Title: The effect of aging on movement related cortical potentials during a face naming task

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ABSTRACT

In the present study a face naming reaction time task was employed in order to evaluate the effect of age on performance and on movement related cortical potentials (MRCPs). In addition, the effect of three response categories with different cognitive demand (DON'T KNOW-don't know the name-, KNOW-correct naming- and TOT-tip-of-the-tongue state) on performance and on MRCPs in a sample of older adults was evaluated. The same MRCPs found in a previous study in a sample of young adults were identified in older adults. The results indicated that older participants were generally slower at providing responses than young adults, and that both age groups showed longer reaction time in TOT than in DON'T KNOW and KNOW categories. The first component of readiness potential (1st-RP) showed larger amplitude and longer duration in older than in young adults, especially in TOT category, which would explain the generally slower responses provided by older participants. In addition, in older adults, the 1st-RP was larger in TOT than in DON'T KNOW category, but a slope reduction and stabilization was observed in TOT from the more demanding stages of stimulus processing. These results may reflect a lengthening in preparation period in TOT category, which probably explains the behavioural slowing in this category. The data of the present study suggest differences in the allocation of processing resources between groups, indicating that the sensoriomotor performance should be compromised more in older than in young adults in tasks with high cognitive load.

KEYWORDS: movement related cortical potentials; aging; face-naming task; complex choice-reaction time paradigm

1. Introduction

It was found that aging process is associated with neural changes that underlie deficits in perceptual, cognitive and motor abilities observed in the elderly (Arnsten, 1998; Cabeza, 2001; Raz, 2000). Although perceptual and cognitive domains have been widely studied, much less is known about age-related changes in brain activity during motor programming and how aging-related behavioural slowing is influenced by such changes.

Cortical motor programming is a stage of information processing during which a movement is planned, structured and activated once the movement parameters have been identified and coded (Labyt et al., 2004). The cortical activity related to motor programming can be studied through changes in *movement related cortical potentials* (MRCPs). Since the discovery of the *Bereitschaftspotential* (BP) (Kornhuber & Deecke, 1965) or *readiness potential* (RP), four MRCP components were typically described: the first part of the readiness potential (named 1st-RP in the present study), which has been associated with a general state of preparation (Gerloff et al., 1998) or considered as an index of resource mobilization (McCallum, 1993); the second part of RP or the negative slope (named NS' in the present study), which has been related to the voluntary choice and the endogenous urge to act (Rektor, 2003) and therefore reflecting the specific preparation of the motor program that will be performed (Kirsch et al., 2010); the motor potential (MP) and the reafferent potential (RAP), that have been considered as correlates of the beginning of motor cortex activity and feedback mechanisms, respectively (Bötzel et al., 1997; Kornhuber & Deecke, 1965; Shibasaki et al., 1980) (for a complete revision, see Shibasaki & Hallet, 2006).

The most frequently used paradigm for studying motor cortical programming has consisted of asking participants to perform repetitive self-paced and self-initiated movements; this is known as the BP paradigm. In this paradigm the nature of the movement is predetermined, which may lead to rather automatic performance of the movements across trials (Jahanshahi & Hallet, 2003) as the motor program is already available and consequently the RP recorded under this type of paradigm does not reflect aspects of movement programming (Lang, 2003).

The BP paradigm has been used in very few studies to investigate the effect of aging on MRCPs and the results are inconsistent. In some studies it was found that the amplitude of the 1st-RP was smaller in older than in young adults (Deecke, 1980; Feve et al., 1991); others found longer latency in older than in young adults in the complete RP (Feve et al., 1991; Ishizuka et al., 1996), and yet others did not find any differences between young and older adults (Loveless, 1980; Singh et al., 1990).

It has been established that the RP can also be recorded prior to sequential button pressing (Cunnington et al., 1995) or when a movement must be selected from among a set of possible responses (Praamstra et al., 1996). Motor programming can also be studied in reaction time (RT) tasks, in which movements are triggered by external stimulation. In a visual and auditory choice-RT task in which subjects had to respond to a series of letters with a predefined finger, Falkenstein et al. (2006) observed longer RTs, and larger and more widely extended MRCPs across the scalp in older than in young individuals.

Some studies have demonstrated that the RP not only reflects changes in the motor activity itself, but also depends on other factors that influence the level of central nervous activation in preparation for motor activities (anticipation, attention, intention, motivation, effort or timing) (Dirnberger et al., 2000, Freude et al., 1988; Freude & Ullsperger, 1987; McAdam & Rubin, 1971). Most of the tasks used to study MRCPs were simple motor tasks and few studies have explored the contribution of complex cognitive processes to RP, or to MRCPs in general. In a previous study, MRCPs were analyzed in a sample of young adults carrying out a face naming choice-RT task (Buján et al., 2009). The task generated three types of responses with different cognitive demand, but requiring similar sequential movements (a manual response with the right or left index finger followed by a verbal response). The three response categories in the task were: 1) DON'T KNOW: the participants did not know the name and said "Don't know"; 2) KNOW: the participants knew the name and stated it correctly, and 3) TOT (tip-of the-tongue-state): the participants were sure they knew the name but could not retrieve it and said "Can't remember". This complex choice-RT task enabled identification, in young adults, of manual- and speech-related movement components, observation of the temporal relationships between stimulus-locked and response-locked averages and determination of how the differences in the cognitive load of the three response categories can affect the motor programming reflected by MRCPs. In the present study, we analyzed the MRCPs produced in a sample of older participants during the execution of the same task used in the previous study (Buján et al., 2009).

It is well known that aging is related to slowed performance in RT paradigms, but the typical pattern found, referred to as “the complexity effect”, is that the slowing is not constant across tasks but increases with increasing task complexity (for a review, see Salthouse, 2000). Indeed, some studies have shown a stronger interdependence between cognitive and sensorimotor processes with advancing age, reflecting poorer motor performance in older adults when a cognitive load is added (Band & Kok, 2000; Li & Lindenberger, 2002).

The complex choice-RT task used in the present study may maximize identification of age-related differences in motor programming and favour investigation of the influences of cortical motor processes on age-related slowing. One issue that has been debated with respect to RT tasks is whether the age-related differences are primarily attributable to stages associated with stimulus processing or to stages associated with motor programming. In two recent studies (Falkenstein et al., 2006; Kolev et al., 2006), the delay in RT in older individuals was accompanied by longer duration and larger MRCPs, whereas the ERPs associated with stimulus processing or response selection stages were not affected by age. In both studies the authors concluded that aging-related behavioural slowing was due to prolongation of central response generation.

In a previous study (Galdo-Álvarez et al., 2009a), the effect of aging on the ERP components associated with the stimulus processing stages was examined by use of the same task used in the present study. As expected, the behavioural results showed that age had a significant effect on RT, with longer RTs in older than in young adults. The latencies of ERP components associated with post-perceptual stages (P2, N400 and Early-P3) were longer in elderly adults than in young adults. Nevertheless, the complete delay caused by these stimulus processing stages was very short (less than 100 ms) and therefore such differences in latency could not entirely explain the behavioural slowing in older than in young adult participants (about 800 ms longer). In addition, in line with the results obtained for young adults (Díaz et al., 2007), the RT was also longer in the TOT response category than in the KNOW and DON'T KNOW response categories. Nevertheless, there were no differences between response categories in relation to the latencies of stimulus-locked ERP components, which may explain the behavioural slowing in the TOT response category.

In the present study, the MRCPs produced in a sample of elderly adults during a face naming choice-RT task used in previous studies (Buján et al., 2009; Díaz et al., 2007; Galdo-Álvarez et al., 2009a) were analyzed, with the following specific objectives:

1. To characterize and evaluate the manual and verbal MRCP components in a sample of elderly adults during execution of a choice-RT task with high cognitive load. It was expected that the same MRCP components would be observed in the older adults as observed in young adults (Buján et al., 2009).

2. To determine the effect of aging on behavioural performance and on MRCPs in a face naming choice-RT task with high cognitive load. In accordance with previous studies, we expected to find slower responses in older participants than in young participants and differences between age groups in MRCPs that may explain the age-related behavioural slowing.

3. To determine whether the differences in cognitive demand among the DON'T KNOW, KNOW and TOT response categories have any effect on RTs and MRCPs in older adults. In accordance with the findings of previous studies, we expected to observe longer RTs in the TOT than in the DON'T KNOW and KNOW responses, as well as differences in time relationships between stimulus-locked and response-locked averages and in MRCP measures among response categories that could explain the slower TOT response in older participants. In addition, we expected to find differences among response categories in older adults in speech-related

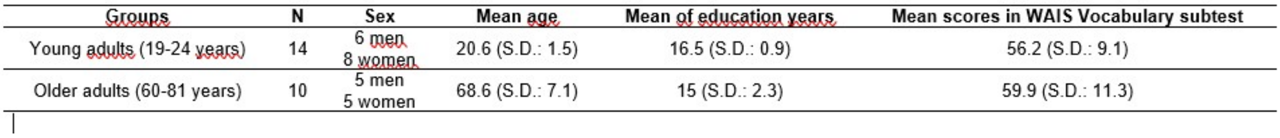
components associated with the greater linguistic demand in the KNOW response category at this stage.

2. Materials and methods

2.1. Sample

A total of 24 healthy volunteers participated in the study, including the same 14 young adults who participated in the previous study of Buján et al. (2009) (age range: 19-24 years) and 10 elderly adults (age-range: 60-81 years). The two groups of participants did not differ in level of education, as measured by years of education ($t_{(11.15)} = 1.94$; $p = 0.08$) or in level of vocabulary, as measured by Vocabulary subtest of Wechsler Adults Intelligence Scale (WAIS, Wechsler, 1988) ($t_{(22)} = -0.88$; $p = 0.38$) (see Table 1). All volunteers were right-handed, with normal or corrected-to-normal vision, and were healthy, with no history of neurological or psychiatric disorders. None of the participants were familiar with the protocols used in the study, which were approved by the local ethics committee. All participants gave their informed consent prior to taking part in the study.

Table 1. Socio-demographic characteristics and mean scores in vocabulary subtest of WAIS (S.D.: standard deviation)



Groups	N	Sex	Mean age	Mean of education years	Mean scores in WAIS Vocabulary subtest
Young adults (19-24 years)	14	6 men 8 women	20.6 (S.D.: 1.5)	16.5 (S.D.: 0.9)	56.2 (S.D.: 9.1)
Older adults (60-81 years)	10	5 men 5 women	68.6 (S.D.: 7.1)	15 (S.D.: 2.3)	59.9 (S.D.: 11.3)

2.2. Procedure

Stimuli were photographs of the faces of famous people. The images were obtained from various sources (i.e., digitized databases from the media or Internet or digitized images from magazines). A total of 800 different faces of famous people (including actors, politicians, sportsmen, TV stars, etc., from Galicia, Spain and other countries) were initially selected from several decades of the 20th century and from the present time. Two test groups (young and older adults) selected the 200 photos that they considered the best known and most representative of the different decades (see Díaz et al., 2007 for a complete list of names). Each participant in the present study was therefore shown 200 photographs (10 x 13 cm), for 314 ms each, at a distance of 1 m, with a subtended visual angle of 5.7º x 8.6º of arc, on a 19" flat screen monitor with a vertical refresh rate of 120 Hz. The photos were all software-edited for homogeneity of background and with respect to contrast and average luminance. All images were in colour, and showed a frontal view of the face, with clear representation of all major features, against a neutral background. Negative facial expressions were avoided, and images with neutral or mildly positive expressions were generally used.

The photographs were presented sequentially in 5 blocks of 40 photographs, and with an interblock interval of 90 s. During the task, the participants maintained a steady position by looking at a cross that appeared in the centre of the screen during intervals without photographs. Before the start of the task, the participants were presented with a practice block of 10 photographs (different from the 200 photographs that formed part of the task) to ensure that they had understood the instructions.

In response to each photo, the participants were required to press the M key (covered with a red sticker) of a computer keyboard, with the index finger of the right hand, as quickly as possible when they were sure that they did not know the name of the person, or the Z key (covered with a green sticker) with the index finger of the left hand as quickly as possible, when they were sure that they did know the name of the person. Immediately after this, the participants had to produce a verbal response. If the participants had pressed the M key they had to say aloud “Don’t know” (DON´T KNOW response category); if they had pressed the Z key they had two options: 1) to say aloud the name of the famous person (KNOW response category) or 2) to say aloud “Can’t remember”, if they were sure that they knew the name and felt that they were on the verge of producing it, but could not remember it at that moment (TOT response category). The TOT states were therefore caused spontaneously by the task, without any type of experimental manipulation. The interval between pressing the key and presenting the next photo was 2500 ms for the KNOW and DON’T KNOW responses. For the TOT responses, this interval was variable because a procedure was used to verify the authenticity of the TOT status, consisting of presenting the photograph again after having presented a series of three words, one of which was a phonological prime for the name of the famous person (see Díaz et al., 2007 for a complete description of procedure).

In the present study we evaluated performance and MRCP parameters for the three response categories. In the case of KNOW category, only the trials and the EEG epochs corresponding to correct responses were considered.

2.3. Electroencephalographic (EEG) recording and processing

The participants were seated on a comfortable chair in a Faraday chamber, with attenuated levels of light and noise, and were instructed to move as little as possible during the recording.

In accordance with the International 10-20 System, EEG activity was recorded at 30 active electrodes (Fp1, Fp2, F7, F3, Fz, F4, F8, FT7 FC3, FCz, FC4, FT8, T3, C3, Cz, C4, T4, TP3, CP3, CPz, CP4, TP4, P7, P3, Pz, P4, P8, O1, Oz, O2) inserted in a cap with a nose reference and frontopolar ground. The signal was passed through a 0.1-50 Hz (24 dB/octave slope) analog band-pass filter and was amplified to 22.5 K. The sampling rate was 500 Hz. Simultaneous to EEG recordings, ocular movements (EOG) were recorded with two electrodes located supra and infraorbitally to the right eye (VEOG) and another two located at the lateral angle of each eye (HEOG). All impedances were maintained below 10 kΩ.

After signal storage, the same processing steps used in the previous study (Buján et al., 2009) were followed. Ocular artefacts were corrected by use of the algorithm of Gratton et al. (1983) and the EEG was then segmented by extraction of synchronized epochs with each manual motor response. The epochs were classified a posteriori as DON'T KNOW, KNOW and TOT, depending on the participant's response. The duration of the epoch was adapted to the maximum mean RT achieved by the participants. Thus, the duration of the epoch in the young adults was 3300 ms (2000 ms pre-response plus 1300 ms post-response) and in the older adults, 4300 ms (3000 ms pre-response plus 1300 ms post-response). The signal was adjusted to a baseline of 500 ms (between -2000 and -1500 ms for young adults and between -3000 and -2500 ms for older adults) and segments exceeding ± 150 µV were automatically rejected. Finally, the signal was passed through a digital band-pass filter (0.1 to 30 Hz, 24 dB/octave slope) and the epochs were averaged.

2.4. Data analysis

The number of responses and the RTs for the manual response (pressing the key) corresponding to each of the response categories (KNOW, DON´T KNOW and TOT) were evaluated.

The EEG epochs corresponding to DON'T KNOW, KNOW and TOT responses were averaged. The values of latency and amplitude for all components were measured at the C3, Cz, C4, P3, Pz, P4, F7, Fz and F8 electrodes.

In the previous study of Buján et al. (2009), the waveforms in young adults revealed 4 MRCP components, in accordance with previous reports (Deecke et al., 1969; Shibasaki et al., 1980): the first component of the readiness potential (1st-RP) occurred at around the 1000 ms prior to the response; the negative slope (NS') was observed between 500 and 100 ms prior to the response; the motor potential (MP) between the 50 ms prior to the response and the next 100 ms; the reafferent potential (RAP) with a maximum amplitude between the 50 and 300 ms posterior to the response. After the RAP, another two components were observed, the speech-related motor potential (Sr-MP), with a maximum peak between the 250 and 700 ms after the manual response, followed by a positive-going phase (the speech-related reafferent potential: Sr-RAP) between the 600 and 1300 ms after the manual response.

In the present study, temporal principal component analysis (tPCA) was applied to the MRCP data obtained in both age groups, and corresponding to the DON'T KNOW, KNOW and TOT categories, in order to determine whether both age groups presented similar temporal components, and therefore, whether it was possible to compare the different components in young and older adults. The decision with regard to the number of components to be selected was based on the results of the scree test (Cattell, 1966). The extracted components were then submitted to a Promax rotation, as Dien (1998) reported that the use of Promax rotation would provide more accurate results in order to reduce problems, such as misallocation of variance. The results revealed similar components in older and young adults, with similar temporal and topographical distributions in both age groups (see Table 2).

To address the second objective, i.e. to determine the effect of age on the execution of the task and the MRCPs, between-group comparisons were made for each response category. As the epochs were different for each age group and there were important differences in the RTs between categories, different intervals were taken into account considering the mean RT in each category and each age group in analyzing the 1st-RP. Thus, for the DON'T KNOW category the mean amplitude in the interval -1600 a -500 ms in the older participants was compared with the mean amplitude in the interval -1100 a -500 ms in the younger participants; for the KNOW category the mean amplitude in the interval -1800 a -500 ms in the older participants was compared with the mean amplitude in the interval -1100 a -500 ms in younger participants; for the TOT category the mean amplitude in the interval -2500 a -500 ms in older adults was compared with the mean amplitude in the -1700 a -500 ms interval in younger participants. For the rest of the components the same intervals were compared: for NS' the mean amplitude between -500 and -100 ms was analyzed; for MP and Sr-MP the peak latencies and amplitudes were measured from the maximum peak to baseline in the intervals between -50 and 100 ms and between 250 and 700 ms, respectively; for the reafferent potentials, the peak latencies and the peak to peak amplitudes were measured in the temporal intervals between 50 and 300 ms for RAP and between 600 and 1300 ms for Sr-RAP.

To address the third objective, the MRCPs produced in older participants were compared among the three response categories. For the 1st-RP the mean amplitude was measured in the temporal intervals indicated by the tPCA (1st-RPa: between -2500 and -1600 ms; 1st-RPb: between -1500 and -1200 ms, and 1st-RPc: between -1100 and -700 ms). For the other components, the same measures were used as for the between-group comparisons. In order to study the time relationships between stimulus-onset and response-onset time-locked ERP components, the mixed plots of the stimulus-onset and response-onset averaged ERP waveforms from older participants were elaborated for each response category.

2.5. Statistical analysis

One-way ANOVAs were used to compare the percentage of responses and RTs between groups for each response category. Repeated-measures ANOVA with a within-subject factor (Response Category, with three levels: DON'T KNOW, KNOW and TOT) was applied to compare the percentage of responses and the RTs in the three response categories within the group of older participants.

To determine the differences in MRCP measures between groups, mixed ANOVAs were applied to each response category, with two within-subject factors (Region with three levels: frontal [F7/Fz/F8], central [C3/Cz/C4] and parietal [P3/Pz/P4]) and Side, with three levels: left [F7/C3/P3], midline [Fz/Cz/Pz] and right [F8/C4/P4]) and one between-subject factor (Age, with two levels: young and older adults). To investigate factors affecting the amplitude and latency of the MRCP components in older adults, a repeated measures ANOVA was used, with three within-subject factors (Response Category, with three levels: DON'T KNOW, KNOW and TOT; Region with three levels: frontal [F7/Fz/F8], central [C3/Cz/C4] and parietal [P3/Pz/P4]), and Side, with three levels: left [F7/C3/P3], midline [Fz/Cz/Pz] and right [F8/C4/P4]).

For both types of comparisons, the Greenhouse-Geisser correction was applied to the degrees of freedom when the condition of sphericity was not fulfilled. When significant effects were detected by ANOVA, Bonferroni tests were applied for post-hoc comparison of the means. Differences in results were considered significant at $p < .05$.

3. Results

Performance

The mean percentages of responses and RTs in each response category in both groups are shown in Figure 1. No differences between age groups or among categories in older adults group were found in the percentage of responses. In the KNOW category the error rate was less than 1%

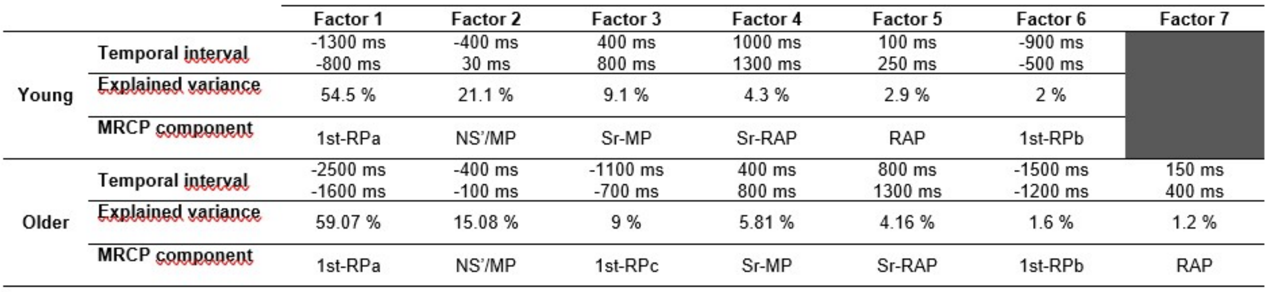
and no differences were observed between the age groups. A significant effect of Age was found for RT in the three categories, as the RT was longer in older than in young adults in the DON'T KNOW ($F_{(1,22)} = 11.22$; $p < .05$), in the KNOW ($F_{(1,22)} = 22.78$; $p < .001$) and in the TOT categories ($F_{(1,22)} = 8.7$; $p < .01$). Also, differences among the categories in the older adults group were found ($F_{(2,18)} = 17.2$; $p \leq .001$), with a significantly longer mean RT in the TOT response category than in DON'T KNOW and KNOW responses.

(Figure 1 about here)

Movement related cortical potentials

Similar components for both age groups were identified in the tPCA for each response category (see Table 2 and Figure 2). The grand average MRCP waveforms for each age group, in each response category, and voltage maps of MRCP components that differed significantly between groups are illustrated in Figure 3. The mean amplitudes of the 1st-RP, NS' and MP for both age groups are shown in Figure 4.

Table 2. Temporal intervals, explained variance and corresponding MRCP components associated to each temporal factor extracted by the temporal principal component analysis (tPCA) in young and older adults.



		Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Factor 6	Factor 7
Young	Temporal interval	-1300 ms -800 ms	-400 ms 30 ms	400 ms 800 ms	1000 ms 1300 ms	100 ms 250 ms	-900 ms -500 ms	
	Explained variance	54.5 %	21.1 %	9.1 %	4.3 %	2.9 %	2 %	
	MRCP component	1st-RPa	NS'/MP	Sr-MP	Sr-RAP	RAP	1st-RPb	
Older	Temporal interval	-2500 ms -1600 ms	-400 ms -100 ms	-1100 ms -700 ms	400 ms 800 ms	800 ms 1300 ms	-1500 ms -1200 ms	150 ms 400 ms
	Explained variance	59.07 %	15.08 %	9 %	5.81 %	4.16 %	1.6 %	1.2 %
	MRCP component	1st-RPa	NS'/MP	1st-RPc	Sr-MP	Sr-RAP	1st-RPb	RAP

(Figure 2 about here)

(Figure 3 about here)

For the 1st-RP, the mixed-ANOVAs for DON'T KNOW and KNOW response categories did not reveal any significant effects for Age. In the TOT response category, Age had a significant effect on the mean amplitude of the 1st-RP component ($F_{(1,22)} = 4.98$; $p < .05$), as it was larger in older (-7.03 μV) than in young adults (-0.91 μV).

In older adults the repeated-measures ANOVA revealed the following significant effects: a) for the 1st-RPa, a marginally significant effect for Response Category was found ($F_{(2,18)} = 2.96$; $p = .07$) and the post-hoc comparisons did not reveal any significant effects. The Response Category × Region interaction was also significant ($F_{(4,36)} = 4.82$; $p < 0.01$), as the mean amplitude was marginally larger ($p = .07$) in TOT (-6 µV) than in DON'T KNOW (2.3 µV) in the central region. In the TOT category, the mean amplitude was significantly larger in the central than in the frontal region (-4.1 µV); b) for the 1st-RPb, the repeated-measures ANOVA revealed significant effects for Response Category ($F_{(2,18)} = 3.65$; $p < .05$) and for the Response Category × Region interaction ($F_{(4,36)} = 4.83$; $p < .01$), as the mean amplitude was significantly larger in TOT (-9.8 µV) than in DON'T KNOW (-0.6 µV) in the central region. In the TOT category, the amplitude was significantly larger in the central and parietal regions (-9.5 µV) than in the frontal region (-5.5 µV); c) for the 1st-RPc, the ANOVA revealed a significant effect for Response Category ($F_{(2,18)} = 3.47$; $p < .05$), as the mean amplitude was significantly larger in TOT (-8.75 µV) than in DON'T KNOW (-0.7 µV).

For the NS', MP and RAP components no differences were found between groups in any of the response categories. In older adults, the repeated-measures ANOVA revealed for NS' a significant effect for Region ($F_{(2,18)} = 6.4$; ε: .619; $p < .05$), as the mean amplitude was significantly larger in the parietal (-7.2 µV) than in the frontal region (-3.65 µV). For MP, the ANOVA did not reveal any significant effect on the latency of the component and revealed a significant effect for Side on the amplitude ($F_{(2,18)} = 4.86$; $p < .05$), as it was significantly larger at the midline (-12.08 µV) than on the left side (-8.7 µV). For RAP, the ANOVA did not reveal any significant effect on either the latency or the amplitude of this component.

(Figure 4 about here)

For Sr-MP, the mixed-ANOVAs did not show significant differences between groups in the DON'T KNOW and KNOW categories. However, in the TOT category the ANOVA showed a significant effect for Age on the latency of the component ($F_{(1,22)} = 4.05$; $p < .05$), as it was significantly shorter in young (397 ms) than in older adults (538 ms). In older adults, the ANOVA revealed a significant effect for Response Category on the latency of the component ($F_{(2,18)} = 3.7$; $p < .05$), as it was shorter in the DON'T KNOW category (410 ms) than in the KNOW (532 ms) and TOT categories (538 ms), although the post-hoc comparisons did not reveal any significant differences. With regard to amplitude, the ANOVA revealed significant effects for Region, Side and the Region × Side interaction ($F_{(4,36)} = 5.21$; $p < .01$), as it was significantly larger in the central (-18.14 μV) and parietal (-18 μV) regions than in the frontal region (-10.1 μV) only on the left side, and over the frontal region the amplitude was larger at the midline (-17.23 μV) than on the left side (-10.1 μV).

Finally, for Sr-RAP component the mixed-ANOVA revealed a significant effect for Age on the latency in the DON'T KNOW category ($F_{(1,22)} = 12.16$; $p < .01$), as it was significantly shorter in older than in young adults (774 ms and 1057 respectively). In KNOW category, significant effects for the Region × Age interaction ($F_{(2,44)} = 14.46$; ε: .576; $p < .001$) and for the Region × Side × Age interaction were found on the Sr-RAP amplitude ($F_{(4,88)} = 5.05$; ε: .510; $p \leq .01$), as it was larger in young than in older adults in the parietal region on the left side (30.22 μV and 19.52, respectively) and at the midline (30.4 μV and 20.23 μV, respectively). No differences were found between age groups in TOT category. In older adults, the ANOVA revealed a significant effect for Response Category on the latency ($F_{(2,18)} = 5.23$; $p \leq .01$), as it was significantly shorter in the DON'T KNOW category (774 ms) than in the KNOW (1006 ms) and TOT (1009 ms) categories. The ANOVA did not reveal any significant effects on the Sr-RAP amplitude.

Relationship between stimulus-locked and response-locked ERPs

The mixed-plots of the stimulus-onset and response-onset averaged waveforms for older adults in each response category are shown in Figure 5.

(Figure 5 about here)

In the young adults group the 1st-RP was clearly appreciated from the time of stimulus presentation in the DON'T KNOW and KNOW categories, whereas in the TOT category appeared to start at around 1700 ms before the manual response, but returned to baseline until approximately 1100 ms before the manual response. The component only reached continuous negative amplitude from time when late-P3 took place in stimulus-onset averaged waveform, around 1100 ms before the manual response (see Buján et al., 2009), and its slope increased until achieve the maximum negative amplitude in the MP (see Figure 4). The mixed-plots for older adults showed that in the DON'T KNOW category, the starting point of the 1st-RP coincided with the temporal interval in which the Late-P3 component in stimulus-locked average took place, around 1000 ms prior to the manual response. In the KNOW category the beginning of the 1st-RP coincided with the interval in which P2/Early-P3 took place, around 1500 ms prior to the manual response. In the TOT category, the 1st-RP was observed from the time of stimulus presentation (2500 ms prior to the manual response), but a decrease in the slowly rising negativity of the readiness potential was observed from the start of the 1st-PRb (see Figure 4), coinciding with the stimulus-locked Late-P3 and LNW components.

4. Discussion

The proportion of responses in each category was very similar in both groups and it was consistent with previous reports in young (Brennen et al., 1990; Díaz et al., 2007) and in older adults (Burke et al., 1991; Rastle & Burke, 1996). Although the older participants produced more TOT responses than young participants, the difference was not significant, in contrast with previous studies that have reported a significantly higher percentage of TOT responses in older adults (Burke & Shafto, 2004; Burke et al., 1991; White & Abrams, 2002). In accordance with Galdo-Álvarez et al. (2009a), the former result may be due to the high intellectual status of the older participants in the present study, together with the fact that the task was designed to minimize age-related differences in the participants in terms of the famous people known by the groups.

Age had an overall effect on RT, with longer RTs in older than in young adults for each response category, in accordance with the age-related behavioural slowing observed in several previous studies, both concerning face processing (Grady et al., 1994; Pfütze et al., 2002) and the processing of other types of stimuli (Falkenstein et al., 2006; Loveless, 1980; Mattay et al., 2002; Sailer et al., 2000). The behavioural slowing in the older adults relative to the younger adults was greater in TOT (800 ms), followed by KNOW (700 ms), with DON'T KNOW in last place (500 ms). These behavioural data support that there is a gradation in the cognitive demand in the different response categories, and that this modulates the RT, in accordance with "the complexity effect" observed in previous studies (Band & Kok, 2000; Salthouse, 1996; Yordanova et al., 2004). As in the young adults (Buján et al., 2009), in the older adults the RT was longer in TOT states than in the other two categories of response.

Six MRCP components were identified in the three response categories in both age groups: the first component of the readiness potential (1st-RP), the negative slope (NS´), the motor potential (MP) and the reafferent potential (RAP), and two components associated with the verbal responses required by the task: the speech-related motor potential (Sr-MP) and the speech-related reafferent potential (Sr-RAP).

The 1st-RP showed a typical central-parietal and symmetrical distribution in both young and older adults for the three response categories, in accordance with previous studies (Deecke et al., 1969; Feve et al., 1991; Shibasaki et al., 1980; Singh et al., 1990).

The amplitude of the 1st-RP in the KNOW and TOT categories was larger in older than in young adults, however only in TOT category the difference was significant. In a classical study it was demonstrated that the amplitude of the 1st-RP was directly related to the moment that it started (Deecke et al., 1976) and therefore with its duration, with the amplitude being greater the longer the duration. These data suggest that in older participants, the response preparation period was lengthened compared with young adults, which would explain the behavioural slowing observed in older participants, especially in the TOT condition. The present results support the data reported in previous studies (Falkenstein et al., 2006; Feve et al., 1991; Ishizuka et al., 1996; Kolev et al., 2006), i.e. that preparation of the response lasted longer and was longer in older adults in more demanding tasks.

Moreover, in older adults the mean amplitude of the component in the intervals in which the 1st-RP was divided was greater in the TOT category than in DON'T KNOW (principally in the central region), with intermediate values in the KNOW category, whereas in our previous study (Buján et al., 2009) no differences among the response categories were found in young participants. Superimposition of the response-locked ERP and the stimulus-locked ERP on time (see mixed plots, Figure 5), revealed the modulation of the amplitude of the 1st-RP by stimulus-locked ERPs, which was different for both age groups.

In young adults the sustained negativity that describes the 1st-RP in TOT began at the moment when stimulus categorization took place (coinciding with the stimulus-locked Late-P3), at approximately 1100 ms before the response. In the older subjects, the sustained negativity began from the moment of presentation of the stimulus (at approximately 2500 ms prior to the response). The slowly rising negativity was maintained until approximately 1600 ms prior to the response (coinciding with finalization of the stimulus-locked Late-P3, correlate of completion of the stimulus categorization), moment at which a change in the 1st-RP slope was observed, with stable negative values being maintained in the subsequent stages (NS' and MP). Taking into account the functional significance of the first part of RP as a index of general resource mobilization (McCallum, 1993), these data might be explained in accordance with previous studies, which have shown that the amplitude of the readiness potential decreased when the subjects' attention was divided (Vaez-Mousavi & Barry, 1993) or when less attention was paid to preparation (Wiese et al., 2004).

In young adults the processing resources were divided from the beginning of motor programming (see Buján et al., 2009), whereas in older adults more motor resources were allocated at the beginning of motor programming and division of the processing resources only started from the most demanding processing stages (stimulus categorization and review of the categorization), when the subject tries unsuccessfully to resolve the conflict between the cognitive and metacognitive levels (the subject is sure that he/she recognises the famous person and knows their name, but is unable to recall the complete phonology of the name) (Brown, 1991; Brown &

McNeill, 1966). This conflict would add a cognitive load, which may interfere in the response selection in accordance with previous studies using demanding tasks in older adults (Band & Kok, 2000); this gives rise to a lengthening of the response preparation with the corresponding behavioural slowing in this category in older adults. Nevertheless, we can not establish reliable conclusions about the timing of the response selection process. One measure that can reflect this process is the lateralized readiness potential (LRP, de Jong et al., 1988; Coles, 1989), but in the present study it could not be calculated because the manual responses were not counterbalanced. In future studies this aspect will be taken into account.

On the whole, the results for the 1st-RP suggest that older adults employed a different processing resource allocation strategy than young adults, especially in TOT category. These results are consistent with the data obtained in studies with a dual-task paradigm. The difficulty found by older adults in carrying out dual tasks is clearly demonstrated (Bock & Schneider, 2002; Holtzer et al., 2005; Wu & Hallett, 2005) and this age-related impairment has been attributed to difficulties associated with dividing attention between processes. The division of resources after the more demanding stages may imply - in accordance with Bock & Schneider (2002) - that older people may need to allocate more of their computational resources for sensoriomotor adaptation. Therefore, the sensoriomotor performance of older adults may be compromised when an attentional load is added, reflecting greater interdependence of sensoriomotor and cognitive abilities with advancing age (Li & Lindenberger, 2002).

In line with the shared resources model of attention (Kanheman, 1973), this interpretation suggests a greater effort in the TOT category in older people and less automatic execution of movement. The reduced attentional capacity in older adults may result in them using motor resources to compensate for cognitive deficits in more demanding situations, as suggested in previous studies (Lindenberger et al., 2000; Maylor & Wing, 1996). In other words, to maintain similar execution as in the young subjects, with regard to the percentage of responses, the older adults make more effort and dedicate more resources to try to resolve the conflict in TOT, which results in a similar percentage of responses, but longer RTs.

The topographical distribution of the NS’, MP and RAP components was similar in both age groups, in accordance with the findings of previous studies (Deecke et al., 1976; Shibasaki et al., 1980). There were no differences between the groups in any of the response categories and therefore, specific preparation of motor programme, movement execution and kinaesthetic feedback phases may not be affected by cerebral aging (Deecke, 1980; Singh et al., 1990). No differences between the response categories were observed in relation to these components in either of the age groups. We therefore consider that these components reflect purely motor aspects and do not appear to be influenced by cognitive ones.

Following the RAP, the tPCA revealed two factors in both age groups corresponded to the Sr-MP and Sr-RAP identified in the study by Buján et al. (2009). In both age groups, the distribution of Sr-MP was central-parietal, which is consistent with the distribution of the motor potential for manual movements (Deecke et al., 1976; Shibasaki et al., 1980). There were no differences in the amplitudes between the groups for any of the response categories. This was surprising taking into account the differences in the waveforms obtained for both groups. In the three categories, the amplitude of this component was clearly smaller in the older group. We attribute the lack of between-group differences to the great variability in the amplitude of this component in older participants, although more research is required to clarify this aspect.

In the TOT category, the latency of the Sr-MP was shorter in young than in older adults. In our previous study (Buján et al., 2009) young participants showed shorter latencies in TOT than in KNOW category. Unlike the young adults, there were no differences in the latency of Sr-MP between KNOW and TOT categories in older adults but the latency was shorter for the DON’T KNOW category than for the KNOW and TOT categories. The lower linguistic complexity involved in pronouncing a learned response that may remain in the working memory during the whole task (“Don’t know”) in comparison with that involved in pronouncing a different name in each task (KNOW category) may give rise to an earlier verbal response. The delay of the Sr-MP component in TOT relative to DON'T KNOW does not appear to be very consistent, as in TOT the verbal response is also learned ("Can't remember"). These results suggest that older adults may experience the same difficulty in activating the phonological repetitive pattern related to the TOT response category as in activating the phonological information about the retrieved name in the KNOW category. We suggest that this difference may be because older participants have difficulties in executive aspects of working memory during the retrieval state in TOT category (Rypma et al., 2001), probably caused by failure to inhibit irrelevant information (Hasher, 1999). These data may reflect an age-related reduction in mental flexibility, since older participants are still searching for the name and do not focus on the task demands, showing a lack of adaptation to the motor task requirements (Labyt et al., 2004). It is also likely, in accordance with Galdo-Álvarez et al. (2009b), that older adults make use of a phonetic strategy (e.g. sub-vocalization) to complete phonological access, which may require more time.

There were some differences between groups in relation to the distribution of the amplitude of the Sr-RAP across the scalp in the KNOW category. The component was larger in parietal than in central and frontal regions only in the group of young adults, and the amplitude was larger in young than in older adults at left and midline locations in the parietal region. The more widespread distribution in older adults and the smaller amplitude relative to young adults may reflect a reduction in somatosensory integration with age, in accordance with Labyt et al. (2004). In contrast, in young adults, correct integration of sensory information resulted in a Sr-RAP of larger amplitude and a specific central-parietal distribution, in accordance with topographical data reported for this component in previous studies (Shibasaki et al., 1980).

In the DON'T KNOW category, the latency of the Sr-RAP was shorter in older than in young adults and it was shorter for the DON'T KNOW than for the KNOW and TOT categories only in older adults. Given the earlier appearance of Sr-MP in the DON'T KNOW category than in the KNOW and TOT categories in older adults, there was an earlier feedback to somatosensorial areas in the former category, resulting in the differences observed for this component between the age groups.

5. Conclusions

The 1st-RP showed larger amplitude and longer duration in older than in young adults, especially in TOT category, which may reflect that the response preparation took longer in the older than in the young participants, and explain the behavioural slowing in the older compared with young adults. The specific slowing down observed in both young and older adults in the TOT category was associated with an interruption in the progression of the 1st-RP, due to division of processing resources between the search for phonological information and motor programming, but at different times in each group. In young adults the interruption took place from the beginning of motor preparation until classification of the stimulus occurred, whereas in older adults more motor resources were engaged in motor preparation at the beginning until review of the selected response (LNW component) when the division of resources took place. On the whole, the data suggest that the processing resource allocation strategies differ between age groups, indicating that the sensoriomotor performance of older adults will be compromised to a greater degree than in young adults when a cognitive load is added in the task.

The NS', MP and RAP do not appear to be modulated by age or by the differential cognitive demand of the response categories studied. These data suggest that these components reflect processes that are specifically related to the motor plan.

In young adults there was a delay in the appearance of Sr-MP in the KNOW category in comparison with the TOT category. However, in older adults, the latencies were similar in TOT and KNOW, whereas in DON'T KNOW the component appeared earlier. Despite the lower linguistic demand in TOT, older participants executed the verbal response at the same time as in the KNOW category, which may indicate some difficulty with conflict management in TOT states. In addition, older participants may display reduced somatosensory integration, as can be inferred from the smaller amplitude and the more widespread topographical distribution of the Sr-RAP component than in young adults.

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References

Arnsten, A.F.T. 1998. Catecholamine modulation of prefrontal cortical cognitive function. Trends Cogn. Sci. (Regul. Ed.) 2, 436-447.

Band, G.P., Kok, A., 2000. Age effects on response monitoring in a mental-rotation task. Biol Psychol. 51, 201-221.

Bock, O., Schneider, S., 2002. Sensorimotor adaptation in young and elderly humans. Neurosci. Biobehav. Rev. 26, 761-767.

Bötzel, K., Ecker, C., Schulze, S., 1997. Topography and dipole analysis of reafferent electrical brain activity following the Bereitschaftspotential. Exp. Brain Res. 114, 352–361.

Brennen, T., Baguley, T., Bright, J., Bruce, V., 1990. Resolving semantically induced tip-of-the-tongue states for proper nouns. Mem. Cognit. 18, 339–347.

Brown, A.S. 1991. A review of the tip-of-the-tongue experience. Psychol. Bull. 109, 204-223.

Brown, R., McNeill, D., 1966. The “tip of the tongue” phenomenon. J. Verb. Learn. Verb. Behav. 5, 325–337.

Buján, A., Lindín, M., Díaz, F., 2009. Movement related cortical potentials in a face naming task: Influence of the tip-of-the-tongue state. Int. J. Psychophysiol. 72, 235-245.

Burke, D., MacKay, D., Worthley, J., Wade, E., 1991. On the tip of the tongue: What causes word finding failures in young and older adults? J. Mem. Lang. 30, 542-579.

Burke, D.M., Shafto, M.A., 2004. Aging and language production. Curr. Dir. Psychol. 13, 21-24.

Cabeza, R., 2001. Functional neuroimaging of cognitive aging. In Cabeza, R., Kingstone, A. (Eds.), Handbook of functional neuroimaging of cognition, MIT Press, Cambridge, MA, pp. 331-337.

Cattell, R.B., 1966. The scree test for the number of factors. Multivariate Behav. Res. 1, 245-276.

Coles, M., 1989. Modern mind-brain reading: psychophysiology, physiology, and cognition. Psychophysiology 26, 251-269.

Cunnington, R., Iansek, R., Bradshaw, J.L., Phillips, J.G., 1995. Movement-related potentials in Parkinsons' disease: Presence and predictability of temporal and spatial cues. Brain 118, 935-950.

de Jong, R., Wierda, M., Mulder, G., Mulder, L.J., 1988. Use of partial stimulus information in response processing. J. Exp. Psychol. Hum. Percept. Perform. 14, 682-692.

Deecke, L., 1980. Influence of age on the human cerebral potentials associated with voluntary movements. In Stein, D.G. (Ed), The psychobiology of aging: problems and perspectives, Elsevier, Amsterdam, pp. 411-423.

Deecke, L., Grozinger, B., Kornhuber, H.H., 1976. Voluntary Finger Movement in Man - Cerebral Potentials and Theory. Biol. Cybern. 23, 99-119.

Deecke, L., Scheid, P., Kornhuber, H.H., 1969. Distribution of readiness potential, pre-motion positivity, and motor potential of the human cerebral cortex preceding voluntary finger movements. Exp. Brain Res. 7, 158-168.

Díaz, F., Lindín, M., Galdo-Álvarez, S., Facal, D., Juncos-Rabadán, O., 2007. An event-related potentials study of face identification and naming: The tip-of-the-tongue state. Psychophysiology 44, 50-68.

Dien, J., 1998. Addressing misallocation of variance in principal component analysis of event-related potentials. Brain Topogr. 11, 43-55.

Dirnberger, G., Reumann, M., Endl, W., Lindinger, G., Lang, W., Rothwell, J.C., 2000. Dissociation of motor preparation from memory and attentional processes using movement-related cortical potentials. Exp. Brain Res. 135, 231-240.

Falkenstein, M., Yordanova, J., Kolev, V., 2006. Effects of aging on slowing of motor-response generation. Int. J. Psychophysiol. 59, 22-29.

Feve, A.P., Bathien, N., Rondot, P. 1991. Les potentiels corticaux liés au mouvement de l'homme âgé. Neurophysiol. Clin. 21, 281-291.

Freude, G., Ullsperger, P., 1987. Changes of the Bereitschaftspotential in the course of muscular fatiguing and non-fatiguing hand movements. J. Appl. Physiol. 56, 105-108.

Freude, G., Ullsperger, P., Kruger, H., Pietschmann, M., 1988. The Bereitschaftspotential in preparation to mental activities. Int. J. Psychophysiol. 6, 291-297.

Galdo-Álvarez, S., Lindín, M., Díaz, F., 2009a. The effect of age on event-related potentials (ERP) associated with face naming and with the tip-of-the-tongue (TOT) state. Biol. Psychol. 81, 14-23.

Galdo-Álvarez, S., Lindín, M., Díaz, F., 2009b. Age-related prefrontal over-recruitment in semantic memory retrieval: Evidence from successful face naming and the tip-of-the-tongue state. Biol. Psychol. 82, 89-96.

Gerloff, C., Richard, J., Hadley, J., Schulman, A.E., Honda, M., Hallett, M., 1998. Functional coupling and regional activation of human cortical motor areas during simple internally paced and externally paced finger movements. Brain 121, 1513–1531.

Grady, C.L., Maisog, J.M., Horwitz, B., Ungerleider, L.G., Mentis, M.J., Salerno, J.A., Pietrini, P., Wagner, E., Haxby, J.V., 1994. Age-related-changes in cortical blood-flow activation during visual processing of faces and location. J. Neurosci. 14, 1450-1462.

Gratton, G., Coles, M.G.H., Donchin, E., 1983. A new method for off-line removal of ocular artifact. Electroencephalogr. Clin. Neurophysiol. 55, 468-484.

Hasher, L., 1999. Inhibitory control, circadian arousal, and age. In Gopher, D., Koriat, A., (Eds.), Attention and performance, XVII, Cognitive regulation of performance: Interaction of theory and application, MIT Press, Cambridge, MA, pp. 653-675.

Holtzer, R., Stern, Y., Rakitin, B.C., 2005. Predicting age-related dual-task effects with individual differences on neuropsychological tests. Neuropsychology 19, 18-27.

Ishizuka, H., Tomi, H., Sunohara, N., 1996. Age-related changes in movement-related cortical potentials. Nippon Ronen Igakkai Zasshi. 33, 586-591.

Jahanshahi, M., Hallett, M., 2003. The Bereitschaftspotential: What does it measure and where does it come from? In Jahanshahi, M., Hallett, M. (Eds.), The Bereitschaftspotential: Movement-related cortical potentials, Kluwer Academics/Plenum Publishers, New York, pp. 117.

Kanheman, D., 1973. Attention and effort, Prentince-Hall, Englewoods Cliffs, NJ.

Kirsch, W., Hennighausen, E., Rösler, F., 2010. ERP correlates of linear hand movements in a motor reproduction task. Psychophysiology 47, 486-500.

Kolev, V., Falkenstein, M., Yordanova, J., 2006. Motor-response generation as a source of aging-related behavioural slowing in choice-reaction tasks. Neurobiol. Aging 27, 1719-1730.

Kornhuber, H.H.Deecke, L., 1965. Hirnpotentialänderungen bei willkürbewegungen und passiven bewegungen des menschen: Bereitschsftspotential und reafferente potentiale. Pflugers Arch Gesamte Physiol Menschen Tiere 284, 1-17.

Labyt, E., Szurhaj, W., Bourriez, J., Cassim, F., Defebvre, L., Destee, A., Derambure, P., 2004. Influence of aging on cortical activity associated with a visuo-motor task. Neurobiol. Aging 25, 817-827.

Lang, W., 2003. Surface recordings of the Bereitschaftspotential in normals. In Jahanshahi, M., Hallet, M. (Eds.) The Bereitschaftspotential: Movement-related cortical potentials, Kluwer Academics /Plenum Publishers, New York, pp. 19-34.

Li, K.Z.H., Lindenberger, U., 2002. Relations between aging sensory/sensorimotor and cognitive functions. Neurosci. Biobehav. Rev. 26, 777-783.

Lindenberger, U., Marsiske, M., Baltes, P.B. 2000. Memorizing while walking: increase in dual tasks costs from young adulthood to old age. Psychol. Aging 15, 417-436.

Loveless, N.E., 1980. Aging effects in simple RT and voluntary movement paradigms. Prog. Brain Res. 54, 547-551.

Mattay, V.S., Fera, F., Tessitore, A., Hariri, A.R., Das, S., Callicott, J.H., Weinberger, D.R., 2002. Neurophysiological correlates of age-related changes in human motor function. Neurology 58, 630-635.

Maylor, E.A., Wing, A.M., 1996. Age differences in postural stability are increased by additional cognitive demands. J. Gerontol. Ser. B-Psychol. Sci. Soc. Sci. 51, 143-154.

McAdam, D.W., Rubin, E.H. 1971. Readiness potential, vertex positive wave, contingent negative variation and accuracy of perception. Electroencephalogr. Clin. Neurophysiol. 30, 511-517.

McCallum, W.C., 1993. Human slow potential research: a review. In: McCallum, W.C., Curry, S.H. (Eds.), Slow Potential Changes in the Human Brain. Plenum Press, New York, pp. 1–11.

Pfütze, E.M., Sommer, W., Schweinberger, S.R., 2002. Age-related slowing in face and name recognition: Evidence from event-related brain potentials. Psychol. Aging 17, 140-160.

Praamstra, P., Cools, A.R., Stegeman, D.F., Horstink, M.W.I., 1996. Movement-related potential measures of different modes of movement selection in Parkinson's disease. J. Neurol. Sci. 140, 67-74.

Rastle, K.G., Burke, D.M., 1996. Priming the tip of the tongue: Effects of prior processing on word retrieval in young and older adults. J. Mem. Lang. 35, 586-605.

Raz, N., 2000. Aging of the brain and its impact on cognitive performance. In Craik, F.I.M., Salthouse, T.A. (Eds.), Handbook of aging and cognition, Erlbaum, Mahwah, NJ, pp. 1-90.

Rektor, I., 2003. Intracerebral recordings of the Bereitschaftspotential and related potentials in cortical and subcortical structures in human subjects. In: Jahanshahi, M., Hallet, M. (Eds.), The Bereitschaftspotential: Movement-related Cortical Potentials. Kluwer Academics /Plenum Publishers, New York, pp. 61–77.

Rypma, B., Prabhakaran, V., Desmond, J.E., Gabrieli, J.D.E., 2001. Age differences in prefrontal cortical activity in working memory. Psychol. Aging 16, 371-384.

Sailer, A., Dichgans, J., Gerloff, C., 2000. The influence of normal aging on the cortical processing of a simple motor task. Neurology 55, 979-985.

Salthouse, T.A., 2000. Aging and measures of processing speed. Biol. Psychol. 54, 35-54.

Salthouse, T.A., 1996. The processing-speed theory of adult age differences in cognition. Psychol. Rev. 103, 403-428.

Shibasaki, H., Barrett, G., Halliday, E., Halliday, A.M., 1980. Components of the movement-related cortical potential and their scalp topography. Electroencephalogr. Clin. Neurophysiol. 49, 213-226.

Shibasaki, H., Hallett, M., 2006. What is the Bereitschaftspotential? Clin. Neurophysiol. 117, 2341–2356.

Singh, J., Knight, R.T., Woods, D.L., Beckley, D.J., Clayworth, C., 1990. Lack of age effects on human brain potentials preceding voluntary movements. Neurosci. Lett. 119, 27-31.

Vaez-Mousavi, S., Barry, R., 1993. Positive and negative shifts of the readiness potential: preparatory effects. Int. J. Psychophysiol. 15, 105-113.

Wechsler, D., 1988. WAIS. Escala de Inteligencia de Wechsler para Adultos, TEA Ediciones, Madrid.

White, K.K., Abrams, L., 2002. Does priming specific syllables during tip-of-the-tongue states facilitate word retrieval in older adults? Psychol. Aging 17, 226-235.

Wiese, H., Stude, P., Nebel, K., Osenberg, D., Ischebeck, W., Stolke, D., Diener, H.C., Keidel, M., 2004. Recovery of movement-related potentials in the temporal course after prefrontal traumatic brain injury: A follow-up study. Clin. Neurophysiol. 115, 2677-2692.

Wu, T., Hallett, M., 2005. The influence of normal human ageing on automatic movements. J. Physiol. 562, 605-615.

Yordanova, J., Kolev, V., Hohnsbein, J., Falkenstein, M., 2004. Sensorimotor slowing with ageing is mediated by a functional dysregulation of motor-generation processes: evidence from high-resolution event-related potentials. Brain 127, 351-362.

Figure legends

Figure 1. Means and standard deviations for the percentage of responses **(A)**, and means and standard deviations for reaction times **(B)** in each response category for older (blank columns) and young adults (shadowed columns).

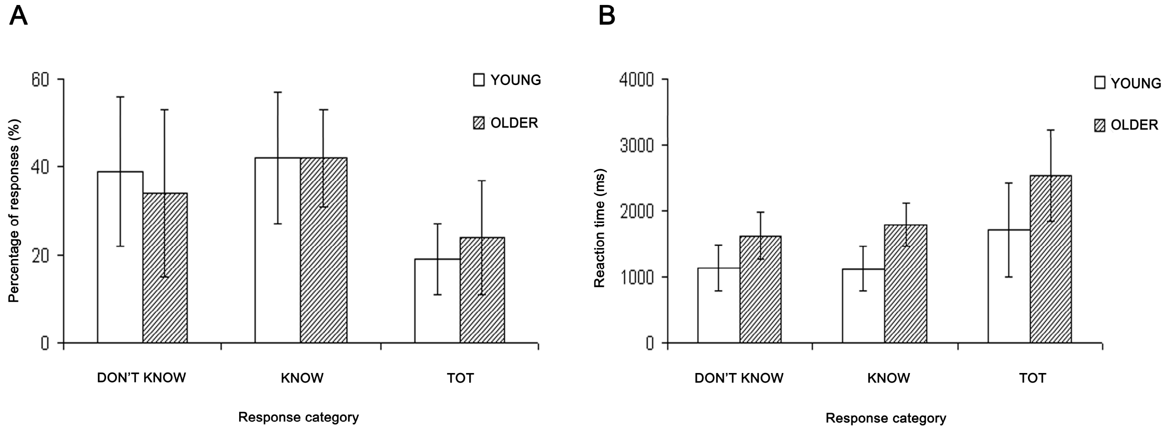

Figure 2. Temporal factors extracted by temporal principal component analysis (tPCA) for young (left) and older (right) adults.

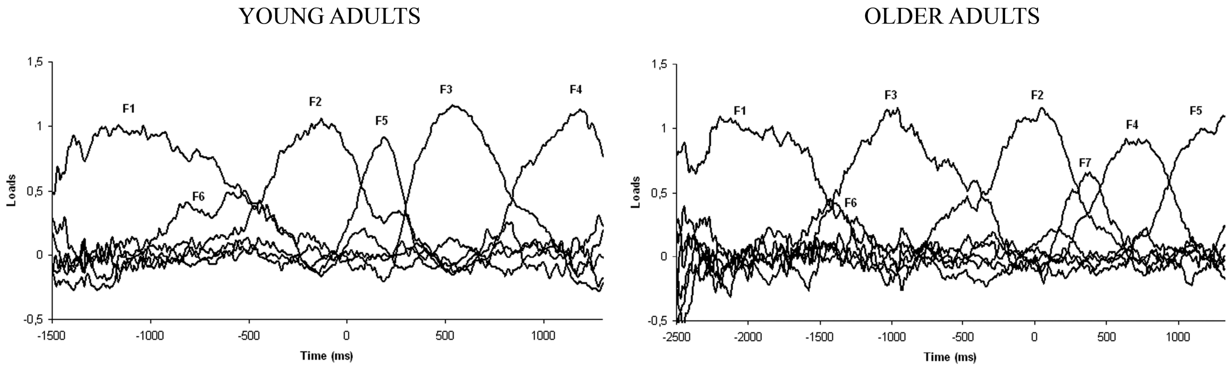

Figure 3. A. Grand-averaged MRCP waveforms for young (upper) and older (bottom) adults, in the DON'T KNOW, KNOW and the TOT categories at the nine electrodes analyzed (1st-RP: first component of readiness potential; NS´: negative slope; MP: motor potential; RAP: reafferent potential; Sr-MP: speech-related motor potential; Sr-RAP: speech-related reafferent potential).

B. Voltage maps for the 1st-RP component, in TOT response category, for young (left) and older (right) adults.

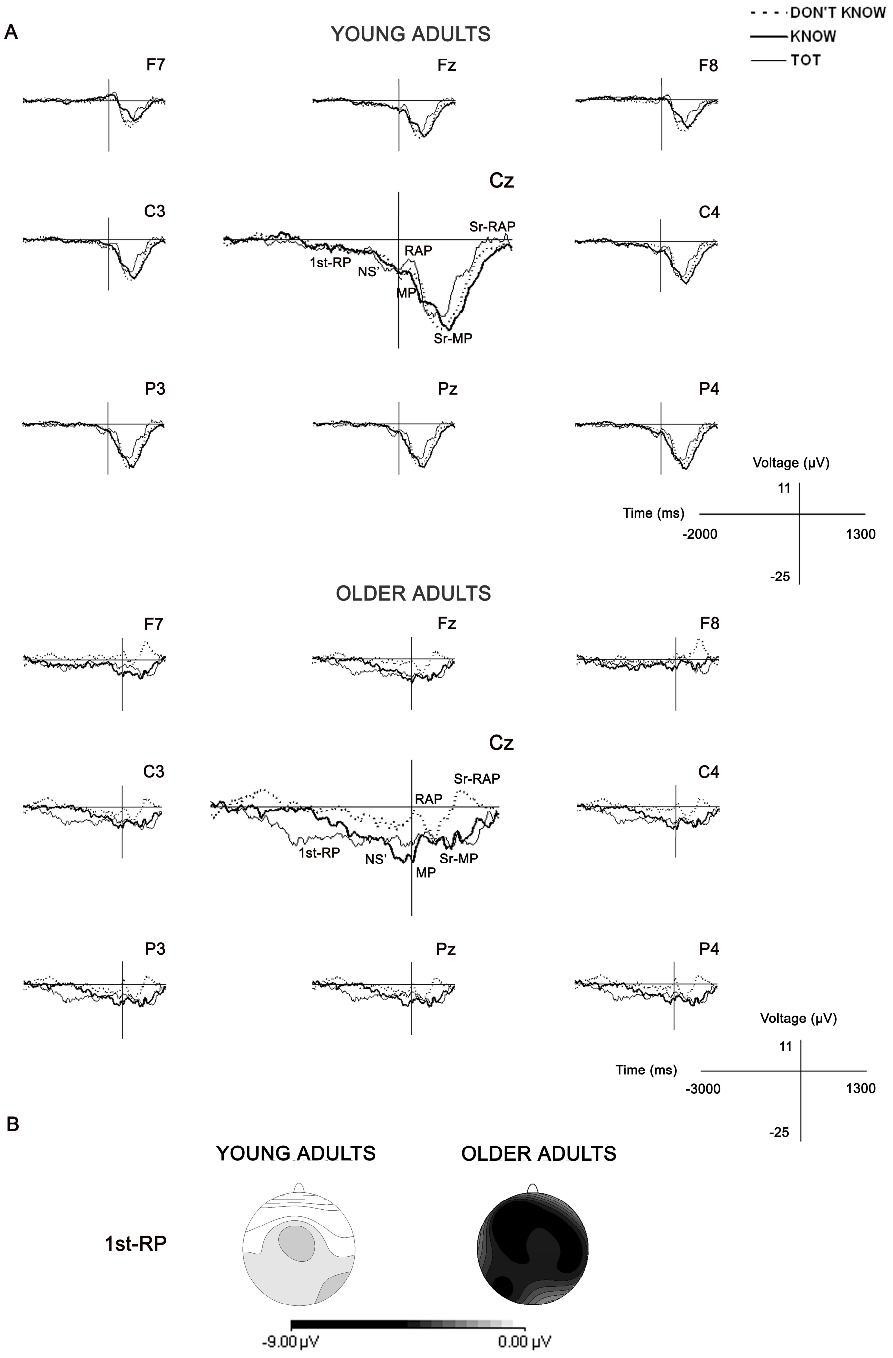

Figure 4. Mean amplitudes for the different intervals of the 1st-RP, the NS' and the MP for young (left) and older (right) adults in the three response categories.

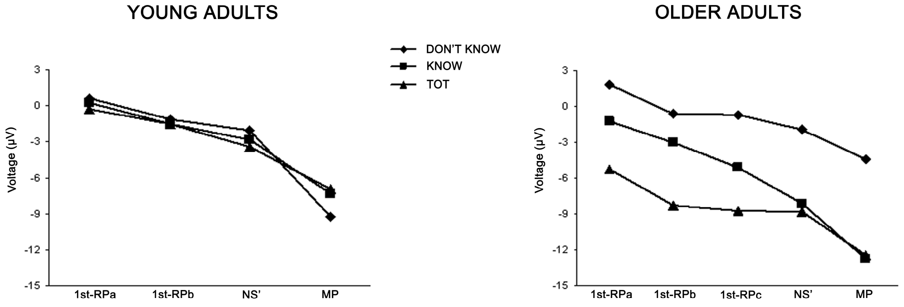

Figure 5. Mixed plots of the grand-averaged stimulus-locked ERP waveforms at the Pz electrode site (thin line) and response-locked ERP waveforms at the Cz electrode site (thick line) for older adults, in the DON'T KNOW (upper row), KNOW (middle row) and the TOT (lower row) categories (S: stimulus presentation; R: response; LNW: late negative wave).