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Developmental trajectories of event related potentials related to working memory

Catarina I. Barriga-Paulino*, Elena I. Rodríguez-Martínez, Antonio Arjona, Manuel Morales, Carlos M. Gómez

Human Psychobiology Laboratory, Department of Experimental Psychology, University of Seville, Spain

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ABSTRACT

Working memory is an important cognitive function, and it is crucial to better understand its neurophysiological mechanisms. The developmental trajectories of the Event Related Potentials related to this important function have hardly been studied. However, these ERPs may provide some clues about the individual state of maturation, as has been demonstrated for anatomical brain images.

The present study aims to determine the behavioral and neurophysiological development of Working Memory (WM) processes. For this purpose, 170 subjects with ages ranging from 6 to 26 years performed a visual Delayed Match-to-Sample task (DMTS). The RTs, total errors, and Event Related Potentials (ERPs) in the phases of encoding, retention, and matching were obtained. Results revealed a decrease in the amplitude of ERPs with age, paralleled by improved performance on the DMTS task (i.e., shorter RTs and fewer errors). None of these variables were affected by gender. To determine whether memory performance was influenced by the individual pattern of maturation beyond age, the amplitude of the different ERP components was correlated with RT and errors on the WM task after removing the effect of age. Frontal N2 and posterior P1 and the Late Positive Component were the only ERPs that presented significant correlations with behavioral errors. Behavioral performance was predicted by age and by the scores on the first component extracted from Principal Component Analysis (PCA) of the ERPs. Age (under 17 years old) explained 85.04% and the PCA component explained 14.96% of the variance explained by the bivariate model predicting behavioral errors (1/age + scores of 1st PCA component). From the age of 17 on, the principal PCA component ceases to be an independent component predicting error performance. The results suggest that the individual maturation of ERP components seems to be of particular importance in controlling behavioral errors in WM, as measured by the DMTS.

1. Introduction

In the past few years, several studies have focused on the neural activation patterns underlying WM processes (Ghetti et al., 2012; Shing et al., 2016; Constantinidis and Klinberg, 2016). The ERP technique applied to the investigation of the cerebral mechanisms of information storage and maintenance is useful for making inferences about the timing and anatomical location of these WM processes. In DMTS paradigms, there are distinctive ERP components related to information processing in each of three different phases of the task: the encoding of the stimulus, its retention (interval between S1-S2), and recovery (matching process between the stored and the presented stimulus). Regarding the encoding phase, some studies using visual tasks have found that P2 consists of an index related to WM (Wolach and Pratt, 2001). This ERP appears approximately 200 ms after visual stimulation (Mecklinger and Pfeifer, 1996), and it seems to reflect a mechanism of attentional selection of the stimulus' features. In addition, in the verbal domain, differences in P2 peak amplitude suggest that anterior and posterior distributional differences are elicited during the encoding of words for rote and elaborative memory tasks (Dunn et al., 1998). During the stimulus' retention period on WM tasks, using S1-S2 paradigms, the typical ERP that arises is a Negative Slow Wave (Ruchkin et al., 1990, 1992). This ERP presents higher amplitude in the left hemisphere during phonological memory operations (Barrett and Rugg, 1990; Rugg, 1984a, 1984b) and higher amplitude in the right hemisphere during visual memory operations (Barrett et al., 1988; Barrett and Rugg, 1989). Moreover, this component is sensitive to task difficulty (Ruchkin et al., 1992) and seems to

* Correspondence to: Human Psychobiology Laboratory, Department of Experimental Psychology, University of Seville, Calle Camilo José Cela, S/N, 41018 Seville, Spain.
E-mail address: cbarriga@us.es (C.I. Barriga-Paulino).

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present a different topographical distribution for spatial WM tasks and object memorization (Ruchkin et al., 1997). Regarding the matching phase of the memorized stimulus, P3 consists of the ERP that has been shown to index processes related to WM updating. This positivity occurs between 300 and 800 ms after stimulus onset and reflects the activation of a processing mechanism responsible for updating the stimulus' representations in the WM (Donchin and Coles, 1988). Its maximum amplitude is located in parietal regions (Johnson, 1993). Although P2 has been related to the encoding phase, as described above, some investigations seem to point in the opposite way, associating this ERP with the matching of the actual visual input with an expected form (Evans and Federmeier, 2009). In addition, Kaan and Carlisle (2014) found higher P2 amplitudes for predictive sequences of stimuli where participants generate an expectation of the form of the next letters, versus non-predictive sequences (random sequences). Although these studies did not use the same type of paradigm as ours (DMTS task), they showed a mechanism related to memory that allows subjects to anticipate, during the delay period, the possible appearance of the previously seen stimulus; thus, it is possible that the ERP amplitudes that appeared were similar to when a classical DMTS is used.

Some studies have described that, during development, a synaptic pruning occurs (Huttenlocher, 1990; Whitford et al., 2007; Giedd et al., 2009), which would produce a reduction in neural sources. This reduction is clearly observed in the decline in absolute power of brain rhythms from delta to beta (Segalowitz et al., 2010). It has been proposed that this decrease in power is related to the reduction in the synaptic connections as age increases, which would be macroscopically observed in the reduction in cortical thickness with age. For ERPs, although not for all components, it is typical to observe a reduction in the amplitude of ERPs with age, for instance, in the visual P1 (Segalowitz et al., 2010) and the visual P3b (Courchesne, 1978; Stige et al., 2007; Flores et al., 2009). The relationship of brain rhythm maturation and ERPs with cognitive improvement has been described, for instance, as a parallel course of theta power and WM maturation (Rodríguez-Martínez et al., 2013). The possible relationship between individual ERP status and maturation, beyond age-related maturation, has also been studied. Segalowitz showed that a higher amplitude in early Contingent Negative Variation was related to performance on executive tasks such as planning and set-shifting (Segalowitz et al., 1992). On the other hand, the possible association between the individual level of brain maturation and individual cognitive performance has been described. Fast changes in cortical thickness during development are associated with a higher IQ (Shaw et al., 2006) and a multivariate parameter extracted from fractional anisotropy correlated with Working Memory and numerical abilities at school entry ages (Ullman and Klingberg, 2016). However, this relationship is lost in adolescence, suggesting a greater contribution of biological factors in early childhood and an increasing contribution of social factors as age increases. This individual rate of maturation is also perceived as an increase in performance variability on cognitive tests in early childhood (Rojas-Benjumea et al., 2013; Roalf et al., 2014). All these results suggest that an individual brain-age is present during child development.

The goal of this manuscript is to describe the developmental trajectories of all the ERPs observed on a DMTS task performed by a wide range of subjects between 6 and 26 years old. No previous study offers such a complete description of the development of the complete series of ERPs on DMTS tasks across age. A reduction in the amplitude of ERPs with age is expected, given the possible reduction in neural sources due to synaptic pruning. From a functional point of view, the possibility will also be explored that the individual maturational state of ERPs, super-imposed on the age-related maturational general trend, would influence WM performance. This possibility is explored in model 2, described in the methodological section. As children have been shown to present a broad temporal window for the maturation of cognitive functions (Rojas-Benjumea et al., 2013; Roalf et al., 2014), it is possible that ERPs would help to establish the cognitive maturational status of subjects during development. For this purpose, two different approaches will be followed: (i) After eliminating the effect of age on the behavioral variables and the ERPs, the age residuals of ERPs and the behavioral variables would be correlated, indicating which ERPs are more related to individual behavioral performance during development; (ii) the ability of age and an ERP maturational component extracted from the PCA of ERPs to predict the WM parameters will be assessed. If ERPs contain information independent from age regarding the maturational status of subjects, the prediction of behavioral performance based on age will improve when the ERP maturational principal component is included as a regressor of behavioral performance. Thus, the present report will provide information about the maturational progress of each ERP during human development and about the value of ERPs in assessing the individual maturational cognitive status of children.

2. Materials and method

2.1. Subjects

One-hundred and seventy subjects between 6 and 26 years old (15.89 years ± 6.12) participated in this study. For each age, 8 subjects were recorded and analyzed (4 males and 4 females), with a total sample of 85 males and 85 females. However, five subjects were excluded due to excessive EEG artifacts. The final sample was composed of 165 subjects, 81 males and 84 females (16.00 years ± 6.07).

Subjects did not report any neurological diseases or psychological impairments, and they were extracted from middle-class socioeconomic backgrounds. The children had good academic records and were recruited from public schools, and the young adults were college students recruited through advertisements on the University Campus.

Experiments were conducted with the informed and written consent of each participant (parents or tutors in the case of children), following the Helsinki protocol. The study was approved by the Ethical Committee of the University of Seville.

2.2. Stimuli and task procedure

Visual stimuli were Pokémon and Digimon-type cartoons. The size of all stimuli was adapted in Picassa to equal dimensions of 142×228 pixels. Uncommon stimuli were used to avoid verbal strategies and to ensure that the memorization processing was mainly visual. The stimulus presentation program used was E-Prime version 2.0, and an SRBOX Cedrus was used to record the subjects' responses.

The paradigm used was a DMTS task composed of a total of 128 trials organized in 4 experimental blocks with 32 trials each. The trials were counterbalanced; i.e., in half of them the target stimulus appeared on the left visual field, and in the other half the target stimulus appeared on the right visual field. The order of presentation was totally random, so that each subject performed a unique sequence of trials. The task was kept relatively simple in order to facilitate the testing of the youngest children.

It is possible that subjects might have certain knowledge of the items presented; however, the experiments were performed in 2010–2012, before the 'Pokémon-GO' game was launched. In any case, 256 figures were presented in the experiment, which is a very large number to remember. Moreover, the experiment was still a working memory experiment, regardless of the type of figures used.

The task started with the appearance of the first stimulus (S1) at the center of the screen. The stimulus covered a visual angle of 4.56° on the horizontal meridian. Fig. 1 shows an example of a trial during the task. The subjects were situated 60 cm from the screen. The stimulus was presented for 1000 ms and had to be memorized by the subject. Then, a