Neuroscience 326 (2016) 1–9

BRAIN SIGNAL COMPLEXITY RISES WITH REPETITION SUPPRESSION IN VISUAL LEARNING

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Abstract—Neuronal activity associated with visual processing of an unfamiliar face gradually diminishes when it is viewed repeatedly. This process, known as repetition suppression (RS), is involved in the acquisition of familiarity. Current models suggest that RS results from interactions between visual information processing areas located in the occipito-temporal cortex and higher order areas, such as the dorsolateral prefrontal cortex (DLPFC). Brain signal complexity, which reflects information dynamics of cortical networks, has been shown to increase as unfamiliar faces become familiar. However, the complementarity of RS and increases in brain signal complexity have yet to be demonstrated within the same measurements. We hypothesized that RS and brain signal complexity increase occur simultaneously during learning of unfamiliar faces. Further, we expected alteration of DLPFC function by transcranial direct current stimulation (tDCS) to modulate RS and brain signal complexity over the occipito-temporal cortex. Participants underwent three tDCS conditions in random order: right anodal/left cathodal, right cathodal/left anodal and sham. Following tDCS, participants learned unfamiliar faces, while an electroencephalogram (EEG) was recorded. Results revealed RS over occipito-temporal electrode sites during learning, reflected by a decrease in signal energy, a measure of amplitude. Simultaneously, as signal energy decreased, brain signal complexity, as estimated with multiscale entropy (MSE), increased. In addition, prefrontal tDCS modulated brain signal complexity over the right occipito-temporal cortex during the first presentation of faces. These results suggest that although RS may reflect a brain mechanism essential to learning, complementary processes reflected by increases in brain signal complexity, may be instrumental in the acquisition of novel visual information. Such processes likely involve long-range coordinated activity between prefrontal and lower order visual areas.

Key words: repetition suppression, EEG, multiscale entropy, learning, tDCS, prefrontal cortex.

INTRODUCTION

The surrounding environment provides a continuous wealth of visual information, which we must learn to use efficiently. Foremost, this requires neurophysiological mechanisms that allow the discrimination of novel and noteworthy items from familiar ones. Inherent to this ability is the need to become familiar with previously encountered stimuli (i.e.: encode visual information). A brain response strongly associated with the process of familiarization, known as repetition suppression (RS), entails a diminished neuronal response for previously presented stimuli relative to novel ones (Desimone, 1996; Grill-Spector et al., 2006; Sayres and Grill-Spector, 2006). RS has been associated with basic learning behaviors, notably, perceptual priming (Dobbins et al., 2004; Schacter et al., 2004) and visual habituation (Snyder and Keil, 2008; Turk-Browne et al., 2008; Rankin et al., 2009). RS has also been observed in more complex learning paradigms and declarative memory formation (Heisz et al., 2006; Schiltz et al., 2006; Williams et al., 2007; Vizioli et al., 2010; Caharel et al., 2011; Pihlajamaki et al., 2011). This suggests that RS is a mechanism embedded in the encoding process of visual information.

Many theoretical models have been proposed to account for the suppression of neuronal activity associated with visual encoding (e.g.: Grill-Spector et al., 2006). In particular, a mounting body of evidence supports a dynamic neuronal interaction model which proposes that higher order regions of the cortex modulate the processing activity of sensory regions (Friston, 2005). This model suggests that through experience (i.e.: repetition), higher order areas come to expect the presentation of certain stimuli. In short, as the difference between what is expected and what is presented diminishes through

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Abbreviations: DLPFC, dorsolateral prefrontal cortex; EEG, electroencephalography; MSE, multiscale entropy; RS, repetition suppression; tDCS, transcranial direct current stimulation.

http://dx.doi.org/10.1016/j.neuroscience.2016.03.059
0306-4522/

repetition (i.e.: reduction of prediction error), visual processing in sensory cortical areas becomes more efficient, leading to decreased brain signal amplitude (Summerfield and Egner, 2009). An interpretation of the expectancy-driven model of RS called *predictive coding* conceptualizes RS as a mechanism that begins with the presentation of an unknown or unexpected stimulus. In this framework, novel or unexpected stimuli require extensive updating, which causes high initial neuronal activity, manifesting as high amplitudes in an electroencephalogram (EEG). This activity diminishes along with the EEG signal's amplitude, as the stimulus is repeated and becomes familiar. This acquisition of familiarity allows higher cortical areas to expect the later reappearance of the stimulus (Summerfield and Egner, 2009; Apps and Tsakiris, 2013; Clark, 2013). The substantial involvement of the dorsolateral prefrontal cortex (DLPFC) in modulating occipito-temporal cortical function during various visual encoding tasks (e.g.: Barcelò et al., 2000; Ishai, 2008; Miller et al., 2011; Zanto et al., 2011) makes it a prominent higher order area that would be involved in a network model of RS. However, in order to build expectations about incoming visual information, previous visual information must be allowed to build up or accumulate, a point that has largely been unaddressed in previous accounts of the predictive coding model. If less updating is required as a stimulus is presented, as manifested by RS, then more information must become available in the brain about the visual features of this stimulus. This available information or representation then becomes the basis (i.e.: expectation) against which incoming stimuli are compared. It is unclear whether RS reflects this process of information acquisition.

In recent years, a measure of EEG signal complexity known as multiscale entropy (MSE) developed by Costa (2005), has proved useful in the study of nonlinear dynamics of neuronal networks. Broadly, MSE estimates the amount of novel information progressively contained in an electrical signal generated by an area of the cortex over multiple timescales. Decreased EEG signal complexity has been repeatedly found to be associated with loss of brain function (e.g.: psychopathology, traumatic brain injury) (Protzner et al., 2010; Catarino et al., 2011; Beharelle et al., 2012), while increased complexity has been associated with brain development (Lippe et al., 2009; Vakorin et al., 2011) and learning (Misic et al., 2010; Deco et al., 2011). It has been proposed that brain signal complexity increases as more information about a stimulus (i.e.: learning) becomes available. Thus, a neuronal network containing more information would produce a signal also containing more information, as measured by MSE (Misic et al., 2010; Deco et al., 2011). In the context of learning, a functional network would form to accommodate increasing amounts of visual and semantic information, which would in turn produce an increasingly complex signal. Support for this hypothesis was found by Heisz et al. (2012) who have shown that EEG signal complexity is higher for familiar faces and increases as unfamiliar faces become familiar. These results suggest that MSE may provide valuable insight into the information acquisition capabilities of the brain.

Transcranial direct current stimulation (tDCS) is a non-invasive brain stimulation method that allows transient modulations of cortical excitability. Such effects are engendered by inducing a weak electrical current flowing from a positively charged anode to a negatively charged cathode placed on the scalp, over cortical areas of interest. Cortical excitability modulation depends on the polarity of the electrode: anodal stimulation increases excitability of the underlying cortex, whereas cathodal stimulation decreases it (Nitsche and Paulus, 2000). tDCS modulates excitability of neuronal populations not by inducing action potentials but rather by changing the threshold for discharge. Depending on polarity, this results in either an increase or a decrease in the probability of discharge of the stimulated cortical area when it is called upon during a specific task (Fritsch et al., 2010). In recent years, many studies using tDCS over the DLPFC have reported effects on a wide range of cognitive functions such as planning (Dockery et al., 2009) and decision-making (Boggio et al., 2010). Such studies suggest that tDCS is a safe and relevant method to investigate the involvement of cortical areas in cognitive functions.

Based on the association between familiarity acquisition, RS and increasing brain signal complexity, we hypothesize that EEG signals recorded during repeated presentations of unfamiliar faces will simultaneously present RS and complexity increase. Specifically, signal amplitude over occipito-temporal areas associated with the second presentation of a face would be significantly lower than the amplitude associated with the first presentation (i.e.: RS), while signal complexity associated with the second presentation would be significantly higher than complexity associated with the first presentation. Moreover, because RS and information acquisition ostensibly rely on cortical network interactions between prefrontal and occipito-temporal areas, alteration of DLPFC function by tDCS should modulate RS and complexity augmentation effects over face processing areas.

EXPERIMENTAL PROCEDURES

Procedures were previously reported (see Lafontaine et al., 2013).

Participants

Fourteen healthy young adults were recruited for this study (8 males and 6 females, range: 21–31 years; mean ± standard deviation: 23.5 ± 2.37 years). All participants were students at *Université de Montréal*. EEG data of one participant were excluded from analyses because of excessive artefacts. Data from two more participants were rejected from analysis because of concerns they were not sufficiently attentive during the encoding task (recognition accuracy ⩽ 50%). Thus, reported analyses include data from 11 participants. The study was reviewed and approved by the *Comité d'éthique de la recherche de la Faculté des arts et des*