Neuroscience and Biobehavioral Reviews xxx (2014) xxx–xxx

Contents lists available at ScienceDirect

Neuroscience and Biobehavioral Reviews

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

Review

The role of high-frequency oscillatory activity in reward processing and learning

Q1 Josep Marco-Pallarés[a,b,*], Thomas F. Münte[c,d], Antoni Rodríguez-Fornells[a,b,e]

[a] Department of Basic Psychology, University of Barcelona, 08035 Barcelona, Spain
[b] Cognition and Brain Plasticity Unit, Bellvitge Research Biomedical Institute (IDIBELL), Hospitalet de Llobregat, Barcelona, Spain
[c] Department of Neurology, University of Lübeck, Lübeck, Germany
[d] Institute of Psychology II, University of Lübeck, Lübeck, Germany
[e] Institució Catalana de Recerca i Estudis Avançats (ICREA), Barcelona, Spain

ARTICLE INFO

Article history:
Received 1 July 2014
Received in revised form 3 November 2014
Accepted 18 November 2014
Available online xxx

Keywords:
Oscillatory activity
Reward
Novelty
Beta
Gamma

ABSTRACT

Oscillatory activity has been proposed as a key mechanism in the integration of brain activity of distant structures. Particularly, high frequency brain oscillatory activity in the beta and gamma range has received increasing interest in the domains of attention and memory. In addition, a number of recent studies have revealed an increase of beta–gamma activity (20–35 Hz) after unexpected or relevant positive reward outcomes. In the present manuscript we review the literature on this phenomenon and we propose that this activity is a brain signature elicited by unexpected positive outcomes in order to transmit a fast motivational value signal to the reward network. In addition, we hypothesize that beta–gamma oscillatory activity indexes the interaction between attentional and emotional systems, and that it directly reflects the appearance of unexpected positive rewards in learning-related contexts.

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1. Introduction

Oscillatory activity is a basic brain mechanism that allows communication between distant brain areas (Buzsaki and Draguhn, 2004). In the last decade, oscillatory activity in the beta (12 to 30 Hz) and gamma (>30 Hz) frequency bands of mammals has been found to be crucial for information processing in the central nervous system and has been related to a variety of motor and cognitive functions including perception, motor control, sensorimotor integration, attention, inhibition, memory and higher level cognition (Chen et al., 2004; Jensen et al., 2007; Llinás et al., 2005; Ribary, 2005; Schnitzler and Gross, 2005; Uhlhaas and Singer, 2006; Wang, 2010). Recently, human electrophysiological studies have described an increase of high beta–low gamma oscillatory activity after reward delivery in gambling and learning tasks (Cohen and Ranganath, 2007; Doñamayor et al., 2012, 2011; Marco-Pallares et al., 2008; Marco-Pallarés et al., 2009).

In the following sections we will review the recent literature on reward processing in humans to propose the hypothesis that beta–gamma oscillatory activity is mediating the interaction between brain systems involved in attention and reward processing, and that it directly reflects the appearance of unexpected positive rewards in learning related contexts. Thus, beta–gamma oscillatory activity will appear whenever a feedback stimulus

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* Corresponding author at: University of Barcelona, Department of Basic Psychology, Facultat de Psicologia, Campus de, Edifici Ponent Passeig de la Va, 08035 Q2 Barcelona, Spain. Tel.: +34 933125156..
E-mail addresses: josepmarco@gmail.com, josepmarco@hotmail.com (J. Marco-Pallarés).

http://dx.doi.org/10.1016/j.neubiorev.2014.11.014
0149-7634/© 2014 Published by Elsevier Ltd.

Please cite this article in press as: Marco-Pallarés, J., et al., The role of high-frequency oscillatory activity in reward processing and learning. Neurosci. Biobehav. Rev. (2014), http://dx.doi.org/10.1016/j.neubiorev.2014.11.014

conveys new information about unexpected positive and significant rewards. This brain oscillatory signature might signal the need to store new information in memory for guiding future actions and, therefore, might represent a key mechanism for orchestrating the cross-talk between learning processes, involving the medial temporal lobe, the ventral striatum, medial prefrontal regions and the midbrain dopaminergic system.

2. Functional role of beta–gamma activity

Studies on reward (Knutson et al., 2005; O'Doherty et al., 2001) or positive feedback processing (Camara et al., 2010, 2009; Nieuwenhuis et al., 2005) have revealed an extended network including the ventral striatum, amygdala, insula, ventromedial prefrontal cortex and anterior cingulate cortex among others. However, the mechanisms that allow the integration of information of the different nodes of this network are largely unknown. Using electroencephalography (EEG) to record the brain electrical activity of large neuronal groups, two independent studies using different experimental paradigms reported an increase of oscillatory activity when participants received a signal indicating a monetary gain (positive feedback, Cohen et al., 2007; Marco-Pallares et al., 2008; Fig. 1B). This increase occurred 200 to 400 ms after the feedback informing about the positive outcome, and was produced at frequencies ranging from 20 to 35 Hz which are traditionally considered to represent high beta–low gamma frequency ranges ($\beta\gamma$ activity from now on). Marco-Pallares et al. (2008) used a gambling task in which the subjects had to choose between a larger and a smaller number that corresponded to the win or loss of the equivalent sum in Euro cent ($p = 0.5$ for wins and losses, Fig. 1A). In this study the win-related $\beta\gamma$ power was more pronounced for larger rewards than smaller rewards, suggesting that this activity could be related to the magnitude of the outcome.

Similarly, Cohen et al. (2007) also found a greater $\beta\gamma$ power after positive feedback. Here, a reversal learning task was used, in which participants had to choose between two squares located at left or right positions. After the selection, a visual feedback indicated whether the participant received a reward (10 cents) or a punishment (−10 cents). During a block (80 to 150 trials) each of the sides was associated to a probability to win. When a new block started, and without informing to the participant, the probabilities changed. The three possible probabilities for left and right locations were, for different blocks, 0.75–0.25; 0.5–0.5 and 0.25–0.75, respectively. Interestingly, $\beta\gamma$ oscillatory activity was more pronounced for unexpected rewards ($p(\text{win}) = 0.25$) than for expected rewards ($p(\text{win}) = 0.75$). Previously, Keil et al. (2001) had also described a similar activity using a paradigm in which participants had to press a button three seconds after a cue and in order to receive a monetary reward. The amount of money depended on how temporally precise the response was. Upon the button press, which was immediately followed by the presentation of feedback indicating the amount of reward, left frontal electrodes showed an increase of power in the 20–30 Hz frequency range, 350 to 500 ms after the button press. This activation was not present when the reward was delivered randomly or when participants just pressed the button, suggesting that the effect was not related to motor activity. Interestingly, in a recent magnetoencephalography (MEG) gambling study, Doñamayor et al. (2011) also found an increase in $\beta\gamma$ power (with peaks at 29 and 34 Hz), 200 to 500 ms after reward delivery (Fig. 1C, Doñamayor et al., 2012, 2011).

These initial studies clearly pointed out the involvement of reward-related processes in the generation or modulation of the $\beta\gamma$ component (Marco-Pallarés et al., 2009). This proposal was further supported by another study showing that the $\beta\gamma$ increase after monetary gains was related to the Catechol-*O*-methyltransferase enzyme (COMT) Val158Met polymorphism (Marco-Pallarés et al., 2009). COMT plays a key role in the degradation of dopamine in the prefrontal cortex. Bilder et al. (2004) proposed an inverse relationship between tonic dopaminergic activity in the prefrontal cortex and phasic activity in striatal areas. Therefore, carriers of the Met allele, which has been associated to low enzyme activity (that is, reduced dopamine degradation in the prefrontal cortex), would show increased tonic activity in the prefrontal cortex which would lead to decreased dopaminergic striatal phasic activity. In contrast, participants homozygous for the Val allele would show decreased prefrontal tonic activity and increased striatal phasic activity. Indeed, participants homozygous for the Val allele showed enhanced $\beta\gamma$ oscillatory activity after gains compared to MetMet carriers, supporting the tonic-phasic hypothesis. Further, Padrão et al. (2013) also showed that individuals with high trait anhedonia presented a smaller $\beta\gamma$ response after rewards than high hedonic participants. Anhedonia is the reduction of the ability to experience pleasure (Meehl, 1975) and has been related to dysfunctions in the reward system, especially in the Nucleus Accumbens (Russo and Nestler, 2013). In addition, following similar rationale, a recent study found a positive correlation between this activity and the trait of sensation seeking (Leicht et al., 2013). Both human studies and animal models have shown that high sensation seekers present and increased mesolimbic dopaminergic activity (Blanchard et al., 2009), especially in the Nucleus Accumbens. These results support the involvement of the reward network and its dopaminergic subcortical components in the generation of $\beta\gamma$ oscillatory activity.

However, while initial studies had shown that $\beta\gamma$ oscillatory activity was elicited by positive reward outcomes, it became subsequently clear that not all positive reward conditions elicit this activity. In HajiHosseini et al. (2012) we investigated its relationship to the difference between expected and obtained rewards and punishments (prediction error) by employing a gambling task in which a cue indicated the probability and magnitude of upcoming outcomes (monetary gains or losses, Fig. 2A). The goal of the experiment was to determine whether $\beta\gamma$ activity was modulated by the probability, magnitude or the expected value of the monetary outcome. A $\beta\gamma$ oscillatory activity increase was observed only after unexpected gains, that is, those gains with low probability (Fig. 2A). In addition, $\beta\gamma$ activity was not related to the expected value, prediction error or to the magnitude of the reward. This result also agrees with a previous finding of an increase of $\beta\gamma$ power after improbable rewards (Cohen et al., 2007). In addition, Cunillera et al. (2012) analyzed feedback processing in a modified version of the Wisconsin Card Sorting Task that required the selection of one of four cards according to a certain rule (color, shape, number, Fig. 2B). After each selection the participant is informed whether the selection has been correct or incorrect. However, at a certain moment, and without informing the participant, the rule changes and the participant has to infer the new rule by trial and error. The study revealed that the $\beta\gamma$ increase appeared only following the first positive feedback after a correct rule change. In other words, $\beta\gamma$ activity appeared after the most informative positive feedback, the one that indicated that the correct rule had been selected. Another relevant study analyzed the effect of contextual novelty in reward processing (Bunzeck et al., 2011). Participants had to learn the relationship of different fractal images to the probability of winning money and subsequently performed a recognition task that required them to determine whether a scene was indoor or outdoor. Some of these scenes were familiar (had been presented in a previous phase of the experiment) and others were novel. After the decision, the fractal image appeared indicating the probability of subsequent monetary reward. $\beta\gamma$ Activity was enhanced for fractal images indicating high reward probability (Fig. 2C) and furthermore this activity was modulated by the familiarity of the context, being higher for the novel condition. According to the

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