Neuronal Mechanisms of Working Memory Performance in Younger and Older Employees

Sergei A. Schapkin and Gabriele Freude

Federal Institute for Occupational Safety and Health, Berlin, Germany
`schapkin.sergei@baua.bund.de, sschapkin@mail.ru`

Abstract. As working memory (WM) is compromised with advancing age, older people may have performance deficits in WM tasks. This is probably due to a great number of WM operations which should be performed for extended periods of time. The reduction of a number of these operations was expected to reduce WM load and age-related deficits in WM performance. Fifty younger (29±3 years) and 49 older (55±3 years) healthy employees had to perform a visual 0-back (oddball) task and a 2-back task. Within the 2-back task, the short (3 or 4 items, low WM load) and long (5 or 6 items, high WM load) target-to-target sub-sequences were analysed separately. Older workers performed worse than younger ones at higher WM loads, except for the oddball condition and low WM load condition. The N2 latency of the event-related potentials (ERPs) increased with WM load and was generally longer in older than younger adults. In addition, the N2 latency decreased with WM load in younger adults but did not change in older ones. Older workers also showed a delayed P3a as well as a delayed and reduced P3b. By contrast, age-related enhancements of the occipital N1 and frontal P2 components under WM load were observed. The parietal slow positive wave (SPW) increased under high WM load but did not vary with age. The results indicate that older adults are able to compensate for age-related WM impairments when the amount of WM operations required does not exceed the limits of their WM capacity. The allocation of cognitive resources to stimulus encoding (N1) and memory retrieval (P2) are putative neuronal mechanisms for these WM improvements. However, older adults have maintenance problems at higher WM loads. This is associated with deficits in neuronal processes relating to response selection (N2), detection of changes in WM representations (P3a) and WM updating (P3b). These results provide a basis for the development of work load criteria and training opportunities for older workers who have to do complex work requiring working memory.

Keywords: aging, working memory, event-related potential.

1 Introduction

Working memory (WM), a system providing temporary storage and processing of information, is essential for flexible action regulation and adjustment to environmental demands [1]. WM decline with advancing age is well documented in the literature and is thought to be accounted for by progressive loss of neurons in the brain

D. Harris (Ed.): EPCE 2014, LNAI 8532, pp. 70–81, 2014.

structures underlying WM [2]. The event-related potentials (ERPs) enable the examination of age differences in the allocation of processing resources to mental operations at different processing stages. The fronto-central N2 and parietal P3 (P3b) components are usually reduced and/or delayed in older people (see [3] for review), suggesting the existence of age-related deficits in executive processes associated with response monitoring [4] and working memory updating [5, 6]. The fronto-centrally distributed P3a component is closely related to the P3b and considered to be an index of attentional reorienting and novelty processing [3], [6]. However, the age effects on P3a in working memory tasks are not usually separated from those of P3b [7, 8, 9], which makes it difficult to disentangle the contribution of both processes to WM performance. The processes of early stimulus encoding also appear to be critical for WM [10]. The occipital N1 is thought to reflect selective amplification of sensory information to facilitate stimulus encoding [11], while a frontally distributed P2 component has been associated with top-down control over visual feature discrimination [12] or task-relevant stimulus evaluation [13] with both components tending to increase with advancing age [3]. However, the age-related changes in N1 and P2 are still matter of debate (see [3], for review). The parietal slow positive wave (SPW) is considered to be an index of effort and sustained attention, as this component increases with WM load [14], while age effects on the SPW are less well documented (e.g., [7]).

The n-back paradigm [15] is very well-suited to examine the key WM processes in real-time interaction while perceptual and motor demands are kept constant. Participants have to memorise a stimulus sequence (encoding, maintenance) and then decide whether a given stimulus matches one that appeared n trials ago (manipulation). This requires the continuous updating of memory representations (updating). A body of research using n-back tasks have demonstrated reliable age effects on performance and psychophysiological measures [7, 8, 9], [16].

Notably, the age-related performance decline in the n-back task has usually been inferred from data averaged across the whole trial block. Schmiedek et al. [16] used "lure" items embedded in a 2-back task and found that the age-related interference effects were only observed for lures up to four items back but not for longer trial sub-sequences. It follows that performance decline for short trial sub-sequences was predominantly due to lures and not to WM load per se. In other words, if no lures were presented, the age differences in performance would be small or absent. Based on the line of this reasoning, the present study analysed performance and ERPs for short and long target-to-target sub-sequences. In the low WM load condition participants had to process 3 to 4 items between two "neighbour" targets, while in the high WM load condition 5 to 6 items had to be processed. As processing of short sub-sequences requires a smaller number of WM operations than processing of long sub-sequences we expected that age differences at lower loads should be much smaller than at higher loads. The age-related increases of the N1 and P2 components were hypothesized to be an index of compensatory allocation of cognitive resources to early processing. The age-related frontal shift of the P3 is considered to be the compensatory activation of frontal brain areas to enhance cognitive control [7], [9]. With this in mind, the P3 frontality effect should be greater in older adults than in younger adults for both low and high WM load conditions than the oddball condition. We also assumed that age-related reallocation of cognitive resources to early processing may deploy resources that are needed for the subsequent and more complex processes of response selection and memory updating. Hence, the delayed and/or reduced N2, P3a and P3b components should be observed in older compared with younger adults. The n-back task requires sustained attention for extended periods of time and older participants may compensate for WM deficits by enhanced on-task effort which may result in a SPW increase [7]. To examine this assumption age differences in the SPW were also analysed.

2 Method

2.1 Participants

Fifty younger (29±3 years) and 49 older (55±3 years) healthy employees were recruited through advertisements in local newspapers. The exclusion criteria were cardiovascular, neurological or psychiatric disorders, head injury, use of psychoactive medications or drugs. All participants were right-handed, native German speakers, had normal or corrected to normal vision, were currently employed with at least 20 hours per week, signed an informed consent and were compensated € 10 per hour.

2.2 Task

Twenty five different 12 x 18 mm Latin letters were presented successively in white on the black background for 200 ms each with an inter-stimulus interval of 1500 ms and a response window of max 1500 ms; each of them appeared with equal probability and was randomly distributed along the trial sequence. In the oddball task participants had to press a key with the right index finger when the letter “X” was displayed. In the 2-back task they had to maintain all incoming stimuli in memory and press a key if a letter was identical to the letter presented two trials previously. The oddball task consisted of 189 trials. The 2-back task consisted of 388 trials, where short (3 or 4 items) and long (5 or 6 items) target-to-target sub-sequences were analysed separately. The target probability (20%), physical and temporal features did not differ between the three conditions to avoid interference with WM load. The “neighbour” target-to-target sub-sequences consisted of letters which were highly different on perceptual features to avoid interference with lures [16]. The sub-sequences comprising 2, 3, 4, or 5 standards were quasi-randomly distributed within the oddball task and the 2-back task. Participants received training blocks in the 0-back task and the 2-back task until they attained 80% correct responses and thereafter conducted the main tasks.

2.3 EEG Recording

The EEG was continuously recorded from 24 electrodes (10-20 system) against Cz reference. The EOG was recorded from electrodes placed above and below the left eye (vEOG) and next to the outer canti (hEOG). The signals were sampled and amplified with 2048 Hz (Brain Products LTD, Germany). Electrode impedance was kept below 10 kΩ. ERPs were re-referenced offline to linked mastoids. Eye movement artefacts were corrected using the Gratton & Coles algorithm. Epochs contained artefacts greater than ± 100 µV were excluded from analysis. The ERPs were filtered digitally with a 10 Hz low pass. The most prominent ERP components were identified by visual inspection of grand means at following sites: N1 at Oz, P2 at FCz, N2 at FCz, P3a at FCz, P3b at Pz, and SPW at Pz. The peak amplitudes and latencies at these sites were measured against 200 ms baseline in following time windows: N1 (100 - 150 ms), P2 (150 - 250 ms), N2 (200 - 300 ms), P3a (300 - 450 ms), P3b (350 - 700 ms), SPW (mean amplitude, 800 - 1200 ms).

2.4 Data Reduction and Statistical Analyses

All responses faster than 200 ms were excluded from the analysis. The correct RTs (raw and log-transformed) to targets, omission rates (OM), and false alarm rates (FA) were computed for the oddball task (baseline condition), short sub-sequences of the stimuli in the 2-back task (3 or 4 items, low WM load condition) and long sub-sequences of the stimuli in the 2-back task (5 or 6 items, high WM load condition). Similarly, the ERP components were also averaged for oddball, low load and high load conditions. Performance measures were subjected to an ANOVA with "Load" (oddball, low, high) as a within-subject factor and Age (younger, older) as a between-subject factor. The amplitudes and latencies of ERP components were subjected to an ANOVA with "Stimulus" (standard, target) and "Load" (oddball, low, high) as within-subject factors and Age (younger, older) as a between-subject factor. The Huynh-Feldt-corrected p-values were computed, if necessary. T-tests were applied to examine significant ANOVA effects. Statistical analyses were conducted using SPSS for Windows 18.0.

3 Results

3.1 Behavioural Data

The main effects of Load were significant on all performance measures (Fs > 109; ps < .001). Error rate was higher under high load (FA: 2.65%; OM: 10.53%) than low load (FA: .95%; OM: 7.25%) which in turn was higher than in the oddball condition (FA: .30%; OM: .28%). Surprisingly, RTs were longer at lower loads (558 ms) than higher loads (464ms) and the shortest in the oddball condition (357 ms). Correlations between speed and accuracy computed separately for each age group and load level did not reveal any speed-accuracy tradeoffs. Older adults performed as well as younger adults in the oddball condition (RT; FA; OM; younger: 358ms; .26%; .30%; older: 356ms; .34%; .25%) and low load condition (younger: 548 ms; .7%; 6.80%; older: 569 ms; 1.21%; 7.7%) but worse than younger adults at higher loads (younger: 449 ms; 2.15%; 8.51%; older: 479 ms; 3.15%; 12.56%) as expressed in an Age * Load interaction (ln RTs: $F(2, 194) = 3.59$, $p < .04$, $\eta^2 = .04$; false alarms: $F(2, 194) = 4.09$,

$p < .02$, $\eta^2 = .04$; omissions: $F(2, 194) = 3.98$, $p < .02$, $\eta^2 = .04$). Moreover, the Age * Load interaction on omission rate was due to the fact that the decline in accuracy going from the low load to the high load condition was significant for older adults but not for younger adults.

3.2 ERP Data

The ERP grand means as a function of age, load, and stimulus type are presented in the Figure 1.

N1. The N1 was larger to targets (-6.08 µV) than standards (-4.45 µV); Stimulus: $F(2,194) = 108.21$, $p < .001$, $\eta^2 = .53$. The N1 decreased under both low load (-4.93 µV) and high load (-5.00 µV) as compared to the oddball condition (-5.85 µV); Load: $F(2,194) = 19.01$, $p < .001$, $\eta^2 = .16$. This effect was seen for targets, while for standards the N1 decrease under low load compared with the oddball condition was found (Stimulus * Load: $F(2,194) = 43.45$, $p < .001$, $\eta^2 = .31$). Older adults showed a larger and later N1 (-6.15 µV, 136 ms) than younger ones (-4.37 µV, 127 ms) irrespective of stimulus type and load (Age, amplitude: $F(1, 97) = 5.58$, $p < .02$, $\eta^2 = .05$; latency: $F(1, 97) = 4.86$, $p < .03$, $\eta^2 = .05$).

P2. The P2 decreased in the low load condition (6.91 µV) as compared to both high load (7.45 µV) and oddball conditions (7.65 µV); Load: $F(2,194) = 4.86$, $p < .01$, $\eta^2 = .05$. This effect was seen for targets but not standards (Stimulus * Load: $F(2,194) = 15.96$, $p < .001$, $\eta^2 = .14$). The P2 latency decreased in both low load condition (167 ms) and high load condition (167 ms) relative to the oddball condition (174 ms), $F(2,194) = 14.05$, $p < .001$, $\eta^2 = .13$. A Load * Age interaction ($F(2,194) = 3.30$, $p < .05$, $\eta^2 = .03$) was attributed to a larger P2 in younger than older adults under both load conditions, while no age differences in the oddball task were found (low load, young: 6.01 µV; old: 7.81 µV; high load, young: 6.62 µV; old: 8.28 µV; oddball, young: 7.33 µV; old: 7.97 µV). Moreover, age groups exhibited a different P2 reactivity to high WM load: the P2 decreased in younger adults but not in older ones.

N2. The N2 was larger and later for standards (-.11 µV, 268 ms) than targets (2.29 µV, 246 ms); Stimulus, amplitude: $F(1, 97) = 64.33$, $p < .001$, $\eta^2 = .40$; latency: ($F(1, 97) = 89.58$, $p < .001$, $\eta^2 = .48$. A main effect of Load on the N2 amplitude ($F(2, 194) = 18.13$, $p < .001$, $\eta^2 = .16$) was due to a larger (i.e. less positive) N2 in the low load condition (-.02 µV) than both high load (1.66 µV) and oddball conditions (1.61 µV) with greater effect for targets than standards (Stimulus * Load: $F(2, 194) = 8.65$, $p < .001$, $\eta^2 = .08$). The N2 latency was longer in both oddball (260 ms) and low load (262 ms) conditions than in the high load condition (250 ms), $F(2, 194) = 12.27$, $p < .001$, $\eta^2 = .11$. The N2 latency decreased in the low load condition for targets (244 ms) compared with standards (280 ms) while no effects in other conditions were found (Stimulus * Load: $F(2, 194) = 10.73$, $p < .001$, $\eta^2 = .10$). A significant main effect of Age on the N2 latency ($F(1, 97) = 24.12$, $p < .001$, $\eta^2 = .19$) was due to a delayed N2 in older (268 ms) compared to younger adults (246 ms) irrespective of memory load. The N2 latency decreased at higher loads compared with both oddball and low load conditions in younger but not older adults (Load * Age: $F(2, 194) = 3.53$, $p < .03$, $\eta^2 = .04$.)

P3a. A main effect of Stimulus was due to a larger and earlier P3a to targets (10.76 μV, 389 ms) than standards (5.20 μV, 404 ms); amplitude: F(1, 97) = 211.81, p < .001, η^2 = .69; latency: F(1, 97) = 4.18, p < .04, η^2 = .04. A main effect of Load on the P3a amplitude (F(2, 194) = 18.66, p < .001, η^2 = .16) was attributed to a P3a reduction in the low load condition (6.63 μV) relative to both high load (8.30 μV) and oddball conditions (9.01 μV); F(2, 194) = 25.65, p < .001, η^2 = .20. The effect was more pronounced for targets than standards (Stimulus * Load: F(2, 194) = 4.13, p < .02, η^2 = .04). A longer P3a latency in both load conditions (low load: 407 ms, high load: 405 ms) than the oddball condition (376 ms) was found (F(2, 194) = 18.93, p < .001, η^2 = .16) with greater effect for targets than standards (Stimulus * Load: F(2, 194) = 21.83, p < .001, η^2 = .18). The P3a was delayed in older adults (420 ms) compared to younger adults (374 ms) irrespective of WM load (F(1, 97) = 26.62, p < .001, η^2 = .21).

P3b. As the P3b component was not reliably detectable in the standard-locked data, we analysed the P3b for targets only. The P3b was reduced and delayed under WM load (low load: 10.28 μV, 431 ms; high load: 12.69 μV, 449 ms) compared to the oddball condition (16.5 μV, 371 ms) as expressed in main effects of Load on the P3b amplitude (F(2, 194) = 18.66, p < .001, η^2 = .16) and latency (F(2, 194) = 30.00, p < .001, η^2 = .24). A reduced and delayed P3b for older adults (11.59 μV, 454 ms) compared to younger adults (14.73 μV, 408 ms) across conditions was also obtained (Age, amplitude*:* F(1, 97) = 12.39, p < .001, η^2 = .12; latency*:* F(1, 97) = 11.36, p < .001, η^2 = .11).

P3 Frontality. To test the "P3 frontality effect" in older adults, an ANOVA with the within-factors "Site" (FCz, Pz) and "Load" (oddball, low load, high load) for targets was performed. A significant "Site * Age" interaction (F(1, 97) = 6.94, p < .01, η^2 = .07) was due to age differences in the P3 amplitude at Pz (young: 14.78 μV, old: 11.57 μV) but not at FCz (young: 11.48 μV, old: 10.05 μV). The post-hoc tests revealed a parietal P3 maximum in younger adults irrespective of WM load (FCz vs. Pz, oddball: 13.19 μV, vs. 18.85 μV, low load: 9.62 μV vs. 11.55 μV, high load: 11.62 μV, vs. 13.93 μV, all ps < .001). By contrast, the P3 in older adults had the parietal maximum in the oddball condition but was more evenly distributed under WM load due to the P3 reduction at Pz (FCz vs. Pz, oddball: 10.90 μV vs. 18.85 μV, p <.001; low load: 8.31 μV vs. 9.03 μV, p < .16; high load: 10.96 μV vs. 11.48 μV, p < .27).

SPW. The SPW was larger for targets (3.44 μV) than standards (2.26 μV), (Stimulus: (F(1, 97) = 24.76, p < .001, η^2 = .20) and increased at higher WM loads (3.75 μV) compared to other conditions (oddball: 2.39 μV, low load: 2.42 μV); F(2, 194) = 16.44, p < .001, η^2 = .14. This increase was observed for targets but not standards (Stimulus * Load: F(2, 194) = 14.20, p < .001, η^2 = .12).

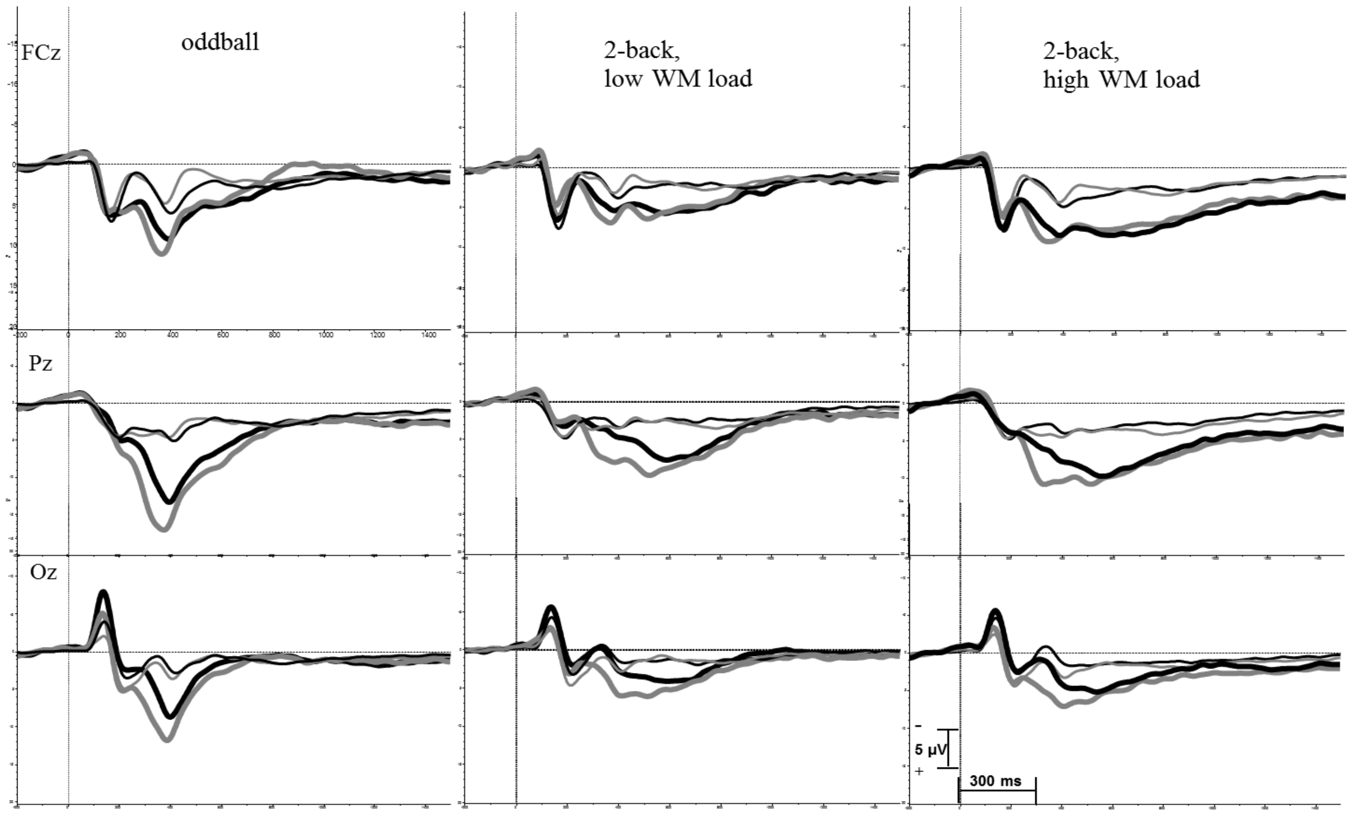

Fig.1. ERPs as function of age, working memory load and stimulus type. Black –old, gray –young, thick –targets, thin –standards.

Correlations between ERPs and Performance. To examine whether age groups differ in the involvement of cognitive processes during task performance, correlations between ERP components and performance measures in the high load condition were computed (Tab. 1). In younger participants, significant correlations between late ERP components and performance measures were found. Better performance (shorter RTs and/or lower error rate) was associated with larger P3a and P3b amplitudes and their shorter latencies to target stimuli. In addition, better performance was related to a reduced N2 and enhanced SPW for targets. Notably, significant correlations were found also for standards where better performance of younger adults was associated with both larger P3a and SPW as well as shorter P3a latency. By contrast, older adults revealed a smaller number of significant correlations between ERP components than younger adults. In older adults the P3a, P3b and SPW amplitudes negatively correlated with RTs while P3b latency positively correlated with omission rate.

Table 1. Pearson correlations between ERP and performance measures in the high WM load condition. RT – reaction time, % OM – omission percentage, % FA – false alarm percentage. Significances are in parentheses.

	Younger			Older		
Standards	RT	% OM	% FA	RT	% OM	% FA
N2 amplitude	-	-	-	-	-	-
P3a amplitude	-.35 (.01)	-	-	-	-	-
P3a latency	-	.36 (.01)	.39 (.005)	-	-	-
P3b amplitude	-	-	-	-	-	-
P3b latency	-	-	-	-	-	-
SPW amplitude	-	-.31 (.03)	-	-	-	-
Targets						
N2 amplitude	-.31 (.03)	-.28 (.05)	-.31 (.02)	-	-	-
P3a amplitude	-.40 (.004)	-	-	-.27 (.05)	-	-
P3a latency	.39 (.005)	.42 (.003)	.36 (.01)	-	-	-
P3b amplitude	-.29 (.03)	-	-	-.39 (.005)	-	-
P3b latency	.38 (.006)	.35 (.01)	.37 (.008)	-	.29 (.04)	-
SPW amplitude	-	-.37 (.008)	-.34 (.01)	-.31 (.03)	-	-

4 Discussion

4.1 Performance Data

The results of the present study largely agree with other literature demonstrating performance decline in older relative to younger adults in the 2-back task [7, 8, 9], [16]. Expanding on previous data we demonstrate that averaging performance in the 2-back task across the whole trial block is not precise enough to assess WM function, at least in this sample of healthy older employees. Nevertheless, analyses of the short and long target-to-target sub-sequences provide a more detailed evaluation of WM performance and putative neuronal mechanisms. The well-trained older individuals performed the 2-back task as well as younger ones when computational demands were low (3 or 4 items). By contrast, at higher computational demands (5 or 6 items), performance is observed to decline with age. The results confirm our assumption that older adults are able to compensate for performance deficits when the amount of WM operations required (e.g. encoding, maintenance, manipulation, updating) is rather small and items can be maintained in short-term memory (i.e. up to 6 seconds). The result is consistent with Cowan's model which postulates that humans are able actively maintain and process up to four items in WM [17].

4.2 ERP Data

Early Processing. Although the age-related increases of the N1 and P2 components have been obtained in different cognitive tasks [8], [10, 11, 12], their putative mechanisms are still unclear. It is known that the N1 and P2 are larger in attended than unattended stimuli and reflect early processes of stimulus encoding and evaluation respectively [11, 12]. Therefore, the age-related N1 increase we found suggests that older adults allocate more resources to stimulus encoding than younger ones irrespective of memory load. We also observed the N1 reduction in the 2-back task relative to the oddball task in both age groups. The result is commensurate with the 2-back task, where each standard stimulus must be assumed to be a possible target and thus processing resources should be shared between standards and targets. However, the N1 remained larger in older adults than in younger adults, suggesting less efficient allocation of processing resources in the former group. Notably, this age-related N1 increase in our study was also evident in the oddball task indicating that age differences in the N1 are unspecific to memory load but rather due to more general changes in executive control over stimulus encoding with advancing age [18].

The anterior P2 component is thought to reflect a top-down control over visual feature discrimination [12] or task-relevant stimulus evaluation [13]. Consistent with other studies [8] we found the P2 increase in older relative to younger adults. In addition to this, the age-related P2 increase was also observed under WM load except for the oddball condition. More importantly, the P2 decreased under WM load in younger adults but not in older adults. As the stimuli in the n-back task were easy to recognise, the P2 increase is unlikely to be a consequence of discrimination difficulty. Older participants were rather highly focused on early evaluation of whether a stimulus has "targetness" properties, in order to select an appropriate response as quickly as possible. By contrast, the P2 reduction in younger participants may be due to the fact that the relevance evaluation proceeded more automatically and recruited fewer resources than in their older counterparts. Another explanation for the P2 increase may be memory retrieval processes which should be persistently active under WM in older adults. Conversely, younger adults may have relied less on retrieval mechanisms as expressed in P2 reduction under WM load. This interpretation is supported by our data from the memory-based switching task where participants had to retrieve stimulus-response (S-R) mappings from memory and apply them to a presented stimulus [19]. In similar fashion, the P2 in the switching task was larger in older than in younger adults. Moreover, the P2 latency positively correlated with RT mixing costs in older adults only suggesting extensive use of the retrieval mechanism to support maintenance of the S-R mappings in WM. Notably, the "retrieval" and "relevance evaluation" explanations for P2 are not mutually exclusive. A relevance evaluation may require extensive retrieval of items held in WM to match them with an incoming stimulus. The matching process is probably associated with the subsequent N2 component. Putting these interpretations together, we can surmise that the age effects on N1 and P2 components may be interpreted as compensatory allocation of processing resources for both stimulus encoding and evaluation via persistent recruitment of memory retrieval mechanisms in older adults.

Response Selection, Change Detection and Memory Updating. The functional role of the fronto-centrally distributed N2 component is still matter of debate [4], [20, 21, 22]. The N2 is elicited when participants are focusing on a stimulus to make a task-relevant decision [22] or have to match a current stimulus with WM representations [4]. The N2 is usually delayed when different S-R mappings should be held in WM [21]. In our n-back task we consider the N2 as an index of an executive control process which provides the priority of a relevant S-R mapping over irrelevant ones. In turn, the selected response inevitably requires changing and updating of WM content which probably elicit the following P3 component. Recent studies stressed a close relationship between the N2 and P3 in tasks requiring WM [19], [21]. Moreover, the shortening of the N2 latency with WM load that we found in younger adults suggests that their response selection is more efficient and/or less resource-consuming than in older adults.

Polich [6] proposed an integrative theory of P3a and P3b components which is well-suited for application to WM. He considers both components as indexes of different sub-processes constituting the common fronto-parietal network. An early attention process stemming from changes in working memory representations elicits the P3a. The attention-driven stimulus signal is then transmitted to parietal structures where WM updating occurs and the P3b is produced. All of this is consistent with the fact that in the present study, the P3a was seen for both standards and targets while the P3b was observed for targets only. It seems likely that the P3a reflects changes in WM representations elicited by each incoming stimulus. By contrast, the target stimuli require more elaborated processing and hence produce larger P3a and P3b. Significant correlations of P3b with reaction time and error rate in both age groups indicate the crucial role of continuous updating of information for WM performance. Younger adults appear to use the mechanism of detection of changes in WM representations more extensively than older adults, as expressed in multiple correlations between performance and P3a for both targets and standards in the younger group. By contrast, only one significant correlation between performance and the P3a in older group was observed.

In agreement with other data ([7], [9]) we found a delayed P3a as well as a delayed and reduced P3b in older adults. The age-related frontal shift of the P3b is considered to be a compensatory activation of frontal brain mechanisms to enhance cognitive control [7]. However, in contrast to other studies using a similar paradigm ([7], [9]), we did not observe a larger frontal P3a in older as compared to younger adults (P3 frontality effect). Nevertheless, we found that the parietal P3 maximum in the oddball task changed to a more evenly distributed P3 under WM load in older adults while the parietal P3 maximum in younger adults persisted across conditions. Therefore, we did not obtain the age-related “P3 frontality effect” but rather a “P3b reduction effect” and cannot interpret the results as compensatory allocation of processing resources to frontal mechanisms.

One may ask which factors contribute to the updating deficits in older adults. Older participants might not be able to maintain their attention and effort during the task. However, the absence of age effects on SPW does not support this interpretation, as the SPW is considered to be an index of sustained attention and effort [14]. Other research has demonstrated that older participants are able to be engaged in demanding tasks and maintain on-task effort over time as well as their younger counterparts [20].

Recent studies suggest that reasons for the P3b reduction may originate in the processes preceding the P3b, namely in response selection. The age-related increase in the N2 latency we found agrees well with previous studies showing that difficulties in response selection may lead to a prolonged N2 which may overlap with the subsequent P3b and in turn reduce and prolong it [21]. Notably, the age-related lengthening of the N2, P3a, P3b latencies and the P3b reduction were already significant in the oddball task. The results indicate that key processes relying on WM weaken with age and this may already be observed in easy cognitive tasks where no WM load is imposed.

Another reason for the P3b reduction in older adults may be an inefficient allocation of cognitive resources. The age-related N1 and P2 increases found in the present study suggest that the compensatory allocation of cognitive resources to stimulus encoding and memory retrieval may result in the shortening of resources that are necessary for later operations like response selection (N2), detection of changes in WM representations (P3a) and WM updating (P3b). This explanation of age-related changes in neuronal mechanisms of working memory should be addressed in further studies.

References

1. Baddeley, A.: Working Memory. Science 255, 556–559 (1992)
2. Rodrigue, K.M., Kennedy, K.M.: The cognitive consequences of structural changes to the aging brain. In: Schaie, K.W., Willis, S.L. (eds.) Handbook of the Psychology of Aging, pp. 73–91. Elsevier, Amsterdam (2011)

3. Friedman, D.: The components of aging. In: Kappenman, E.S., Luck, S.J. (eds.) Oxford Handbook of Event-Related Potential Components. Oxford University Press, New York (2011)
4. Folstein, J.R., Van Petten, C.: Influence of cognitive control and mismatch on the N2 component of the ERP: a review. Psychophysiol. 45, 152–170 (2008)
5. Donchin, E., Coles, M.G.H.: Is the P300 component a manifestation of context updating? Behav. Brain Sci. 11, 355–425 (1988)
6. Polich, J.: Updating P300: An integrative theory of P3a and P3b. Clin. Neurophysiol. 118, 2128–2148 (2007)
7. Daffner, K.R., Chong, H., Sun, X., Tarbi, E.C., Riis, J.L., McGinnis, S.M., Holcomb, P.J.: Mechanisms underlying age- and performance-related differences in working memory. J. Cogn. Neurosci. 23, 1298–1314 (2011)
8. McEvoy, L.K., Pellouchoud, E., Smith, M.E., Gevins, A.: Neurophysiological signals of working memory in normal aging. Cogn. Brain Res. 11, 363–376 (2001)
9. Wild-Wall, N., Falkenstein, M., Gajewski, P.D.: Age-related differences in working memory performance in a 2-back task. Front. Psychol. 2, 186 (2011)
10. Gazzaley, A., Clapp, W., Kelley, J., McEvoy, K., Knight, R.T., D'Esposito, M.: Age-related top-down suppression deficit in the early stages of cortical visual memory processing. PNAS 105, 13122–13126 (2008)
11. Hillyard, S.A., Anllo-Vento, L.: Event-related brain potential in the study of visual selective attention. PANAS 95, 781–785 (1998)
12. Luck, S.J., Hillyard, S.A.: Electrophysiological correlates of feature analysis during visual search. Psychophysiol. 31, 291–308 (1994)
13. Potts, G.F.: An ERP index of task relevance evaluation of visual stimuli. Brain and Cogn. 56, 5–13 (2004)
14. Ruchkin, D.S., Johnson Jr., R., Canoune, H., Ritter, W.: Short-term memory storage and retention: an event-related brain potential study. Electroencephalogr. Clin. Neurophysiol. 76, 419–439 (1990)
15. Gevins, A., Smith, M.E., McEvoy, L., Yu, D.: High-resolution, E.E.G.: EEG mapping of cortical activation related to working memory: effects of task difficulty, type of processing, and practice. Cereb. Cortex 7, 374–385 (1997)
16. Schmiedek, F., Li, S.C., Lindenberger, U.: Interference and facilitation in spatial working memory: age-associated differences in lure effects in the n-back paradigm. Psychol. Aging 24, 203–210 (2009)
17. Cowan, N.: The magical number 4 in short-term memory: A reconsideration of mental storage capacity. Behav. Brain Sci. 24, 87–185 (2001)
18. Chao, L.L., Knight, R.T.: Prefrontal deficits in attention and inhibitory control with aging. Cereb. Cortex 7, 63–69 (1997)
19. Schapkin, S.A., Gajewski, P.D., Freude, G.: Age differences in memory-based task switching with and without cues: An ERP study. Journal of Psychophysiology (in press, 2014)
20. Falkenstein, M., Hoormann, J., Hohnsbein, J.: Inhibition-related ERP components: variation with modality, age, and time on-task. J. Psychophysiol. 16, 167–175 (2002)
21. Gajewski, P.D., Falkenstein, M.: Diversity of the P3 in the task-switching paradigm. Brain Research 1411, 87–97 (2011)
22. Ritter, W., Simson, R., Vaughan Jr., H.G., Friedman, D.: A brain event related to the making of a sensory discrimination. Science 203, 1358–1361 (1979)