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Review

Electrophysiological underpinnings of reward processing: Are we exploiting the full potential of EEG?

Garance M. Meyer[a,b,c,d], Josep Marco-Pallarés[e,f], Philippe Boulinguez[a,b,c,d,#,*], Guillaume Sescousse[a,b,c,d,#]

[a] *Université de Lyon, F-69622, Lyon, France*
[b] *Université Lyon 1, Villeurbanne, France*
[c] *INSERM, U 1028, Lyon Neuroscience Research Center, Lyon, F-69000, France*
[d] *CNRS, UMR 5292, Lyon Neuroscience Research Center, Lyon, F-69000, France*
[e] *Department of Cognition, Development and Educational Psychology, Institute of Neurosciences, University of Barcelona, Spain*
[f] *Cognition and Brain Plasticity Unit, Bellvitge Biomedical Research Institute, Spain*

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ABSTRACT

Understanding how the brain processes reward is an important and complex endeavor, which has involved the use of a range of complementary neuroimaging tools, including electroencephalography (EEG). EEG has been praised for its high *temporal* resolution but, because the signal recorded at the scalp is a mixture of brain activities, it is often considered to have poor *spatial* resolution. Besides, EEG data analysis has most often relied on event-related potentials (ERPs) which cancel out non-phase locked oscillatory activity, thus limiting the functional discriminative power of EEG attainable through *spectral* analyses. Because these three dimensions -temporal, spatial and spectral- have been unequally leveraged in reward studies, we argue that the full potential of EEG has not been exploited. To back up our claim, we first performed a systematic survey of EEG studies assessing reward processing. Specifically, we report on the nature of the cognitive processes investigated (i.e., reward anticipation or reward outcome processing) and the methods used to collect and process the EEG data (i.e., event-related potential, time-frequency or source analyses). A total of 359 studies involving healthy subjects and the delivery of monetary rewards were surveyed. We show that reward anticipation has been overlooked (88% of studies investigated reward outcome processing, while only 24% investigated reward anticipation), and that time-frequency and source analyses (respectively reported by 19% and 12% of the studies) have not been widely adopted by the field yet, with ERPs still being the dominant methodology (92% of the studies). We argue that this focus on feedback-related ERPs provides a biased perspective on reward processing, by ignoring reward anticipation processes as well as a large part of the information contained in the EEG signal. Finally, we illustrate with selected examples how addressing these issues could benefit the field, relying on approaches combining time-frequency analyses, blind source separation and source localization.

1. Introduction

Reward processing is at the very heart of goal-directed behavior and decision-making. It has been shown to be impaired across a wide range of psychiatric disorders (Balodis and Potenza, 2015; Ng et al., 2019; Nusslock and Alloy, 2017), making it a potentially valuable transdiagnostic marker of mental health (Hägele et al., 2015). Understanding how the brain processes rewards is thus crucial, but remains a complex endeavor. First, reward processing comprises both anticipatory and outcome phases, each of them involving several processes co-occurring at various times scales. While reward anticipation corresponds to the cognitive operations that precede an incoming reward, including incentive valuation, probability estimation or motor preparation, reward outcome corresponds to those operations triggered by the actual delivery of the reward, including hedonic feelings, reward value update and behavioral reinforcement. Broadly speaking, incentive salience (‘wanting’), hedonic impact (‘liking’), and learning can be seen as the three core components of reward (Berridge et al., 2009; Berridge and Robinson, 2003). Second, reward processing involves large brain networks as well as various neuromodulators (Haber and Knutson, 2010; Kranz et al., 2010; Liu et al., 2011). This complexity thus requires the use of complementary neuroimaging techniques

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[*] Corresponding author at: Centre de Recherche en Neurosciences de Lyon, 95 boulevard Pinel, 69500 Bron, France.
E-mail address: philippe.boulinguez@univ-lyon1.fr (P. Boulinguez).
[#] Co-last authors listed in alphabetical order.

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in order to gain a global understanding of reward processing in the brain.

Functional MRI and PET have been among the most popular techniques used to investigate reward processing and have helped characterize the underlying brain networks and neurochemistry. On the other hand, electroencephalography (EEG) has been leveraged for its fine temporal resolution, which can reveal the rapid brain dynamics that remain out of reach for fMRI and PET (Luck, 2014). As such, many EEG studies have tracked specific timed events associated with reward processing, most often through event-related potentials (ERPs) (see for reviews: Brunia et al., 2011; Foti and Weinberg, 2018; Glazer et al., 2018; Luft, 2014; Marco-Pallarés et al., 2015; Proudfit, 2015; Sambrook and Goslin, 2015; San Martín, 2012; Walsh and Anderson, 2012). However, a major limitation of EEG in general, and ERPs in particular, is that the signal recorded at the scalp is a mixture of a number of different brain activities arising from a number of different brain regions. The resulting mixing of brain activities is exacerbated by volume conduction, which causes activity from a single region to spread across a large part of the scalp (see Jackson and Bolger, 2014 for a comprehensive review on EEG signal generation). But confounds do not only arise from the limited spatial resolution inherent to the method. Simply considering event-related voltage deflections recorded between two sensors also neglects the fact that electrophysiological brain activity can occur through different frequency bands. Disentangling the temporal, spatial and functional overlaps of electrophysiological activities is thus a central issue to consider in order to optimally benefit from EEG . More or less advanced signal processing methods can enhance the discriminative power of EEG, by (1) considering the frequency content of the signal that provides functional signatures of neurocognitive processes, (2) using mathematical solutions to separate the functional sources of activity mixed in the overall electroencephalogram, and (3) estimating the anatomical origin of an electrophysiological marker.

Indeed, because brain activity recorded with EEG is composed of oscillations that occur in different frequency bands, their separation via time-frequency analyses (which assess the spectral characteristics of the signal as a function of time) constitutes a first way to isolate activities that would otherwise overlap in time or space. Moreover, recent methodological advances, not specific to the EEG domain, offer various computational solutions to recover a set of source signals[1] from the mixed signals recorded at the sensor level. These are termed *Blind Source Separation* (BSS). BSS-based analyses are able to unmix most sources of the ongoing brain activity without a priori knowledge about the source signals or the mixing process. Additionally, *source localization* is a class of methods that aim to retrieve the anatomical generator(s) of an observed EEG activity. It relies on an inverse problem that, as an ill-posed problem, is non-unique and unstable (i.e., cannot be solved but only estimated). However, when applied on "clean" unmixed signals, source localization offers the opportunity to take full advantage of the spatial information contained in the EEG signal (He et al., 2018; Huster and Calhoun, 2018; Michel and Murray, 2012).

To summarize, the discriminative power of EEG analyses relies on three axes that are mutually beneficial: the temporal, spectral, and spatial dimensions (Fig. 1). Here, we perform a systematic survey of EEG studies investigating how the different methodological options that might contribute to disentangling brain activities confounded in the EEG signal have been employed to address current theoretical issues about reward processing. In other words, we aimed to check whether the full power of EEG has been exploited in the field. Specifically, we report on (1) the nature of the cognitive processes investigated (reward anticipation vs reward outcome processing) and (2) the methods used to collect and process the EEG data. Based on the results, we argue that a large proportion of previous studies investigating reward processing have used EEG in a suboptimal way. Indeed, we show that (1) reward anticipation has been overlooked and (2) the three axes for discriminative power have been unequally leveraged, revealing that some methodological developments have not been widely adopted by the field yet. We then discuss and illustrate with selected examples how doing so could bring novel insights to the field.

2. Systematic analysis

2.1. Methods

We searched the Pubmed and Web of Science databases for EEG studies of reward processing on 8/10/2019. To be included, studies had to (1) include a group of healthy subjects; (2) involve the delivery of monetary rewards; (3) report statistical analyses of brain activity related to the anticipation and/or receipt of rewards. Based on these criteria, 359 articles (out of 2469 retrieved records) were considered for our survey. Detailed information about the selection process as well as a flow chart are provided in the Supplementary Materials.

The following information was extracted from the abstracts or method sections of these articles: (1) nature of the cognitive processes investigated, i.e. reward anticipation and/or reward outcome processing; (2) methods used to collect and process the EEG data, i.e. technique used (e.g., EEG, EEG-fMRI…), and presence of ERP, time-frequency and/or source analyses. We chose to extract this information regarding data processing because it captures the use of the three axes for discriminative power of EEG. Indeed, while both ERPs and time-frequency analyses make use of the temporal dimension, only time-frequency analyses exploit the spectral dimension. By source analyses, we here refer to the methods that can contribute to enhanced spatial information, in particular source separation and/or localization methods.

2.2. Results

Among the 359 surveyed studies, a majority was interested in reward outcome processing (88%, 316 studies) as compared with reward anticipation (24%, 86 studies). While 92% (331 studies) reported ERP analyses, only 19% (70 studies) reported time-frequency analyses. Twelve percent (44 studies) performed source analyses (here meant as source separation and/or localization), and only 2% (8 studies) performed both time-frequency and source analyses. Finally, 4% of studies used EEG combined with another neuroimaging technique (EEG-fMRI: 14 studies, EEG-Magnetoencephalography (MEG): 1 study, EEG-PET: 1 study). Figs. 2 and 3 display the evolution of these proportions over the last 20 years.

3. Considering the diversity of reward processes

Our analysis revealed that EEG studies have investigated reward outcome processing more often than reward anticipation (88% vs 24%, Fig. 2). Incidentally, it is interesting to note that the field of EEG has mostly relied on gambling/guessing tasks (e.g., Gehring and Willoughby, 2002; Kujawa et al., 2013) as well as reinforcement learning tasks (e.g., Bellebaum et al., 2010; Cohen et al., 2007), well-suited to investigate reward outcome processing, while the field of fMRI has been more strongly influenced by paradigms such as the Monetary Incentive Delay task (Knutson et al., 2000) which was specifically developed to investigate anticipatory processes. We speculate that the overrepresentation of EEG studies investigating reward outcome processing might result from the combination of a theoretical interest for a trendy issue and the ease of use of available tools and markers. Indeed, the field has historically focused on the feedback-related negativity (FRN) and other feedback-related ERPs in the context of error processing and learning, in particular in relation with the influential reward prediction

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[1] Note that in the context of blind source separation, "source" should not be understood as an anatomical generator, but a functional generator. See section "Considering spatial information: localization and source separation" for discussion.

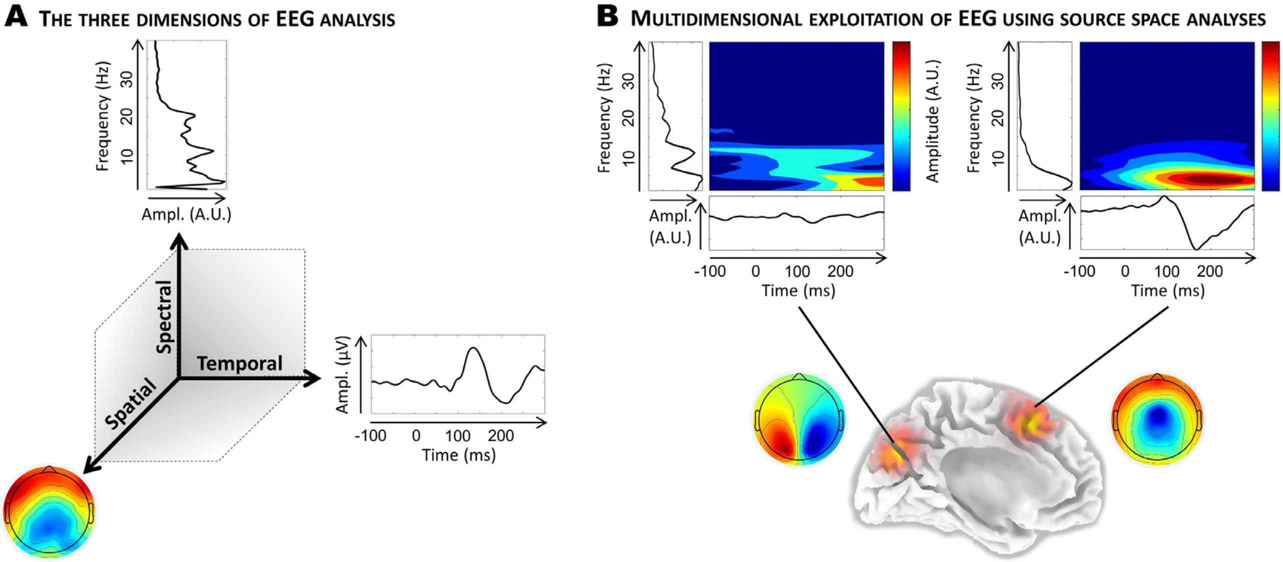

Fig. 1. The discriminative power of EEG relies on the exploitation of three analytical dimensions. The EEG signal recorded at the sensors is a time-series, which can be resolved along different analytical dimensions. (A) The high temporal resolution of the recorded time-series allows one to examine how it unfolds with time (*temporal* dimension) as well as its underlying oscillatory rhythmicity (*spectral* dimension). Considering the spectral content of the signal can help to distinguish brain processes or functions, because these may occur in different frequency bands. These two dimensions are often examined in isolation, using ERP analyses (that ignore the spectral dimension), or spectral analyses (that ignore the temporal dimension). ERP and static spectrum at electrode FCz are shown as illustrations. The third dimension, *spatial*, is reconstructed from the known position of the different sensors on the scalp. It is often considered as the weakness of EEG, and hence ignored. Indeed, while the topography of scalp activity can be examined (here, topography at 210ms is shown as an example), it may be poorly informative due to volume conduction. Yet, a range of solutions is available to take full advantage of the spatial information hidden in the scalp signal, including source separation and source localization methods. (B) Optimal discriminative power may be obtained when the three dimensions -temporal, spectral, spatial- are leveraged in combination, e.g., by using time-frequency analyses (that combine the temporal and spectral dimensions to examine event-related changes in the amplitude and phase of oscillations at specific frequencies) performed in the source space. Illustrations show, for two distinct sources, the static spectrum, back-projected ERP (at electrodes B4 and FCz, respectively), time-frequency map, topography, and localization (obtained using sLORETA). All illustrations are adapted from Albares et al., 2014. The reader is referred to the main text for details about the different signal processing options presented here.

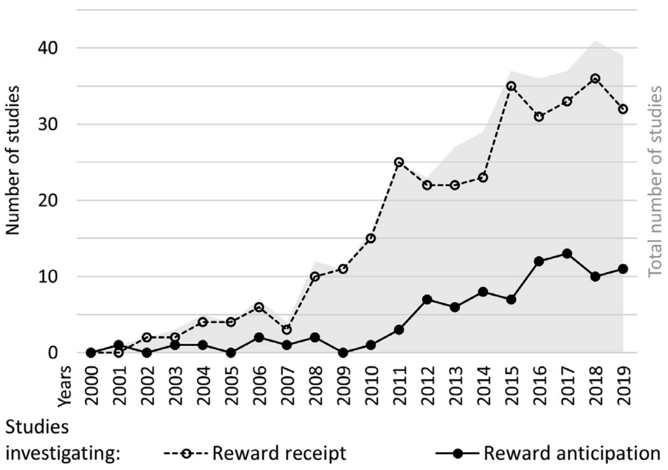

Fig. 2. EEG studies investigating reward outcome processing vs. reward anticipation. Much more studies have investigated reward processing at the outcome stage (by means of analyses of the feedback period, using comparisons such as win vs. loss or small vs. large gain), as compared with reward anticipation (for instance, analyses of the cue period, using comparisons such as expected win vs. expected loss).

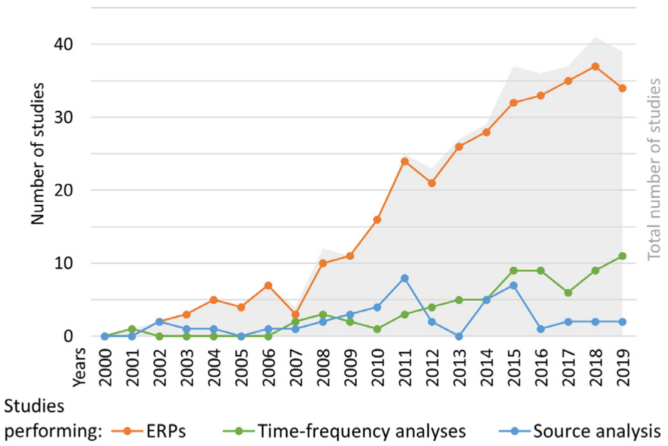

Fig. 3. EEG studies of reward processing made unequal use of the three dimensions for discriminative power. Most studies over the last 20 years have relied on ERP analyses. In contrast, time-frequency and source analyses have been performed by only a minority of studies. This demonstrates limited use of the spatial and spectral information. Note that no clear temporal evolution in the proportion of studies using ERPs, time-frequency analyses or source analyses can be seen.

error (RPE-FRN) framework (Holroyd and Coles, 2002; Sambrook and Goslin, 2015; Walsh and Anderson, 2012). Only later, the focus shifted to reward processing *per se* (Foti and Weinberg, 2018), putting reward anticipation in the spotlight. Additionally, reward anticipation processes were initially associated with subcortical areas (Schultz et al., 1997), which logically made EEG a less appropriate technique to investigate them, due to the difficulty of reaching deep brain areas.

Consistent with our observation, Glazer et al. (2018) noted that EEG studies neglect the “rich temporal heterogeneity of reward processing”, by focusing on the reward outcome stage and disproportionately relying on the FRN. Glazer et al. thus called for “broadening the time course” of EEG components investigated in relation to reward processing. Based on the data presented here, we fully endorse this recommendation. It should be emphasized that the high temporal resolution of EEG is particularly valuable here, since the brain signals related to reward anticipation and reward outcome processing are often problematically confounded when studied with fMRI, due to the sluggishness of the BOLD signal (e.g., Pornpattananangkul and Nusslock, 2016). However, "broadening the time course" may not be sufficient. Below, we discuss other equally important limitations that the field must overcome for using EEG in an optimal way to disentangle the neurocognitive processes of reward.

4. Considering oscillatory components

Although the informativeness and added value of time-frequency analyses have been previously highlighted in the context of reward processing and feedback learning (Cohen et al., 2011b; Marco-Pallarés et al., 2015), our systematic survey reveals that a large majority of studies keeps relying on ERPs to date, with only a small minority of studies reporting time-frequency analyses (e.g., in 2018, 37 out of 41 papers reported ERP analyses, while only 9 reported time-frequency analyses; Fig. 3). The problem is that ERP analyses are intrinsically limited in the insight they can provide about the neurocognitive mechanisms supporting reward processing.

The first reason is that ERP analyses only exploit a small part of the information contained in the EEG signal, as they ignore the spectral information and cancel out non-phase locked activity. For example, the ERPs following reward receipt show two characteristic components, the FRN and P300. Time-frequency analyses have shown that these components correspond to overlapping phase-locked delta and theta oscillatory activities (Bernat et al., 2015, 2011; Cohen et al., 2007). But, in the same time range (~250-450ms), time-frequency analyses have also shown a clear increase in high-beta band activity (20-35Hz) at frontal electrodes for gains compared with losses (Cohen et al., 2007; Doñamayor et al., 2012; HajiHosseini et al., 2015, 2012; HajiHosseini and Holroyd, 2015; Marco-Pallares et al., 2008; Marco-Pallarés et al., 2009; Mas-Herrero et al., 2015). Because this high-beta band activity is induced rather than phase-locked (as revealed by analyses considering evoked and induced activity separately, Li et al., 2016; or by using phase coherence analysis, Cohen et al., 2007), it does not contribute to the ERPs. More generally, it is common for high frequency oscillatory activity to be induced rather than phase-locked, and it is therefore rarely captured by ERP analyses.

The second reason is what is termed the component overlap issue. As summarized by Luck (2014), an ERP component is often conceptualized as "a scalp-recorded neural signal that is generated in a specific neuroanatomical module when a specific computational operation is performed" (p.66). In practice though, the EEG signal is a mixture of a number of different brain activities (because of their inherent temporal and/or spatial overlap, and because of volume conduction). As a consequence, ERP waveforms at the scalp are most often composed of several overlapping signals from different generators (Luck, 2014). As a result, the components under scrutiny (which are classically defined based on peaks and troughs in these waveforms) often have unclear generators. For example, the FRN is generally believed to be generated by the anterior cingulate cortex, but the contribution of other generators is still a matter of debate, even while this is the most studied EEG feature in the context of reward processing (Walsh and Anderson, 2012). Also, the functional meaning of ERP components can also be obscured because of overlapping cognitive operations. For example, the FRN was named as such because it was first understood as a negativity present in loss and not in gain conditions, but it was later suggested to reflect a positive-going deflection that would be present only in gain conditions, and would sum up with the "standard" response to feedback, a N200 (Holroyd et al., 2008; Proudfit, 2015). In other words, the FRN was thought to be due to the addition of a loss-related process, before being reinterpreted as being due to the addition of a gain-related process (Proudfit, 2015). To work around the component overlap issue, some of the studies analyzed here have used difference waves or principal component analysis (e.g. Foti et al., 2011a; Sambrook and Goslin, 2016). However, the issue of whether these outputs reflect a discrete process still stands (Dien, 2012; Luck, 2014). Considering spectral information provides an efficient solution capitalizing on the fact that temporally or spatially co-occurring processes may occur in different frequency bands. For instance, time-frequency analyses have shown that the FRN harbors two overlapping components (i.e., increased phase-locked delta activity to gains and increased phase-locked theta activity to losses) that have different generators and relate to different aspects of reward processing (Foti et al., 2015). It was also demonstrated that the phase-locked delta and theta activities giving rise to the ERPs waveforms in the FRN-P300 time range reflect more independent processes than their ERP counterparts (Bernat et al., 2015, 2011; Watts et al., 2017). However, time-frequency analyses are not a magic-wand solution to the component overlap issue. Volume conduction still applies, and there is obviously no one-to-one mapping between frequency bands and cognitive processes. There are numerous possible generators of a single oscillation, and a single oscillation potentially reflects different processes in different circuits (Cohen, 2017a; Karakaş and Barry, 2017). In other words, there may be situations where a same frequency band supports different processes that are close in time and/or space (see e.g. Mas-Herrero and Marco-Pallarés, 2016 for an illustration of co-occurring medial frontal theta band activities supporting distinct feedback-related processes).

Importantly, oscillations have a direct neurophysiological significance, and are not a mere by-product of brain function (Buzsáki and Draguhn, 2004). As a consequence, studying oscillations allows to adopt a more mechanistic perspective, as they can be directly linked to neurophysiological phenomena (see Cohen et al., 2011b for instance for a discussion in the context of feedback learning). In particular, they are thought to play an important role in neuronal communication, by allowing synchronization within local neuronal populations or between distant brain areas (Bonnefond et al., 2017; Buzsáki and Draguhn, 2004; Canolty and Knight, 2010; Fries, 2015; Varela et al., 2001). As such, studying oscillations offers a glimpse into the neural computations underlying cognitive processes (Donner and Siegel, 2011; Karakaş and Barry, 2017; Lopes da Silva, 2013; Siegel et al., 2012). In the context of reward processing, it has been proposed that the high-beta band activity following reward feedback may be a mechanism supporting the coupling within a frontostriatal-hippocampal network involved in the processing of unexpected or highly-relevant rewards in the context of learning (Marco-Pallarés et al., 2015; Wang et al., 2019). We note that this kind of network perspective justifies the use of connectivity analyses (see Bastos and Schoffelen, 2015; He et al., 2019 for reviews of connectivity approaches for EEG data). Indeed, EEG (or MEG) connectivity analyses are the only way to uncover rapid network dynamics non-invasively in humans (with the limitation that deep brain components of the target network may be more challenging to assess, see section "Considering spatial information: localization and source separation"). However, they are rarely performed in EEG studies of reward processing.

In conclusion, time-frequency analyses are a valuable complementary approach to the traditional ERP analyses, since scanning the frequency spectrum can provide a much more detailed picture of brain reward processing. We note that studies of reward anticipation using time-frequency analyses are particularly scarce (22 out of 359 surveyed studies to date, e.g., Pornpattananangkul and Nusslock, 2016; Reinhart and Woodman, 2014). Importantly, because time-frequency analyses alone do not circumvent the component overlap issue, it is essential to go beyond the study of power modulations in a specific frequency band at one or several electrodes. Rather, source separation and in-depth source-space analyses should be considered to get maximal discriminative power in the study of neurocognitive processes.

Box 1
Source localization issues.

The generators of brain electric fields are macroscopic post-synaptic potentials created by synchronized populations of pyramidal cells oriented perpendicularly to the cortical surface (Jackson and Bolger, 2014). The EEG signal thus captures only part of the neural activity of interest, and requires caution for functional interpretation of the localization of its generators. Nonetheless, when using dipole modelling -an approach that aims to model the recorded activity with a single or a few dipoles on the basis of a priori assumptions with respect to the number of these dipoles (model-driven inverse solutions)-, source localization is fatally biased if the number of dipoles is misestimated (Michel and Brunet, 2019). In contrast, distributed source modelling discretizes the source space into a large number of locations in the brain volume. It estimates the amplitude of all equivalent current dipole locations simultaneously to recover the source distribution with minimum overall energy that best fits scalp measurements (minimum norm solutions). This class of data-driven inverse solutions is theoretically more appropriate when the number of dipoles to model is unknown, which is particularly the case when complex cognitive tasks are used or when data are very noisy (Hauk and Stenroos, 2014; He et al., 2018; Yao and Dewald, 2005). Based on the observation that minimum norm solutions are biased toward superficial sources, weighting parameters have been introduced and form the class of weighted minimum norm solutions on which successful tools like sLORETA are based (Pascual-Marqui, 2002). These methods are accurate from a mathematical point of view in ideal noise conditions (Greenblatt et al., 2005; Pascual-Marqui, 2007; Sekihara et al., 2005). But despite convincing empirical comparisons, it is difficult to validate the accuracy of each solution for real EEG data (Grech et al., 2008), and issues of physiological plausibility remain. For instance, distributed methods which use norm constraints applied to the overall source space might provide too smooth solutions to be perfectly realistic (Pascual-Marqui et al., 2002). Moreover, representing an active segment of the cortical sheet by a small subset of focal dipoles can raise some issues of biological interpretability.

5. Considering spatial information: localization and source separation

EEG is reputed as having poor spatial resolution. In the traditional ERP approach, spatial information is thus simply ignored, by averaging the signal at one or several electrodes (Michel and Murray, 2012). Indeed, drawing conclusions from electrodes' position could be misleading, as there is no straightforward correspondence between the position of the electrode(s) at which an EEG feature is best observed and the brain area(s) generating it (i.e., an ERP which has a fronto-central topography does not necessarily have fronto-central areas as main generators). Source localization methods were developed to exploit the spatial information contained in the EEG signal, with the aim of countering the effects of volume conduction. These methods allow one to estimate the anatomical generators of an EEG feature of interest, based on head models and resolution of the inverse problem, for which several approaches exist (see He et al., 2018 for review, and Box 1 for details).

In our survey, 19% of studies used source localization, with most aiming to localize the source of ERPs. However, because ERPs are most often composed of several signals from different generators (the component overlap issue, see previous section), this approach runs the risk of lacking precision in most cases regardless of the computational reliability of the localization method used (e.g., Pascual-Marqui, 2002). As a consequence, uncertainties remain in studies using source localization to track the anatomo-functional bases of reward processing. For example, while many studies suggest that the anterior cingulate cortex is the main generator of the FRN (e.g., Bellebaum and Daum, 2008; Gehring and Willoughby, 2002; Hewig et al., 2007; Luu et al., 2003; Polezzi et al., 2010; Potts et al., 2006; Ruchsow et al., 2002; Zhou et al., 2010), some suggested a wider picture, by revealing a range of other potentially contributing generators (e.g., the inferior frontal gyrus, Martin and Potts, 2011; Ruchsow et al., 2002; the superior frontal gyrus, Bellebaum and Daum, 2008; the medial or superior temporal cortex, Bellebaum and Daum, 2008; De Pascalis et al., 2010; Kokmotou et al., 2017).

Unmixing the signals contributing to the overall electrical activity recorded on the scalp therefore appears as a major issue to disentangle the underlying neurocognitive mechanisms that are, by virtue of their overlap in time and space, potentially mixed in the experimental design. Blind source separation (BSS) methods can tackle this issue (Makeig et al., 2002). BSS is a data-driven ensemble of techniques originally from signal processing sciences, with a wide range of applications besides neuroscience (Comon and Jutten, 2010). In particular, BSS methods allow the separation of intermixed sources without a priori knowledge about the source signals or the mixing process. Thus, when applied to EEG data, they assume no a priori biophysical or topographical information. In other words, here the term "sources" does not refer to anatomical generators, but to functional entities that are separated based on their statistical properties (see Box 2 for details). In practice, source separation provides the researcher with a set of source estimates, which are composed of reconstructed source activities and topographies. By working directly on source activities, it is possible to move from classical electrode-space analyses to source-space analyses (either time-frequency or ERP analyses). Besides, topographies (i.e., the spatial projection of the source to the scalp) can be fed to source localization algorithms (Figure 4). Although separated on the basis of their statistical properties, the components resulting from BSS can still be expected to reflect the activity of distinct cortical areas (Delorme et al., 2012). For this reason, applying source localization on separated sources can maximize the use of the spatial information contained in the EEG signal (Onton et al., 2006). As an example, the current density map (obtained through distributed source modeling) of an ERP recorded at the scalp might be difficult to interpret when it is itself composed of a large number of generators that are distant and whose dynamics are not perfectly aligned in time. Separating (and localizing) sources might help to disentangle the different neural activities contributing to the overall ERP recorded at the scalp, thus limiting the superposition between neurocognitive mechanisms when interpreting current density maps. Indeed, BSS has proven useful in decomposing ERP responses into distinct events (e.g., Bridwell et al., 2015; Onton et al., 2006).

Source-space analyses offer other advantages. Because the signal of interest is better isolated, the method provides access to less energetic but potentially interesting features of the data that may be missed with classical analyses (Sutherland and Tang, 2006). Moreover, since connectivity analyses performed at the sensor level are compromised by volume conduction patterns, connectivity measures may best be derived from source activities after BSS (Brunner et al., 2016; Schoffelen and Gross, 2009)[2]. Despite these advantages, source separation and source-space analyses have been used by only one of the surveyed studies (Silvetti et al., 2014). In this study, independent component analysis was used to isolate one component for each subject on the basis of a topography consistent with a medial frontal source and an activity consistent with the error-related negativity (an ERP that is time-locked to the motor response and more negative following errors, and is believed to be generated by the medial frontal cortex). The activity of this component was then assessed during reward anticipation and outcome processing periods, providing arguments for the hypothesis that the same medial frontal source could be responsible for encoding error-related processes as well as reward expectation and prediction error.

To enhance spatial information, another possibility is to combine the millimeter resolution of fMRI with the unique ability of EEG to probe fast neural dynamics (He et al., 2018). This has been done by 14 (4%) of the studies included in our analysis, using a variety of approaches. For example, Mas-Herrero et al. (2015) used joint independent component analysis and showed that the high beta band activity induced by gains cor-

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[2] When applied to source signals, vector autoregressive (VAR) models are useful tools for assessing information flow through lagged dependencies between source signals (e.g., Directed Transfer Function, Kaminski and Blinowska, 1991; Partial Directed Coherence, Baccalá and Sameshima, 2001).

Box 2
Blind source separation general principles and applications.

Numerous BSS approaches and algorithms can be applied to EEG signal processing in order to unmix potential overlapping neural processes. In contrast to source localization methods, these approaches do not aim to localize the generators based on biophysical assumptions. Rather, the general method relies on the assumption of a certain degree of independence between sources. Independent Component Analysis (ICA) is the most popular approach (Hyvärinen et al., 2001). It decorrelates the signals and reduces higher-order statistical dependencies in order to make the source signals as independent as possible (Delorme et al., 2007; Onton and Makeig, 2006). Various higher order statistics (HOS) algorithms use data distribution characteristics to perform the decomposition, with the main separation criteria being maximization of non-gaussianity (e.g., FASTICA, EFICA) or minimization of mutual information (e.g., INFOMAX, ExtINFOMAX). These algorithms decompose the EEG signal obtained from a specific number of electrodes into the same number of statistically maximally independent components. They are robust to Gaussian noise in the dataset but temporal information is lost. Second order statistics algorithms (SOS; e.g., SOBI, UWSOBI, WASOBI, AJDC; Sutherland and Tang, 2006; Tang et al., 2006, 2005) are interesting alternatives. They use time-frequency information to perform the decomposition, with spectral diversity as the main separation criterion. Indeed, they allow applying BSS on shorter time intervals and are more robust with respect to outliers (Congedo et al., 2008; Lio and Boulinguez, 2013; Tang, 2010).

Choosing a BSS method is not trivial. For instance, HOS-based BSS algorithms are optimal for removing non-brain artifacts and most of the Gaussian noise from the data (e.g., Lio and Boulinguez, 2013), while the benefits of SOS-based BSS algorithms in the temporal domain are well-suited for capturing trial-to-trial variations and analyzing single-trial ERPs (Sutherland and Tang, 2006; Tang et al., 2011; Zhang et al., 2014). SOS-based BSS is also especially adapted to group BSS, a method which aggregates data from all subjects to form a unique estimation of the mixing matrix for the whole group (Congedo et al., 2010; Eichele et al., 2011; Huster et al., 2015; Kovacevic and McIntosh, 2007; see Huster & Calhoun, 2018 for a special issue on multi-subject decomposition of EEG). Group BSS solves one of the major concerns with source separation, which is generalization across subjects. Indeed, when using BSS at the individual level, single-subject components have to be selected by hand (e.g., based on topography and time course similar to an ERP of interest, Silvetti et al., 2014) or matched across subjects by means of clustering algorithms for group analysis. This introduces subjectivity (in the selection or when setting the criteria for clustering), and difficulties with statistical analyses when only a subset of subjects contributes to a cluster. Indeed, because of interindividual anatomo-functional variability, building a unique mixing matrix for a group of subjects on the basis of their aggregated data violates the mandatory assumption that the mixing matrix is stationary (Lio and Boulinguez, 2018, 2013). Yet, SOS-based algorithms are more robust to mixing matrix distortions, leading more easily to generalization when similar spectral patterns are identified at neighboring locations, as compared with HOS-based algorithms which show a tendency for overlearning and over-separation (extraction of spurious information from non-stationary events) (Lio and Boulinguez, 2018, 2013). Importantly, even though using group BSS with SOS-based algorithms like SOBI allows direct matching of functionally equivalent components across subjects on the basis of their spectral signature, it does not prevent from analyzing the inter-individual variability of these sources by using the group filter to extract and compare individual component time-series (Huster and Raud, 2018).

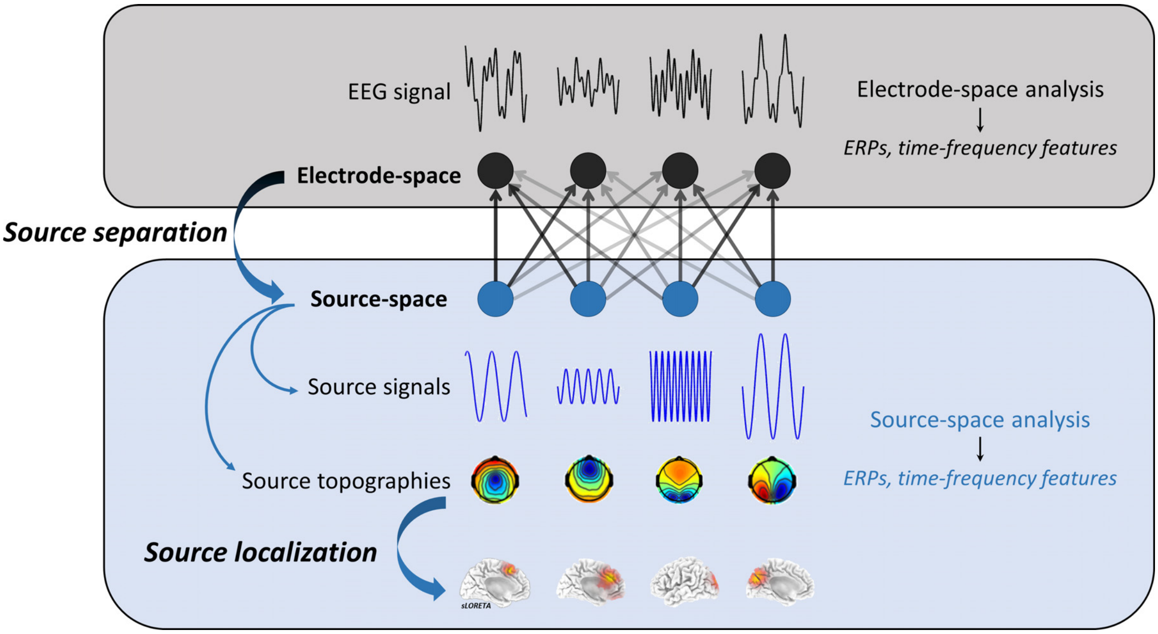

Fig. 4. Source separation at a glance. Source separation allows to unmix most sources of the ongoing brain activity. In practice, source separation returns the estimated source signals and topographies. Working directly with the source signals allows switching from classical electrode-space analyses to source-space analyses, regardless of the kind of analysis one aims to perform (ERP or time-frequency analyses). Besides, the source topographies can be used for localization (see text for details).

responds to the engagement of a fronto-striatal-hippocampal network identified with fMRI, providing support for previous hypotheses (Marco-Pallarés et al., 2015). Using regression of oscillatory power changes onto BOLD signal changes, Mas-Herrero and Marco-Pallarés (2016) showed that the sensitivity of midfrontal theta band activity to outcome valence and unsigned prediction error was correlated with the activation of the supplementary motor area and dorsomedial prefrontal cortex, respectively. Given the close proximity of these subregions of the medial frontal cortex, it would have been difficult with EEG alone to determine that the sensitivity of theta band activity to these variables reflects the engagement of two distinct regions rather than that of one single region encoding both processes.

Finally, the fact that a substantial part of the reward network is subcortical calls for a word of caution. While some authors have claimed that part of the reward feedback-related EEG activity may be generated by the striatum (Carlson et al., 2011; Foti et al., 2011a, 2015), the possibility to access subcortical, deep activity with EEG remains highly controversial (see Cohen et al., 2011a; Foti et al., 2011b for discussion) and cannot be considered as a genuine opportunity yet (but see Attal et al., 2012, 2009; Seeber et al., 2019). In any event, it is reasonable to consider that the activity we can observe with EEG is mostly cortical. Because of this major limitation of the EEG technique, standard and complementary neuroimaging tools will still be highly needed in the future.

6. Conclusion

Our survey of the literature reveals that a majority of EEG studies on reward processing have been designed to investigate how ex-

Box 3
How advanced methods in EEG analysis can help answer outstanding questions on reward processing.

- Using time-frequency and connectivity analyses to uncover the oscillatory mechanisms supporting the integration and transfer of information within the reward network
- Using source-space connectivity analyses to unravel the interaction between the reward network and the attentional, executive, or motor networks, that mediates the behavioral effects of reward
- Using source-space analyses to identify precise markers of neurocognitive dysfunctions in pathology (e.g., major depressive disorder, substance use disorder, behavioral addiction; McLoughlin et al., 2014)
- Leveraging the three axes for the discriminative power of EEG to isolate motivational from motor and attentional processes during reward anticipation (e.g., Reinhart and Woodman, 2014)
- Exploiting the fine temporal resolution of EEG to separate the brain signals related to reward anticipation and reward outcome processing, that are often problematically confounded when studied with fMRI (e.g., Alicart et al., 2015)

perimental manipulation of feedback valence, likelihood or magnitude, among other attributes, impacts the FRN amplitude (Glazer et al., 2018; Sambrook and Goslin, 2015; Walsh and Anderson, 2012). This approach provides limited insight. First, it overlooks reward anticipation. Second, investigating variations of one ERP at one or a few electrodes ignores a lot of the (spatial and spectral) information contained in EEG signal, providing a biased perspective on how the brain actually processes rewards. Indeed, time-frequency analyses of reward outcome processing unsurprisingly showed that different processes are confounded (e.g., those reflected in the evoked delta and theta band activities) or missed (e.g., those reflected in the induced beta band activity) in classical time-domain analyses. Paying more attention to reward anticipation and employing more recent methodological advances as discussed here will undoubtedly help to build a more comprehensive picture of the neurocognitive mechanisms underlying reward processing. We believe that it can help answer outstanding questions on reward processing (Box 3).

We want to highlight that, even though the analyses we describe here are more difficult to apply than classical ERP analyses, and may also require more resources (e.g., time, or data storage capacity), they are now greatly facilitated by available software (e.g., Fieldtrip, EEGlab; see Michel and Brunet, 2019 for a list of packages including source localization tools). Still, some precautions should be taken when applying them, as soon as the initial setup of the experiment. For instance, source localization requires higher density recordings (at least 64 electrodes, Seeck et al., 2017), efficient source separation needs long continuous time-series (e.g., Lio and Boulinguez, 2013), and accessing subtle features of the data requires a large number of trials (e.g. while 20 trials are enough to obtain a stable FRN in healthy subjects -Marco-Pallares et al., 2011-, a minimum of 50 can usually be recommended for time-frequency analyses, Cohen, 2017b). For more details, we refer the reader to the useful recommendations made in all the listed references of interest.

In conclusion, because EEG is inexpensive, non-invasive, and portable, there is great interest in using EEG features as potential biomarkers of cognitive processes or pathologies. We believe that using the methods discussed here could provide more precise and interpretable markers in reward studies.

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Data code availability

The data supporting the survey presented in this paper was extracted from published literature following a procedure described in the Supplementary Material. The full list of references and the derived data are available from the corresponding author on simple request.

Code availability: Not applicable.

Declarations of Competing Interest

None.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2021.118478.

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