Contribution of Hand Motor Circuits to Counting

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Abstract

■ The finding that number processing activates a cortical network partly overlapping that recruited for hand movements has renewed interest in the relationship between number and finger representations. Further evidence about a possible link between fingers and numbers comes from developmental studies showing that finger movements play a crucial role in learning counting. However, increased activity in hand motor circuits during counting may unveil unspecific processes, such as shifting attention, reciting number names, or matching items with a number name. To address this issue, we used transcranial magnetic stimulation to measure changes in corticospinal (CS) excitability during a counting task performed silently and using either numbers or letters of the alphabet to enumerate items. We found an increased CS excitability of hand muscles during the counting task, irrespective of the use of numbers or letters, whereas it was unchanged in arm and foot muscles. Control tasks allowed us to rule out a possible influence of attention allocation or covert speech on CS excitability increase of hand muscles during counting. The present results support a specific involvement of hand motor circuits in counting because no CS changes were found in arm and foot muscles during the same task. However, the contribution of hand motor areas is not exclusively related to number processing because an increase in CS excitability was also found when letters were used to enumerate items. This finding suggests that hand motor circuits are involved whenever items have to be put in correspondence with the elements of any ordered series. ■

INTRODUCTION

Functional imaging studies have repeatedly shown that processing numbers activates a frontoparietal cortical network partly overlapping that involved in the finger movement control (Pinel, Piazza, Le Bihan, & Dehaene, 2004; Connolly, Andersen, & Goodale, 2003; Piazza, Mechelli, Butterworth, & Price, 2002; Zago et al., 2001; Harrington et al., 2000; Pesenti, Thioux, Seron, & De Volder, 2000; Binkofski et al., 1999). Although it is tempting to regard these activations as reminiscent of the use of a finger-counting strategy in childhood (Butterworth, 1999), the actual contribution of hand motor circuits to number processing remains largely unknown.

Several observations support a close interaction between finger representation and numerical abilities. Indeed, in patients with Gerstmann syndrome, numerical deficits are sometimes observed in association with finger agnosia (Martory et al., 2003; Mayer et al., 1999; Gerstmann, 1930). A similar association of deficits has been found following a transient lesion of the left angular gyrus by means of either electrical (Roux, Boetto, Sacko, Chollet, & Tremoulet, 2003) or transcranial magnetic stimulation (TMS; Rusconi, Walsh, & Butterworth, 2005). Another observation supporting this privileged relationship between fingers and numbers is the use of finger-counting strategies, a universal behavior observed in several different cultures (Butterworth, 2000). In children, it has been shown that the performance in finger discrimination tasks better predicts the results in arithmetical tasks than standard developmental tests (Fayol, Barouillet, & Marinthe, 1998). This unique relationship between fingers and numbers is also suggested by anthropological observations showing, for example, that, in several languages, the word ''five'' has common ancestors with ''fingers,'' ''fist,'' or ''hand'' (Menninger, 1969).

The aim of the present study was to investigate the possible contribution of hand motor circuits to number processing in a dot counting task. Based on the aforementioned observations, it is sensible to assume that if hand motor circuits are involved in number representation, their excitability should be modulated during this task. However, before assigning a specific role to hand motor circuits in number processing, their possible contribution to nonspecific aspects of counting must be discarded. Indeed, even a simple dot counting task involves several processes, some of them being unrelated to access to number representation. These processes can be segmented as follows: (1) shifting attention to isolate each item, (2) reciting number names, (3) matching each item with a number name in a serial order, and (4) accessing cardinality. These different operations will be detailed in the next sections.

First, a crucial process in counting tasks is attention allocation in order to individuate each item. Indeed, the finding that the reaction time (RT) increases as a

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function of the item number suggests that counting relies on serial visual processes that necessitate attentional shifts (Trick & Pylyshyn, 1994; van Oeffelen & Vos, 1984). However, when only a few items (1–4) are presented simultaneously, they may be processed in parallel, in a much faster way, a phenomenon known as *subitizing* (Mandler & Shebo, 1982; Kaufman & Lord, 1949). Subitizing is characterized by a much shorter RT than counting and by a marginal increase in RT as a function of item number (Trick & Pylyshyn, 1994). The hypothesis that these two individuation strategies mobilize attentional resources in a different way is further supported by functional imaging studies showing an increased activation as the item number becomes larger than four, both in the posterior parietal cortex and in the frontal eye fields, two brain regions involved in attention allocation (Wardak, Ibos, Duhamel, & Olivier, 2006; Piazza, Giacomini, Le Bihan, & Dehaene, 2003; Piazza et al., 2002; Wardak, Olivier, & Duhamel, 2002, 2004; Sathian et al., 1999).

Second, the ability to enumerate number series correctly depends on the integrity of language processes. Seron et al. (1991) have shown that aphasic patients experience difficulties in counting large dot arrays and rely more often than control subjects on compensatory strategies such as counting aloud. Logie and Baddeley (1987) also underlined the role of the articulatory loop to update the intermediate result of counting in verbal working memory. Along the same lines, Piazza et al. (2002, 2003) have shown an increased activation in Broca's area during silent counting.

Third, counting also relies on the appropriate matching of each separate item with a number name in a serial order. According to the one-to-one correspondence principle, each item has to be associated with a unique number name (Fuson, 1988; Gelman, 1982). Developmental studies have suggested that accurate pointing with the hand may be a precursor in the acquisition of this principle because children apply the one-to-one correspondence principle in pointing movements before they are able to apply it with number names (Graham, 1999).

Fourth, the interpretation of the counting result relies on the understanding of cardinality (Gelman, 1982). Whereas the one-to-one correspondence principle can be applied to any ordered series, the notion of cardinality is specific to numbers. Some recent observations have suggested that finger representation could provide a support for cardinality. Indeed, Di Luca, Grana, Semenza, Seron, and Pesenti (2006) have found that the identification of Arabic digits ranging between 1 and 10 is performed faster when the finger used to press the response button matches the presented number, in accordance with a canonical representation of numbers on fingers. Moreover, telling how many fingers are raised on a hand picture activated regions in the left and right intraparietal sulci, similar to those activated by magnitude judgments on Arabic digits or number words (Thompson, Abbott, Wheaton, Syngeniotis, & Puce, 2004). This overlapping activation suggests that finger configurations may share common processes with symbolic numerical knowledge.

Whether hand motor circuits are involved in one, or several, of these processes is unknown and will be investigated in the present study. To do so, the corticospinal (CS) excitability of hand muscles was assessed during a counting task by recording motor evoked potentials (MEPs) induced by TMS applied over the primary motor cortex (M1). This method has proved successful in revealing subtle changes in CS excitability in different cognitive tasks (Pelgrims, Andres, & Olivier, 2005; Vargas et al., 2004; Fadiga, Craighero, Buccino, & Rizzolatti, 2002; Fadiga et al., 1999). If hand motor circuits are involved in number processing, we predict a specific increase in CS excitability of hand muscles during dot counting.

EXPERIMENT 1

Dots were presented simultaneously on a computer screen and participants had to enumerate them by using either numbers (numerical task) or letters of the alphabet (alphabetic task); CS excitability of hand muscles was measured during the task performance. If the involvement of hand motor circuits in counting is specific to number processing, we predict that MEP amplitude should be larger in the numerical than in the alphabetic task. The use of arrays containing different dot numbers should also allow us to investigate whether CS excitability is modulated differentially in subitizing and counting. In order to rule out the possible effect of attention on CS excitability, we designed a control task where subjects had to detect, in the same arrays, whether two adjacent dots had the same color (Figure 1A).

Methods

Participants

Twelve right-handed volunteers (7 women; age range, 20–30 years) participated in this experiment after providing informed consent. None of them reported neurological or visual impairments or mathematical disabilities. All participants were screened for adverse reactions to TMS by using the Transcranial Magnetic Stimulation Adult Safety Screen Questionnaire (Keel, Smith, & Wassermann, 2001). The TMS protocol was approved by the ethical committee of the Université catholique de Louvain.

TMS and Electromyography

TMS was delivered through a figure-eight coil (7-cm-diameter windings), connected to a Magstim 200 stimulator (Magstim, Whitland, UK). The coil was held tangentially over the left M1 hand area, with the handle pointing backward and forming an angle of 45° with the sagittal plane.

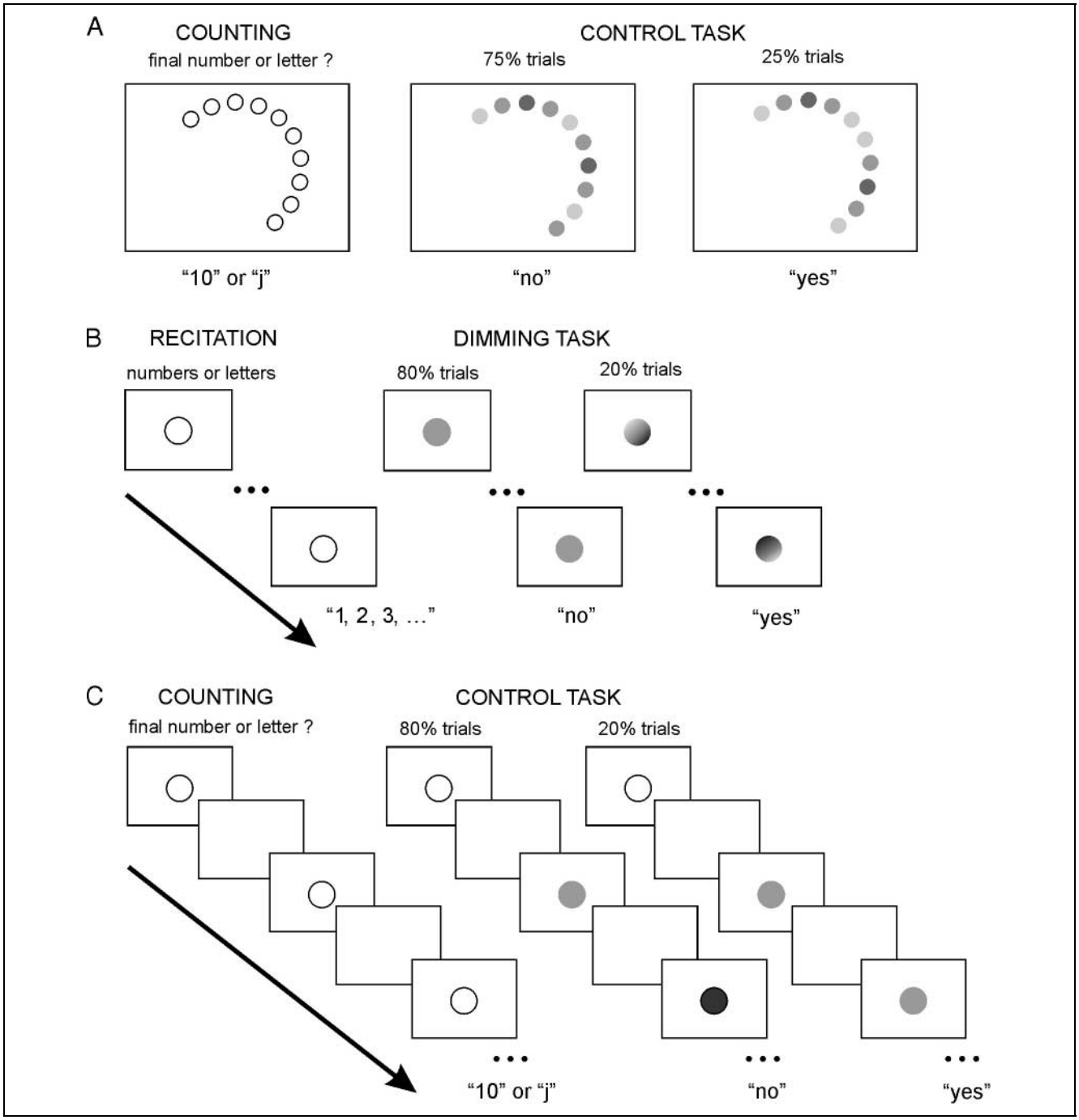

Figure 1. (A) Experiments 1 and 2. Dots were displayed simultaneously and participants were instructed to give the number of dots or the corresponding letter of the alphabet, in the counting tasks, and to detect whether two contiguous dots had the same color, in the control task. (B) Experiment 3. Participants were asked to recite silently the number series or the alphabet at 2 Hz while a single dot remained on the screen for a variable duration. The control task consisted in the detection of a brief dimming during the continuous dot display. (C) Experiment 4. Instructions were the same as in Experiments 1 and 2 but dots were flashed at an average frequency of 2 Hz.

Electromyographic (EMG) recordings were made from surface electrodes (Neuroline; Medicotest, Ølstykke, Denmark) placed on the right first dorsal interosseus (FDI) muscle. Participants wore earplugs to attenuate the coil noise. First, the hot spot in M1 was located by searching the stimulation site where TMS elicited the largest MEPs in the FDI. This position was marked on a closely fitting EEG cap and the TMS coil was held at that position by means of a mechanical arm for the whole duration of the experiment. TMS intensity was set at 120% of the motor threshold at rest, defined as the minimum intensity required to generate an MEP in 5 out of 10 trials (peak-to-peak amplitude, $\geq$50 μV). The average intensity ($\pm$ *SD*) was 47 $\pm$ 6% of the maximal stimulator output. EMG recordings started 2000 msec before the TMS pulse and lasted for 5000 msec. The raw EMG signal was

amplified (gain, 1000) and high-pass filtered at 10 Hz (Neurolog; Digitimer, Welwyn Garden City, UK), digitized at 5 kHz (CED 1401; Cambridge Electronic Design, Cambridge, UK) and stored on a PC for off-line analyses (Signal, Cambridge Electronic Design).

Stimuli

Stimuli consisted in dot arrays containing either 1–4 or 9–12 dots presented on a computer screen placed at a distance of 60 cm. In the numerical and alphabetic tasks, stimuli were white dots displayed on a black background. In order to reduce the use of perceptual grouping strategies, the dots were displayed along a fictive circle (diameter 25, 30, or 35 cm) centered on the screen center (see Figure 1A). The first dot of the array could appear, with equal probability, at 12 possible locations along this circle (steps of 30°). Moreover, to avoid guessing strategies based on an explicit relationship between the length of the array and numerosity, both dot size (0.5, 0.7, or 0.9 cm) and spacing (0.4 or 0.5 cm) were varied systematically across trials. However, in a given trial, dot size and spacing were constant. For each numerosity, 12 arrays of different lengths and curvatures were created and each of them was used only once in each task. The visual angle of the stimuli varied as a function of the number of dots but never exceeded 12°. The same stimuli were used in the control task (see below) but the dot color varied between light and dark gray (20%, 40%, or 60% black). In control trials, each neighboring dot had a different color (maximal 20% step) except in 25% of the trials, where two contiguous dots had the same color; the location of these two identical dots varied randomly in the array.

Procedure

Each trial began with the presentation of a cross on the screen center for 500 msec; this fixation cross was then turned off and the dot array was displayed 500 msec later. The array remained on the screen till the participant provided a response. The next trial started 3000 msec after the participant's response. A personal computer was used to control the dot display (E-Prime V1.0; Psychology Software Tools, Pittsburgh, PA).

Counting was performed by using either the numbers or letters. In the numerical task, participants were asked to report the number of dots; in the alphabetic task, they were instructed to assign a letter to each dot following the alphabetic order and to report the letter corresponding to the last dot. The control task consisted in detecting arrays where two contiguous dots of the same color were present; the response was either ''yes'' or ''no'' (Figure 1A). These three tasks were performed silently with both hands completely relaxed. Only the final answer had to be given aloud, triggering the microphone used to measure the RT. Responses were also tape-recorded to analyze the error rate off-line. The instructions emphasized the need to answer fast and accurately.

At the beginning of each session, participants also had to perform a naming task in order to take into account possible differences in the time necessary to retrieve number and letter names (i.e., naming RT). Participants were asked to name as quickly as possible Arabic digits randomly selected between 1 and 20, uppercase letters between A and T, or the words yes and no. Each stimulus was presented five times. Naming RTs were collected in the absence of TMS.

Each task started with 10 practice trials. The numerical and alphabetic tasks consisted of 72 trials each, presented in two successive blocks of 36 trials. Each numerosity between 1 and 4 was presented 6 times and each numerosity between 9 and 12 was presented 12 times in each task. The control task included two successive blocks of 48 trials where the proportions of small (1–4) and large (9–12) numerosities were identical to those reported for the counting task.

Single-pulse TMS was applied over the left M1 200 msec after the display of small arrays (1–4 dots) and either 200 or 1700 msec after the display of large arrays (9–12 dots). We could not test the 1700-msec delay for small arrays because the mean RT for this condition was around 1000 msec. Array size and TMS timing were randomly intermingled within each block. In the control task, trials where two contiguous dots had the same color were randomly intermingled. The task order was counterbalanced across the 12 participants.

Data Analysis

Error rates were computed separately with respect to the task (numerical, alphabetic, and control) and range (1–4 and 9–12) and a repeated measures analysis of variance (ANOVA) was performed with these two factors as within-subject variables. The control trials where two identical neighboring dots were present (25%) were not incorporated in the data analysis because, in these trials, it is unlikely that the entire array was processed. Therefore, *misses* (i.e., nondetection of two neighboring dots of the same color) were excluded from the ANOVA (mean ± *SD*, 18.8 ± 10.1%). As a consequence, analysis of errors in the control task was exclusively based on *false alarms* (i.e., an affirmative answer when no identical neighboring dots were present in the array).

For RT and MEP amplitude analyses, trials were discarded if (1) the MEP or the verbal response failed to be recorded properly (2.6%), (2) the answer was incorrect (5.4%), (3) the background EMG activity in the FDI exceeded 50 μV (0.6%), and (4) the MEP amplitude was outside the individual range of ± 3 *SD* (1.3%). In the remaining trials (90.1%), RTs were computed for each numerosity (1–4 and 9–12) and corrected with the cor-

responding naming RT. The regression line between the corrected RTs and numerosity was calculated for each task and range. Each slope value was then used as a dependent variable in a 3 (task: numerical vs. alphabetic vs. control) × 2 (range: 1–4 vs. 9–12) repeated measures ANOVA. For MEP analysis, because of their large inter-individual variability (Rossini & Rossi, 1998; Kiers, Cros, Chiappa, & Fang, 1993), peak-to-peak amplitudes were first normalized by computing z scores for each subject and then averaged with respect to task, range and TMS timing. A first ANOVA was performed on the normalized MEP values gathered when TMS was delivered 200 msec after the display in order to investigate the effect of the task (numerical vs. alphabetic vs. control) and range (1–4 vs. 9–12) on MEP amplitude. For the range 9–12, a second ANOVA was performed to determine the effect of the task and TMS timing (200 vs. 1700 msec) on normalized MEP values. Post hoc comparisons were made using bilateral paired t tests ($\alpha < .05$).

Additional ANOVAs were also performed to rule out that the effect of the task described in the Results section was due to differences in background EMG activity. These analyses showed that none of the aforementioned factors (task, range, and timing) influenced the root-mean-square (RMS) of the EMG signal recorded from the FDI during a 200-msec delay before the TMS (all p values $>.1$).

Results

Behavioral Results

The mean error rate ± *SD* was 2.8 ± 4%, 4.4 ± 5%, and 4.7 ± 6.7% in the numerical, alphabetic, and control tasks, respectively. As shown in Figure 2, the error rate was influenced by the range, $F(1,11) = 13.37$, $p < .01$, irrespective of the task ($F < 1$). Indeed, the mean error rate computed for the three tasks increased from 1.6 ± 3.6%, for the 1–4 range, to 5.2 ± 6.6%, for the 9–12 range.

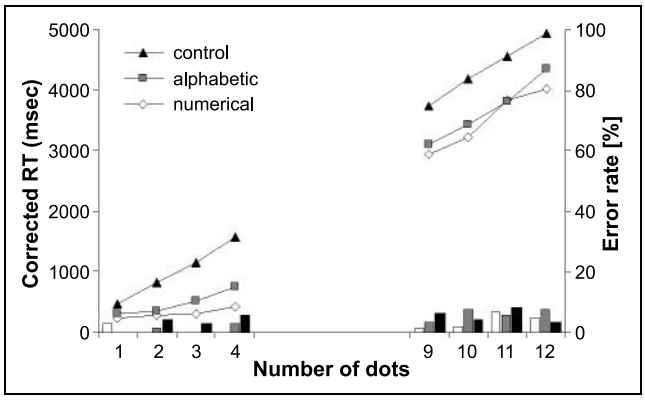

Figure 2. Error rate and RTs for the three tasks, as a function of the number of dots displayed on the screen (Experiment 1). RTs were corrected by subtracting the naming RT obtained for each possible answer in a separate task.

The slopes of the regression lines between the corrected RTs and dot number were computed for each task separately (see Methods). In all conditions, the slopes of the regression lines were different from 0 ($p < .05$). However, as illustrated in Figure 2, RTs were specifically influenced by dot number. In the 1–4 range, the slopes of the regression lines were different for the three tasks and increased from the numerical to the alphabetic and control tasks; in the 9–12 range, the three slopes were identical. The ANOVA performed on the slopes revealed a main effect of the task, $F(2,22) = 6.67$, $p < .001$, and range, $F(1,11) = 62.87$, $p < .001$, as well as an interaction between these two factors, $F(2,22) = 24.13$, $p < .001$. RTs gathered in the numerical and alphabetic tasks showed a classical dissociation between subitizing (small dot arrays) and counting (large dot arrays), as indicated by steeper slopes in the 9–12 range (numerical task, 381 ± 140 msec per item; alphabetic task, 415 ± 115 msec per item) than in the 1–4 range [numerical task, 61 ± 42 msec per item, $t(11) = 8.70$, $p < .001$; alphabetic task, 100 ± 192 msec per item, $t(11) = 9.45$, $p < .001$]. In contrast, in the control task, we failed to find evidence for an effect similar to subitizing, as shown by the absence of difference between the slopes measured in the 1–4 range (367 ± 125 msec per item) and 9–12 range [397 ± 167 msec per item, $t(11) = .71$, *ns*] in this condition.

Electrophysiological Results

The mean MEP amplitudes (± *SD*) for each condition are given in Table 1. We first investigated the effect of the task and range on the normalized MEP amplitude for the 200-msec TMS delay. Figure 3A illustrates typical MEPs gathered for one subject during these three tasks. An ANOVA showed a main effect of the task, $F(2,22) = 5.09$, $p < .01$, indicating that the MEP amplitude was smaller in the control task than in the numerical, $t(11) = 2.72$, $p < .05$, and alphabetic tasks, $t(11) = 2.19$, $p < .05$, whereas there was no significant difference between the MEP amplitude recorded in these two tasks, $t(11) = .32$, *ns*. The range had no influence on MEP amplitude and did not interact with the task (Fs <1; see Figure 3B).

Table 1. Mean MEP Amplitude in mV (± *SD*) as a Function of Task, TMS Timing, and Range of Dots in Experiment 1

	Control	*Numerical*	*Alphabetic*
TMS 200 msec			
Range 1–4	1.968 ± 0.94	2.432 ± 1.249	2.334 ± 1.122
Range 9–12	1.926 ± 0.91	2.378 ± 1.187	2.341 ± 1.169
TMS 1700 msec			
Range 9–12	2.223 ± 1.069	2.606 ± 1.453	2.599 ± 1.477

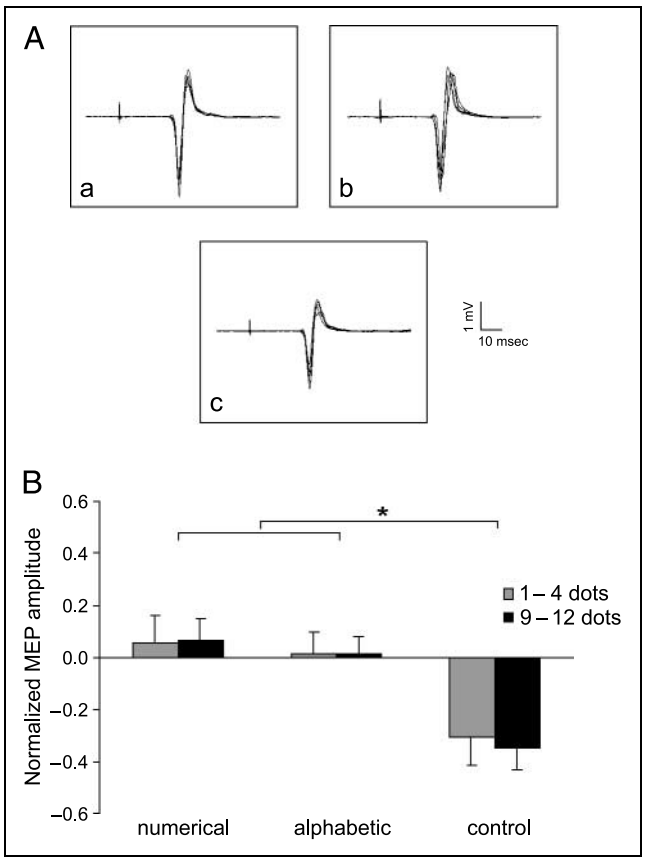

Figure 3. (A) Five representative MEPs, recorded in a sample participant, during the (a) numerical, (b) alphabetic, (c) and control tasks in Experiment 1. (B) Average values (± *SE*) of intrasubject normalized MEP amplitude for each task, as a function of the range of dots (Experiment 1).

The effect of the TMS timing on the MEP amplitude was investigated for these three tasks by comparing the amplitude of MEPs gathered at two different delays (200 and 1700 msec). Because of the very short RTs for the 1–4 range, this analysis was only possible for the 9–12 range (see Methods). Both the task, $F(2,22) = 4.17$, $p < .05$, and timing, $F(1,11) = 13.13$, $p < .01$, had a significant effect, but the two-way interaction was not significant, $F(2,22) = 1.52$, *ns*. MEP amplitude was larger in the numerical task than in the control task, $t(11) = 2.78$, $p < .05$, irrespective of the timing. A marginal difference was also found between the alphabetic task and control task, $t(11) = 2.13$, $p < .06$, whereas MEP amplitude in the numerical and alphabetic tasks was not different, $t(11) = .31$, *ns*. Regarding the main effect of timing, TMS applied 1700 msec after dot presentation yielded larger MEPs than when delivered at 200 msec (Figure 4).

EXPERIMENT 2

Results from Experiment 1 have demonstrated an increase in CS excitability of FDI when either numbers or letters were used to enumerate dots. In order to determine whether this effect was specific to hand muscles, as expected if reminiscent of a finger-counting strategy, a similar experiment was conducted for hand, arm, and foot muscles. This issue was investigated only for the 1700-msec delay and for large numerosities (range, 8–13) and only in the numerical and control tasks, because Experiment 1 did not evidence a difference between results gathered for the alphabetic and numerical tasks.

Methods

Participants

Twelve right-handed volunteers (6 women; age range, 21–29 years) were recruited following the same criteria as in Experiment 1. Three of them had already participated in Experiment 1.

TMS and Electromyography

The experimental setup was the same as in Experiment 1. MEPs were recorded from the right FDI, the right biceps brachialis (BB), and the right tibialis anterior (TA). A common hot spot was used for both the FDI and the BB and the coil was placed over an intermediate position between the hand and arm areas of the left M1, with the handle pointing backward and forming an angle of 45° with respect to the sagittal plane. The motor threshold for the FDI and the BB was defined as the minimal TMS intensity required to elicit MEPs in 5 out of 10 trials simultaneously in both muscles. For the TA, the largest MEPs were evoked with the coil placed over the vertex, perpendicularly to the sagittal plane and with the handle pointing rightward. For the whole experiment, TMS intensity was set at 120% of the motor threshold at rest, corresponding to 46 ± 6% (mean ± *SD*) of the maximal stimulator output for the FDI and BB and to 68 ± 9% for the TA.

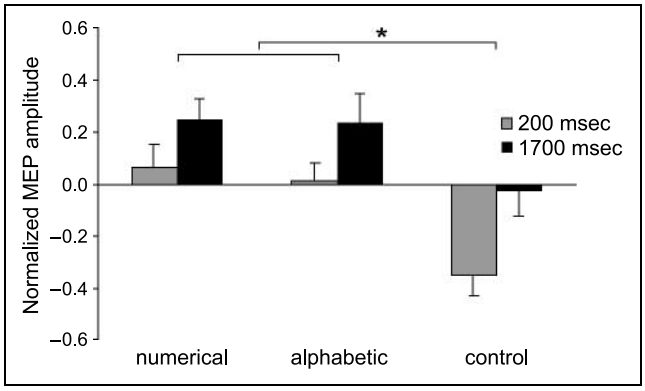

Figure 4. Average values (± *SE*) of intrasubject normalized MEP amplitude as a function of the task and TMS timing (Experiment 1).

Stimuli and Procedure

Participants performed only the numerical and control tasks (Figure 1A). Stimuli consisted of arrays of 8 to 13 dots. Eight different arrays were created for each numerosity by varying the curvature, dot size, and spacing (see Experiment 1). The setup used to display the stimuli and record the RTs was the same as in Experiment 1. Instructions emphasized the need to keep hand, arm, and foot muscles completely relaxed. Naming RTs were also collected at the beginning of the experiment to correct the RTs for both tasks. Subjects performed 10 practice trials from each task in the absence of TMS. Then, participants performed two blocks of 24 trials for the numerical task and two blocks of 32 trials for the control task. In the numerical task, each numerosity was presented eight times. The control task was the same as in Experiment 1: In each block, there were eight trials with two neighboring dots of the same color. In the remaining 24 trials, each numerosity was presented in equal proportions. Numerosity, curvature, dot size, and spacing were randomly intermingled within each block.

In every trial, an MEP was recorded by applying a single-pulse TMS over the left M1 1700 msec after the stimulus display. Half of the participants started Experiment 2 with a block from each task while MEPs were recorded from the upper limb muscles; another series of two blocks was then performed while MEPs were recorded from the TA. In other participants, MEPs were first recorded from the TA and then from the FDI and BB. Task order was counterbalanced across participants but remained unchanged during the recording of upper and lower limb muscles.

Data Analysis

We used the same procedure as in Experiment 1 to analyze errors in the numerical and control tasks. In the control task, the rate of misses reached 18.8 ± 12.8%; only the false alarms were included in the error analysis (see Data Analysis of Experiment 1). For the analysis of RT and MEP amplitude, trials were discarded if (a) the MEP or the verbal answer failed to be recorded (0.8% of the data); (b) subjects gave an incorrect response (4.5%); (c) the background EMG activity exceeded 50 μV in the FDI (1%), the BB (0.4%), or the TA (0.3%); and (d) the MEP amplitude was outside the individual range of ± 3 *SD* (1.3%).

In the remaining trials (91.7%), RTs were averaged for each combination of task and numerosity and corrected by subtracting the corresponding naming RT. For each subject, we computed the slope of the regression line between the corrected RTs and numerosity for the two tasks. The individual slopes were compared across tasks using paired t tests ($\alpha < .05$). Moreover, the peak-to-peak MEP amplitude was normalized by computing z scores for each subject and muscle, and unilateral paired t tests were used to test the hypothesis that CS excitability was larger in the numerical than in the control task; this a priori hypothesis was based on results of Experiment 1 gathered for the FDI. Complementary analyses failed to reveal any effect of the task on the RMS of the EMG signal recorded in the FDI, BB, and TA over a period of 200 msec before TMS (all p values $>.1$).

Results

Behavioral Results

The mean error rate (± *SD*) was 3.1 ± 4.3% in the numerical task and 1.2 ± 2.9% in the control task, $t(11) = 1.69$, $p < .1$ (Figure 5). In both tasks, the corrected RTs increased significantly with the number of dots in the array (p values $<.001$; Figure 5). However, the slope of RTs was steeper in the numerical task (385 ± 123 msec) than in the control task (230 ± 108 msec), $t(11) = 4.47$, $p < .001$.

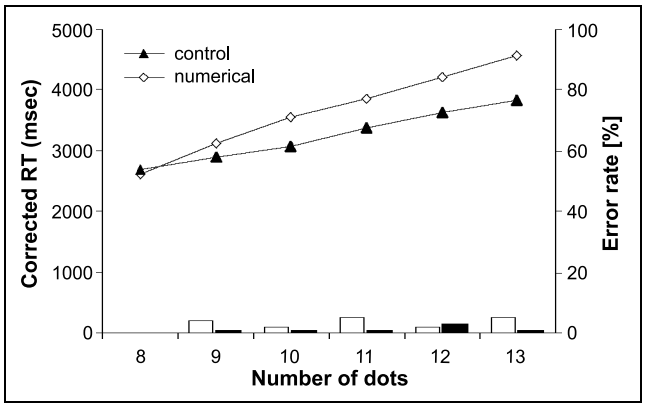

Figure 5. Error rate and RTs for the numerical and control tasks, as a function of the number of dots displayed on the screen (Experiment 2). RTs were corrected as described in Experiment 1.

Electrophysiological Results

The mean amplitude (± *SD*) of the MEPS gathered in the numerical and control tasks is given in Table 2 for each muscle. As in Experiment 1, larger MEPs were found in the FDI during the numerical task than in the control

Table 2. Mean MEP Amplitude in mV (± *SD*) as a Function of Task and Muscle in Experiment 2

	Control	*Numerical*
FDI	2.95 ± 2.146	3.435 ± 2.504
BB	0.674 ± 0.488	0.693 ± 0.469
TA	0.712 ± 0.408	0.714 ± 0.414

task, $t(11) = 1.86$, $p < .05$. In contrast, as illustrated in Figure 6, the MEP amplitude in BB, $t(11) = .93$, *ns*, and TA, $t(11) = .25$, *ns*, were identical in both the control and numerical task.

EXPERIMENT 3

Although in Experiments 1 and 2 the participants were asked to perform the counting tasks in silence, we cannot rule out that the increased CS excitability of hand muscles resulted from subvocal articulation. Indeed, several studies have suggested interactions between Broca's area and the M1 hand area (Oliveri et al., 2004; Meister et al., 2003; Seyal, Mull, Bhullar, Ahmad, & Gage, 1999; Tokimura, Tokimura, Oliviero, Asakura, & Rothwell, 1996). To investigate whether subvocal articulation could explain the increase in hand muscle activity we observed in the counting tasks, we measured CS excitability of the FDI during a mental recitation task. Mental recitation of either numbers or letters was performed at 2 Hz while a dot was continuously displayed on the screen for the whole trial duration. A dimming task was used as control (Figure 1B).

Methods

Participants

Twelve participants (7 women; age range, 20–45 years) were recruited according to the same criteria as in Experiment 1. Five of them had already participated in Experiment 1 or 2.

TMS and Electromyography

The experimental setup was the same as in Experiment 1. MEPs were recorded from the right FDI by using the same procedure as in Experiment 1. TMS intensity was set at 120% of the individual motor threshold at rest, that is, 49 ± 10% (mean ± *SD*) of the maximal stimulator output. To ensure that enumeration was performed silently, electrodes were also placed on the right zygomatic muscle.

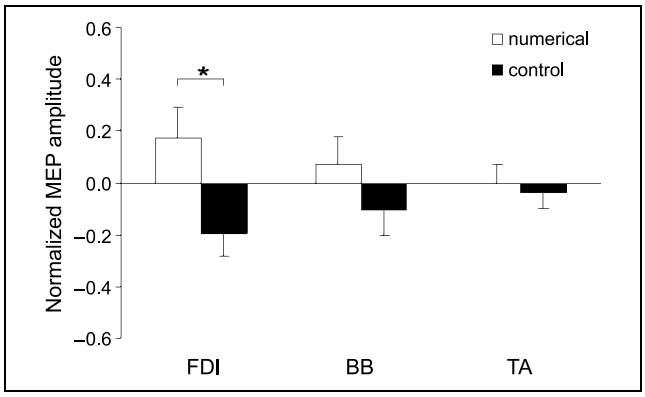

Figure 6. Average amplitude (± *SE*) of the MEPs recorded in hand (FDI), arm (BB), and foot (TA) muscles during the numerical task and the control task (Experiment 2). MEPs were normalized as described in Experiment 1.

Stimuli and Procedure

Each trial started with the display of a central fixation cross for 500 msec and, after a 500-msec delay, a white dot (diameter, 3 cm) on a black background was displayed at the screen center for 4500, 5000, 5500, or 6000 msec. The dot color remained constant, except in 20% of the control trials where a brief dimming (500 msec) occurred at a random time. A trial ended with the presentation of a question mark that appeared 1000 msec after the dot offset. The next trial started 1000 msec after the participant's response. The setup used to display the stimuli was the same as in Experiments 1 and 2.

Participants were asked to recite mentally the number series or the alphabet at 2 Hz. A metronome was used before the TMS session to get the participants acquainted with that rhythm. Mental recitation started when the dot appeared on the screen and participants had to report their response (i.e., last number or letter at dot offset) when the question mark was displayed. Instructions emphasized the importance of using a constant rate during mental recitation. In the control task, participants were asked to report whether dot color had dimmed or not during the display (Figure 1B). Responses were tape-recorded; each task was preceded by 10 practice trials without TMS.

The numerical and alphabetic tasks included 32 trials each, equally counterbalanced across the four display durations, that is, 4500, 5000, 5500, or 6000 msec (expected responses, 9 or I, 10 or J, 11 or K, 12 or L, respectively). The control dimming task included 40 trials: in 32 of them, a ''no'' answer was expected; a ''yes'' answer was expected in the others. In half of the trials, TMS was delivered over the left M1 hand area at the beginning of the trial, that is, 1000 or 1500 msec after the dot appeared. In the other half, the TMS was applied at the end, that is, with a 3500- or 4000-msec delay. These four TMS delays were randomly intermixed in each block.

Data Analysis

In the recitation tasks, answers were not classified as correct or false but a correlation was measured between the observed and predicted answers, as expected if recitation was performed at 2 Hz. Control trials where a dimming occurred were discarded from statistical analyses. Trials were also excluded if (a) the TMS-induced MEP failed to be recorded (0.5% of the data), (b) the answer to the dimming task was incorrect (0.3%), (c) the

background EMG activity exceeded 50 μV in the FDI (0.5%) or 100 μV in the zygomatic muscle (0.2%), and (d) the MEP amplitude was outside the individual range of ± 3 *SD* (1.1%).

The remaining trials (97.4%) were entered in the following analyses. Peak-to-peak MEP amplitude was normalized as in Experiments 1 and 2 and those values were used as a dependent variable in an ANOVA with task (numerical, alphabetic, and control) and timing (1000–1500 vs. 3500–4000 msec) as within-subject factors. EMG background activity in the FDI and zygomatic muscles did not differ across the different conditions, as shown by complementary analyses performed on the RMS of the EMG signal recorded over a 500-msec time window before the TMS pulse (all p values >.1).

Results

Behavioral Results

The average rate of recitation was 1.96 ± 0.16 Hz for numbers and 2.02 ± 0.17 Hz for letters. The correlation between the observed and predicted answers was .95 ($p < .001$) in number recitation and .98 ($p < .001$) in letter recitation. In the dimming task, we found 1 ± 4% of misses and 1 ± 2% of false alarms.

Electrophysiological Results

The mean MEP amplitude (± *SD*) is reported in Table 3 for each condition. MEP amplitude was not influenced by the task ($F < 1$), indicating that CS excitability of hand muscles while reciting numbers and letters did not differ from the control condition. The main effect of the timing and the interaction between the task and timing were not significant (p values >.1).

EXPERIMENT 4

Results from Experiment 3 suggest that the increased CS excitability found in Experiments 1 and 2 is not due to subvocal articulation but is rather specific to a process involved in the use of ordered series to enumerate items. In order to investigate further this process, we examined whether hand motor circuits are involved in counting tasks that do not require spatial processing. Indeed, it could be hypothesized that CS excitability increased in the counting tasks of Experiment 1 because these tasks involved the matching of numbers and letters with items presented at different spatial locations. To address this issue, we replicated Experiment 1 but while presenting dots sequentially at a unique spatial location (Figure 1C).

Table 3. Mean MEP Amplitude in mV (± *SD*) as a Function of Task and TMS Timing in Experiment 3

	Control	*Numerical*	*Alphabetic*
TMS 1000–1500 msec	1.541 ± 1.043	1.541 ± 1.053	1.532 ± 1.048
TMS 3500–4000 msec	1.546 ± 1.045	1.535 ± 1.046	1.538 ± 1.053

Methods

Participants

Subjects were the same as those of Experiment 3. Half of them performed the recitation task (Experiment 3) before Experiment 4.

TMS and Electromyography

The TMS protocol was the same as in Experiment 3.

Stimuli and Procedure

In the counting tasks, 9 to 12 white dots (diameter, 3 cm) on a black background were flashed sequentially at the screen center. In the control task, dot color was white, light, or dark gray (i.e., 0%, 40%, or 80% black). During a given trial, each dot was different from the previous one (40% step) except in 20% of the trials where two successive dots had the same color.

At the beginning of each trial, a fixation cross was displayed for 500 msec and dots were flashed 500 msec later. Each dot was displayed for 200 msec and, in a given trial, the time interval between dots ranged between 200 and 400 msec. The time interval between dots varied pseudorandomly in order to make sure that the participants could not provide a correct response simply by reciting numbers or letters at a constant rate. However, in a given trial, the mean display rate was always equal to 2 Hz and the duration of 9-, 10-, 11-, and 12-dot series was, as in Experiment 3, equal to 4500, 5000, 5500, and 6000 msec, respectively. Each trial ended by a question mark that appeared 1000 msec after the last dot and was turned off after the participant's response; the next trial started after a delay of 1000 msec.

As in Experiment 1, participants were instructed to enumerate silently the flashed dots, using either the numbers or letters. The answer (i.e., last number or letter) was given aloud after the question mark display. The control task consisted in detecting two successive dots of the same color and participants had to answer yes or no when the question mark was displayed on the screen (Figure 1C). Responses were tape-recorded. Each task was preceded by 10 practice trials without TMS. The timing of TMS and the proportion of trials

in the numerical, alphabetic, and control tasks was the same as in Experiment 3. Task order was counterbalanced across participants.

Data Analysis

We discarded from statistical analyses all control trials where two successive dots had the same color (30 ± 16% of misses) because, in this condition, participants did not have to process all dots. Therefore, as in Experiment 1, only false alarms were taken into account to compute the error rate in the control task. Trials were also excluded if (a) the TMS-induced MEP failed to be recorded (1.5% of the data), (b) an erroneous response was provided (16%), (c) the background EMG activity exceeded 50 μV in the FDI (1.1%) or 100 μV in the zygomatic muscle (0.3%), and (c) the MEP amplitude was outside the individual range of ± 3 *SD* (1.1%). In the remaining trials (80%), MEP amplitude was normalized as in previous experiments and used as a dependent variable in an ANOVA with task (numerical, alphabetic, control) and timing (1000–1500 vs. 3500–4000 msec) as within-subject factors. There was no difference between conditions in EMG background activity in the FDI and zygomatic muscles (all p values >.1).

Results

Behavioral Results

The error rates were 13 ± 11%, 15 ± 15%, and 19 ± 13% in the numerical, alphabetic, and control tasks, respectively ($t < 1$).

Electrophysiological Results

The mean MEP amplitude (± *SD*) is reported for each condition in Table 4. As illustrated in Figure 7, CS excitability of hand muscles increased during number and letter enumeration when compared with the control task, $F(2,22) = 4.60$, $p < .05$. As in Experiment 1, we found that MEP amplitude was significantly smaller in the control task than in the numerical, $t(11) = 2.99$, $p < .01$, and alphabetic tasks, $t(11) = 2.04$, $p < .07$, whereas these two tasks did not differ from each other, $t(11) = 1.24$, *ns*. We also found a significant effect of the timing, $F(1,11) = 4.80$, $p < .05$, on MEP amplitude. Indeed, MEP amplitude was larger when TMS was delivered after 3500–4000 msec than after 1000–1500 msec (Figure 7). The interaction between the task and timing was not significant ($F < 1$).

Table 4. Mean MEP Amplitude in mV (± *SD*) as a Function of Task and TMS Timing in Experiment 4

	Control	*Numerical*	*Alphabetic*
TMS 1000–1500 msec	1.502 ± 1.374	1.932 ± 1.744	1.672 ± 1.473
TMS 3500–4000 msec	1.698 ± 1.497	2.164 ± 1.755	1.765 ± 1.626

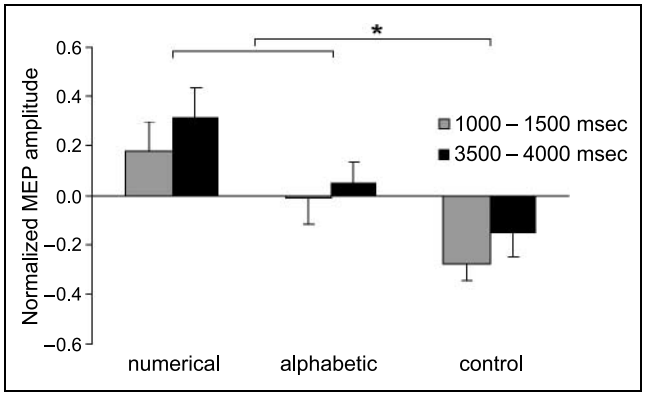

Figure 7. Average values (± *SE*) of intrasubject normalized MEP amplitude as a function of the task and TMS timing (Experiment 4).

DISCUSSION

The present results demonstrated an increased CS excitability of hand muscles in counting tasks irrespective of the use of numbers or letters to enumerate items. This finding challenges the hypothesis that hand-motor-related areas play a specific role in number processing. Before discussing these results, some important methodological issues regarding the interpretation of such changes in CS excitability during cognitive tasks have to be clarified.

Methodological Issues: Interpretation of CS Excitability Changes

Several points have to be taken into account before interpreting the present findings. First, the absence of task-related changes in background EMG activity allows us to rule out the influence of voluntary motor activity on MEP amplitude. Second, it is noteworthy that, although TMS was applied over M1, any change in CS excitability may result not only from an increased M1 excitability but also from excitability changes in any nonprimary motor area connected with M1 or even in the spinal cord circuitry. Therefore, TMS does not allow us to determine the exact origin of the task-related increase in CS excitability we observed. However, because functional imaging studies have repeatedly found an increased activation in the premotor and parietal areas during number processing (Piazza et al., 2002; Zago et al., 2001; Pesenti et al., 2000), it is sensible to assume that they are re-

sponsible for the increased CS excitability we reported in the present study.

Role of Hand Motor Circuits in Counting

We found that CS excitability increased in counting tasks irrespective of the use of numbers or letters, suggesting that the contribution of motor-related areas is not specific to number processing. Moreover, because this increased CS excitability was identical when counting small (1–4) or large (9–12) dot arrays, it indicates that this change in MEP amplitude was not related to the use of subitizing or counting strategies (Experiment 1). In addition, we found that this increase in CS excitability is specific to hand muscles because no comparable changes were observed for arm and foot muscles (Experiment 2). Finally, we demonstrated that changes in CS excitability during counting are not due to mental recitation of numbers and letters (Experiment 3), an interpretation suggested by the finding that speech may influence hand muscle excitability (Oliveri et al., 2004; Meister et al., 2003; Seyal et al., 1999; Tokimura et al., 1996).

Although neither the individuation strategy (subitizing or counting) nor mental recitation seems to be sufficient on its own to explain the increased CS excitability we found during counting, it could be hypothesized that the combination of these two processes may lead to larger MEP amplitude, because such a combination could require additional resources. Indeed, in the counting tasks (Experiments 1 and 2), the assignment of a number or a letter name to items presented in multiple spatial locations relies on a successful interaction between these two processes. However, Experiment 4 showed that the CS excitability also increased when dots were presented sequentially at a unique spatial location, suggesting that it is not related to the association of number/letter names with spatially distributed items. Therefore, it is sensible to assume that motor-related areas are involved in counting tasks whenever items have to be put in correspondence with the elements of an ordered series.

However, this interpretation has to be put together with the finding that counting led to a larger CS excitability only in intrinsic hand muscles and not in arm and foot muscles (Experiment 2). One possible explanation for this specificity comes from developmental studies. Indeed, as already mentioned in the Introduction, it has been shown that children apply the one-to-one correspondence principle in pointing movements before applying it to number names (Graham, 1999). In addition, they make fewer counting errors when they perform the pointing movements themselves than when the gestures are performed by the experimenter (Alibali & DiRusso, 1999). These results illustrate how hand and finger movements contribute to structure counting abilities during development by linking object individuation with the recitation of the number names. Moreover, Fuson (1988) has suggested that finger movements in children reflect the one-to-one correspondence principle not only in space but also in time: The pointing–object correspondence ensures the spatial correspondence between the gesture and object location, whereas the word–pointing correspondence allows the temporal adjustment between the production of a number name and gestures.

Because fingers provide a bodily counterpart to abstract number names, it has also been proposed that finger movements could facilitate the assignment of symbols to numerosities in children (Fayol & Seron, 2005). In particular, raising fingers in a given order, while reciting numbers, helps learning the sequence of number names. Moreover, the combined use of finger and verbal counting allows a transition from approximate to exact numerical knowledge, by linking the relations between objects and those between number names (Wiese, 2003). Therefore, it can be concluded that the specific involvement of hand motor circuits in counting may be reminiscent of the use of fingers to keep track of serial associations between items and number names. Our results suggest that such a strategy can be applied to items presented either simultaneously or sequentially and using elements from any ordered series.

Possible Involvement of Premotor Areas in Counting

Based on the present results, we propose a premotor theory of counting, similar to that proposed for spatial attention (Rizzolatti, Riggio, Dascola, & Umilta, 1987). As covert attentional shifts are thought to correspond to saccades that are planned but not executed, counting in adults could consist in building a motor plan for moving fingers sequentially without executing it. This hypothesis is supported by several studies on the role of premotor areas in finger movements. Indeed, activation of the premotor cortex is known to increase with the number of transitions in sequences of finger movements (Harrington et al., 2000). The involvement of the premotor cortex has also been demonstrated for imagined finger movements (Kuhtz-Buschbeck et al., 2003; Haslinger et al., 2002), a finding compatible with the idea that finger counting could be planned at a premotor stage, even in the absence of actual movements. Moreover, experiments on monkeys have shown that the premotor areas F2 and F4 contain neurons discharging in response to specific target locations during the preparation of goal-directed movements (Kakei, Hoffman, & Strick, 2001; Kurata, 1993). During counting, the tuning properties of such neurons would be particularly relevant to assure the pointing–object correspondence.

Subitizing in Letter Enumeration

Processing numbers and letters may share common features, as suggested by the finding that the use of

letters to enumerate dots led to the same dissociation between subitizing and counting as classically reported for numbers. Indeed, results of Experiment 1 revealed that, when using numbers or letters to enumerate 9–12 dots, RTs increased as a function of the number of dots by about 400 msec per item. This RT increase can be attributed to multiple processes, including attentional shifts and number or letter name retrieval. In contrast, in the 1–4 range, the slopes were 61 msec per item for number enumeration and 100 msec per item for letter enumeration. These values are consistent with results from the literature and suggest a parallel processing of collections of 1–4 items (Trick & Pylyshyn, 1993). To our knowledge, this is the first report of subitizing in letter enumeration.

The question arises as to what could explain the slight difference between the slopes obtained for number (61 msec per item) and letter enumeration (100 msec per item) in the subitizing range. Although subitizing does not require attentional shifts, the serial recall of the number or letter names is nonetheless necessary to perform the task. This operation could be responsible for the small but significant RT increase in the 1–4 range, as suggested by previous studies on number enumeration (Trick & Pylyshyn, 1993, 1994). Because the alphabetic task is less natural, we propose that it is more time consuming to recall the letter than the number names. In the counting range (9–12), this difference between the numerical and alphabetic tasks disappeared, probably because of the dominant influence of attentional shifts on RTs.

An intriguing question is whether subitizing for letters resulted from a fast conversion between numbers 1–4 and the first letters of the alphabet or from a parallel process unspecific to number processing. Subitizing has long been considered as a nonverbal process (also known as ''object-tracking system'') that yields discrete representations of small numerosities (Feigenson, Dehaene, & Spelke, 2004; Kaufman & Lord, 1949). However, because object individuation takes place in a preattentive stage of vision, it has been argued that subitizing is not specific to number processing (Nieder, 2005). Further research, using, for example, other letters of the alphabet, will be necessary to address this issue.

Conclusion

In conclusion, our study showed that CS excitability of hand muscles increased during counting because of the need to match individual items with the elements from an ordered series. This interpretation is compatible with developmental data showing that finger movements contribute to structure counting activities in children. We propose that, in counting tasks, the one-to-one correspondence between items and number names could involve the premotor cortex because of its role in conditioning finger movements to external and internal cues. Further research will be necessary to investigate the possible contribution of motor circuits to other arithmetical tasks.

Acknowledgments

This work was supported by Grant 01/06-267 from the Communauté Française de Belgique—Actions de Recherche Concertées (Belgium), Grant P5/1/5 IAP program from the Belgian Federal Government, and Grant 3.4508.02 from the Fonds pour la Recherche Scientifique Médicale (FRSM, Belgium). This project was also supported by a grant from the Fondation Médicale Reine Elisabeth (FMRE, Belgium). M. A. is research assistant at the Fonds National pour la Recherche Scientifique (FNRS, Belgium).

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