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BIOLOGICAL SCIENCE, Psychology

Touch perception reveals the dominance of spatial over digital representation of numbers

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Abstract

We learn counting on our fingers and the digital representation of numbers we develop is still present in adulthood (Rusconi et al. 2005; Andres et al. 2007). Such an anatomy-magnitude association establishes tight functional correspondences between fingers and numbers (Di Luca et al. 2006). However, it has long been known that small-to-large magnitude information is arranged left-to-right along a mental number line (Dehaene et al. 1993; Walsh 2003; Hubbard et al. 2005). Here, we investigated touch perception to disambiguate whether number representation is embodied on the hand (“1”=thumb; “5”=little finger) or disembodied in the extrapersonal space (“1”=left; “5”=right). We directly contrasted these number representations in two experiments using a single, centrally located effector (the foot) and a simple postural manipulation of the hand (palm-up vs. palm-down). We show that visual presentation of a number (“1” or “5”) shifts attention crossmodally, modulating the detection of tactile stimuli delivered on the little finger or thumb. With the hand resting palm-down, subjects perform better when reporting tactile stimuli delivered to the little finger after presentation of number “5” than number “1”. Crucially, this pattern reverses (better performance after number “1” than “5”) when the hand is in a palm-up posture, in which the position of the fingers in external space, but not their relative anatomical position, is reversed. The human brain can thus use either space-based or body-based representation of numbers, but in case of competition the former dominates the latter, showing the stronger role played by the mental number line organization.

Andres, M., Seron, X., and Olivier, E. (2007). *J. Cogn. Neurosci.* 19, 563-576.

Dehaene, S., Bossini, S., and Giraux, P. (1993). *J. Exp. Psychol. Gen.* 122, 371-396. Di Luca, S., Grana, A., Semenza, C., Seron, X., and Pesenti, M. (2006). *Q. J. Exp. Psychol.* 59, 1648-1663. Hubbard EM, Piazza M, Pinel P, Dehaene S. (2005) *Nat Rev Neurosci.* 6: 435-448. Rusconi, E., Walsh, V., and Butterworth, B. (2005). *Neuropsychologia*, 43, 1609-1624. Walsh, V. (2003). *Trends Cogn. Sci.* 7, 483-488.

It has long been considered that literate humans associate numbers (e.g., “1” and “5”) with fingers (e.g., thumb and little finger) by virtue of learning processes such as counting on fingers. Such an embodied finger counting strategy, developed during numerical acquisition in childhood, might result in a finger-number association that is still present in adulthood when the same numerical manipulations can be carried out mentally^{1,2}. Accordingly, activation of the precentral gyrus and parietal areas participating in hand-shaping control and finger movements³ are commonly reported during numerical tasks⁴⁻⁹ and have been suggested to underlie implicit finger counting strategies⁴⁻⁶. Neuropsychological studies of Gerstmann’s syndrome¹⁰⁻¹¹ and transcranial magnetic stimulation (TMS) approaches in healthy subjects^{3,12,13} have also suggested tight functional correspondences between fingers and numbers. However, a disembodied form of numerical representation is also well-established: Numbers are represented in a spatial format along the so called “mental number line”, whereby smaller numbers occupy relatively leftward locations compared to larger numbers¹⁴⁻¹⁵. This phenomenon, which has become known as the spatial numerical association of response codes (SNARC) effect, suggests that magnitude information may be analogically arranged from left-to-right (in most Western cultures): In parity judgment tasks, large numbers are responded to faster with the right hand (and small numbers faster with the left hand) by virtue of the spatial compatibility between the location of a given number on the mental number line and the location of the correct response effector in external space. Neuropsychological evidence from neglect patients and TMS studies on subjects bisecting numerical intervals has further supported the left-to-right spatial organization of numbers¹⁶⁻²¹. Moreover, visual attention and action can be enhanced according to the magnitude of a visually presented number, larger numbers boosting performance on the right, and

smaller numbers on the left side^{22,23}. The few existing attempts to contrast hand/finger-based (embodied) and space-based (disembodied) representations of numbers have led to mixed results. Dominance of the space-based representation has been suggested by Dehaene and colleagues¹⁴, who asked subjects to perform a crossed-hand version of their original parity-judgement task and found that the SNARC effect was not dependent upon the left-right hand identity, but the left-right hand location in the response space. In contrast, finger-based dominance has been suggested by Di Luca and colleagues²⁴, who asked subjects to perform a visuo-motor finger-number compatibility task and found better performance when the mapping was congruent with the prototypical finger-counting strategy. In addition, a certain degree of flexibility in number representation has been recently suggested²⁵⁻²⁸, as the mapping between numbers and space can vary to some extent with instructional context²⁵ and task demands¹⁷.

Previous findings are thus not definitive with regard to number representation, as both the embodied and the disembodied hypotheses have received empirical support. In this study we used a novel approach to disambiguate between such representations within a corporeal modality, by investigating the attentional effects induced by numbers on the perception of touches delivered to the fingers. A postural manipulation of the hand (palm-up vs. palm-down) allowed us to directly contrast the embodied and disembodied representations of numbers. A further manipulation was critically introduced to avoid any left-right arrangement in the response space, potentially favouring a space-based representation, as well as any motor bias in the response effector, potentially favouring a finger-based representation: Subjects had to respond to tactile stimulation by pressing a centrally located pedal with the foot.

Results and Discussion

Participants performed a simple tactile detection task, by making speeded foot-pedal responses to a tactile stimulus delivered to either the thumb or little finger of their right (preferred and counting) hand. Tactile intensity was set in a previous session in order to obtain an equal detection probability for the two fingers (see Supporting Information). In the first experiment, the task instructions were given as to emphasize the fingers (i.e., “you will feel a touch on either your thumb or little-finger”). With a variable delay, an electrocutaneous stimulus followed the presentation of a task-irrelevant number (“1”, “2”, “4” or “5”) on a screen in front of their hand (Figure 1). The tactile task was performed with the unseen hand passively resting either in a palm-down or palm-up posture.

Insert Figure 1 about here

Two main results were found: First, visual presentation of a number crossmodally affects tactile performance; Second, this numerical cueing of touch does not follow a number-finger association, but a number-space association, akin to the mental number line¹⁴. A descriptive illustration of the results for all experimental conditions including all the numbers (“1”, “2”, “4” and “5”) is provided by Figure 2a (see Methods and Supporting Information). When the right hand was in the palm-down posture, placed centrally with the middle finger aligned with the visually presented number, subjects’ detection of brief tactile stimuli applied to the little finger improved as a function of the preceding number magnitude. The larger the number, the better the

performance in terms of inverse efficiency (IE) score, jointly indexing accuracy and response latency. The opposite pattern of results was found when the same little finger was stimulated with the hand in the palm-up posture. In this condition, subjects' tactile performance actually decreased as the preceding number increased. The statistical comparison showed a significant Finger x Posture interaction ($F(1,13) = 9.80; p < 0.01$): Figure 2b shows that for stimuli applied on the little finger, a difference was present between the slopes of IE regression lines in the palm-down and in the palm-up position (-4.55 vs. +3.70 respectively, $p < 0.05$, Figure 2b, yellow bars). Results for the thumb mirrored those for the little finger (Figure 2b, blue bars). When the hand was in the palm-down posture, subjects' detection improved as a function of the number's magnitude. For the thumb, the smaller the preceding number was, the better the performance, the regression line having a positive slope. On the contrary, when the hand was in the palm-up position, subjects' detection of brief stimuli on the thumb tended to worsen with decreasing magnitude of the presented number (+5.94 vs. -2.04 for the palm-down and the palm-up postures, respectively, $p = 0.053$, Figure 2b).

Insert Figure 2 about here

To further establish the dominant role played by the space-based organization of numbers, an additional analysis of tactile performance was run by focusing on those conditions with presentation of numbers "1" and "5" (i.e., excluding conditions "2" and "4"). The four-way ANOVA revealed a significant main effect of Delay on tactile

performance [$F(3,39) = 15.35$; $p < 0.01$]. Newman-Keuls post-hoc test revealed that subjects' performance was worst in the longer delay (1300 ms), as compared to shorter delays (550, 800 and 1050 ms, $p < 0.01$ for all comparisons). However, the variable Delay was not involved in any significant interaction (Figure 2c). The hypothesis of an embodied representation of numbers predicts that the thumb is more closely associated with, and thus would be more efficiently primed by, number "1" than number "5", independently of the hand's posture, with the opposite association for the little finger. Contrary to these predictions, a significant Posture x Finger x Number interaction ($F(1,13) = 14.43$; $p < 0.01$) confirmed that the numerical cueing of touch is mapped in extrapersonal space. Subjects' performance was better in perceiving a touch on the thumb after number "1" than "5" in the palm-down posture (IE score: 447 vs. 470 ms, respectively, $p < 0.05$), but the opposite tendency was obtained when the hand posture was reversed (IE score: 428 vs. 417 ms, respectively). Similarly, when considering the little finger, subjects' performance mirrored that of the thumb: In the palm-down posture stimuli on the little finger were detected more efficiently when preceded by number "5" than number "1" (408 vs. 439 ms, respectively, $p < 0.05$), but the opposite was true in the palm-up posture, in which performance was better when touches were preceded by number "1" than "5" (429 vs. 447 ms respectively, $p < 0.05$). The same significant pattern of results was also obtained when subjects' accuracy was separately tested, response latencies showing the same tendency. In other words, the same touch delivered to the same little finger was better perceived if preceded by number "5" than number "1" in the palm-down posture, but was better perceived if preceded by number "1" than number "5" in the palm-up posture.

To further explore the potential role played by instructional and task-setting variables, we performed a second experiment whereby tactile stimuli were always delivered on the thumb or on the little finger, but the side of the hand was stressed (i.e., “you will feel a touch on either the left or right side of your hand”). Moreover, to provide a finer description of the time-course of the effect of numerical cueing of touch, a shorter delay was tested: tactile stimuli were delivered either 550 ms after number onset (i.e., as the shortest delay in the first experiment), or 250 ms after number onset (i.e., when the task-irrelevant number was still present on the screen, see Methods section for details).

Results replicated the findings of the previous experiment. As shown in Figure 3b, tactile performance was crossmodally affected by the visual presentation of a number and numerical cueing of touch again followed a number-space association, as revealed by the significant Finger x Posture interaction ($F(1,12) = 6.02$; $p < 0.03$). In the palm-down posture, subjects’ tactile detection at the little finger improved with increasing number magnitude, the opposite pattern being observed in the palm-up posture. For stimuli applied on the little finger, the slopes of IE regression lines in the palm-down and in the palm-up position differed (-11.69 vs. +12.12 respectively, $p < 0.04$, Figure 3b, yellow bars). Again, results for the thumb mirrored those for the little finger (Figure 3b, blue bars). When the hand was in the palm-down posture, subjects’ detection improved with decreasing number magnitude, the opposite tendency being present when the hand was in the palm-up position, (+23.22 vs. -3.35 for the palm-down and the palm-up postures, respectively, $p = 0.07$, Figure 3b). When considering only number “1” and “5”, the ANOVA revealed a significant Posture x Finger x Number interaction ($F(1,12) = 8.20$; $p < 0.01$), which further confirmed that the numerical cueing of touch was mapped in extrapersonal space. Figure 3c illustrates

that this effect was also present at the shortest delay, this variable being neither significant nor involved in any interaction (Figure 3c), thus suggesting a rather early space-based mapping of numbers.

The findings of both experiments clearly demonstrate that the human brain takes into account magnitude information presented in the visual modality when processing tactile stimuli at the fingers, but in so doing it refers to an extrapersonal, spatial representation of numbers. Indeed, very similar and consistent results were observed both when task instructions emphasized the (left or right) sides of the hand (second experiment), and the (little-finger or thumb) fingers of the hand (first experiment), as further confirmed by the omnibus ANOVA run on data from the common delay (550 ms after number onset), whereby the between-subject variable Emphasis was not involved in any interaction. Therefore, even when emphasis was given to fingers, and might have in principle favoured a finger-based numerical representation, the results were clear in showing a space-based dominance in number representation. When compared to previous studies, it is noteworthy that the present findings were obtained within a novel approach, best suited to disambiguate between number representations: First, number magnitude was totally task-irrelevant, at odds with previous visuo-motor number-finger mapping task²⁴; second, a single, centrally located effector was employed, at variance with SNARC tasks whereby two, left-right horizontally aligned effectors are typically used^{14,17}; finally, the foot was used as response effector, i.e., a body-part that is not used to learn counting.

Here, the case for a connection between space and numbers²⁹ was studied in direct reference to the body. Our manipulation of hand posture³⁰ was effective in distinguishing between the spatial reference frames in which tactile perception is biased by numerical cueing. By using an embodied approach based on tactile

perception we not only show for the first time that number-based attentional cueing crosses sensory modalities, but also demonstrate that number-based tactile priming is early mapped according to an extrapersonal spatial representation, thus providing a compelling support for the dominant role played by the spatial representation of numbers known as the 'mental number line'.

METHODS

Subjects. The first experiment was run on fourteen (7 female, mean age 30.9; SD 10.1, range 20 to 51 years) neurologically healthy subjects. Thirteen (7 female, mean age 29.3; SD 8.1, range 21 to 51 years) healthy subjects participated to the second experiment. Three subjects took part in both experiments. All participants gave their informed consent to take part in this study, which was approved by the local ethics committee. They were asked to show how they usually count with their fingers, without specifying in the request which hand to use first. However, to induce subjects to use both hands, they were asked to count up to "8". Only subjects who employed the conventional (for Italian and French subjects) counting system (1–thumb, 2–index, 3–middle, 4–ring, 5–little finger) starting from the right thumb were admitted to the experimental session. Subjects were all right-handed according to the Edinburgh Handedness Inventory. They had normal or corrected visual acuity and reported no somatosensory problems and were naïve as to the purpose of the study.

Apparatus and Procedure

Both experiments were run with the same set-up and procedures were identical, unless otherwise stated. A PC (Dell, Optiplex GX270, Intel Pentium 4) equipped with a visual stimuli generator (ViSaGe, Cambridge Research Systems, Rochester, UK)

was used to control stimulus presentation and response collection. Arabic numerals ("1", "2", "4", or "5") were presented singly at the center of a CRT monitor (Eizo FlexScan T931; resolution, 800×600 pixels; refresh rate, 160 Hz), located 57 cm from the subjects' eyes, subtending 1x1 degrees of visual angle. Subjects' right hidden hand laid in front of them, the middle finger aligned with the vertical meridian of a monitor, where a fixation point appeared. Thumb and little finger were thus to the right or to the left with respect to the middle finger. Two different postures could be assumed: Hand pronation (palm-down posture), or supination (palm-up posture). Subject's fixation and eye-movements were constantly monitored throughout each trial via an eye tracking system (Cambridge Research Systems, Rochester, UK; 250 Hz). After the subject succeeded in keeping the fixation within a (non visible) circular window centred on the fixation point (2.5° side-by-side) for 500 ms, one of the four equiprobable numbers ("1", "2", "4" or "5") appeared (300 ms). In the first experiment, a brief (100 µs) electro-cutaneous stimulus was equiprobably delivered via self-adhesive disposable electrodes (Neuroiline 700-K, Ambu) to the thumb or little finger after one of four possible delays from the number onset (550, 800, 1050 or 1300 ms). In the second experiment, the electro-cutaneous stimulus was equiprobably delivered to the thumb or little finger after one of two possible delays: 550 ms after the number onset (i.e., same as the shortest delay in the first experiment), or 250 ms after the number onset (i.e., 300 ms earlier, when the number was still present on the screen). In both experiments, subjects had to respond as fast as possible to the tactile stimulation by pressing a central foot-pedal with their right foot. Eye movements were monitored up to the foot-pedal response. If central fixation was broken at any time during the trial, the trial was aborted and randomly reintroduced to ensure that the same number of trials was recorded for each condition. The tactile stimulus intensity

was set to obtain approximately 80% correct detections for both fingers with a titration procedure that was run in a pre-experimental session (see Supporting Information). Each stimulator (DS7A, Digitimer Ltd, UK) current was varied independently for each finger so that detection performance was comparable between the two fingers. Subjects were told that the number was totally irrelevant for the tactile detection task. To ensure that number magnitude was processed (see Supporting Information) they were also told they could be asked without warning which number appeared in the immediately preceding trial.

Accuracy and reaction time (RT) were combined in the “inverse efficiency” (IE) score, a standard way to combine RT and accuracy data into a single performance measure, computed as the median RT divided by the proportion of correct trials for a given condition; a higher IE value indicates worse performance, just as for RT and error measures. The IE score was submitted to a four-way ANOVA with Delay, Posture, Finger and Number (“1” vs. “5”) as variables. Each posture was further analysed by a three-way ANOVA. Regression line beta values between IE score and numbers were also calculated and submitted to a three-way ANOVA with Delay, Posture and Finger as within-subject variables. Significant sources of variance were explored by Newman-Keuls post-hoc tests and planned comparisons.

Supporting Information

Supporting Information includes additional procedures and results, one figure and two tables.

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Figure Captions:

Figure 1. Experimental Set up and Procedures

The subjects' right hand lay in front of them with their middle finger aligned with the central fixation point on the monitor. Following a fixation period of 500 ms, a number appeared for 300 ms in the center of the monitor. A tactile stimulus was delivered either to the thumb or the little finger after a variable delay: four delays were possible in the first experiment (550, 800, 1050 or 1300 ms after offset of the task-irrelevant number), and two in the second experiment (250 ms or 550 ms after onset of the task-irrelevant number). The subjects were instructed to respond to the tactile stimulus as quickly as possible, by pressing a centrally located pedal with their right foot.

Figure 2. Visual numerical cueing of touch is modulated by hand posture: emphasis on fingers.

a

Regression lines of the inverse efficiency score as a function of number magnitude for all conditions. Regression equations reflect the averaged data in each panel. Performance for the thumb (blue panels) in palm-down posture (upper row), decreased as a function of number magnitude from the smallest ("1") to the largest ("5") number ($y = +5.9x + 436$, $r^2 = 0.81$); the pattern is opposite for the same stimulus on the same thumb but in palm-up posture (bottom row, $y = -2.0x + 430$, $r^2 = 0.65$). Little finger results (yellow panels) mirror those for the thumb ($y = -4.6x + 437$, $r^2 = 0.39$, palm-down posture, upper row; $y = +3.7x + 425$, $r^2=0.77$ palm-up posture, bottom row).

b

Beta values of the regression lines (mean \pm S.E.M) relating the inverse efficiency score to number magnitude are presented for the palm-down (left side of the graph) and the palm-up posture (right side) for little finger (yellow bars) and thumb (blue bars) [finger X posture interaction, $F(1,13) = 9.80$, $p < 0.01$]. Hand posture modulates the visual numerical cueing of touch. Indeed, for stimuli applied to the thumb, positive beta values in the palm-down posture become negative in the palm-up posture ($+5.94 \pm 2.10$ vs. -2.04 ± 2.53 , respectively). The opposite is true for the little finger (-4.55 ± 1.95 vs. $+3.70 \pm 2.58$, respectively).

c

Time course of the visual numerical cueing of touch. Inverse efficiency scores (mean + S.E.M.) for stimuli to the little finger (yellow panels) and thumb (blue panels) after presentation of number "1" (black bars) and "5" (green bars) are presented for each delay (550, 800, 1050 and 1300 ms from number off-set). The spatial bias induced by the number is not modulated by the delay: in the palm-down posture (upper row), the pattern of performance for touches delivered to the little finger was better after number "5" than number "1" while performance for touches delivered to the thumb was better after number "1" than after number "5". The reversed pattern is observed in the palm-up posture (bottom row), irrespective of the delay.

Figure 3. Visual numerical cueing of touch is modulated by hand posture: emphasis on the sides of the hand

a

Regression lines of the inverse efficiency score as a function of number magnitude for all conditions. Regression equations reflect the averaged data in each panel. Performance for the thumb (blue panels) in palm-down posture (upper row), decreased as a function of number magnitude from the smallest (“1”) to the largest (“5”) number ($y = +20.1x + 458$, $r^2 = 0.97$); the pattern is opposite for the same stimulus on the same thumb but in palm-up posture (bottom row, $y = -4.26x + 421$, $r^2 = 0.84$). Little finger results (yellow panels) mirror those for the thumb ($y = -12.4x + 551$, $r^2 = 0.92$, palm-down posture, upper row; $y = +12.9x + 489$, $r^2=0.52$ palm-up posture, bottom row).

b

Beta values of the regression lines (mean \pm S.E.M) relating the inverse efficiency score to number magnitude are presented for the palm-down (left side of the graph) and the palm-up posture (right side) for little finger (yellow bars) and thumb (blue bars) [finger X posture interaction, $F(1,12) = 6.02$; $p < 0.03$]. Hand posture modulates the visual numerical cueing of touch, also when emphasis in task instruction is given to the side (left or right) of the hand. For stimuli applied to the thumb, positive beta values in the palm-down posture become negative in the palm-up posture ($+3.4 \pm 4.9$ vs. -23.2 ± 12.6 , respectively). The opposite is true for the little finger (-11.69 ± 7.3 vs. $+12.12 \pm 6.6$ respectively).

c

Time course of the visual numerical cueing of touch. Inverse efficiency scores (mean + S.E.M.) for stimuli to the little finger (yellow panels) and thumb (blue panels) after presentation of number “1” (black bars) and “5” (green bars) are presented for each delay: 250 from the number onset (i.e., during number presentation) and 250 ms from the number offset (i.e., after number presentation). Even at the shortest delay, the spatial bias induced by the number on tactile perception shifts according to whether the hand is in the palm-down (upper row), or the palm-up posture (bottom row).