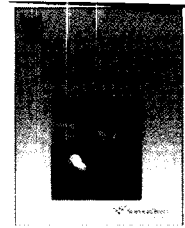


available at www.sciencedirect.comjournal homepage: www.elsevier.com/locate/cortex**Special issue: Original article**

Time course of number magnitude interference during grasping

Michael Andres^{a,b,*}, David J. Ostry^{c,d}, Florence Nicol^a and Tomas Paus^{e,f}

^aUnité de Neurosciences Cognitives, Faculté de Psychologie, Université Catholique de Louvain, Louvain-la-Neuve, Belgium

^bUnité de Neurophysiologie, Faculté de Médecine, Université Catholique de Louvain, Brussels, Belgium

^cDepartment of Psychology, McGill University, Montreal, Quebec, Canada

^dHaskins Laboratories, New Haven, CT, USA

^eMontreal Neurological Institute, McGill University, Montreal, Quebec, Canada

^fBrain and Body Centre, University of Nottingham, Nottingham, United Kingdom

ARTICLE INFO

Article history:

Received 6 April 2007

Reviewed 27 May 2007

Revised 16 July 2007

Accepted 20 August 2007

Published online 23 December 2007

Keywords:

Control

Planning

Number

Finger

Semantic

Action

ABSTRACT

In the present study, we recorded the kinematics of grasping movements in order to measure the possible interference caused by digits printed on the visible face of the objects to grasp. The aim of this approach was to test the hypothesis that digit magnitude processing shares common mechanisms with object size estimate during grasping. In the first stages of reaching, grip aperture was found to be larger consequent to the presentation of digits with a high value rather than a low one. The effect of digit magnitude on grip aperture was more pronounced for large objects. As the hand got closer to the object, the influence of digit magnitude decreased and grip aperture progressively reflected the actual size of the object. We concluded that number magnitude may interact with grip aperture while programming the grasping movements.

© 2008 Elsevier Masson Srl. All rights reserved.

1. Introduction

Several observations suggest that number magnitude and the size of objects to grasp are processed in the dorsal visual pathway by a common system of magnitude (Walsh, 2003). Indeed, recent brain imaging studies have shown that judgements on numerical magnitude and physical size are both associated with increased activity in the intraparietal sulcus (IPS) and premotor cortex (Fias et al., 2003; Kadosh et al., 2005; Pinel et al., 2004). Because these two regions contribute to the

programming of grasping movements (Binkofski et al., 1999; Culham et al., 2003; Ehrsson et al., 2000; Frey et al., 2005; Davare et al., 2006), it is reasonable to assume that number magnitude processing interacts with the visuo-motor processes involved in shaping the handgrip to object size. In line with this view, electrophysiological recordings in monkeys have shown that neuronal activity in the IPS and premotor cortex is modulated by both the object size and the appropriate hand posture (Raos et al., 2006); such neuronal responding fits the requirements of number magnitude

* Corresponding author. Unité de Neurophysiologie, Faculté de Médecine, Université Catholique de Louvain, Avenue Hippocrate 54, 1200 Brussels, Belgium.

E-mail address: michael.andres@psp.ucl.ac.be (M. Andres).
0010-9452/\$ – see front matter © 2008 Elsevier Masson Srl. All rights reserved.
doi:10.1016/j.cortex.2007.08.007

processing, as defined by computer simulations, because it involves a size estimate independent of the object's visual appearance (Dehaene and Changeux, 1993).

In a previous experiment, we asked participants to perform either a grip closure or opening depending on the parity of a visually presented digit (Andres et al., 2004). Electromyographic (EMG) recordings revealed that grip closure was initiated faster in response to digits with a low value whereas grip opening was initiated faster in response to digits with a high value. However, these results did not allow us to infer common processes for the coding of number magnitude and object size because the task required imitating grasp movements in the absence of objects. A recent study extended these results to natural grasping movements performed in response to visually presented digits (Lindemann et al., 2007). Depending on digit parity, participants had to grasp a physical object using either the finger and thumb (i.e., precision grip) or the whole hand (i.e., power grip). Results showed that movement initiation was speeded up when participants performed a precision grip in response to digits with a low rather than a high magnitude, consistent with the specificity of this hand configuration for grasping small objects. Moreover, during the reaching phase, the maximal grip aperture was found to be larger following the presentation of high than low digits, irrespective of the selected grip. Altogether, these results confirm the existence of interactions between number magnitude processing and the adjustment of grip aperture to object size. However, little is known about the time course of these interactions during grasping. In the study by Lindemann et al. (2007), digit magnitude was found to influence the maximal grip aperture, which is classically observed in the second half of the reaching phase, but their results did not tell us anything about the effect of digit magnitude in the first stages of the reaching phase.

Glover (2004) proposed that the reach-to-grasp movement is characterized by a gradual cross-over between planning and on-line control of the grasping movement. These two systems are assumed to involve different parts of the parietal lobe. The purpose of planning is to select the appropriate motor program for a given action. For on-line control, the requirement is to minimize the spatial error of the movement through fast correction mechanisms. The inputs of the planning stage include both spatial and semantic information about the object to grasp, whereas on-line control is mainly influenced by the spatial dimensions of the object such as its size, orientation or position. Planning is responsible for the initial determination of all movement parameters and continues to be highly influential in the first stages of the reaching phase. As the movement unfolds, the control system exerts an increasing influence on spatial parameters. Regarding the possible effect of number magnitude on grip aperture, Glover's model predicts maximal interference in the first stages of the reaching phase, when grip aperture is thought to reflect the integration of both spatial and semantic information by the planning system. Because it is essential that the final grip reflects the actual object size, visual control mechanisms should contribute to reduce number magnitude interference later on during movement execution.

To test these predictions, we conducted the present experiment where participants were asked to reach and grasp

objects of different size, with either low (i.e., 1 and 2) or high digits (i.e., 8 and 9) printed on the visible face. All objects were grasped using a precision grip and kinematic recordings were used to investigate the effect of number magnitude on grip aperture. Based on previous results (Lindemann et al., 2007), we hypothesized that grip aperture should increase when a high, relative to a low, digit was printed on the object to grasp. Moreover, we predicted that digit magnitude interference should be maximal in the first stages of the reaching phase and vanish progressively as the hand gets closer to the object.

2. Methods

2.1. Participants

Sixteen English-speaking students from McGill University gave their informed consent to participate in this experiment (11 females; range of age: 19–35 years). They were all right-handed and had normal, or corrected-to-normal, vision. They reported no history of neurological or mathematical disabilities. The protocol was approved by the Research Ethics Board of the Montreal Neurological Institute and Hospital.

2.2. Stimuli and procedure

Subjects sat at a table covered by a black tissue secured with tape, with both hands at rest on the table. A 10-mm piece of pen was attached to the table in a starting position located at 250 mm on the right of the body midline and 200 mm from the edge of the table nearest to the subject. Subjects were instructed to hold the piece of pen, between their right finger and thumb, at the beginning of each trial. The task consisted in grasping a white 25 mm (height) \times 20 mm (width) rectangular wooden block; the length of the block was either 400, 500, or 600 mm. The wooden block was placed in front of the subject, at a distance of 250 mm from the starting position, with the long axis of the block orthogonal to the direction of movement. The block was positioned on an inclined plane facing the subject and forming a 45° angle with the table surface in order to improve the view of the stimuli. An Arabic digit with either a low (i.e., 1 or 2) or a high magnitude (i.e., 8 or 9) was printed centrally on the visible face of the block. Digits were black stickers, with a 7–9 mm width and a 15 mm height. In total, all possible combinations between the three block sizes and the four digits were presented. The experimenter sat at the right edge of the table in order to change the presented block between trials; 1.5 \times 1.5 m black panels prevented the subject from seeing the experimenter manipulating the blocks.

At the beginning of each trial, subjects had their eyes closed and held their right hand in the starting position. A low tone was then delivered through headphones and the subjects were instructed to open their eyes, reach and grasp the block using exclusively the bidigital grip formed by the index finger and the thumb, and place it either in front of or behind the inclined plane. Half of the subjects were asked to place it forward if the printed digit was even and backward if the digit was odd, whereas others received the reverse instructions. The goal of the grasp movement was related to

a parity judgement in order to force the subjects to attend to the presented digit, while keeping the processing of number magnitude implicit. Instructions emphasized the need to grasp the blocks with maximal accuracy by placing only the tips of the finger and thumb on the lateral ends of the block. At the end of the trial, a high tone was delivered in the headphones to remind the participants to come back to the starting position, close their eyes again and wait for the next trial. One series of 10 practice trials and two series of 60 experimental trials were completed by the subjects, resulting in 20 observations for each combination of block size (40, 50, 60 mm) and digit magnitude (1–2 vs 8–9). The blocks were presented in a random order, with the double constraint that the same digit could not appear in more than two consecutive trials and that block size could not be the same in more than three consecutive trials.

2.3. Kinematic recordings

The kinematic parameters of grasp movements were recorded using an Optotrak motion tracking system (Northern Digital, Waterloo, Ontario). An infrared light emitting diode (IRED) was taped on the thumb (near the right inferior corner of the nail, palm facing down) and on the index finger (near the base of the nail on the left side, palm facing down) of the right hand. As a control, we also taped an IRED on the styloid process of the radius of the right wrist. Finally, a reference IRED was fixed 5 cm behind the inclined plane. The camera was attached to the wall facing the subject, at a distance of 5 m, and was inclined at about 45° to cover the whole workspace. During grasp movements, the IRED positions were sampled with a 200 Hz frequency. The recording was triggered by the low tone and lasted 3000 msec. In order to measure the spatial resolution of the Optotrak system in the present workspace, we secured 10 cm spaced IREDs on a wooden stick and moved it in several directions above the table (Haggard and Wing, 1990). The average distance between the two IREDs, as measured by the Optotrak system, showed a standard deviation of 0.02 mm across all sampled frames. So, we considered that an IRED displacement superior to 0.1 mm reflected actual movement.

Movement onset was thus determined by taking the time point where the grip aperture increased by more than 0.1 mm, with the additional constraint that such a change should be observed in 30 successive samples (i.e., for a 150 msec duration). The first frame in each sequence of 30 successive samples matching these two criteria was considered as the movement onset; likewise, the movement offset corresponded to the first frame where changes in grip aperture remained smaller than 0.1 mm for a continuous period of 150 msec. We calculated the following parameters: (1) the RT, i.e., the time interval between the low tone and movement onset; (2) the movement time (MT), i.e., the time interval between movement onset and offset as defined according to the aforementioned criteria; (3) the grip aperture throughout the movement. It is worth noting that grip aperture was measured by computing the three dimensional distance between the IREDs placed on the nails of the finger and thumb. As a result, when the hand contacted the object at 100% of the MT, grip aperture was overestimated relative to the size of the presented object, which was seized between the tips of finger and thumb. Importantly, the overestimation was the same across

conditions because the position of the IREDs on the fingers was fixed throughout the experiment.

Trials were excluded from the analyses if: (a) the IREDs placed on the fingers were not visible by the camera during the grasp movement; (b) the subject made errors in placing the block forward or backward depending on digit parity; (c) the RT was shorter than 200 msec or longer than 1200 msec; (d) the MT fell outside a 500–1500 msec range. Analyses of variance (ANOVA) were performed on the remaining trials (92%) and unilateral t-tests were used for post-hoc comparisons (α corrected for multiple comparisons).

3. Results

The mean RT (\pm S.D.) was 692 ± 151 msec and the mean MT was 1038 ± 101 msec. We entered the RT and MT values in two separate ANOVAs with block size (40, 50, 60 mm), digit magnitude (low: 1 and 2 vs high: 8 and 9) and target location (forward vs backward) as within-subject factors and response assignment (i.e., forward if the digit was odd and backward if the digit was even vs forward if the digit was even and backward if the digit was odd) as between-subject factor. Results showed that RT and MT remained unchanged across conditions (all p -values $> .12$). In particular, there was no effect of block size on the RT ($F(2,28) = .97$, $p < .39$) and on the MT ($F(2,28) = .41$, $p < .67$), indicating that the initiation and duration of the reaching phase were not affected by the size of the target.

In order to test the influence of block size and digit magnitude on grip aperture, we also performed a repeated measure ANOVA on the maximal grip aperture observed during the MT. A main effect of block size was found ($F(2,28) = 431.97$, $p < .001$, $\eta^2 = .97$), showing that maximal grip aperture differed significantly between the three sizes of blocks (40 mm: 76.9 ± 5.2 mm; 50 mm: 84.4 ± 5.9 mm; 60 mm: 91.1 ± 6.7 mm; all p -values $< .001$). In contrast, the maximal grip aperture only increased by 0.3 ± 0.7 mm when high relative to low digits were presented, resulting in a marginal effect of digit magnitude ($F(1,14) = 4.00$, $p < .07$, $\eta^2 = .22$). Target location and response assignment had no effect on the maximal grip aperture (p -values $> .1$) and were not taken into account in the rest of the analyses.

We hypothesized that digit magnitude had little influence on the maximal grip aperture because this maximum was typically observed in the second half of the movement (i.e., between 66 and 82% of the total MT), at a time where grip aperture is likely to be exclusively determined by block size (Jeannerod, 1984). We further investigated this hypothesis by dividing, for each individual trial, the total MT in 21 intervals of equal duration. These intervals were then expressed as a percentage of the total MT, allowing us to measure, and average across subjects, the grip aperture evolution during the reaching phase. As illustrated in Fig. 1A, the correlation between grip aperture and block size increased with the percentage normalized MT. Fig. 1B shows the digit magnitude effect, as measured by computing the difference in grip aperture between the movements performed in response to high and low digits, irrespective of the block size. Positive values indicate a larger grip aperture following the presentation of digits with a high rather than a low value. In contrast to the block

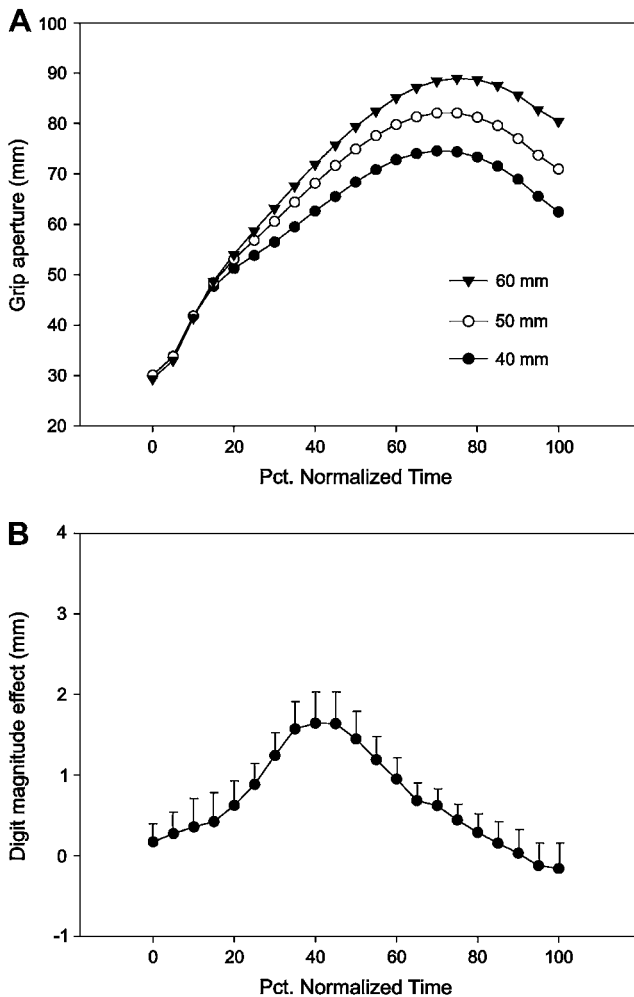


Fig. 1 – (A) Grip aperture as a function of block size over time. Time was normalized across subjects to a percentage of the total movement duration in each individual trial: the fingers started to move at 0% and contacted the object at 100%. (B) Differences (\pm S.E.) in grip aperture between the movements performed in response to a high digit and the ones performed in response to a lower digit, irrespective to object size. Positive values indicate a larger grip aperture following the presentation of digits with a high rather than a low magnitude. The time scale is the same as in (A).

size effect, the grip enlargement caused by high digits was maximal in the first half of the reaching phase (i.e., 40% of the total MT) and decreased afterwards. Before 20% of the MT, grip aperture was too small to reflect a substantial effect of either block size or digit magnitude.

We entered the values of grip aperture at 20, 40, 60, 80 and 100% of the MT in a 3 (block size) \times 2 (digit magnitude) \times 5 (timing) repeated measure ANOVA. Results showed a main effect of block size ($F(2,30) = 255.09$, $p < .001$, $\eta^2 = .94$) and digit magnitude ($F(1,15) = 32.37$, $p < .001$, $\eta^2 = .68$), as well as an interaction between these two factors ($F(2,30) = 3.36$, $p < .05$, $\eta^2 = .18$). As shown in Fig. 2, when grasp movements aimed a 60-mm block, the presentation of high digits increased grip aperture by 1.38 ± 1.6 mm relative to the presentation of low digits (Bonferroni t-test, $t(15) = 3.49$, $p < .01$). Although it does

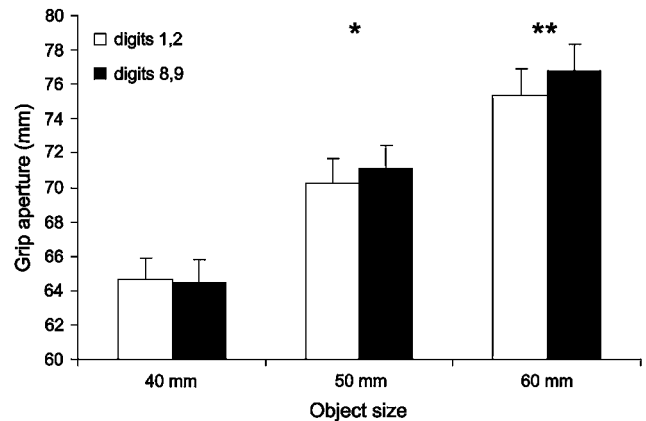


Fig. 2 – Average grip aperture (\pm S.E.) as a function of block size and digit magnitude. Asterisks signal the object size conditions where grip aperture was significantly increased by the presentation of digits with a high rather than a low magnitude (* $p < .05$, ** $p < .01$).

not exceed 0.81 ± 1.4 mm, a significant increase in grip aperture was also found when testing the effect of digit magnitude on the grasping of a 50-mm block (Bonferroni t-test, $t(15) = 2.27$, $p < .05$). In contrast, digit magnitude did not influence the grasping of the smallest block ($t(15) = .5$, $p < .31$).

A block size by timing interaction was also observed ($F(8,120) = 52.96$, $p < .001$, $\eta^2 = .78$). Although the effect of block size was highly significant whatever the timing (all p -values $< .001$), the differences in block size were better reflected in grip aperture at the end of the movement than at the beginning. Indeed, the mean difference in grip aperture between the 40-mm and 60-mm conditions increased linearly throughout the MT (linear trend: $F(1,15) = 184.97$, $p < .001$, $\eta^2 = .93$): it was equal to 2.8 ± 3 mm at 20%, 9.3 ± 5.1 mm at 40%, 12.3 ± 4.3 mm at 60%, 15.3 ± 3 mm at 80% and 18 ± 2.5 mm at 100%.

Furthermore, an interaction between digit magnitude and timing suggests that, contrary to the increasing effect of block size, the grip enlargement caused by high digits decreased throughout MT ($F(4,60) = 6.26$, $p < .001$, $\eta^2 = .30$). The digit magnitude by timing interaction remained significant when the 100% data points were removed from the analysis ($F(3,45) = 4.7$, $p < .01$, $\eta^2 = .24$), indicating that it cannot be totally explained by the fact that the hand had contacted the object at 100% of the MT and grip aperture could therefore not reflect an effect of digit magnitude. When compared to low digits, the presentation of high digits increased grip aperture by 0.6 ± 1.1 mm at 20%, 1.7 ± 1.5 mm at 40%, 1 ± 1 mm at 60% and 0.3 ± 0.8 mm at 80% (quadratic trend: $F(1,15) = 7.75$, $p < .01$, $\eta^2 = .34$). The increase in grip aperture was significantly different from 0 at 20, 40 and 60% of the MT (all p -values $< .05$) but not on later timings.

4. Discussion

In the present study, the distance between the finger and thumb was measured during the reaching phase of grasping movements performed towards objects of different size. Grip

aperture was found to be larger when digits with a high value were printed on the object to grasp than when digits with a low value were presented. This finding agrees with previous studies suggesting interference between number magnitude and grip aperture (Andres et al., 2004; Lindemann et al., 2007).

Moreover, we found that the effects of number magnitude and object size on grip aperture had a distinct time course. Whereas the correlation between object size and grip aperture increased as the hand approached the object, the interference of digit magnitude peaked in the first half of the reaching phase (i.e., 40% of the MT) and decreased progressively in the second half. These results indicate that information related to number magnitude is processed during the planning stage of grasping movements, where both semantic and spatial informations are taken into account to select the appropriate hand shape. In line with Glover's (2004) model, our results also suggest the existence of control mechanisms that counteract the interference of number magnitude during movement execution to allow the precise adjustment of grip aperture to object size.

This finding parallels the results of similar experiments showing that the initial grip aperture is larger when subjects read words related to large objects (e.g., apple) than when they read words related to small objects (e.g., grape; Glover and Dixon, 2002; Glover et al., 2004). It is worth noting that the digit magnitude effect on the maximal grip aperture was marginal in the present study. Because this maximum is classically observed at about 75% of the MT (Jeannerod, 1984), we hypothesized that it was mainly determined by object size and showed little effect of digit magnitude. However, in a similar study, Lindemann et al. (2007) found that the maximal aperture was significantly influenced by the previous presentation of digits. Such discrepancy may be explained by the fact that, in the study by Lindemann et al., participants were trained to perform the grasping movements without visual feedback. In accordance with the model of Glover (2004), we can assume that the semantic information relative to digit magnitude kept on influencing grip aperture in the latest stages of the movement due to the absence of visual control.

Our view predicts that the interference of digit magnitude with grip aperture should be exacerbated in patients with a selective impairment of the on-line visual control of grasping movements (i.e., optic ataxia). Because these patients cannot rely on spatial information during movement execution, numbers could also be used as quantitative cues to calibrate grip aperture anticipatively. Milner et al. (2001) studied a patient who failed to scale her handgrip appropriately when reaching an object, except when, after training, she was able to use memorized visual information about the object to grasp. Additional experiments should assess the potential benefits of using numbers to calibrate handgrip in ataxic patients. Future studies should also investigate the interactions between number and finger representations in patients with mathematical disabilities. Although the association between numerical and finger deficits has been underlined many times since Gerstmann (1930) described a syndrome combining acalculia and finger agnosia, the relationship between these two deficits is still poorly understood (e.g., Mayer et al., 1999).

Furthermore, we found that the grip aperture increase consequent to the presentation of high digits, relative to low ones,

was modulated by object size. Indeed, we found that the increase in grip aperture following the presentation of digits with a high magnitude was larger during the grasping of 60 mm blocks than that of 50 mm blocks. No effect of digit magnitude was found during the grasping of 40 mm blocks. Following the additive-factor method (Sternberg, 2001), the effects of digit magnitude and object size should simply add up if each magnitude estimate was computed in independent modules. In contrast to this prediction, we observed an interaction between the effects of digit magnitude and object size, suggesting that the two factors influence a common processing stage. The present data do not allow us to determine whether such interaction occurs at a central or peripheral level. One could argue, for example, that the digit magnitude effect vanished when movements were directed towards small blocks due to a more difficult finger positioning, as predicted by Fitt's law. Indeed, the duration of the reaching movement classically increases as object size decreases (Gentilucci et al., 1991; Jakobson and Goodale, 1991). In the present experiment, this possibility seems unlikely because the MT did not increase during the grasping of the smallest block. Moreover, although the blocks had different lengths, it is worth mentioning that the graspable surfaces were always the same. However, the question remains whether digit magnitude and object size were integrated into a single representation before the selection of the handgrip or whether both magnitudes were processed separately to converge at the response selection stage.

We specifically addressed this question in a recent experiment where participants had to make judgements about the possibility to grasp objects of different size following the presentation of digits with low or high values (Badets et al., 2007). If digit magnitude directly influences the representation of the grip aperture, the maximal size of graspable objects, as evaluated by the participants, should be underestimated after the presentation of low digits and overestimated following that of high digits. In contrast to this prediction, we found that participants felt able to grasp larger objects after the presentation of low digits than in the control condition, whereas the presentation of high digits led them to underestimate the maximal size of graspable objects. This result rather suggests that digit magnitude interfered with the computation of the object size estimate, which in turn biased the decision about the ability to grasp the given object. Importantly, digit magnitude did not affect the performance in a perceptual estimation task where the same objects had to be classified as smaller or larger than a reference object. These results support the view that the effect of digit magnitude on grip aperture is mediated by a representation of the object size, which is involved in the programming of grasping movements but not in perceptual judgements (Badets et al., 2007).

Finally, in the present study, digit magnitude had no effect on RTs whereas the digit magnitude and grip aperture interaction was initially observed using chronometric methods (Andres et al., 2004; Lindemann et al., 2007). However, previous studies used a choice-RT paradigm where participants had to select one of two possible hand configurations based on digit parity, whereas our task required the use of a precision grip in all trials and the grasping movement involved a reaching phase characterized by both an opening and closing of the

grip. Only the goal of the movement varied across trials: the grasped object had to be placed either in front of or behind its initial position depending on digit parity. Because number and space interactions have been reported in several studies (Hubbard et al., 2005), one could still expect to observe shorter RTs when the object had to be placed forward than backward in response to low digits, and backward than forward in response to high digits. Indeed, such an association is reminiscent of the alignment of numbers along the vertical axis of a thermometer. However, statistical analyses failed to reveal any significant interaction between digit magnitude and target location. So, the number and space interactions reported in the literature are likely to involve different processes from those required to perform grasping movements.

Acknowledgements

We thank G. Houle, M. Davare, E. Olivier, O. White and J.-L. Thonnard for their helpful contribution to this study. M.A. is a research assistant at the Fonds National pour la Recherche Scientifique (FNRS, Belgium).

REFERENCES

- Andres M, Davare M, Pesenti M, Olivier E, and Seron X. Number magnitude and grip aperture interaction. *Neuroreport*, 15: 2773-2777, 2004.
- Badets A, Andres M, Di Luca S, and Pesenti M. Number magnitude potentiates action judgements. *Experimental Brain Research*, 180: 525-534, 2007.
- Binkofski F, Buccino G, Posse S, Seitz RJ, Rizzolatti G, and Freund H. A fronto-parietal circuit for object manipulation in man: evidence from an fMRI-study. *The European Journal of Neuroscience*, 11: 3276-3286, 1999.
- Culham JC, Danckert SL, Desouza JF, Gati JS, Menon RS, and Goodale MA. Visually guided grasping produces fMRI activation in dorsal but not ventral stream brain areas. *Experimental Brain Research*, 153: 180-189, 2003.
- Davare M, Andres M, Cosnard G, Thonnard JL, and Olivier E. Dissociating the role of ventral and dorsal premotor cortex in precision grasping. *The Journal of Neuroscience*, 26: 2260-2268, 2006.
- Dehaene S and Changeux JP. Development of elementary numerical abilities. *Journal of Cognitive Neuroscience*, 5: 390-407, 1993.
- Ehrsson HH, Fagergren A, Jonsson T, Westling G, Johansson RS, and Forssberg H. Cortical activity in precision- versus power-grip tasks: an fMRI study. *Journal of Neurophysiology*, 83: 528-536, 2000.
- Fias W, Lammertyn J, Reynvoet B, Dupont P, and Orban GA. Parietal representation of symbolic and nonsymbolic magnitude. *Journal of Cognitive Neuroscience*, 15: 47-56, 2003.
- Frey SH, Vinton D, Norlund R, and Grafton ST. Cortical topography of human anterior intraparietal cortex active during visually guided grasping. *Brain Research Cognitive Brain Research*, 23: 397-405, 2005.
- Gentilucci M, Castiello U, Corradini ML, Scarpa M, Umiltà C, and Rizzolatti G. Influence of different types of grasping on the transport component of prehension movements. *Neuropsychologia*, 29: 361-378, 1991.
- Gerstmann J. Zur symptomatologie der hirnläsionen im übergangsgebiet der unteren parietal-und mittleren occipitalwindung. *Nervenarzt*, 3: 691-695, 1930.
- Glover S. Separate visual representations in the planning and control of action. *The Behavioral and Brain Sciences*, 27: 3-78, 2004.
- Glover S and Dixon P. Semantics affect the planning but not control of grasping. *Experimental Brain Research*, 146: 383-387, 2002.
- Glover S, Rosenbaum DA, Graham J, and Dixon P. Grasping the meaning of words. *Experimental Brain Research*, 154: 103-108, 2004.
- Haggard P and Wing AM. Assessing and reporting the accuracy of position measurements made with optical tracking systems. *Journal of Motor Behavior*, 22: 315-321, 1990.
- Hubbard EM, Piazza M, Pinel P, and Dehaene S. Interactions between number and space in parietal cortex. *Nature Reviews Neuroscience*, 6: 435-448, 2005.
- Jakobson LS and Goodale MA. Factors affecting higher-order movement planning: a kinematic analysis of human prehension. *Experimental Brain Research*, 86: 199-208, 1991.
- Jeannerod M. The timing of natural prehension movements. *Journal of Motor Behavior*, 16: 235-254, 1984.
- Kadosh RC, Henik A, Rubinsten O, Mohr H, Dori H, Van Deven V, Zorzi M, Hendler T, Goebel R, and Linden DEJ. Are numbers special? The comparison systems of the human brain investigated by fMRI. *Neuropsychologia*, 43: 1238-1248, 2005.
- Lindemann O, Abolafia JM, Girardi G, and Bekkering H. Getting a grip on numbers: numerical magnitude priming in object grasping. *Journal of Experimental Psychology: Human Perception and Performance*, 33: 1400-1409, 2007.
- Mayer E, Martory MD, Pegna AJ, Landis T, Delavelle J, and Annoni JM. A pure case of Gerstmann syndrome with a subangular lesion. *Brain*, 122: 1107-1120, 1999.
- Milner AD, Dijkerman HC, Pisella L, McIntosh RD, Tilikete C, Vighetto A, and Rossetti Y. Grasping the past: delay can improve visuomotor performance. *Current Biology*, 11: 1896-1901, 2001.
- Pinel P, Piazza M, Le Bihan D, and Dehaene S. Distributed and overlapping cerebral representations of number, size, and luminance during comparative judgments. *Neuron*, 41: 983-993, 2004.
- Raos V, Umiltà MA, Murata A, Fogassi L, and Gallese V. Functional properties of grasping-related neurons in the ventral premotor area F5 of the macaque monkey. *Journal of Neurophysiology*, 95: 709-729, 2006.
- Sternberg S. Separate modifiability, mental modules, and the use of pure and composite measures to reveal them. *Acta Psychologica*, 106: 147-246, 2001.
- Walsh V. A theory of magnitude: common cortical metrics of time, space and quantity. *Trends in Cognitive Sciences*, 7: 483-488, 2003.