Chapter 2
Dexterous Manipulation: From High-Level Representation to Low-Level Coordination of Digit Forces and Positions

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Abstract The ability to perform fine object and tool manipulation, a hallmark of human dexterity, is not well understood. We have been studying how humans learn anticipatory control of manipulation tasks to characterize the mechanisms underlying the transformation from multiple sources of sensory feedback to the coordination of multiple degrees of freedom of the hand. In our approach, we have removed constraints on digit placement to study how subjects explore and choose relations between digit forces and positions. It was found that the digit positions were characterized by high trial-to-trial variability, thus challenging the extent to which the Central Nervous System (CNS) could have relied on sensorimotor memories built through previous manipulations for anticipatory control of digit forces. Importantly, subjects could adjust digit forces prior to the onset of manipulation to compensate for digit placement variability, thus leading to consistent outcome at the task level. Furthermore, we found that manipulation learned with a set of digits can be transferred to grips involving a different number of digits, despite the significant change in digit placement distribution. These results have led us to propose a theoretical framework based on high-level representation of manipulation tasks can be learned in an effector-independent fashion and transferred to some, but not all that contexts. We discuss these findings in relation to the concept of motor equivalence and sensorimotor integration of grasp kinematics and kinetics.

2.1 Introduction

Goal-directed dexterous manipulation is accomplished by controlling the distribution of digit forces among multiple digits that grasp the object to generate or resist object motions. It should be emphasized that most hand-object interactions humans encounter in activities of daily living do not constrain where each digit is placed on

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the object, or how many digits are used. Therefore, for a given manipulation a given object can be grasped in many different ways. Mechanically, both digit positions and forces contribute to meet the manipulation task requirement. Therefore, studying grasping kinematics or digit forces in isolation limits the extent to which we can advance our understanding of how the CNS resolves the classic problem of redundant degrees of freedom in dexterous manipulations [1]. Specifically, focusing on either grasping kinematics or kinetics overlooks the underlying sensorimotor transformations from multiple sources of sensory feedback to multiple motor commands necessary to modulate multiple digit forces to positions.

The vast majority of grasping studies over the past 30 years has examined either digit positions or forces. For instance, studies of grasp kinematics have shown that subjects tend to maximize the end-state comfort by choosing sub-optimal hand locations for the initial grasp when the object has to be transported to a different location [2]. Hand shaping can be also changed according to the task goals [3] and learned object dynamics [4, 5], even though the hand degrees of freedom are controlled through synergistic motion patterns [16, 17]. However, these studied did not measure digit forces. In contrast, studies of grasp kinetics have examined the control and coordination of digit forces by using objects that constrained digit contacts, hence removing the natural digit placement variability that occurs when subjects can choose where to grasp an object. For constrained grasping studies, subjects are usually required to grasp force/torque sensors mounted at fixed locations on the object. These studies have revealed that, similar to what had been reported for reach-to-grasp kinematics, digit forces are also modulated as a function of object properties and task goals, such as object weight [6], surface friction [7], and shape [8]. Furthermore, it has been shown that digit forces can be controlled in the form of synergies, effectively reducing the number of independent degrees of freedom [9, 10]. Although research of grasp kinematics and kinetics in isolation has revealed important insights, a major question remained: *how are digit forces and positions synergistically controlled as a unit?*

To illustrate the above scenario of grasping at unconstrained contacts, let us consider the task of two-digit grasping, lifting, and balancing an object whose mass distribution is asymmetrical. This particular object would tilt towards the heavier side if one does not actively produce a torque to counterbalance the external torque, i.e., a compensatory torque. In order to prevent the tilt, one has to first position the digits on the object, then gradually exert forces through the digit-object contacts to generate a torque at object lift onset in the direction opposite to the torque caused by object mass distribution (Fig. 2.1a). Whereas the task space in this example is only three dimensional (i.e., translations and rotation in the x-y plane; Fig. 2.1a), the actions of the hand lie within a space that consists of the grip forces (normal to the surface, f_x), load forces (tangential to the surface, f_y), and positions of the contacts from at least two digits $C_i = (x_i, y_i)$. Mathematically, a two-digit planar grasp can be represented as

$$F_0 = Gf_c \quad f_c \in FC \tag{2.1}$$

where F_o is the task space consisting of net forces exerted in the horizontal and vertical directions as well as the torque in the x-y plane, G is a 3×4 'grasp matrix'

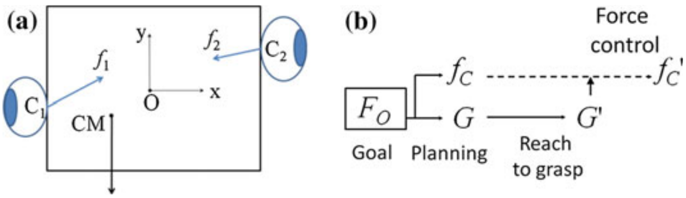

Fig. 2.1 Redundancy in two-digit dexterous manipulation. **a** Example of two-digit planar manipulation. **b** Temporal evolution of a manipulation task. *G* and *G*' denote planned and actual digit contact distributions, f_C denotes planned digit forces, and f_C' denotes the digit forces required to attain the manipulation task goal

determined by digit positions (x_1, y_1) and (x_2, y_2), f_c is a vector consisting of digit forces [f_{x1}, f_{y1}, f_{x2}, f_{y2}], and *FC* is the frictional constraints.

This redundancy poses three major challenges to the CNS. First, without physical constraints on the objects' contact locations, the CNS has to determine where to position the digits among many possible locations. Note that some contact locations may enable a grasp matrix *G* that is more suitable (e.g., less force is required) for the upcoming manipulation than other contact locations. Second, the actual contact sites may be quite variable from trial to trial due to noise in motor planning and/or execution [11] (Fig. 2.1b). Variability in digit placement implicitly requires the CNS to select appropriate digit forces to ensure task completion. This means that simply reproducing the digit force distribution used in the manipulation performed in the previous trial (i.e., stored as sensorimotor memory [12]) may not generate the same outcome at the task level if the current and previous digit contact distribution are significantly different. In this case, the digit forces required for the manipulation will not match planned digit forces (f_C and f_C', respectively; Fig. 2.1b). Lastly, once the manipulation is successfully learned, are the neural representations of learned hand-object actions independent from the effectors used during learning? If so, one would predict that humans should be able to perform the same manipulation task by using a set of effectors, e.g., digits or hand, that differs from that used to learn the manipulation.

In this chapter we review our work addressing the above three question and highlight open questions for future research. Specifically, we investigated the coordination of digit positions and forces by using a novel apparatus that allows subjects to choose where they grasp while still providing measurement of digit forces. The results reviewed here are the first direct evidence about how the CNS exploits the sensorimotor redundancy in both grasp kinematics and kinetics.

2.2 Materials and Methods

Subjects. Twenty-four right-handed subjects (12 females and 12 males, ages 20–26) and ten right-handed volunteers (4 males and 6 females, ages 19–24) participated in the first and second study, respectively. They had normal or corrected-to-normal

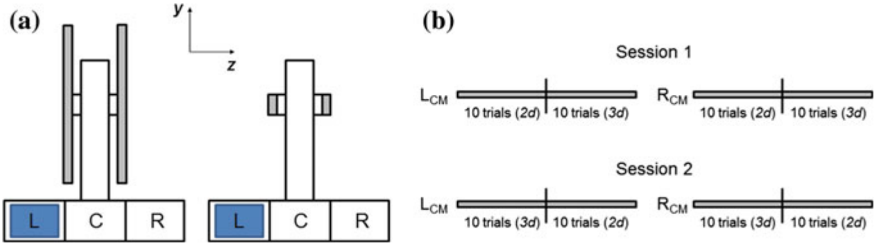

Fig. 2.2 Experimental setup. **a** The unconstrained (*left*) and constrained (*right*) devices used in Experiments 1 and 2. **b** The experimental sequence used in Experiment 2. The labels "2*d*" and "3*d*" denote two- and three-digit grip, respectively, whereas L_{CM} and R_{CM} denote left and right center of mass, respectively

vision, no previous history of orthopedic, neurological trauma, or pathology of the upper limbs and were naive to the purpose of the study. Subjects gave their informed consent according to the declaration of Helsinki and the protocols were approved by the Office of Research Integrity and Assurance at Arizona State University.

Apparatus. We used a custom-made grip device to measure digit forces and their points of application during manipulation tasks (Fig. 2.2a; see [13] for details). Forces and torques exerted by the thumb and fingers were recorded by two six-component force/torque (F/T) transducers (Nano-17, ATI Industrial Automation) mounted collinearly on each side of the object handle. Force and torque data were sampled at 1 kHz by 12 bit analog-to-digital converter boards (PCI-6225, National Instrument). To allow unconstrained placement of the digits, the grip surfaces consisted of two parallel long PVC plates (length and width: 140 mm and 22 mm, respectively) each mounted vertically on an F/T transducer and were covered with 100-grit sandpaper. These two plates were replaced by two small circular plates (diameter: 22 mm) during constrained grasping experiment (Fig. 2.2a). The distance between the two grip surfaces (grip width) was always 6.07 cm. A Plexiglass box attached underneath the grip apparatus was used to change the mass distribution to the left, right or center of the grip device by inserting a mass (400 g) into one of three compartments. The total mass of the grip device and load was 790 g. A torque in the frontal plane of −255 or +255 N/mm is introduced when the load was placed in the left or right compartment (L and R), respectively. For Experiment 1, we also placed the mass in the center such that no compensatory torque was required to lift the object straight. The visual identification of the actual object center of mass (CM) was blocked from view by a lid.

For Experiment 1, object kinematics was recorded with a magnetic tracker at 120 Hz. For Experiment 2, hand and object kinematics were recorded using an active marker 3D motion capture system at a sampling rate of 480 Hz. Subjects were outfitted with active markers on the fingernails of thumb, index, and middle fingers.

Experimental Procedures. Subjects sat comfortably with the hand resting on a table with the elbows flexed. The apparatus was placed at a distance of 30 cm from the hand start position, and the midpoint of the apparatus was aligned with subjects' right shoulders. For each trial, after a verbal signal from the experimenter, subjects reached from this start location, grasped the grip surfaces with the tip of a required set of digits of the right hand, lifted the grip device at a natural speed to a height of ∼10 cm, held it for ∼1 s, and replaced it. Subjects were instructed to extend the non-involved fingers throughout the task. At the beginning of each block of trials, we instructed subjects to minimize object roll during the lift. The between-trial interval within a block was ∼10 s.

Experiment 1. Subjects were assigned to one of two groups ($n = 12$ for each group): the unconstrained group used the apparatus with long graspable surfaces, whereas the constrained group used the apparatus with small circular graspable surfaces (left and right object, respectively; Fig. 2.2a). Both subject groups were given the same task instructions. After three practice trials (with center CM location), subjects performed three blocks of ten consecutive trials per CM location for a total of 30 experimental trials. Subjects were informed that CM location would remain the same for the entire block of trials, but they could not anticipate CM location at the beginning of each block of trials as changes of object CM across blocks of trials were performed out of view. The consecutive presentation of a given object CM location was used to allow subjects to learn implicitly the magnitude and direction of the external torque caused by the added mass. The order of CM blocks of trials was counterbalanced across subjects. On average, the time between blocks of trials was 1 min, respectively.

Experiment 2. Each subject performed the task the unconstrained grasp surfaces with two grip types: (1) two-digit grasping (thumb and index finger; $2d$) and (2) three-digit grasping (thumb, index, and middle fingers; $3d$). Subjects performed 10 $2d$ trials followed by 10 $3d$ trials ($2d \rightarrow 3d$) with left CM (L_{CM}). After a short break (∼ 20 s), subjects performed the $2d \rightarrow 3d$ experimental condition with right CM (R_{CM}). Each subject was tested again two weeks later but on a trial sequence opposite to that experienced on his/her first experimental session, i.e., $3d \rightarrow 2d$ on the L_{CM} condition followed by $3d \rightarrow 2d$ on the R_{CM} condition (Fig. 2.2b). The break between the two experimental sessions was designed to minimize potential positive or negative learning transfer effects from one sequence to the next. Prior to the experiment, subjects lifted the object once with each grip type ($2d$ and $3d$) with the load placed in the center compartment to familiarize with the task, texture, and weight of the grip device. Subjects were informed that the load could be placed either in the left or right compartment of the Plexiglass box and would remain the same for two blocks of trials. At the beginning of each block, subjects were told the number of digits to be used for the upcoming block of trials.

Data Processing. Force and position data were temporally aligned offline and analyses were performed using MATLAB. We analyzed the following variables (see [13, 14] for details): (1) Object lift onset: the time at which the vertical position of the grip device crossed and remained above a threshold for 200 ms; (2) Object roll: the angle between the gravitational vector and the vertical axis of the grip device, and peak roll is the peak of object roll shortly (∼150 ms) after object lift onset; (3) Digit forces: force perpendicular (grip force, GF) and parallel (load force, LF) to the grip surface; (4) Digit center of pressure (CoP): the vertical coordinate of the point of resultant digit force application, calculated for each digit using the force and torque output of each sensor (positive and negative values CoP denoted higher and lower CoPs relative to the center of transducer, respectively). Note that GF, LF, and CoP recorded on the finger side of the grip device are the resultant net forces and net center of pressure of both index and middle finger when subjects performed the task using the 3*d* grip. To quantify the modulation of individual digit position, we used the fingertip marker position defined as the vertical position of the marker on the nail of the thumb, index, and middle fingers.

We then used digit forces and CoP to compute the following performance variables: (a) the average of the digit grip forces (F_{GF}), (b) the difference between load forces exerted on the thumb and finger side of the grip device (ΔF_{LF}), and (c) the vertical distance between the thumb and index finger CoP on the thumb and finger side of the grip device (d_y). How these three variables are coordinated dictates whether the compensatory torque (T_{com}) necessary for minimizing object roll is attained before the object is lifted to balance the external torque caused by the added mass (see [15]). We use the following equation to approximate the relationship among these variables

$$T_{com} = F_{GF} \times d_y + \Delta F_{LF} \times \frac{w}{2} \tag{2.2}$$

where *w* is the distance between the graspable surfaces. To further understand how digit placement changed when there is a change in grip type (Experiment 2), we also computed the vertical distance between thumb and index finger markers (d_{tip}). Note that all of these performance variables were computed at object lift onset. Our analysis focused on object lift onset because this event allows for an unbiased estimation of *anticipatory* modulation of digit forces as a function of digit positions, i.e., prior to experiencing the external torque that occurs as soon as the object is lifted (for more details on this rationale, see [13]).

2.3 Experiment 1: Digit Force and Position Coordination in Unconstrained Grasping

In the first experiment, we studied how digit positions and forces are modulated and coordinated during learning the manipulation as well as throughout stable performance of our manipulation task. We also compared the results obtained using unconstrained grasps with the same task performed with constrained contacts as this model has been used by most grasp studies. Overall, subjects learned to generate compensatory torque equally well and at similar rates in both grasp conditions, even though the underlying control mechanisms differed significantly between the two subject groups.

Learning Constrained Versus Unconstrained Grasping. At the task level, compensatory torque generation (i.e., object roll minimization) was learned within the first three trials by both constrained and unconstrained subject groups (Fig. 2.2). Therefore, only data from the unconstrained group is described here. On trial 1, subjects exerted little or no compensatory torque (mean ± SE: −26.6 ± 16.9 N·mm, −14.1 ± 33.8 N·mm, and 22.5 ± 17.5 N·mm for left, center and right CM, respectively). Unlike the compensatory torques developed after trial 1, the direction and magnitude of these torques were not correctly scaled to the external torque. On trials 2 and 3, however, the compensatory torque gradually approached the external torque and settled at a mean value of −188.3 (±13.9) N·mm and 189.7 (±17.0) N·mm (right and left CM, respectively) from trial 4 through 10 (Fig. 2.3). The compensatory torque at lift onset for the center CM condition changed little after trial 1, reaching a mean value of 11.3 (±13.1) N·mm. Despite the fact that subjects' performances were different for center vs. left and right CM locations (CM × Trial interaction $p < 0.001$), post hoc comparisons between neighboring trials (1 vs. 2, 2 vs. 3, and so forth) revealed that subjects learned to generate anticipatory compensatory torque to minimize object roll early in the trial sequence, the only significant

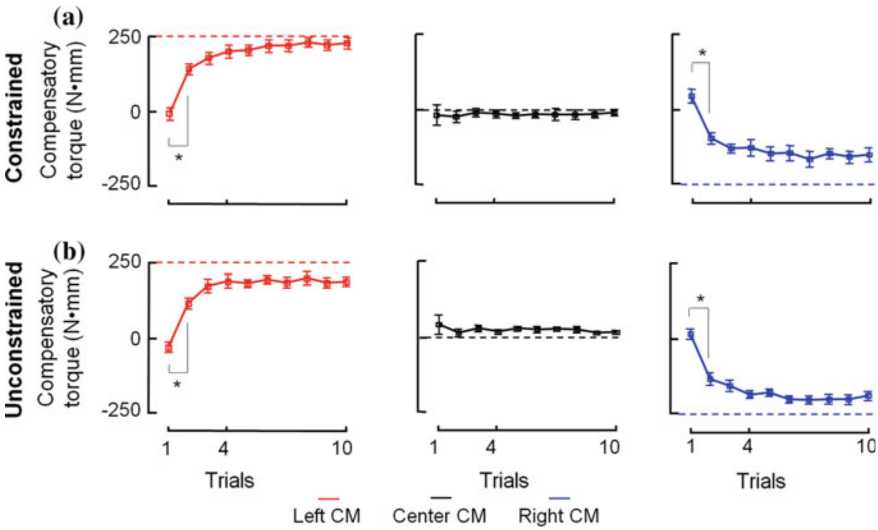

Fig. 2.3 Anticipatory control of compensatory torque as a function of trial. Data in **a** and **b** denote compensatory torque for the constrained and unconstrained grasp conditions, respectively. *Dashed horizontal lines* denote the external torque caused by the added mass. For graphical purposes, the external and compensatory torques are plotted with the same sign. All data are means averaged across subjects (±S.E.). *Asterisks* indicate significant differences ($p < 0.05$) between trials. Adapted from [13]

difference in compensatory torque occurring between trial 1 and trial 2 ($p < 0.05$ for both right and left CM in both groups). The relation between peak object roll and trials paralleled the relation between compensatory torques and trials shown in Fig. 2.3.

For digit positions, the centers of pressure (CoP) of thumb and index finger at object lift onset were modulated as a function of trial and object CM location. Figure 2.4a shows d_y averaged across all subjects as a function of trial for each CM location and subject group. On the first trial, subjects tended to position the digits collinear to each other regardless of CM location. After trial 1, when lifting the object during the center CM condition, thumb and index finger CoP tended to remain collinear across all subsequent trials in both groups. In contrast, left and right CM locations elicited opposite patterns of digit CoP modulation. Specifically, the thumb CoP tended to be positioned progressively higher and lower relative to the index CoP for the left and right CM locations, respectively, and for both subject groups (CM × Trial interaction, $p < 0.001$; Group × Trial interaction, $p > 0.05$). Similar to the above results on compensatory torque, post hoc comparisons between neighboring trials revealed that the only significant change in dy occurred between trial 1 and 2 but only for right and left CM in both groups ($p < 0.05$).

For digit forces, grip forces (F_{GF}) tended to increase as a function of trial for left and right CM conditions and decrease for center CM in both subject groups (Fig. 2.4b; CM × Trial interaction, $p < 0.001$, Group × Trial interaction, $p > 0.05$). However, post hoc analyses showed that these trends were significant only for the left CM condition in both groups ($p < 0.001$ and $p < 0.005$ for unconstrained and constrained groups, respectively). Subjects also used different patterns of load force

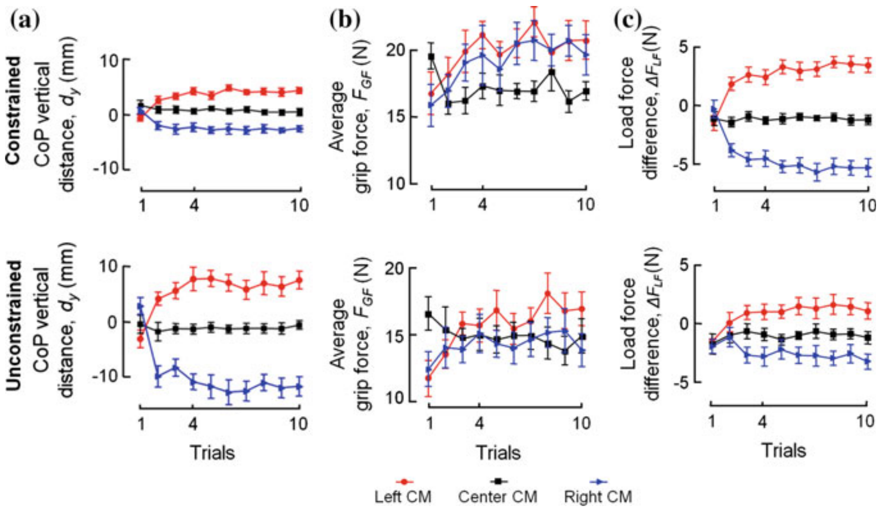

Fig. 2.4 Learning of digit placement and forces. All data averaged across subjects (±S.E.). *Top* and *bottom rows* show data from constrained and unconstrained groups, respectively. Adapted from [13]

distribution across CM locations (Fig. 2.4c). Specifically, thumb and index finger load forces remained symmetrical across all trials in both subject groups in the center CM condition. In contrast, the difference between thumb and index finger load forces (ΔF_{LF}) tended to be modulated as a function of trial early in the trial sequence to then remain relatively constant for left and right CM conditions for both subject groups. On the first trial, subjects tended to use nearly symmetrical load forces for both CM and subject groups. After trial 1, load forces applied by the thumb and index finger were applied asymmetrically to counteract the CM asymmetries. Specifically, the thumb load force tended to be progressively larger and smaller relative to the index load force for the left and right CM conditions, respectively, in both subject groups (CM × Trial interaction, $p < 0.001$; Group × Trial interaction, $p > 0.05$). However, post hoc comparisons between neighboring trials revealed that only the constrained group modulated ΔF_{LF} significantly from trial 1–2 for both CM conditions (both $p < 0.05$).

Since stable level of task performance was attained within the first 3 trials (Fig. 2.3), we used trial 3 as the cut-off after which (trial 4 through 10) we defined subjects' performance as stable, i.e., where further practice with the manipulation task did not lead to statistically significant improvements in compensatory torque at object lift onset and object roll minimization. Therefore, we examined the magnitude of digit forces and CoP during the last seven trials of each block. The two subject groups exhibited significant differences in their overall strategy. Specifically, constrained grasp trials relying mostly on modulation of grasp kinetics (force application), and unconstrained grasp trials relied primarily on modulation of grasp kinematics (digit placement on the object). Digit position modulation in the constrained group was significantly smaller than that exhibited by the unconstrained group in left and right CM conditions (Fig. 2.4a; 3-way analysis of variance, ANOVA, on factors Group, CM, and Trial; CM × Group interaction, $p < 0.001$; post hoc tests on Group effects within right CM: $p < 0.05$; non-significant Group effects within left CM). Furthermore, the constrained group used larger grip force than the unconstrained group across trial 4–10 (Fig. 2.4b; main effect of CM, $p < 0.01$; main effect of Group, $p < 0.001$). Post hoc tests also revealed that subjects used significantly larger grip force only for left and right CM conditions ($p < 0.05$). Lastly, the constrained group showed larger asymmetry of digit load forces than the constrained group in left and right CM conditions (Fig. 2.4c; CM × Group interaction $p < 0.001$; post-hoc tests on Group effects within left and right CM: both $p < 0.05$). These results suggested that, despite inter-subject variability, the subjects had common strategies according to the object physical properties. We speculate that such strategies were implemented to optimize the motor output by reducing the total digit force, thus minimizing the energy cost and motor noise [13]. Note that unlike the result obtained from random perturbation trials presented in the Chap. 3 by Naceri and colleagues, all subjects adapted similar preferred strategies in an anticipatory fashion in our experiment. This is because the perturbation induced by the added mass following object lift is predictable.

Covariation of Digit CoPs and Digit Forces. The above analysis revealed that digit forces and positions at object lift onset were controlled differently depending

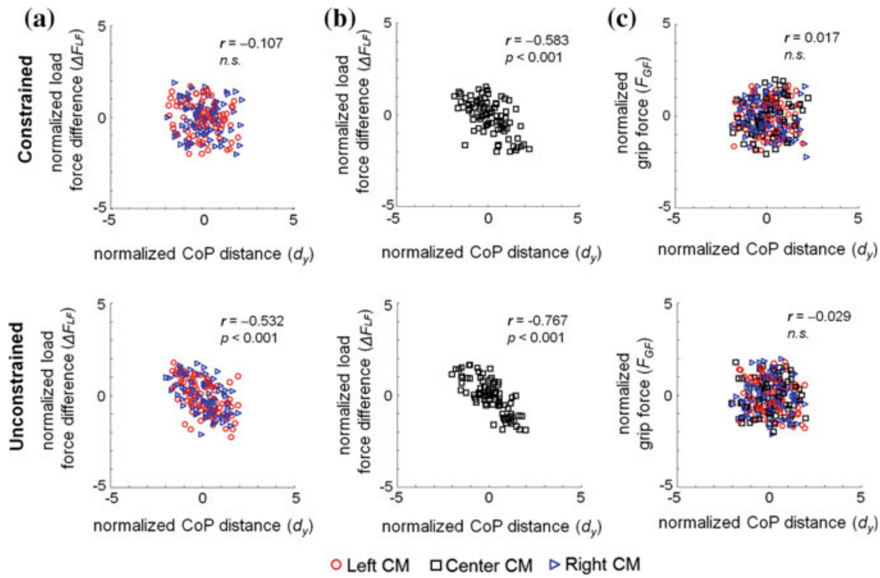

Fig. 2.5 Relations between digit centers of pressure, grip force, and load force. Data are from constrained and unconstrained grasp trials 4 through 10 from each subject and CM condition (*top* and *bottom row*, respectively) and are shown in normalized form. Data in **a** and **c** are from *left* and *right* CM conditions, whereas data in **b** are from the center CM condition. The Pearson's r-value and corresponding p-value are shown in each panel (n.s. = not significant, $p > 0.05$). Adapted from [13]

on whether or not the grip device constrained digit placement. Surprisingly, however, subjects from the unconstrained and constrained groups learned to generate compensatory torques with similar consistency (Fig. 2.3). This was confirmed by a lack of a significant Group effect on the standard deviation of T_{com} of the mean compensatory torque averaged from trial 4–10 ($p > 0.05$). This result is remarkable particularly when considering that the variability of digit placement at object lift onset of the unconstrained group was significantly larger than the constrained group. With regard to standard deviation of individual digit CoP, we found only a significant main effect of Group ($p < 0.001$). The standard deviation of d_y was significantly different across subject groups and CM (both $p < 0.001$).

In contrast, there was no significant difference between the two groups with regard to the standard deviation of either digit load forces or grip forces ($p > 0.05$). As T_{com} is the net result of d_y, F_{GF}, and ΔF_{LF} (Eq. 2.2), the large variability in digit placement in the unconstrained group was effectively compensated by digit force modulation such that trial-to-trial variability of T_{com} was similar to the constrained group. We therefore examined how subjects modulated, on a trial-to-trial basis, digit forces as a function of position. Linear regression analyses on data normalized to zero mean and unit standard deviation (see [13] for details) was performed. We observed significant negative correlations between d_y and ΔF_{LF} in both the unconstrained group (r =

−0.615, $p < 0.001$) and constrained group ($r = -0.263$, $p < 0.001$). Furthermore, the correlation coefficient of the unconstrained group was significantly larger than that of the constrained group ($p < 0.001$). We also found that center CM was different from left and right CM conditions. Specifically, for the center CM condition, both subject groups showed negative correlations between d_y and ΔF_{LF} (Fig. 2.5b). This correlation was significantly larger in the unconstrained than in the constrained group ($p < 0.05$). Interestingly, for left and right CM conditions, the constrained group did not exhibit a significant correlation. In contrast, negative correlations were still found for the unconstrained group (Fig. 2.5a). Lastly, the strength of the correlation between d_y and ΔF_{LF} was significantly larger in the unconstrained than in the constrained group ($p < 0.05$). We found no significant correlation between d_y and F_{GF} or between ΔF_{LF} and F_{GF} in either subject group.

2.4 Experiment 2: Transfer of Learned Manipulation Between Different Grip Types

Experiment 1 revealed that natural trial-to-trial variability occurs when subjects can choose where to grasp an object. Remarkably, such variability persists even after the manipulation has been learned (trials 4–10). An important result was that subjects actively compensate for digit placement variability by modulating digit forces such that the required compensatory torque is attained at object lift onset. As this trial-to-trial variability in digit placement was relatively small, in a second experiment we introduced a large change in digit position after subjects had learned the manipulation task. This was achieved by asking subjects to use a different grasp configuration by adding or removing one digit relative to the grasp configuration used to learn the task. The ability to transfer learned manipulation across grasp types was examined at both task and digit level. Overall, we found complete transfer of task performance despite significantly different digit position and force patterns.

Learning and Learning Transfer of Compensatory Torque. Subjects were able to learn the manipulation task with both two-digit and three-digit grasp, in a similar fashion to that described for Experiment 1. Specifically, T_{com} averaged across all subjects changed significantly as a function of consecutive practice in the pre-switch block (main effect of Trial, $p < 0.001$; Fig. 2.6). On average, all subjects learned to anticipate the T_{com} necessary to minimize object roll within the first 3 trials regardless of grip type and CM location, after which T_{com} did not change any further on subsequent trials (all tests on trials 4–10: $p > 0.05$).

Following a change in grip type, i.e., at the beginning of the second block (trial 11, Fig. 2.6), we performed ANOVA for each CM location to examine the immediate effect of changing grip type on T_{com}. Subjects were able to generate T_{com} whose magnitude was statistically indistinguishable from that generated on the pre-switch trial (trial 10) for all but one experimental condition ($3d \rightarrow 2d$, L_{CM}, $p = 0.035$).

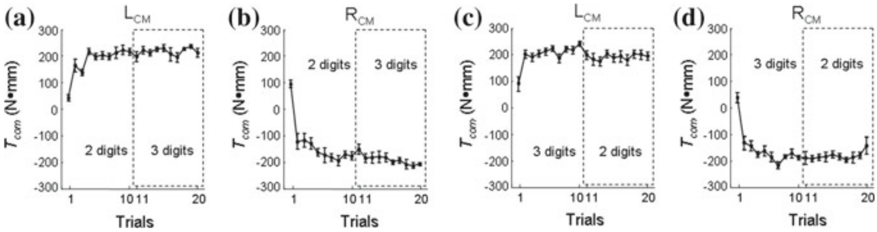

Fig. 2.6 Learning curves of compensatory torque: pre- and post-grip type switch. Trials within the *dashed box* (11–20) indicate the grip type subjects switched to after learning the manipulation with a different grip type. T_{com} denotes compensatory torque, whereas L_{CM} and R_{CM} denote left and right center of mass, respectively. Data in **a** and **b** are from the $2d \rightarrow 3d$ condition, whereas data in **c** and **d** are from the $3d \rightarrow 2d$ condition. "L_{CM}" and "R_{CM}" denote left and right center of mass, respectively. Data are averages of all subjects (±S.E.). Adapted from [14]

However, no significant differences were found when comparing peak object roll on trial 10 versus 11 on any of the four experimental conditions. This indicates that the statistically significant difference for the $3d \rightarrow 2d$ L_{CM} condition did not have significant behavioral consequences on the manipulation, thus suggesting that anticipatory control of T_{com} in the pre- and post-switch trials was equally appropriate to attain the task goal. Furthermore, we examined average differences between 7 trials pre- versus post-switch in grip type using ANOVA with repeated measures for each CM location with within-subject factors of Trial (7 levels; 7 pre- and 7 post-switch) and Grip type (2 levels, pre- and post-switch). We found no significant main effect of Trial, Grip type, or interaction ($p > 0.05$ for each experimental condition). This suggests that no further learning of T_{com} occurred before and after the switch in grip type, the average T_{com} being statistically similar for the two grip types. Similarly, no significant main effect of Trial, Grip type, or interaction were found on peak object roll as well ($p > 0.05$ for each experimental condition).

Change of Digit Positions and Forces Following a Change of Grip Type. The positive learning transfer of T_{com} to a different grip type implies that subjects were able to coordinate, in an anticipatory fashion, the components that generate the T_{com}: d_y, ΔF_{LF}, F_{GF}. Since there are infinite number of combination of these components (see Eq. 2.2), we analyzed each T_{com} component separately.

Digit Center of Pressure. Subjects used significantly different vertical separations between digit center of pressure (d_y) after switching grip type on all but one experimental condition ($3d \rightarrow 2d$, R_{CM}; Fig. 2.7). For the left CM location, subjects significantly increased d_y when adding middle finger to the grip and decreased d_y when removing one finger from the grip, whereas an opposite pattern was found for the right CM location. In addition to the change found in the net center of pressure on the finger side when adding or removing a finger, we found that the distance between thumb and index finger marker (d_{tip}) was significantly modulated such that the index finger was positioned higher when adding the middle finger and lower when remov-

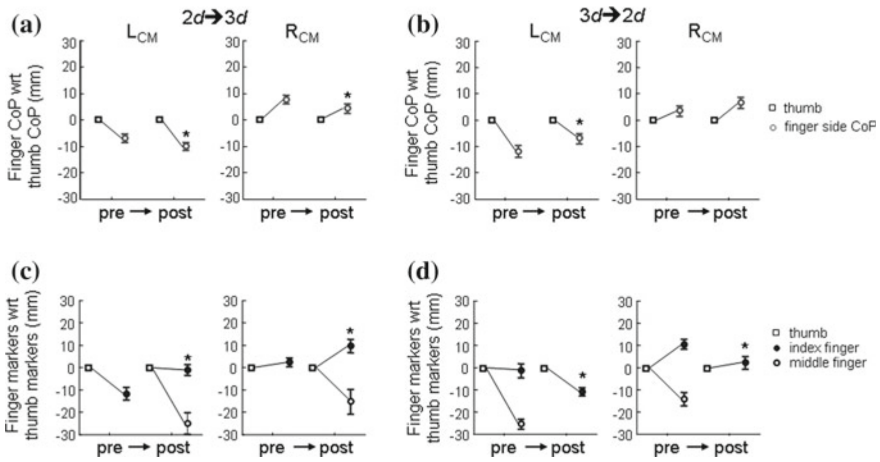

Fig. 2.7 Immediate learning transfer of digit center of pressure and position from pre- to post-grip type switch trials. *Asterisks* denote a statistically significant difference ($p < 0.05$) between pre- and post-switch trials. **a** and **b** are digit center of pressure measured by F/T sensors. **c** and **d** are digit position measured by motion tracking. Data are averages of all subjects (± S.E.). Adapted from [14]

ing the middle finger (Fig. 2.7). Therefore, subjects *immediately* used significantly different digit placement distribution when changing grip type.

After the immediate adaptation (i.e., trial 11) following a change in grip type, there were no further significant modulation of d_y (no significant Trial effect or Trial × Grip interaction, $p > 0.05$). Specifically, the new digit placement was maintained for all but one experimental condition (significant Grip effect for three conditions and non-significant Grip effect for one condition, $3d \rightarrow 2d$, R_{CM}; Fig. 2.8a). With regard to the relative fingertip positions, d_{tip} was significantly modulated in a similar fashion to that observed in the immediate adaptation in all conditions (significant Grip type effect only).

Digit Load Forces. Subjects used significantly different load force sharing (ΔF_{LF}) after switching grip type on only one experimental condition ($2d \rightarrow 3d$, L_{CM}). However, unlike the immediate adaptation in the ΔF_{LF}, three out of four experimental conditions showed long term modulation of ΔF_{LF} throughout the first post-switch trials in response to the modulation of d_y (significant Grip effect; $p < 0.05$). ΔF_{LF} remained unchanged only in $3d \rightarrow 2d$, R_{CM} condition in which d_y was not modulated significantly (Fig. 2.8b). However, there were no significant Trial effect or Trial × Grip type interaction on ΔF_{LF}. In general, subjects tend to use larger load force difference in $2d$ than $3d$ grip.

Digit Grip Force. No significant main effect of Grip type ($p > 0.05$ for each experimental condition) were found on the immediate post-switch trial, indicating that subjects exerted similar net grip forces regardless of the number of digits used for

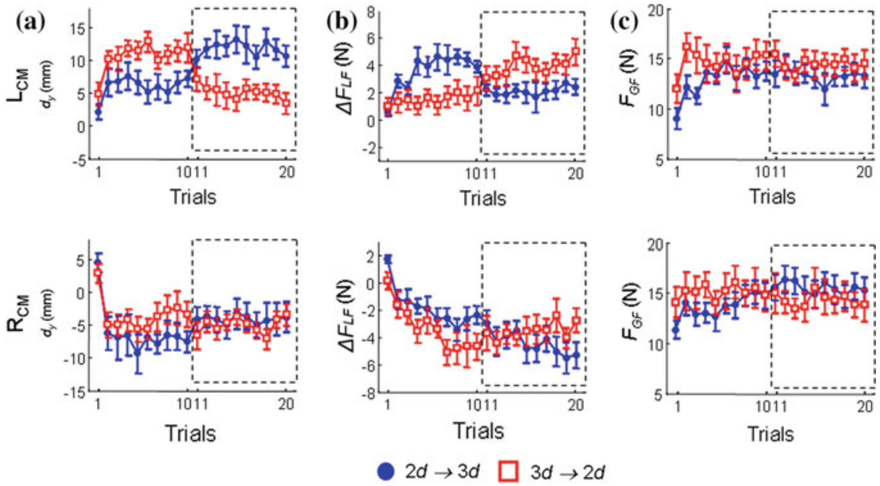

Fig. 2.8 Learning curves of digit center of pressure and forces: pre- and post-grip type switch. Each plot shows data from two-digit grip trials followed by three-digit grip trials (*squares*) and trials performed in the reverse order (*circles*). **a**–**c** are dy, ΔF_{LF}, F_{GF}, respectively, across pre- and post- transfer blocks. Data are averages of all subjects (±S.E.). Adapted from [14]

the grasp. However, whereas grip force is provided by index finger only in 2*d* grip on the finger side, the middle finger may contribute substantially in 3*d* grip for left CM condition. In the trials following the switch in grip type, subjects also exerted similar grip forces to those exerted before the switch (Fig. 2.8c), with lack of significant main effects of Grip type, Trial, or interaction ($p > 0.05$ for each experimental condition).

2.5 Discussion

This chapter reviewed recent evidence describing how the CNS addresses the redundancy of available kinematic and kinetic solutions to perform dexterous manipulation. It should be noted that the control of grasp kinematics and kinetics are part of a continuum, i.e., digit force distribution must take into account digit contact distribution. Nevertheless, until recently most of the literature on grasping has focused on either kinematic or kinetic synergies. Specifically, biomechanical analyses of multi-digit grasping have characterized prehension synergies that emerge from 'chain effects' through which obligatory and non-obligatory relations among digit forces and torques emerge (for review, see [10]). Similarly, studies of hand shaping during reach-to-grasp have characterized kinematic synergies, i.e., systematic covariation patterns of digit joint angles that can be described by a very small number of principal components across a wide variety of object shapes and sizes ([16, 17]; for review see [18]). Both of these approaches have revealed significant insights into motor control strategies that result in dimensionality reduction across the available degrees of freedom (i.e., joints, forces). However, and given the above-mentioned continuum of grasp kinematic and kinetics, a major gap remains: *How does the CNS control synergies that combine the control of digit positions and forces?* Here, the term ‘synergy’ is used as a broader term that describes the covariation of variables in a high-dimensional space that consists of both kinematic and kinetic components. Kinematic or kinetic synergies are throught to originate from biomechanical and neural constraints. However, the synergy between kinematic and kinetic variables discussed here denotes the ability of the CNS to integrate sensory information in the continuum of reaching-grasping-manipulation. This allows the system to make corrections to accomplish high-level goals that are independent of the configuration and forces of the hand.

2.5.1 Redundancy of Kinematic and Kinetic Solutions Through Digit Force-to-Position Modulation

As described in the Results section, learning of dexterous manipulation appears to occur despite execution and/or planning noise causing trial-to-trial variability in digit placement [13]. These observations were confirmed using a virtual reality environment where digit placement variability was induced by changing object width across trials [19]. Even when differences in digit placement are not accidental, but intentional, i.e., when we grasp an object using a set of digits that was not used to learn a given manipulation, the sensorimotor system can still re-organize digit force distribution to a new digit contact distribution [14]. These two scenarios, characterized by small and large variability in digit placement, respectively, capture a critically important sensorimotor ability, digit force-to-position modulation, which we propose as a hallmark of dexterous manipulation in humans. It should be noted that modulation of digit forces to positions requires a synergy-based mechanisms, whereby multiple sources of sensory feedback are integrated and used to generate a set of forces that can satisfy the task requirements. Remarkably, and despite the large number of degrees of freedom involved in object manipulation, subjects are able to adjust multiple digit forces as a function of digit contact distribution *within a few 100 ms*, i.e., between contact and onset of manipulation.

Equation 2.2 describes the relation between two contacts and their forces for generating a given torque in two dimensions. As mentioned in the Methods, the desired compensatory torque can theoretically be attained through a number of infinite digit force-position relations, i.e., an example of the Bernstein’s problem of redundant degrees of freedom [1]. However, we found that subjects respond to trial-to-trial variability in digit placement by (a) exerting similar grip forces, thus reducing a free variable to a constant, and (b) linearly modulating the difference between thumb and index finger load forces as a function of the vertical distance between the digits (Fig. 2.5) [13]. This relatively simple relation describes a family of digit position-force relations that ensure the attainment of the same compensatory torque. Further studies have provided additional supporting evidence on the covariations of digit positions and forces as a way of synergistic control in other dexterous manipulation tasks (see Chap. 3 for details).

Although the mechanisms responsible for digit force-to-position modulation remain to be determined, behavioral evidence suggests that humans are particularly skilled at sensing digit placement during digit force production for large vertical distances between the fingertips [20]. Yet, how this sensory feedback is used to select the appropriate digit force distribution is not known. However, a recent study suggests that feedback-mediated force corrections occur to a greater extent when grasping an object at unconstrained than constrained contacts [21]. This result is compatible with the notion that the control of digit forces for constrained grasps benefits from the fact that the same digit forces can be used across trials, and therefore one would expect a greater reliance on sensorimotor memory of digit forces used in previous manipulations. In contrast, trial-to-trial variability in digit placement found for unconstrained grasps demands that forces are distributed in a way that reflects the actual digit contact distribution. Hence, corrective forces responses occurring between contact and onset of manipulation in unconstrained grasping may reflect such compensatory mechanisms triggered by sensing the mismatch between planned and actual digit placement (Fig. 2.1b).

2.5.2 High-Level Representation of Learned Manipulation

The above-described digit force-to-position modulation has led to the proposition that the sensorimotor system builds a high-level representation of learned manipulation, which for the above-reviewed studies corresponds to the desired compensatory torque [13, 14]. This concept, which is a fundamental component of the theoretical framework underlying motor equivalence [22–25], is based on the notion that the neural representation of learned motor behavior can be dissociated from the effectors (muscles, joints, limbs, etc.) with which the behavior was learned. Therefore, a learned motor behavior could be performed at a similar level of performance even when the effectors engaged in learning the behavior differ from those used to perform it. For the case of dexterous manipulation at unconstrained contacts, the ability to transfer a compensatory torque learned with two digits to three digits, or vice versa, could be interpreted as an example of motor equivalence. It has been pointed out, however, that effector-independence for motor execution is not routinely observed. Specifically, a number of notable exceptions have been reported in the literature, whereby changing the context of a learned manipulation prevents subjects to perform the same manipulation. For example, subjects are unable to transfer a learned compensatory torque after the object is rotated 180° ([15, 26]). Failure to generate the same torque in the opposite direction to that learned through previous manipulations indicates that manipulation learning transfer is sensitive to the congruency between the frame of reference of the learned action and the object. Such congruency is maintained when exerting a learned compensatory torque in the same direction despite a change in grip type [14], but not when rotating the object, in which case subjects have to perform a mental rotation of the action [15, 26]. Additional examples of failure to transfer learned manipulation to different contexts [27–29] indicate that there are circumstances that prevent high-level representations of learned manipulation to be transferred. This experimental evidence, combined with evidence indicating successful transfer of learned manipulation [14], indicate that the sensorimotor system's ability to build synergies for coordinating multiple digit positions with forces and retrieve them is sensitive to several factors, including previous manipulation history and frames of references associated with the 'old' versus 'new' manipulation context.

2.5.3 Open Questions and Future Research

Our understanding of the factors underlying humans' ability to control multiple position or force variables in a synergistic fashion to perform dexterous manipulation has improved significantly over the past two decades, leading to the characterization of kinematic and kinetic synergies. The work reviewed in this chapter is the first attempt at answering the question of how the CNS combines kinematic and kinetic grasp synergies. Nevertheless, further work is needed to characterize the underlying sensorimotor mechanisms. Specifically, behavioral data suggest that unconstrained grasping is mediated by more corrective force responses than constrained grasping [21]. However, it remains to be determined how cortical areas within the so-called 'grasp circuit', which has been characterized in human and non-human primate studies of grasping and manipulation [30], interact when sensory feedback of digit placement must be integrated with digit force control. Similarly, to date there is no comprehensive theoretical framework describing the key features of manipulation tasks that allow or prevent learning transfer to different task contexts. Furthermore, we do not know why a given manipulation task can be transferred to some, but not all contexts. Lastly, another critical open question is: how does the CNS transition from kinematic synergies before contact to kinetic synergies after contact? It remains unclear whether kinetic synergies are simply a result of kinematic synergies interacting with the environment or originate from different neural mechanisms. Future work should combine complementary experimental approaches to study unconstrained grasping and manipulation, including brain imaging, non-invasive brain stimulation, virtual reality environments, and sensorized objects and/or gloves, to gain insight into sensorimotor mechanisms responsible for dimensionality reduction in dexterous manipulation.

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