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ORIGINAL ARTICLE

Maintenance and manipulation of object sequences in working memory: a lifespan study

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Abstract Many studied reported that working memory components receive remarkable changes during lifespan. In order to better investigate this, we evaluated working memory components on human subjects belonging to five groups (10 subjects each) at different ages 6, 8 and 10 years old, young adult (age) and old adult (age). Our pattern of results shows a major transition in object sequence manipulation performance between ages 8 and 10 years. If related to young adults results, both 10-year-old children and old adults differed in accuracy and RT (specificare cosa significa) in both maintenance and manipulation conditions. In particular, young adults and old adults differ in RTs in the manipulation condition. Our results also suggest that a change in response strategy from 6 to 8 years of age, to prioritize accuracy may be present. Our findings appear consistent with recent neuroscientific findings, and lead to novel predictions.

Keywords Working memory · Development · Aging · Executive functions · Prefrontal cortex · Lifespan

Introduction

Working memory is the system responsible for temporarily maintaining and manipulating information (e.g., [3], [4]). It functions as a limited capacity mental workspace that can be flexibly used to support everyday cognitive activities. Developmental changes in the ability to maintain information active for processing in working memory are observed in school-aged children and adolescents (e.g., [1, 12, 19, 25]). Developmental changes in working memory functions are more pronounced when subjects are required to manipulate this information, rather than merely to maintain it [9, 10, 14, 15]. Recently, a process-specific account of working memory development, in which maintenance and manipulation are dissociable components, has been suggested [11, 18, 23]. In this account, information manipulation is characterized by a longer developmental time course than maintenance since it implies additional brain regions with slower development as compared to the prefrontal areas underlying pure maintenance. To differentiate the involvement of brain areas in manipulation and maintenance of information in working memory, with special reference to prefrontal cortex, Crone et al. [10] tested performance and brain activity patterns in three groups of subjects of different age (8–12, 13–17 and 18–25 years). The task involved recognition of forward (maintenance) and backward (manipulation) serial position of a nameable visual object presented in a sequence of three objects. The most remarkable finding in this study was that participants (aged 8–12) showed a lower performance as compared to the other two groups in the manipulation task condition. Interestingly, participants in the age ranging 8–12 years did not show the activation of dorsolateral prefrontal cortex (with superior parietal cortex) in the manipulation condition, which was contrarily reported in adolescents and adults supporting the hypothesis that dorsolateral prefrontal cortex is involved in working memory manipulation.

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In order to describe the evolution of these working memory functions in the lifespan, here we focused our experiments on 6, 8 and 10 years old groups, a young adult group and an old adult group investigating the cognitive abilities of maintaining and manipulating information in working memory in a lifespan approach. These two abilities seem to differentially involve the central executive, and to be characterized by different developmental trends.

Methods

Participants

A total of 123 subjects, 82 children aged between 6 and 10 years, 21 young adults and 20 old adults participated in the study. All childrens' parents gave informed consent. The children sample was divided into three age groups (mean age 6 years and 4 months = 30, mean age 8 years and 2 months = 24, mean age 10 years and 3 months = 28). The young adults were recruited from the university students at the University "Sapienza" (mean age 27 years and 3 months). The old adults were aged between 60 and 82 years (mean age 68 years and 7 months) without known pathological neurologic dysfunctions. Mini Mental State test was evaluated in all old adults and only the subjects scored in the normal range (>24) were included in the study.

Stimuli

A total of 72 images consisting in simple and easily nameable ClipArt items (object pictures), selected from a previous study by Crone et al. [10] were used as experimental stimuli. During a pre-experimental phase, the experimenter verified if the images were easy to name by presenting the participants a printed version of all the stimuli and asking them to name each one of the figures. Children were instructed to name the images in the easiest possible way, and they were also told that there were no correct or wrong answers. The experimenter checked if the names were compatible with the objects, and whether the participants were consistent in their labeling of a given object over the two presentations. As a result of the pre-experimental naming session, we excluded from the experimental material 18 pictures associated to naming difficulties.

In order to prepare children to promptly recall the verbal labels of the pictures, a brief naming session was also performed before starting the experiment.

Procedure

All participants were individually tested in a quiet and dim lighted room. The experimental procedure is illustrated in Fig. 1a. The task was to press one of three keys ("z", "v" and "m") to indicate whether the probe corresponded to the first, the second, or the third memory item, in the presentation order with the instruction "forward" (maintenance), and in the reverse of the presentation order with the instruction "backward" (manipulation). We excluded the trials with reaction times which were two standard deviations above the mean for each condition. The experimental block consisted in 60 trials. Before starting the experimental block participants were given 16 practice trials in different conditions.

Results

We ran a two-factor ANOVA analysis with age group (5 levels: 6, 8, 10, young and old adults) as a between-subjects factor and condition (2 levels: "forward" versus "backward") as a within subjects factor. Results on accuracy data (Fig. 1b) showed a significant age group effect ($F_{4,117} = 27.46$, $p < 0.0001$, a significant condition (forward, backward) effect ($F_{1,117} = 16.55$, $p < 0.0001$), and a non-significant interaction effect. The post hoc analysis by planned comparisons on accuracy (percentage of correct responses) revealed significant differences between all age groups in both forward and backward conditions, except for the comparison between 10 year old and old adult subjects (forward 6 vs 8 years: $F1,117 = 5.59$, $p < 0.05$; 8 vs 10 years old: $F_{1,117} = 4.29$, $p < 0.05$; 10 years old vs young adults: $F_{1,117} = 12.06$, $p < 0.001$; young adults vs old adults: $F_{1,117} = 6.57$, $p < 0.05$; 10 years old vs old adults: $F_{1,117} = 0.47$, $p =$ n.s.; backward 6 vs 8 years: $F_{1,117} = 8.37$, $p < 0.005$; 8 vs 10 years old: $F_{1,117} = 5.53$, $p < 0.05$; 10 years old vs young adults: $F_{1,117} = 14.81$, $p < 0.001$; young adults vs old adults: $F_{1,117} = 4.38$, $p < 0.05$; 10 years old vs old adults: $F_{1,117} = 2{,}43$, $p =$ n.s. The difference in accuracy between forward and backward conditions was only significant for the age group 6 years ($p < 0.01$) (Fig. 1b).

The ANOVA age group × condition on reaction time (RT) data (Fig. 1c) showed a significant group effect ($F_{4,117} = 30.18$, $p < 0.0001$), a significant condition effect ($F_{1,117} = 66.04$, $p < 0.0001$), and a significant interaction effect ($F_{4,117} = 3.69$, $p < 0.01$). The post hoc analysis by Tukey test revealed no significant RT differences between 6 and 8-year-old groups in both forward and backward conditions, a significant difference between 8 and 10-year-old groups only in the backward condition ($p < 0.001$), significant differences in the comparisons between 10-year old and young adults (forward $p < 0.001$; backward $p < 0.001$), and young adults with old adults (forward $p < 0.001$; backward $p < 0.001$), in both conditions. Finally, a significant difference between old adult and

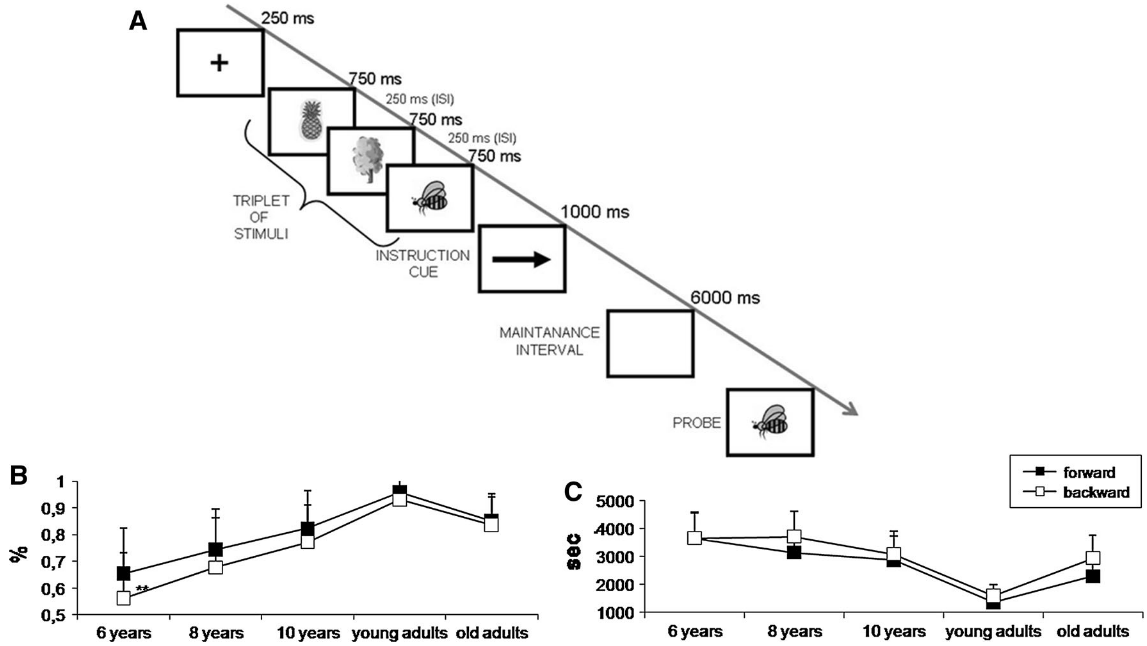

Fig. 1 Experimental procedure and results. **a** Illustration of the experimental procedure. A sequence of three nameable visual objects is presented, followed by a visual instruction for either forward or backward retrieval, a maintenance interval and a test display, in which one of the three objects (probe) is presented. Subjects had to associate the correct serial position to the probe, as a function of the memory sequence array and the forward/backward instruction. **b**, **c** Performance in terms of accuracy (percentage of correct responses) and response time (RT) of the five age groups in forward and backward conditions (see text for more explanations)

10-year-old groups was found only in the forward condition ($p < 0.001$). The difference in RT between forward and backward conditions was only significant for age groups 8 years ($p < 0.001$) and old adults ($p < 0.001$) (Fig. 1c).

Discussion

Our results lead to several conclusions regarding the lifespan evolution of the cognitive abilities implied in object sequence representation and processing in working memory. We observed a major transition in object sequence manipulation performance between developmental ages 8 and 10, as revealed by accuracy and reaction time measures. Crone et al.'s [10] previous study with the same experimental paradigm considered children with age between 8 and 12 years included in the same age group; this can mask eventual developmental differences in a critical period of brain morphological and functional development, showing discordant data if related to ours. Given that Crone et al. [10] found a key association between the manipulation performance and the activation of dorsolateral prefrontal and superior parietal cortex, it can be hypothesized that such brain circuits are characterized by a critical development between the ages 8 and 10 years.

These data appear consistent with developmental neuroanatomical studies. In fact nonlinear increases in gray matter (GM) have been observed till adolescence, peaking at about 12–16 years (depending on the brain region), after which a reduction in total GM accompanied by a relatively more linear increase in white matter (WM) in frontal, temporal and parietal brain regions is evident (e.g., [13, 22]). This nonlinear reduction in the GM/WM ratio has been related to progressive myelination processes [22] and is characterized by regional heterogeneity and heterochronicity [13, 26]: in particular dorsal prefrontal, posterior parietal, and temporal lobes mature relatively late in contrast with the early maturation of lower order sensorimotor and occipital brain regions and the frontal pole [13, 17].

Central executive functions have been of particular interest in the developmental functional imaging literature, as they are known to be mediated by the frontal lobes and their connections [5, 16, 21, 24], with later development, peaking during adolescence. Interestingly, these authors consider the onset of adolescence at the age of 10 years, placing our 8 years old subjects at the end of childhood, and our 10 years old subjects at the onset of adolescence.

In a lifetime perspective, we found that 10 years old children and old adults displayed a similar performance pattern in the task, differing only in the RT measure in the object sequence maintenance condition. This evidence suggests a comparable level of efficiency of the brain circuits for working memory functions between such age groups, except for a faster access to stored information in 10-year-old children. However, in old adults we found longer RTs in the manipulation condition, suggesting a slower operation of manipulation or related working memory access to enable a certain level of accuracy in performance in this task condition.

Moreover, a simple computational model of executive control suggests that a variety of cognitive deficits observed in the elderly could be explained by a deficit in the ability to represent, maintain and update contextual information in working memory [6–8].

We found also that both groups of 10 years old children and old adults differed from young adults in accuracy and RT in both maintenance and manipulation conditions. In particular, young adults and old adults differ in RTs in the manipulation condition. The last evidence can be related to the observation that the grey matter volume decreases in frontal lobes associated with age proceeds from dorsal to ventral areas [27].

In developmental age we also found differences in the pattern of performance between 6 years old and 8 years old children. Specifically, we observed a significant difference in accuracy between maintenance and manipulation conditions in 6 years old children. In 8 years old children we found longer RTs in the manipulation condition as compared to the maintenance condition. Therefore, a change in response strategy from 6 to 8 years of age, to prioritize accuracy can be hypothesized. Related to this evidence, Pickering et al. [20] found that for short-term serial recall, scores on verbal and spatial tasks were dissociable in 5 and 8-year olds.

This indicates that while different storage components are implicated in verbal and spatial short-term memory, a common mechanism underlying the reconstruction of serial order contributing to performance in both domains may be present [2].

Finally, based on Crone et al.'s [10] findings, our study predicts that the differences in performance found in our data may be linked to differential activations of dorsolateral and ventral prefrontal cortex, as well as superior parietal cortex, depending on the task condition and age group. These brain processing differences for object sequence maintenance and manipulation among the involved lifespan age groups can be tested by fMRI investigations. In particular, we predict a large difference in activation of dorsolateral prefrontal cortex and superior parietal cortex in an object sequence manipulation condition, between 8 and 10 years old children. We also predict lower differences in the fMRI activation contrast between maintenance and manipulation conditions for dorsolateral prefrontal cortex and superior parietal cortex in 6-year old children (as related to accuracy) and old adults (as related to RTs), as compared to other age groups in our study. Further evidence can be gained by event related potential (ERP) studies with emphasis on the temporal dimension of processing, which is in particular expected to lead to latency differences related to the probe for old adults in the manipulation. In conclusion our results demonstrate that the two functions of maintenance and manipulation of object sequence information are dissociated during both development and aging, and that manipulation is characterized by a later development and an earlier decline as compared to maintenance.

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