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Finger pressure adjustments to various object configurations during precision grip in humans and monkeys

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Abstract

In this study, we recorded the pressure exerted onto an object by the index finger and the thumb of the preferred hand of 18 human subjects and either hand of two macaque monkeys during a precision grasping task. The to-be-grasped object was a custom-made device composed by two plates which could be variably oriented by a motorized system while keeping constant the size and thus grip dimension. The to-be-grasped plates were covered by an array of capacitive sensors to measure specific features of finger adaptation, namely pressure intensity and centroid location and displacement. Kinematic measurements demonstrated that for human subjects and for monkeys, different plate configurations did not affect wrist velocity and grip aperture during the reaching phase. Consistently, at the instant of fingers-plates contact, pressure centroids were clustered around the same point for all handle configurations. However, small pressure centroid displacements were specifically adopted for each configuration, indicating that both humans and monkeys can display finger adaptation during precision grip. Moreover, humans applied stronger thumb pressure intensity, performed less centroid displacement and required reduced adjustment time, as compared to monkeys. These pressure patterns remain similar when different load forces were required to pull the handle, as ascertained by additional measurements in humans. The present findings indicate that, although humans and monkeys share common features in motor control of grasping, they differ in the adjustment of fingertip pressure, probably because of skill and/or morphological divergences. Such a precision grip device may form the groundwork for future studies on prehension mechanisms.

Introduction

In dexterous primate species, precision grip is defined as the opposition of the pulpar surface of the distal phalanges of the index and thumb (Jeannerod *et al.*, 1995; Sustaia *et al.*, 2013). Albeit this ability is a key behavior in everyday activities, how this skill appeared, evolved and acts still remains unclear. The origin, evolution, and mechanisms of human prehension can be better understood by comparing it with grasping features in non-human primates. In both humans (Johansson & Westling, 1984; Soechting & Flanders,

2008) and macaques (Salimi *et al.*, 1999; Brochier *et al.*, 2004), the grip strategy is adapted to the object configuration, namely its shape, surface orientation, and degree of slipperiness. Previous studies performed on human subjects demonstrated that fingers placement on a to-be-grasped object is crucial for grip control and to counteract the object roll/slip during lifting (Lukos *et al.*, 2007, 2008). The grip is optimized probably by modifying the distribution of forces applied by the fingers (Salimi *et al.*, 2000) and by integrating sensorimotor memories with sensory feedback on finger positions (Fu *et al.*, 2010). The control of grip force represents a key component for performing a successful grip (Forssberg *et al.*, 1991; Schieber & Santello, 2004). A grip force that is too weak can cause accidental slip and fall of objects, while an excessive grip force can result in damaging fragile objects or even cause hand injuries (Galea & Darian-Smith, 1997; Hermsdörfer *et al.*, 2003; Nowak & Hermsdörfer, 2005). There is a substantial need for improved methodologies, in

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clinical conditions as well as in a translational animal model, to unravel the finger pressure adaptations induced by particular object configurations. The present study was undertaken to test whether different object configurations may induce specific finger adjustments, namely pressure intensity, centroid location at the first touch, and centroid displacement over object surface during grasping. Data were collected from 18 human subjects and two macaque monkeys, the most commonly studied non-human primates in grasping-related experiments. The custom-made experimental device allowed to manipulate the orientation of two plates composing a small handle that had to be grasped through a precision grip. Each plate was covered with capacitive sensor arrays, allowing the assessment of several finger pressure parameters. In addition, to reveal eventual differences during the reaching phase, hand kinematics was collected using a 3D-motion optical analyzer.

Materials and methods

Subjects

The experiments were performed in 18 healthy volunteers (nine females and nine males) and in two adult macaque monkeys (*Macaca fascicularis*, one female and one male, 4.5 and 6.3 kg, respectively). Fourteen human subjects (seven females and seven males, 20–40 years, seven right-handed and seven left-handed) participated to the main experiment and four additional subjects (two females and two males, 20–40 years, two right-handed and two left-handed) participated to an additional control experiment on load force effects. Human subjects were tested after providing informed consent and were all naïve as to the purpose of the study. The hand preference was ascertained by the Edinburgh Handedness Inventory (Oldfield, 1971). Human subjects were tested without training using their preferred hand. Subjects were seated comfortably in front of the device and were instructed to perform the reach, grasp, and pull task using their 'natural' velocity and grip force. By contrast, the monkeys were daily trained for 2 months to accept handling by the investigators, to sit on a primate chair and to perform the task. During training, the monkeys received a food reward if they succeeded to grasp and pull the device. Data were collected when the monkeys showed a constant and reproducible performance using the trained hand. The experiments performed in humans were undertaken with the understanding and written consent of each subject, were authorized by the Ethics Committee of the University/Hospital of Ferrara (n. 140690), and the study conforms with World Medical Association Declaration of Helsinki published on the website of the Journal of American Medical Association. The experiments performed in macaques are in accordance with the Council Directive 2010/63/EU of the European Parliament and the Council of 22 September 2010 on the protection of animals used for scientific purposes and were approved by the Animal Care Ethics Committee of the University of Ferrara, were authorized by the Italian Ministry of Health (n. 1139/2016-PR) and complied with the European laws on the use of laboratory animals. To optimize the number of animals, the present study was performed according to 3R principle originally formulated by Burch and Russel (see Griffin *et al.*, 2014).

Precision grip device

The device was formed by a handle (Fig. 1A) that, if correctly pulled, opens a Plexiglas drawer (160 mm height \times 190 mm width \times 160 mm depth) embedded in an aluminum/Plexiglas box (190 mm height \times 240 mm width \times 300 mm depth). The drawer is mounted

on a rail that could slide along the sagittal axis (travel distance, 70 mm). The handle was formed by two small horizontal aluminum plates (3 mm height \times 18 mm width \times 30 mm depth) buried in a vertical groove (100 mm height \times 25 mm width \times 25 mm depth) to force the precision grip and to protect the internal components. Each plate could be independently rotated along the horizontal and vertical planes by two high-precision stepping micro-motors (2224SR; Faulhaber, Schönaich, Germany) with planetary gearheads (20/1; Faulhaber, Schönaich, Germany) connected to a PC and power supplied by 24 V. The combination of various spatial orientations of the upper and lower plates defined various configurations of the handle. The distance between the two plates (at 9 mm from the frontal and the two lateral edges) was preserved at a fixed measure (reference axis). Each plate of the handle was covered on its outer side by a 6×4 capacitive sensor array (18 \times 24 mm each; Fig. 1B). Capacitive sensors are transducers designed, produced and tested in our laboratories (Roncone *et al.*, 2016). To make it working as pressure sensor, the array was covered with a soft layer of polychloroprene (neoprene) with a thickness of 1 mm covered by a conductive layer. Three boards were needed to allow the data flow. Data coming from the two boards connected to the capacitive sensors were connected via I2C communication-bus to a third board which processed the data and in turn was connected via RS232 communication-bus to the PC using a USB-RS232 converter cable (FTDI-TTL-232R-3V3, FTDI Chip, Glasgow, UK). Each capacitive sensor sampled finger pressure at 22 Hz and provided a pressure value (in arbitrary unit) between 200 (for no grip pressure) and 11 (for saturated grip pressure). These data were off-line rescaled in percentage of the maximal sensor response (Fig. 1C). Sensors were never saturated during the experiment. Note that capacitive sensors did not express pressure values in absolute terms. The pressure can be expressed also in g/cm², as preliminarily calculated by applying objects of different weight on the sensor array (Fig. 1D). However, the goal of the present study was comparative and, thus, data are reported in arbitrary units (in the 0–2400 range for each plate). A microswitch (V15T16, Honeywell International, Morristown, USA) was integrated into the drawer to signal the start of pull. These signals were acquired by a DAQ-NI-USB-6229 device (National Instruments, Austin, USA) and were used to reconstruct and temporally align pressure data during the analysis. To control the aforementioned hardware as well as to visualize and record data, a custom Virtual Instrument (VI) was created by LabVIEW graphical programming language (National Instruments, Austin, USA).

Precision grip task

Each trial started with the hand of the human subject or monkey positioned on a pad in front of the chest. The precision grip device was positioned at 30 cm (humans) or 20 cm (monkeys) from the chest, 5 cm below the chin, so that the subject could easily see the to-be-grasped handle. The handle could be pulled by a minimum force of 1 N as measured by an isometric force transducer (ZP-50N dynamometer, IMADA, Toyohashi, Japan). This value appeared appropriate to allow both humans and macaques to easily perform the task (Ehrsson *et al.*, 2000; Brochier *et al.*, 2004; our preliminary observation). However, to avoid differential force effects due to the different pull force of the two species (i.e., a device easy to pull for humans could be harder for macaques), we performed a control experiment on humans where different masses (50, 100, and 200 g) were applied to the device in order to increase the load force required to pull it (load force; 1.5, 2.5, and 3.5 N, respectively).

The go instruction was a verbal instruction of the experimenter (humans) or the opening of a custom-made Plexiglas diaphragm

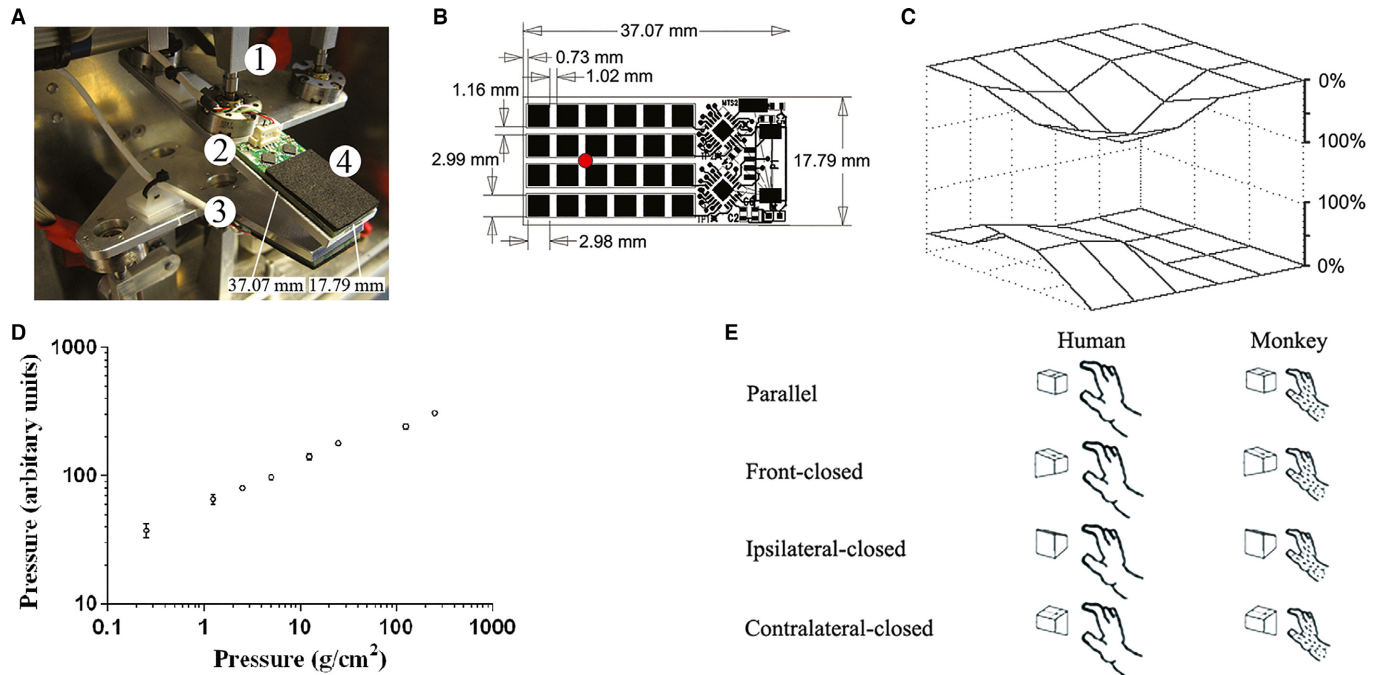


FIG. 1. (A) Photograph of the handle inserted in the drawer showing the two plates controlled by the micro-motors. Numbers within white circles indicate the piston of a micro-motor (1), the upper (2), and lower (3) plates of the handle, and the sensor array covered by neoprene (4). Length and width of sensor array is indicated within white rectangles. In this photograph, the front panel containing the vertical groove was removed to make the handle more visible. (B) Representation of the sensor array, indicating the dimension of its components. The red point indicates the reference axis, i.e., where the distance of the two plates remains constant. (C) Reconstruction of the pressure exerted on the handle by the fingers, as elaborated by the custom-made software. (D) Pressure detected (in arbitrary units) in function of different weights (in g/cm^2) applied to the sensor array. All measurements are expressed as mean \pm SEM of three determinations. (E) Different handle configurations used for the present experiments. Note that the size of hands were not in proportion with the handle to improve the legibility of figure. [Colour figure can be viewed at wileyonlinelibrary.com].

placed between the monkey and the handle. Overall, the task involved the following steps: (i) start of movement, corresponding to the lift of the hand from the pad; (ii) touch, corresponding to the contact of both the index and thumb with the corresponding plates of the handle; and (iii) start of pull, corresponding to the beginning of drawer displacement. TTL signals characterizing each step were recorded and used off-line for data synchronization.

As each sensor can assume a value in the 0–100 range (Fig. 1C), the 24 sensors of each plate gave altogether a maximal value of 2400 arbitrary units. The touch is determined by the same sensors used to measure the pressure. When pressure value on both plates exceeded 4% of the maximum value (2400 arbitrary units), a TTL pulse was generated to mark the event. If only one finger touched the plate and generated a pressure above the 4% threshold, the TTL was not generated until the other finger exceeded the threshold as well. This allowed us to exclude from the analysis grips performed partially. This was true also for temporally incorrect sequences. For example, the sequence (i) index touch, (ii) index lift, (iii) thumb touch, (iv) index touch, was discarded from the study. Overall, although no errors have been detected for humans, about 10% of monkey trials were discarded.

Four-handle configurations were selected based on the orientation of the two plates (Fig. 1E), namely, parallel in the horizontal plane (parallel), closed on the front side (front-closed), closed on the same side as the hand used for grasping (ipsilateral-closed), and closed on the side opposite to the hand used to grasp (contralateral-closed). Angles between each plate and the horizontal plane were fixed to 12° for the front-closed configuration and 15° for the ipsilateral- and contralateral-closed configurations. The distance between the two plates, measured at 9 mm from the front and lateral edges (i.e., the reference axis), was fixed to 30 mm (for human subjects) and

20 mm (for monkeys) for all configurations (Fig. 1B). These values were based on preliminary observations and represented the optimal slope/distance relationship allowing humans and monkeys to correctly perform the task (i.e., in the more reproducible manner across trials). For human subjects, the distance between the plates surface was adjusted at 30 mm, a value that represent the average measurement of the index thumb distance at their insertion on the palm when kept parallel (C-shaped). On the other hand, for monkeys, the same measurement during a similar finger posture gave a value of about 17 mm. For this reason, the distance between the two plates was adjusted to 20 mm for the monkeys, as this value represents the minimum possible for our device because of mechanical constraints. Indeed, a further reduction of the distance did not allow the rotation of the two surfaces around the pistons of the micro-motors. To exclude the systematic repetition of stereotyped movements, the order of presentation of the four-handle configurations and time interval between two consecutive trials were randomly varied on a trial-to-trial basis. The analysis was performed off-line using a custom program in MATLAB (MathWorks, Natick, USA). The data processing program was used to calculate (i) pressure intensity, calculated for each plate in an arbitrary unit (0–2400) by summing pressure values of all sensors (0–100), and (ii) the coordinates (in mm) of the centroid in antero-posterior (AP) and medio-lateral (ML) directions, corresponding to the average of sensor coordinates weighted by their pressure contribution. During each session, human subjects performed 20 trials for each handle configuration, monkeys 10 trials. Each human subject performed a single session. In the first monkey, nine sessions for the right and five for the left hand were performed, whereas in the second monkey, 8 for the right and 15 for the left hand (maximum two sessions per week).

Kinematics recording

Hand movements during the task were recorded by a 3D-motion optical analyzer (Qualisys Motion Capture System; Qualisys, Charlotte, USA) and were synchronized by using the TTL signal of pad release. Setup and procedure were similar to those described by a previous work (Fadiga *et al.*, 2013). Three small adhesive infrared-reflective spheres (diameter 3.0 mm, weight 40 mg) were placed over three anatomical landmarks: the wrist (head of the ulna) and the last interphalangeal joint of thumb and index finger. Three infrared cameras, placed at ~ 1.5 m from the subject, were used to record the position of the markers. The motion analysis software reconstructed the 3D coordinates of the markers in space and time, enabling off-line reconstruction of the movement of each marker. Movements were recorded at a sampling rate of 200 Hz, a value considered more than appropriate for the biological motion of primates (Saleh *et al.*, 2012; Fadiga *et al.*, 2013). Using TTL signals from the pad (at the release) and from the handle (at touch), we analyzed wrist velocity and grip aperture, i.e., the distance between the two markers placed on the fingers. Analyses were performed off-line using the Qualisys Track Manager software (Qualisys Motion Capture System; Qualisys, Charlotte, USA). During each session, human subjects performed 20 trials per handle configuration and monkeys performed 4–12 trials depending on their motivation. Each human subject performed one single session. Each monkey performed four sessions for the right and four for the left hand (maximum two sessions per week).

Statistical methods

Data are presented as mean \pm SEM (standard error of mean) of 14 human and 4 monkey hands. All variables were averaged across trials for each session. Data are analyzed using two-way ANOVA (Fig. 2C–D, 3C and 5B–C) with Handle configuration (parallel, front-close, ipsilateral-close, contralateral-close) and Species (human, monkey) as factors. When interaction between the factors was not significant, unpaired *T*-tests were performed between the two species for each handle configuration. To analyze pressure intensity values (Fig. 3B), regression analysis and one-way ANOVA on slopes were performed. In the supplemental experiment investigating different effect of load forces, one-way ANOVA was performed on pressure intensity and centroid coordinate values. Newman–Keuls *post hoc* test was used for multiple comparisons ($P < 0.05$).

Results and statistical analysis

No training was required for human subjects and they were tested using their preferred hand (see Materials and methods). By contrast, the two monkeys were tested using either hand and were able to perform the task only after a period of training (~ 1 month per hand). After training, no major difference was observed between right and left hand in terms of kinematics or grip pressure. For this reason, monkey data resulting from both hands were grouped together.

Fingers/wrist kinematics

Kinematic data of the hand during the reaching-to-grasp phase (i.e., before handle touch) were analyzed in order to test the effect of different handle configurations on reaching performance. Representative examples of the time-course of wrist velocity (Fig. 2A) and grip aperture (Fig. 2B) for each handle configuration are shown for

one representative human subject (left panels) and one monkey (right panels). Both wrist velocity and grip aperture profiles were substantially similar in all handle configurations, albeit some difference emerged between two species. To quantitatively characterize these kinematic data, statistical analyses were performed on the maximal wrist velocity and grip aperture. Two-way ANOVA on maximal wrist velocity values (Fig. 2C) showed no effect of Handle configuration, but a significant effect of Species ($F_{1,64} = 230.10$, $P < 0.0001$) and a nonsignificant Handle configuration \times Species interaction. *T*-tests between the two species revealed that monkeys performed reaching at smaller velocity as compared to human subjects for all handle configurations ($t_{16} = 7.56$, $P < 0.0001$; $t_{16} = 7.75$, $P < 0.0001$; $t_{16} = 7.16$, $P < 0.0001$ and $t_{16} = 7.85$, $P < 0.0001$ for parallel, front-, ipsilateral-, and contralateral-closed, respectively). Consistently, two-way ANOVA on maximal grip aperture values (Fig. 2D) showed no effect of Handle configuration, but a significant effect of Species ($F_{1,64} = 439.50$, $P < 0.0001$) and a nonsignificant Handle configuration \times Species interaction. *T*-tests between the two species confirmed the obvious smaller finger aperture in monkeys as compared to human subjects for all handle configurations ($t_{16} = 10.40$, $P < 0.0001$; $t_{16} = 10.07$, $P < 0.0001$; $t_{16} = 10.72$, $P < 0.0001$ and $t_{16} = 10.76$, $P < 0.0001$ for parallel, front-, ipsilateral-, and contralateral-closed, respectively).

Characterization of finger pressure during grip

Pressure parameters of fingers during the grip phase (i.e., after handle touch) were analyzed in order to test whether different handle configurations induced peculiar grip adaptation.

Pressure intensity

Representative examples of the time-course of pressure intensity (Fig. 3A) for each handle configuration are shown for one human subject (left panels) and one monkey (right panels). The touch instant was identified by using the same threshold (96 arbitrary units) for humans and monkeys (see Materials and methods). This threshold was reached at $\sim 50\%$ of maximal pressure in monkeys and at $\sim 25\%$ of maximal pressure in humans. This justifies the difference showed in pressure parameters between the two species (due to technical constraints). The pressure profiles were substantially similar in all handle configurations, albeit some difference emerged between the two species. To quantitatively assess the pressure intensity on each plate at the beginning (touch) and the end (start of pull) of pressure adjustments preceding the pull, sensor values in the area directly contacting the finger pads were summed together (Fig. 3B). Considering the index, two-way ANOVA on pressure intensity values performed at touch or start of pull failed to detect any difference between Handle configuration or Species factors. Considering the thumb, two-way ANOVA on pressure intensity performed at both events showed no effect of Handle configuration, but a significant effect of Species (touch: $F_{1,64} = 70.07$, $P < 0.001$; start of pull: $F_{1,64} = 87.75$, $P < 0.001$) and a nonsignificant Handle configuration \times Species interaction. *T*-tests between the two species showed that thumb pressure was lower in monkeys than in human subjects, at both touch and start of pull for all handle configurations (touch: $t_{16} = 4.41$, $P = 0.0004$; $t_{16} = 5.35$, $P < 0.0001$; $t_{16} = 4.10$, $P = 0.0008$; and $t_{16} = 3.30$, $P = 0.0045$; start of pull: $t_{16} = 5.25$, $P < 0.0001$; $t_{16} = 5.95$, $P < 0.0001$; $t_{16} = 4.46$, $P = 0.0004$; and $t_{16} = 3.67$, $P = 0.0021$ for parallel, front-, ipsilateral-, and contralateral-closed, respectively). To compare the pressure tuning during the grip adjustment (occurring between touch and start of pull) in the different

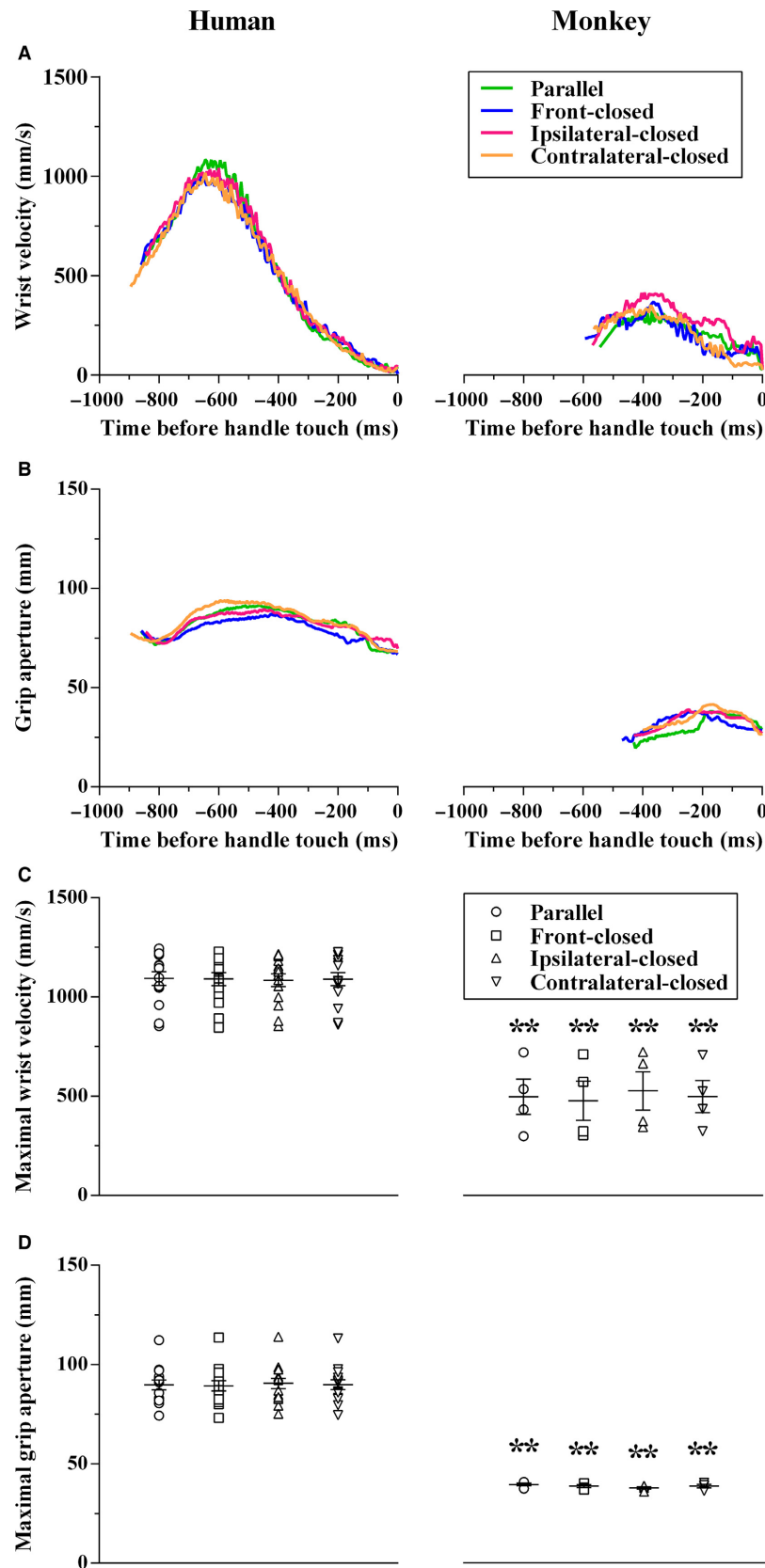


FIG. 2. Kinematic features during the task. (A) Representative examples of the time-course (in ms) of the wrist velocity (in mm/s) in human subjects (left panel) and monkeys (right panel). (B) Representative examples of the time-course (in ms) of the size of grip aperture (in mm) in human subjects (left panel) and monkeys (right panel). (C) Maximal wrist velocity (in mm/s) in human subjects (left panel) and monkeys (right panel). (D) Maximal grip aperture (in mm) in human subjects (left panel) and monkeys (right panel). All measurements are expressed as mean \pm SEM of 14 human or four monkey hands. $**P < 0.01$ different from human (two-way ANOVA and unpaired *T*-test). [Colour figure can be viewed at wileyonlinelibrary.com].

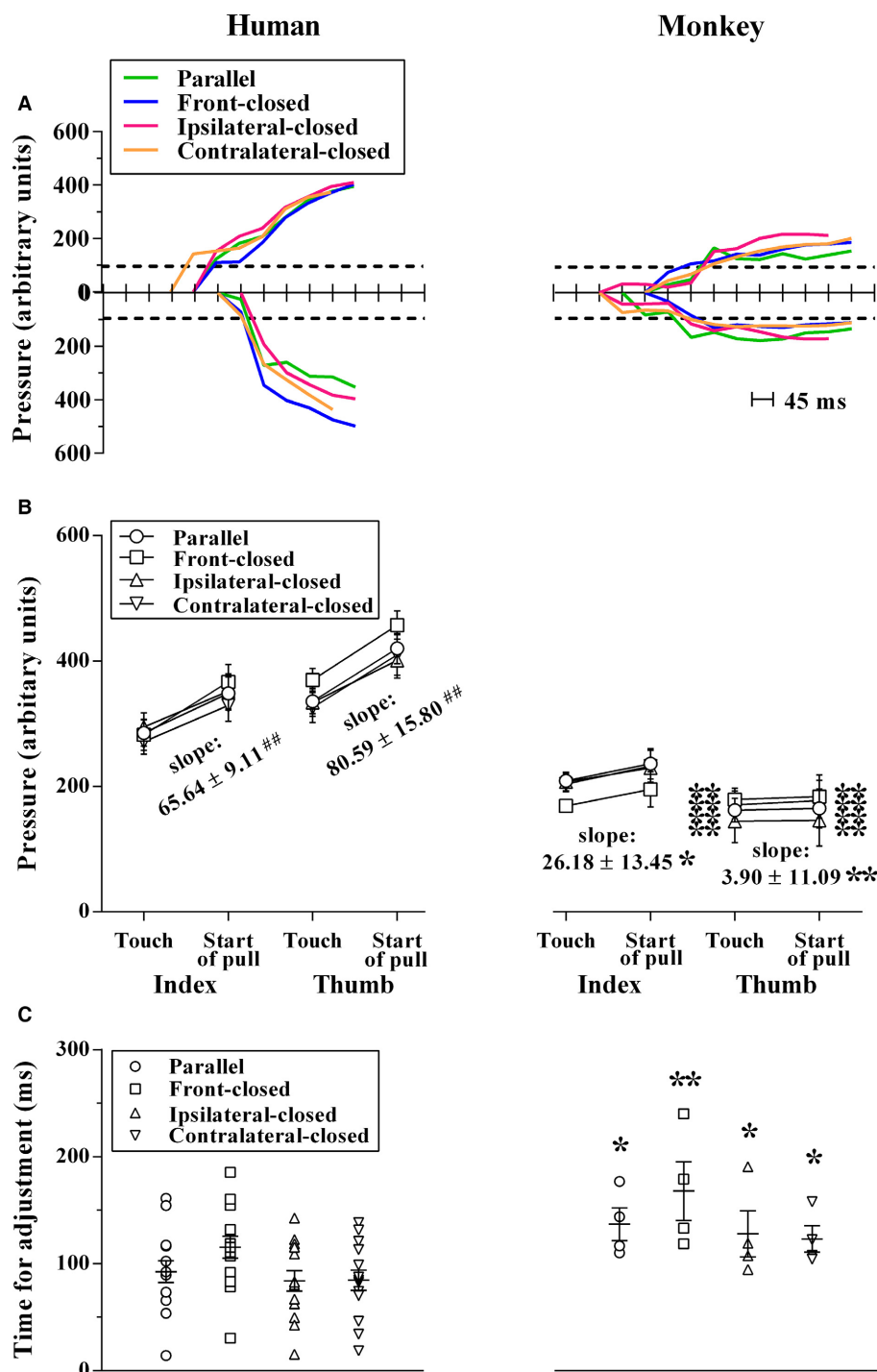


FIG. 3. Intensity of the pressure of the fingers on the handle. (A) Representative examples of the time-course (in ms) of the pressure intensity (in arbitrary units) applied by the index on the upper plate and the thumb on the lower plate, in human subjects (left panel) and monkeys (right panel). Horizontal dotted lines represent the 4% threshold for the touch. (B) Pressure intensity (in arbitrary units) applied by the index on the upper plate and the thumb on the lower plate, from touch to start of pull, in human subjects (left panel) and monkeys (right panel). (C) Time (in ms) spent between the touch and the start of pull in human subjects (left panel) and monkeys (right panel). All measurements are expressed as mean \pm SEM of 14 human or 4 monkey hands. $^{##}P < 0.01$, different from zero (linear regression test); $^*P < 0.05$, $^{**}P < 0.01$ different from human (one- or two-way ANOVA followed by the Newman–Keuls test and unpaired *T*-test). [Colour figure can be viewed at wileyonlinelibrary.com].

handle configurations, a linear regression analysis was performed. A single regression line was calculated for each finger combining all handle configurations, in human subjects as well as in monkeys. In humans, linear regression analysis demonstrated a slope significantly different from zero (index: $F_{1,6} = 51.92$, $P < 0.001$; thumb: $F_{1,6} = 26.03$, $P < 0.01$). By contrast, in monkeys, the slope was not

significantly different from zero. These results indicate that the pressure increase observed during the adjustment period was significantly detectable only in human subjects. Consistently, one-way ANOVA performed on slope values of these four regression lines showed relevant differences ($F_{3,28} = 7.82$, $P < 0.001$). *Post hoc* analysis revealed the larger slope of humans as compared to monkeys.

Adjustment time

An additional difference between the two species emerged also when considering the time duration for the grip adjustment (Fig. 3C). Two-way ANOVA performed on time values showed no effect of Handle configurations, but a significant effect of Species ($F_{1,64} = 43.61$, $P < 0.001$) and a nonsignificant Handle configuration \times Species interaction. *T*-tests between the two species revealed that adjustment time was longer in monkeys than in humans for all handle configurations ($t_{16} = 4.11$, $P = 0.0008$; $t_{16} = 4.08$, $P = 0.0009$; $t_{16} = 3.72$, $P = 0.0019$; and $t_{16} = 4.05$, $P = 0.0009$ for parallel, front-, ipsilateral-, and contralateral-closed, respectively).

Pressure centroid at touch

To study the adjustments of finger positions during the grip, AP and ML coordinates of pressure centroid were computed by weighting the contribution of each sensor in each plate of the handle. Examination of coordinates of pressure centroid at touch for the index and thumb (Fig. 4) for human subjects (first and second panel) and monkeys (third and fourth panel) demonstrated that $95.5 \pm 4.5\%$ and $94.9 \pm 3.9\%$ of the points (for humans and monkeys, respectively) were located in correspondence of the four sensors around the point corresponding to the reference axis of the handle (see Materials and methods). This revealed that the pressure centroids for all handle configurations were clearly clustered in the region where the distance between plates remained constant.

Pressure centroid displacement during grip

During finger adjustments, the pressure centroid was shifted differently depending on the handle configuration and on the considered species. A representative example of the coordinates of the centroid displacement is shown in a bi-dimensional system (Fig. 5A) for human subjects (first and second panel) and monkeys (third and

fourth panel). In these plots, centroid positions calculated at touch were spatially normalized, so that finger adjustments start at the same point in all trials. To quantitatively assess the centroid adjustment in each handle configuration, displacements along AP and ML direction were analyzed separately for each finger. Considering the AP displacement (Fig. 5B), two-way ANOVA on index finger values showed a significant effect of Handle configuration ($F_{3,64} = 84.86$, $P < 0.001$), Species ($F_{1,64} = 4.28$, $P < 0.05$), and Handle configuration \times Species interaction ($F_{3,64} = 6.24$, $P < 0.001$). *Post hoc* analysis revealed that the front-closed handle configuration induced a larger displacement in the direction of pull, as compared to other configurations, this displacement being significantly stronger for monkeys than for humans. Similarly, two-way ANOVA on thumb values showed significant effect of Handle configuration ($F_{3,64} = 73.75$, $P < 0.001$), Species ($F_{1,64} = 1079.00$, $P < 0.001$), and Handle configuration \times Species interaction ($F_{3,64} = 7.26$, $P < 0.001$). *Post hoc* analysis revealed that the front-closed handle configuration induced a more important displacement in the direction of pull, as compared to other configurations. Differently from index finger, the displacement of the thumb was stronger for monkeys than for humans, considering all handle configurations. Additional differences were highlighted when analyzing the ML displacement (Fig. 5C). Two-way ANOVA on index finger values showed a significant effect of Handle configuration ($F_{3,64} = 233.30$, $P < 0.001$), a nonsignificant effect of Species and a significant Handle configuration \times Species interaction ($F_{3,64} = 19.43$, $P < 0.001$). *Post hoc* analysis revealed that the pressure centroid in the ipsilateral-closed and in the contralateral-closed handle configurations strongly shifted in opposite directions (lateral and medial, respectively). Moreover, ML displacement for these two-handle configurations was more pronounced for monkeys than for humans. Similarly, two-way ANOVA on thumb values showed a significant effect of Handle configuration ($F_{3,64} = 235.80$, $P < 0.001$), but not of Species and a significant Handle configuration \times Species interaction ($F_{3,64} = 29.81$,

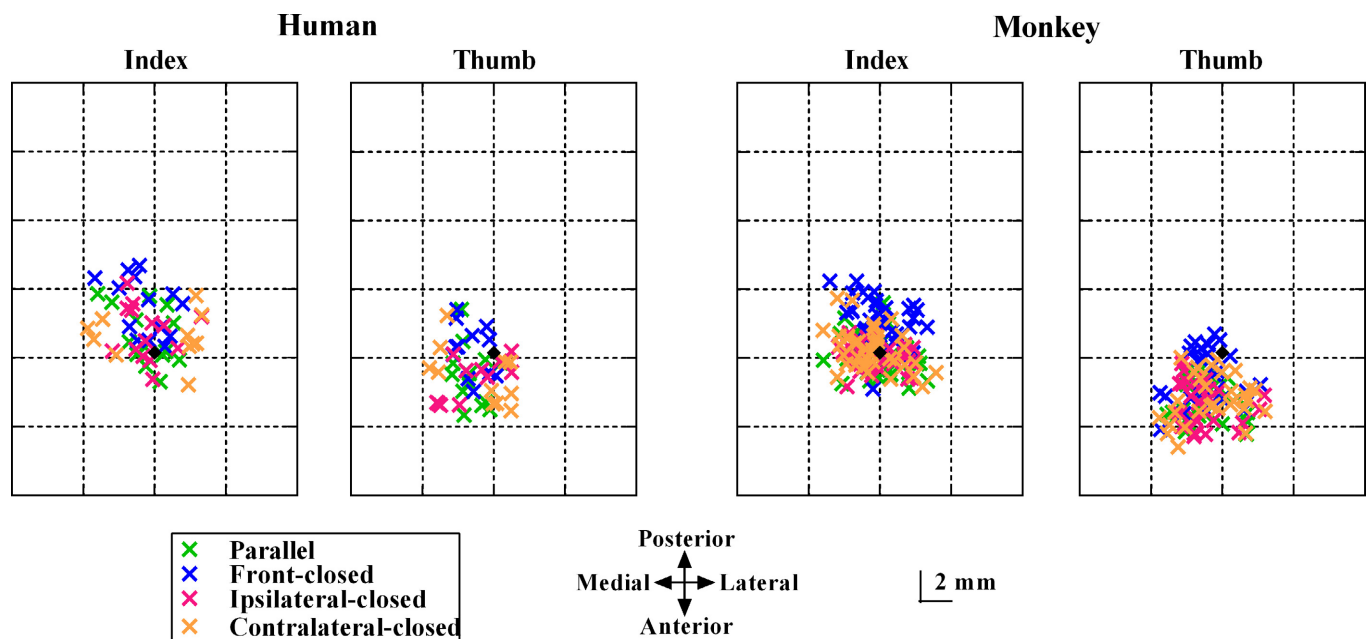


FIG. 4. Localization of the pressure centroid of the fingers on the handle. Cumulative representation of the pressure centroid of the index on the upper plate and the thumb on the lower plate at touch in human subjects (first and second panel, respectively) and monkeys (third and fourth panel, respectively). Each point corresponds to one subject (human) or session (monkey). The small black diamond represents the point corresponding to the reference axis of the handle, i.e., where the distance between plates remained constant. [Colour figure can be viewed at wileyonlinelibrary.com].

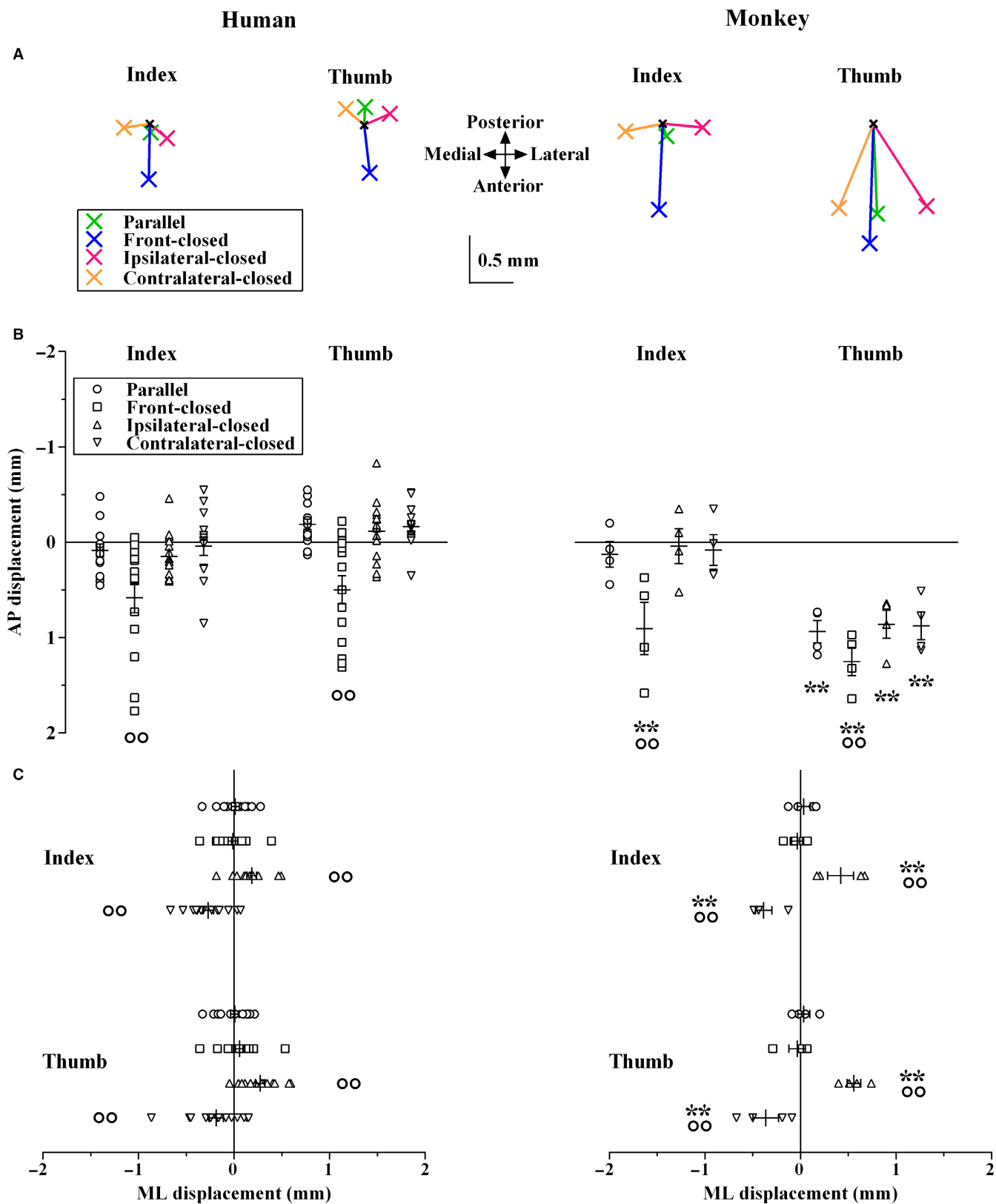


FIG. 5. Displacement of the pressure centroid of the fingers on the handle. (A) Representative examples of the displacement of the pressure centroid for index and thumb in human subjects (first and second panel, respectively) and monkeys (third and fourth panel, respectively). (B) Antero-posterior (AP) displacement (in mm) of the pressure centroid of the index on the upper plate and the thumb on the lower plate in human subjects (left panel) and monkeys (right panel). (C) Medio-lateral (ML) displacement (in mm) of the pressure centroid of the index on the upper plate and the thumb on the lower plate in human subjects (left panel) and monkeys (right panel). All measurements were performed between the touch and the start of pull and are expressed as mean \pm SEM of 14 human or four monkey hands. $**P < 0.01$ different from human, $^{\circ\circ}P < 0.01$ different from other configurations (two-way ANOVA followed by the Newman-Keuls test). [Colour figure can be viewed at wileyonlinelibrary.com].

$P < 0.001$). As for the index finger, *post hoc* analysis for thumb revealed that the pressure centroid in the ipsilateral-closed and in the contralateral-closed handle configurations strongly shifted in opposite directions (lateral and medial, respectively). Moreover, ML displacement for these two handle configurations was more pronounced for monkeys than for humans.

Finger pressure evaluation at different load forces (control experiment)

To assess whether pressure parameters were dependent on the load force required to pull the handle, additional human subjects were tested on a supplemental experiment.

Pressure intensity

For each handle configuration, considering index and thumb at touch (Fig. 6A), one-way ANOVA on pressure intensity values revealed no major difference among load forces. This lack of significance was also found at start of pull (Fig. 6B), albeit a trend to increase the intensity was detected in the front- and ipsilateral-closed handle configurations.

Pressure centroid displacement during grip

For each handle configuration, considering the AP displacement (Fig. 6C), one-way ANOVA on index values revealed no major difference among different load forces. One-way ANOVA performed on thumb values in the front-closed handle configuration showed important differences ($F_{3,12} = 6.316$, $P < 0.01$). *Post hoc* analysis revealed a specific increase in displacement when a force of 3.5 N was needed to pull the handle. Finally, considering the ML displacement for both index and thumb (Fig. 6D), one-way ANOVA failed to detect differences.

Discussion

The present experiment was designed to evaluate finger pressure adjustments during precision grip in humans and macaques on a handle allowing to keep constant the size while varying the degree of parallelism of the to-be-grasped surfaces. This causes different moduli and directions of force vectors acting in the opposition space (Oztop & Arbib, 2002) determined by the fingers. During reaching, we verified that the different handle configurations induced similar kinematics. This concurs with the idea that modifying the handle configuration did not constitute a significant perturbation of kinematics during the reaching phase. During the grip phase, both in human subjects and monkeys, pressure intensity and adjustment time was not modulated by handle configuration. However, humans employed stronger thumb pressure intensity and shorter adjustment time, as compared to monkeys. Moreover, humans displayed a marked increase of pressure throughout the grip, contrary to monkeys, who performed finger adjustments at constant pressure. In addition, these results displayed that each handle configuration induced specific adjustments of pressure centroid position for both fingers. This was verified in both species albeit clearly amplified in monkeys as compared to humans.

Assessment of finger adaptation to object shape

In this study, we considered the preferred (right or left) hand of 18 human subjects, as well as the right and left hands of two macaque

monkeys. In order to account for right/left anatomical/biomechanical differences, we defined handle configurations as ipsilateral- and contralateral-closed, with respect to the hand used for grasping. Moreover, centroid displacement was studied along medial and lateral, rather than right and left, directions. Therefore, possible effects of handle configuration could hardly be attributed to different right/left biomechanics.

In agreement with previous experiments (Saleh *et al.*, 2010), the kinematic profile revealed that in humans, as in monkeys, the prehensile movement began with an extension (aperture) of the fingers and, as the hand approached the handle, both the index and thumb flexed for grasping in a similar spatiotemporal sequence for all handle configurations. Human subjects performed the reaching with similar maximum wrist velocity and grip aperture for all handle configurations. A similar approach was employed by monkeys despite remarkable differences between the two species, such as greater wrist velocity and grip aperture in humans (Roy *et al.*, 2000). The kinematic similarities between humans and macaques might be reflected by similarities in neural mechanisms of prehension in the two species (Castiello, 2005). Indeed, larger maximal grip aperture in humans is consistent with larger hand dimension and handle size. However, it is difficult to directly compare our results with other studies, as the experimental conditions differ by several aspects (e.g., training, position of subjects, distance, and dimension of object; Gentilucci *et al.*, 2001; Roy *et al.*, 2002; Sartori *et al.*, 2013a,b).

Consistent with the reaching kinematics, pressure centroids at touch were clearly clustered around the point corresponding to the reference axis of the handle. Furthermore, in humans, pressure intensity at the two main steps of the grip, namely touch and start of pull, as well as the duration of pressure adjustments, were similar for all handle configurations. A similar result was obtained for monkeys. Taken together, these results suggest that, both in humans and macaques, the four handle configurations were processed as the same object, or as objects with similar properties (Kudoh *et al.*, 1997; Paulignan *et al.*, 1997). These similarities confirm that these two species share common aspects of the motor control of grasping (Roy *et al.*, 2000; Christel & Billard, 2002; Castiello, 2005).

Despite these similarities, some differences emerged between humans and monkeys. In particular, humans applied stronger thumb pressure to all handle configurations, as compared to monkeys, at both touch and start of pull. This result highlights species differences in thumb anatomy and biomechanics during grasping (Marzke, 1997; Sustaita *et al.*, 2013; Feix *et al.*, 2015). By contrast, for the index finger, only a mild effect was detected for the front-closed configuration, at start of pull. Divergences between humans and monkeys were further highlighted when considering pressure adjustments throughout the grip procedure. Humans displayed a clear pressure increase from touch to start of pull, whereas in monkeys, the pressure change was negligible. The duration for pressure adjustment from touch to start of pull was also shorter in humans than monkeys. Altogether, these findings indicate that, in our experimental conditions, humans could adapt grip pressure during the task and adjust grip parameters in a relatively short time interval, contrary to macaques. One possibility, not incompatible with the above interpretation, is that monkeys applied their maximum force at touch, so that no further force increase could be generated afterwards.

The major discrepancy between humans and macaques was observed in the displacement of index and thumb pressure centroids on handle surfaces. Both in humans and in monkeys, each handle configuration induced a significant centroid displacement in the handle slope direction, probably due to the low friction induced by the

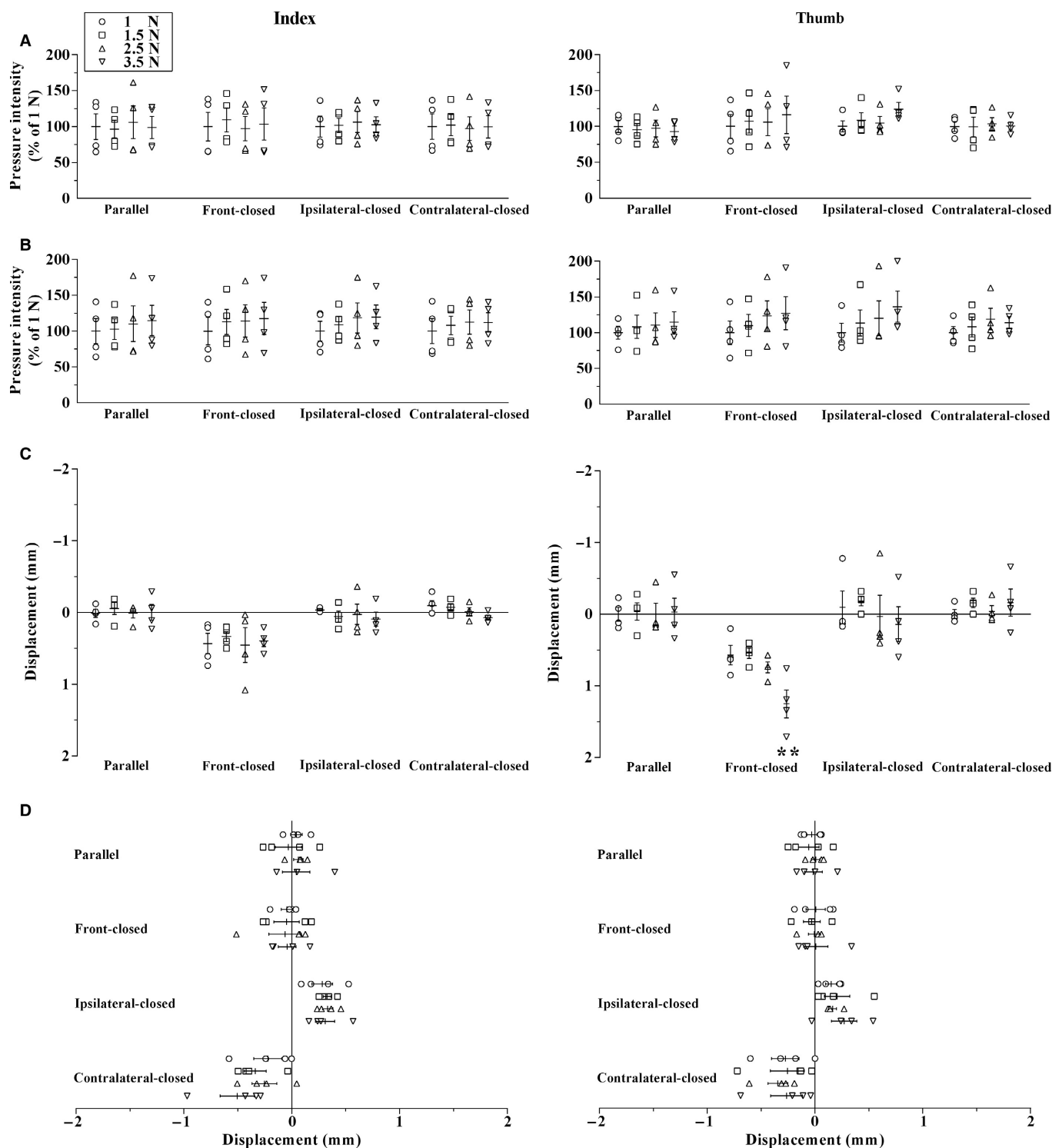


FIG. 6. Finger pressure evaluation at different load forces in human subjects. (A) Pressure intensity (in % of 1 N force) applied at touch by the index on the upper plate (left panel) and the thumb on the lower plate (right panel). (B) Pressure intensity (in % of 1 N force) applied at start of pull by the index on the upper plate (left panel) and the thumb on the lower plate (right panel). (C) Antero-posterior (AP) displacement (in mm) of the pressure centroid of the index on the upper plate (left panel) and the thumb on the lower plate (right panel). (D) Medio-lateral (ML) displacement (in mm) of the pressure centroid of the index on the upper plate (left panel) and the thumb on the lower plate (right panel). All measurements are expressed as mean \pm SEM of four human hands. ** $P < 0.01$ different from 1 N force (one-way ANOVA followed by the Newman-Keuls test).

slopes of the surfaces (Salimi *et al.*, 1999; Johansson & Flanagan, 2009). However, in monkeys, displacements induced by handle configurations were clearly amplified as compared to humans. This amplification was even more substantial when considering it relative

to finger length (human: index, 99.5 ± 4.5 mm, thumb, 65.0 ± 5.0 mm; monkey: index, 36.3 ± 1.3 mm, thumb, 22.3 ± 1.3 mm). Besides, in monkeys, the AP displacement of the thumb was particularly marked regardless of handle configuration. One possible

reason could be the lesser ability, in macaques, to adjust to low levels of frictions (Salimi *et al.*, 1999). Alternatively, the morphological constraint of the finger joint could compel the movement (Christel & Billard, 2002). Macaques present important morphological differences with humans, including hypertrophied arm muscles consistent with the use of their forelimbs for locomotion (Cheng & Scott, 2000; Christel & Billard, 2002). Comparatively, in humans, precision grip and manipulative abilities are facilitated by musculoskeletal traits such as long digits, robust metacarpals and phalanges, large joint surface and mobility and hypertrophic thenar muscles (Marzke, 1997; Schieber & Santello, 2004; Rolian *et al.*, 2011; Sustaita *et al.*, 2013; Feix *et al.*, 2015).

However, given the device structure, plates configuration evoked always the same wrist/fingers orientation, i.e., index on the upper plate, thumb on the lower plate. Changing the whole device configuration, e.g., placing the plates vertically in order to change wrist orientation may give origin to different effects (Werremeyer & Cole, 1997). Furthermore, an additional factor to keep in consideration when comparing the pressure centroid displacements in human subjects and monkeys may be represented by the different ratio between finger length and handle dimension in the two species. The lower ratio between finger length and distance of handle surface for the monkeys with respect human subjects could explain, at least partially, the larger pressure adjustments performed by the monkeys.

It is worth mentioning that, in our experiment, the grasping device was calibrated to the minimum load force, thus corresponding to a weak grip force in humans (Ehrsson *et al.*, 2000; our data). In macaques, this value concurred with previous work (Brochier *et al.*, 2004), and allowed the most reproducible performance across trials. To further validate the choice of this load force for our comparison of the two species, we verified in human subjects that the modulation of load force required to pull the handle did not constitute a major perturbation for specific pressure adjustments. Our results showed that pressure intensity and centroid displacements during grip are not affected by different load forces between 1.0 and 3.5 N, a range of force compatible with precision grip (Ehrsson *et al.*, 2000).

Considering the notable flexibility of handle configurations, load force, or texture of the handle surfaces, the present precision grip device can be used at both clinical and experimental levels for the evaluation of deficits in manual dexterity associated with injuries or neurological diseases as well as to test the effectiveness of therapeutic approaches (Nowak, 2008; Prodoehl *et al.*, 2009). Finally, in non-human primates, the device can be useful to study how cortical neurons controls grip adaptation, also in parallel to other grip devices (Bury *et al.*, 2009; Nowak & Hermsdörfer, 2003).

Conclusion

Overall, the present study demonstrated that, although humans and monkeys share common features in the motor control of grasping, they differ in the adjustment of fingertip pressure during the execution of a precision grip. This finding sheds light on the prehensile specializations that can be derived from the ancestral motor pattern (Sustaita *et al.*, 2013). Moreover, our precision grip device may form the groundwork for future studies to usefully characterize fingers adaptation in both clinical and experimental scenarios.

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Conflict of interest

The authors declare no conflict of interest.

Author contributions

Riccardo Viaro and Banty Tia: conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, and wrote the paper. Gino Coudé: conceived and designed the experiments, contributed reagents/materials/analysis tools, and performed the experiments. Rosario Canto, Andriy Oliynik, Paola Salmas, Lorenzo Masia, and Giulio Sandini: contributed reagents/materials/analysis tools. Luciano Fadiga: conceived and designed the experiments, contributed reagents/materials/analysis tools, and wrote the paper.

Data accessibility

The data of the present report are all available upon request. Requests should be addressed to riccardo.viaro@unife.it.

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