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RESEARCH ARTICLE

Grasping numbers

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Abstract Both theoretical and empirical studies suggest that numerical processing is intimately linked to representations of goal-directed hand actions. Further evidence for this possibility is provided here by the results of two experiments, both of which revealed a powerful influence of numerical magnitude on the selection of hand grasping movements. Human participants performed either power or precision grip responses based on the semantic properties (e.g., parity) of visual Arabic numerals, in Experiment 1, or depending on their surface characteristics (e.g., colour), in Experiment 2. In both the experiments, it was found that small numerical values facilitated precision grip (commonly used to grasp small objects), while large numerical value potentiated power grip (commonly used to grasp large objects). These findings reveal that perceiving numbers can automatically prime grasping gestures, in a similar manner to viewing physical objects. This result is coherent with the view that processing of symbolic (numerical) and physical quantitative information converges onto a shared magnitude system representing the coordinates of action.

Keywords Number processing · Numerical magnitude · Grasping · Parietal lobe · Stimulus–response compatibility · Action selection · Hand–object interaction · Visuomotor transformation

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Introduction

Numbers pervade almost every aspect of our everyday life. We use them to measure, quantify and symbolically represent different dimensions of objects and events in the world. Links between number and space, as well as between number and time have been shown in several behavioural and functional studies (see Walsh 2003; Hubbard et al. 2005; Nieder 2005 for recent reviews). Dehaene et al. (1993), for example, showed that participants asked to classify numbers as even or odd (parity judgement) were quicker to respond to larger numbers when responses were made on the right side of space, whereas they were quicker to respond to smaller numbers when the responses were made on the left. This effect was labelled the SNARC (Spatial–Numerical Association of Response Codes) effect, and has been taken as evidence that representations of numerical magnitude are spatially coded and can be conceptualized as a "mental number line" on which numbers are arranged in ascending order from left to right.

Theoretical and empirical work, however, also argue in favour of a close connection between number representations and hand actions. Neuroimaging studies, for instance, have identified partly overlapping parieto-frontal circuits for numerical processing and goal-directed hand actions (Rueckert et al. 1996; Dehaene et al. 1996; Stanescu-Cosson et al. 2000; Pesenti et al. 2000; Zago et al. 2001; Simon et al. 2002; Pinel et al. 2004 Gobel et al. 2004; Cohen Kadosh et al. 2007). Similarly, physiological studies in nonhuman primates have reported neurons selective for numerical quantity within the part of the monkey parietal cortex housing the representation of the forelimb used for responding (Sawamura et al. 2002). Moreover, transcranial magnetic stimulation (TMS) studies have shown increased excitability of hand motor circuits in adults performing number processing tasks (Sato et al. 2007; Andres et al. 2007). Finally, neuropsychological, developmental and linguistic evidence also suggests that numerical representations in the parietal cortex may be related to hand and finger response processes in the same area (Butterworth 1999a, b).

Despite several converging lines of evidence, however, the exact functional relationship between number and hand action representation remains unclear. One interesting hypothesis (Walsh 2003) has suggested that a nonsymbolic, analogue-representation of magnitude, thought to be located in the parietal cortex (Dehaene 1997; Hubbard et al. 2005), is crucial in mediating the interaction between symbolic numerals (e.g., the digit 5, or the spoken or written word “five”) and actions. According to this view, a representation of numerical magnitude can emerge naturally from the properties of the action system that transforms visual information about the physical magnitude (e.g., size, weight, speed) of external objects into the corresponding motor responses. Because these magnitude-related visuomotor transformations are performed within the dorsal visual pathway (Goodale et al. 1991; Goodale and Milner 1992), numerical and action representations might have converged onto shared neural circuits in the parietal cortex.

To date, relatively few studies have directly tested the functional interaction between numerical magnitude and hand/finger responses. A pioneering behavioural study (Andres et al. 2004) has shown that the magnitude of Arabic numbers can interfere with grip opening/closure movements, such that small numbers are responded to more quickly by closing the thumb and forefinger, while large number by opening them. In that study, however, participants were not required to grasp an object but rather to shape thumb and forefinger to mimic components of grasping actions. More recently, Lindemann et al. (2007) investigated the effect of number processing on the planning and execution of memory-guided, reach-to-grasp actions. They reported that precision grip movements were initiated faster in response to relatively small numbers (digits 1 and 2), whereas power grip movements were initiated faster in response to large numbers (digits 8 and 9). Furthermore, analysis of grasping kinematics revealed that maximum grip aperture was larger in the context of large numerical magnitude, regardless of whether precision grip or power grip was used to respond. These results indicate interference effects between number processing and the programming of prehension movements, thereby supporting the hypothesis of a common magnitude code between symbolic numerals and reach-to grasp actions.

The two experiments reported in this paper set out to obtain a further understanding of the interaction between number and action processing, by using a modified version of the stimulus–response compatibility paradigm employed in previous research (Andres et al. 2004; Lindemann et al. 2007). Three critical issues were addressed.

First, we examined the effect of number processing on the selection of manual responses that did not require overt arm movement (i.e., the transport component of prehension) and consisted of isolated grasping components (Ellis and Tucker 2000; Ehrsson et al. 2000; Grezes et al. 2003). In the study by Lindemann et al. (2007), Arabic numerals affected the onset times of whole prehension acts, which included both reaching and grasping components. Thus, the question remains as to whether numbers can selectively influence the control of goal-directed grip formation regardless of reaching movements.

Second, we investigated whether the interference effect of numerals on grasping actions is monotonically related to numerical values, as it is known from the SNARC effect (Dehaene et al. 1993; Fias et al. 1996). Precisely, we expected that precision grip responses would be selected progressively faster as numerical magnitude decreases, while the reverse was predicted for power grip. Accordingly, in the current study, all Arabic digits in the range 1–9 (not only relatively small and large numbers, as in the previous study by Lindemman and colleagues) were presented, and the associations between numerical value and grasping responses were assessed with a statistical regression analysis (Lorch and Myers 1990).

Third, we examined whether the priming of grasping responses by visual numerals is an automatic and obligatory process that manifests itself even when accessing a number semantic representation is completely irrelevant for the task performance (Fias et al. 2001).

Experiment 1

In Experiment 1, participants were asked to indicate whether a visually presented single Arabic digit was even or odd (e.g., a parity judgement) by making a precision or power grip response. Humans tend to grasp small objects, such as coins and pins, with a precision grip, with the object held between the tips of index finger and thumb. In contrast, larger objects, such as bottles and tennis balls, are usually grasped with a power grip between the palm and the fingers (Napier 1960). If the mental representation of numerical magnitude influences the selection of hand grip, then stimulus–response compatibility effects should be observed between the magnitude of the visually presented number and the grasping response, despite the fact that the task itself has nothing to do with number magnitude. More specifically, we predicted that facilitation effects (e.g., faster and more accurate responses) should be obtained when a small digit number is indicated by a precision grip and a large digit number is indicated by a power grip (congruent number-grasping pairing), whereas interference effects should be observed with the reverse mappings (incongruent number-grasping pairings).

Participants performed the grasping responses (i.e., precision or power grip) with their right hands either with palms up-oriented (hand supine), or down-oriented (hand prone), in separate conditions. The purpose of this hand orientation manipulation was to ensure that each type of grip (i.e., precision and power) was performed equally on the left and right side of space, thereby controlling for the SNARC effect (Dehaene et al. 1993) as a potential confounding factor in the interpretation of the results. Specifically, we hypothesized that true number-grasping associations should not be affected by the supine/prone orientation of the hand, as small numbers should be responded to faster with precision grip, and large numbers faster with power grip, irrespective of where each type of grasping action is performed (i.e., when the hand is supine/palms up, precision grip involves the rightmost fingers of the hand, but these fingers are located on the left side of the hand in the prone/palms down orientation). By contrast, if the hypothesized differences in the latencies of grasping responses are driven by a SNARC-like effect, then small numbers should be responded to faster when precision grip is on the left side of space (i.e., hand prone condition), but not so if precision grip in on the right side of space (i.e., supine hand condition).

Method

Participants

Twenty-four Italian students (16 females) at the University of Bologna, aged between 18 and 29 years (mean age 24.12 years, SD 3.1 years), took part in the Experiment 1. Informed consent was obtained from each subject prior to commencing the Experiment. All the participants were right-handed, as shown by the Edinburgh Handedness Inventory (Oldfield 1971), and had normal or corrected-to-normal vision. They were blind regarding the nature of the experiments and received partial course credit for their participations. None of the participants reported neurological or psychiatric disorders. The experiment was performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki, and was approved by the Ethical Committee of the Department of Psychology, University of Bologna.

Apparatus and stimuli

An IBM-compatible Pentium IV computer running E-Prime software (Psychology Software Tools, Inc., 2002) controlled the presentation of stimuli, timing operation, and data collection. Stimuli consisted of Arabic digits ranging from 1 to 9 (5 excluded), presented one at a time at the centre of a computer screen, in white Arial font (size 40, approximately 9 × 13 mm) on a black background. Stimuli were displayed on a 21-in VGA monitor (1,024 × 768 spatial resolution, 16 colour bit). A custom-made glove device connected with E-Prime software was used to measure reaction times (RTs) of hand grasping responses (see Fig. 1). The timing was millisecond accurate (average error <0.5 ms). The glove device had two components. The first component measured precision grip responses and consisted of a small micro-switch, 1 cm square and 0.5 cm thick, attached to the inside tip of the glove's thumb. The second component measured power grip responses and consisted of an aluminium cylinder, 10 cm tall and 3 cm in diameter, glued to the palm of the glove. A micro-switch was attached to the free side of the cylinder, so that the switch was depressed when the hand squeezed the cylinder. Participants wore the glove device on their right hand, grasping one micro-switch between their thumb and index finger, and the cylinder between the surface of the palm and the remaining three fingers, thus performing power and precision grips [see Ellis and Tucker (2000) for method using a similar response device to measure latency of precision and power grip responses].

Procedure

Participants sat in front of a computer screen in a dimly illuminated room with their eyes at the distance of about 57 cm from the centre of the monitor. At the start of the procedure, participants had their right forearm and elbow resting on the table, with the right hand (wearing the glove) positioned

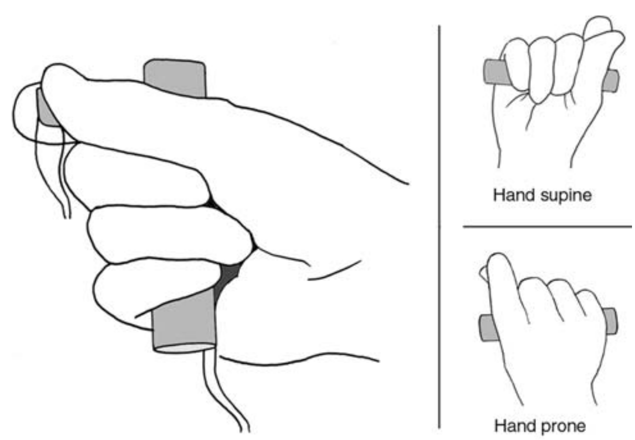

Fig. 1 *Left panel*: schematic illustration of the glove device used in the study (not in scale). *Right panels*: illustration of the hand supine and hand prone conditions of Experiment 1. Note that when the hand is supine/palms up, precision grip involves the rightmost fingers of the hand (*right upper panel*), but these fingers are located on the left side of the hand in the prone/palms down orientation (*right bottom panel*)

mid-sagittally in the frontal plane, approximately 30 cm from the trunk. They were asked to decide whether each presented number was odd or even by making one of two grasping movements (e.g., precision grip or power grip). The instruction emphasized both speed and accuracy. The words “small” and “large” were never used in the instructions and no reference at all was made to numerical magnitude. Participants were randomly assigned to one of two hand-orientation conditions: hand prone and hand supine, according to whether their right hand was placed in a prone or supine posture at the start of each trial (see Fig. 1).

Each trial was initiated by a white fixation cross acting as a warning signal. After 1,000 ms the fixation cross was replaced by a randomly selected digit number, which was presented in exactly the same central location as the fixation cross. The target stimulus remained in view for 2 s, or until a response was made. A blank screen followed for 2,000 ms, after which the next trial started. Incorrect responses ended the trial and were immediately followed by a short visual error feedback. Participants were timed out if they did not respond within 2,000 ms. There were two blocks of trials for each hand-orientation condition. In the first block, half of the participants used one mapping rule (even number/precision grip, odd number/power grip), whereas the others used the reverse mapping. In a second block, the assignment of responses was reversed in all participants. Each block consisted of 12 presentations of each digit in a pseudorandom order for a total 96 target numbers per block. Twenty-four practice trials were performed before the first block to familiarize the participants with the assignment of responses. The experimental session lasted for approximately 30 min.

Results

Response times. Anticipations (reaction times, RTs < 100 ms), omitted responses (RTs > 2,000 ms), and incorrect responses (0.5, 0.7 and 3.1% of the total trials, respectively) were excluded from analysis. Median RTs for correct answers were computed for each target number, each type of grasping response, and each subject. The data were subjected to a mixed design ANOVA, with Hand Grip (two levels: precision or power) and Number Magnitude (four levels: 1–2, 3–4, 6–7, or 8–9) as the within-subject factors, and with Hand Orientation (two levels: prone or supine) as the between-subject factor.

First, the main effect of Hand Orientation was not significant $F(1,22) < 1$, nor did Hand-Orientation enter in any significant interactions [Hand Grip × Hand Orientation, $F(1,22) = 2.3$, $P = 0.14$, Number Magnitude × Hand Orientation, $F(3,66) < 1$, three-way interaction, $F(3,66) < 1$)]. The main effect of Number Magnitude was not significant, either $F(3,66) < 1$. The main effect of Hand Grip was significant, $F(1,22) = 13.7$, $P < 0.0001$, revealing that precision grip responses was executed faster than power grip responses (619 vs. 691 ms, respectively). More important for the present purpose, however, was that the predicted interaction between Hand Grip and Number Magnitude was significant, $F(3,66) = 18.5$, $P < 0.0001$. This effect is clearly illustrated in Fig. 2, in which it can be seen that precision grip responses tended to be performed faster to relatively small numbers (576 and 613 ms, for magnitudes 1–2 and 3–4, respectively) than to relatively large numbers (630 and 656 ms, for magnitudes 6–7 and 8–9, respectively). In striking contrast, power grip responses tended to be faster when large numbers were presented (650 and 682 ms, for magnitudes 8–9 and 6–7, respectively) than in the presence of small numbers (701 and 730 ms, for magnitudes 3–4 and 1–2, respectively).

To further investigate the nature of the interaction between number magnitude and grasping responses, a regression analysis for repeated measures data (Lorch and Myers 1990) was performed on the RT difference between power grip minus precision grip responses (dRT) with the number magnitude as the predictor variable.

The analysis consisted of first calculating the regression weights for each participant separately, and then running a group t test to see whether the mean group values differed significantly from zero. As reported in the study by Fias et al. (1996), there are several advantages to this analysis.

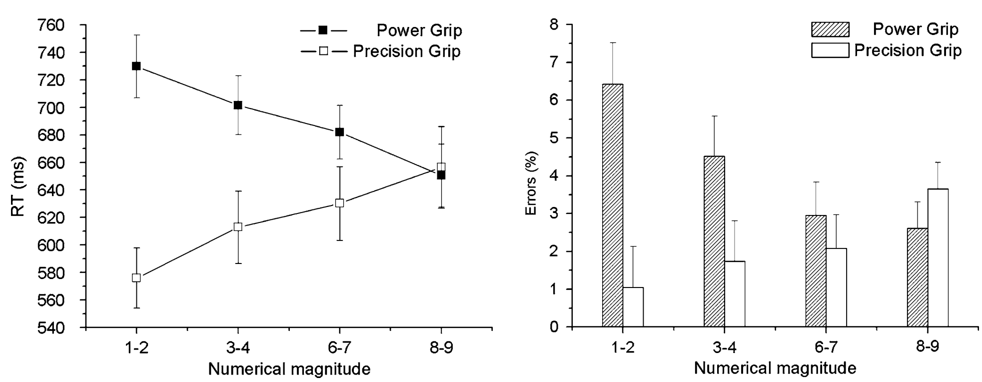

Fig. 2 Mean reaction time (RT) and percentage errors as a function of numerical magnitude and hand grip response (power and precision grip) for Experiment 1. *Bars* refer to 1 standard error of the mean

For example, the presence of a numerical-grasping association is judged by a main effect (does the mean slope coefficient obtained from individual regression equations differ from zero?), rather than by the presence of a significant interaction between magnitude and grasping type. In addition, the regression analysis allows a direct quantification of the size of the effect, rather than a qualitative judgment about the presence or absence of an interaction. Finally, the method evaluates the linear relation between number value and dRT for each participant, reducing the chance of misestimating the numerical-grasping effect due to group averaging.

The resulting regression equation was: dRT = 200.1 − 51.6 (magnitude), with number magnitude contributing significantly, $t(23) = -8$, SD = 30.7, $P < 0.0001$, with a negative slope in all participants. Indeed, as shown in Fig. 3, dRTs between power grip and precision grip responses decreased linearly as numerical magnitude increased, indicating that relatively small number elicited faster precision grip responses, resulting in positive dRTs, whereas relatively large number elicited faster power grip responses, and thus negative dRTs.

Error rates. The same ANOVA as above was performed on error rates. The main effect of Hand Grip was significant, $F(1,22) = 5.5$, $P < 0.05$, showing that less error were made with precision grip than with power grip responses (2.1 vs. 4.1%, respectively). The main effect of Number Magnitude, $F(3,66) = 2.2$, $P = 0.09$, and Hand Orientation, $F(1,22) < 1$, were not significant. Importantly, there was a significant interaction between Hand Grip and Number Magnitude, $F(3,66) = 12.4$, $P < 0.0001$. Post hoc analysis with the Newman–Keuls test revealed that there were fewer errors with small numbers than with large numbers when making precision grip responses (1.4 and 2.9%, respectively; $P < 0.05$); while the pattern was reversed for the power grip responses (5.4 and 2.7%, respectively; $P < 0.05$). The Hand Grip × Hand Orientation interaction, $F(1,22) < 1$, the Number Magnitude × Hand Orientation interaction, $F(3,66) < 1$, and the three-way interaction, $F(3,66) < 1$, were not significant. Finally, there was no sign of speed–accuracy trade-off, as indicated by the presence of a positive correlation between RTs and errors computed over the 16 cells of the design (4 number magnitudes, 2 hand grips, and 2 hand orientations), $r = +0.80$, $n = 16$, $P > 0.001$.

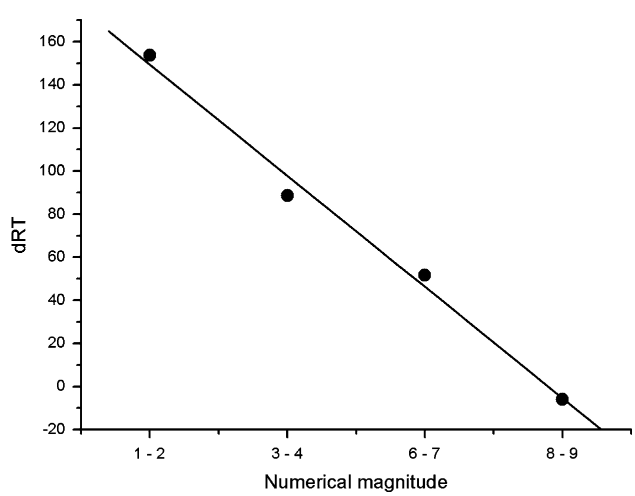

Fig. 3 Differences in RT (dRT) between hand grip responses (power grip–precision grip) as a function of numerical magnitude for Experiment 1. *Filled circles* indicate the observed dRTs. The *continuous line* depicts the predicted dRTs on the basis of the regression analysis

Discussion

The results of Experiment 1 were straightforward. As expected, participants found it easier, both in terms of accuracy and speed, to pair a small digit number with a precision grip, and a large digit number with a power grip. This stimulus–response compatibility effect occurred regardless of the prone or supine posture of the responding hand. That is, small numbers were classified faster by using a precision grip both when the subjects performed this action toward the left side (e.g., hand prone condition) and toward the right side (e.g., hand supine condition) of extracorporal space. Conversely, large numbers were classified faster by using a power grip in both the left and right side of space. The data therefore appear to rule out an explanation of the interaction between number magnitude and grasping responses in terms of the spatial–numerical association of response codes, the so called SNARC effect (Dehaene et al. 1993).

Experiment 2

In Experiment 2, we sought to provide evidence that the association of numerical value and grasping actions may operate as an automatic and obligatory process. In Experiment 1, the numerical-grasping effect emerged even if magnitude-related information was completely irrelevant to the parity judgement task, thus supporting the hypothesis that seen numbers can automatically influence the selection of finger responses. In the preceding experiment, however, successful task completion (e.g., number parity judgment) required access to numerical semantic information (number parity status). Here, we investigated whether the observed interaction between number size and grasping can occur also with a completely nonnumerical task (Dehaene and Akhavein 1995; Fias et al. 2001). To this aim, participants were asked to report the colour of number digits by either performing a precision or a power grip response. If numerical-grasping interaction arises automatically, then it should show up even when the digit itself is noninformative and completely irrelevant to the task. It is worth noting that previous studies of the SNARC effect (Fias et al. 2001; Lammertyn et al. 2002) found that this effect was reduced or abolished when participants were asked to report the colours of the digits. Thus, the results of the present experiment might be critical to differentiate the numerical-grasping associations from the numerical–spatial (SNARC) effects.

Method

Participants

Fourteen Italian students (ages ranging from 19 to 27 years, mean age 23.8 years, SD = 2.6 years; 9 females) at the University of Bologna, who had not taken part in the previous experiment, were recruited. The participants were all right handed and had normal or corrected-to-normal vision. They were blind regarding the nature of the experiments, and received partial course credit for their participations. The experiment was performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki, and was approved by the Ethical Committee of the Department of Psychology, University of Bologna.

Apparatus, stimuli and procedure

They were identical to those used in Experiment 1, except for the following variations. Numbers (1 to 9, 5 excluded) were presented in standard red or blue colour, as defined in E-Prime 1.1 library, on a back background. Participants were asked to decide whether each presented number was red or blue by making one of two grasping movements (e.g., precision grip or power grip). At the start of each trial, subjects had their right, responding hand in a mid-prone posture (with the palm facing left). The experiment was composed of two blocks of trials. In the first block, half of the participants used one mapping rule (red number/precision grip, blue number/power grip), whereas the others used the reverse mapping. In a second block, the assignment of responses was reversed in all participants. Each block consisted of 12 presentations of each digit, shown half of the times in blue and the other half in red, thus yielding a total of 96 target numbers per block.

Results

Responses times. As in Experiment 1, anticipations (RTs < 100 ms), omitted responses (RTs > 2,000 ms), and incorrect responses (0.3, 0.5, and 3% of the total trials, respectively) were excluded from analysis. Median RTs for correct answers were computed for each target number, each type of grasping response, and each subject. The data were subjected to a repeated-measures ANOVA, with Hand Grip (two levels: precision or power) and Number Magnitude (four levels: 1–2, 3–4, 6–7, or 8–9) as the within-subject factors. The analysis reveal a significant main factor of Hand Grip, $F(1,13) = 6.8$, $P < 0.02$, indicating that power grip responses (572 ms) were slower than precision grip responses (504 ms). Conversely, the main factor of Number Magnitude was not significant, $F(1,13) < 1$. More importantly, there was a significant interaction between hand grip and number magnitude, $F(3,39) = 6.2$, $P < 0.001$. As illustrated in Fig. 4, precision grip responses tended to be quicker when small numbers were presented (477 and 482 ms, for magnitudes 1–2 and 3–4, respectively), than when large numbers were shown (518 and 530 ms, for magnitudes 6–7 and 8–9, respectively), while the opposite occurred with power grip responses (595, 574, 573, and 544 ms, for magnitudes 1–2, 3–4, 6–7. and 8–9, respectively). The regression analysis for repeated measures data, conducted as in Experiment 1, revealed the following equation (presented in Fig. 5): dRT = 156.6 34.6 (magnitude). The regression weights of magnitude deviated significantly from 0, $t(13) = 3.6$, SD = 34.5, $P < 0.003$, with a negative slope in 12 out of 14 participants.

Error rates. The same ANOVA as above showed that the main factor of Hand Grip just missed significance,

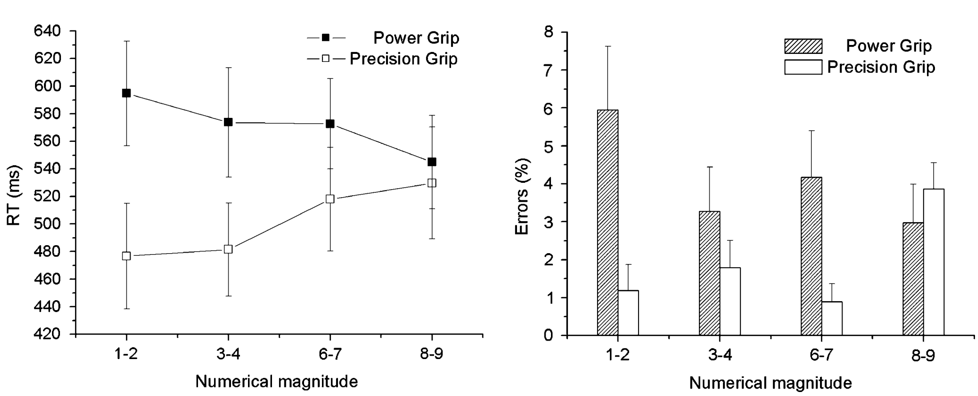

Fig. 4 Mean reaction time (RT) and percentage errors as a function of numerical magnitude and hand grip response (power and precision grip) for Experiment 2. *Bars* refer to 1 standard error of the mean

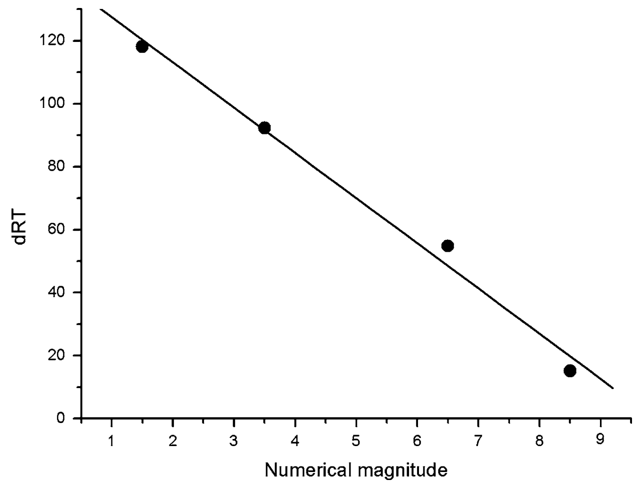

Fig. 5 Differences in RT (dRT) between hand grip responses (power grip–precision grip) as a function of numerical magnitude for Experiment 2. *Filled circles* indicate the observed dRTs. The *continuous line* depicts the predicted dRTs on the basis of the regression analysis

$F(1,13) = 3.8$, $P = 0.07$, and that the main factor of Number magnitude was not significant, $F(3,39) = 2$, $P = 0.13$. More importantly, the interaction between Hand Grip and Number Magnitude was significant, $F(3,39) = 6.8$, $P < 0.001$. Post hoc analysis with the Newman–Keuls test revealed that there were fewer errors with small numbers than with large numbers with precision grip responses (1.2 and 3.8%, respectively with magnitudes 1–2 and 8–9; $P < 0.05$); while the pattern was reversed for the power grip responses (5.9 and 2.9%, respectively with magnitudes 1–2 and 8–9; $P < 0.05$). Finally, as can be seen in Fig. 4, no speed-error trade off was apparent in the case of the important hand grip by magnitude interaction.

Comparison across experiments. In the final analysis, we compared the observed interference effects across the two experiments. To this end, a mixed design ANOVA, with Hand Grip (two levels: precision or power) and Number Magnitude (four levels: 1–2, 3–4, 6–7, or 8–9) as the within-subject factors, and Experiment (two levels: Experiment 1 and Experiment 2) as the between-subject factor, was performed on the latency data. The main effect of Experiment was significant, $F(1, 36) = 11$, $P < 0.01$, showing that overall RTs in Experiment 1 were slower than those in Experiment 2 (655 and 536 ms, respectively), perhaps because the parity judgement task in Experiment 1 was more difficult than the colour discrimination task in Experiment 2. Of most importance for our purpose, however, the factor Experiment did not enter in any significant interaction [Hand Grip × Experiment, $F(1,36) < 1$, Number Magnitude × Experiment, $F(3,108) < 1$, three-way interaction, $F(3,108) < 1$], thus indicating that numerical magnitude effects on grasping actions were of similar size and direction in both Experiments 1 and 2.

In addition, the slope values of the regression analyses of the dRTs from Experiment 1 and Experiment 2 were compared. The analysis revealed no significant difference across experiments, $t(36) = 1.5$, $P = 0.1$.

General discussion

Disparate lines of evidence suggest a close relationship between number processing and goal-directed hand actions (Walsh 2003; Hubbard et al. 2005; Andres et al. 2004; Lindemann et al. 2007). Further behavioural evidence for this possibility is provided by the data from the two experiments reported here, both of which revealed a powerful influence of numerical magnitude on the selection of hand grasping movements.

Participants were required to perform either a power or precision grip depending on the parity (odd or even) of visual Arabic numerals in Experiment 1, or based on their colour (red or blue) in Experiment 2. In both experiments, it was found that small numerical values facilitated precision grip, a type of hand movement commonly performed to grasp and manipulate small objects. Conversely, large numerical value potentiated power grip, a grasping gesture associated with using large objects. Furthermore, a linear increase of response latencies with number size was found when the response was a precision grip, whilst a decrease was observed when the response was a power grip. This indicates that the current numerical effect on grasping actions follows the same linear trend as it is known from the SNARC effect (Dehaene et al. 1993; Fias et al. 1996), thus suggesting that the spatial and motor associations of numbers may rely on similar functional mechanisms (Walsh 2003).

Importantly, these grasping-numerical interactions occurred independently of whether the fingers performing the grasping responses were directed toward the left or right side of space. This allows us to rule out an interpretation of the current data based on the well-established link between number magnitude and the left–right coordinates of external space, namely the SNARC effect, according to which small numbers are responded to faster on the left side, and large numbers faster on the right of side space (Dehaene et al. 1993; Zorzi et al. 2002). Finally, the interaction between number magnitude and grasping responses seems to be obligatory and automatic, in the sense that it arises from the visual presentation of number, even when the task does not explicitly require processing numeric magnitude (i.e., parity judgement in Experiment 1), or accessing a semantic representation of numbers (i.e., colour judgement in Experiment 2; see Dehaene and Akhavein 1995).

Taken together, these findings clearly demonstrate that the mere presentation of symbolic numerical stimuli can automatically activate motor representations that interact (e.g., facilitate or interfere) with the selection of specific grasping movements. This supports the hypothesis that number processing and the representation of manual gestures are strictly coupled, thereby revealing that the conceptual, semantic representation of numerical magnitude includes motor properties.

These observations appear highly consistent with the results of earlier studies that have demonstrated an effect of numerical magnitude on grip aperture programming (Andres et al. 2004), as well as on latencies and kinematics of (memory-guided) reach-to-grasp actions (Lindemann et al. 2007). In reach-to grasp paradigms, however, the respective role of reaching and grasping in determining the interactions between numbers and prehensive actions remains unclear. By employing an experimental task that only required participants to plan and execute power and precision grips, with no reaching involved, the current study directly demonstrates that the interference effect originates at the level of grasp planning. Moreover, the use of finger responses rather than memory-guided (i.e., without visual feedback) reach-to-grasp movements made it possible to observe magnitude priming effects not only on grasping latencies but also on error rates, thereby providing additional support for the hypothesis of grasping-numerical interaction. It is possible that the unavailability of vision during reach-to-grasp movements in the study of Lindemann et al. (2007) discouraged participants to begin responding until they were sure of the required grip, thus eliminating interference effects on error rates.

Previous behavioural (Tucker and Ellis 1998; Ellis and Tucker 2000) and physiological (Grezes et al. 2003) studies with normal subjects have shown that perceiving objects (for example, small vs. large objects) that afford a particular type of grasp (precision vs. power grip), or words denoting those objects (Gentilucci and Gangitano 1998; Glover et al. 2004; Bub et al. 2008), automatically evoke motor programs relevant to their use. The present study further demonstrates that viewing numbers activates action tendencies in a similar manner to seeing physical objects and reading words, thereby implying that the mechanisms of visuomotor transformations underlying hand–object interaction are sensitive to a large array of high-level, cognitive variables (here, numerical magnitude). Overall, previous (Andres et al. 2004; Lindemann et al. 2007) and current findings are broadly consistent with a planning-control model of action (Glover and Dixon 2002; Glover et al. 2004; Glover 2004), in which effects of semantic information occur early in the movement (thereby reflecting cognitive influences on action planning), and tend to decline as action progresses (i.e., control phase). Interestingly, number magnitude effects can also influence imagined grasping actions (Badets et al. 2007). As motor imagery can be conceived as form of planning in which the movement is not executed (Jeannerod 1994), this latter finding further supports the hypothesis that numbers affect the planning phase of action. Conversely, numerical magnitude effects on action are more difficult to incorporate in a perception–action model of visuomotor control (Goodale and Milner 1992) according to which action planning should generally be immune to high-level, cognitive influences.

Evidence from recent TMS studies in humans also supports the hypothesis that activation of motor representation is critical for mediating the semantic association between numbers and hand/fingers. A selective increase of the corticospinal excitability of hand muscles has been described in adult participants who were performing a visual parity judgement task (Sato et al. 2007) and a counting task (Andres et al. 2007). Interestingly, this effect has been interpreted as evidence for the use of finger-counting strategy developed during numerical acquisition in childhood (Butterworth 1999a, b), but still automatically activated in adults when performing numerical tasks. Indeed, a recent study has shown that the performance of Italian participants, in a digit-finger mapping task, reflects systematic association of digits 1–5 with the fingers of the right hand (from thumb to little finger), and digits 6–10 with the fingers of the left hand (from thumb to little finger), in accordance with the prototypical Italian finger-counting (Di Luca et al. 2006). Although one could argue that automatically evoked finger-counting strategy may have contributed to the present findings (i.e., response to small digits faster with the right thumb and index finger, and to large digits faster with the remaining three right fingers), this account does not fit well with our results. Since the participants in this study were native Italian, the finger-counting hypothesis predicted significantly faster response times to digits 3–4 than to digits 8–9 when power grip (i.e., right middle finger, ring finger and little finger flexed against the palm) was used for responding (Di Luca et al. 2006), yet the opposite was found here. These results do not, of course, rule out the contribution of finger-counting to number semantics (Butterworth 1999a; Andres et al. 2007; Sato et al. 2007), but they show that it may not be the only way through which abstract numerical concepts and hand/finger visuomotor processing may be functionally linked [see Di Luca and Pesenti (2008) for a similar proposal].

Similarly, the current results argue against the possibility that different number of fingers used while performing precision grip actions (two fingers) versus power grip actions (three fingers in the present paradigm) was responsible for the present interference effects. This hypothesis predicted faster and more accurate power grip responses with digits 3 and 4 (matching the number of fingers used in power grip) rather than with digits 8 and 9, whereas the opposite occurred here. Furthermore, this conclusion is perfectly consistent with the findings of Lindemann et al. (2007) who reported that numerical effects on prehension actions remained present regardless of the number of fingers used to grasp objects.

How can symbolic numerical stimuli affect the selection of specific grasping gestures? In the triple code model of number processing, (Dehaene et al. 1998) proposed that numbers are mentally represented in three basic formats: modality-specific codes in the visual–arabic and auditory–verbal domain, and a supramodal, abstract code (i.e., “number sense”) which provides a semantic representation of numerical magnitude. Several neuroimaging studies (Chochon et al. 1999; Pesenti et al. 2000; Stanescu-Cosson et al. 2000; Naccache and Dehaene 2001; Simon et al. 2002; Eger et al. 2003; Fias et al. 2003; Pinel et al. 2004; Piazza et al. 2007) and studies of neurological patients (e.g., of the Gerstmann type; Mayer et al. 1999) have repeatedly shown that areas in and around the intraparietal sulcus (IPS) host an abstract representation of number magnitude. It should be noted that this parietal region is not devoted exclusively to number processing but is engaged whenever subjects attend to the dimension of size, whether symbolic (numerical) or physical (Pinel et al. 2004; Kaufmann et al. 2005; Cohen Kadosh et al. 2007). Crucially, functional imaging studies in humans have clearly demonstrated that the programming of goal-directed hand actions (grasping movements in particular) activates the anterior part of the IPS region (Binkofski et al. 1999; Grefkes et al. 2002; Culham et al. 2003; Castiello 2005; Frey et al. 2005), in close proximity, if not overlapping, with the region that is selectively activated by calculation and number processing (Simon et al. 2002).

Moreover, single-unit recording studies in nonhuman primates (Sawamura et al. 2002) reported number-encoding neurons intermingled within the part of the monkey IPS containing the representation of the forelimb used to make responses.

Collectively, these results indicate that a parietal representation of magnitude, activated by quantitative processing of symbolic and nonsymbolic stimuli, is intimately linked with the representation of hand movement responses and intentions (Gobel et al. 2004). It is possible that partly overlapping neural representations dedicated to numbers and hand actions reflect the fact that processing of numerical quantity may share common properties with the computation of magnitude for object–hand interaction, thereby accounting for the behavioural interference between numbers and grasping responses reported here (Andres et al. 2004; Badets et al. 2007). This conclusion finds support in Walsh’s theory of magnitude (2003) which proposes that the parietal lobe hosts a general magnitude system that extracts information across disparate dimensions of quantity (space, time, and numbers) for the purpose of guiding goal-directed actions.

In this context, it is particularly interesting to note that, in Experiment 2, we found semantic effects of numerical value on grasping responses even when participants attended to a stimulus dimension (e.g., colour) which is deemed to rely only minimally on parietal resources. This result contrasts with earlier behavioural studies (Fias et al. 2001; Lammertyn et al. 2002) that failed to observe a SNARC effect when participants were asked to report the colours of the digits. Fias et al. (1996) attributed this null result to the reduced amount of overlap between neural circuits for number (dorsal pathway) and colour (ventral pathway). However, functional studies both in humans (Claeys et al. 2004) and monkeys (Toth and Assad 2002) show that parietal cortex does encode colour if colour is behaviourally relevant for guiding motor responses. This is in line with the results of the present study, in which an effect of the task-irrelevant digit on response times to colour stimuli was observed. Whether the discrepant results between this and Fias et al.’s (2001) study reflect a fundamental difference between the SNARC effect and grasping-numerical interaction, or other (methodological) differences, requires additional studies.

In conclusion, this study provides direct behavioural evidence of a close relationship between numerical magnitude and the selection of grasping gestures. This result is coherent with the view (Walsh 2003) that processing of symbolic and physical quantitative information converges onto a shared magnitude system representing the coordinates of action. In this sense, the representation of magnitude in humans may be quite similar to the representation of magnitude in nonhuman primates (Sawamura et al. 2002; Brannon 2006).

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