Consciousness and Cognition 54 (2017) 36–46

Contents lists available at ScienceDirect

Consciousness and Cognition

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

Awareness in the crowd: Beta power and alpha phase of prestimulus oscillations predict object discrimination in visual crowding

Luca Ronconi[a,b,*], Rosilari Bellacosa Marotti[c]

[a] Center for Mind/Brain Sciences (CIMeC), University of Trento, Rovereto, TN, Italy
[b] Scientific Institute IRCCS "E. Medea", Bosisio Parini, Lecco, Italy
[c] International School for Advanced Studies (SISSA), Trieste, Italy

ARTICLE INFO

Keywords:
Perception
Consciousness
Peripheral vision
Letter processing
Dyslexia
Autism

ABSTRACT

Visual crowding is among the factors that most hamper conscious object perception. However, we currently ignore the neural states that predispose to an accurate perception within different crowding regimes. Here, we performed single-trial analyses of the electroencephalographical (EEG) oscillations, evaluating the prestimulus power and phase differences between correct and incorrect discrimination during a letter-crowding task, where irrelevant letters were placed nearby (strong crowding) or far (mid crowding) relative to the target. Results show that prestimulus alpha (8–12 Hz) power was related to target discrimination in the mid, but not in the strong, crowding condition. Importantly, accurate discrimination in the strong crowding condition was predicted by the phase of alpha and by the power of beta (13–20 Hz) oscillations. These evidence suggest that both periodic visual sampling mechanisms, reflected in the alpha phase, and network predisposition to extract local information, reflected in the beta power, predispose to object discrimination in a crowded scene.

1. Introduction

Visual crowding represents one of the fundamental bottleneck for conscious object perception, hampering the processing of visual information at the higher levels of the visual hierarchy (Levi, 2008). Crowding is defined as the difficulty in perceiving a target in the presence of nearby flankers. It limits recognition, not detection, and it is observable especially in peripheral vision. Crowding can affect the conscious perception of visual objects with different complexities, from simple stimuli, such as oriented gratings, to more complex objects, such as letters and faces (Pelli, 2008; Whitney & Levi, 2011).

Studying the neural activity associated to visual discrimination in a crowding regime could thus provide important insights into the neural mechanisms that underlie conscious visual experience. Studying crowding has also clinical implications, in particular in some neurodevelopmental disorders: individuals with developmental dyslexia suffer more of visual crowding (Bouma & Legein, 1977; Martelli, Di Filippo, Spinelli, & Zoccolotti, 2009; Zorzi et al., 2012; see Franceschini et al., 2015; Gori & Facoetti, 2015 for reviews), whereas individuals with autism spectrum disorder seem to be less influenced by it (Baldassi et al., 2009; Keita, Mottron, & Bertone, 2010; Ronconi, Molteni, & Casartelli, 2016).

Despite the large number of studies investigating the psychophysical factors that influence visual crowding, direct attempts to find its neural correlates have started only very recently and they limited the investigation to post-stimulus activity. In particular, some

* Corresponding author at: Centre for Mind/Brain Sciences (CIMeC), University of Trento, Corso Bettini 31, 38068 Rovereto, TN, Italy.
E-mail address: luca.ronconi@unitn.it (L. Ronconi).

http://dx.doi.org/10.1016/j.concog.2017.04.020
Received 29 October 2016; Received in revised form 26 April 2017; Accepted 29 April 2017
Available online 11 May 2017
1053-8100/

authors have used functional magnetic resonance imaging (fMRI) (Anderson, Dakin, Schwarzkopf, Rees, & Greenwood, 2012; Bi, Cai, Zhou, & Fang, 2009; Fang & He, 2008; Freeman, Donner, & Heeger, 2011; Kwon, Bao, Millin, & Tjan, 2014; Millin, Arman, Chung, & Tjan, 2014) and electroencephalography (EEG) (Chen et al., 2014; Chicherov, Plomp, & Herzog, 2014; Ronconi, Bertoni, & Marotti, 2016) to study the neural correlates of the phenomenon.

To date, however, there are no studies investigating pre-stimulus neural correlates of visual crowding. In other terms, we currently ignore what are the brain states that predispose to accurate perception within different crowding regimes. High-temporal resolution techniques such as EEG or MEG are particularly suitable for this aim since they allow to measure the ongoing neural oscillations before the onset of the relevant stimulus. Single-trial analyses of the electrophysiological signals, where the oscillatory activity is compared for the different possible perceptual outcomes (e.g. seen vs. unseen, correct vs. incorrect), can then be used to probe the causal influence of different properties of the ongoing brain oscillations (such as amplitude and phase) on conscious perception (for a review see VanRullen, 2016a).

In recent years, increasing evidence show that different aspects of pre-stimulus oscillatory activity are predictive of various aspects of perception (for reviews see Frey, Ruhnau, & Weisz, 2015; VanRullen, 2016a). The phase of brain oscillations at low frequencies, especially in the alpha and theta bands (8–12 and 3–7 Hz respectively) has been found to be related to trial-by-trial fluctuations in threshold-level perception in the visual (Busch, Dubois, & VanRullen, 2009; Fiebelkorn, Saalmann, & Kastner, 2013; Hanslmayr, Volberg, Wimber, Dalal, & Greenlee, 2013; Mathewson, Gratton, Fabiani, Beck, & Ro, 2009) and auditory (Ng, Schroeder, & Kayser, 2012; Strauß, Wöstmann, & Obleser, 2014) domains. Phase also predicts different suprathreshold visual discrimination, for example in reaction times tasks (Callaway & Yeager, 1960; Drewes & VanRullen, 2011), temporal segregation/integration of visual stimuli (Mathewson et al., 2012; Milton & Pleydell-Pearce, 2016; Valera, Toro, John, & Schwartz, 1981; Wutz, Muschter, van Koningsbruggen, Weisz, & Melcher, 2016), and spatial attention tasks (Busch & VanRullen, 2010; Buschman & Miller, 2009; Landau, Schreyer, van Pelt, & Fries, 2015). As a further confirmation of the relationship between oscillatory phase and perception, many large-scale signatures of stimulus processing such as ERPs, BOLD response and connectivity have been shown to relate to the phase of oscillations in the time period before the stimulus onset (Gruber et al., 2014; Hanslmayr et al., 2013; Scheeringa, Mazaheri, Bojak, Norris, & Kleinschmidt, 2011).

Perception also correlates with the amplitude of pre-stimulus oscillations. Most studies in the visual domain have reported that amplitude variations in alpha frequency band of the EEG determine the detection of subsequent stimuli. Alpha power is considered an index of cortical excitability, with lower power associated to higher excitability (Romei et al., 2008). Consistently, spontaneous high alpha oscillations in the occipital sites before the stimulus presentation impair detection of near-threshold stimuli (Ergenoglu et al., 2004; Hanslmayr et al., 2007; van Dijk, Schoffelen, Oostenveld, & Jensen, 2008). Hanslmayr et al. (2007) found that observers in a detection task could be categorized as either "perceivers" or "non perceivers" according to prestimulus alpha amplitude. It has been proposed that alpha oscillations might exert an inhibitory control over cortical processing, and amplitude is inversely proportional to inhibition: indeed, alpha oscillations increase over the regions that represent unattended or non-relevant stimuli and decrease over relevant stimuli (Bonnefond & Jensen, 2012; Foxe & Snyder, 2011; Mathewson et al., 2009; Min & Herrmann, 2007; Worden, Foxe, Wang, & Simpson, 2000; Yamagishi, Callan, Anderson, & Kawato, 2008). As recently suggested by Samaha, Gosseries, and Postle (2017), however, distinct frequency bands are possibly reflecting cortical processing within different regions. They used transcranial magnetic stimulation (TMS) to test excitability of occipital and parietal cortex, with concurrent EEG recording. They replicated previous findings of an inverse relationship between prestimulus power and TMS-induced phosphene perception, but while alpha oscillations (both power and phase) were predictive of occipital cortex excitability, parietal cortex excitability was predicted by the power of beta oscillations. This idea would fit previous evidence, for example those showing that beta suppression is correlated to the expectation of an upcoming tactile stimulation in somatosensory cortex (van Ede, Jensen, & Maris, 2010).

These studies showing an inverse relationship between pre-stimulus power and performance contrast with others linking enhanced prestimulus beta power and increased attentional activation (Basile et al., 2007; Buser & Rougeul-Buser, 2005; Montaron, Bouyer, & Rougeul-Buser, 1979; Wróbel, 2000), improved detection of weak tactile stimuli (Linkenkaer-Hansen, Nikulin, Palva, Ilmoniemi, & Palva, 2004), shorter reaction times (Liang, Bressler, Ding, Truccolo, & Nakamura, 2002; Zhang, Wang, Bressler, Chen, & Ding, 2008) and reduced Gestalt/increased local perception (Zaretskaya & Bartels, 2015). Moreover, a similar positive correlation between prestimulus oscillatory power and visual performance seems to emerge from studies looking at pre-stimulus alpha activity in temporal attention paradigms such as the attentional blink (AB; Raymond, Shapiro, & Arnell, 1992; for a review see Martens & Wyble, 2010). In the AB, two target letters have to be discriminated in a rapid visual presentation stream (RSVP). When the second target is presented within 200–500 ms relative to the first target, its recognition is markedly impaired. Studies found that higher alpha power in the period of task preparation (pre-RSVP) characterized trials in which the second target was consciously reported (MacLean & Arnell, 2011; Petro & Keil, 2015; Ronconi, Bertoni, et al., 2016). These evidence were supported by recent studies showing that an auditory rhythmic entrainment at 10 Hz leads to higher discriminability of the second target in AB paradigms, which is reflected both in a more accurate second target discrimination (Ronconi, Pincham, Szucs, & Facoetti, 2016d) and in an increased amplitude of its N2 ERP component (Ronconi, Pincham, Cristoforetti, Facoetti, & Szucs, 2016c).

In the present study, we tested the pre-stimulus oscillatory correlates (power and phase) of accurate visual discrimination during a visual crowding task. The distance between the target and flankers (i.e. critical space) is one of the factors that most influences visual crowding (Bouma, 1970; Whitney & Levi, 2011). Specifically, the identification of a cluttered object improves as the critical spacing between the target and the flankers increases. In the present task, we manipulated the critical space between the target and the flanker letters in order to induce different levels of crowding. In the 'strong' crowding condition, the flanker letters were presented nearby the target letter, while in the mid crowding condition the flankers were presented at a farther spatial distance relative to the target. Letter crowding paradigms similar to those employed in the present study have been largely used in previous psychophysical