

When is the brain ready for mental actions? Readiness potential for mental calculations

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While the preparatory neural mechanisms of real and imagined body movements have been extensively studied, the underpinnings of self-initiated, voluntary mental acts are largely unknown. Therefore, using electroencephalography (EEG), we studied the time course and patterns of changes in brain activity associated with purely mental processes which start on their own, without an external or interoceptive stimulation. We compared EEG recordings for decisions to perform mental operations on numbers, imagined finger movements, and actual finger movements. In all three cases, we found striking similarities in slow negative shifts of brain electrical activity lasting around 1 s and, therefore, characteristic for readiness potential. These results show that the brain not only needs time to be ready for a purely mental task but also that a required preparatory interval involves neural changes analogical to the ones observed before intentional body movements. As such, the readiness potential represents a universal process of unconscious preparatory brain activity preceding any, including purely mental, voluntary action.

Key words: volition, mental actions, readiness potential, mathematical ability, Libet's experiment

INTRODUCTION

Imagine that you are a skillful crossword puzzle solver and have just bought your favorite new brain teaser. You start reading the clues and stop by one which seems easy to answer. It does not mean that the correct word simply pops up in your mind. You must perform a sequence of operations: find candidates for a solution, examine them carefully and select the one which best fits the meaning expressed in the clue. After solving this task, you choose the next clue and engage in further mental efforts until all the blanks are filled in. Assuming that every process of selecting the clue and finding a solution was freely initiated and performed without any external support from friends, books, or electronic devices, one could say that it is a paradigmatic example of an important kind of a cognitive task. Its aim is not to find out what is happening

in the immediate surroundings but to set the mind in motion to produce a purely mental result. This finding can later be expressed verbally but then it is only an announcement of a previous solution. Such an announcement is completely different from, for example, an “intention to move” because the effect of the latter is a real or imagined movement (expressed either as covert or overt bodily change), not a purely mental result.

There are many examples of these kinds of mental exercises, including the classic ones, such as mathematical calculations performed without any external supports. Could such mental acts be studied from an outside, non-egocentric perspective? To address this question, we focused on the brain's electrical activity associated with the initiation of digit addition as a purely voluntary mental act.

The most commonly studied voluntary motor actions so far are typically preceded by specific brain activity

called readiness potential (RP). Although RP was identified in the 1960s (Kornhuber and Deecke, 1965; Deecke et al., 1969), nearly 20 years passed until Libet and collaborators (1983, 1985) demonstrated that it occurs before a conscious decision to move a body part. From then on (Lang, 2003; Shibasaki and Hallett, 2006), the concept of RP was used to refer solely to preparatory neural activity in the cerebral motor system. Indeed, philosophers and neuroscientists have typically associated this phenomenon exclusively with motor acts. Likewise, the issue of volitionality was previously studied only in the context of overt behavior (Brass et al., 2013). Yet, later studies suggest that contributions from motor-related processes may not be necessary for RP generation (Alexander et al., 2016), or may be associated mainly with action consequences or outcomes, not the movement itself (Jo et al., 2014; Wen et al., 2018). For example, when a response is prepared and then abandoned (as in a NoGo condition), it is still preceded by RP (Alexander et al., 2016). Interestingly, when a prepared response is always followed by the associated non-motoric effect, the generated RP can be even greater (Wen et al., 2018).

Capitalizing on these findings, we hypothesized that RP is in fact a more general neural mechanism of getting ready to act. Thus, a volitional action could be of a physical as well as mental kind. If this hypothesis holds, then RP should be registered even before a voluntary initiation of purely mental actions; skilled activities of the mind which are neither directly triggered by physical stimuli nor expressed in bodily changes. Although, so far, negative potentials have been reported before some kinds of mental actions (i.e., imagining of movements), these actions were always stimulus driven (Beisteiner et al., 1995; Cunnington et al., 1996; Jankelowitz and Colebatch, 2002). The only exception, wherein stimulus-driven responses were not involved, was the seminal study by Libet et al. (1983) in which, while observing a spot of light revolving on an oscilloscope screen (for a HTML5 open source version of the Libet's clock see Garaizar et al., 2016), participants voluntarily initiated finger movements, and only later reported the clock position of the revolving spot. (That is, participants reported when they decided to initiate their actions.) Yet, these were manual, not mental actions. Furthermore, we needed an experiment with a freely initiated mental activity, but still in the presence of a stimulus to be later used for a reliable determination of the beginning of such mental action.

To this end, we simplified the Libet clock to two time points (12 and 6 o'clock), as shown in Fig.1, and let participants decide at will on one of these two possible points for action initiation. Then we asked them to report after 2.56 seconds what point on the clock's face was actually selected for performance of the mental action, or control the imagined manual action. The

beginnings of responses in the third condition, real manual actions, were recorded by button presses. Such a procedure allows the measure of starting points for both mental and physical actions. Using electroencephalography (EEG), we then investigated whether RPs can be also observed prior to purely mental voluntary actions. Thus, in addition to preparation for actual finger movements – a kind of replication of a study by Kornhuber and Deecke (1965), or imagined index finger movements (cf. Jankelowitz and Colebatch, 2002), the key task was preparation for performance of a simple mental action (here: arithmetic calculation).

Measuring the time course of preparatory activity occurring before a mental (or any) task is not possible in functional magnetic resonance imaging (fMRI) studies (Soon et al., 2013). It merely enables a precise localization of their neural substrates. Specifically, one can only conclude that whereas the vague “when” of a mental act is correlated with the pre-supplementary motor area (pre-SMA) activity, the “what” (mental act) decision is linked to the medial prefrontal and parietal cortex activity. Similarly, when an EEG study on mental actions is focused on spatial attention (Bengson et al., 2014), the occipital alpha-band power (8–13 Hz) merely allows to predict the location of attentional focus, rather than its timing. All in all, despite earlier attempts to investigate the neural processes preceding mental actions, none of the previous studies have addressed the issue of their detailed temporal characteristics.

In this report, we have adopted a standard motor paradigm to examine the temporal patterns and direction of modulations in neural activity preceding purely mental actions, wherein participants perform the summation of components of three-digit numbers at a freely chosen time. As already indicated, the classic paradigm was modified to overcome the main challenge in such a task; identification of the exact moment when the mental activity starts. The purpose of our study was to investigate if any specific regularities in neural activity could be observed in EEG signals preceding the initiation of purely mental actions. If the answer is “yes”, the next question is whether these EEG readings resemble RPs registered for typical motor acts?

In all three action kinds studied here, we found slowly increasing negative charges in the electrophysiological signals before the beginning of a particular task. These findings show that RPs occur prior to voluntary action execution regardless of its physical or mental nature. Such outcomes clearly demonstrate that previous reports have not recognized one of the most critical features of RPs. From a more general viewpoint, counter to common expectations that the brain needs time to set the body in motion, as opposed to setting the mind which can be done in an instant (almost immediately),

we discovered that preparations for both physical and mental acts take a similar time. We interpret this striking result as an indication of a deeper regularity in neural processing: the action – be it physical or mental – has to be preceded by brain activity of similar duration.

METHODS

Participants

Nineteen volunteers (10 women) aged 21 to 27 (mean=23.4, SD=1.31) took part in this study. None had history of psychiatric or neurological illnesses. All participants declared right handedness. Yet, because the dependent measure (i.e., readiness potential) is hardly influenced by handedness (Brunia et al., 1985), there was no need to verify hand preference by any objective measure. As our paradigm involved dots with changing colors, participants were tested with Ishihara Color Test (plates 3, 6, 12, 16, 18) to confirm that they were able to properly recognize the four colors used. Written informed consents were obtained from all participants prior to the study.

Study location and ethical approval

Our experiment was conducted in Action and Cognition Laboratory in the Institute of Psycholo-

gy at Adam Mickiewicz University in Poznan. The research project was approved by the local Ethics Committee for Research Involving Human Subjects, which reviewed the adopted ethical standards for participants' recruitment, experimental protocols, and debriefing. As such, all procedures performed in our study were in accordance with the 1964 Helsinki declaration and its later amendments or comparable ethical standards.

Experimental tasks

All participants performed three blocks of tasks: mental additions of components of three digit numbers, imagined movements of the right index finger (as if a keyboard button was pressed), and actual performances of the right index finger movements, namely real button presses. Each block of tasks was run in a random order assigned to study participants. In each condition, a simplified clock face with a spot rotating every 2.56 s was shown on a flat 19" (48.26-cm) CRT screen with a refresh rate of 75 Hz, and positioned at a distance of 70 cm from participants' eyes. The look of the clock was inspired by the one originally used by Libet (1983; 1985) and remained identical across conditions except for the colors of dots involved, and centrally presented three-digit numbers necessary for mental addition. The simplified clocks used in this study are shown in Fig. 1.

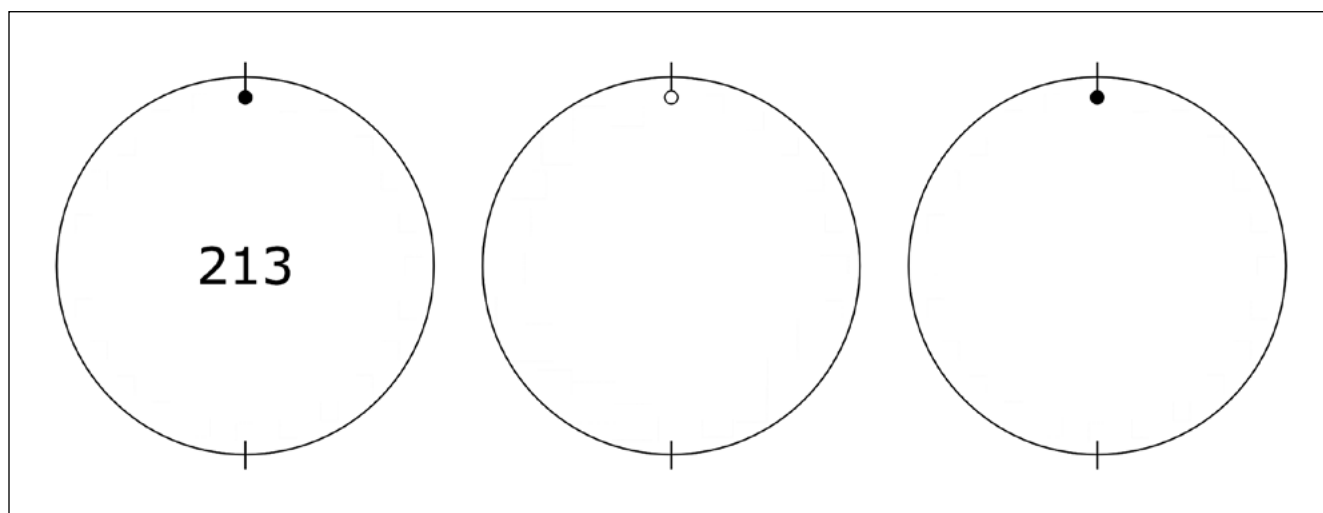


Fig. 1. The simplified Libet clocks. Left panel: the clock with the spot revolving as in Libet (1983) experiment, with additional three-digit numbers shown in the middle and changing every 1.28 s. Participants decided at will on one of the two possible points for action initiation, added the three numbers composing a given digit, and reported the outcome after 2.56 s, which also indicated what point on the clock's face was actually selected for performance of the mental action. Middle panel: the clock with revolving spots which changed colors every 1.28 s. Participants' task was to imagine index finger movements, again starting at will on one of the two possible points for action initiation. Right panel: the clock with the revolving black spot, whose top or bottom position was at will selected for real button presses. The three different clocks, associated with respective study conditions, were presented in separate blocks whose order was randomized for different participants.

Because the beginnings of mental actions, due to a lack of associated overt behavior, cannot be determined by objective measurements (with the problem becoming even more acute when actions must be performed voluntarily), the main challenge of this study was to overcome this limitation. To this end, we simplified the Libet clock leaving only two critical marks – vertical dashes – on the clock’s face. The first one was at the 12 and the other at the 6 o’clock position. Therefore, participants could freely choose the moment of action initiation, whether physical or mental, from this limited range of options. It is of note that, in contrast to other experiments involving non-overt actions (Beisteiner et al., 1995; Cunnington et al., 1996; Jankelowitz and Colebatch 2002), such restrictions did not deprive participants from their freedom of making choices, thus allowing them to retain some scope of volitionality. This way, the expected neural activity would not be stimulus driven, as in the case of contingent negative variation (Walter et al., 1964) or stimulus preceding negativity (Brunia, 1988), the two potentials similar in shape to RP but associated with stimulus anticipation (Brunia et al., 2012). Notably, in mental calculations a hypothetical time span between a direct intention to act and the onset of mental action might be so short that it could be negligible. Therefore, the exact moment a person consciously starts to perform mental action would be reflected in neural activity changes that differ from the ones observed in classic RP.

Mental actions in the current study, as indicated above, involved summation of three digits forming a number. The stimuli were presented in the center of the simplified Libet clock, and the digits changed randomly every 1.28 s, each time when the rotating spot crossed the top or bottom dash of the clock face. The actual moment when the three digits were to be added was voluntarily chosen, yet limited either to the 12 or 6 o’clock position. Participants were asked to report the obtained sum exactly after the spot ran a full circle (i.e., after 2.56 s). Specifically, the task required from our participants to add the three digits in three digit numbers (e.g., 123, 504, 341). For example, for the number 123 the answer would be $(1+2+3 =) 6$. The displayed numbers were selected in such a way that a sum of their digits ranged from 3 to 9, and none of the presented numbers included two zeros as its components.

Imagined right index finger movements were initiated when the color of the revolving spot changed randomly (into red, green, blue or yellow), yet again only when the spot reached either the top or bottom of the clock face. Specifically, in this condition, participants freely chose positions 12 or 6 (where the dots changed colors) as the starting point for imagined movements.

As before, they were also asked to report the moment when they imagined the movement exactly after the spot ran a full circle (i.e., after 2.56 s). Notably, participants were requested to imagine that they kinesthetically move their fingers (from the first person’s perspective), rather than to imagine a movement of a finger (i.e., a displacement of an alien finger, or the third person’s perspective), because a first-person/subjective motor imagery of moving something can have a different neural substrate than a visual imagery of an external moving object (cf. Guillot et al., 2009). In order to make kinesthetic imagery easier, their right hands were covered with a scarf.

The actual right index finger movements were also performed when the rotating spot reached either the top or bottom of the clock’s face. In short, participants were instructed to press the keyboard space bar at a freely chosen moment, yet only when the spot reached either the 12 or 6 o’clock.

Notably, participants were asked to avoid using any strategy in deciding the time of an action (e.g., to avoid starting their actions always when the spot reached 12 o’clock) and to act with no hurry. Strategic timing of a response would be completely different from spontaneous selection of one of the two possible time points for action, and as “stimulus driven” would not give rise to typical RP. Participants were acquainted with task rules twice: first with verbal instructions from an experimenter, and then in the form of written instructions. Additionally, to check the proper understanding of instructions, participants were requested to describe the tasks in their own words.

The research paradigm was implemented in SuperLab ver. 5 (Cedrus®, San Pedro, CA) and the study was carried out in a moderately lit room. The task blocks were performed until at least 80 trials from each participant were collected. The duration of a particular block ranged from 10 to 20 minutes.

Recording technique and pre-processing

EEG data were acquired using sampling rate of 2048 Hz with a 64-channel BioSemi system with active electrodes. The electrode placement was in accordance with the 10/20 system (Jasper, 1958). The impedance was kept below 5 k Ω for all electrodes. Electro-oculographic activity, which was recorded from two pairs of electrodes positioned around the eyes (horizontally near the outer corners of the left and right eye, as well as above and below the left eye), was used to filter out signal artifacts related to eye movements and blinking. Signal processing and the visualization of brain activity was carried out with Brain Vision Ana-

lyzer 2.0. The obtained EEG recordings were re-sampled to 150 Hz frequency, then filtered with low-frequency cut-off of 0.1 Hz, high-frequency cut-off of 30 Hz, and a notch filter of 50 Hz. In each condition the signal was subsequently divided into segments preceding task performance by 1,000 ms, with the baseline defined as the average activity from 300-ms intervals prior to the 1,000-ms segments. For additional analyses, longer periods of inactivity (i.e., time intervals within the blocks of tasks when participants decided not to undertake any actions) were also segmented into 1,000-ms intervals prior to the dot passing either 12 or 6 o'clock, with the baseline again defined as the average activity from the 300-ms window preceding such 1,000-ms segments.

Data analyses

In all participants whose data were included in the analyses, each individual trial was evaluated for correctness (adherence to instructions). As a result, in 14 participants an insignificant number of trials (~5%) with clear anticipations or delays (i.e., responses at least 300 ms prior to or after the rotating spot crossed the top or bottom dash of the clock face), with incorrectly named colors of the dots, or incorrect summations of the displayed digits, were excluded from analyses. All data obtained from five participants had to be excluded from analyses for the following reasons: errors during signal registration (one participant), and unintentional nonadherence or forgetting of instructions which led to incorrect task performance (four participants, despite their in-depth training). Notably, given the testing paradigm that was used here, the correctness of performance could be assessed – based on audio-video recordings – only after the completion of the experimental session.

As in previous studies dealing with RPs (Kornhuber and Deecke, 1965; Libet et al., 1983), the Cz electrode with the highest negative average signal in the 1,000-ms window prior to task performance was selected for the main analysis of the scalp-recorded slow negative shifts in brain electric potentials, including negativity slopes. Yet, to be more consistent with current approaches, analogical signals were also extracted from six most active electrodes in this vicinity – Cz, FCz, C1, FC1, C2, and FC2 – regardless of study condition (i.e., electrode selection was based on brain activity averaged across all three conditions, and was therefore orthogonal to any potential differences between conditions of interest, e.g., Driel et al., 2012). While these results are also depicted in the main text, because they are virtually identical their detailed descriptions can be found in supplemental materials.

Although the beginning of RP can be loosely defined at this stage as a steady increase in negative potential relative to baseline (or comparable intervals of inactivity), its statistical significance can be further ascertained (Guthrie and Buchwald, 1991). Given specific parameters of the time interval of interest, number of participants, and autocorrelation parameter, seven successively significant point-to-point differences revealed by t-tests (performed on the 150 data points acquired from resampling of the signal within each of the 1000-ms intervals) must be obtained to consider the signal change as significant. Between-tasks comparisons of RPs were also performed separately for each of the 150 time points to test whether or not the observed signal modulations were significantly different.

To make comparisons between and within conditions easier, mean signal amplitude changes within three time intervals (starting from -900 to 0 ms) were also calculated and subjected to a 3 (condition: mental action, imagined finger movement, the actual finger movement) by 3 (time interval: -900 to -600, -600 to -300, and -300 to 0 ms) by 2 (task: action, inactivity) repeated-measures analysis of variance (rmANOVA). Instead of an a priori 1,000-ms window prior to task performance, the 900-ms window, additionally divided into three equal time intervals, was selected because this is where real increases of activity were observed in our study. Interestingly, even Libet (1985, see also commentaries) argues that a short (300-ms) interval of cerebral activity is needed to invoke the “neuronal adequacy” for conscious experience.

The obtained effect sizes are provided here as the proportion of variance accounted for, using partial eta squared [$[\eta^2]$]. For completeness, the observed power (OP) is also reported.

To investigate if any lateralization of the RP signal, corrected for the average signal from a corresponding time window with no activity, can be observed on the electrodes in the vicinity of Cz, two groups of electrodes (right: FC2, FC4, FC6, C2, C4, C6, CP2, CP4, CP6, and left: FC1, FC3, FC5, C1, C3, C5, CP1, CP3, CP5), and ten 100-ms intervals were selected for further analyses. To calculate the contralateral-ipsilateral difference between potentials, the average signal from the right-sided electrodes was contrasted with the left-sided electrodes for each of the ten time intervals.

RESULTS

The overall signal changes observed for mental actions were similar to the ones observed for imagined finger movements. Furthermore, even though the movements were imagined or performed with the

dominant hand, the readiness potential signals registered on electrodes in the vicinity of Cz were barely lateralized to any of the hemispheres, except for some subtle effects observed in the very late phase of preparatory activity for imagined finger movements. These results are illustrated in Fig. 2. Specifically, back-averaging of EEG signals observed prior to performance of the three kinds of tasks showed clear-cut affinities between the temporal and directional modulations of neural activity. In all three conditions – i.e., mental addition (the main task), as well as imagined, and actual index finger movements (the two control tasks), wherein participants freely chose the moment the re-

quired action was initiated – we observed the greatest changes of signal amplitude in the 1,000-ms time window on the Cz electrode placed over the vertex of the head (Jasper, 1958).

As shown in Fig. 3, through most of the time courses the readiness potentials observed in the three conditions did not differ significantly between each other, except for a few time points. Specifically, pairwise comparisons for the 150 RP time points for the Cz electrode depicted in Fig. 3A revealed that the only interval wherein significant differences between conditions were observed was located between -833 ms and -773 ms (i.e., ten consecutive time points), but it was

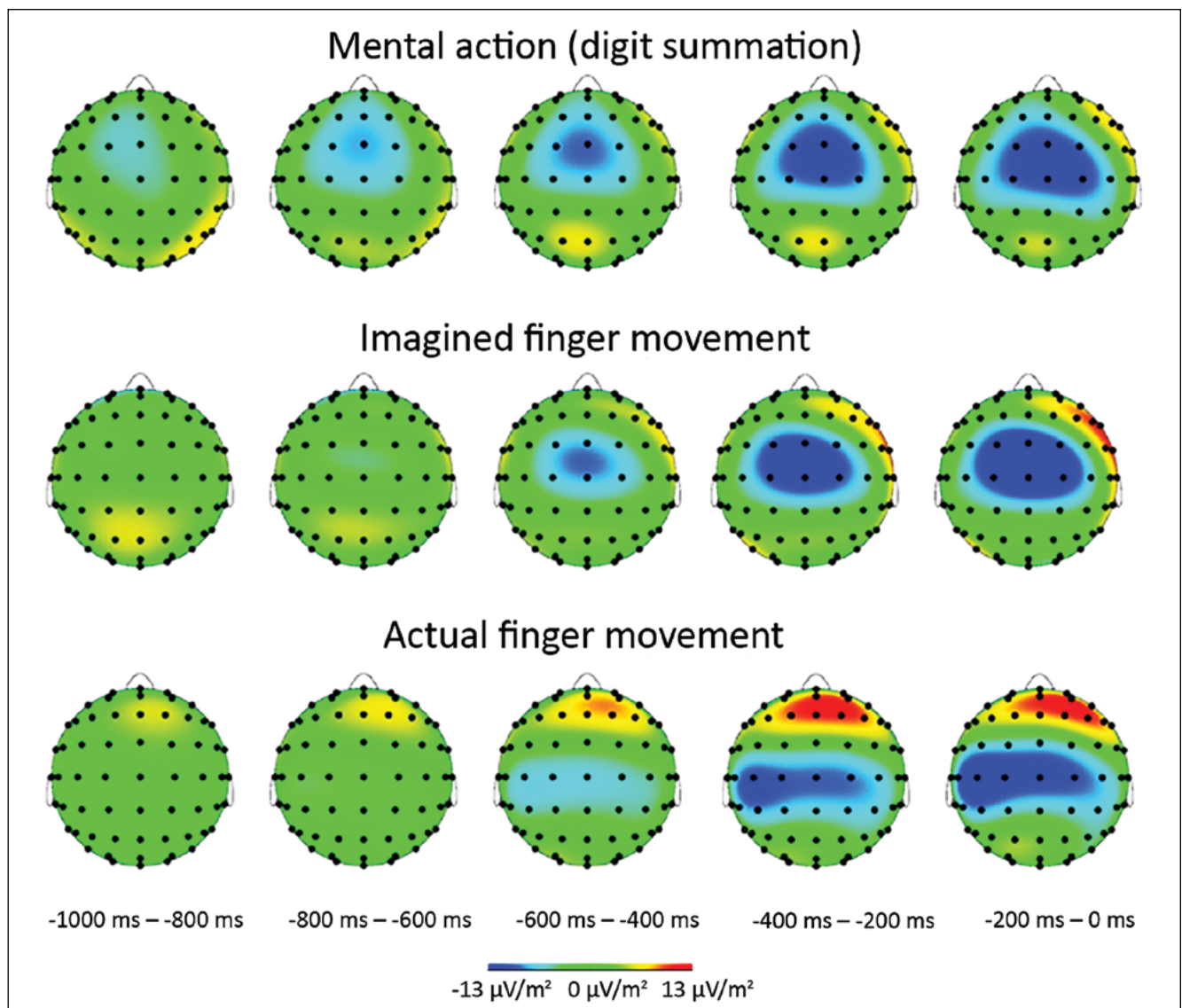


Fig. 2. Average changes of signal amplitudes for the three tested conditions. In the case of mental addition (upper row) and imagined movement (middle row) similar distributions of signal changes over central areas were observed. Notably, in the latter case, the signal seemed more lateralized to left hemisphere in the late phase. In the case of the index finger movement (lower row) the potential seemed to be lateralized to the left hemisphere in the late preparatory phase. Yet, the differences between the left and right hemisphere were not significant.

limited only to a direct comparison of mental action and imagined finger movement. No further significant differences between conditions were observed (with the provision that at least seven consecutive comparisons must be significant). As shown in Fig. 3B, the same results were obtained when relevant signals in this vicinity were extracted from the six most active electrodes for each of the studied conditions.

The characteristic shape of signal amplitude envelope, typically linked to readiness potential associated with physical body movements, was found in each of the studied tasks. Fig. 4A-C shows these effects with reference to control intervals of inactivity. During mental calculation (digit addition), as shown in Fig. 4A (top panel), the beginning of readiness potential was observed as early as 907 ms before task

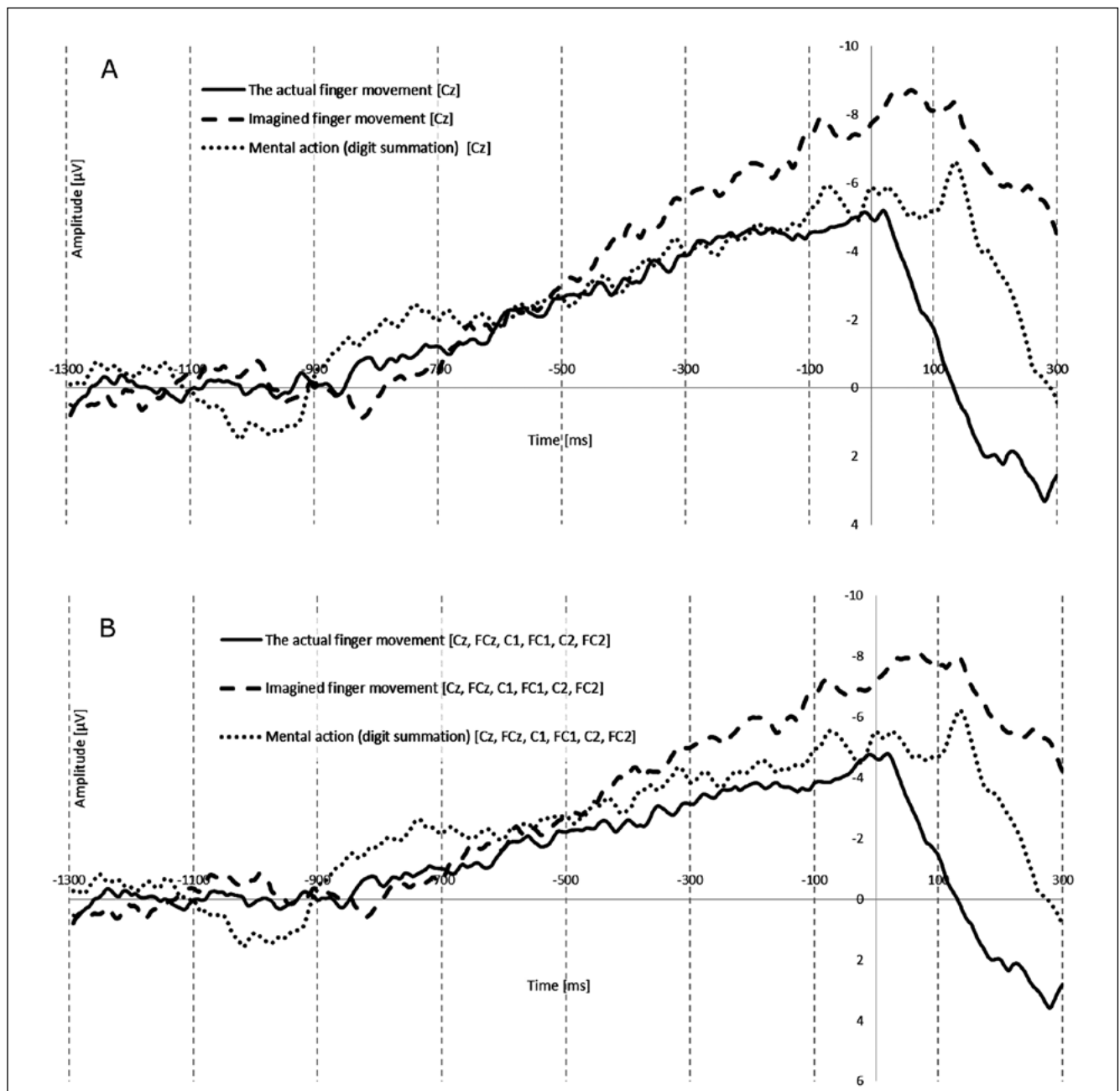


Fig. 3. Average traces for action-related potentials (readiness potentials, RPs) registered in each of the three studied conditions. (A) RPs extracted for each study condition with the use of the Cz electrode (as in all classic studies on related reports). (B) RPs extracted for each condition with the signal averaged across six most active electrodes. 0 on the X axis indicates the moment of action execution. Prior to this point, before 500 ms, clear convergence of all three potentials is observed, regardless of the signal extraction method.

performance. All t-tests between individual data samples contrasted with baseline (-1,300 to -1,000 ms before action initiation), with at least seven consecutive significant point-to-point differences required to be meaningful (Guthrie and Buchwald, 1991), starting from this time point were significant (at 907 ms, $t_{13}=-2.330$, $P<0.05$). Indeed, exactly the same time point was revealed as the beginning of this slow shift in negative potential when we compared mental action to control time intervals of inactivity from this task block. The observed gradient of RP change was $6 \mu\text{V/s}$ ($r=0.918$).

When, instead of a point by point analysis of RPs, the signal was collapsed across three equal time intervals (starting from -900 to 0 ms), the outcomes were very similar. As shown in the bottom panel of Fig. 4A, with mean signal amplitude changes averaged separately for each of the three time intervals, significant signal increases as compared to corresponding intervals of inactivity were found in each of the tested intervals. This effect was, in fact, found regardless of the study condition, as revealed by a significant time by task interaction from the rmANOVA (described in the Methods section), $F_{1,101,14,310}=20.88$, $P<0.001$, $\eta^2=0.616$, and $OP=0.992$ (with Greenhouse-Geisser corrected degrees of freedom). The effect was such that increases of RP-related activity in the first time interval, as compared to the remaining two intervals, were small but still significant (with Bonferroni-corrected P [BFP]=0.008). All the results from the omnibus rmANOVA are described in Supplemental Materials.

There was no evidence for the lateralization of signal in this condition. Specifically, in the immediate vicinity of the Cz site, no significant differences were observed for any of the 100-ms windows in the contralateral-ipsilateral comparisons of the selected electrodes.

As shown in Fig. 4B (top panel), a comparison between RP preceding imagined finger movement and control time intervals indicated that, despite signal increases above baseline which started at 787 ms before movement onset ($t_{13}=-4.06$, $P=0.001$), a significant signal modulation in this condition started 687 ms (as compared to periods of inactivity) before this action was performed ($t_{13}=-2.155$, $P=0.05$). From then on, the observed increases in negative signal were significant (except for few time points), and the observed gradient of RP change was $9.4 \mu\text{V/s}$ ($r=0.96$). As the bottom panel of Fig. 4B shows, but somewhat counter to the effect indicated above (see a description of the bottom panel of Fig. 4A), significant RP signal increases (vs. intervals of inactivity) were found in the second and third time intervals (if a separate rmANOVA was performed for this condition) only.

Interestingly, only in this condition the contralateral-ipsilateral comparison of the selected electrodes revealed significant differences in the last two of the 100-ms windows (namely between 200 and 0 ms prior to imagined finger onset: from -200 ms to -100 ms, $t_{13}=-2.191$, $P<0.05$, and from -100 ms to action execution $t_{13}=-2.563$, $P<0.05$). Yet, these differences would not survive the Bonferroni correction.

Finally, as shown in the top panel of Fig. 4C, a comparison between RP preceding actual finger movements and control time intervals indicated that, despite signal increases which started 847 ms before movement onset ($t_{13}=-2.91$, $P<0.05$, as compared to baseline), several points of significant signal modulation in this condition (as compared to periods of inactivity) were observed only as late as 727 ms before this action was performed ($t_{13}=-2.299$, $P<0.05$). Yet, the observed increases in negative signal were not continuously significant (until -367 ms, $t_{13}=-2.395$, $P<0.05$). The observed gradient of RP change was $5.8 \mu\text{V/s}$ ($r=0.977$). Consistent with the weaker initial increases of RP in the point by point analysis, with signals collapsed within the three time intervals, and as the bottom panel of Fig. 4C shows, there would be significant signal increases only in the second and third time interval (if a separate rmANOVA for this particular condition was performed).

As before, we did not find any evidence for the lateralization of RP signal in this condition. In the immediate vicinity of the Cz site, similarly to mental action, no significant difference between the selected electrodes was observed for any of the 100-ms windows in the contralateral-ipsilateral comparison.

Virtually identical results were obtained when the signals were extracted from the six most active electrodes in this vicinity, including the Cz electrode. These effects are shown in Fig. 4D-F, and described in more detail in the supplemental materials.

It is also worthy to directly compare a depiction of the time points in Fig. 4A, 4B and 4C (see also Fig. 3, where RPs in the three conditions are shown only vs. baseline), that is, with respect to each other. One could in fact argue that mental actions are more engaging and start differing from inactivity intervals even earlier. Yet, inactivity-related reference signals seem to differ among the three blocks and therefore, such differences should be interpreted with caution. Conversely, an examination of signal changes following the beginnings of actions (i.e., after their execution) would immediately reveal long-lasting significant signal differences. Yet, because they are no longer related to preparatory processes taking place exclusively “in the head”, and are no doubt related to differences in action modes, they will not be considered here.

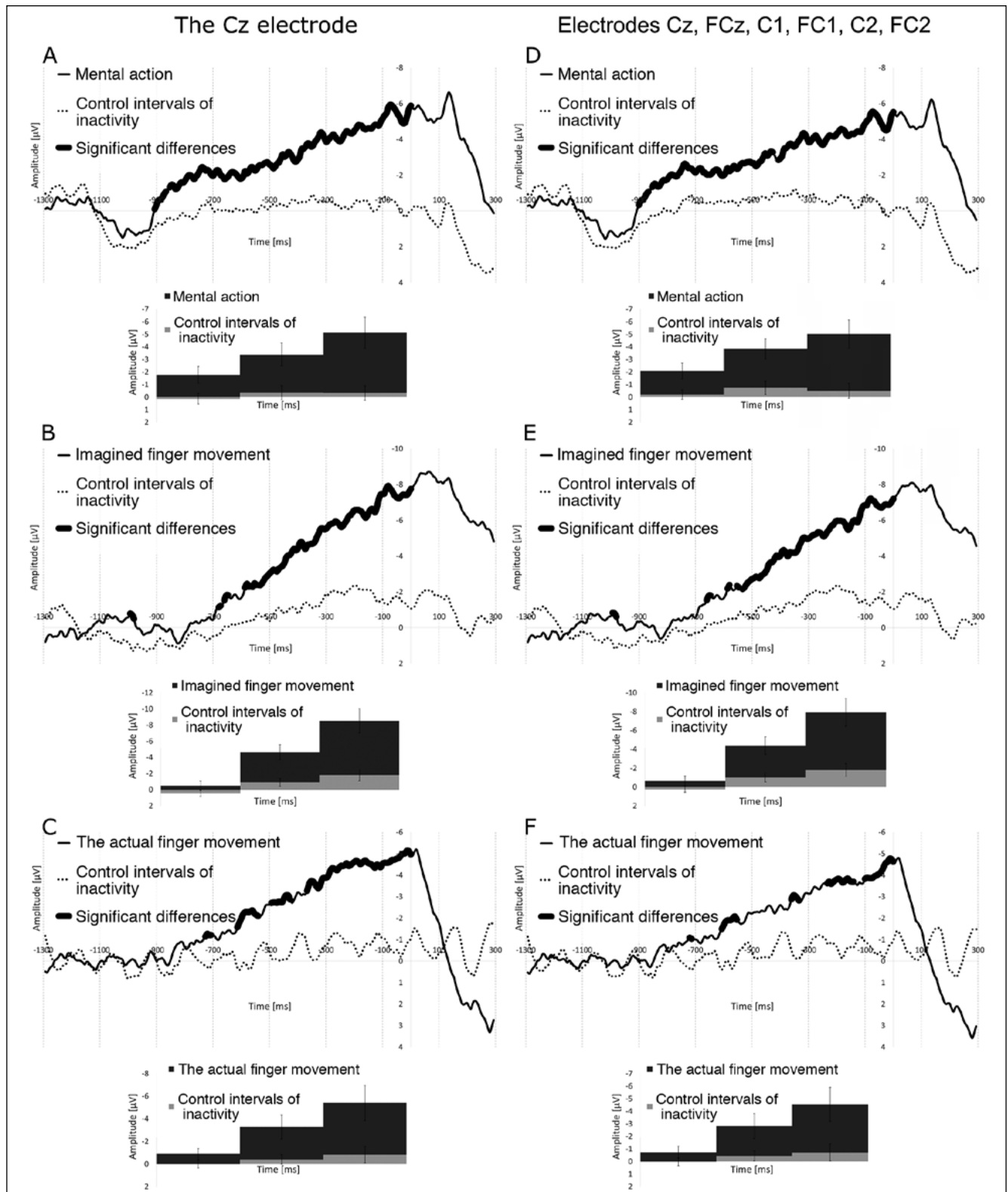


Fig. 4. Preparatory activity for the voluntary performance of the three tasks contrasted with respective periods of inactivity. (A-C) Readiness potentials (RPs) extracted from the Cz electrode. (A) Mental action (arithmetic). (B) Imagined finger movement. (C) The actual index finger movement. (D-F) RPs for the three tasks, extracted from the six most active electrodes, regardless of the study condition. Top panels: 150 RP time points for each condition. Bottom panels: RP changes collapsed across three equal time intervals (starting from -900 to 0 ms). In all panels, 0 on the X axis reflects the moment of action execution.

DISCUSSION

While it seems indisputable that the brain needs processing time during preparation for physical actions, whether or not getting ready for mental actions also requires any time is a question for debate. The results of this study clearly show that there is no difference in the temporal and directional patterns of intention-related neural activity, i.e., regardless of whether signals recorded before the volitional initiation of purely mental acts, imagined bodily movements, or physical motor responses are concerned. The characteristic, slowly increasing negative potentials starting around one second prior to any of these self-initiated actions, with the strongest effect observed on an electrode with the highest negative values of their amplitudes, indicate that the same electrophysiological readiness potential (Kornhuber and Deecke, 1965; Jankelowitz and Colebatch, 2002; Shibasaki and Hallett, 2006) precedes mental operations (here: digit addition). If motor and mental activity is led by processes or mechanisms of the same kind, the resulting conclusion is such that the human brain initiates any actions in the same way, regardless of their physical or mental nature.

The potentials registered in the three different conditions studied here did not differ significantly through most of their time courses, even though some divergence between them was expected as a result of putative differential contribution from supplementary and premotor cortical regions. For example, the initiation of intentional movement is typically headed by pre-SMA and SMA activity in the early preparatory phase, and then accompanied by more posterior dorsal premotor involvement (Praamstra et al., 1995; Erdler et al., 2000; Cunnington et al., 2002; Fried et al., 2011; Makoshi et al., 2011). For the latest phase of purely mental actions we expected to see a decrease in RP in this particular vicinity, since these motor regions should not be engaged in their preparation. To our surprise, no change in the RP profile was detected. While our experiment does not disentangle the exact source of the observed similarities in brain processes preceding actions of such different kinds, a few critical questions emerge. Is it a single mechanism that is common to both mental and physical actions? Alternatively, are there two (or more) different brain mechanisms that develop in a similar way in their temporal domains? Given the obtained results, there must be one common mechanism which is responsible for selection and initiation of the appropriate cognitive or motor system which will subsequently execute the selected task. If this is the case then the standard concept of RP – previously described as a potential preceding only the motor activity (Shibasaki and Hallett, 2006) – requires in fact an extension to all kinds of intentional actions. All things considered, RP can be regarded as a general phenomenon that occurs before execution of volitional

action independently of its bodily or mental character, and independent of cognitive attitudes (Kornhuber and Deecke, 1965; Taylor, 1978; Slobounov et al., 2004).

From this perspective, Libet's experiment (1983, 1985), and particularly the concept of an intention to move a body part requires some reinterpretation too. Regardless of the compulsory initial brain activity, that is RP which always precedes a physical action, an "intention to move" – that in Libet's experiment was reported to occur about 200 ms prior to movement onset – cannot be considered a purely mental act. Thus, the failed attempts to find separate or additional RPs that should occur before such a conscious decision (i.e., an intention) to physically start a movement (Libet, 1985) are not that surprising. Yet, based on the flawed reasoning that "intention" is "a typical example of mental action", RPs should not occur prior to mental actions. The results of our experiment indicate otherwise, but also call for a clarification of a concept of mental action.

Although mental actions may not necessarily require effort, many of them do. This is definitely the case for mental calculations but not necessarily for a simple "intention to move" – a prerequisite of any voluntary motor activity. Unlike the latter, such effortful mental operations that lead to a specific outcome, even though still mental, must be also preceded by RPs. In sharp contrast, a simple intention to move is not in our view that different from, or is even equivalent to, a simple command (e.g., "Move a finger now!") and is apparently issued without RP.

The temporal characteristics of signal changes observed prior to mental addition, that is increases in negative potentials which are indistinguishable from RPs observed before motor acts, suggest a common underlying neural mechanism. This may also indicate that elementary arithmetic operations, such as addition, are less abstract than usually assumed. If this were the case then mental summation of digits would be a kind of embodied action, even though not linked to any overt movement. A support for this view comes from evidence that mathematical abilities and finger representations have overlapping neural substrates (Andres et al., 2007, 2012; Penner-Wilger and Anderson, 2013). Yet, these common underpinnings are typically located in the inferior parietal lobule, as in Gerstmann's syndrome linked to damage to the angular gyrus. On the other hand, there is clear behavioral evidence that finger movements interfere with mathematical abilities (Michaux et al., 2013). Indeed, unskilled finger counting takes much longer than mental operations on numbers. Therefore, even if the latter are mediated by processes taking place in brain areas responsible for movement control, it does not simply entail that arithmetic calculations are of motoric nature (Klichowski and Króliczak, 2017).

CONCLUSION

The observation that the cerebral cortex needs around one second to be ready for a mental effort shows that former intuitions about activities of the mind (and brain) clearly require some revisions. In a common view, switching from a particular mental action to another one differs from switching between different actions of the body. Therefore, it is natural to expect that a new kind of movement, which is not a continuation of a previous one, cannot be initiated at an instant. Yet, we do believe and commonly experience that a new kind of mental effort is not preceded by a time gap. The results of this study convincingly show that such a universal mental experience is a misleading one.

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SUPPLEMENTAL MATERIALS

The outcomes for the pooled signal from the six most active electrodes

For the electrodes with the highest activity – recorded in the vicinity of, but also including, the Cz electrode – pairwise comparisons between mental actions and imagined finger movements revealed some significant differences located between -827 ms and -780 ms (i.e., in eight consecutive time points). In the case of real and imagined movements, the potentials preceding them were significantly different only between -113 and -73 ms (i.e., for seven consecutive but late time points). The RPs related to these three conditions are shown in Fig. 3B.

Similarly to between-condition comparisons, the comparisons within conditions vs. respective control intervals of inactivity do not differ much from the main, Cz-limited analysis, either. In the case of mental actions, the RP started at 853 ms before action initiation ($t_{13}=-2.223$, $P<0.05$), and almost all further time points were significantly different from inactivity-related signal (except for time points between -420 ms and -413 ms, where p-values were slightly above the 0.05 threshold). For imagined finger movements the RP was significantly different from -533 ms ($t_{13}=-2.227$, $P<0.05$) to the very moment of action execution. Finally, in the case of the actual finger movements only several points of significant signal modulations (vs. respective inactivity points) were observed, and they started to occur as late as 720 ms before action performance ($t_{13}=-2.380$, $P<0.05$). For the visualization of these results, see top panels of Fig. 4D-F in the main text.

The outcomes of rmANOVA for the three time intervals immediately preceding action execution

The results for the Cz electrode alone

When mean signal amplitude changes within three time intervals (starting from -900 to 0 ms) were calculated, and subjected to a 3 (condition: mental action, imagined finger movement, the actual finger movement) by 3 (time interval: -900 to -600, -600 to -300, and -300 to 0 ms) by 2 (task: action, inactivity) repeat-

ed-measures analysis of variance (rmANOVA), the following results emerged. There was a main effect of time interval ($F_{1,016,13,205}=14.349$, $p<0.01$, partial eta squared [$_{p}\eta^2$]=0.525, the observed power [OP]=0.94), such that regardless of the study condition and task, the pooled signals within each of the time intervals differed significantly from each other (with Bonferroni-corrected p value [BFp]=at least 0.012). Moreover, there was a significant main effect of task ($F_{1,13}=26.658$, $p<0.001$, $_{p}\eta^2=0.672$, OP=0.997) and it was such that regardless of the condition and time interval, the RP associated with action preparation was significantly different from inactivity-related signal. There was also a significant time interval by task interaction ($F_{1,101,14,310}=20.88$, $P<0.001$, $_{p}\eta^2=0.616$, OP=0.992) and, as already mentioned in the main text, this effect was such that increases of RP-related activity in the first time interval, as compared to the remaining two intervals, were the smallest but still significant (BFp=0.008).

Finally, there was also a significant condition by time interval interaction ($F_{2,272,29,536}=6.252$, $P<0.01$, $_{p}\eta^2=0.325$, OP=0.89), and it indicated that the consecutive between-interval signal changes did not significantly differ from each other for the mental actions (BFp \geq 0.08), they did significantly differ from each other for imagined finger movements (BFp<at least 0.006), whereas for actual finger movements the outcomes were quite similar to the former with the exception that there was only a trend towards a significant signal increase between the second and third time interval (BFp=0.06). There were no further significant effects (neither the main effect of condition nor any remaining interaction, $F\leq 1.228$).

The results for the six most active electrodes (including the Cz electrode)

When mean signal amplitude changes within the three time intervals (-900 to -600, -600 to -300, and -300 to 0 ms) were calculated, and subjected to a 3 (conditions) by 3 (time intervals) by 2 (tasks) rmANOVA, the outcomes were the following. As for the Cz electrode alone, there was a main effect of time interval ($F_{1,026,13,332}=11.994$, $p<0.01$, $_{p}\eta^2=0.480$, OP=0.898), such that regardless of the study condition and task,

the signals within each of the time intervals differed significantly from each other (BFp=at least 0.024). As before, there was also a significant main effect of task ($F_{1,13}=22.601$, $p<0.001$, $p\eta^2=0.635$, $OP=0.992$) and it was such that regardless of the condition and time interval, the action-related RP was significantly different from inactivity-related signal. Similarly to Cz alone, there was also a significant time interval by task interaction ($F_{1,114,14,477}=19.703$, $P<0.001$, $p\eta^2=0.602$, $OP=0.990$) and this effect, again, was such that increases of RP-related activity in the first time interval, vs.the remaining two intervals, were the smallest but still significant (BFp=0.015). Finally, there was also a significant

condition by time interval interaction ($F_{2,26,29,395}=5.684$, $P<0.01$, $p\eta^2=0.304$, $OP=0.856$), and, as before, the consecutive between-interval signal changes did not significantly differ from each other for the mental actions (BFp \geq 0.127), but they did significantly differ from each other for imagined finger movements (BFp<at least 0.012), whereas for actual finger movements the same exception emerged - a trend towards a significant difference between the second and third time interval (BFp=0.082). Similar to the classic analysis on the Cz electrode, there were no further significant effects (neither the main effect of condition nor any remaining interaction, $F\leq 1.152$).