specifically, the ERN would be generated when a phasic negative prediction-error dopamine signal disinhibits the apical dendrites of neurons in the ACC. The

opposite ERP positivity would be produced by a positive dopamine signal inhibiting the apical dendrites of neurons in the ACC.

A complete account of the interaction between the dopamine system and the ACC, together with the "signature" of this activity in the form of ERN can be found in Holroyd and Coles, (2002). In this work, the integration of the ACC in a more general valuation system is proposed. As mentioned in the previous section, these results have to be compared with the OFS-located ongoing valuation system proposed by Montague and Berns (2002), as well as with results in Knutson *et al.* (2001a,b), related to monetary reward. The model proposed by Holroyd and Coles is reproduced next:
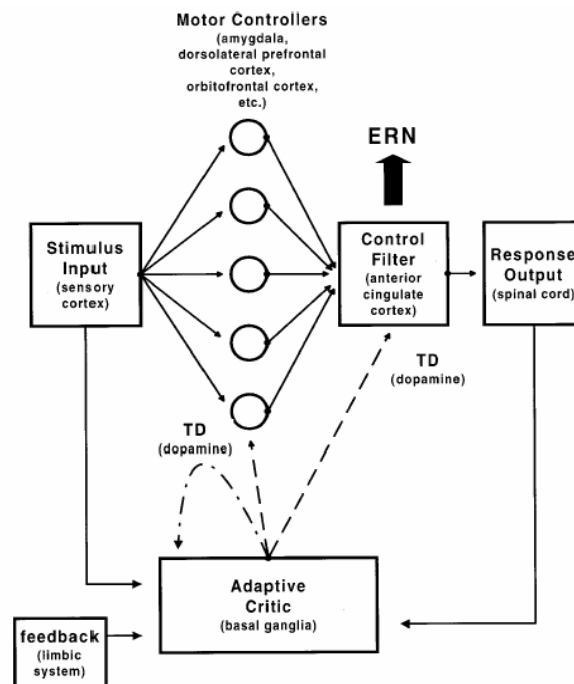

Figure 1: Graphical description of the role of ACC as "executive controller", mediating between "motor controller" neural assemblies and responses. Reproduced with the permission of the authors.

Central to this model is the idea that there exist several motor controllers corresponding to neural command structures that project to the ACC, which, acting as a "motor control filter", decides which motor command structures actually take control. Importantly, this gating role is learned through experience mediated by the dopamine system. It is impossible to avoid the comparison of this proposition with the temporal binding hypothesis of Engel *et al.* (2001) described in the previous section: An expectancy signal emitted by the ACC might influence

the synchrony of neural assemblies' oscillation patterns, priming some of them and, therefore, supporting the "executive control" features of this brain region.

Alternatively, in an interesting twist to the argument that confers a role to synchronization of oscillations as a signature of integration of top-down processes, Amzica et al. (1997) report the use of reward (water) to condition the increase of synchronization of gamma oscillations in a specific area of the brain of a water-deprived cat. This is followed by the disappearance of the synchrony due to the extinction of the conditioning. The highest gamma-oscillation synchrony was found to take place in the intralaminar centrolateral nucleus and the lateral genicular nucleus which are supposed to be important for large-scale gamma-band thalamo-cortical circuits.

Summary

The dopamine system, quite thoroughly studied from anatomical and functional points of view, has been shown as the basic element of brain reward processing that feeds other neural systems in the cortex, responsible for top-down processes. Several recent studies have been surveyed here, in which the role of high-level cognitive areas, such as the orbitofrontal and anterior cingulated cortices, in the processing of reward has been described. These systems influence integrative oscillatory pattern mechanisms that may be part of the whole reward processing framework. Only recently, this oscillatory activity has started to be explored by means of its EEG-measured manifestation.

It has been hypothesized that the ACC's proposed role as an "executive controller", mediating between "motor controller" neural assemblies and responses, might be explained resorting to its generation of an expectancy-valuing signal. This signal would have an influence on the synchronization of neural assemblies' oscillations, selectively enhancing certain response saliencies. This bridges elements of the theories put forward by Engel *et al.* (2001), Holroyd and Coles (2002), Montague and Berns (2002), and the workings of the dopamine system summarized in Schultz (2002).

This work also intends to provide a global and up-to-date review of a series of developments that could facilitate the interpretation of EEG results obtained from experiments based on reward-related tasks.

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