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Numbers within our hands: Modulation of corticospinal excitability of hand muscles during numerical judgment

Marc Sato[CA], Luigi Cattaneo, Giacomo Rizzolatti, Vittorio Gallese

Dipartimento di Neuroscienze, Sezione di Fisiologia, Università degli studi di Parma

Via Volturno 39, 43100, Parma, ITALY

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[CA] Corresponding author
Dipartimento di Neuroscienze, Sezione di Fisiologia, Università degli studi di Parma
Via Volturno 39, 43100 Parma, Italy
E-mail address: marc.sato@nemo.unipr.it

ABSTRACT

Developmental and cross-cultural studies show that finger-counting represents one of the basic number learning strategies. However, despite the ubiquity of such an embodied strategy, the issue of whether there is a *neural* link between numbers and fingers in adult, literate individuals remains debated. Here, we used transcranial magnetic stimulation to study changes of excitability of hand muscles of individuals performing a visual parity judgment task, a task not requiring counting, on Arabic numerals from 1 to 9. While no modulation was observed for the left hand muscles, an increase in amplitude of motor evoked potentials was found for the right hand muscles. This increase was specific for smaller numbers (1 to 4) as compared to larger numbers (6 to 9). These findings indicate a close relationship between hand/finger and numerical representations.

Keywords: Numerical cognition; Transcranial magnetic stimulation; Motor cortex; Embodiment.

INTRODUCTION

The issue of how numbers are represented (and manipulated) in the human brain has been for long time matter of debate. Recently, thanks to combined efforts of developmental psychology, psychophysics and neuroscience our understanding of numerical abilities and their neural basis has significantly improved. It has been shown that numerical competence related to approximate processing of quantity can be considered as a basic independent faculty, present early in infancy (Dehaene, 1997; Nieder, 2005). This competence, however, appears to be limited in its representational power, failing to support certain numerical concepts, such as negative numbers or even exact integers (Feigenson, Dehaene and Spelke, 2004). The development and maturation of these concepts are thought to depend on cultural and educational processes. From this perspective, a fundamental question concerns the role of language in developing numerical concepts and arithmetic abilities. Studies on numerical competence in populations in which the verbal counting system is limited have underlined a distinction between a system of number approximation not linked to language and a language-based counting system for exact number and arithmetic (Gordon, 2004; Pica et al., 2004). Individuals of these populations are unable to perform exact calculation when the answer exceeds their naming range, but exhibit normal approximate number processing. These results suggest that numerical competence depends on a language-based counting system, and reinforce the long-standing idea that learning a communicable number notation with exact numerical references may play a role in the emergence of a fully formed conception of number (Gelman and Butterworth, 2004; Gelman and Gallistel, 2004).

Neuropsychological and brain imaging studies focusing on the localization of numerical processing and arithmetic in the brain also support the distinction between a verbal code for exact arithmetic processing and a language-independent analogue magnitude code for approximate processing. Neuroimaging studies with healthy individuals show that number processing rests on a distinct neural circuitry, involving a set of parietal, frontal and cingulate areas (Dehaene et al., 1996; Rueckert et al., 1996; Chochon et al., 1999; Stanescu-Cosson et al., 2000; Zago et al., 2001; Simon et al., 2002; Eger et al., 2003; Pinel et al., 2004). While the cortex lying in the horizontal segment of the intraparietal sulcus seems to play a crucial role in language-independent semantic representation of numerical quantity, the activation of the left inferior frontal gyrus, a region commonly associated with language functions, has been suggested to reflect exact mental calculation and to be involved in retrieval of arithmetic facts (Dehaene et al., 2003; Dehaene et al., 2004). Consistent with these findings is the observation that patients with lesions in the left frontal cortical areas are unable to perform exact calculations such as multiplication, but do not exhibit significant difficulties in quantity comparisons (Dehaene and Cohen, 1997; Lemer et al., 2003). In contrast, patients with damage to areas within the inferior parietal lobe are proficient at performing exact numerical computations involving rote retrieval but may have striking deficits in their ability to perform tasks requiring a representation of numerical quantity (Dehaene and Cohen, 1997; Delazer and Benke, 1997; Lemer et al., 2003). Altogether, these studies provide convincing evidence that number comprehension and calculation are mediated by both analogue magnitude and verbal codes.

Another important semiotic means for representing numbers, also described in populations with extremely limited or no verbal counting, is the one based on the use of body-parts, such as fingers or hands. Several lines of evidence argue in favor of a close relationship between number and hand/finger representations. Developmental and cross-cultural studies have shown that finger-counting is a basic numerical learning strategy, that develops spontaneously (Butterworth, 1999). Also, performance on finger discrimination tasks (e.g., digital gnosia and digital discrimination) in 5- to 6- year-old children is considered as one of the best predictor of arithmetic abilities (Fayol, Barouilette and Marinthe, 1998). Another connection between hand/finger representation and numerical knowledge stems from the study of Gerstmann syndrome (Gerstmann, 1924, 1940; Mayer et al., 1999) and of Developmental Gerstmann Syndrome (Kinsbourne and Warrington, 1963; Suresh and Sebastian, 2000), where an association of finger agnosia and dyscalculia can be observed. Accordingly, a recent repetitive transcranial magnetic stimulation (rTMS) study (Rusconi, Walsh and Butterworth, 2005) on healthy volunteers showed that stimulation of the left angular gyrus disrupts the capacity to execute tasks requiring access to finger representations and numerical judgment. Finally, several functional imaging studies showed that arithmetic tasks activate that part of the left precentral gyrus where hand movements are represented (Dehaene et al., 1996; Rueckert et al., 1996; Pesenti et al., 2000; Stanescu-Cosson et al., 2000; Zago et al., 2001; Pinel et al., 2004).

In the present study, we explored whether numerical judgment may automatically induce changes in the excitability of corticospinal output to hand muscles of educated adults despite the absence of any conscious necessity to use an embodied strategy for solving the task. In a first experiment, we used single-pulse TMS applied to the hand region of the motor cortex in individuals orally performing a visual parity judgment task on Arabic numerals from 1 to 9 (5 excluded). The parity judgment task was chosen because a motor strategy is irrelevant in order to perform the task. The focal TMS was delivered 200 ms after the onset of the number presentation to either the left or right hemisphere and motor-evoked potentials (MEPs) were recorded from the contralateral *abductor pollicis brevis* (APB) and *abductor digiti minimi* (ADM) hand muscles. These two muscles were chosen within the complex system of intrinsic hand muscles in order to select a broad spectrum of counting-like hand postures (Weiss and Flanders, 2004). We hypothesized that changes in the corticospinal excitability of hand muscles during the task could be directly related to the way of representing numbers by means of fingers.

Preliminary behavioral observations showed a clear tendency for Italian adults to use their right hand to represent numbers from 1 to 5 and, subsequently, their left hand to represent numbers from 6 to 10. Accordingly, processing smaller digits (i.e., from 1 to 4) and larger digits (i.e., from 6 to 9) should induce an increase in corticospinal excitability of the right and left hand muscles, respectively. Finally, a behavioral experiment, measuring reaction-time in a parity judgment task, was performed in order to assess possible differences in terms of complexity when processing smaller and larger digits.

EXPERIMENT 1: TMS STUDY

METHODS

Participants

Two separate groups of eight subjects (nine males and seven females; mean age ± SD, 24 ± 4 years) participated in Experiment 1A and Experiment 1B. All were right-handed, according to a standard handedness inventory (Oldfield, 1971) and had normal or corrected-to-normal vision. Participants were screened for neurological, psychiatric, and other medical problems, and contraindications to TMS (Wassermann, 1998). Informed consent was obtained for all subjects and they were paid for their participation. The protocol was approved by the Parma University Ethical Committee and was carried out in accordance with the ethical standards of the 1964 Declaration of Helsinki.

Electromyography

Continuous electromyography (EMG) recordings from *abductor pollicis brevis* (APB) and *abductor digiti minimi* (ADM) muscles were simultaneously acquired with a CED Micro 1401 analog-to-digital converting unit (Cambridge Electronic Design, Cambridge, U.K.). The EMG signal was amplified (1000x), digitized (sampling rate: 8 kHz, off-line band-pass filter: 5-4000 Hz), and stored on a computer for offline analysis. The APB and ADM muscles were recorded from either the right or the left hand, according to the experimental session, using

Ag/AgCl surface electrodes with a bipolar montage. The active electrode was placed on the muscle belly and the reference electrode on the corresponding tendon. Electrodes were therefore placed laterally to the metacarpal bone of the thumb for APB and on the medial border of the palm for ADM.

Transcranial Magnetic Stimulation

Either the left or the right hemisphere was magnetically stimulated by means of monophasic single pulses delivered through a figure-of-eight coil connected to a transcranial magnetic stimulator (ESAOTE Biomedica, Italy). The coil was moved over the scalp in order to determine the optimal site from which maximal amplitude MEPs were elicited in the APB and ADM muscles. For optimal stimulation of the hand motor cortex, the intersection of the coil was placed tangentially to the scalp with the handle pointing backward and laterally at a 45° angle away from the midline (Mills, Boniface and Schubert, 1992). The coil handle was fixed on a mechanical arm, in order to suppress movements of the coil itself from the original position on the scalp. The resting motor threshold (rMTh) of the APB and ADM muscles was determined according to standard methods as the minimal intensity capable of evoking MEPs (Rossini et al., 1994) in 5 out of 10 consecutive trials from the two relaxed muscles with an amplitude of at least 50 μV. A single optimal spot on the scalp was searched for in order to evoke MEPs from the two muscles with similar thresholds. In this way, no individual differences in rMTh between the two muscles on the same side were found in any subject. The output of the stimulator was set to 120% of rMTh for the stimulations applied during the experimental session. The complete muscle relaxation before TMS was verified by means of on-line visual monitoring of the EMG signal by the experimenter.

Procedure

The experiments were programmed using Matlab (The Mathworks Inc., Natick, MA), Cogent (Functional Imaging Laboratory, Queen Square, London) and Signal (Cambridge Electronic Design, Cambridge, U.K.) software to control the stimulus presentation and to trigger the TMS and EMG recordings.

Participants were comfortably seated on an armchair with their elbow flexed at 90° and their hands half-pronated in a totally relaxed position. The head was lying on a headrest in order to maintain a comfortable and stable position. They were required to orally make a parity judgment on one-digit Arabic numerals. Stimuli were single Arabic digits ranging from 1 to 9 (5 excluded), presented one at a time in the center of the screen and written in black Arial font on a white screen (~ 0.3 x 0.3°). Stimulus presentation was delivered through a 19 inch monitor with a viewing distance of approximately 60 cm.

Each trial started with a fixation cue (the ‘+’ symbol, presentation time 500 ms) followed by the target number (presentation time 500 ms) and by a blank screen (presentation time1000 ms). Then a question mark (the '?' symbol, presentation time 2500 ms) was shown, followed by a blank screen (presentation time 1000 ms). The question mark prompted the participants to tell whether the observed number was odd or even.

Both Experiment 1A and Experiment 1B consisted of two different experimental sessions in which the hand motor cortex of the left and right hemispheres was separately stimulated while recording from the contralateral hand muscles. The order of sessions was counterbalanced across subjects. In Experiment 1A, every digit was presented 5 times in a randomized sequence for a total of 40 trials in both sessions. In each trial the TMS pulse was delivered 200 ms after the onset of the number presentation. The delay of 200 ms was extrapolated on the basis of previous studies indicating that lexical and semantic processes during word recognition entail activation in the frontal cortex as early as 150-200 ms after onset of written word stimuli (Pulvermuller, Shtyrov and Ilmoniemi, 2005; Hauk et al., 2006). This interval also appears to be consistent with ERP studies focusing on the timecourse of access to numerical representations (Dehaene, 1996; Posner and Temple, 1998). Experiment 1B was identical to Experiment 1A, except for an additional control condition where TMS was applied simultaneously with stimulus presentation. Each digit was presented 9 times in a randomized sequence for a total of 72 trials. For each digit, the TMS pulse was delivered 200 ms after the onset of the number presentation in 6 trials and at 0 ms from the onset of the number presentation in the 3 other trials. Trials for which the pulse was delivered at the onset of the stimulus presentation were considered as control trials.

Data Analysis

Data were processed offline. The mean percentage of errors was 1% in both Experiment 1A and Experiment 1B (SD: 0.58 / 0.90). Error trials and trials with EMG activity before TMS were discarded from the analyses (overall less than 5% in both experiments). The negative to positive peak amplitude of the MEPs was measured and subsequently *z*-score normalized to the grand average of all MEPs from the same muscle and the same hemisphere within the same subject in order to allow a comparison between subjects. In Experiment 1A, data were averaged for each subject within the same muscle and hemisphere according to both the numerical and parity categories (i.e., small/odd, '1/3', small/even, '2/4', large/odd, '7/9', large/even, '6/8'). A four-way analysis of variance was performed on these data. The considered within-factors were related to the stimulated side (left hemisphere and right hemisphere), the numerical category (smaller digits, i.e., 1 to 4, and larger digits, i.e., 6 to 9), the parity category (odd and even digits) and the recorded muscle (APB and ADM). In experiment 1B, two distinct ANOVAs were performed. In the first analysis, data were averaged for each subject within the same muscle and hemisphere according to the numerical category (i.e., smaller digits, larger digits and control trials). A three-way ANOVA was performed on these data with the stimulated side, the numerical category and the recorded muscles as within-factors. To further investigate a possible parity effect in Experiment 1B, data related to smaller and larger numbers were averaged within the same muscle and hemisphere according to the numerical and parity categories (i.e., small/odd, '1/3', small/even, '2/4', large/odd, '7/9', large/even, '6/8') and submitted to a four-way ANOVA. The considered within-factors were related to to the stimulated side, the numeral category, the parity category and the recorded muscle. Whenever appropriate, post-hoc analyses were performed using Bonferroni correction. The significance level was always set at $p = .05$. For each analysis, a Mauchly test showed that the sphericity assumption was not violated.

RESULTS

Two TMS experiments were carried out. Experiment 1A consisted of two sessions in which we stimulated the motor cortex representations of the right and left hand respectively, while recording EMG from the contralateral APB and ADM muscles. In each trial, the TMS pulse was delivered 200 ms after the onset of the number presentation. A four-way ANOVA (with the hemisphere, the numerical category, the parity category and the recorded muscle as within-factors) showed that the presentation of smaller (1-4) and larger numbers (6-9) (the digit 5 was not used) differentially affected MEP amplitude of hand muscles ($F(1,7) = 12.02$, $P < .01$). A significant interaction was present between the side of stimulation and the numerical category ($F(1,7) = 7.78$, $P < .03$). Post-hoc analysis revealed that the interaction was due to the fact that, during stimulation of the left hemisphere, mean MEP amplitudes were larger when processing smaller numbers than larger numbers ($P < .02$ - see Figure 1A) while, during stimulation of the right hemisphere, mean MEP amplitudes were not influenced by the two numerical categories ($P > .68$ - see Figure 1B). No interaction was observed between the recorded muscle and the numerical category ($F(1,7) = 0.25$), nor between the recorded muscle, the side of stimulation and the numerical category ($F(1,7) = 0.12$). These later results indicate that the MEP modulation equally affected both APB and ADM muscles. Finally, neither the effect of the parity category ($F(1,7) = 0.16$) nor the interaction between the parity and numerical categories were significant ($F(1,7) = 0.43$). All the remaining interactions were not significant.

Insert Figure 1 about here

In Experiment 1B, we further investigated the excitability of the right and left hand muscles during the parity judgment task by adding a control condition, in which the pulse was delivered simultaneously with the stimulus onset. As in the first experiment, the motor cortex representations of the right and left hand were respectively stimulated while recording from the contralateral APB and ADM muscles. MEPs induced by focal TMS, delivered either 0 ms or 200 ms after the onset of the number presentation, were recorded simultaneously from the APB and ADM muscles. ANOVA showed a significant interaction between the side of stimulation and the numerical category ($F(2,14) = 8.79$, $P < .003$) but no effect of the numerical category ($F(2,14) =$

0.93). Post-hoc analysis revealed that the interaction was due to the fact that, during stimulation of the left hemisphere, mean MEP amplitudes were larger when processing smaller numbers than both larger numbers and control trials (small vs. large: $P < .05$; small vs. control: $P < .05$; large vs. control: $P > .99$ - see Figure 2A) while, during stimulation of the right hemisphere, mean MEP amplitudes were not influenced by the three numerical categories (small vs. large: $P > .99$; small vs. control: $P > .49$; large vs. control: $P > .52$ - see Figure 2B). These results, coming from a separate group of subjects, thus replicate those observed in Experiment 1A. No interaction was observed between the recorded muscle and the numerical category ($F(2,14) = 0.04$), as well as between the recorded muscle, the side of stimulation and the numerical category ($F(2,14) = 0.45$). As in Experiment 1A, these latter results indicate that the MEP modulation affected equally both APB and ADM muscles.

To further investigate a possible parity effect in Experiment 1B, data related to smaller and larger numbers were entered into a further ANOVA (see Methods). This analysis showed a significant interaction between the side of stimulation and the numerical category ($F(1,7) = 6.98$, $P < .04$) but no effect of the numerical category ($F(1,7) = 2.06$). Post-hoc analysis revealed that the interaction was due to the fact that, during stimulation of the left hemisphere, mean MEP amplitudes were larger when processing smaller numbers than when processing larger numbers ($P < .05$) while, during stimulation of the right hemisphere, mean MEP amplitudes were not influenced by the two numerical categories ($P > .99$). No interaction was observed between the recorded muscle and the numerical category ($F(1,7) = 0.04$), as well as between the recorded muscle, the side of stimulation and the numerical category ($F(1,7) = 0.41$). Finally, neither the effect of the parity category ($F(1,7) = 0.52$) nor the interaction between the parity and numerical categories ($F(1,7) = 2.38$) were significant. All the remaining interactions were not significant.

At the end of both TMS experiments participants were asked to '*count with their fingers from 1 to 10*', without indications on the hand(s) to be used. All subjects but two (14 out of 16), used first their right hand to count from 1 to 5 and then their left hand to count from 6 to 10. The two other subjects used a counting strategy involving only the right hand. None of the subjects stated to have used such an embodied strategy to perform the task during the experimental session.

Insert Figure 2 about here

EXPERIMENT 2: BEHAVIORAL STUDY

METHODS

Participants

Twenty-four subjects (fifteen males and nine females; mean age ± SD, 27 ± 4 years) participated in Experiment 2. All were right-handed and had normal or corrected-to-normal vision. None of them participated in the previous TMS experiments.

Procedure

The experiment was carried out in a sound-attenuated room. Participants were seated at a table with the monitor placed in front of them with a viewing distance of approximately 60 cm. The experiment, requiring a unimanual go/no-go paradigm, consisted of four experimental sessions (hand x parity judgment) in which participants were asked to make either an odd or an even parity judgment to one-digit Arabic numerals by pressing a key aligned with their midline with either their right hand or left hand. Participants were instructed to give a motor response, as fast and accurately as possible, when the stimulus fulfilled the parity criteria response instructions and refrain from responding when not. The order of sessions was fully counterbalanced across subjects (latin-square randomization). Stimuli were single Arabic digits ranging from 1 to 9 (5 excluded), presented one at a time in the center of the screen and written in black Arial font on a white screen (~ 0.3 x 0.3°). Each trial started with a fixation cue (the '+' symbol) presented during 500 ms, immediately followed by the target number. The maximum response time was 2 s. The inter-trial interval, consisting of a blank screen, was 2 s. For each session, every digit was presented 8 times for a total of 40 trials organized in a randomized sequence.

Data Analysis

The mean percentage of errors was 1% (SD: 1.21), no subjects exceeded the limit of 10% of errors. For each participant, median RT values were calculated for correct trials in relation to each session and numerical category (i.e., small/odd, '1/3', small/even, '2/4', large/odd, '7/9', large/even, '6/8'). A three-way ANOVA was conducted on these data with the effector (left or right hand), the parity category (odd/even) and the numerical category (smaller/larger digits) as within-factors. The significance level was always set at $p = .05$. A Mauchly test showed that the sphericity assumption was not violated.

RESULTS

Statistical analyses of RTs showed a reliable effect of the parity category ($F(1,21) = 8.17$, $P < .01$), with RTs slower when responding for odd than for even numbers (average: 456 ms vs. 436 ms) but no reliable effect of the numerical category ($F(1,21) = 3.46$) nor interaction between the two factors ($F(1,21) = 1.61$). Finally, neither significant effect of the hand response (F(1,21)

= 0.01) nor interactions between the independent variables were found (see Figure 3).

As in the TMS experiments, participants were asked at the end of the behavioral experiment to '*count with their fingers from 1 to 10*', without indications concerning the hand(s) to be used. All subjects but two (22 out of 24), used first their right hand to count from 1 to 5 and then their left hand to count from 6 to 10. The two other subjects used a counting strategy involving first the left-hand than the right-hand. These subjects were discarded from the analysis.

Insert Figure 3 about here

DISCUSSION

The present results highlight a close relationship between number and finger cortical representations by showing a specific increase of the corticospinal excitability of the right hand muscles during a visual parity judgment task on Arabic numerals. This excitability increase was very robust across the two TMS experiments. Three main results were observed. First, the increase of excitability of right hand muscles was observed only during the presentation of smaller numbers (1-4), as compared to larger numbers (6-9) or to a control condition. Second, no modulation due to presentation of smaller or larger numbers was observed when stimulating the right motor cortex. Third, the modulation observed for the right hand muscles was present 200 ms after the onset of the number presentation. Because pre-TMS electromyography activities showed complete relaxation of the hand muscles and no participant stated to have used a strategy based on finger counting to perform the task, these results clearly demonstrate that number processing for smaller numbers automatically induces an increase of the corticospinal excitability of the right hand muscles.

What is the relation between the numerical judgment and the enhanced motor output to the right hand muscles, and how can this relationship be explained? In our view, the finger/number relation derives from an embodied finger counting strategy developed during numerical acquisition in childhood to represent, manipulate and communicate numbers, and still unconsciously recalled by adults when dealing with numbers.

Evidence in favor of this interpretation comes from different sources. Body parts, such as hands, fingers or even toes, appear as a natural means for counting and representing numbers in many cultures (Butterworth, 1999). At the ontogenetic level, the acquisition of numerical skills and arithmetical knowledge can be seen as an increasingly sophisticated understanding of numerosity that begins well before the development of full competent language (Butterworth, 2005). From this view, developmental research provided converging evidence on the relationship between gesturing and the acquisition of mathematical knowledge. It is well established, for example, that hand/arm gesturing helps pre-schoolers in improving their knowledge of one-to-one correspondence, and contributes to accurate counting performance (Alibali and DiRusso, 1999; Butterworth, 2005). Similarly, the study of hand gestures/speech mismatches, produced by school children when solving mathematical problems, showed that they possess mathematical knowledge they cannot articulate in speech (Goldin-Meadow, Alibali and Church, 1993; Goldin-Meadow, Kim and Singer, 1999; Goldin-Meadow and Wagner, 2005). Taken together, these findings suggest a tight connection between the development of symbolic representations of numbers and the use of fingers. Furthermore, in many cultures, manipulating and representing numbers by means of fingers precedes the use of more abstract codes, such as the verbal or written codes, and therefore provides a bridge between the child's likely innate capacity for numerosity and more advanced mathematical achievements (Siegler and Shrager, 1984; Fuson, 1988). As previously noted, it is also worthwhile to point out that performance on finger discrimination tasks (e.g., digital gnosia and digital discrimination) in 5- to 6- year-old children is considered as one of the best predictor of arithmetic abilities (Fayol, Barouillet and Marinthe, 1998).

Another source of evidence for a close relationship between numbers and hand/finger representations is given by brain-imaging studies. fMRI signal increase in the part of the left precentral gyrus where hand movements are represented (Binkofski et al., 1999), was repeatedly reported during numerical processing. This activation was described during additions (Pesenti et al., 2000; Stanescu-Cosson et al., 2000), multiplications (Dehaene et al., 1996; Zago et al., 2001), subtractions (Rueckert et al., 1996) and number comparisons (Dehaene et al., 1996; Pesenti et al., 2000; Pinel et al., 2004). In agreement with our view, some authors have suggested that the activations of the left precentral gyrus, together with those observed in the parietal cortex, might reflect the involvement of a finger-movement network, and, by extension, underlie a finger counting strategy used during the tasks (Pesenti et al., 2000; Zago et al., 2001). However, because the precentral gyrus was also found to be activated during a comparative judgment task on numbers based on their luminance properties, it has been argued that this region might rather reflect response selection and decision processes (Pinel et al., 2004). In the light of the present results, the fact that the task did not involve any hand response and, most importantly, that the observed modulation of the corticospinal excitability of right hand muscles was strictly related to smaller numbers seems to rule out the idea that the activation of the precentral gyrus was exclusively based on response selection and decision processes. Moreover, the fact that the modulation of the corticospinal excitability of the right hand muscles was observed 200 ms after the onset of the number presentation suggests that this modulation was present during early representational processing stages.

The finger embodiment hypothesis has also been directly investigated in a recent behavioral study where Italian adults had to identify Arabic digits by pressing 1 of 10 keys with the corresponding finger (Di Luca et al., 2006). These results showed that, when any of the 10 fingers can be used, a mapping congruent with the prototypical finger-counting strategy reported by the participants (i.e., using first their right hand to count from 1 to 5 and then their left hand to count from 6 to 10) leads to better performance than does a mapping congruent with a left-to-right oriented mental number line. These results thus provide evidence that finger-counting strategies may influence the way that numerical information is mentally represented and processed. In our Experiment 2, given that the participants started to count with their right hand when asked to do it, one could expect faster responses to smaller numbers when using the right hand compared to the left one, and conversely. However, the results did not confirm such prediction, possibly because number and finger interactions were restricted to unimanual left or right index presses. Interestingly, both experiments failed to reveal an interaction between the magnitude of the digit and the hand used to respond. This finding contradicts the well-established effect of Spatial-Numerical Association of Response Code (SNARC) effect, originally described by Dehaene and colleagues (1993). This effect - interpreted as evidence that the relative magnitude of numbers is encoded analogically in terms of left-right spatial-numerical associations along a mental number line - refers to the fact that, when participants were required to make bimanual parity judgments on digits by pressing a left or a right key, smaller numbers were responded to faster with the left hand than with the right hand, whereas larger numbers were responded to faster with the right hand than with the left hand. Although they do not rule out the existence of numerical representation based on a left-to-right oriented mental line, both our Experiment 2 and the study of Di Luca and colleagues (2006) stress the importance of controlling the finger-counting preference of subjects together with the experimental protocol when studying space and number interactions.

Although the present TMS findings fit well with these developmental, behavioral, neuropsychological and neuroimaging data and suggest a close relationship between number and finger representations, alternative interpretations of our results have to be discussed.

Firstly, the observed cortical modulation might be due to possible differences in terms of complexity when processing smaller and larger numbers. The fact that RTs were significantly faster when responding to even numbers than to odd numbers in Experiment 2 may indeed reflect the higher complexity required for processing odd numbers. A similar effect has been previously reported during a parity judgment task and attributed to the linguistic complexity of the odd concept (Hines, 1990; Nuerk, Iversen and Willmes, 2004). However, the fact that no reliable effect of the parity category was found in both Experiments 1A and 1B rules out a possible interpretation of our TMS results based on a higher complexity for processing odd numbers.

Secondly, the present modulation was confined to the left hemisphere and might thus reflect some verbal-motor components related to covert naming of numbers or retrieval of numerical knowledge based on verbal routines. Accordingly, an increase in the corticospinal excitability of the right hand muscles has been previously described during reading aloud (Tokimura et al., 1996) and even during silent reading (Papathanasiou et al., 2004). The observed increased motor output might therefore reflect a linguistic contribution of the left hemisphere, with the observed asymmetry reflecting the lateralized cortical organization of language. The specificity of the present modulation, strictly related to smaller numbers, argues against this hypothesis. However, a more cautious interpretation of the present results could be based on the lexical frequency of numbers. Indeed, it has been shown that the lexical frequency of counting words is inversely correlated with their numerosity: thus, the word one is more frequent than the word two, two is more frequent than three, and so forth (Dehaene and Mehler, 1992). Therefore, one could argue that, because of lower lexical frequencies, the visual presentation of larger Arabic digits might activate to a lesser extent the symbolic representations involved in covert naming. However, this prediction does not fit well with our results. Indeed, previous brain imaging studies investigating the effect of lexical frequency on visual word processing during a lexical decision task have reported an increased activation of the left inferior frontal gyrus for low frequency words as compared to high frequency words (e.g., Fiebach et al., 2002; Nakic et al., 2006; Prabhakaran et al., 2006). These results are thought to reflect the role of the left inferior frontal gyrus in graphene-to-phoneme conversion and, more generally, in phonological processing, and are consistent with the view that lexical search for high frequency words requires less phonological mediation because they can be rapidly identified on the basis of visual word information. In addition, a recent fMRI study failed to show any significant effects of low vs. high lexical frequency words during reading aloud (Carreiras, Mechelli and Price, in press). Given these results, it is difficult to interpret the increase in the corticospinal excitability of the right hand muscles here reported for smaller numbers as compared to larger numbers as reflecting greater demand on lexical/phonological processes involved in covert naming. Furthermore, this interpretation based on lexical frequency does not appear to be in accordance with the results of Experiment 1B, in which no significant differences between larger numbers and control trials were found when stimulating the left motor cortex

Another possible interpretation of our results could come from an elegant neuroimaging study by Longcamp and colleagues (2003), showing that the visual presentation of letters automatically activates writing-related areas in the left premotor cortex. The increased corticospinal excitability found in the present study could then result from the implicit activation of handwriting movements in response to the visual presentation of digits. However, the absence of modulation between larger numbers and control trials observed in Experiment 1B makes this interpretation unlikely.

Hence, although the present study does not allow to fully reject a linguistic contribution of the left hemisphere, either through covert naming of the presented number or by implicit activation of handwriting movements, this modulation is much more likely to reflect the more frequent use of a finger embodiment strategy for representing smaller numbers. Accordingly, the use of the embodiment strategy should then primarily involve, at least for right-handed subjects, the right hand rather than the left one. This is particularly evident during childhood. At an early stage, it is obvious that representing numbers by means of finger is firstly restricted to numbers from 1 to 5 (Gelman and Gallistel, 2004; Butterworth, 2005). This period is considered to be crucial for the acquisition of meanings of cardinal numbers and, therefore, might represent a fundamental passage towards the development of a mature language-based counting system and the mastery of arithmetical operations. Also consistent with this view is the fascinating case report of a child who was born without forearms but experienced phantom hands and actually used their phantom fingers to count and solve arithmetic problems (Poek, 1969; cited by Ramachandran and Hirstein, 1998).

Finally, an important question raised by the present study concerns the specificity of the effect. Indeed, the use of only one ordinal sequence, that of numbers, does not allow us to distinguish between number related processes in particular and ordinal sequence processing in general (e.g. when processing months, days of the week or letters) for which the necessity of a one-to-one mapping is the common factor. Further experiments are required to test if other ordinal sequences than numbers might also be embodied to some degree in the sensory-motor system.

In conclusion, we suggest that the present results may reflect a trace, an echo, of a finger embodiment strategy, developed in childhood and used to represent and manipulate numbers. This strategy, constrained by our bodily experience (Lakoff and Nunez, 2000) and mapped within the sensory-motor system, might still be automatically evoked during number processing.

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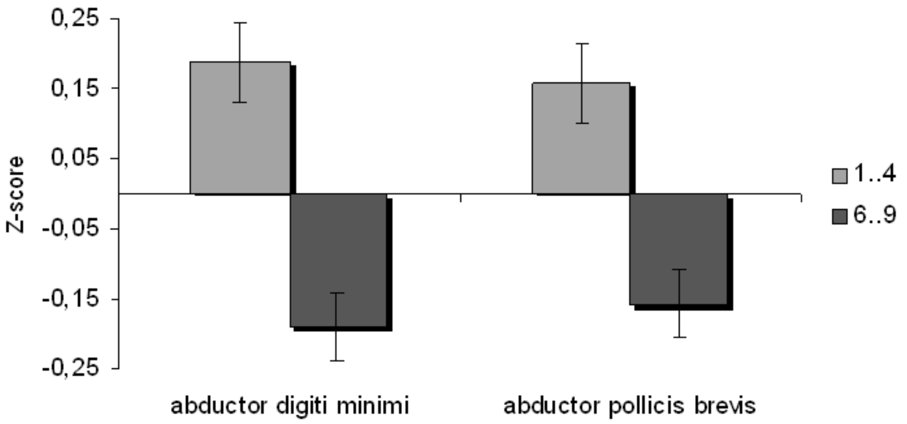
FIGURES

Figure 1. Average value of normalized MEP amplitudes of the contralateral *abductor digiti minimi* and *abductor pollicis brevis* muscles during parity judgment for smaller (1-4) and larger (6-9) numbers in Experiment A. (A) Stimulation of the left motor cortex; (B) Stimulation of the right motor cortex. Error bars represent standard errors of the mean (n = 8).



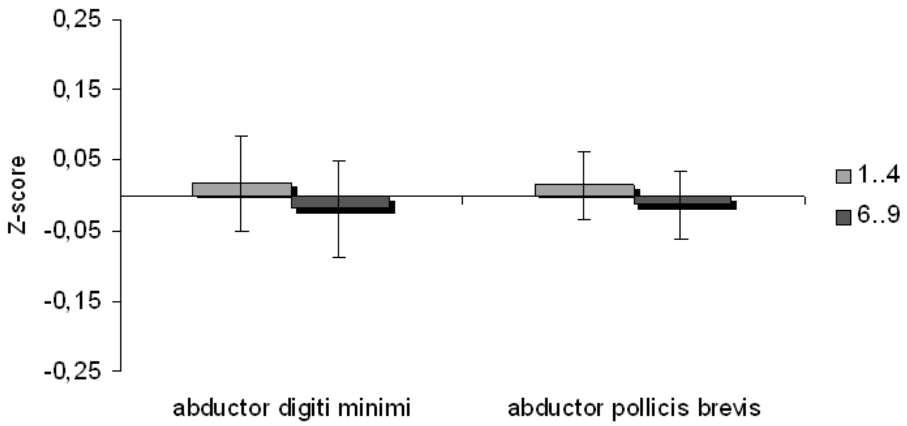
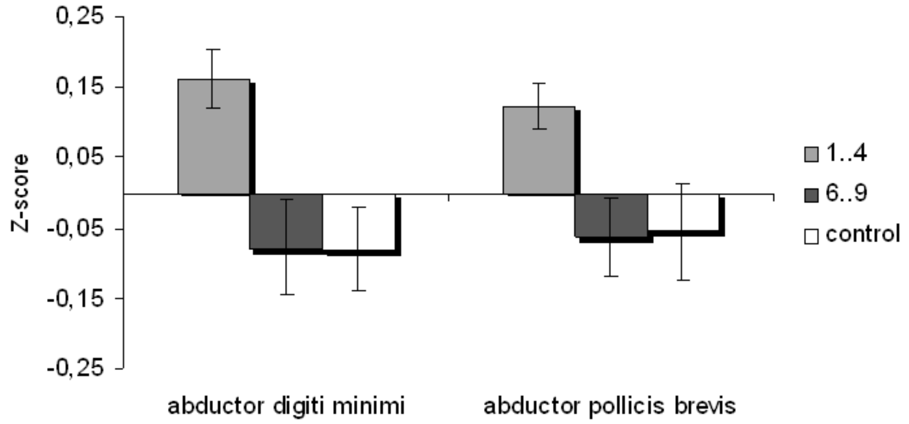


Figure 2. Average value of normalized MEP amplitudes of the contralateral *abductor digiti minimi* and *abductor pollicis brevis* muscles during parity judgment for smaller (1-4) and larger (6-9) numbers and control trials in Experiment B. (A) Stimulation of the left motor cortex; (B) Stimulation of the right motor cortex. Error bars represent standard errors of the mean (n = 8).



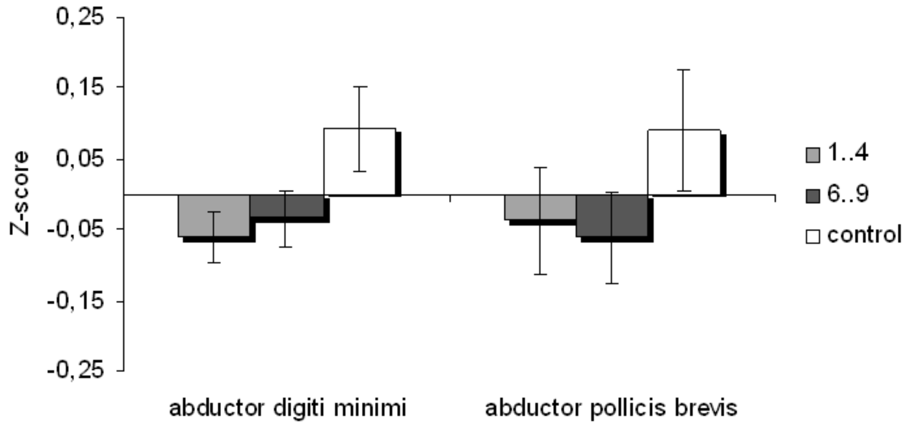


Figure 3. Mean reaction times observed in Experiment 2 according to the hand response (left/right) and the parity criteria (odd/even). Error bars represent standard errors of the mean (*n* = 22).