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Numerosity processing in early visual cortex

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ABSTRACT

While parietal cortex is thought to be critical for representing numerical magnitudes, we recently reported an event-related potential (ERP) study demonstrating selective neural sensitivity to numerosity over midline occipital sites very early in the time course, suggesting the involvement of early visual cortex in numerosity processing. However, which specific brain area underlies such early activation is not known. Here, we tested whether numerosity-sensitive neural signatures arise specifically from the initial stages of visual cortex, aiming to localize the generator of these signals by taking advantage of the distinctive folding pattern of early occipital cortices around the calcarine sulcus, which predicts an inversion of polarity of ERPs arising from these areas when stimuli are presented in the upper versus lower visual field. Dot arrays, including 8–32 dots constructed systematically across various numerical and non-numerical visual attributes, were presented randomly in either the upper or lower visual hemifields. Our results show that neural responses at about 90 ms post-stimulus were robustly sensitive to numerosity. Moreover, the peculiar pattern of polarity inversion of numerosity-sensitive activity at this stage suggested its generation primarily in V2 and V3. In contrast, numerosity-sensitive ERP activity at occipito-parietal channels later in the time course (210–230 ms) did not show polarity inversion, indicating a subsequent processing stage in the dorsal stream. Overall, these results demonstrate that numerosity processing begins in one of the earliest stages of the cortical visual stream.

Introduction

Numerosity is a fundamental visual attribute that the brain must process to achieve a detailed representation of the external world. While there exist different views on the mechanisms underlying the perception of numerosity (e.g., Durgin, 1995; Durgin and Proffitt, 1996; Durgin, 2008; Dakin et al., 2011), one proposal is that numerosity is perceived directly as a primary perceptual feature—similar to contrast, color, orientation, shape, etc. (Burr and Ross, 2008; DeWind et al., 2015; Anobile et al., 2016; Cicchini et al., 2016; Fornaciai et al., 2016; Park et al., 2016).

Most neural investigations of numerosity representation have implicated the parietal cortex, and particularly the intraparietal sulcus (IPS) (i.e. Zorzi et al., 2011; Anobile et al., 2016; Nieder, 2016; Piazza and Eger, 2016). On the one hand, functional magnetic resonance imaging (fMRI) studies have reported that neural activity in the parietal cortex shows selectivity and sensitivity to numerosity of a stimulus even in passive viewing paradigms (Piazza et al., 2004, 2007; Harvey et al., 2013). On the other hand, electroencephalogram (EEG) studies have shown that brain responses are strongly sensitive to changes in numerosity, especially at relatively later latencies (~ 180–200 ms), with a scalp pattern of activity consistent with the involvement of parietal cortex (Temple and Posner, 1998; Libertus et al., 2007; Hyde and Spelke, 2009; Park et al., 2016; Fornaciai and Park, 2017).

Nevertheless, from a theoretical point of view, such parietal mechanisms may be insufficient for explaining all of the processing stages needed to successfully extract numerosity from a visual scene. Indeed, one of the most influential computational models of numerosity perception (Dehaene and Changeux, 1993) posits that physical inputs collected by the retina first pass through a normalization stage, in which the visual array is normalized and encoded in an object-location map to create a size-invariant code. Subsequently, the activity elicited by the items in the object-location map is summed by number-sensitive neurons, and then conveyed toward number-selective units, which allow a representation of the approximate number of items.

Despite the theoretical influence of the Dehaene and Changeux (1993) model, very little attention has been paid to the neural basis of

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the early processing stages that might underlie these effects. Roggeman et al. (2011) exploited the fMRI adaptation technique and provided evidence for an occipito-parietal pathway conveying numerosity information, and identified the three processing stages proposed by models such as those provided by Dehaene and Changeux (1993) and Verguts and Fias (2004) – namely, the first stage of the object-location map (inferior occipital gyrus), a stage transforming the object locations into a summation code (middle occipital gyrus), and finally a number-selective stage (superior parietal lobe). At the same time, recent studies exploiting visual evoked potentials (VEPs) have demonstrated evidence for the early steps of numerosity processing in the visual stream (Park et al., 2016; Fornaciai and Park, 2017). Recently, we reported neural responses to dot arrays that were strongly sensitive to changes in the number of items presented, with sensitivity to numerosity far exceeding sensitivity to other non-numerical, continuous visual attributes such as field area (or convex hull), individual dot surface area, and density (Park et al., 2016). The results showed strong sensitivity over occipito-parietal scalp sites at around 180 ms of latency – consistent with a modulation at the level of the P2p ERP component observed in previous studies (Temple and Posner, 1998; Libertus et al., 2007)- but also strong sensitivity to numerosity at much earlier latencies after stimulus onset (75 ms) over midline occipital scalp sites. These findings suggest that numerosity information may be processed very early in the visual stream. Interestingly, early responses to dot-array stimuli modulated in numerosity have also been observed by Gebuis and Reynvoet (2013) over medial (albeit superior) occipital channels around 100 ms post-stimulus, although the effect of numerosity there did not reach statistical significance in their report.

In the present study, we investigated whether this early sensitivity to numerosity for stimuli in the postulated approximate number system range (numerosities roughly comprised between 5 and 100; see Anobile et al., 2016 for a review) arises from the early stages of visual processing, such as V1 or V2, using an approach previously developed to help identify the neural source of early ERP activities. More specifically, ERPs are thought to arise from dendritic trees of the large pyramidal neurons aligned orthogonally to the cortical surface, giving rise to dipoles oriented perpendicular to the cortical surface (Luck, 2014), which can thus vary according to the folding pattern of the brain. It is well known that primary visual cortex (i.e., striate cortex) in primates presents a unique representation along and around the calcarine sulcus, in which upper visual-field stimulation is represented in the ventral portion of the striate cortex on the bottom bank of the calcarine sulcus and lower visual field stimulation in the dorsal part on the upper bank (e.g. Halliday and Michael, 1970; Michael and Halliday, 1971). Thus, according to the original cruciform model of visual processing (Jeffreys and Axford, 1972a), stimulation in the upper versus lower visual field produces local field potentials of opposite polarity, which in turn result in opposite polarity signals recorded on the scalp surface – an approach that has been used in a number of studies concerning the sources of early visual evoked potentials (e.g., Kriss and Halliday, 1980; Clark et al., 1995; Di Russo et al., 2002; Lesevre and Joseph, 1979; Maier et al., 1987).

One key visual ERP component that has been shown to be sensitive to the location of the stimuli, showing opposite polarities for stimuli presented in the upper versus lower visual hemifield, is the C1 component. The C1 represents the first major component evoked by visual stimuli, typically occurring at a latency between 60 and 100 ms (Di Russo et al., 2002). The brain generator of this component was originally thought to be the primary visual cortex (e.g. Jeffreys and Axford, 1972b; Kriss & Halliday, 1980; Clark et al., 1995), although other authors have instead proposed that extrastriate cortices such as V2 and V3 are responsible for the C1 component (Lesevre & Joseph, 1979; Maier et al., 1987). More recent studies have led to the conclusion that both V1 and V2/V3 can contribute to the scalp-recorded C1 component, with clear predictions about the expected direction of the polarity inversion: while signals originating in V1 should present negative polarity for upper visual field stimuli and positive polarity for lower visual field stimuli, the opposite pattern is expected for signals originating in V2/V3 (Ales et al., 2013; Kelly et al., 2013a, 2013b). Here, given the similarity between the early activity found by Park and colleagues (2016) and the timing of the C1 component, we exploited this polarity inversion paradigm to test for the role of early visual areas in numerosity perception. While the results of Park and colleagues (2016) already provide some hints about the role of early visual processing in numerosity perception – as their first peak of activity was consistent with the timing of the C1 component – no firm conclusion could be drawn from a timing measure alone, and the coarse spatial resolution of scalp-EEG could not pinpoint any particular candidate as the generator of the early numerosity-sensitive activation. Even if the same spatial resolution limitations of the EEG technique apply to the present study, we aimed to employ the polarity inversion effect to provide direct evidence indicating whether early numerosity processing occurs in the primary visual cortex (V1), in early extrastriate cortex (V2/V3), or elsewhere in higher-level visual areas. Critically, our approach based on the high-temporal resolution EEG allowed us to pinpoint the exact timing at which such activity occurs. Indeed, without information about timing, signals arising from early visual cortices (i.e. from fMRI) could reflect either the initial feed-forward activity or later activation due to feedback signals, while our primary focus of interest is the initial sensory processing step. Thus, for the aim of testing the involvement of early visual cortex in numerosity processing, the current paradigm provides a substantial advantage compared to other techniques that cannot disentangle different stages of processing occurring in the same brain areas.

Materials and methods

Participants

Thirty subjects (16 females, average age = 22 years) took part in the study for course credits, after signing a written informed consent. All participants were naïve to the purpose of the study, and had normal or corrected-to-normal vision. Experimental procedures were approved by the Duke University Institutional Review Board and were in line with the Declaration of Helsinki.

Apparatus and stimuli

Stimuli were generated using the Psychophysics Toolbox (Pelli, 1997; Kleiner et al., 2007), for Matlab (version r2013b; The Mathworks, Inc.), and presented on an LCD monitor screen located at approximately 90 cm from the participant. The screen encompassed approximately 34 ×19 degrees, and was set to run at 60 Hz.

Stimuli were dot-arrays, presented in white on a gray background, comprising five different levels of numerosity evenly spaced in a $\log_2$ scale: 8, 11, 16, 23 or 32 dots. The arrays were built following the design previously used by Park et al. (2016), which allows for systematically constructing stimuli ranging equally in three orthogonal dimensions: numerosity (N), size (Sz), and spacing (Sp). Beside number, the other two dimensions (Sz and Sp) – which were orthogonal to the number of items – were derived by combining the logarithmically scaled values of the individual area of the items (IA), the total area occupied by the items (TA), the area of the virtual circular field in which the items were positioned (FA), and sparsity, defined as the inverse of item density ($Spar$) (for details of this innovative design, see also DeWind et al., 2015).

To give a more specific definition, Sz is defined as the dimension along which both TA and IA changes at the same rate, while N is held constant: $\log(Sz) = \log(TA) + \log(IA)$. Sp, on the other hand, is defined as the dimension along which both FA and $Spar$ change concurrently while N is held constant: $\log(Sp) = \log(FA) + \log(Spar)$. Moreover,