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Older adults exhibit a more pronounced modulation of beta oscillations when performing sustained and dynamic handgrips

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ABSTRACT

Muscle contractions are associated with a decrease in beta oscillatory activity, known as movement-related beta desynchronization (MRBD). Older adults exhibit a MRBD of greater amplitude compared to their younger counterparts, even though their beta power remains higher both at rest and during muscle contractions. Further, a modulation in MRBD has been observed during sustained and dynamic pinch contractions, whereby beta activity during periods of steady contraction following a dynamic contraction is elevated. However, how the modulation of MRBD is affected by aging has remained an open question. In the present work, we investigated the effect of aging on the modulation of beta oscillations and their putative link with motor performance. We collected magnetoencephalography (MEG) data from younger and older adults during a resting-state period and motor handgrip paradigms, which included sustained and dynamic contractions, to quantify spontaneous and motor-related beta oscillatory activity. Beta power at rest was found to be significantly increased in the motor cortex of older adults. During dynamic hand contractions, MRBD was more pronounced in older participants in frontal, premotor and motor brain regions. These brain areas also exhibited age-related decreases in cortical thickness; however, the magnitude of MRBD and cortical thickness were not found to be associated after controlling for age. During sustained hand contractions, MRBD exhibited a decrease in magnitude compared to dynamic contraction periods in both groups and did not show age-related differences. This suggests that the amplitude change in MRBD between dynamic and sustained contractions is larger in older compared to younger adults. We further probed for a relationship between beta oscillations and motor behaviour and found that greater MRBD in primary motor cortices was related to degraded motor performance beyond age, but our results suggested that age-related differences in beta oscillations were not predictive of motor performance.

1. Introduction

Aging is a multifaceted process, which involves alterations in brain structure and biochemistry. It is associated with reduced grey matter volume, cortical thinning, decreases of white matter myelination and neurotransmitter depletion (Minati et al., 2007). Motor functions tend to decline in old age in a broad array of motor tasks, manifesting in decline of fine motor control and coordination, slowing of movements, and impairments related to gait and balance, which in turn affect quality of life (Maes et al., 2017; Rosso et al., 2013; Seidler et al., 2010). Most common motor tasks require the combination of different types of muscle contraction, in which switches from static to dynamic force production occur frequently. However, age-related effects in brain dynamics during complex contraction sequences remain largely unknown.

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Understanding how aging affects motor-related neural oscillations is fundamental to better understand the mechanisms of motor control in humans. A robust brain response induced by motor tasks is the modulation of beta sensorimotor rhythms. Beta oscillations are stronger during rest and are abolished during preparation and execution of motor tasks. This strong decrease in beta power relative to resting levels is known as movement-related beta desynchronization (MRBD) (Cheyne, 2013), and lasts as long as there is a muscle contraction (Erbil and Ungan, 2007; van Wijk et al., 2012). Several studies have reported age-related changes in beta oscillations during movement, such as a greater MRBD in both motor and premotor areas during right-hand finger extensions (Sailer et al., 2000), sequences of finger movements (Heinrichs-Graham et al., 2018; Heinrichs-Graham and Wilson, 2016), cued button presses (Bardouille et al., 2019), bimanual button presses in a go/no-go task (Schmiedt-Fehr et al., 2016), unimanual hand grips (Rossiter et al., 2014), as well as during a right-hand precision grip force modulation task (Hübner et al., 2018a). Interestingly, despite displaying increased MRBD, older adults exhibit higher absolute beta power during muscle contractions compared to younger adults (Heinrichs-Graham and Wilson, 2016). This is mostly due to the fact that older adults exhibit higher resting-state beta activity compared to their younger counterparts (Gómez et al., 2013; Heinrichs-Graham et al., 2018; Heinrichs-Graham and Wilson, 2016; Hübner et al., 2018a; Koyama et al., 1997; Veldhuizen et al., 1993). Pharmacological manipulations of GABA have shown that increased levels of intracortical GABAergic inhibition lead to higher resting beta power and accentuated MRBD during dynamic contractions (Hall et al., 2011, 2010; Jensen et al., 2005; Muthukumaraswamy et al., 2013). These observations are closely related to the ones observed in aging, which seems to indicate that age-related changes are associated with changes in GABAergic inhibition. Following a motor task, beta oscillations exhibit increased amplitude relative to resting levels, known as post-movement beta rebound (PMBR). PMBR overshoots around 1–2 s after the cessation of a motor task and is stronger over the hemisphere contralateral to the moving limb (Fry et al., 2016; Jurkiewicz et al., 2006). Reduced PMBR has been observed in older adults (Bardouille et al., 2019; Liu et al., 2017). This suggests that altered brain structures and biochemistry due to aging have consequences on the observed motor-related neural activation patterns.

Steady muscle contractions are maintained by a continuous drive from the motor cortex to spinal motoneurons (Scott, 2012), during which there is a relative increase in beta power compared to dynamic contractions (Baker, 2007; Cassim et al., 2000; Espenhahn et al., 2017; Kilner et al., 2003, 1999; Schoffelen et al., 2008; Spinks et al., 2008; van Wijk et al., 2012). The functional role of this elevation in beta synchrony remains unclear; however, previous studies have suggested that it reflects the integration of afferent information to promote a stable motor output (Androulidakis et al., 2007, 2006; Gilbertson et al., 2005; Omlor et al., 2007). A study from Rossiter and colleagues (Rossiter et al., 2014) examined unimanual sustained handgrips in healthy aging, and found an increased beta suppression with age in the ipsilateral but not in the contralateral primary motor cortex (M1). This may suggest a heterogeneous effect of the aging process in different brain regions. However, the modulation of beta activity during sustained muscle contractions has not yet been formally examined in the context of healthy aging.

The aim of the present study was to examine the modulation of beta oscillations during sustained and dynamic contractions in healthy aging. We used a motor paradigm that included periods of steady handgrips and force modulation, both uni- and bimanual. Exploiting the high spatio-temporal resolution of MEG (Baillet, 2017), we investigated whole-brain age-related changes in spectral dynamics beyond the M1s. We also probed the association between age-induced differences in beta oscillations and motor performance. Based on previous results, we expected greater resting beta power in older adults in motor areas (Heinrichs-Graham and Wilson, 2016; Rossiter et al., 2014) and hypothesized that age-related increases in resting beta activity would be present beyond the motor cortex since aging is associated with structural alterations in multiple brain regions. We further anticipated that older adults would exhibit increased MRBD during dynamic contractions (Heinrichs-Graham and Wilson, 2016; Hübner et al., 2018a; Sailer et al., 2000; Schmiedt-Fehr et al., 2016). In turn, this would indicate that greater beta desynchronization is required to produce muscle contractions, compensating for elevated resting-state beta power levels in the older population. Finally, we sought to investigate whether the increase in beta synchrony during sustained handgrips would exhibit age-specific differences.

2. Materials and methods

2.1. Participants

We studied 12 younger (age range 19–28 years) and 12 older (age range 60–74 years) healthy individuals recruited via advertisements. All participants were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971). Subject characteristics are detailed in Table 1. Recruitment criteria included young subjects between 18 and 30 years and older adults above 60 years, and excluded subjects with a personal history of neurological and psychiatric disorder, as well as MEG exclusion criteria related to presence of ferromagnetic material (e.g. dental braces, metal implants and/or crowns). The study was approved by the McGill University Ethical Advisory Committee. All participants signed a written informed consent and were compensated for their participation. Measurements were carried out using the MEG facility at the McConnell Brain Imaging Centre (BIC) of the Montreal Neurological Institute (MNI), McGill University.

At the beginning of the session, participants completed the following behavioral assessment tests: Nine Hole Peg Test (9HPT) (Mathiowetz et al., 1985b), Box and Blocks Test (BBT) (Mathiowetz et al., 1985a), Purdue Pegboard Test (PPT) (Lindstrom-Hazel and VanderVlies Veenstra, 2015), and Hand Grip Strength (HGS) (Bohannon et al., 2006). All tests were performed using both hands to cover a range of upper limb motor abilities, from manual dexterity to strength. The 9HPT was measured in seconds, reflecting how quickly each participant placed and removed nine pegs into the holes of a board. The BBT was quantified as the number of blocks moved from one compartment of a box to another of equal size within 60 s. The HGS was measured in kilograms. The PPT was quantified as the number of pins placed into holes of a board within 30 s (dominant, non-dominant and both hands) or the number of assembled pins, collars and washers within 60 s (assembly test with both hands). Of note, PPT was not collected for two older subjects. All participants were screened for mental status by means of the mini mental state examination (MMSE) (Folstein et al., 1975). Wilcoxon rank-sum tests were used to determine whether behavioral assessments were significantly different between younger and older adults.

Table 1
Subject characteristics and behavioral scores: mean ± SD.

		YOUNGER (n = 12)	OLDER (n = 12)	*p* value
Age		24.2 ± 2.8	67.7 ± 3.7	
SEX		4 F/8 M	3 F/9 M	
Education		16.7 ± 1.9	15.3 ± 2.8	> 0.1
mmse		29.2 ± 1.0	28.7 ± 1.3	> 0.1
9HPT (sec)	RH	17.2 ± 1.8	20.5 ± 2.1	<0.0005
	LH	19.4 ± 2.4	22.7 ± 3.4	<0.01
BBT (blocks)	RH	68.3 ± 5.6	57.7 ± 3.9	<0.001
	LH	67.1 ± 6.1	57.4 ± 4.6	<0.001
HGS (kg)	RH	48.4 ± 14.6	39.4 ± 9.0	> 0.1
	LH	39.2 ± 9.9	35.3 ± 7.7	> 0.1
PPT (pins)	RH	16.9 ± 1.8	13.3 ± 1.6	<0.001
	LH	15.0 ± 1.5	12.7 ± 1.8	<0.01
	RH-LH	12.8 ± 2.0	10.1 ± 1.1	<0.005
	A	42.8 ± 5.1	28.2 ± 5.7	<0.0001

F = female, M = male, MMSE = mini mental state examination, 9HPT = nine hole peg test, BBT = box and blocks test, HGS = hand grip strength, PPT = purdue pegboard test, RH = right hand, LH = left hand, RH-LH = right hand and left hand, A = assembly.

2.2. Experimental paradigm

The protocol carried out inside the MEG scanner consisted of two motor tasks alternated by three 5-min resting-state periods (Fig. 1a). During the resting-state periods, subjects were instructed to stare at a white cross displayed on a screen in front of them. They were also instructed not to think of anything in particular and not to manipulate the hand grippers. After the 1st rest period, the maximum voluntary contraction (MVC) was obtained for each participant, using the same hand grippers later employed for the motor tasks. The first motor task consisted of a unimanual isometric right handgrip, during which the subjects had to apply force to track a ramp target as accurately as possible. At the onset of the trial, an orange circle appeared on the screen and the subjects had 2 s to increase their force to reach a white target block at 15% of their MVC. This force was held for 3 s. Subsequently, participants tracked a linear increase of the force to reach 30% of their MVC over a 3-s period, during which they had to maintain the circle inside the white target block, followed by a 3-s hold at this force (Fig. 1b). A single trial lasted 11 s and was repeated 50 times for a total task duration of about 13 min. The second motor task consisted of bimanual steady isometric handgrips. At the onset of the trial, two circles (blue and red) appeared on the screen and the subjects had 2 s to increase the force produced by both hands to 15% of their MVC. This force was sustained for 6 s (Fig. 1c). A single trial lasted 8 s and was repeated 50 times for a total task duration of about 10 min. Visual feedback was provided throughout the experiment. For both tasks, the inter-trial interval was jittered between 3 and 5 s, during which subjects stared at a white cross. All subjects practised both motor tasks prior to the MEG acquisition to familiarise themselves with the experiment. Note that the order of the unimanual and bimanual conditions was not counter-balanced.

2.3. Data acquisition and pre-processing

2.3.1. Hand grippers: grip force fiber optic response pad

A pair of non-magnetic, non-electronic hand grippers made from plastic to prevent noise in the MEG environment were used (Current Designs Inc, USA). The hand grippers consisted of a machined black enclosure with a protruding force bar that moved in when gripped to produce a linear force measurement output based on the pressure applied. We used a spring with a range of 500 N. The dimensions of the force grip were 17.8 × 3.2 cm, with a force bar of 12.7 × 1.3 cm placed 2.5 cm outside the main enclosure. The maximum travel of this bar was 0.127 cm. The grippers were connected to a 932 interface through a 3-m long fiber pigtailed connector, which received the optical signals from the hand grippers in the MEG suite, and converted them into electrical signals that were transferred to a computer.

2.3.2. Neuroimaging data acquisition and pre-processing

MEG recordings were acquired with a 275-channel CTF whole-head system. Participants changed into non-magnetic clothes and performed the experiment in a seated position while their arms rested on the armchairs. Bipolar electrocardiogram (ECG) and vertical bipolar electrooculogram (EOG) were acquired to correct for cardiac artifacts and eye movements. All signals were amplified and digitized at a sampling rate of

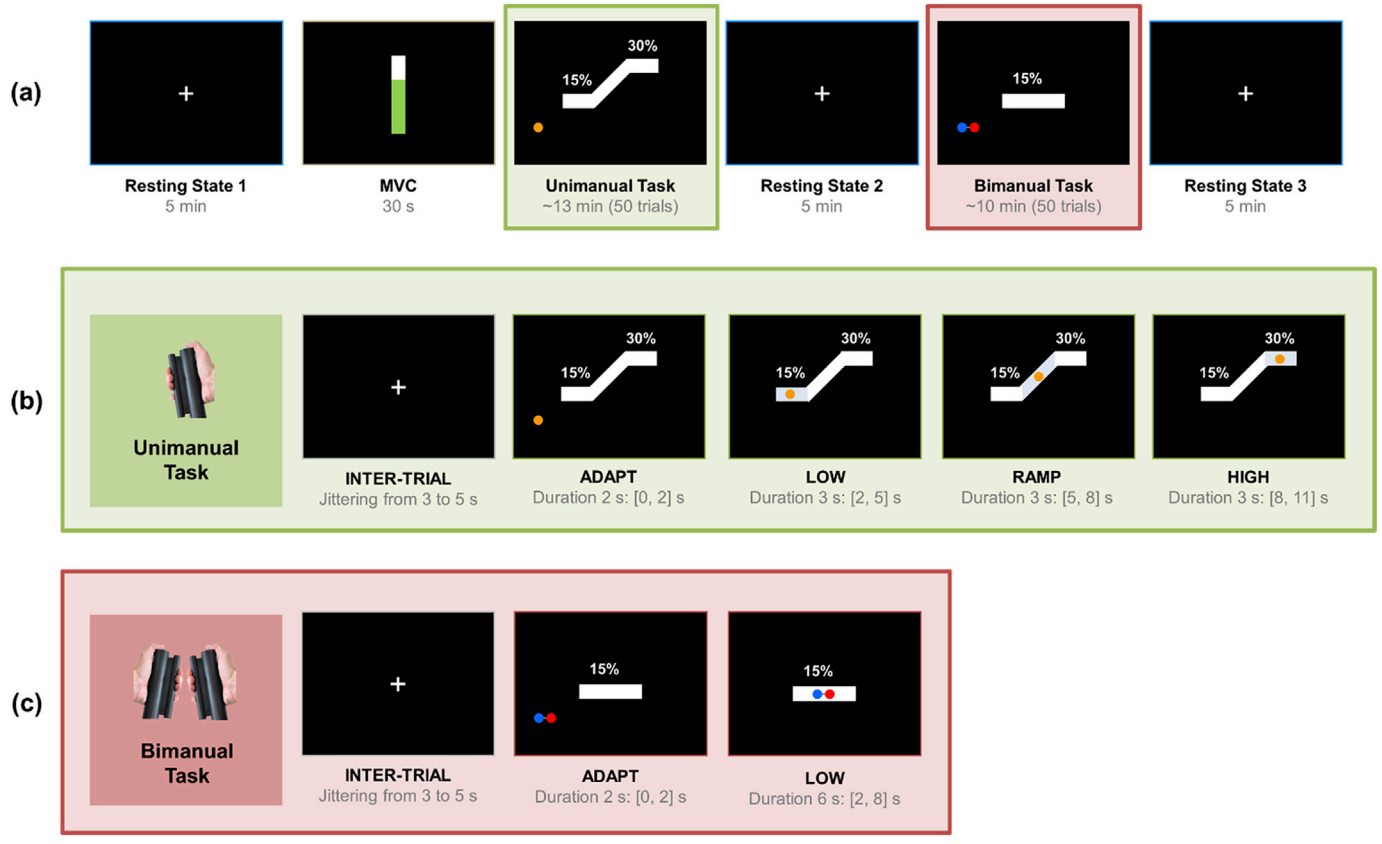

Fig. 1. (a) Illustration of the protocol. Participants carried out two motor tasks inside the MEG scanner, alternated by three periods of rest, during which subjects fixated on a crosshair for 5 min. After the first rest period, the maximum voluntary contraction (MVC) was obtained for each participant. (b) Unimanual task. Participants fixated on a crosshair for a few seconds, for a jittered period lasting between 3 and 5 s. This was followed by the appearance of an orange circle on the screen, where participants had 2 s to apply force to reach 15% of their MVC. A steady grip was then maintained for 3 s, which was followed by a guided ramp period where participants had to apply force to reach 30% of their MVC and sustain this grip strength for another 3 s. (c) Bimanual task. Participants fixated on a crosshair for a jittered period lasting between 3 and 5 s. Subsequently, two circles (blue and red) appeared on the screen. Participants had 2 s to apply force to reach 15% of their MVC, which they sustained for 6 s.

2400 Hz, and MEG files were saved after performing third order gradient correction. An empty-room noise recording was collected prior to the acquisition of each session to capture environmental noise conditions and was used in subsequent offline data analyses. The 3-D digitization of the head shape was done with a Polhemus Fastrak device, using around 100 head points distributed uniformly. Individual T1-weighted MRI images were acquired on a 3T MRI scanner (Siemens Prisma; TR = 2300 m s; TE = 2.32 m s; field of view = 240 mm; voxel size = 0.9 × 0.9 × 0.9 mm). The position of the head localization coils (nasion, left and right pre-auricular) and the head-surface points were used as anatomical references for coregistration between the MEG and MRI coordinate systems.

Offline data were processed using the open-source toolbox Brainstorm (Tadel et al., 2011). Notch filters were applied to remove power line artifacts around 60 Hz and harmonics. MEG data were band-passed from 1 to 150 Hz. Cardiac and eye movement artifacts were detected using the ECG and EOG signals and corrected using signal-space projection (SSP). Artifacts due to external magnetic fields were removed visually using independent component analysis (ICA). Segments that presented motion artifacts or where subjects moved more than 5 mm between head position measurements were discarded from the analysis. MEG signals were down-sampled to a 120-Hz sampling rate.

Resting-state periods. The 5-min recordings were segmented in epochs of 5 s. Epochs that had previously been found to be contaminated by motion artifacts were discarded. The average number of epochs after artifact rejection was $58.6 \pm 1.2/57.6 \pm 4.6$ for younger/older adults (Resting-state 1), $58.3 \pm 2.4/56 \pm 5.4$ for younger/older adults (Resting-state 2), and $56.3 \pm 9.3/57.4 \pm 2.2$ for younger/older adults (Resting-state 3). The difference in the number of epochs between groups was not significant across any of the resting-state periods, as assessed using the Wilcoxon rank-sum test (Resting-state 1: $p = 0.473$; Resting-state 2: $p = 0.185$; Resting-state 3: $p = 0.679$).

Motor tasks. Data from the unimanual task were epoched from −2.5 to +14 s, and data from the bimanual task were epoched from −2.5 to +11 s. Time 0 indicates onset of the visual cue for analysis. The average number of trials after artifact rejection was 40.4 ± 10.4/40.3 ± 9.1 for younger/older adults (Unimanual task), and 44.3 ± 8.4/41.1 ± 8.8 for younger/older adults (Bimanual task). The difference in the number of trials between groups was not significant for any of the tasks, as assessed using the Wilcoxon rank-sum test (Unimanual task: $p = 0.954$; Bimanual task: $p = 0.277$).

2.4. Data analysis

2.4.1. Behavioral analysis

The force exerted by the subjects was recorded using the calibrated hand grippers. The x and y screen positions of the applied force were also recorded for offline analysis. Task accuracy was quantified as the root mean squared error between the position on the screen and the target profile (defined as the middle of the target ramp), averaged over time and trials. Trials that exceeded 3 standard deviations were considered outliers and therefore not used in the computation of task accuracy. This was the case for two trials of a younger subject, which were also manually rejected in the MEG data.

2.4.2. MRI structural analysis

Cortical reconstruction and volumetric segmentation were performed with the FreeSurfer image analysis suite version 5.3.0 (http://surfer.nmr.mgh.harvard.edu/). The technical details of these procedures are described in prior publications (Dale et al., 1999; Dale and Sereno, 1993; Fischl et al., 1999a,b; Fischl et al., 2004, 2002; 2001; Fischl and Dale, 2000; Han et al., 2006; Jovicich et al., 2006; Reuter et al., 2012, 2010; Ségonne et al., 2004). Procedures for the measurement of cortical thickness have been validated against histological analysis (Rosas et al., 2002) and manual measurements (Kuperberg et al., 2003; Salat et al., 2004). Thickness measurements were mapped on the inflated surface of each participant's reconstructed brain and projected to the ICBM152 template using Brainstorm (Tadel et al., 2011). Maps were subsequently smoothed using a circularly symmetric Gaussian kernel across the surface with a full-width-half-maximum (FWHM) of 5 mm. Finally, cortical maps were compared between groups using non-parametric permutation tests combined with independent Student's *t*-tests of unequal variance. The null distribution was estimated with 10,000 permutations and results corrected for multiple comparisons using the false discovery rate (FDR) (number of signals 15,000). The structural analysis was done to identify the brain areas that presented differences in cortical thickness between groups. Particularly, we wanted to assess whether age-related differences in cortical thickness could have accounted for the differences observed in MRBD, reported in a previous study within the primary motor cortex (Provencher et al., 2016).

2.4.3. MEG source imaging

Lead fields were obtained using an overlapping spheres head model, which computes locally-fitted spheres under each sensor (Huang et al., 1999). Source reconstruction was performed using an extension of the linearly constrained minimum variance (LCMV) beamformer (Van Veen et al., 1997). A set of 15,000 elementary current dipoles distributed over the cortical surface was used, whereby the dipoles were assumed to be perpendicular to the cortical envelope. The empty room recording of a 2-min duration was used to estimate the noise covariance matrix. The data covariance matrix was estimated directly from the MEG recordings. The LCVM regularization parameter applied to the data covariance matrix was set as its median eigenvalue.

Resting-state periods. Normalized source power was computed using Morlet wavelets averaged across the 5 s segments (time resolution = 3 s, central frequency = 1 Hz) over the entire brain volume for the following frequency bands: alpha (8–12 Hz) and beta (16–28 Hz). The resulting source maps were smoothed with a 5 mm FWHM circularly symmetric Gaussian kernel and projected onto a standard space (ICBM152 template). Grand-averaged surfaces were computed across subjects for each group and frequency band.

Motor tasks. Single trial source waveforms were extracted per subject and decomposed to the time-frequency (TF) domain using Morlet wavelets (time resolution = 3 s, central frequency = 1 Hz). The evoked response was removed from each trial before computing the TF decomposition, a step that has been recommended for the evaluation of the TF decomposition of neurophysiological signals (Tadel et al., 2011). An average whole-brain TF map across trials was computed and subsequently averaged within the following frequency bands related to sensorimotor rhythms: alpha (8–12 Hz) and beta (16–28 Hz). We selected the 16–28 Hz frequency range to avoid including any power from the contiguous alpha and gamma bands. For both bands, relative power (*RP*%) was calculated as follows: $\boldsymbol{RP}\% = \frac{\mathbf{P}(t) - \mathbf{B}}{\mathbf{B}} \times 100\%$ (Pfurtscheller and Lopes da Silva, 1999), where $P(t)$ is the absolute power at time t and B is the baseline power. B was defined as the mean power obtained from the 1st resting-state period (see section *2.4.7.* for the effects of using different baselines). The *RP*% related to the beta band is denoted as MRBD and PMBR during and after a muscle contraction, respectively. Subsequently, the *RP*% was averaged across several time windows for each subject. For the unimanual task, *RP*% was averaged within three 3-sec time windows: sustained contraction at 15% MVC (2–5 s), guided dynamic contraction from 15% MVC to 30% MVC (5–8 s), and sustained contraction at 30% MVC (8–11 s). For the bimanual task, the behavioral analysis showed that task accuracy did not reach the desired thresholds until around 4–5s after the onset of the trial, which suggests that subjects were not performing a sustained contraction in the first few seconds of the trial (Supp. Fig. 1). Hence, *RP*% for the bimanual task was averaged within two 3-sec time windows: unguided dynamic contraction (2–5 s), and sustained contraction at 15% MVC (5–8 s). Cortical surfaces were obtained per participant, smoothed with a 5 mm FWHM circularly symmetric Gaussian kernel, and projected onto a standard space (ICBM152

template). Grand-averaged surfaces of each task time window were computed across subjects for each group and frequency band.

Statistics. For both rest and task, permutation testing was used to test for group differences across the whole brain. The test statistic used was the independent Student's *t*-test of unequal variance. For each comparison, 10,000 permutations were computed to build the null distribution. Significance testing was performed with a threshold of 5% using FDR correction for multiple comparisons (number of signals 15,000).

2.4.4. Modulation of beta oscillations

We were interested in examining whether the MRBD modulation observed during sustained and dynamic contractions in young subjects was altered in older subjects. To this end, regions of interest (ROIs) were selected for subsequent analysis. The peak MRBD ROIs were identified as the vertices showing the strongest MRBD (top 5%) within the motor cortex. Since dynamic contractions elicit increased MRBD compared to sustained contractions, the windows containing dynamic contractions (Unimanual: 5–8 s; Bimanual: 2–5 s) were grand-averaged across all subjects and used to define the ROIs related to MRBD. Supp. Fig. 2 displays the peak MRBD ROIs, located within left and right M1, and Supp. Table 1 provides the coordinates of the peak vertex of each MRBD ROI in MNI space. ROI power time-courses were then extracted and averaged across vertices. An ROI was also created from the whole-brain analysis that combined the brain regions identified to exhibit stronger MRBD in older adults for both unimanual and bimanual tasks, henceforth called "*ageMRBD*". The three ROIs are depicted in the first row of Fig. 5.

The following *Modulation metrics* were used to quantify the depth of variations to which subjects modulated their beta power:

$$\textbf{\textit{Modulation Unimanual}} = abs\left(\beta_{[2,5]} - \beta_{[5,8]}\right) + abs\left(\beta_{[5,8]} - \beta_{[8,11]}\right)$$

$$\textbf{\textit{Modulation Bimanual}} = abs\left(\beta_{[2,5]} - \beta_{[5,8]}\right)$$

where $\beta_{[t_1,t_2]}$ is the averaged beta activity between time-points t_1 and t_2. The beta activity used to compute $\beta_{[t1,t2]}$ was the absolute beta power instead of MRBD and was extracted for all three ROIs (left peak MRBD, right peak MRBD, *ageMRBD*). In this fashion, we can quantify a relative measure of how much beta oscillations were modulated without confounds related to the resting beta power.

Statistics. The *Modulation metrics* were used to test for age-related differences. The data was transformed using the Box-Cox transformation (Box and Cox, 1964) to ensure that the assumption of normality was not violated. We conducted two separate mixed-model ANOVA's for each task, in which "brain region" (left peak MRBD, right peak MRBD, *ageMRBD*) was the within-subjects factor, and "age" (younger, older) was the between-subjects factor. The dependent variable was the modulation metric. A Greenhouse–Geisser correction was applied whenever Mauchly's test indicated a lack of sphericity. *Post hoc* Bonferroni-adjusted *t*-tests were performed whenever a main effect was detected, with an α-level of 0.05.

2.4.5. PMBR analysis

We were interested in examining whether PMBR exhibited differences between tasks, hemispheres and/or groups. PMBR is a brain response measure strictly localized in the motor cortex after a motor task, thus we did not perform a whole-brain analysis but focused on ROIs in the motor cortex. Windows starting 1.5 s after each trial and lasting 1 s (Unimanual: 12.5–13.5 s; Bimanual: 9.5–10.5 s), were grand-averaged across all subjects and used to define the peak ROIs related to PMBR (top 5%). PMBR was localized more anterior than MRBD in both hemispheres (Supp. Fig. 2), consistent with previous studies (Fry et al., 2016; Jurkiewicz et al., 2006; Salmelin et al., 1995; Stancák and Pfurtscheller, 1995). Supp. Table 1 provides the coordinates of the peak vertex of each PMBR ROI in MNI space. ROI power time-courses were then extracted and averaged across vertices.

Statistics. PMBR ROI time-courses were averaged within the previously defined 1-sec window for each task. These averaged PMBR values were used to test for power differences. The data was transformed using the Box-Cox transformation (Box and Cox, 1964) to ensure that the assumption of normality was not violated. Note that the data had to be translated prior to applying the transformation since the Box-Cox transformation cannot handle negative values. We conducted two separate mixed-model ANOVA's for each task, in which hemisphere (left, right) was the within-subjects factor, and age (younger, older) was the between-subjects factor. The dependent variable was the averaged PMBR. *Post hoc* Bonferroni-adjusted *t*-tests were performed whenever a main effect was detected, with an α-level of 0.05.

2.4.6. Association between beta oscillations and motor performance

To examine the relationship between beta oscillations and motor performance, we carried out separate linear regression analyses, using task accuracy and behavioral scores as the dependent variable respectively. Linear regression was applied separately for each task (unimanual and bimanual); hence in total 4 regressions were performed. The explanatory variables included in all regressions were:

1) Age
2) ***ageMRBD* ROI:** Modulation metric, averaged MRBD (Unimanual: 5–8 s, Bimanual: 2–5 s), averaged resting-state beta power.
3) **Peak MRBD ROIs (top 5%):** Modulation metric, averaged MRBD (Unimanual: 5–8 s, Bimanual: 2–5 s), averaged resting-state beta power.
4) **Peak PMBR ROIs (top 5%):** Averaged PMBR (Unimanual: 12.5–13.5 s, Bimanual: 9.5–10.5 s).

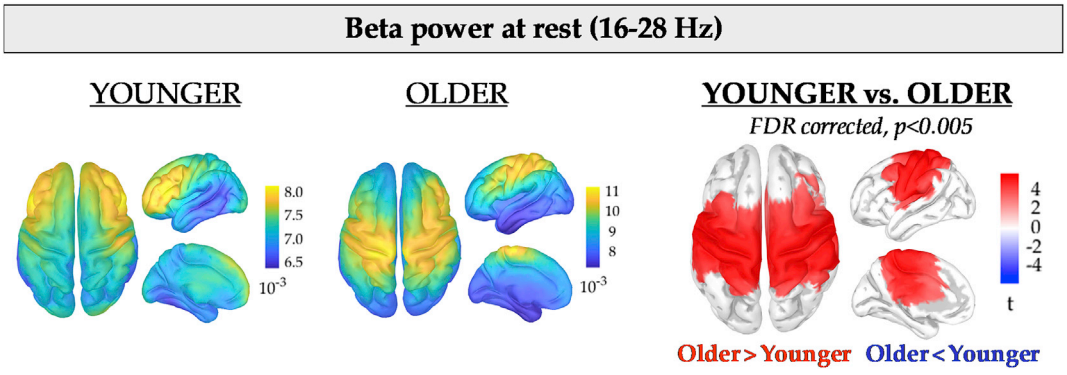

Fig. 2. Beta power during the 1st resting-state. Left and middle panels: grand-averaged images across younger and older participants, respectively. Right panel: differences in oscillatory power at rest between groups (FDR-corrected, $p < 0.005$). Older adults exhibited greater spontaneous beta power compared to younger adults.

Neural features were extracted from both hemispheres separately. Thus, in total 12 and 8 features were used for the unimanual and bimanual tasks respectively. Principal component analysis (PCA) was used to summarize the behavioral scores that involved unimanual (9HPT, BBT, PPT (Right hand)) and bimanual movements (PPT (Both hands and assembly)). The first PC was used as the dependent variable in the regression. To investigate whether any individual feature was significantly correlated to motor performance, we first divided the observations into two sets: training (90%) and testing (10%). We then permuted the labels, performed linear regression in the training set, used the linear model to predict the motor performance in the testing set, and calculated the root-mean-squared-error (RMSE) for the testing set. We carried this out 5,000 times to build the null distribution of the testing RMSE. During the second stage of analysis, we repeated the same procedure using the correct labels, and thus obtained the observed testing RMSE. This cross-validation analysis was done for each of the 4 regressions.

2.4.7. Effect of baseline on relative power calculation

An important step when examining motor-related oscillatory activity is to express it as a percentage of power change relative to baseline levels. This baseline period is usually defined between 0.5 and 3 s prior to task onset. However, the duration of the PMBR depends on the motor task characteristics and can last several seconds (Fry et al., 2016), which may result in contamination of the baseline if the inter-trial period is not long enough. Careful selection of the baseline is thus a crucial step. Further, it has been shown that older adults exhibit higher absolute beta power during muscle contractions compared to their younger counterparts, despite a larger decrease in beta power relative to baseline (Heinrichs-Graham et al., 2018; Heinrichs-Graham and Wilson, 2016). Therefore, it has been suggested that, to obtain a more holistic understanding of the age-related power changes during a motor task, both absolute and baseline-corrected power should be examined (Hübner et al., 2018a). To this end, we examined three scenarios: 1) Absolute beta power, 2) *RP*% with respect to an inter-trial baseline period (−1 to 0 s), 3) *RP*% with respect to the 1st resting-state period. The latter is the method used for all the subsequent analyses presented in this study.

3. Results

3.1. Behavioral analysis

Behavioral scores are summarized in Table 1. Finger dexterity measured with 9HPT/PPT and unilateral gross manual dexterity measured with BBT were significantly worse in the older group for both hands. Bimanual finger dexterity coordination measured with PPT was also significantly inferior in older adults.

Regarding the motor tasks carried out inside the MEG scanner, all participants successfully completed both tasks. Differences in task accuracy during the tasks were not significant between age groups (Unimanual task: $t_{22} = -0.32$, $p = 0.752$; Bimanual task: $t_{22} = 1.54$, $p = 0.138$).

3.2. MRI structural analysis

No brain volume differences were found between groups ($p = 0.16$) (Supp. Fig. 3a). Cortical thickness was decreased in the older group mainly in frontal and temporal areas (FDR-corrected, $p < 0.01$), as shown in Supp. Fig. 3b.

3.3. Resting-state oscillatory power

Spontaneous beta power was higher in frontal and parietal areas, particularly in older adults (Fig. 2, left and middle panels), and showed a significant age effect. Older adults exhibited higher beta power compared to their younger counterparts (Fig. 2, right panel). This effect of age on beta power was more pronounced in motor areas, and extended to frontal, parietal and temporal brain areas.

These age-related differences in spontaneous beta power were present in all three resting-state recordings. Spontaneous alpha power was greater in visual areas, in both younger and older adults (Supp. Fig. 4). However, no significant age effects were detected in the alpha band.

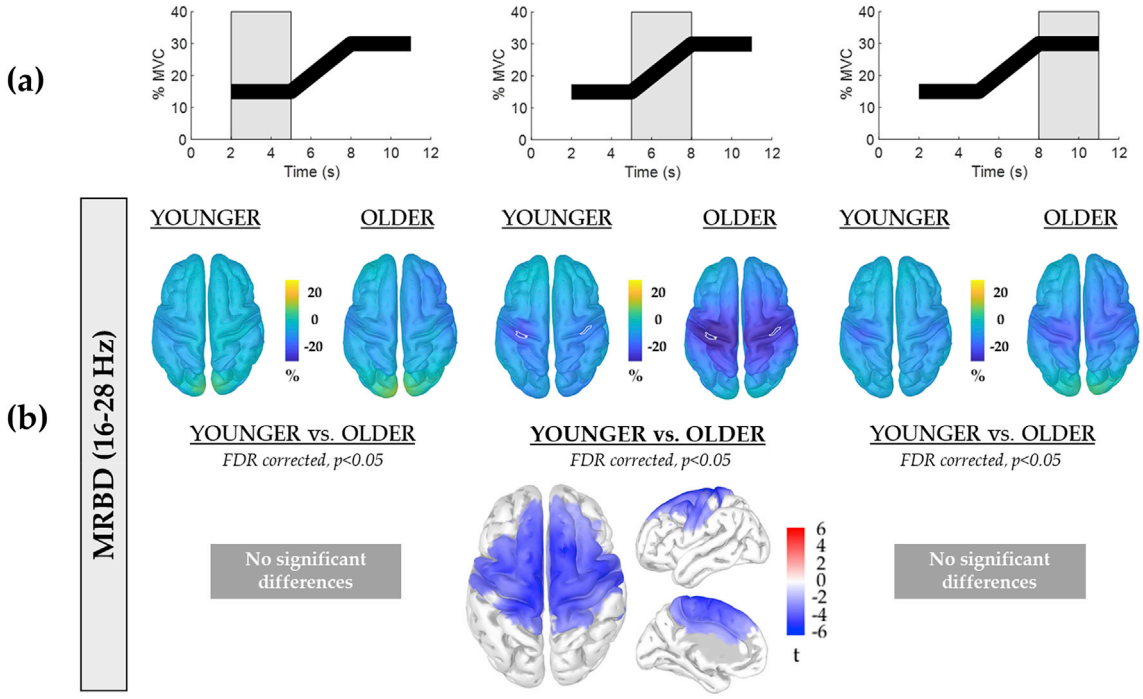

Fig. 3. Unimanual task: (a) Illustration of the different stages of the task. Grey shaded areas indicate the period displayed in the images on the same column. **(b)** Upper panel: grand-averaged images of MRBD across each group. MRBD ROIs are delineated in white. Lower panel: differences in MRBD between groups (FDR-corrected, $p < 0.05$).

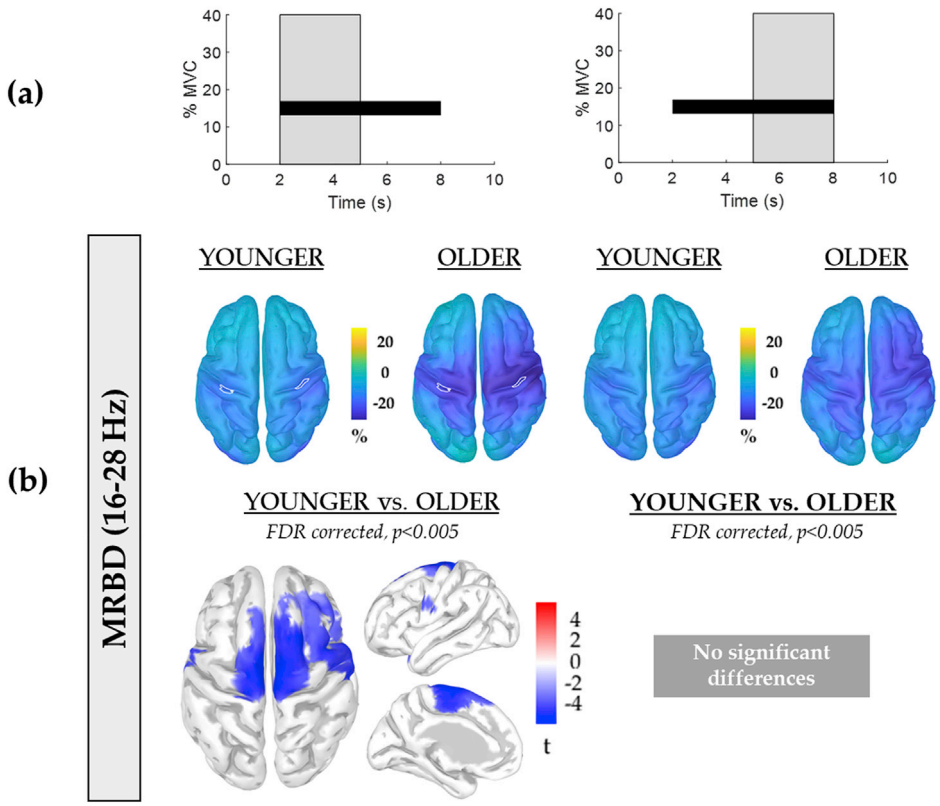

Fig. 4. Bimanual task: (a) Illustration of the two 3-s subperiods of the task (grey shaded areas). (b) Upper panel: grand-averaged images of MRBD across each group. MRBD ROIs are delineated in white. Lower panel: differences in MRBD between groups (FDR-corrected, $p < 0.05$).

3.4. Whole-brain MRBD analysis

Unimanual task. Grand-averaged surfaces displaying MRBD are shown in Fig. 3b (upper panel). We found significant differences in MRBD magnitude underlying dynamic force production between the two age groups (Fig. 3b, bottom panel): older adults exhibited increased (i.e. more negative) MRBD during the guided dynamic contraction (5–8 s). No significant differences between groups were found during sustained contractions.

Bimanual task. Grand-averaged surfaces showing MRBD are shown in Fig. 4b (upper panel). Similarly to the unimanual task, we found significant differences in MRBD magnitude between the two age groups only at the beginning of the trial (2–5s) (Fig. 4b, bottom panel), during which older adults exhibited greater (i.e. more negative) MRBD. This specific time interval corresponds to the period when subjects had not yet accomplished a sustained grip and were thus still performing a dynamic contraction (Supp. Fig. 1). The peak location of MRBD (denoted in white in Fig. 4b, top row) did not exhibit significant age-related differences.

Results in the alpha frequency band for the unimanual and bimanual tasks are shown in Supp. Figs. 5 and 6, respectively. Alpha desynchronization did not exhibit significant differences between groups.

During the guided dynamic contraction period, older adults exhibited a significantly greater and more widespread MRBD compared to younger adults. During sustained contraction periods, no significant differences in MRBD were found between groups.

During the first 3-sec period, older adults exhibited a significantly stronger and more widespread MRBD compared to younger adults. During the second 3-sec period, during which subjects achieved the bimanual sustained contraction, no significant differences were found between groups.

3.5. Modulation of beta oscillations

To investigate more precisely the modulation of beta oscillations between different brain regions in younger and older adults, we extracted a power modulation metric from all ROIs (depicted in the first row of Fig. 5) for both task paradigms.

Unimanual task. The unimanual task induced modulations in beta power in several brain regions (Fig. 5). The modulations can be observed both in the relative (with respect to resting-state power) and absolute power subfigures. Results of the mixed ANOVA (Table 2) revealed a significant main effect of "Age", which suggests an overall difference in the amplitude of beta power modulation between groups. *Post-hoc* testing revealed a significantly larger modulation in older compared to younger adults ($t_{70} = -3.43$, $p = 0.001$). We also observed a significant main effect of "Brain Region", which suggests that there was an overall difference in beta power modulation between brain regions. *Post-hoc* testing of the "Brain Region" effect showed a significantly greater modulation in the left and right ROIs (peak MRBD, located at the primary motor cortices) compared to the *ageMRBD* ROI (left peak MRBD vs. *ageMRBD*: $t_{23} = -2.79$, $p = 0.010$; left peak MRBD vs. *ageMRBD*: $t_{23} = -3.68$, $p = 0.001$), but no significant difference between left and right ROIs ($t_{23} = -0.02$, $p = 0.983$). Finally, there was no significant interaction between the factors. The statistical analysis quantified through ANOVA can be evaluated qualitatively in Fig. 5.

Bimanual task. The bimanual task induced weaker modulations in MRBD compared to unimanual muscle contractions (Fig. 5). Nonetheless, the mixed ANOVA (Table 2) revealed the same significant main effects as in the unimanual task. A significant main effect of "Age" was observed, and *post-hoc* testing again showed significantly greater modulation in older adults ($t_{70} = -3.56$, $p < 0.001$). We also detected a significant main

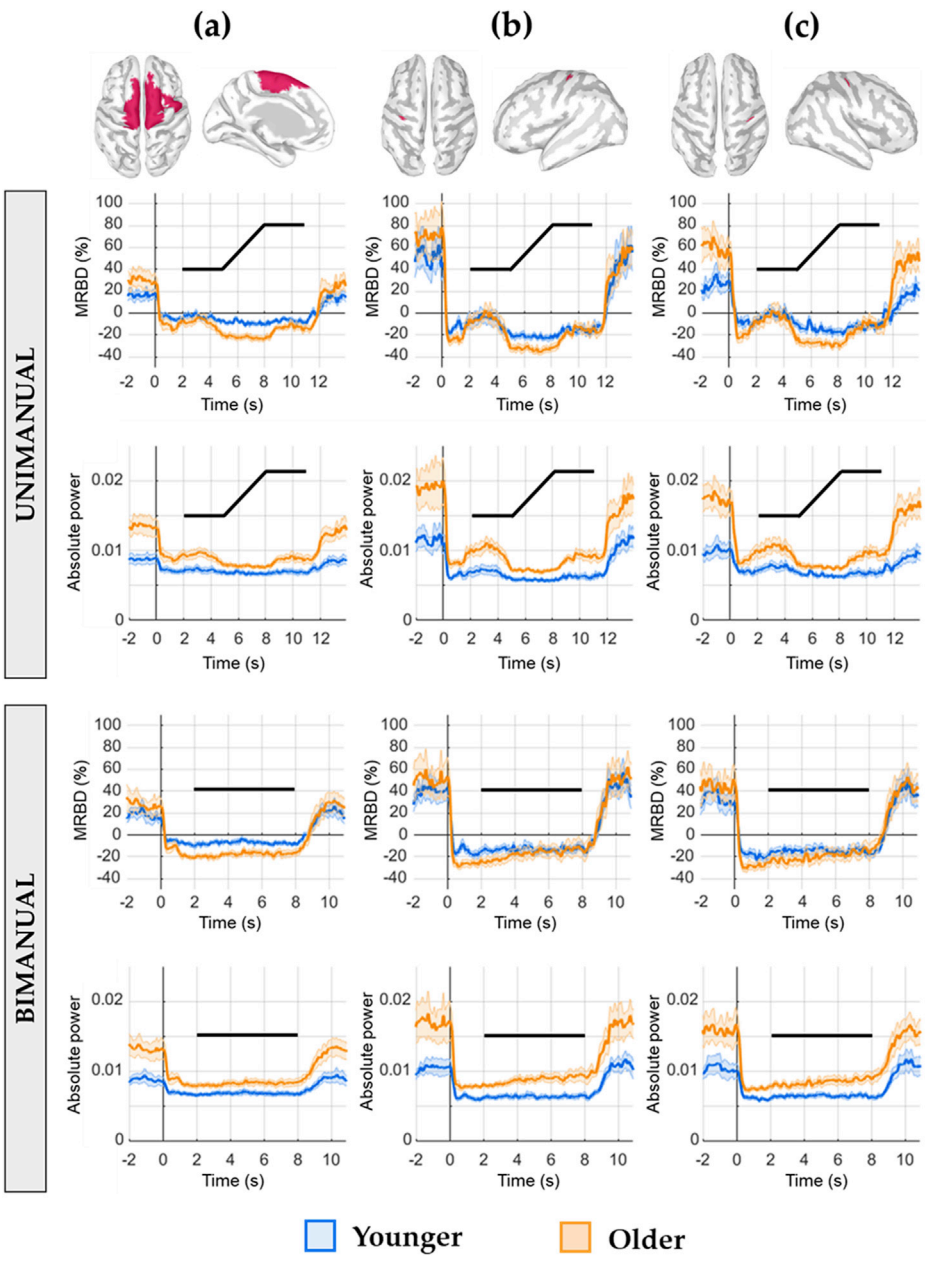

Fig. 5. Unimanual and Bimanual tasks: Temporal evolution of the MRBD (upper row) and absolute beta power response (lower row) in **(a)** *ageMRBD* ROI, i.e. brain regions identified to exhibit stronger MRBD in older adults, **(b)** peak MRBD ROI (left M1) and **(c)** peak MRBD ROI (right M1). Older adults exhibited higher absolute beta power throughout the entire movement execution for both tasks. During the unimanual task, we observed a greater (more negative) MRBD during the guided dynamic contraction compared to sustained contraction periods (15%MVC and 30%MVC) for both groups. During the bimanual task, older adults exhibited greater (more negative) MRBD at the beginning of the trial compared to their younger counterparts.

effect of "Brain region", and *post-hoc* testing revealed, as before, a significantly larger modulation in the left and right ROIs (peak MRBD, located at the primary motor cortices) compared to the *ageMRBD* ROI (left peak MRBD vs. *ageMRBD*: $t_{23} = -2.65$, $p = 0.014$; left peak MRBD vs. *ageMRBD*: $t_{23} = -2.69$, $p = 0.013$), but no significant difference between left and right ROIs ($t_{23} = 1.52$, $p = 0.142$). Finally, there was no significant interaction between the factors. The statistical analysis quantified through ANOVA is illustrated qualitatively in Fig. 5.

3.6. PMBR analysis

We examined possible differences in PMBR between younger and older adults for both tasks. The ROIs used are depicted in Supp. Fig. 2.

Unimanual task. We found no significant main effect of hemisphere or age; however, there was a significant age-by-hemisphere interaction (Table 3). This interaction indicates that the effect of hemisphere on PMBR was different in younger compared to older adults. To investigate this interaction, 4 *post-hoc* tests were conducted using paired and independent *t*-tests as appropriate, and a Bonferroni correction was applied (significance at $0.05/4 = 0.0125$). Paired *t*-tests between hemispheres did not reveal any significant difference (Younger: $t_{11} = 2.47$, $p = 0.031$, Older: $t_{11} = -1.35$, $p = 0.204$). Independent *t*-tests yielded a marginally significant greater PMBR in the right hemisphere (ipsilateral) for the older group compared to the younger group ($t_{22} = -2.66$, $p = 0.014$), whereas no significant difference was found in the left hemisphere (contralateral) ($t_{22} = -0.28$, $p = 0.780$).

Bimanual task. We did not find a main effect of hemisphere, age, or any age-by-hemisphere interaction (Table 3).

3.7. Associations between beta oscillations and motor performance

We carried out four linear regression analyses between beta oscillations and motor performance scores. The cross-validation analysis is shown in Supp. Fig. 7. The prediction of task accuracy during the unimanual task was not significantly different compared to using permuted labels, hence no further analysis was done. For the other three

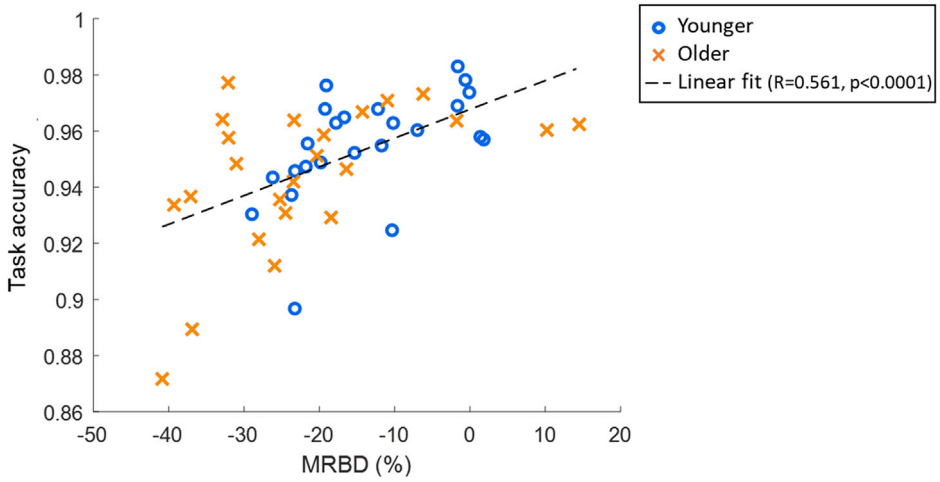

Fig. 6. Relationship between MRBD at the peak location (primary motor cortex) and task accuracy for the bimanual task. Subjects that exhibited greater (i.e. more negative) MRBD performed worse in the task.

Table 2
Results of the mixed-model ANOVAs for the modulation of beta oscillations – unimanual and bimanual tasks.

			F-statistics		
	SS	*df*	*MS*	*F*	*p* value
UNIMANUAL					
Age	8.80	1	8.80	6.94	**0.015**
Residuals	27.9	22	1.27		
Brain region	3.82	2	1.91	31.51	**< 0.001**
Age:Brain region	0.05	2	0.02	0.38	0.685
Residuals	2.67	44	0.06		
BIMANUAL					
Age	1.65	1	1.65	5.12	**0.034**
Residuals	7.08	22	0.32		
Brain region	0.59	2	0.30	6.22	**0.005**
Age:Brain region	0.03	2	0.02	0.31	0.714
Residuals	2.10	44	0.05		

Table 3
Results of the mixed-model ANOVAs for PMBR – unimanual and bimanual tasks.

			F-statistics		
	SS	*df*	*MS*	*F*	*p* value
UNIMANUAL					
Age	31.5	1	31.5	1.87	0.185
Residuals	370	22	16.8		
Hemisphere	4.77	1	4.77	2.12	0.159
Age:Hemisphere	17.8	1	17.8	7.91	**0.010**
Residuals	49.4	22	2.25		
BIMANUAL					
Age	<0.01	1	<0.01	<0.01	0.993
Residuals	2488	22	113		
Hemisphere	7.09	1	7.09	0.97	0.336
Age:Hemisphere	6.50	1	6.50	0.89	0.356
Residuals	161	22	7.32		

cases, the prediction of the dependent variables was significantly better when using the correct labels ($p < 0.05$), hence further analysis was done. For the model predicting task accuracy during the bimanual task, beta desynchronization at the peak locations of MRBD (i.e. left/right M1) was the only identified significant feature. A reduced regression model using only this feature was implemented. Fig. 6 displays the correlation between MRBD and task accuracy, which suggests that subjects with stronger (i.e. more negative) MRBD exhibited worse task performance. For the models predicting behavioral scores, a reduced model revealed no significant features beyond age.

3.8. Effect of baseline on relative power calculation

We extracted averaged time-courses from the left and right MRBD ROIs corresponding to absolute beta power, beta *RP*% calculated with respect to an inter-trial baseline, and beta *RP*% calculated with respect to the 1st resting-state. We found that absolute beta power levels were always greater for older participants before and during the motor tasks (Supp. Fig. 8a–b) compared to their younger counterparts. When inter-trial beta power levels were selected as baseline, we observed that older adults exhibited greater MRBD compared to younger adults across the entire trial (Supp. Fig. 8c–d). In contrast, when resting beta power levels were selected as baseline, older adults exhibited greater MRBD compared to younger adults only during dynamic contractions (Supp. Fig. 8e–f).

4. Discussion

We examined the influence of healthy aging on motor-related beta oscillations using two motor paradigms: unimanual and bimanual handgrips. Extending previous studies that have focused on M1s, we investigated whether whole-brain age-related differences are present during both sustained and dynamic contractions. Consistent with prior literature, we found greater beta power at rest, as well as increased (i.e. more negative) MRBD in older adults compared to their younger counterparts. Interestingly, although older adults exhibited increased MRBD compared to younger adults during periods of dynamic contraction, the same was not observed during periods of sustained force production. As a result, we showed that older adults exhibit a more pronounced modulation of beta oscillations during dynamic muscle contractions. Furthermore, we found a significant correlation between MRBD during dynamic contractions and behaviour. Below we discuss the implications of this work in the context of understanding the functionality of beta oscillations in motor control.

4.1. Behavioral analysis

We did not observe differences in terms of task accuracy between groups during the motor tasks performed inside the MEG scanner. This was expected, since the force applied by each subject was the same predefined percentage of their MVC, which implies that task-level difficulty was comparable among participants and that differences observed in this study in terms of brain activity patterns are attributable to age rather

than other factors, such as increased effort (Aine et al., 2006).

On the other hand, older adults exhibited deteriorated fine motor control in the corresponding behavioral assessments (Table 1), which is in line with the expected motor decline in older adults (Desrosiers et al., 1995; Grice et al., 2003; Lindstrom-Hazel and VanderVlies Veenstra, 2015; Mathiowetz et al., 1985a). Handgrip strength was not significantly different between groups due to high variability between individuals.

4.2. Structural analysis

Older adults were characterized by a significant decrease in cortical thickness, particularly in frontal and temporal brain areas (Supp. Fig. 3). The affected regions are in notable agreement with previous studies that included larger sample sizes (Fjell et al., 2009; Hogstrom et al., 2013; Salat et al., 2004). These brain regions were overall in correspondence with areas that exhibited age-related increases in MRBD (Figs. 3 and 4); however, the magnitude of MRBD and cortical thickness were not found to be significantly correlated ($R = -0.14$, $p = 0.35$), which suggests that the observed age-related functional differences may not be directly associated with this specific neurodegenerative process.

4.3. Age-related changes in power at rest

We found that older adults exhibited increased resting beta power compared to younger adults (Fig. 2). We did not find significant differences in resting alpha power between groups. Our results agree with several prior studies regarding age-related differences in power at rest, where it was reported that older adults exhibited similar levels of alpha power (Duffy et al., 1984; Heinrichs-Graham and Wilson, 2016; Koyama et al., 1997; Veldhuizen et al., 1993) and increased beta power (Gómez et al., 2013; Heinrichs-Graham et al., 2018; Heinrichs-Graham and Wilson, 2016; Hübner et al., 2018a; Koyama et al., 1997; Veldhuizen et al., 1993). However, previous studies only evaluated specific brain areas and/or performed the analysis in sensor space. Our whole-brain analysis demonstrated that the motor cortex was the area that showed the most significant differences in spontaneous beta power between younger and older subjects. This aligns with the evidence that beta-band activity is pathologically increased in movement disorders such as Parkinson's disease (Brown et al., 2001; Silberstein et al., 2005), which suggests that increased beta oscillations at rest may be related with a deterioration of flexible behavioral and cognitive control (Engel and Fries, 2010). However, when we probed whether spontaneous beta power was a good predictor of motor performance, we did not find any relationship that linked increased spontaneous beta power with poorer motor performance.

4.4. Whole-brain age-related MRBD changes during muscle contractions

The majority of past studies that examined aging effects on motor control have used motor paradigms whereby the subjects performed a dynamic contraction, and they consistently reported age-related increases in MRBD – i.e. more negative desynchronization (Bardouille et al., 2019; Heinrichs-Graham et al., 2018; Heinrichs-Graham and Wilson, 2016; Hübner et al., 2018a; Rossiter et al., 2014). In line with these studies, during periods of dynamic contraction we found a significant increase in MRBD in older adults compared to younger adults. Our whole-brain analysis further revealed a more widespread MRBD in older adults, in contrast with younger adults, for which the desynchronization was mainly located in the M1s (Figs. 3b–4b, upper panel). Specifically, our results suggest a significant age-related increase in MRBD that covered frontal and premotor brain regions (Figs. 3b–4b, lower panel). Moreover, we observed that during periods of steady contractions, no differences were found between groups across the entire brain (Figs. 3b–4b, lower panel). Thus, our results align with the study from Rossiter and colleagues that reported no differences in MRBD in M1 contralateral to the moving hand during steady contractions (Rossiter et al., 2014), however our observations seem to indicate that the ipsilateral primary motor cortex does not show differences in MRBD either, in contrast with the study from Rossiter and colleagues (Rossiter et al., 2014).

4.5. Age-related changes in beta power modulation during muscle contractions

Both younger and older adults exhibited the expected modulation of beta oscillations that emerges when sequentially performing sustained and dynamic contractions (Baker, 2007; Cassim et al., 2000; Kilner et al., 1999, 2003; Schoffelen et al., 2008; Spinks et al., 2008; van Wijk et al., 2012). This implies that the motor performance decline observed in healthy aging is not due to an impairment in the capacity to modulate beta oscillations. In fact, we observed a larger modulation in older compared to younger adults (Table 2). The increase in synchronized beta oscillations that emerges when producing a steady muscle contraction has been suggested to provide an efficient processing platform for promoting the maintenance of a steady motor output whilst compromising initiation of new movements (Androulidakis et al., 2007; Engel and Fries, 2010; Gilbertson et al., 2005; Omlor et al., 2007; Pogosyan et al., 2009). Further, it has been recently suggested that absolute beta power needs to reach a certain threshold level in order to initiate a muscle contraction, regardless of age (Heinrichs-Graham and Wilson, 2016). Beta oscillations at rest are greater in older adults; this suggests that an increased desynchronization is needed for the required threshold to initiate a muscle contraction to be reached. If we only consider the results we obtained during dynamic contractions, our findings align well with this theory, since older adults exhibited increased cortical beta suppression with respect to resting beta levels compared to younger adults. Yet, considering that we baseline-corrected the motor-related beta power using the spontaneous power observed at rest, our results also show that during sustained contractions there were no differences between groups beyond the ones observed at rest. Our findings may suggest that the threshold in terms of absolute beta power for the maintenance of a sustained contraction is shifted in aging, whereas the threshold for executing a dynamic contraction remains the same.

4.6. Relationship between MRBD and motor performance

Two main theories have aimed to explain over-recruitment in aging: *compensation* and *dedifferentiation* (Reuter-Lorenz and Park, 2010). The basic idea of *compensation* is that brain reorganization in older adults is a compensatory mechanism to counterbalance impaired function. Alternatively, the *dedifferentiation* hypothesis argues that older adults inefficiently recruit additional brain areas because of less precise brain structure-function interactions. Hence, this over-activation is not seen as a compensation mechanism to achieve better performance, rather as a less selective activation pattern. Several studies have provided evidence of a positive correlation between over-recruitment and performance during a motor task (Mattay et al., 2002; Heuninckx et al., 2008). Other studies have reported that greater brain activity during a cognitive task was correlated to poorer performance (Logan et al., 2002; Stebbins et al., 2002). In another study it was reported that there was no correlation between brain activity and increased difficulty during a motor task (Riecker et al., 2006). These discrepancies suggest that the association between increased activity in a specific brain region and performance in older adults may be task-specific or dependent on the task demands and the behavioral measure used. Therefore, in an attempt to unravel whether the age-related overactivation of frontal/premotor/motor areas during dynamic contractions and the increased modulation of beta oscillatory power between sustained and dynamic contractions in aging represent a *compensation* or *dedifferentiation* mechanism, we examined its association with motor performance.

Features related to the brain regions that showed significantly increased MRBD in aging (*ageMRBD*) did not reveal any association with

behavioral measures. This suggests that they were recruited in a non-selective fashion. Taken together with the fact that these brain regions exhibited decreased cortical thickness in the older participants, the overactivation of these regions in older adults might be indicative of a loss of functional specificity, and therefore supporting the *dedifferentiation* hypothesis. Recent observations that increased prefrontal cortex activity in healthy aging does not contribute to maintain cognitive function (Morcom and Henson, 2018) would align with these results. Further, the modulation metric that quantified the depth of variations of beta oscillatory power did not show a relation with behaviour in any of the considered regions.

We identified one electrophysiological measure (beta desynchronization at the peak MRBD ROIs) that associated beta oscillations and motor performance, but only during bimanual muscle contractions inside the MEG scanner. An explanation could be that the implemented unimanual task was not sensitive enough for the explanatory values to significantly predict performance. Participants with stronger (i.e. more negative) MRBD at the peak location (M1) exhibited worse task performance. However, these regions did not show significant age-related increases in MRBD (Fig. 4b), thus we cannot interpret this association as a *compensation* or *dedifferentiation* mechanism. This finding is supported by observations that after acute exercise, better performance is coupled with decreased (i.e. less negative) MRBD (Dal Maso et al., 2018; Hübner et al., 2018b). We speculate that, since increased MRBD at the peak location is correlated with greater resting-state beta power (Heinrichs-Graham and Wilson, 2016), the need to attenuate resting beta power to reach the beta threshold for proper motor execution may cause inferior task performance. However, further research is needed to understand the underlying mechanisms that link beta oscillatory activity and behaviour.

4.7. Age-related changes in PMBR

Recent studies reported that older adults exhibited reduced PMBR in the contralateral hemisphere to the moving hand during a finger tapping task compared to younger adults (Bardouille et al., 2019; Liu et al., 2017). On the other hand, our results suggest that older adults did not exhibit significant differences in PMBR in the contralateral (left) hemisphere to the moving hand during the unimanual task, but rather an increased PMBR in the ipsilateral (right) hemisphere (Fig. 5, Table 3). Furthermore, during the bimanual task, no significant differences in PMBR were found between groups. It has been proposed that PMBR reflects active inhibition of the motor network (Solis-Escalante et al., 2012) and it has been specifically linked to the inhibitory neurotransmitter γ-aminobutyric acid (GABA) (Gaetz et al., 2011; Jensen et al., 2005). This suggests that PMBR plays a role in preventing the generation of unwanted movements. While speculative, our results may reflect a case of *dedifferentiation*, whereby inhibition of both cortices after a motor task occurs in older adults, in contrast with younger adults for which PMBR occurs only in the contralateral hemisphere to the executing hand. However, the precise mechanism underlying how PMBR is affected by aging remains to be fully elucidated.

4.8. Effects of baseline on relative power calculation

In agreement with previous studies, absolute beta power levels were consistently higher in older participants before and during the motor tasks (Supp. Fig. 8a–b) (Heinrichs-Graham et al., 2018; Heinrichs-Graham and Wilson, 2016; Hübner et al., 2018a). When inter-trial beta power levels were used as baseline, older adults exhibited greater MRBD compared to younger adults across the entire trial (Supp. Fig. 8c–d). In contrast, when resting beta power levels were used as baseline, older adults exhibited greater MRBD compared to younger adults only during dynamic contraction. The reason for this discrepancy is that beta power levels during the inter-trial period were significantly higher in both groups compared to resting levels (Supp. Fig. 8e–f), an indication that inter-trial power levels were contaminated by PMBR. This is due to the fact that the rebound effect can last several seconds after the end of a motor task, and has been associated with force output, such that higher force output results in greater PMBR (Fry et al., 2016). Nevertheless, the inter-trial interval has been traditionally selected as baseline in motor studies focused on MRBD and PMBR. Our results highlight the importance of investigating whether the inter-trial power levels are artificially high due to PMBR contamination by comparing with resting power levels, as also suggested in recent studies (Heinrichs-Graham et al., 2018; Heinrichs-Graham and Wilson, 2016). In cases where the inter-trial is short, resulting in PMBR contamination, the usage of a resting-state recording for baseline normalization is strongly recommended.

4.9. Limitations

It has been suggested that resting beta levels and MRBD are modulated by the circadian rhythm (Toth et al., 2007; Wilson et al., 2014). In the present experiment, participants were scanned between 10 a.m. and 6 p.m. (Morning session: 8 younger/6 older; Afternoon session: 4 younger/6 older). Albeit somewhat balanced between groups, we cannot exclude circadian/ultradian effects on the results due to differences in the scanning time.

The inter-trial duration is a crucial parameter to consider when designing protocols to study motor-related beta oscillations. As we exemplify in Supp. Fig. 8, PMBR levels may contaminate the inter-trial baseline, leading to possibly biased results. In this paper, we used the resting-state beta power levels as baseline to take into account this issue. Still, we cannot exclude the possibility that the MRBD was contaminated by the elevated PMBR, since the inter-trial duration was not long enough for the PMBR to fully return to its baseline levels. Nevertheless, the PMBR is mostly localized within the M1s, whereas we observed most of the age-related differences in premotor and pre-frontal areas. This suggests that the obtained results are not biased by excessive contamination by the elevated PMBR levels.

The force applied during the experiment was based on each subject's own MVC, from 0 to 30% MVC (unimanual) and from 0 to 15% MVC (bimanual), to ensure that the required effort, and consequently the resulting fatigue level, was the same across participants. To investigate whether fatigue modulated the observed age-related differences in MRBD, we repeated our analysis using the initial and final 25 trials corresponding to each task. We subsequently tested for whole-brain differences in MRBD between younger and older adults for trials in the first and second trial set. For the unimanual task, the analysis revealed age-related differences only during the ramp block and generally in the same brain regions as the results using all trials (Supp. Fig. 9). These findings suggest that, for the unimanual task, physical fatigue was either non-existent or its effect did not differ between age groups. Specifically, if fatigue did occur, these results suggest that for the resulting fatigue levels, the corresponding cortical adaptions did not differ between age groups. Nevertheless, age-related fatigue modulations were out of the scope of this paper, as we did not expect participants to experience fatigue to a large extent based on the low MVC levels used in our paradigms. However, in future studies the use of the Borg scale to monitor fatigue perception could be a good way to quantify fatigue levels (Borg, 1982). For the bimanual task, age-related differences were obtained during the initial 3s segment of the trial, but only when using the last 25 trials (Supp. Fig. 10). However, it is not likely that this observation is related to physical fatigue, since the bimanual task required considerably less force (15%MVC) compared to the unimanual task (30%MVC), and its duration was shorter (6 s/trial) than the unimanual task (9 s/trial). Therefore, the observation seen in Supp. Fig. 10 is more likely related to low statistical power resulting from splitting the trials in half. However, because the motor tasks were not counterbalanced, we cannot discard the possibility that physical and/or mental fatigue may have had an effect on the results obtained for the bimanual task.

5. Conclusions

Older adults exhibited significantly higher beta oscillations at rest, and our results showed that the motor cortex is the brain area that exhibits the highest increase in resting beta oscillatory activity. The present study confirms that older adults produce a larger MRBD during dynamic muscle contractions compared to younger adults. Our results also suggest that during sustained contractions, there are no differences in beta power between age groups beyond the ones observed at rest. We further probed the relationship between motor performance and age-related differences in beta oscillations during rest and task, but our results suggest that this altered beta activity in aging did not carry additional information.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuroimage.2019.116037.

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