Transfer and Generalization of Learned Manipulation between Unimanual and Bimanual Tasks

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Abstract

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Successful grasping and dexterous object manipulation relies on the ability to form internal representations of object properties that can be used to control digit kinetics and kinematics. Sensory cues and sensorimotor experience enable the updating of these internal representations. Aside from the weight of the object, the center of mass of the object results in object torque that needs to be represented and compensated for. In order to counter object torque, digit forces and centers of pressure are modulated to generate a compensatory moment to prevent object roll. Generalization studies can be used to examine whether this learning is represented on a low effector-specific level or a high task-specific level. Previous studies have shown that the internal representation of object torque does not generalize after object rotation or contralateral hand switch suggesting an effector level of representation. However, it has been shown that switching from two to three digits and vice versa does lead to full generalization suggesting a high level representation in certain circumstances. Thus, an understanding of whether learned manipulation would generalize when adding or removing the number of degrees of freedom and effectors would provide more information on these levels of representation. We asked 30 participants to lift a visual symmetrical object with an asymmetrical center of mass. Participants lifted the object 10 times in one grasp type (right hand unimanual, bimanual, or left hand unimanual). Following that, they switched to another grasp type and lifted the object another 10 times. Through various different orders of these transfer blocks, we examined their ability to generalize between unimanual and bimanual grasping by comparing the pre- and post-transfer trials. Our results show the partial generalization of learned manipulation when switching
between unimanual and bimanual grasps. This is shown from the reduction in peak roll after transfer compared to novel trials and the generation of compensatory moments in the appropriate direction (but insufficient magnitude) after transfer. Moreover, after transfer to the right hand unimanual and bimanual grasps, moment generation was driven by digit center of pressure modulation while transfer for left hand unimanual grasps was driven by load force modulation. In addition, we also show failed generalization after contralateral hand switch as evidenced by large post-transfer rolls and minimal moments. We suggest that learned manipulation of object torque is a high level of representation but that this representation can only be accessed by either digit kinematics or kinetics, depending on the hand used.
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The grace of the Lord Jesus Christ, the love of God, and the communion of the Holy Spirit be with all of you.
Dedication

To: Mom, for your love and sacrifice.
Chapter 1: Introduction

Skilled object manipulation is accomplished through the sensorimotor control of effector kinetics and kinematics to the task goal (Cohen and Rosenbaum 2004; Fu et al. 2010; Santello 2018). Much of the early work done on reach-to-grasp movements looked into the temporal kinematics of different arm segments, from the proximal shoulder joint and arm movement to distal finger span and kinematics (Jeannerod 2009). During reach-to-grasp movements, before contact with the object, digits of the hand are also shaped to the contour of the object to be grasped (Santello and Soechting 1998; Winges et al. 2003). This shows that hand kinematics are influenced by the object to be manipulated and are planned in advance of object contact. Additionally, in order to successfully lift an object off a surface, forces must be applied to grip the object and lift it while overcoming the object’s weight (for review see: Johansson and Flanagan 2009). Normal (grip) and tangential (load) forces are increased in parallel to overcome the coefficient of friction between the digits and the contact surface to prevent slippage (Cadoret and Smith 1996; Johansson and Westling 1984; Westling and Johansson 1984). This is accomplished through the use of sensory cues and prior grasping experience to form estimates of object properties that allow for the planning of forces before feedback at object contact (Baugh et al. 2012; Buckingham et al. 2009; Gordon et al. 1991; Gordon et al. 1993; Johansson and Westling 1988b; Salimi et al. 2003).

Aside from weight and texture, forces are also controlled to, and in anticipation of, object torque (Johansson et al. 1999; Wing and Lederman 1998). Salimi et al (2000) showed that when the center of mass, of a visually symmetrical object, was closer to either the thumb or index finger side, initial performance was characterized by large object rolls. Stable successful
performance, roll minimization, was achieved within three to five lifts through the anticipatory control of digit forces to generate a moment that countered object roll. Specifically, the load forces of the digit on the side of the center of mass were larger than the other digit. Thus, sensorimotor experience enables the central nervous system to form an internal representation of object dynamics that can be used for successful performance. A similar finding was shown in whole hand grasping where the grip forces of the fingers were coordinated and varied for different object centers of mass (Santello and Soechting 2000).

All the above studies into the control of grip and load forces employed objects with constrained contact points at the location of the force transducer. A major limitation of constraining contact points is that most objects of daily living allow contact points to vary (Heald et al. 2018) and object manipulation thus involves controlling both effector kinetics and kinematics.

The coordination between effector kinetics and kinematics was initially explored by examining the choice of digit contact point. This choice is influenced by the intention of the task with contact points varying by end-goal height (Cohen and Rosenbaum 2004), whether the goal is to lift or pour a grasped bottle (Craje et al. 2011), or to prevent object roll (Lukos et al. 2007). More recent research has examined the combined influence of kinetic and kinematic control and determined that there exists a continuum of control between grasp kinetics and kinematics (Fu et al. 2010; Lukos et al. 2008). Specifically, learned manipulation relies on a force-to-placement coordination to successfully perform the task when the grasp surface is unconstrained (Fu et al. 2010; Lee-Miller et al. 2016) (Appendix B).

One of the paradigms used to examine force-to-placement coordination is similar to previous studies on object torque control through varying object center of mass (Johansson et al. 2010).
1999; Salimi et al. 2000; Wing and Lederman 1998). Learned manipulation thus involves the modulation of digit forces and placement to generate a compensatory moment that counters object roll (Fu et al. 2010; Lukos et al. 2008). Specifically, successful (minimal object roll) grasping and manipulation of an object with an asymmetrical center of mass occurs by 1) partitioning digit placement by placing the digit on the side of the center of mass higher, and/or 2) applying larger load force on the digit closer to the center of mass. Feedback from digit contact is used to adjust digit forces accordingly to generate the appropriate compensatory moment prior to lift-off (Davare et al. 2019; Mojtahedi et al. 2015; Toma et al. 2019). This covariation of digit forces-to-placement allows the generation of a stable compensatory moment despite trial-to-trial variability in digit placement (Fu et al. 2010; Lukos et al. 2013). This force-to-placement covariation is similar to the concept of motor equivalence which refers to the ability to vary different performance variables while maintaining the same performance outcome (Bernstein 1966; Cole and Abbs 1986; Lashley 1930; Wing 2000). Thus, the generation of a stable compensatory moment despite variability in digit forces and placement indicates a high-level representation of torque information. Aside from two-digit precision grasping, we have recently shown that this feature is seen in whole-hand (Marneweck et al. 2016) (Appendix D) and bimanual (Lee-Miller et al. 2019)(Appendix E) manipulation. Thus, this is a general feature of grasping and manipulation across multiple effectors.

A possible theoretical framework to describe this general feature relies on internal representations of object properties that can be accessed through feedforward and feedback processes to enable successful performance (Flanagan et al. 2009; Gordon and Salimi 2004; Haruno et al. 2001; Johansson and Edin 1993; Salimi et al. 2000; Witney 2004). Based on this framework, successful object manipulation relies on the use of sensory cues and prior
sensorimotor memories to form an internal representation of the object and task. The feature of force-to-placement covariation and variability while maintaining a stable compensatory moment has been suggested to show a high-level representation (Fu et al. 2011; Fu et al. 2010; Marneweck et al. 2016). In these instances, a high-level of representation corresponds to learning that generalizes to the task goal (reducing object roll by generating a compensatory moment) as opposed to a low-level of representation where digit force and placement are learnt separately. Thus, this high-level of representation includes an internal representation of object properties and the corresponding kinetics and kinematics required for the task. Additionally, because of the asymmetry of the object, the digits/hands placed on both sides of the object apply different load forces and thus have to be coordinated to ensure appropriate performance. The extent to which this high-level representation is task- or effector-specific has been studied with varying conclusions.

Table 1 provides a summary of the results of various studies examining the transfer of grasping and manipulation tasks. Learned representations of object weight or texture correspond to a high-level of generalization as evidenced by the positive contralateral hand transfer of weight information (Chan et al. 1990; Chang et al. 2008; Gordon et al. 1994; Gordon and Salimi 2004; Westling and Johansson 1984; Westling and Johansson 1987). In contrast, information about object torque does not transfer as readily across most contexts. Learned object torque in one direction (e.g. clockwise for an object with a center of mass located towards the right of midline), does not transfer across hands (Bursztyn and Flanagan 2008; Fu et al. 2014; Gordon and Salimi 2004). Additionally, 180° object rotations, which rotate the center of mass from the right to the left or vice versa, do not lead to transfer (Fu et al. 2010; Salimi et al. 2003; Zhang et al. 2010). The lack of transfer across the hands could be due to the mirror symmetry mapping of
digit forces between the hands where forces learned in the right thumb would transfer to forces of the left (Fu et al. 2014). As such, it was suggested that object rotation followed by contralateral hand switch would enable transfer as it maintains the intrinsic reference frame of the body. However, further studies have failed to show a transfer of torque after hand switch and object rotation (Albert et al. 2009; Bursztyn and Flanagan 2008). Thus, learned manipulation of object torque seems to be specific to the frame of reference between the object and body.

**Table 1: List of previous studies examining the transfer of learned manipulation**

<table>
<thead>
<tr>
<th>Authors</th>
<th>Learned Manipulation</th>
<th>Transfer condition</th>
<th>Results</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chang et al 2008</td>
<td>Object weight in a two-digit lift</td>
<td>Open palm hefting to contralateral hand</td>
<td>Transfer of forces across hand</td>
</tr>
<tr>
<td>Chan et al 1990; Gordon et al 1994</td>
<td>Object weight in a two-digit lift</td>
<td>Contralateral hand transfer</td>
<td>Transfer of forces across hand</td>
</tr>
<tr>
<td>Gordon and Salimi 2004</td>
<td>Object weight and torque in a two-digit lift</td>
<td>Contralateral hand transfer</td>
<td>Transfer of weight but not torque</td>
</tr>
<tr>
<td>Salimi et al 2003; Zhang et al 2010</td>
<td>Object torque in a two-digit lift</td>
<td>Rotation of asymmetrical object</td>
<td>Negative transfer (interference) after rotation</td>
</tr>
<tr>
<td>Albert et al 2009; Bursztyn and Flanagan 2008</td>
<td>Object torque in a two- or three-digit lift</td>
<td>Rotation and Contralateral transfer</td>
<td>No transfer of torque</td>
</tr>
<tr>
<td>Bursztyn and Flanagan 2008</td>
<td>Object Torque in a constrained two-digit lift</td>
<td>Hand rotation, Contralateral hand rotation, Hand and object rotation</td>
<td>Partial transfer of torque</td>
</tr>
<tr>
<td>Marneweck et al 2015</td>
<td>Object torque in an unconstrained two-digit lift</td>
<td>Hand rotation</td>
<td>No transfer of torque</td>
</tr>
<tr>
<td>Fu et al 2014</td>
<td>Object torque in an unconstrained two-digit lift</td>
<td>Contralateral hand transfer, Object rotation, Contralateral hand transfer and object rotation</td>
<td>Negative transfer (interference) after object rotation, no transfer otherwise</td>
</tr>
<tr>
<td>Fu et al 2011</td>
<td>Object torque in a two- or three-digit lift</td>
<td>Two to three digit or Three to two digit transfer</td>
<td>Transfer of torque when adding or removing digits</td>
</tr>
</tbody>
</table>

Further studies examining how maintaining the object reference frame while altering the effectors such as 180° hand rotation or contralateral hand rotation showed partial transfer (Bursztyn and Flanagan 2008). 180° hand rotations involve wrist flexions that rotate the digits
such that the fingertips are facing the body. Such rotation, with constrained contact points, places a biomechanical constraint on the hand and limits the range of motion, which could be the reason for the positive performance. Additionally, most of the studies constrained digit placement collinearly and thus only load forces contributed to the generation of compensatory moments. To examine the effect of changing the body and/or hand, to object frame of reference on unconstrained grasping, we performed a similar study where the frame of reference was varied across trials (Marneweck et al. 2015) (Appendix C). In this study, we examined how maintaining or modifying the object-body or object-hand frame of reference might affect learned manipulation. Object-body and object-hand frame of reference was maintained through i) 360° object rotations, ii) 360° subject rotations, iii) 360° object and subject rotations, and iv) 180° object and subject rotations. Object-body and object-hand relations were modified through v) 180° object rotations, and vi) 180° subject rotations. Object-hand relations were modified while maintaining object-body relations by vii) 180° hand rotations. Object-body relations were modified while maintaining object-hand relations by viii) 180° hand and subject rotations. Overall, we found that only when maintaining these frames of reference (i-iv) was there positive transfer. Conditions that modified any of the learned frames of reference (v-viii) disrupted the ability to transfer. Additionally, in contrast to the previous study, when the grasp surface was unconstrained, participants failed to transfer learned object torque after 180° hand rotation. We argue that the biomechanical constraints placed on the hand during these rotations makes it difficult to examine learned behavior. Further studies on unconstrained grasping showed similar lack of transfer during contralateral hand switch, object rotation, and contralateral hand and object rotation (Fu and Santello 2014). These studies further reinforce the understanding that the
high-level learning of compensatory moment generation exists in a specific body/hand and object frame of reference.

Generalizability can also be examined by observing the influence of changing the number of digits/degrees of freedom in contact with the object. To study effector-specificity, Fu et al (2011) performed a set of experiments where transfer of learned torque was examined by changing the degrees of freedom between two and three-digit grasping. Successful transfer of compensatory moment was shown both when switching from two to three digits, and when switching from three to two digits. Additionally, it was found that initial transfer was driven by digit center of pressure. Specifically, adding or removing digits resulted in a change of the overall center of pressure while load forces were evenly redistributed according to pre-transfer estimates. A high-level representation of task enabled the sensorimotor system to use feedback about digit center of pressure after changing degrees of freedom to modulate digit load forces accordingly. Thus, even though learned manipulation of object torque is sensitive to the object-body and object-hand frame of reference, it is not digit specific. Correspondingly, contralateral hand transfer does not generalize because it changes the object-hand frame of reference while adding or removing digits maintains this reference frame.

Aside from the addition or removal of the number of digits, effector specificity can also be examined through changing the number of hands used to grasp the object. Changing from unimanual to bimanual grasping or vice versa is a more complex task than adding or removing fingers of one hand. This change challenges the congruence of the hand-object reference frame by requiring the fingers of one hand to take over the role of the contralateral thumb and vice versa. Thus, even though the object-body frame of reference needs to be maintained for learning to generalize, the extent to which transferring between unimanual and bimanual grasping
maintains or modifies the object-hand frame of reference and if this leads to positive transfer is not known. Additionally, how changing the degrees of freedom affects transfer and generalization is not fully known.

In the present study, we aim to determine if learned manipulation of object torque generalizes to different effectors and degrees of freedom between whole-hand unimanual and bimanual grasping. **The specific aims of the study are to determine if learned manipulation of object torque generalizes from 1) unimanual to bimanual grasping, and/or 2) bimanual to unimanual grasping, regardless of the hand used in unimanual grasping. A secondary aim will be to replicate previous results showing lack of contralateral hand transfer.**

Participants grasped and lifted a visually symmetrical small box with varying centers of mass using either a unimanual or bimanual grasp. After 10 lifts with the same center of mass and grasp, we examined the transfer to another grasp type. In this way, we examined transfer between unimanual to bimanual grasps and contralateral transfer between right hand unimanual and left hand unimanual grasps. The ability to successfully transfer learned manipulation was studied by measuring the peak roll before and after transfer and examining the generation of compensatory moment. When switching from a 5-digit unimanual grasp to a 10-digit bimanual grasp, the forces and placement of the thumb have to be transferred to the contralateral hand, while the opposite is true when switching from a bimanual to unimanual grasp. In both cases, the contribution of the fingers remains relatively the same. We expected that it would be more complex for the thumb to match the forces and placement of the hand while it would be less complex for the digits of the hand to match to forces and placement of the thumb. Thus, we hypothesize that learned manipulation would generalize when adding degrees of freedom and effectors (unimanual to bimanual transfer) but would fail to generalize when removing degrees
of freedom and effectors (bimanual to unimanual transfer). This would be shown by similar peak rolls and compensatory moments between the pre- and post-transfer trials when transferring from unimanual to bimanual grasps but not for bimanual to unimanual grasps. We also hypothesize a lack of transfer when switching to a contralateral unimanual grasp.

To test the hypothesis that learned manipulation generalizes between unimanual and bimanual grasps, participants performed lifts with a right hand unimanual grasp, followed by a bimanual grasp, and then a left hand unimanual grasp (first grasp order condition: right hand – bimanual – left hand). To ascertain that the results of the bimanual to unimanual transfer are not due to hand dominance, a second grasp order condition was performed (left hand – bimanual – right hand). We do not expect that learning from the initial unimanual trials to interfere with the subsequent contralateral unimanual blocks after the bimanual transfer because performance has been shown to be influenced by the most recent sensorimotor experience (Baugh et al. 2012; Flanagan et al. 2001; Quaney et al. 2003; Shibata et al. 2014). However, to ensure that the order of grasp type did not influence the results we introduced a third grasp order condition (bimanual – right hand – left hand). This third condition also confirmed previous findings showing a lack of contralateral transfer (Fu et al. 2014) while also allowing a comparison between novel and transfer trials with a bimanual grasp. Thus, using these three grasp order conditions, we aim to show that learned manipulation of object torque generalizes across multiple effectors and degrees of freedom. If our results support these hypotheses, it would mean that object torque is learned on a high level of representation that can be accessed through multiple effectors but that the ability to generalize is based on whether the number of degrees of freedom and effectors are increased or decreased.
Chapter 2: Materials and Methods

2.1 Participants

30 healthy adults (median age: 26 yr., range: 19-34 yr.; 16 women) with normal or corrected-to-normal vision and no upper limb orthopedic impairments were recruited to participate in the study. Participants were right-handed with handedness determined using the Edinburgh Handedness Inventory (laterality quotient >90). Written informed consent was obtained prior to participation in compliance with the Declaration of Helsinki. The study is part of a larger group of studies that was approved by the Teachers College, Columbia University Institutional Review Board.

2.2 Apparatus

For the object, a custom-made device similar to that in a previous study was used (Marneweck et al. 2016)(Appendix D). Figure 1A shows the schematic of the box (height, width, depth = 165, 80, 85 mm) that was used for the study. The box is visually symmetrical with compartments within the box to change its center of mass. Adding lead weights to the compartments generated object torques of ± 20 Ncm depending on if the weights were placed on the left or right compartments. Sandpaper (100 grit) covered the carbon fiber grip surfaces on either side (height, width, thickness = 150, 80, 3 mm). A 6-axis force transducer (Mini 40, ATI Industrial Automation, NC, USA) was attached onto each of the grip surfaces. These force transducers measured grip and load forces, as well as the overall torque exerted on the surface with a resolution of 0.02 N, 0.01 N, and 0.125 Nmm respectively. An electromagnetic sensor (Polhemus Fasttrack, 0.005mm range, 0.025° resolution) was attached to the top of the device to measure vertical distance and object roll.
Figure 1: Experimental Apparatus. A. Physical appearance of the object as presented to the participants and the inner components. B. Schematic layout of the grasped object showing the total forces produced by the digits on each side and the direction of resultant compensatory moment and object roll.
2.3 Procedure

Each of the 3 conditions was performed by 10 participants (Table 2). Prior to the start of the experiment, markers were attached to the fingertips of the participants. Participants were seated in front of a height-adjustable table, with their elbows flexed 90° in the parasagittal plane. Their hands were placed on the edge of the table. They then performed 3 practice trials per grasp type in their respective grasp order on a practice box with a symmetrical center of mass. Participants were instructed to lift the box at a smooth and self-directed pace. After an audio tone, participants reached and grasped the object on the lateral surface with the appropriate grasp type, anywhere on the respective grip surfaces, and lifted the object vertically upwards. A 10 cm reference marker was placed next to the object to indicate the minimum lift height. The object was held at that height until presentation of a second audio tone (5 s after first tone), after which they placed the object back on the table and returned their hands to the start point awaiting the start of the next trial. At the end of the practice trials, the experimental box was placed in front of the participant, without lifting the box up. Participants then performed blocks of 10 lifts in each grasp type in their grasp order with the same center of mass. After a 5-minute rest, participants repeated the practice (using the same practice device) and condition (using the actual device) with the opposite center of mass. Condition and center of mass order were counterbalanced.

Table 2: Grasp order of each condition

<table>
<thead>
<tr>
<th>Condition</th>
<th>Grasp Order</th>
<th>Grasp Order</th>
<th>Grasp Order</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Trial 1-10</td>
<td>Trial 11-20</td>
<td>Trial 21-30</td>
</tr>
<tr>
<td>1</td>
<td>Right hand Unimanual</td>
<td>Bimanual</td>
<td>Left hand Unimanual</td>
</tr>
<tr>
<td>2</td>
<td>Left hand Unimanual</td>
<td>Bimanual</td>
<td>Right hand Unimanual</td>
</tr>
<tr>
<td>3</td>
<td>Bimanual</td>
<td>Right hand Unimanual</td>
<td>Left hand Unimanual</td>
</tr>
</tbody>
</table>

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2.4 Data Processing

Throughout the lifts, effector forces and torques applied to the grip surfaces recorded by the force transducers, and position data of the box recorded by the electromagnetic sensor were sampled at 500 and 120 Hz, respectively, using custom written software in WinSC/Zoom (Umeå University, Sweden). Digit placement data was sampled at 120 Hz. A second-order low pass Butterworth filter with a cutoff frequency of 6 Hz was used to filter the data collected. To examine anticipatory planning, measures will be recorded at lift-onset, before performance-specific feedback mechanisms influence grasp control (Fu and Santello 2014). Lift onset was defined as the point at which the vertical position of the object went above 1 mm and subsequently remained above this value. Object roll and all other force variables occurred in the frontal plane. Figure 1B shows how the forces and placement are applied in a right handed and bimanual grasp. The outcome measures included:

1. Peak object roll, defined as the angle of the object in the frontal plane. Peak object roll was recorded within 250 ms after lift onset. It denotes the participants’ ability to accomplish the task goal (object roll minimization). Positive values represent counterclockwise roll (towards the left) and negative values represent clockwise roll (towards the right).

Measures recorded at lift onset:

2. Load force (LF), measured in Newton (N), is the tangential component of the force exerted on each grasp surface.
   a. Load force difference \( (LF_{\text{diff}}) = LF_{\text{left}} - LF_{\text{right}} \)

   Positive values indicate larger left than right side LF while negative values indicate larger right than left side LF. It should be noted that using this
formula, a positive value for the right hand indicates larger thumb LF while a positive value for the left hand indicates larger finger LF.

3. Grip force (GF), measured in Newton (N), is the average normal component of the force exerted on each grasp surface.

4. Center of pressure (COP), measured in centimeters (cm), is the equivalent vertical point of application of all the digits on each grasp surface. For multiple digits, this is the net COP after considering all individual digit COPs. This was computed using the formula (Fu et al. 2010; Zhang et al. 2010):

\[
COP_{\text{side}} = \frac{Tx_{\text{side}} - (LF_{\text{side}} \times \text{thickness of grip surface})}{GF_{\text{side}}}
\]

where \( Tx \), torque applied in the frontal plane, is the torque generated on each side of the grasp surface measured in Newton centimeter (Ncm). The thickness of the grip surface was 0.5 cm.

a. Center of pressure difference \((COP_{\text{diff}}) = COP_{\text{left}} - COP_{\text{right}}\)

Positive values indicate higher left than right side COP, while negative values indicated higher right than left side COP. Similar to \( LF_{\text{diff}} \), a positive value for the right hand indicates higher thumb COP while a positive value for the left hand indicates higher finger COP.

5. Compensatory moment (Mcom), measured in Newton centimeter (Ncm), is defined as the anticipatory torque generated by the hand/s, to counter object torque. This was computed using a similar formula (Fu et al. 2010; Latash and Zatsiorsky 2009; Zhang et al. 2010):

\[
Mcom = \left( (LF_{\text{diff}}) \times d/2 \right) + \left( GF_{\text{average}} \times COP_{\text{diff}} \right)
\]

14
where \(d\) is the width of the box (8.1 cm). A positive Mcom denotes a clockwise moment while a negative Mcom denotes a counter-clockwise moment.

6. Digit placement (DP) is the relative height of all the digits to the bottom of the box and was measured using Vicon® motion capture.

### 2.5 Data Analysis

Peak roll was used to determine accomplishment of task goal. Anticipatory planning of digit forces and placement were analyzed using the resultant Mcom, LF\(_{\text{diff}}\), GF, COP\(_{\text{diff}}\), and HP\(_{\text{diff}}\) at lift onset. Peak roll, Mcom, GF, LF, and COP were analyzed using a custom written software in WinZoom (Umeå University, Sweden). Digit placement was analyzed using Vicon® Nexus (Lake Forest, CA).

To examine the generalization of learned manipulation across grasp types, we performed a repeated measures ANOVA with grasp type (right hand, bimanual, left hand), trial (first, tenth), and center of mass (left, right) as the within-subjects factor to compare the peak roll, Mcom, COP\(_{\text{diff}}\), average GF, and LF\(_{\text{diff}}\) for each condition. To compare digit placement across the trials, we performed a repeated measures ANOVA with digit (thumb, index, middle, ring, little finger), trial (first and last), center of mass (left and right), and hand (right hand, bimanual right hand, bimanual left hand, left hand) as the within-subjects factors. To determine if grasp order (novel or transfer trial) affected each grasp type, we performed a one-way ANOVA comparing each grasp type across the conditions for peak roll, Mcom, COP\(_{\text{diff}}\), LF\(_{\text{diff}}\), and DP. For grip force, to determine if GF\(_{\text{left}}\) was different from GF\(_{\text{right}}\), we performed a mixed model ANOVA with grasp, COM (left, right), and side (left, right) as the within-subjects factor and condition as the between-subjects factor. Additionally, we wanted to examine the respective contribution of the
two components of Mcom (LF_{diff} and COP_{diff} x GF) across each condition before and after transfer. To do this, we computed the actual torque generated by these two components and ran the same one-way ANOVA on the results. We also examined learning by performing repeated measures ANOVAs on peak roll and Mcom with COM (left, right) and trial (1 to 10) as the within-subjects factor for each hand and condition. Effect sizes were reported using partial eta squared, \( \eta^2_p \). Bonferroni corrections were used where applicable. Sphericity assumptions were also tested and corrected using the Greenhouse-Geisser correction where appropriate. Significance was considered at the \( p < 0.05 \) level.

**Chapter 3: Results**

In the present study, we examined generalization of learned dexterous manipulation through the transfer of torque information from unimanual to bimanual grasps and from bimanual to unimanual grasps. To examine transfer, we quantified participants’ ability to minimize the roll of an object with an asymmetrical center of mass and their ability to generate a compensatory moment (Mcom) to counter object torque. We also examined contralateral hand transfer. The reduction of object roll after transfer and the generation of Mcom in the appropriate direction but not amplitude was evidence to show the partial generalization of learned manipulation.

### 3.1 Learning of Mcom Generation within 3 trials during Novel and Transfer Lifts

To examine the time course of learning, we compared the peak roll and Mcom of each hand over the 10 trials during the novel lift blocks (condition 1 for the right hand, condition 2 for the left hand, and condition 3 for bimanual). Figure 2 shows the peak roll and Mcom for each trial averaged across the participants in both the left and right COM. Results showed that by trial
2. peak roll was reduced due to the generation of an appropriate Mcom, which stabilized by trial 3. Thus, similar to previous findings, learning of task dynamics occurs within the first few trials.
Figure 2: Novel learning of Mcom and reduction of peak roll. Average (± S.E) Mcom and peak roll across the 10 trials for the right hand (A, B), bimanual (C, D), and left hand (E, F) for each COM. Data for each grasp are taken from the novel condition block. Significance indicated by the asterisk for peak roll and plus sign for Mcom.
Similar to the learning on novel trials, on the transfer trials for the unimanual grasps, roll reduction and Mcom generation was stabilized after 3 trials. However, on the first transfer trial, Mcom generation was generated in the appropriate direction but insufficient magnitude leading to larger peak rolls (Figure 3). This improved on trial 2 with peak roll minimization and Mcom generated similar to the target Mcom by the third trial. In contrast, roll reduction for the bimanual transfer trials were minimized by trial 2 while Mcom generation stabilized similar to the other grasps, at trial 3. Thus, even though initial performance on the transfer trials was better, novel and transfer blocks have similar learning rates with reduction of peak roll after bimanual transfer occurring earlier.
Figure 3: Transfer learning of Mcom and reduction of peak roll. Average (± S.E) Mcom and peak roll across the 10 trials for the right hand (A, B), bimanual (C, D), and left hand (E, F) for each COM. Data for each grasp are taken from the transfer condition block. Significance indicated by the asterisk for peak roll and plus sign for Mcom.
3.2 Learned Generation of Mcom Differs between Unimanual and Bimanual Grasps

On the 10th lift (last pre-transfer trial), all participants performed the task successfully through the minimization of peak roll and generation of the appropriate Mcom. However, even though Mcom was similar across the different grasps, the way in which Mcom was generated differed between the grasps. Figure 4 shows the representative plots of the outcome measures at trial 10 with a left center of mass (COM) for lifts with the right hand, bimanually, and left hand. Minimization of peak roll (> -2°, or < 2°) and generation of the appropriate Mcom (~ 20 Ncm) was seen for all grasps. Where the grasps differ was in the way that Mcom was generated. For effector center of pressure (COP), in right hand grasps, learned manipulation was characterized by generally higher thumb (left side) COP than that of the fingers (right side). Similarly, in the bimanual grasps, the left hand exerted a higher COP than the right hand. However, left-handed grasps showed collinear COP of the thumb (right side) and the fingers (left side). It should be noted that the COP measured in this study is the equivalent COP of all the digits on the corresponding side. For the load forces (LFs), both right- and left-hand unimanual grasping showed larger LFs of the fingers (right and left side respectively) while bimanual grasps showed larger LFs of the left compared to the right hand. Grip forces (GFs) of the right side were slightly higher than those of the left side for all 3 grasp types. Additionally, GF of the right and left hand were larger than the GF of the bimanual grasp.
Figure 4: Representative plots for trial 10 of the left COM for the right hand, bimanual, and left hand grasps. Vertical dotted lines represent time at lift onset.
Figure 5 shows the representative plots with the object having a right COM. Learned manipulation of the right COM was similar to that with the left COM in the minimization of peak roll and generation of appropriate Mcom (~ - 20 Ncm). Right hand Mcoms were generated by generally collinear COPs, larger finger than thumb LFs, and slightly larger thumb than finger GFs. Mcoms of bimanual grasps were generated by higher COPs and larger LFs of the right compared to the left hand, and slightly higher GF of the left hand. Mcoms for the left hand unimanual grasps were generated by higher thumb COP than COP of the fingers, larger finger LFs than thumb, and slightly larger finger GFs. Similar to the left COM, GFs of the right and left hands during unimanual grasps were larger than GFs of the hands during bimanual grasps.

Overall, in unimanual grasping, the COP of the thumb was either collinear or higher than the equivalent COP of the fingers while the combined LF of the four fingers was always larger than the LF of the thumb. The magnitude of these differences was determined by the COM of the object and the required Mcom. For the bimanual grasps, similar to two-digit grasping with the dominant hand, COP difference and LF difference were modulated in the direction of Mcom generation. These findings are similar to our previous studies on whole-hand grasping (Marneweck et al. 2016), and bimanual grasping (Lee-Miller et al. 2019) of asymmetrical objects.
Figure 5: Representative plots for trial 10 of the right COM for the right hand, bimanual, and left hand grasps. Vertical dotted lines represent time at lift onset.
3.3 Reduction of Peak Roll after Unimanual to Bimanual Transfer

Explicit performance of the task goal was observed by recording the peak roll after lift onset to determine if Mcom generation was able to counter object torque. Figure 6 shows the average peak roll across all participants in each condition and grasp. Analysis of the results showed that 1) all participants were able to successfully minimize roll by trial 10, 2) unimanual to bimanual grasp transfer resulted in a reduction in peak roll compared to novel trials in all grasp types, and 3) contralateral switch did not result in a reduction of peak roll. Figures 6A and B show the results of the first transfer condition (right hand – bimanual – left hand). Results of the repeated measures ANOVA showed that there was a statistically significant interaction between COM, grasp, and trial $F(2,18) = 7.49, p < 0.05, \eta^2_p = 0.45$. Post hoc tests revealed that trial 10 had a smaller peak roll than trial 1 for all grasps ($p$’s < 0.05). On the transfer trials, trial 1 of the bimanual transfer had a smaller peak roll than trial 1 for the novel right-hand lift for both the left and right COM. No significant difference was found between the peak roll of trial 1 in the left hand unimanual transfer trial and that of the novel right hand trial. Similar results were seen for condition 2 (left hand – bimanual – right hand) where there was a statistically significant interaction between COM, grasp, and trial $F(2,18) = 11.15, p < 0.05, \eta^2_p = 0.55$ with post hoc tests revealing a reduction in roll after bimanual transfer (Figures 6C, D). Additionally, for the left COM, trial 1 of the right hand transfer trial had a smaller peak roll than trial 1 of the novel left hand trial (Figure 6C). For condition 3 (bimanual – right hand – left hand) only significant interactions between COM and trial $F(2,18) = 152.87, p < 0.001, \eta^2_p = 0.94$, and between COM and grasp $F(2,18) = 11.43, p < 0.05, \eta^2_p = 0.56$ (Figures 6E, F) were observed. Post hoc tests revealed that trial 10 had a smaller peak roll than trial 1 for all grasps ($p$’s < 0.001). There was no
significant difference found between pre and post-transfer trials across the grasps for condition 3 ($p > 0.05$).

One-way ANOVAs were performed for each grasp to determine if peak roll minimization was due to smaller rolls in the bimanual grasps in general. There was a statistically significant difference between trial 1’s for the left center of mass bimanual grasp ($F(2,27) = 5.984, p < 0.05$). A Tukey post hoc test revealed that for the bimanual grasp, peak roll at trial 1 was statistically significantly lower after transfer ($3.89° \pm 0.41, 2.88° \pm 0.97$) compared to the novel trial in condition 3 ($6.80° \pm 0.91, p’s < 0.05$). There was no statistically significant difference between the other grasps and conditions ($p > 0.05$). Taken together, the results showed that peak roll was reduced immediately after unimanual to bimanual transfer but only minimized after a few trials suggesting partial transfer of torque information in this condition. Additionally, contralateral transfer did not result in a reduction in peak roll. This suggests either a lack of transfer or a lack of ability to use the transferred torque information to significantly affect performance for the unimanual transfer trials.
Figure 6: Average peak roll across all conditions. Averaged peak rolls for the first and last trials for all grasps in condition 1 (A, B), condition 2 (C, D), and condition 3 (E, F) for the left and right COM. Significance indicated by the asterisk.
3.4 Transfer Leads to Generation of Mcom in the Appropriate Direction

Aside from peak roll, implicit performance of the task can also be determined by examining the generation of Mcom that is used to counter object torque. Figure 7 shows the average Mcom across all participants in each condition and grasp. Analysis of the results showed that 1) all participants were able to generate the appropriate Mcom by trial 10, 2) unimanual to bimanual grasp transfer resulted in generation of Mcom in the appropriate direction but not magnitude, 3) bimanual to unimanual grasp transfer resulted in generation of Mcom that was smaller in magnitude than unimanual to bimanual transfers, and 4) contralateral switch did not result in appropriate Mcom generation. Results of the repeated measures ANOVA for condition 1 showed that there was a statistically significant interaction between COM, grasp, and trial $F(2,18) = 30.02, p < .001, \eta_p^2 = 0.77$ (Figures 7A, B). Post hoc tests revealed that trial 10 had larger Mcoms than trial 1 for all grasps ($p$’s < 0.05). Trial 1 of the bimanual transfer had a larger Mcom than trial 1 for the novel right-hand lift for both left and right COM. Additionally, trial 1 of the left-hand transfer had a larger Mcom than trial 1 for the novel right-hand lift for the right COM. Comparing between COMs showed that Mcom was different for all except trial 1 of the right hand (Figure 7 ‘+’ sign). These results showed that unimanual to bimanual transfer resulted in Mcom generation that was more than half the required Mcom to minimize roll. In the bimanual to unimanual transfer trials, depending on the COM, Mcom was applied in the right direction but insufficient magnitude in the first post-transfer unimanual trials. These results were confirmed with condition 2 where results revealed a similar statistically significant interaction between COM, grasp, and trial $F(2,18) = 20.21, p < 0.001, \eta_p^2 = 0.69$ (Figures 7C, D). Bimanual transfer similarly resulted in Mcoms larger than trial 1 for the novel lifts. Right hand transfer resulted in larger Mcoms for only the left COM but smaller than after bimanual transfer.
Significant interaction results from condition 3 \((F(1.29,11.58) = 12.57, p < 0.05, \eta^2_p = 0.58)\) further confirmed the small Mcom for unimanual transfer and showed that contralateral switch resulted in close to no Mcom generation (Figures 7E, F).

For bimanual grasps a significant difference between trial 1’s for the left COM \((F(2,27) = 21.87, p < 0.001)\), and right COM \((F(2,27) = 17.21, p < 0.001)\) was observed. Tukey post hoc tests revealed that Mcom at trial 1 was statistically significantly closer to the target Mcom after bimanual transfer (condition 1 and 2) compared to the novel trial in condition 3 \((p’s < 0.001)\) for the left and right COM. For the right hand grasps there were differences between trial 1’s for the left COM \((F(2,27) = 5.357, p < 0.05)\). Tukey post hoc test revealed that Mcom at trial 1 was larger after unimanual transfer (condition 2 and 3) compared to the novel trial in condition 1. For left hand grasps, differences between trial 1’s were seen for the left COM \((F(2,27) = 5.75, p < 0.05)\), and right COM \((F(2,27) = 3.459, p < 0.05)\). A Tukey post hoc test revealed that Mcom at trial 1 was closer to the target Mcom after unimanual transfer (condition 1) compared to the novel trial in condition 2 and the contralateral trial in condition 3 \((p’s < 0.05)\) for the left and right COM. Taken together, these results show that peak roll reduction after bimanual transfer was due to Mcom generation in the appropriate direction. After unimanual transfer, even though Mcom was generated in the appropriate direction, Mcoms were too small to result in a reduction of peak roll. For the right hand, partial transfer was only seen when object COM was on the thumb side. For the left hand, partial transfer was seen on both COM locations. Contralateral hand switch did not result in any Mcom generation and thus the large peak rolls.
Figure 7: Average Mcom across all conditions. Averaged Mcom for the first and last trials for all grasps in condition 1 (A, B), condition 2 (C, D), and condition 3 (E, F) for the left and right COM. Horizontal dotted line represents the target Mcom. Significance indicated by the asterisk for within COM and by the plus sign for across COM differences.
3.5 Post-Transfer Generation of Mcom was due to COP Modulation

As reported above, the contribution of COP to Mcom differs depending on the grasp type. For unimanual grasps, the thumb generally has a higher COP than the equivalent COP of the fingers regardless of COM location while bimanual grasps have varying COP depending on COM location. For a left COM, a positive COP\textsubscript{diff} would assist in Mcom generation in the appropriate direction to counter object roll. For a right COM, negative COP\textsubscript{diff} would have the same effect. A positive COP\textsubscript{diff} results from a higher thumb COP for the right hand and higher finger COPs for the left hand and vice versa for a negative COP\textsubscript{diff}. Figure 8 shows the average COP\textsubscript{diff} across all participants in each condition and grasp. The results showed that 1) contribution of COP to Mcom generation at trial 10 depended on the grasp type and COM, 2) unimanual to bimanual grasp transfer resulted in COP\textsubscript{diff} that was in the same direction as Mcom, 3) bimanual to unimanual grasp transfer resulted in COP\textsubscript{diff} in the same direction as Mcom only when Mcom required thumb COP to be higher, and 4) contralateral switch did not result in any change in COP\textsubscript{diff}. For condition 1, post hoc tests performed after a significant interaction between COM, grasp, and trial ($F(2,18) = 3.90, p < 0.05, \eta^2_p = 0.30$) revealed that trial 10 had a different COP\textsubscript{diff} than trial 1 for all grasps ($p$’s < 0.05) except the left hand in the right COM condition (Figures 8A, B). For the left COM, trial 1 of the bimanual transfer and novel right hand showed a higher left side (left hand, right thumb respectively) than right side (right hand, right fingers) COP. Comparatively, trial 1 for the left hand transfer trial had a higher right side (left thumb) than left side (left fingers) COP. For the right COM, trial 1 of the novel right hand had a higher thumb to fingers COP while the bimanual and left hand transfer trials showed a higher right side (right hand, left thumb) to left side (left hand, left fingers) COP. Left to right COM was different for all except trial 1 of the right hand. In condition 1 for unimanual grasps, COP\textsubscript{diff}
differentially contributes to Mcom generation. Additionally, unimanual to bimanual transfer trials resulted in COP$_{\text{diff}}$ that assisted in the generation of the appropriate Mcom. Bimanual to unimanual trials showed positive transfer only when the direction of COP$_{\text{diff}}$ was in the stereotypical direction of the unimanual grasp (i.e. higher thumb than finger COP). Similar results were seen in condition 2 where post hoc tests showed a difference between trial 1 and trial 10 for all grasp types (COM and trial interaction, $F(2,18) = 52.23$, $p < 0.001$, $\eta_p^2 = 0.85$). Additionally, COP$_{\text{diff}}$ at trial 10 depended on the COM (COM and grasp interaction, $F(2,18) = 47.26$, $p < 0.001$, $\eta_p^2 = 0.84$). Post hoc tests revealed similar results to condition 1 for the bimanual transfer trials, and opposite results for the right hand transfer trials in condition 2 compared to the left hand transfer trials in condition 1. This further shows that positive unimanual transfer only results when the trial requires a higher thumb than finger COP. Similar bimanual to unimanual results were seen for condition 3 (COM, grasp, and trial interaction, $F(2,18) = 7.04$, $p < 0.05$, $\eta_p^2 = 0.44$). Contralateral switch did not result in transfer of COP$_{\text{diff}}$ (Figures 8E, F).

Comparison of the first novel to transfer trial within each grasp type showed that bimanual transfer resulted in COP$_{\text{diff}}$ that assisted Mcom generation (left COM, $F(2,27) = 8.16$, $p < 0.05$, and right COM $F(2,27) = 5.43$, $p < 0.05$) while only in the left COM did right hand unimanual transfer result in COP$_{\text{diff}}$ that assisted Mcom generation ($F(2,27) = 4.13$, $p < 0.05$). For bimanual grasps, Tukey post hoc tests revealed that COP$_{\text{diff}}$ at trial 1 was statistically significantly larger after bimanual transfer (condition 1 and 2) compared to the novel trial in condition 3 ($p$’s $< 0.05$). For the right hand grasp, COP$_{\text{diff}}$ at trial 1 was statistically significantly higher after unimanual transfer (condition 2 and 3) compared to the novel trial in condition 1. Taken together, partial generation of Mcom after bimanual transfer was due to COP modulation
regardless of the COM while partial generation of Mcom after right hand unimanual transfer was seen when object COM was on the thumb side and due to higher thumb to finger COPs. After left hand transfer, appropriate generation of Mcom when object COM was on the side of the fingers (left COM) was not due to COP transfer. Contralateral hand switch did not result in the transfer of COP modulation.
Figure 8: Average COP\text{diff} across all conditions. COP\text{diff} for the first and last trials for all grasps in condition 1 (A, B), condition 2 (C, D), and condition 3 (E, F) for the left and right COM. Significance indicated by the asterisk for within COM and by the plus sign for across COM differences.
3.6 Digit Placement not Modulated across Condition

Overall changes in COP\textsubscript{diff} could have been caused by either changes in digit placement (DP) or changes in the contribution of individual digit COPs to the overall COP\textsubscript{diff}, this in turn being caused by changes in digit GFs. Analysis of kinematic data of DP showed that 1) condition did not affect DP, 2) DPs of unimanual grasps were different from DPs of bimanual grasps, and 3) there were small differences in a few DPs between trials 1 and 10. There were no significant differences across the conditions thus DP was averaged across all the conditions. Figure 9 shows the results of DP averaged across all conditions for the right hand (Figures 9A, B), the right hand of the bimanual grasps (Figures 9C, D), the left hand of the bimanual grasps (Figures 9E, F), and the left hand (Figures 9G, H) (COM, hand, trial, and digit interaction, $F(4.89,102.78) = 5.46, p < 0.001, \eta_p^2 = 0.21$). Post hoc results show that when comparing the digits across the hands, individual digit placement was different between unimanual and bimanual grasps ($p$'s < 0.05). No significant differences were found when comparing between the right and left unimanual grasps or between the right hand and left hand of the bimanual grasps ($p$'s > 0.05). Overall, our results show that DP was not modulated to generate Mcom.
Figure 9: Average DP across all conditions. DP for the first and last trials for all grasps averaged across the conditions for the left and right COM. Significance indicated by the asterisk for within COM and by the plus sign for across COM differences.
3.7 GF Differed across Grasps but not Condition

As mentioned above, it is the combination of COP\textsubscript{diff} and grip force (GF) that result in the generation of one torque component. Thus, analysis of GF would provide further insight into the transfer of torque information. Analysis of GF results showed that 1) average GF (averaged between the left and right grasp sides) did not differ by condition, 2) Unimanual GF was larger than bimanual GF, and 3) COM affected which side had a slightly larger GF. There was not a significant effect of COM. Figure 10 thus shows the average GF (averaged between the left and right COM) across all conditions for trials 1 and 10, each of the grasps. For condition 1 (Figure 10A), post hoc tests revealed difference between novel trial 1 and 10 for the right hand only (grasp and trial interaction, $F(2,18) = 17.98$, $p < 0.001$, $\eta^2_p = 0.67$). For trial 1, GF of the left hand was higher than GF of right hand and bimanual grasps, which did not differ. For trial 10, GF of the left and right hand were higher than that of the bimanual grasp. Results of the condition 2 (Figure 10B) showed similar findings to condition 1 (grasp and trial interaction, $F(2,18) = 9.76$, $p < 0.05$, $\eta^2_p = 0.52$). Post hoc tests showed smaller GF on the first novel trial and smaller bimanual than unimanual GFs. For condition 3 (Figure 10C), trial 1 had a smaller GF than trial 10 for all grasps (main effect of trial $F(1,9) = 18.90$, $p < 0.05$, $\eta^2_p = 0.68$). Bimanual GF was also smaller than unimanual GF (main effect of grasp $F(2,18) = 27.16$, $p < 0.001$, $\eta^2_p = 0.75$). Taken together, our results show that GF of the first novel trial was smaller than subsequent GFs while unimanual GFs were larger than bimanual GFs. Additionally, it is possible that GF of either side might be affected by the conditions. Mixed model ANOVA on the grasp sides showed a significant interaction between grasp, side, and COM $F(3.22, 6.45) = 18.68$, $p < 0.001$, $\eta^2_p = 0.41$. Post hoc tests showed that for the left COM, the right side had a
larger GF for all trials except for the first trial of the bimanual grasp. For the right COM, the left side had a larger GF for all trials except the first trial of the bimanual and left-hand grasps.
Figure 10: Average GF across all conditions. GF averaged across COM for the first and last trials for all grasps in condition 1 (A, B), condition 2 (C, D), and condition 3 (E, F). Significance difference indicated by the asterisk.
3.8 LF Difference only Contributed to Mcom Generation on Left Hand Transfer

Trials when the COM was on the left

Similar to COPdiff, for unimanual grasps, the torque direction that LFdiff generates depends on whether LF of the thumb or fingers is higher. For a left COM, a positive LFdiff would assist in Mcom generation in the appropriate direction to counter object roll. For a right COM, negative LFdiff would have the same effect. A negative LFdiff results from higher finger LF for the right hand and higher thumb LF for the left hand and vice versa for a positive LFdiff. Analysis of the results of LFdiff showed that 1) LF of the fingers was always higher than LF of the thumb for unimanual grasps, 2) only left hand left COM transfer trials affected the magnitude of LFdiff. Figure 11 shows the results of LFdiff across the conditions. For condition 1, figures 11A and B, post hoc tests revealed that trial 1 and 10 did not differ for the left COM but differed for the right COM (COM and trial interaction, $F(2,18) = 9.58, p < 0.05, \eta_p^2 = 0.52$). For the left COM, LFdiff of all grasp types differed from each other while for the right COM, LFdiff of left hand grasps differed from that of the right hand and bimanual grasps (COM and grasp interaction, $F(2,18) = 8.16, p < 0.05, \eta_p^2 = 0.48$). Condition 2 showed similar results with a main effect of grasp type $F(2,18) = 45.52, p < 0.001, \eta_p^2 = 0.84$ and a significant interaction between COM and trial $F(2,18) = 39.14, p < 0.001, \eta_p^2 = 0.81$ (Figures 11C, D). Condition 3 confirmed these results and showed that contralateral switch did not result in LFdiff transfer (Figures 11E, F).

Comparing novel to transfer trial within each grasp type, load forces only differed for the left hand between trial 1’s for the left COM ($F(2,27) = 5.38, p < 0.05$). A Tukey post hoc test revealed that LFdiff at trial 1 was statistically significantly higher after unimanual transfer (condition 1) compared to the novel trial in condition 2. Taken together, our results show that LFdiff only contributed to Mcom generation on the left hand unimanual transfer trials (left COM)
and that $LF_{\text{diff}}$ was characterized by larger finger LF for all unimanual grasps. Additionally, we do not have sufficient evidence to show that $LF_{\text{diff}}$ of bimanual grasps was modulated in the direction of Mcom on the post-transfer trials.
Figure 11: Average LF_{diff} across all conditions. LF_{diff} for the first and last trials for all grasps in condition 1 (A, B), condition 2 (C, D), and condition 3 (E, F) for the left and right COM. Significance indicated by the asterisk.
3.9 Transfer of Torque Information Results in Modulation of COP Difference and GF

As mentioned, Mcom is generated from the combined torques generated from $\text{COP}_{\text{diff}}$ and GF, and $\text{LF}_{\text{diff}}$. Specifically, the GF of the digits act on the COPs to generate one of the torques ($\text{GF} \times \text{COP}_{\text{diff}}$). Additionally, LFs contribute to torque generation by acting on the width between the grasp surfaces (8.1 cm) as the moment arm. Thus, multiplying $\text{LF}_{\text{diff}}$ by half this width (4.05 cm) results in the second torque component. Plotting these components together might provide further insight into the mechanisms of torque transfer. Figures 12-14 show the relative contribution of both torque components to the resultant Mcom in each of the grasps across trials 1 and 10 for all conditions. Our results from above showed that $\text{LF}_{\text{diff}}$ did not differ within the grasps (except for the left hand), as such we will focus our results on GF and $\text{COP}_{\text{diff}}$, which we term the “COP torque”. For bimanual grasps, transfer resulted in higher COP torque compared to novel trials (left COM $F(2,27) = 8.18, p < 0.05$, right COM $F(2,27) = 7.321, p < 0.05$). A Tukey post hoc test revealed that COP torque at trial 1 was closer to the target Mcom after bimanual transfer (condition 1 and 2) compared to the novel trial in condition 3 ($p$’s $< 0.001$) for both left and right COM (Figure 12). Thus, unimanual to bimanual transfer of Mcom was driven by modulation of $\text{GF} \times \text{COP}_{\text{diff}}$. 
Figure 12: Bimanual grasp contribution of torque components to Mcom. Stacked bar graph showing how \(LF_{\text{diff}}\) and \(GF\) with \(COP_{\text{diff}}\) affected Mcom for trial 1 and 10 in all conditions for the left (A) and right (B) COM. Horizontal dotted line indicates target Mcom. Significance indicated by the asterisk.
For the right hand unimanual grasps, transfer resulted in higher COP torque compared to novel trials only for the left COM ($F(2,27) = 8.17, p < 0.05$). A Tukey post hoc test revealed that COP torque at trial 1 was statistically significantly higher after unimanual transfer (condition 2 and 3) compared to the novel trial in condition 1 (Figure 13). Thus, bimanual to unimanual transfer of the right hand was a result of GF x COP$_{diff}$ modulation but only when the COM was on the side of the thumb (left COM).
Figure 13: Right hand grasp contribution of torque components to Mcom. Stacked bar graph showing how LF\textsubscript{diff} and GF with COP\textsubscript{diff} affected Mcom for trial 1 and 10 in all conditions for the left (A) and right (B) COM. Horizontal dotted line indicates target Mcom. Significance indicated by the asterisk.
For the left hand unimanual grasps, aside from a difference between trial 10 of the right COM ($F(2,27) = 4.073, p < 0.05$), COP torque showed no difference in all other conditions. (Figure 14). Additionally, post hoc tests for $\text{LF}_{\text{diff}}$ showed that $\text{LF}_{\text{diff}}$ of the transfer trial in condition 1 was higher than that in the novel trial of condition 2 (Figure 14A). Thus, our results show that for the left hand, when the COM was on the side of the fingers, Mcom generation was due to LF modulation. When the COM was on the side of the thumb (right), Mcom generation could have been due to COP modulation in the direction of Mcom or reduction in the LF of the fingers.
Figure 14: Left hand grasp contribution of torque components to Mcom. Stacked bar graph showing how LF\textsubscript{diff} and GF with COP\textsubscript{diff} affected Mcom for trial 1 and 10 in all conditions for the left (A) and right (B) COM. Horizontal dotted line indicates target Mcom. Significance indicated by the asterisk.
3.10 Individual Change of LF difference and COP difference after transfer

To observe the individual differences between the last pre-transfer trial and the first post-transfer trial, we examined how \( LF_{\text{diff}} \) and \( COP_{\text{diff}} \) changed before and after transfer for each transfer condition (Figure 15). The left COM resulted in a counter-clockwise object torque that required a positive Mcom to prevent while the right COM resulted in a clockwise torque and was countered with a negative Mcom. There are three possible solution to generate a positive Mcom; 1) positive modulation of both \( LF_{\text{diff}} \) and \( COP_{\text{diff}} \), top right quadrants of each graph in Figure 15, 2) more positive \( LF_{\text{diff}} \) and a less negative \( COP_{\text{diff}} \), top left quadrants, 3) more positive \( COP_{\text{diff}} \) and a less negative \( LF_{\text{diff}} \), bottom right quadrants. The opposite is required to generate a negative Mcom. Whether or not different strategies differ in their ability to generalize remains to be seen.

For the left COM, positive Mcom generation would be represented by data points in the top left, top right, or bottom right quadrant (Figures 15A-D), learned manipulation of the right hand was characterized by Mcom generation that was due to higher thumb COPs (positive \( COP_{\text{diff}} \)) and larger finger LFs (negative \( LF_{\text{diff}} \)). However, some participants also applied larger thumb COP while LF between the thumb and fingers was similar (Figure 15A purple data points). One participant applied larger thumb LF and higher thumb COP than that of the fingers (top right quadrant). After bimanual transfer, this same participant maintained the same \( COP_{\text{diff}} \) but applied larger LF on their right hand compared to their left hand (bottom right quadrant) resulting in a smaller Mcom (Figure 15A blue arrows and points). Most other participants either maintained or applied a smaller \( COP_{\text{diff}} \) while also applying more positive \( LF_{\text{diff}} \) compared to the pre-transfer trials (bottom right to top right quadrant). One other participant showed poor transfer by applying smaller \( COP_{\text{diff}} \) and \( LF_{\text{diff}} \) (bottom right quadrant). When transferring from a bimanual grasp to a right hand unimanual grasp (blue points to purple arrows and points), higher
COP and larger LF of left hand during pre-transfer bimanual grasp (top right quadrant) was transferred to higher thumb COPs but larger finger LFs (bottom right quadrant) for the post-transfer right hand (Figure 15B). For one participant, \( \Delta L F \) was negative on the bimanual pre-transfer trial (bottom right quadrant). For this participant, right hand transfer did not result in COP transfer but the same \( \Delta L F \) with smaller COP\( \Delta \) than pre-transfer (bottom right quadrant). For the left hand, learned manipulation was characterized by varying COP\( \Delta \) and higher finger LFs (Figure 15C, top left and right quadrants, yellow points). On bimanual transfer, \( \Delta L F \) was reduced while positive COP\( \Delta \) (higher left hand) was applied (Figure 15C, top and bottom right quadrants, blue arrows and points). This was the general trend among most of the participants. The opposite was seen for bimanual to left hand transfer where positive COP\( \Delta \) and \( \Delta L F \) transferred to negative COP\( \Delta \) and positive \( \Delta L F \) (Figure 15D, top right to top left quadrant). Thus, for generalization in the left COM condition, transfer results in COP\( \Delta \) that facilitate Mcom generation, for bimanual and right hand transfer, while individual differences affect the overall trajectory of transfer. For left hand transfer, the inherent positive \( \Delta L F \) drives that transfer.

For the right COM, negative Mcom would be represented by data points in the top left, bottom left, or bottom right quadrant (Figures 15E-H), learned manipulation of the right hand for most participants involved collinear COPs and larger finger LFs (Figure 15E bottom quadrants, purple data points). Bimanual transfer resulted in more collinear LFs while COPs of the right hand were larger than that of the left hand (Figure 15E left quadrants, blue arrows and points). Two participants applied a positive \( \Delta L F \) (top left quadrant) during their pre-transfer trials, for one participant bimanual post-transfer trial retained a similar COP\( \Delta \) while the other participant applied a more collinear COP\( \Delta \) but a more negative \( \Delta L F \) (bottom left quadrant). For novel
bimanual trials, learned manipulation was characterized by higher right to left hand COPs and larger right to left hand LFs that on right hand transfer trials resulted in larger finger LFs but higher thumb COPs showing a lack of positive transfer (Figure 15F, bottom right quadrant blue points to bottom left quadrant purple arrows and points). However, one participant showed positive transfer by maintaining a similar pre-transfer COP\_diff after right hand transfer (bottom left to top left quadrant). Left hand to bimanual transfer showed more individual differences in LF\_diff after transfer while COP\_diff after transfer was similar to pre-transfer the COP\_diff (Figure 15G). However, one participant showed negative transfer of COP\_diff (bottom left to bottom right quadrant). Bimanual to left hand transfer showed the similar characteristic of larger finger LFs after unimanual transfer (Figure 15H bottom left blue points to top left yellow points). One participant maintained a larger thumb LF but near collinear COPs (bottom left quadrant close to 0). Thus, results of the right COM are similar to the left COM showing individual transfer driven by COP\_diff for bimanual and left hand transfer, and no transfer for the right hand.

Taken together, our results show the individual differences among participants in Mcom generation that is due to the range of possible solutions to counter object torque and highlight the modulation of COP\_diff as a driving factor of post-transfer Mcom generation.
Figure 15: Pre- and post-transfer effect on LF and COP difference. Individual data points showing trial 10 of the pre-transfer grasp and trial 1 of the post-transfer grasp for the left COM (A-D) and right COM (E-H). Arrows represent direction of transfer from pre- to post-trials. Arrow color represents post-transfer grasp.
Chapter 4: Discussion

In this study, we used the paradigm of a visually symmetrical object with an asymmetrical center of mass to investigate the transfer of learned object dynamics in the generalization between unimanual and bimanual dexterous manipulation. Our initial hypotheses were that 1) learning would generalize when adding the number of degrees of freedom (5 to 10 digits) and effectors (one to two hands) in a unimanual to bimanual task, 2) learning would fail to generalize in the opposite direction, and 3) learning would fail to generalize after contralateral hand switch. By showing partial generalization in both transfer directions, our results partially supported the first hypothesis, showed the opposite for the second, and fully supported the third hypothesis. Overall, we have shown the partial generalization of learned manipulation when switching from unimanual to bimanual grasps and vice versa. This was accomplished through the transfer of torque information that resulted in the reduction of peak roll after unimanual to bimanual transfer and the generation of compensatory moments in the appropriate direction after unimanual and bimanual transfer, and bimanual to unimanual transfer. The post-transfer generation of compensatory moment was driven mainly by modulation of digit center of pressure with load force modulation assisting left hand unimanual transfer. Aside from the transfer of torque information, generalization of learned manipulation during transfer trials also results in the transfer of weight information as seen from the appropriate control of grip forces at lift-off. Grip forces are controlled in anticipation of object weight (Flanagan et al. 2003; Johansson and Westling 1988a; Witney et al. 1999). In the present study, on initial novel trials, grip forces were smaller than learned trials regardless of the grasp type. However, during the first transfer trials, grip forces were already applied similarly to learned trials due to the transfer of object weight.
dynamics. This characteristic is seen in all grasps. Here, we report on these findings and discuss the implication of generalization on the ability to form high level internal representations.

4.1 Characteristics of Torque Generation in the Partial Generalization of Learned Manipulation

Full generalization of the learned manipulation would be characterized by a small peak roll (similar to the preceding pre-transfer roll) on the first transfer trial, caused by the generation of a compensatory moment that is equivalent to the external torque of the object. The relative contribution of digit centers of pressure, grip forces, and load forces would depend on the grasp type. In instances of partial generalization, as shown in this study, the characteristic of moment generation would reveal important information on the ability to generalize across grasps. Previous studies have already shown that learned compensatory moment generation is caused by center of pressure and load force modulation that each show trial-to-trial variability while generating a stable moment (Fu et al. 2010; Lee-Miller et al. 2019; Marneweck et al. 2016). Thus, partial generalization could be due to 1) high level transfer of torque information represented as a stable compensatory moment generation with subject-to-subject variability in centers of pressure and load forces but of insufficient magnitude, 2) low level transfer of only center of pressure or load force difference information resulting in smaller moments, or 3) high level transfer of compensatory moment that can only be accessed by either center of pressure or load force modulation. Our results showing the overall lack of an effect of transfer on load force modulation with moment generation driven primarily by center of pressure differences rule out the first possible mechanism of transfer. However, the dependence of center of pressure and load force difference on grasp type requires a closer look at the effect of transfer on individual grasp types before forming a conclusion on the other two possible mechanisms.
From our results of learned manipulation in dexterous bimanual grasping (Figure 12), peak roll minimization is due to compensatory moment generation as characterized by higher equivalent digit centers of pressure and larger total load force of all the digits on the side of the object that corresponds with the center of mass (heavier side). On the transfer trials, partial generalization resulted in smaller peak rolls through moment generation that was due to a higher equivalent digit center of pressure on the heavier side, than lighter side, compared to novel trials. However, this difference in center of pressure between the heavier and lighter side on transfer trials was still smaller than the difference after multiple trials. Load forces were not affected by transfer. Thus, on initial bimanual transfer trials, digit center of pressure difference was modulated to generate compensatory moments that partially countered object roll. After more experience with the same bimanual grasp, center of pressure difference was larger and load forces were modulated accordingly. This characteristic was the same regardless of object center of mass. Thus, for bimanual transfer, it is possible that generalization is represented by a low-level center of pressure modulation. However, when examining the pre- and post-transfer centers of pressure (Figure 8), center of pressure modulation after bimanual transfer is in the appropriate direction regardless of the magnitude of the preceding unimanual center of pressure difference. Thus, regardless of whether the unimanual center of pressure difference is large or collinear, bimanual transfer results in center of pressure modulation that is relatively large. That center of pressure after bimanual transfer does not mimic pre-transfer center of pressure, but rather, favors the appropriate direction of moment generation alludes to a possible high-level transfer of torque information.

In dexterous unimanual grasping (Figures 13 and 14), learned manipulation is similar to bimanual grasping in the minimization of peak roll through compensatory moment generation.
However, unlike bimanual grasping, unimanual grasping is characterized by higher or collinear thumb to finger center of pressure, and larger load force of the fingers compared to the thumb. Because of this, moment generation differs by object center of mass and hand used. When the center of mass is on the thumb side, a higher thumb than finger center of pressure contributes to compensatory moment generation. However, because the load forces of the fingers are always larger than that of the thumb, the moment generated by the load forces assists object torque instead of countering it. As a result, the compensatory moment generated by the center of pressure difference has to compensate for this by generating an even higher compensatory moment to account for object torque and moment from load force difference (Figures 13A and 14B, trial 10). The opposite occurs when the center of mass is on the finger side. In this scenario, it is the larger load forces of the fingers that contributes to compensatory moment generation. The higher thumb or collinear thumb to finger center of pressure does not contribute much to compensatory moment generation, and in instances where the thumb has a higher center of pressure, assists object torque (Figures 13B and 14A, trial 10). Thus, because partial generalization is due to moments generated by the center of pressure difference, positive transfer should only be seen when this difference results in a moment that counters object torque, i.e. right-hand left center of mass (Figure 13A), left-hand right center of mass (Figure 14B). That transfer was also seen in the left-hand left center of mass transfer, due to load force difference modulation (Figure 14A), adds to the understanding that the generalization results in the transfer of torque information as opposed to individual center of pressure or load force information.

Through the various transfer conditions of our study, we conclude that partial generalization of learned manipulation between unimanual and bimanual grasping is due to the transfer of object torque information that can be more easily assessed by center of pressure
modulation to generate a compensatory moment in the direction to counter object torque. This is similar to a previous study that observed learning of torque information through multiple 180° object rotations (Zhang et al. 2010). In that study, the authors found that on initial rotations, moment generation fails to generalize. However, after repeated rotations, digit center of pressure difference was modulated in anticipation of object torque to reduce roll. The authors conclude a differing ability of sensorimotor memory retrieval for learned kinematics (center of pressure) and kinetics (load forces). Separately, other authors have shown the distinct sensorimotor memories between the different aspects of moment generation (Cole et al. 2008; Quaney et al. 2003). In the first study, it was shown that even after a static pinch task, grip forces transfer to the subsequent lift resulting in larger grip forces. The second study showed that this effect does not occur for load forces thus the authors conclude that the sensorimotor memory for load forces is less likely to be influenced by preceding tasks. Our results extend these findings and show the differential effect of transfer on learned manipulation of kinematics and kinetics. Specifically, there is a high level of representation of object torque that can only be assessed partially during generalization and is due to the modulation of kinematics and a failure of kinetics modulation unless moment generation favors the stereotypical larger finger kinetics.

An additional measure of transfer aside from the initial transfer trial could be to examine the rate of subsequent learning. In these instances, transfer would be characterized by increased rates of learning. From our results, both novel and transfer trials experienced stable roll reduction and moment generation by the third trial; i.e., there was not a change in learning rate for transfer trials compared to pre-transfer trials. Note that this is a very short time course of learning, that highlights the learning of object dynamics as opposed to the learning of how to generate compensatory moment. Thus, because learning is already so quick for novel trials, there is likely
a ceiling effect which might mean that observing a change in learning rates is not suitable in this current paradigm.

4.2 Effect of Adding or Removing Degrees of Freedom and Effectors on Generalization

Ecologically, our decision to use a smaller or larger number of degrees of freedom in grasping is strongly determined by the properties of the object to be grasped. It has been shown, in an object transportation task, that the decision to grip an object using two, three, four, or five digits unimanually, or 2 hands bimanually can be predicted by comparing the length and mass of the object to the anthropometric properties of the individual (Cesari and Newell 2000; 1999). For the present study, the grip width and mass of the object placed it between the 5 digit and 2 hand grasp configurations. Specifically, the relatively small grip width of 8 cm preferences a unimanual grasp while the larger weight of 1.27 kg biases the preference closer to a bimanual grasp. Thus, the object properties allow the examination of generalization between a unimanual and bimanual grasp. Additionally, by only using the fingertips, this generalization can be explored within the characteristics of a dexterous precision grasp (Feix et al. 2009; Feix et al. 2015). Our results of partial generalization when switching from a unimanual to bimanual grasp and from a bimanual to unimanual grasp show that generalization is less affected by a change in the number of degrees of freedom and effectors but more so by the intrinsic characteristics of each grasp type. Specifically, the greater ability of a bimanual grasp to generate moments using a large variety of forces and centers of pressure compared to a unimanual grasp where moment generation is characterized by larger finger load forces.

In the present study, generalization of the right hand was due to digit center of pressure modulation while left hand generalization was due to digit load force modulation. This could
indicate a possible effect of handedness on generalization. Previous studies have shown a
difference in neural control strategies linked to handedness (for review see (Sainburg 2005).
Specifically, it has been shown that the dominant hand is more efficient in torque generation
during reaching movements (Bagesteiro and Sainburg 2002). The degree of handedness has also
been shown to affect interlimb transfer (Chase and Seidler 2008). Thus, the difference in
interlimb control could have contributed to the different strategies of generalization between the
right and left hand. Most studies examining object grasping comparing between the dominant
and non-dominant hand have observed that grip forces are similar between both grasps (Rearick
and Santello 2002; Salimi et al. 2000). To the best of our knowledge, no studies have compared
the specific aspects of load force and center of pressure modulation between the dominant and
non-dominant hand. For the dynamics of the arm, a dynamic dominance hypothesis has been
proposed that suggests dominant control of trajectories with a non-dominant control of final
position (Sainburg 2002). Based on this hypothesis, partial transfer of load forces of the non-
dominant hand might be due to the feedback control of the non-dominant hemisphere controlling
load forces appropriately. To elaborate, when the right hand reaches for the device, trajectory
control relies more on feedforward mechanisms determining digit center of pressure. After
contact, feedback about digit center of pressure is used to control load forces as if the object were
novel, i.e. without transfer of torque information. For the left hand transfer trials, digit centers of
pressure are controlled as though the object were novel, however, feedback about digit contact is
used to modulate load forces to the object center of mass. However, more studies are needed to
determine the specific effect of handedness on the ability to generalize object torque information.

A previous study examining generalization through changing degrees of freedom showed
that adding or removing a digit resulted in full generalization through the transfer of moment
generation (Fu et al. 2011). In this study, the authors examined the transfer of torque information when generalizing between a two (thumb and index finger) and three (thumb, index, and middle finger) digit precision grasp. Post-transfer compensatory moments were similar to pre-transfer moments (target moment) when both adding and removing the middle finger. Although pre- and post-transfer moments were similar, digit center of pressure and load force difference differed depending on the number of fingers involved. The authors conclude that the full generalization was indicative of a high level representation of object torque while the ability to generate the same moment despite different digit kinetics and kinematics is similar to the concept of motor equivalence. This conclusion is similar to the findings of the present study in that generalization is due to the transfer of torque information that is then used to generate a compensatory moment through varying digit kinetics and kinematics. However, that study showed full generalization as shown by similar pre and post-transfer moments whereas our results of larger pre to post-transfer moments showed partial generalization. This difference is likely to be due to the difference in the number of degrees of freedom changed. Changing from a two-digit to a three-digit grasp and vice versa requires the adaptation of one additional degree of freedom whereas changing from unimanual to bimanual grasping requires not only double the number of degrees of freedom but also requires reconciling an additional effector. This added complexity adds to the difficulty of generalization. However, a high level representation should be able to compensate for this added change in degrees of freedom. A possible explanation for the partial transfer could be the inherent difference in unimanual and bimanual kinetic and kinematic control. The load force of the fingers during unimanual grasping are always larger than the load force of the thumb, while bimanual grasping does not show this same characteristic. This is arguably not the most efficient strategy, especially since depending on object center of mass, torque from digit kinetics may
counter the torque from digit kinematics. Thus, when changing from a unimanual to a bimanual grasp, repeating similar kinetic and kinematic strategy places a restriction on bimanual moment generation. As a result, the system chooses not to mimic the same strategy, but as a result, kinetic transfer fails. However, this could still be a more favorable strategy than repeating the same forces as the pre-transfer unimanual grasp. Specifically, if the object has a left center of mass, using the same load force modulation as the pre-transfer unimanual right hand would mean that the digits of the right hand exert a larger load force than the digits of the left hand. This immediately places a restriction on the ability to vary moment generation thus reducing the efficiency of the grasp. As a result, a partial generalization may be the preferred strategy because it allows both bimanual kinetics and kinematics to assist in moment generation to counter object torque. However, more studies exploring the sequential changes in the number of degrees of freedom are needed before this can be confirmed.

The difference in compensatory moment generation between unimanual and bimanual grasping suggests that the optimal strategy or strategies are determined by the characteristics of the grasp type. It has been shown that grasp characteristics are chosen to favor the comfort of the end-state (Cohen and Rosenbaum 2004; Rosenbaum and Jorgensen 1992; Rosenbaum et al. 1996). Based on this research, comfortable final postures of hand-object interactions are favored more than comfortable initial postures. How moment generation is controlled and whether or not the modulation of load forces and centers of pressure are modulated to attain some end-goal comfort is an interesting question. We have shown through this study and others that there exists large individual differences and inter-trial variability of force and center of pressure modulation. A possible explanation for this would be the adaptation to noise within the system leading to variability in digit contact and center of pressure. For unimanual grasps, it is likely that the larger
load forces of the fingers are an inherent feature to control for the biomechanics of unimanual grasping. For example, the position of the thumb is typically in line with the index or middle finger (Latash and Zatsiorsky 2009). Thus, center of pressure modulation favors wrist supination. Larger finger load forces are thus underwritten to control for this, by favoring wrist pronation. When a compensatory moment is needed to be generated, depending on if the end-goal was favoring wrist pronation or supination, load forces or center of pressure are controlled accordingly. For bimanual grasping, load forces and centers of pressure are modulated together in favor of the desired direction of compensatory moment. However, our results indicate that center of pressure modulation contributes more to moment generation than load force modulation (Fig 12). The narrow grip width could account for this characteristic. Because of the narrow grip width (8 cm), in order for load forces to generate torque, load force difference needs to be much larger than if the grip width was wider. As a result, the end-state comfort effect favors smaller load force differences while relying on center of pressure modulation to generate the compensatory moment. Further studies exploring this specifically could reveal a deeper understanding into the flexibility of moment control.

The transfer of motor skill learning is an important aspect of motor control and understanding the mechanisms of transfer has wide ranging implications (for review see: (Magill and Anderson 2007). Aside from the conditions of transfer that are specific to grasping and manipulation as outlined in table 1, the transfer of motor learning has been examined in numerous other ways. The transfer of sport skills has already been extensively investigated (for review see: (Issurin 2013), more recently, with the advent of new technology, learning transfer has been studied for virtual environments (for review see: (Levac et al. 2019), and with brain-machine interfaces (for review see: (Azab et al. 2018). With regards to the transfer of motor
abilities, transfer has been shown to be affected by the skill level of the performer, various neural and physiological considerations, and the diversity of practice. However, the precise mechanisms of transfer are not yet fully understood. On an individual anatomical level, transfer has been shown to be greater for proximal tasks compared to distal tasks (Aune et al. 2017). Thus, this could be a possible explanation for the lack of transfer effects for many grasping tasks that require torque control such as ours, where the end effectors lie distal to the body. Furthermore, it may underlie a difference between the control of object weight and that of object torque leading to the difference in generalizability. Our current finding of partial generalization of torque information across changing effectors adds to this and shows the difference in kinematic and kinetic control with regards to transfer.

4.3 Theoretical Framework for Generalization Across Multiple Effectors

The generalizability of weight information that can be transferred after object translation, rotation, or contralateral hand switch has suggested that weight information is stored as a high (task) level of representation (Albert et al. 2009; Chang et al. 2008). In contrast, the failure of learned manipulation to generalize after object rotation or contralateral hand switch has been used to suggest that learning of object torque occurs in an effector specific manner (Edin et al. 1992; Salimi et al. 2003; Salimi et al. 2000). Thus, the ability to generalize object weight dynamics while failing to generalize object torque suggests separate models of control (Gordon and Salimi 2004; Ingram et al. 2017; Wolpert and Kawato 1998). Our study shows that though not full, partial generalization occurs after learned manipulation of object torque suggesting that an effector specific explanation is insufficient.

Generalization of learned movement can also be examined based on the concept of coordinate frames/systems. Specifically, coordinate reference frames refer to intrinsic systems as
those associated with the coordinate frame of the body (joint/body-based) while extrinsic systems comprise the dynamics of the object (object/environment-based). Early work on the adaptation and generalization of reaching movements has suggested that learning and generalization of visuomotor rotations (Krakauer et al. 1999; Krakauer et al. 2000) and interlimb transfer (Criscimagna-Hemminger et al. 2003) occur in extrinsic systems while force field learning occurs in intrinsic systems (Shadmehr and Moussavi 2000). However, more recent work suggests that learning within a task may occur in both coordinate systems (Bays and Wolpert 2006; Berniker et al. 2013; Berniker and Kording 2008; Brayanov et al. 2012). Bays and Wolpert (2006) suggested that when learning a movement, kinematic trajectories are represented extrinsically while forces are represented intrinsically. These findings have similar implications for the neural substrates and the coordinate frames that different cortical areas (such as the primary motor cortex, premotor cortex, and posterior parietal cortex) represent learning in (Brayanov et al. 2012; Criscimagna-Hemminger et al. 2003). In an attempt to reconcile the need to examine generalization in both intrinsic and extrinsic coordinates, Berniker and Kording (2008) tested a model that theorizes that learning occurs through the estimation of the sources of errors. The authors propose that when a movement error is experienced, a decision is made as to whether that error was due to the environment (e.g. heavier ball than expected) or to the body (e.g. not enough force applied). Once the nervous system assigns and attributes error sources to either the environment (extrinsic) or the body (intrinsic), it generates a weighting ratio of the two sources that is then used in the generalization task. Indeed, it has been shown that the internal representation of visuomotor rotations does not generalize in fully intrinsic or extrinsic coordinates, but instead, generalization occurs in a combination of intrinsic and extrinsic coordinates (Brayanov et al. 2012). The authors suggest that the transfer of this combination
depends on the distance across both coordinate spaces. To further examine the effect of reference frames, the contralateral hand transfer of learned movement through force-fields was observed by altering the intrinsic and extrinsic coordinate frames (Carroll et al. 2015). Specifically, the authors had participants learn reaching movements made in the sagittal or transverse plane. When force-field learning was in the sagittal plane, contralateral transfer maintains the same extrinsic and intrinsic coordinates. When learning was in the transverse plane, the intrinsic coordinates were different. Results of that study showed that learning generalizes more (but only partially) when transfer maintains the same extrinsic and intrinsic coordinates. Thus, the congruency of coordinate frames before and after transfer affects the ability to generalize. Partial generalization between unimanual and bimanual reaching movements was also shown when learning was in a fixed direction (Nozaki et al. 2006) but full when learning to reach towards varying targets (Wang et al. 2013). These studies have shown that after transfer, learned information is only partially accessible by the hand that did not experience the learning directly. This is similar to the present study, further showing that transfer when switching from one grasp condition to another is only partial. Additionally, even though learning in the present study was only in one direction, the partial transfer could be attributed to the fact that at least four digits of one hand would have experienced the object torque before transfer. Thus, unlike after contralateral hand switch, when switching from unimanual to bimanual grasps, some digits of the prior grasp type (index, middle, ring, and little finger) maintain the same object-body reference after transfer.

Using coordinate reference frames to explain learning of object torque information seems to suggest, from the lack of transfer after rotation or hand switch, that learning of object torque is represented in intrinsic coordinates or that the system attributes larger sources of error to the
body thus the generation of compensatory moment is specific to the digits used. The results of the present study showing partial generalization offer further insight into these processes. Specifically, if the error (large peak roll) on initial trials is attributed mainly to the body (grasp that was used), the nervous system mainly makes corrections on that particular grasp type. Thus, when transferring to the new grasp type, there is partial generalization because some elements of the previous grasp type are used in the new grasp. For example, when lifting the left center of mass object with the right hand for the first time, errors could be attributed to the right hand not applying the appropriate force and center of pressure modulation. After transferring to a bimanual grasp, only the right hand is able to make corrections for the object torque thus resulting in the partial transfer. Thus, partial generalization is seen because when transferring between unimanual and bimanual grasps, only the intrinsic coordinates conflict. However, this does not fully explain the transfer of center of pressure and not load forces. As mentioned, it has been suggested that kinematic trajectories are represented in extrinsic coordinates while forces are represented in intrinsic coordinates (Bays and Wolpert 2006). Thus, since digit centers of pressure are kinematic variables, their learning in extrinsic coordinates implies that the learning is specific to object torque and thus could explain transfer. In contrast, since load forces are represented intrinsically, their modulation is specific to the grasp type employed and thus switching to a new grasp type does not result in transfer. Transfer to the left hand would thus be driven by the inherent properties of kinetic control (larger finger load forces) and since the object dynamics (left center of mass) favor this property, positive transfer is seen. This could be a possible explanation for why generalization is only partial and due to the appropriate partitioning of digit centers of pressure after right hand and bimanual transfer, and due to the modulation of load forces after left hand transfer.
On top of the intrinsic and extrinsic coordinate frames, an aspect of sensorimotor control that may influence generalizability is related to the use of sensory cues. Prior to contact with the object, during the reach-to-grasp phase, digit kinematics are molded to the contours of the object’s shape (Santello and Soechting 1998; Winges et al. 2003). Additionally, during the reach visual and proprioceptive cues assist in the formation of finger span to object size (Santello and Soechting 1997). Thus, digit placement during learned manipulations is planned and controlled during the reach. Due to the noise of sensory cues and motor commands prior to contact with the object, estimation of contact points and actual contact points often differ (Shibata et al. 2013; Shibata et al. 2014). Consequently, this mismatch might affect planned digit forces. However, previous studies have shown that digit forces are controlled and modulated once sensory feedback of digit placement is obtained after object contact (Mojtahedi et al. 2015; Shibata and Santello 2017; Toma et al. 2019). Because digit center of pressure can be sensed from visual, tactile, and proprioceptive cues (even in the event of an erroneous efference copy), it has been suggested that center of pressure and digit placement are controlled explicitly. Load forces, being modulated through feedback of digit center of pressure are controlled more implicitly. This distinction could be an additional explanation for the transfer of digit center of pressure but not load forces. The explicit control would mean that after transfer, the sensorimotor system would attempt to match the same center of pressure as the pre-transfer trials. The implicit load forces are less able to be transferred and errors in matching the centers of pressure may have contributed to the lack of load force modulation.

4.4 Limitations and Future Work

Aside from the thumb during unimanual grasps, our study examined the combined forces and equivalent center of pressure of all the digits. Although the digits work synergistically to
generate the compensatory moments, examining individual digit forces and centers of pressure would provide more insight into the control of the kinetics and kinematics of grasping. This could be achieved through subsequent studies that are able to examine individual digit forces and placements while also keeping the grasping unconstrained. Additionally, even though the purpose of the study was to examine dexterous manipulation, the functionality of the bimanual grasp may be limited. When interacting with a similar object, a full palmar grasp might be the more preferred way to grasp the object. The purpose of keeping the current grasp points isolated on the distal fingertips maintains this similarity between unimanual and bimanual grasping but the functional aspect of changing the grasp type might be affected. As mentioned above, the choice of grasp type is determined by the size and weight of the object (Cesari and Newell 2000; 1999). However, the authors did not specify whether the bimanual grasp was a palmar grasp or a dexterous digit grasp. Whether or not there is any difference in these two types of bimanual grasping is still to be understood. The modulation of center of pressure can be achieved in two ways. The first is by directly changing digit placement, the second involves maintaining the same digit placement but modulating the contribution of the individual digit centers of pressure. Our study found that modulation of center of pressure was not due to actual changes in digit placement. This is different from our previous finding showing modulation of hand placement to center of pressure (Lee-Miller et al. 2019). However, in that study, participants used a bimanual palmar grasp and grasped a larger box. How the height of the grasp surface affects the decision to modulate center of pressure is still not known. Additionally, all our participants were right-handed. Handedness might influence the pattern of generalization and transfer of object information. Indeed, our results that right hand transfer was due to center of pressure modulation while left hand transfer was due to load force modulation seems to indicate that possibility.
Though we have controlled for the possible influence in the direction of transfer by examining transfer from the right and left hand to a bimanual grasp and vice versa, we do not know if this would generalize to predominantly left-handers.

In this study, object torque was modified by changing the center of mass from the left and the right. Aside from the direction, the overall torque was the same. Whether or not our findings can generalize to different torques is yet unknown. We did not find that digit load forces were modulated to prevent object roll after transfer. Whether this is due to the magnitude of object torque would be an interesting question to examine. Additionally, our study focused on the sensorimotor experience of object torque as opposed to pre-lift visual cues of object torque. Thus, our use of a visually symmetrical box with an asymmetrical center of mass. Aside from boxes whose contents might shift to one side, such objects are not common and as such, the ecological validity may be limited. It should be noted that, as reviewed, whole hand grasps with four fingers on one side and the thumb on the other, have to inherently account for torque during dexterous manipulation even when the center of mass is symmetrical (Appendix A).

Our study has examined generalization when switching from a 5-digit unimanual to a 10-digit bimanual grasp. We chose grasp type based on hand and object size and weight. The small object size (8 cm grip width) favored a unimanual grasp while the larger object weight (1.27 kg) made a bimanual grasp more favorable. If participants placed more emphasis on grip width, the bimanual grasp would force participants into an unnatural configuration. This might limit our understanding of generalizability. Previously, generalization was shown when switching from a 2-digit to a 3-digit grasp. Examining generalization when switching in incremental increases in the number of degrees of freedom might further reveal information about our ability to generalize learned manipulation. Our finding of partial generalization may be due to the
complexity when doubling the number of degrees of freedom and effectors. Future studies could examine generalizability by changing the number of degrees of freedom while keeping the number of effectors the same. This can be accomplished by switching between 2 and 5-digits during a unimanual grasp or switching between 8 and 10-digits during a bimanual grasp.

Similar to Zhang et al (2010) that showed learning of digit center of pressure after multiple rotations, it would be interesting to examine how learning would improve after multiple rotations. Additionally, more insight could be gained into the learning and generalization of object manipulation when comparing generalization after learning in single or multiple contexts. For example, would learning generalize if the initial trials of one grasp type involved lifts with the object rotated and grasped in a variety of angles? Indeed, as mentioned above, it has been shown in a reaching study, that unimanual to bimanual generalization is partial when trained in a fixed direction, but full when trained in multiple directions (Takiyama and Sakai 2016).
Conclusion

The present study showed partial generalization of dexterous learned manipulation when switching between unimanual and bimanual grasping through the transfer of torque information about the object. This partially supported our first hypothesis that increasing the number of degrees of freedom would lead to full generalization but failed to support our second hypothesis that decreasing the number of degrees of freedom would not generalize. Additionally, supporting our third hypothesis, we have shown that a whole hand contralateral switch does not lead to generalization.

Initial lifts of the visually symmetrical object resulted in large peak rolls due to the object’s asymmetrical center of mass. On subsequent lifts, a compensatory moment was generated that countered object torque, stabilizing by the third lift. This compensatory moment was due to two torque components generated from digit kinetics and kinematics. Learned manipulation of these two components differed between unimanual and bimanual grasps. For unimanual grasps, the torque component generated from digit load forces almost always facilitated wrist pronation. This was due to the larger load forces of the four fingers compared to the thumb. For bimanual grasps, digit load forces generated torque that countered object roll by applying more load force on the side closer to the object’s center of mass. The second torque component was generated through modulation of digit kinematics in the form of the equivalent center of pressure. For unimanual grasps, if the center of mass was on the thumb side, center of pressure of the thumb would be higher than the equivalent center of pressure of the other fingers. If the center of mass was on the side of the fingers, this difference would be reduced to a collinear center of pressure. For bimanual grasps, similar to digit load forces, object roll is
countered by applying a higher equivalent center of pressure on the side close to the object’s center of mass. After unimanual to bimanual transfer, moment generation is retained but of a smaller magnitude resulting in a reduction of peak rolls from novel trials that are still larger than learned trials. Moment generation on these bimanual transfer trials was due to the torque generated by modulating digit centers of pressure. Load forces were only modulated after subsequent trials. After bimanual to unimanual transfer, compensatory moments were generated but the magnitude of these were too small to result in reductions of peak rolls. For the right hand, moment generation on transfer trials was due to the modulation of digit centers of pressure. Specifically, transfer was only seen when the center of mass was on the thumb side, which resulted in higher thumb center of pressure than that of the fingers. For the left hand, when the center of mass was on the side of the fingers, moment generation was due to larger finger load forces. Thus, we conclude that there is a high level of internal representation for object torque that can be used in generalization across multiple degrees of freedom and effectors. However, the ability of the sensorimotor system to generate the required moment to counter object torque is driven mainly by digit kinematics. Additionally, we have also shown the lack of transfer after whole hand contralateral switch.
References


Bays PM, and Wolpert DM. Actions and consequences in bimanual interaction are represented in different coordinate systems. Journal of Neuroscience 26: 7121-7126, 2006.


Buckingham G, Cant JS, and Goodale MA. Living in a material world: how visual cues to material properties affect the way that we lift objects and perceive their weight. J Neurophysiol 102: 3111-3118, 2009.


Johansson RS, and Westling G. Coordinated isometric muscle commands adequately and erroneously programmed for the weight during lifting tasks with precision grip. 1988b.


Lashley KS. Basic neural mechanisms in behavior. Psychological review 37: 1, 1930.


APPENDIX A

Literature Review: General Feature and Generalization: An Understanding of Grasping across Multiple Degrees of Freedom

Introduction

An understanding of our ability to use our hands has far reaching implications in a multitude of varying domains; from evolution to robotics. The ability of the human hand to grasp and manipulate objects, coupled with the cognitive ability to enable advanced use, stands out as a uniquely human trait (Key and Lycett 2011; Rolian et al. 2011; Schieber and Santello 2004). It is precisely this trait of intentional grasping and object manipulation (“prehension”) that places the hand at an optimal position for the study of sensorimotor integration in the brain. The past two decades has seen significant advances in our understanding of the hand as a sensorimotor system while also shedding light on the numerous gaps that still exist (Fu and Santello 2018). For example, only recently have we begun to attempt to reconcile the combination of kinematic and kinetic aspects in the motor control of the hand’s prehensile capabilities (Santello 2018). This kinematic kinetic continuum forms the basis of a general feature of grasping and manipulation. The next step towards an understanding of the sensorimotor control of hand-object interactions is determining if the feature, learned in one context, can be transferred or generalizes to another context (for review see: (Shadmehr 2004). This would provide an understanding as to whether the learning lies at a low, effector-specific, level of control or on a higher level. In this literature review, we first summarize studies that have added to our understanding of hand-object interactions and lead towards a general feature of grasping and object manipulation. Next, we
move on to uncover how and under what contexts does learned manipulation generalize and why, and suggest possible directions for future research to fill in the gaps of our understanding.

**Kinematic and Kinetic Control in Grasping**

The inherent sequential actions of grasping and manipulation provides a clear opportunity to examine kinematic and kinetic control of the movements and has been described extensively by dividing these movements into phases (for review see (Johansson and Flanagan 2009). The first is the reach phase, which ends when the digits make contact with the object. This begins the pre-load phase where grip forces begin to increase prior to any increases in lift forces. Soon after this, lift forces are increased in parallel to the increasing grip force, signaling the load (or loading) phase. Once the lift forces are enough to overcome object weight, lift onset occurs. Subsequent phases depend on the task goals and include the hold, transport, replace, and unload phase. Tactile feedback is used throughout the movement to track and monitor the various phases (Johansson and Westling 1984). Kinematic and kinetic sequencing can thus be understood by examining their control in accomplishing the goals of each phase.

Kinematically, grasping can be understood to involve the movement and motor control of the joints and segments that make up the arm and hand. This can be seen in the involvement of proximal arm segments during reach-to-grasp movements (Jeannerod 2009), molding of the digits of the hand to the shape of the object (Santello and Soechting 1998; Winges et al. 2003), and choice of contact point from geometric cues (Fu and Santello 2012; Gilster et al. 2012; Voudouris et al. 2010) and task goal (Ansuini et al. 2008; Ansuini et al. 2006; Craje et al. 2011). From a kinetic point of view, in order to successfully lift an object off a surface, during the pre-load and load phases, the object needs to be appropriately gripped while forces must be applied to the load that overcome the object’s weight (for review see: (Johansson and Cole 1992)).
Furthermore, grip and lift forces are controlled to minimally prevent the object from slipping through the digits after lift onset (Westling and Johansson 1984). This is known as the safety margin and is the value at which the ratio of grip to lift force is just enough to overcome the coefficient of friction between the digits and the contact surface (Cadoret and Smith 1996; Edin et al. 1992). Once contact with an object is made, tactile afferents in the glabrous receptors on the fingertips send information about the texture of the surface to the central nervous system to control the safety margin (Johansson and Westling 1984). Most of this understanding was achieved by examining how participants grasped objects using the two-digit precision grip, where the object is held between the thumb and index or middle finger. However, a similar control of forces to the contact surface can also be found in whole hand grasping (for review see (Latash and Zatsiorsky 2009). Aside from vertical lifts, establishing the appropriate safety margin has also been seen in horizontal movements (Flanagan and Wing 1993), and weight perturbations during lifting (Johansson et al. 1992).

**Kinematic and Kinetic Coupling in Torque Generation**

Aside from weight and texture, grip forces are also controlled to object torque. For example, when grasping one end of a long horizontal column to lift it horizontally, to prevent the object from rolling, grip force is increased the further the object was gripped from its center of mass (Wing and Lederman 1998). This increase in grip force is done in anticipation of a change in object torque (Johansson et al. 1999). Additionally it has been shown in a precision grip task when the center of mass of an object was closer to either the thumb or index finger side, a similar torque is generated to resist object roll (Salimi et al. 2000). Specifically, the lift forces of the digit on the side of the center of mass was larger than the other digit. This generation of torque to oppose object center of mass has also been shown to be elicited by visual cues of object
geometry (Fu and Santello 2012). A similar finding was shown in whole hand grasping (Rearick and Santello 2002; Reilmann et al. 2001; Santello and Soechting 2000).

The generation and control of torque during grasping and object manipulation, because of its definition as the cross product between position and force, naturally involves the coupling of kinematic (position) and kinetic (forces) components. This generation involves the control of digit forces and moment arms (Zatsiorsky et al. 2002; Zhang et al. 2010). Specifically, as each finger exerts grip and lift forces, it generates a torque where the pivot is the midpoint between the digits and the moment arms are the respective digit centers of pressure and the width of the object (Figure 1). Embedded within the moments are the safety margin and the required forces to lift the object from the table (Westling and Johansson 1984; Zhang et al. 2011). Despite the coupling of kinematic and kinetic components during grasping, most early work examined grasping while constraining the digit kinematics by restricting digit placement to one contact point. Thus, when examining grasp control through torque generation, most of the studies reviewed above constrained digit placement onto single digit contact force transducers. In doing so, digit centers of pressure were predetermined, and control of torque generation was determined solely by forces. In experiments examining digit placement for torque generation during object grasping, it was shown that digit position was modulated in anticipation as the desired torque to be generated (Lukos et al. 2007; Lukos et al. 2008). Additionally, other examples of how the task goal affects digit placement include grasp height being influenced by the height of the target position (Cohen and Rosenbaum 2004), and varying digit placement in whole hand grasping depending on whether the object is lifted vertically, lifted to pour out its contents (Craje et al. 2011), passed to someone else (Ansuini et al. 2008), or placed in a specific slot (Ansuini et al. 2006). This understanding is in line with a previously suggested prehension
strategy known as the principle of superposition that was initially used in robotic hand control (for review see: (Latash and Zatsiorsky 2009; Zatsiorsky and Latash 2004). Based on this principle, the central nervous system controls force and torque generation in order to satisfy two commands; 1) avoid slippage during grasping, 2) prevent the object from tilting if not necessary.

Figure 1: Torque control in dexterous manipulation. Free body diagram of the forces and placement required to lift an object.

Anticipatory Torque Control as a General Feature of Precision Grasping

Clearly there was a need to examine the combined influence of kinematic and kinetic control on grasping and manipulation. Using a precision grip (thumb and index finger) task, Fu et al (2010) showed that when the contact surface was unconstrained, forces and digit placement are controlled in a continuum to generate torque. In order to overcome the asymmetrical object center of mass to prevent object roll, the hand needed to produce a counter torque or compensatory moment prior to lift onset. With the unconstrained grip surface, it was shown that
digit placement and forces were indeed modulated to the desired moment. Thus, successful (no roll) grasping and manipulation of an object with an asymmetrical center of mass occurs through the 1) partitioning of digit placement by placing the digit on the side of the center of mass higher, and/or 2) applying larger load force by the digit closer to the center of mass. When lifting an object that is geometrically symmetrical but has an asymmetrical center of mass, large rolls occur on the first lift because participants expect the object to be symmetrical. Thereafter, digit force and placement modulation begins to be employed by the 3rd or 4th lift (Zhang et al. 2010). The modulation and forces and placement were done in an anticipatory manner, i.e. before lift-off. Additionally, it was found that on top of force and placement modulation, digit forces and placements showed strong negative covariation (Fu et al. 2010). Thus, in order to generate the desired compensatory moment, a digit placement strategy could be employed where digits are placed non-collinearly while digit load forces are similar, or a digit load force strategy could be employed where the digits are placed collinearly while digit load forces differ. Alternatively, the compensatory moment could be generated from any combination of these two strategies and thus lies on a continuum of kinematic and kinetic control (Santello 2018).

An interesting aspect of the covariation of forces and placement is that a stable compensatory moment was found to be generated despite trial-to-trial variability in forces or placement (Fu et al 2010, Zhang et al 2010). It has been further shown that sensory feedback of digit placement after contact is used to modulate digit forces in order to generate the desired moment (Davare et al. 2019; Mojtahedi et al. 2015; Toma et al. 2019). The generation of a stable outcome despite variation in its components is similar to the concept of motor equivalence. Motor equivalence is the generation of a unique output despite the use of different variables or effectors (Bernstein 1966; Lashley 1930). Motor equivalence has been shown in handwriting.
where an individual’s handwriting or signature remain invariant even when using effectors other than their hand such as their mouth or feet (Wing 2000). It was also shown that finger span between two digits can be kept the same despite different joint angles and kinematics (Cole and Abbs 1986). The principle of motor equivalence is thus a concept that can be used to describe the trial-to-trial variability of digit load forces and placement despite a stable trial-to-trial compensatory moment. Turvey (1990) postulated that motor equivalence could be a strategy employed by the sensorimotor system to reconcile the large number of degrees of freedom within the body. Given the large number of joints, muscles, and segments in the body, the system must devise a way to control these degrees of freedom while maintaining stable performance and minimizing effort. Motor equivalence allows variability in the degrees of freedom, and noise, to exist while achieving stable performance.

If anticipatory torque control through the generation of moments from digit force and position modulation is a general feature of precision grasping, these characteristics should be found in most if not all of the variations of the precision grip. Variety within precision grasps include the number of fingers used and the curvature of the object. On objects with a relatively flat grip surface, torque generation has been shown in two-digit (Fu et al. 2010; Lee-Miller et al. 2016), three-digit (Fu et al. 2011; Fu and Santello 2012), and five-digit (Marneweck et al. 2016; Naceri et al. 2017) precision grasps. Specifically, successful manipulation involves generation of a compensatory moment through the modulation of digit forces from feedback of digit position after contact. The interaction of the kinematics and kinetics is such that a stable moment is achieved despite trial-to-trial variability of digit position and forces as seen through the covariation of forces-to-position. Even though evidence would point to the same feature existing in four-digit grasps, further research could be done to confirm this. Additionally, we have
recently shown that the pattern is seen in a bimanual palmar precision grip task (Lee-Miller et al. 2019). Thus, anticipatory torque generation through the modulation and covariation of digit force and position is a general feature of object manipulation during precision grasping.

As mentioned, almost all the studies used to obtain this general feature of grasping employed the precision grasp. However, there are many different variations of grasp types that humans can perform. Given the larger number of bones, joints, and muscles in the hand, it is easy to see how these many degrees of freedom can give rise to multiple grasp types (Cutkosky and Howe 1990; Gracia-Ibáñez et al. 2018). Recently, an effort was made to quantify a taxonomy of human hand grasp types (Stival et al. 2019). The taxonomy divided grasp types by various elements, for example, thumb abduction or adduction, whether the palm is involved (power grip), and whether the grasp involves fingertips or the entire pad. Using these elements, the authors identified over 30 different grasp types. It would be interesting to examine if the general feature of precision grasping would generalize to the other different grasp types.

**Differing Characteristics of the General Feature across Multiple Effectors**

Even though the main characteristics of force and center of pressure modulation and force-to-center of pressure covariation exist across the above-mentioned grasps, the control of the degrees of freedom to achieve these characteristics are slightly different, especially when examining across varying object centers of mass (Figure 2). For two-digit grasping, as mentioned above, torque generation is achieved through the larger modulation of digit forces and position/center of pressure on the side of the torque direction while zero torque can be accomplished through equal load forces and collinear digit placement (Figure 2A).
Figure 2: General feature across different grasp types. Distribution of digit placement and load forces on an object with asymmetrical center of mass. Thicker arrows represent larger load forces. A. Two-digit grasp. B. Three-digit grasp. C. 5-digit whole hand grasp. D. Bimanual grasp.

In three-digit grasps, larger forces and centers of pressure are applied similarly (Figure 2B). However, with the unequal distribution of digits on each side, digit placement is such that thumb placement is never below the placement of the middle finger. For example, Fu et al (2011) found that when the object has a left center of mass the thumb is placed in-line with the index finger (Fig 2B top), while for a right center of mass object, the thumb is placed along the midline between the index and middle fingers (Fig 2B bottom). Thus, the resultant center of pressure difference is influenced by the number of fingers used. This becomes clearer when observing a whole hand five-digit grasp.

Using a five-digit grasp, we have shown that compensatory moment generation is generated through digit kinematics where the thumb center of pressure is always higher than the
total center of pressure applied by all four fingers on the other side (Marneweck et al. 2016). Additionally, the load forces are modulated such that the combined load force of the four fingers is always larger than the load force of the thumb (Fig 2C). Although the study was one of the first studies to show this, mostly due to the unconstrained digit placement, it had been shown previously that depending on the object properties, thumb load force can even be negative (Reilmann et al. 2001). It is possible that the biomechanical properties of the whole hand during a precision grip could give rise to this characteristic. For example, in a five-digit precision grip, the end state comfort (Cohen and Rosenbaum 2004) effect could result in the higher thumb center of pressure. Additionally, the forces generated by the thumb might rarely exceed the forces of the four fingers thus leading to an accommodation of digit placement to compensate for this. However, the reason for this unequal distribution of forces, even during the grasping and lifting of a symmetrical object, is yet to be determined.

In unimanual grasping, the anatomy of the hand is such that force produced within one digit causes force production in other digits (Schieber et al. 2001). This interdependence has been explored in various theories of hand control such as synergies (Santello et al. 2016), and enslaving (Zatsiorsky et al. 2000). Thus, grasping and object manipulation must take into account these anatomical characteristics of the hand. In bimanual grasping, the two hands are not as anatomically linked as the digits of the individual hands. That the general feature of grasping exists even in bimanual grasps might point to a certain robustness of the feature and show that it is not merely a result of the interdependence of the fingers. From our study mentioned above, we found that in terms of the general feature of torque generation through force and position modulation, bimanual grasping is similar to two-digit grasping (Lee-Miller et al. 2019). With bimanual grasping, the left and right hands act in similar ways to the thumb and index finger in
two-digit grasping (Fig 2D). Specifically, the hand that is on the side that corresponds to the object center of mass, is placed higher and exerts a larger load force.

Overall, the general feature of object manipulation is seen in multi-digit and multi-hand grasps, while the way in which the torques are generated differs depending on the grasp configuration.

**Generalization of the General Feature of Forces and Torques**

In order to apply the general feature of appropriate torque to successfully grasp and lift an object, we need to have an understanding of the internal properties of the object, such as its weight and center of mass. Prior to any physical interaction with the object, we rely on sensory cues (e.g. vision) and previous sensorimotor experiences to estimate these internal representation of object properties (Gordon et al. 1991; Jenmalm and Johansson 1997; Krakauer et al. 2006; Lee-Miller et al. 2016; Lukos et al. 2008). This enables the dynamics of object manipulation to be predicted and controlled before even grasping the object. Successful manipulation thus involves the generalization of learned manipulations, of familiar objects, to the sensory estimates of the object to be lifted. Sensorimotor experienced gained thereafter can be used to update the existing representations. We will now examine what visual sensory cues have been shown to enable successful manipulation, how feedback affects subsequent performance, and the scenarios that have shown generalization of learned interactions to multiple contexts and suggest potential areas of future research to fill in the existing gaps.

**Generalization of Visual Cues enable Anticipatory Control**

We have already mentioned how visual cues of object shape are used to control finger span and molding during the reach phase (Jeannerod 1986; Santello and Soechting 1998; 1997; Winges et al. 2003). It has also been shown that when lifting objects of different sizes, grip and
load forces are scaled according to the expected weight of the object from visual size cues (Gordon et al. 1991). Scaling occurs during the load phase before object lift-off. Larger objects result in larger grip and load forces and peak force rates. This scaling to object size occurs even without explicit knowledge of object size (Cole 2008). Cole (2008) showed that when lifting a slightly smaller bottle after having previously lifted a larger one, participants scaled their forces to the smaller bottle even though they did not notice a difference when asked verbally.

Additionally, visual cues can also be used to identify familiar objects to allow the retrieval of prior representations for appropriate grasp control (Gordon et al. 1993). During the course of our everyday grasping experience, we form representations of the expected weight of certain materials which can then be used to predict the weight of objects made with those materials (Buckingham et al. 2009). When given similar sized boxes but made with different materials (plastic, wood, metal), participants scaled their forces to the expected weight of the boxes showing that we possess certain priors aligned to the experiences weight of different materials. Thus, in order for size and material cues to allow us to successfully predict object weight, we must have certain priors about the properties associated. To further examine the use and update of priors and the interaction between size and material cues, the authors in (Baugh et al. 2012) designed an experiment where participants lifted wooden blocks that had either a plastic or metal cover. On the first lift, forces were scaled in anticipation of the cover material. On subsequent lifts, forces were scaled to the new weight of the boxes. When asked to lift larger boxes, forces were scaled higher but still in line with the expected weight class of the box. They conclude that we use priors to predict object properties and that when faced with new objects, new priors are formed that can be used for further manipulation. In addition to visual size and material cues, visual cues of surface curvature can also be used in grasp control (Jenmalm and Johansson
When faced with upwards or downwards sloping surfaces, the authors showed that participants scaled their forces to the expected curvature prior to contact.

In terms of the general feature of torque control, it has been shown that visual geometric cues can be used to obtain an understanding of the internal torque of the object (Fu and Santello 2012; 2015). Using an L-shaped and a U-shaped object where the grasp surface is the vertical arm of each object, participants were able to use the geometric cues to apply compensatory moments on the first lift. However, the ability of these shape cues to elicit successful performance varied. On the first lift of the L-shaped object, compensatory moment was applied in the appropriate direction, but the magnitude was too small to completely compensate for object torque thus resulting in object tilt/roll. Only on lifting the U-shaped object did participants apply a compensatory moment in the appropriate direction and magnitude. Thus, object torque is not as easily predicted and internally represented as weight. It has also been shown that when comparing between the use of verbal and visual cues, only visual geometric cues result in a reduced object roll (Salimi et al. 2003). Additionally, when the object geometric cue and density (center of mass) cue differ, participants are unable to apply an appropriate compensatory moment even though they had explicit understanding of the object’s center of mass (Craje et al. 2013). To explore this further, and with unconstrained contacts, we examined the effect of congruency between visual geometric and density cues (Lee-Miller et al. 2016). The experiment employed three objects, an inverted-T shaped object, and two L-shaped objects. Visible metal and plastics weights were placed on the objects such that the inverted-T was geometrically symmetrical with asymmetrical density distribution. Both the L-shapes were geometrically asymmetrical, but one had an asymmetrical density and the other a symmetrical density. We found that only when the geometric cues indicated and were congruent with the density cues did participants apply a
compensatory moment. Similar to Fu and Santello (2012) this compensatory moment was in the appropriate direction but inappropriate magnitude. In both other cases, when geometric and density cues were incongruent, participants lifted the objects as though they were symmetrical.

Overall, visual cues aid in the extraction of object properties by the central nervous system that allow the appropriate control of forces and torques to grasp the object. In this sense, our prior sensorimotor experience allows us to generalize and form an internal representation of the properties of the object to be grasped from visual cues of the object.

**Sensorimotor feedback updates Generalization Models**

Without prior experience with an object, sensory cues are used to generate internal representations of object properties. After experience with the object, sensorimotor feedback is used to update the internal representations for subsequent movement (for review see: Wolpert et al. 2011). Sensorimotor experience can even override any perceptual errors (such as in the size-weight illusion) that existed prior to lifting the object (Buckingham and Goodale 2013; Flanagan and Beltzner 2000; van Polanen and Davare 2015). There is still some debate as to the interaction between initial sensory cues and sensorimotor experience. For example, it was shown that the weighting of visual cues was reduced after sensorimotor experience was gained (Mon-Williams and Murray 2000). However, as we have seen, Baugh et al (2012) showed that visual size cues are used together with sensorimotor experience equally to generate new internal representations of object properties. Our study (Lee-Miller et al 2016) showed that unreliable visual cues are weighted low compared to sensorimotor memories. Additionally, sensorimotor experience need not directly involve the object in order to elicit these updates. For example, merely pinching a device can influence the grip force on another object (Quaney et al. 2003).

The authors asked participants to pinch and squeeze a static device with a certain force. Then the
participants lifted an object. Grip forces were larger when the prior experience was the pinch. They argue that force control can be influenced by actions alone, instead of task performance. Cole et al (2008) used a similar protocol but instead of pinching, participants exerted an upwards force. They showed that the prior upwards force did not affect subsequent load forces. They extend the findings and argue that grip force is less outcome based and thus can be influenced by sensorimotor actions whereas load forces directly involve the task performance and sensorimotor experience must reflect the task to be useful. Regardless of the specific interaction, sensorimotor experience is a strong mechanism for the updating of internal representations of object properties.

Generalization of Learned Manipulation across Multiple Contexts

In instances where the visual cues are not enough to form full representations of the object properties, how does sensorimotor experience affect the generalization of learned manipulation across different contexts? An understanding of the generalization of behavior to multiple contexts will provide insights into the neural control of movement and whether the level of representation is high (task-specific) or low (effector-specific) (Fu et al. 2011; Fu and Santello 2014). In terms of the context that learning can generalize in, studies into the generalization of reaching movements have suggested the use of coordinate systems (Bays and Wolpert 2006; Berniker et al. 2013; Brayanov et al. 2012; Criscimagna-Hemminger et al. 2003; Ghahramani et al. 1996; Krakauer et al. 2000; Sadeghi et al. 2018; Shadmehr and Moussavi 2000). These studies have used the two contexts of visuomotor rotations and varying dynamics in reaching arm movements to show that learning and generalization occurs in different coordinate frames based on the context (Brayanov et al. 2012; Krakauer et al. 2000; Shadmehr and Moussavi 2000). Insights gained from these studies can be used to inform generalization across different
contexts in grasping and object manipulation tasks. Based on coordinate reference frames, an intrinsic system is associated with the coordinate frame of the body (joint-based) while an extrinsic system comprises the dynamics of the object (object-based). It should be noted that in the force-field generalization of reaching movements, extrinsic and object-based systems can be distinguished (Berniker et al. 2013). However, in the current paradigm, the extrinsic coordinates are a result of the object features and thus, are interchangeable. The different contexts where generalization in coordinate reference frames can be examined include contralateral hand transfer, object rotations, and changes in the degrees of freedom used.

**Contralateral hand transfer.** If learning generalizes in extrinsic coordinates, learned forces applied to lift the object will be formed into an internal representation of object weight and/or torque that can be accessed by other effectors. It has been shown that learned load forces from lifting an object can be transferred from one hand to the contralateral hand (Chan et al. 1990; Gordon et al. 1994). For individuals with right hemiparesis, repeated lifting on their affected hand did not result in appropriate force control. However, lifting the object with their unaffected hand allowed the transfer of the appropriate load force scaling when subsequently lifting with the affected hand (Raghavan et al. 2006). Similar results were seen in children with Cerebral Palsy (Gordon et al. 1999). Even without grasping the object, hefting it allows the transfer of weight information for successful force control when lifting with the contralateral hand (Chang et al. 2008). However, when lifting an object with an asymmetrical center of mass, only weight information but not torque transfers across the hand, in two-digit (Gordon and Salimi 2004; Salimi et al. 2000) and three-digit grasping (Albert et al. 2009). The failure to transfer torque information across the hands might be due to the inability to match digit placement and in turn modulate digit load forces differentially (Shibata et al. 2013). Thus, within
the general feature, weight information is interpreted as belonging to the object (extrinsic) and as a result, generalizable across effectors. The lack of transfer of torque generation might indicate that torque information is represented in intrinsic coordinates and thus not accessible to other effectors.

**Object rotation.** Similar to contralateral hand transfer, if learning is in extrinsic object-based coordinates, object rotation would result in a similar rotation of the forces and torque. However, for objects with asymmetrical centers of mass, studies have shown that torque control is not transferrable after object rotation (Fu et al. 2010; Marneweck et al. 2015; Salimi et al. 2003). Not only did the information for torque not transfer but performance from the previous lifts interfered with performance on the post-rotation lifts to result in poorer performance. However, after repeated object rotations, it has been shown that performance does improve, and that the improvement is due to the modulation of digit placement instead of forces (Zhang et al. 2010). The authors thus suggested separate memory representations between digit placement and forces and that the differential learning rate was due to the explicit learning of digit placement compared to the implicit learning (only from tactile feedback) of forces.

In line with the concept of coordinate reference frames, a study was designed to explore how changing these frames affects generalizability of torque generation (Fu et al. 2014). Three scenarios were considered; i) object rotation, ii) hand switch, iii) hand switch and object rotation. The first two conditions have been explored above and seem to indicate that learning is in an intrinsic coordinate frame and thus not generalizable to object rotation or hand switch. These results were confirmed with object rotation resulting in poorer performance (interference) while hand switch resulted in zero transfer. Due to the mirror symmetry of the hand, the authors argued that switching the hand and rotating the object would maintain the intrinsic properties necessary
for successful manipulation. However, they found that there was still zero transfer in this condition suggesting the inability of the contralateral hand to access the intrinsic forces and torques even when maintaining mirror symmetry. Similar results were found while also showing positive transfer for 180° hand rotations (Bursztyn and Flanagan 2008). This is contradictory to our findings that 180° hand rotation did not result in effective transfer (Marneweck et al. 2015). However, Bursztyn and Flanagan (2008) used constrained contacts while we used unconstrained contacts. The biomechanical restriction of the hand places it at an awkward angle once flexed and rotated about the object 180° thus we argue that this is the reason for the differing results. By constraining the contact surfaces, the previous authors were removing the biomechanical restraint and forcing participants hand into a surprisingly favorable, but unnatural, position. It should be noted that in these studies examining object rotation, digit forces and placement after object rotation were almost collinear. This suggests a recognition by the central nervous system that there has been a change in the internal properties of the object. Overall, the lack of transfer of torque information after object rotation further indicates that learning most likely occurs in intrinsic coordinates. It would be interesting to explore smaller degrees of both object and hand rotations to continue examining the robustness of the intrinsic representation.

**Changing degrees of freedom.** Thus far, it seems like the general feature of torque generation is learned in intrinsic coordinates and thus not generalizable outside of an intrinsic coordinate frame. As mentioned in the first section of this review, the digits of the hand are anatomically and neurologically linked such that their movements are interconnected and “enslaved” (Zatsiorsky et al. 2000). This apparent enslaving has led to the suggestion of a theoretical framework based around the interdependency of the digits and hand synergies (for review see: (Santello et al. 2016). Thus, it is possible that grasping and manipulation if learned in
the intrinsic coordinates of the hand, can generalize across the digits by changing the degrees of freedom. This can be done by changing the number of fingers used (Budgeon et al. 2008) or switching between unimanual and bimanual movements (Takiyama and Sakai 2016). It has been shown that torque information can be transferred across effectors where the addition or removal of one finger, i.e. from a two-digit to three-digit grasp or vice versa, resulted in successful performance (Fu et al 2011). Thus, the intrinsic coordinates are shared amongst at least the thumb, index, and middle finger resulting in generalization across these different degrees of freedom. However, generalizing from one to two fingers is different from generalizing from one to four fingers or five digits to two hands. By continuing to probe this generalization template, we will gain more insight into the robustness of the intrinsic representation of torque generation.

It is possible that instead of weight and torque information being represented in different coordinate frames, the use of this information may be weighted differently depending on the dynamics of the task goal (Berniker and Kording 2008; Takiyama and Sakai 2016). There have not been many studies exploring this and this gap has the potential to provide clues into the generalizability of learned manipulation with regards to the general feature of grasping.

**Conclusion and Future Directions**

In this review, we have explored two key aspects of sensorimotor integration and control: a general feature of grasping and object manipulation, and the generalizability of learned manipulations from sensory cues and experience. We have shown through studies examining precision grasping, that learned manipulation involves generating the appropriate compensatory moment through the modulation and covariation of digit forces and placement while maintaining an appropriate safety margin to prevent slippage. This feature has been shown in a variety of different digit and hand combinations. In order to successfully manipulate an object, the
performer needs to form an accurate internal representation of the object’s properties. Before physical interaction with an object, we show a remarkable ability to use visual cues to form internal representations of the object to be lifted. If visual cues do not provide enough information, feedback from sensorimotor experience is used to update these internal representations. The central nervous system then uses these representations to control the forces and placement of the digits. The resultant compensatory moment generation represents a high level of control where varying digit forces and placements can be applied to generate the same compensatory moment. However, it is resistant to different modes of transfer such as contralateral hand switches and object rotation. However, weight information is generalizable across different effectors and can be transferred contralaterally. The only context that has shown positive transfer is in the addition or removal of the number of digits used. Learned manipulation may thus occur in different coordinate frames where weight information is represented in extrinsic coordinates while torque information is represented in intrinsic coordinates. If there is a change in the physical environment, the system defaults to pre-sensorimotor experience levels and lifts the object as though it is lifting it for the first time. This may be done to prevent larger sources of error, or discomfort, especially in torque generation where applying the wrong torque may assist the unintended motion. More research needs to be done to conclude whether or not learning of weight and torque information are in different coordinate frames or a mixed representation, and what this represents (Berniker and Kording 2008).

Early studies into prehension constrained digit placement by requiring the digits to be placed on specific force transducers. The advantage of this was that individual digit forces could be measured independently. In the studies employing unconstrained grasp surfaces, individual digit forces were replaced by the summed force and center of pressure of all four fingers.
Creating devices that can measure individual digit forces and placement on an unconstrained surface will provide a deeper understanding into the control of this general feature. Additionally, exploring grasping across multiple grasp types would highlight the expanse of the general feature. Finally, as generalizability of torque information has only been shown in two-to-three digit transfer conditions, exploring more combinations of degrees of freedom transfer would strengthen our understanding of generalizable behavior within this context.

In conclusion, the understanding of the sensorimotor control of grasping has made several key advancements over the past few years. The closer we get to examining functional tasks, the greater the impact of the insights gained towards real-life scenarios. This understanding will impact various fields and inform neuroscientific approaches, rehabilitative techniques, and robotic protocols.


Bays PM, and Wolpert DM. Actions and consequences in bimanual interaction are represented in different coordinate systems. Journal of Neuroscience 26: 7121-7126, 2006.


Buckingham G, Cant JS, and Goodale MA. Living in a material world: how visual cues to material properties affect the way that we lift objects and perceive their weight. J Neurophysiol 102: 3111-3118, 2009.


APPENDIX B

RESEARCH ARTICLE

Visual Cues of Object Properties Differentially Affect Anticipatory Planning of Digit Forces and Placement

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Abstract

Studies on anticipatory planning of object manipulation showed initial task failure (i.e., object roll) when visual object shape cues are incongruent with other visual cues, such as weight distribution/density (e.g., asymmetrically shaped object with an asymmetrical density). This suggests that shape cues override density cues. However, these studies typically only measured forces, with digit placement constrained. Recent evidence suggests that when digit placement is unconstrained, subjects modulate digit forces and placement. Thus, unconstrained digit placement might be modulated on initial trials (since it is an explicit process), but not forces (since it is an implicit process). We tested whether shape and density cues would differentially influence anticipatory planning of digit placement and forces during initial trials of a two-digit object manipulation task. Furthermore, we tested whether shape cues would override density cues when cues are incongruent. Subjects grasped and lifted an object with the aim of preventing roll. In Experiment 1, the object was symmetrically shaped, but with asymmetrical density (incongruent cues). In Experiment 2, the object was asymmetrical in shape and density (congruent cues). In Experiment 3, the object was asymmetrically shaped, but with symmetrical density (incongruent cues). Results showed differential modulation of digit placement and forces (modulation of load force but not placement), but only when shape and density cues were congruent. When shape and density cues were incongruent, we found colinear digit placement and symmetrical force sharing. This suggests that congruent and incongruent shape and density cues differentially influence anticipatory planning of digit forces and placement. Furthermore, shape cues do not always override density cues. A continuum of visual cues, such as those alluding to shape and density, need to be integrated.
**Introduction**

Skilled object manipulation relies on precise anticipatory planning processes that in turn rely on visual estimates of object properties and prior grasping experience [1–3]. Specifically, visual cues of size, shape and density allow for inference of object properties, such as center of mass (CM) [4–6], which we use with sensorimotor memory representations obtained from prior grasping experience [7–9] to plan for skilled object manipulation.

Object properties inferred from visual shape cues may be different from actual object properties, such as an object with a symmetrical shape cue and an asymmetrical density distribution (e.g., inverted T-shaped object with one side of the base heavier than the other side). Studies investigating anticipatory planning processes in initially manipulating such objects have shown failed performance as indicated by an inability to maintain the vertical angle of the object in the frontal plane (i.e., large object roll), even when subjects had knowledge of the density distribution [6,10–12]. For example, when presented with a symmetrical inverted T-shaped object consisting of a brass bar on the one side and a hollow plastic bar on the other side, subjects accurately estimated the location of the CM (by pointing). However, during initial lifts with such objects, instead of partitioning load forces to generate an appropriate compensatory moment (Mcom) in the opposite direction of the CM, subjects applied symmetrical load forces, resulting in a roll [6].

The results of the above studies [6,10] suggest that visual shape cues may initially override visual density (i.e. weight distribution) cues (when these cues are incongruous) during planning of manipulating such objects. However, these studies constrained digit placement to be collinear (i.e., on force sensors). It has recently been shown that unconstrained digit placement during manipulation of such objects (i.e., with incongruent shape and weight distribution) results in partitioning of both digit position and load forces (i.e., higher digits and forces on the heavier side) to generate torques to counter object roll [3,11,13,14]. Furthermore, we know from studies that investigate effects of rotation of these objects that appropriate digit placement is learned faster than digit force partitioning, although modulation of digit placement alone was not sufficient to prevent roll entirely [11]. Based on the faster learning of placement, the authors suggested that digit placement is an explicitly controlled process that is independent from digit forces that are implicitly controlled. Thus, it is conceivable that subjects could modulate digit placement, but not forces, during initial trials with objects such as that used in the Craje et al. study [6] (incongruent shape and weight distribution).

In the present study, we tested the overall hypotheses that shape and weight distribution (density) cues will differentially influence digit placement and forces (e.g., placement but not force modulation on initial lifts). Furthermore, we tested the hypothesis that shape cues will override weight distribution cues when these cues are incongruent. We first replicated the Craje et al. study [6] to determine whether symmetrical shape cues override density cues during initial manipulation, when the information they provide is incongruent. However, unlike that study, digit placement here was unconstrained. Next, we investigated whether anticipatory planning might be improved when shape and density cues are congruent (i.e. an L-shaped object with an asymmetric weight distribution), with digit placement unconstrained. This condition was similar to that tested in previous studies [10,15] which found subjects applied an Mcom to reduce object roll on the first trial, but the Mcom was of insufficient magnitude to prevent object roll. Again, here, unlike previous studies, we examined the contributions of both digit placement and forces in generating an Mcom that was appropriate to the object’s weight distribution. Lastly, we investigated anticipatory planning of manipulating an object with an asymmetric shape cue and a symmetric weight distribution cue (e.g., an inverted T-shaped object with equal lengths of brass on each side, but with hollow plastic extending one side of...
the T). This condition created incongruence unlike that tested in prior studies, since here the shape was asymmetrical whereas the CM was still at the object’s center. Thus, we tested whether asymmetrical shape cues would override symmetrical density cues (resulting in incorrect partitioning of digit placement and forces compared to correct symmetrical digit placement and forces).

**Materials and Methods**

**Participants**

Sixty healthy young adults (median age: 26 years, range: 20–37 years; 21 males), recruited between January 2014 and April 2014, participated in the study. Participants were right-handed, had normal or corrected-to-normal vision, and had no upper limb orthopedic impairments. Written informed consent was obtained prior to participation in compliance with the Declaration of Helsinki. The study was approved by the Teachers College, Columbia University Institutional Review Board.

**Apparatus**

A custom-made grip device with a central vertical column and 3 interchangeable horizontal bases was used to measure the torques and forces of the thumb and index finger (Fig 1). The central vertical column of the device consisted of two balsa wood-covered plastic rectangular grip surfaces (height: 70 mm, width: 20 mm, thickness: 4 mm, distance between grip surfaces: 80 mm) attached to two multi-axis force sensors (Nano 17 Force/Torque transducer, ATI Industrial Automation, NC) that were mounted onto a Plexiglass block (height: 130 mm, width: 24 mm, depth: 40 mm). The force sensors measured grip force, load force, and torques applied (resolution = 0.05 N, 0.025 N, 0.125 Nmm respectively). Using a right-handed precision grip, the thumb could be placed anywhere on the left grip surface and the index finger could be placed anywhere on the right grip surface. An electromagnetic sensor (Polhemus Fasttrack, 0.005 mm of range, and 0.025° resolution) was mounted on the top of the Plexiglas block to measure vertical position and roll of the grip device.

The congruency of visual cues of object shape and object density distribution was manipulated to probe its effect on anticipatory planning of digit placement and forces during initial trials. To manipulate visual cues of object shape, 3 interchangeable horizontal bases were made of Plexiglass with different lengths (180 mm, 130 mm, 105 mm, respectively). Each base could be attached to the central vertical column resulting in the three differentially shaped objects (see Fig 1): a visually symmetrical inverted T-shaped object, a visually asymmetrical L-shaped object, and a visually asymmetrical inverted T-shaped object with one end shorter than the other. To manipulate visual cues of object density distribution and thus CM, we used 4 different weights (height: 25 mm, depth: 25 mm): a solid metal bar (width: 75 mm, mass: 405 g), a hollow plastic bar (width: 75 mm, mass: 10 g), a solid metal cube (width: 25 mm, mass: 135 g), and a solid metal cube affixed to a hollow plastic bar (width: 75 mm, mass: 140 g). These weights were placed on the horizontal bases of the object resulting in three different configurations (Fig 1c). The first configuration, used in Experiment 1, a symmetrical inverted T-shape with asymmetrical density distribution, was arranged with the metal bar on the thumb side with the plastic bar on the index finger side. The CM of this configuration was on the side of the metal bar (thumb). The second configuration, used in Experiment 2, an asymmetrical L-shape with asymmetrical density, was arranged with the solid metal bar on the thumb side of the base. The CM of this configuration was on the side of the metal bar (thumb). The third configuration, used in Experiment 3, an asymmetrical inverted T-shape with symmetrical density, was arranged with the solid metal cube on the shorter side of the base (index finger) and the
solid metal cube and hollow plastic bar on the longer side of the base (thumb). The CM of this configuration was the center of the device. Therefore, the configurations in each of the three experiments, varied in their shape and density arrangement. The configuration in Experiment 1 resulted in incongruence between visual cues of object shape and visual cues of density distribution where shape cues indicated a centered CM while density cues indicated an off-centered...
CM (towards the thumb/left side). The configuration in Experiment 2 resulted in congruence between visual cues of object shape and visual cues of density distribution where both indicated an off-centered CM (towards the thumb/left side). The configuration in Experiment 3 resulted in incongruence between visual cues of object shape and visual cues of density distribution where shape cues indicated an off-centered CM (towards the thumb/left side) while density cues indicated a centered CM.

Each experiment had two conditions. In Experiment 1 and 2, the CM location was on the left in one condition and on the right in the other condition. In Experiment 3, the shape cue (the longer base-side) was on the left in one condition and on the right in the other condition. A possible limitation of our previous studies [6] was that all participants experienced all conditions. Thus, even if the data did not suggest it, there could have been proactive interference preventing appropriate force scaling. To prevent this, in this study, participants performed only one condition (condition 1 or 2 in either Experiment 1, 2, or 3), with ten participants per condition.

Procedure

Participants were seated in front of a height-adjustable table, with their right elbow flexed 90° in the parasagittal plane, with their right shoulder in line with the midpoint of the object, and their right hand on a start marker on the table. Participants performed a hefting task of the individual parts, then a CM estimation task of the object with its shape and density configuration in place. The object was then placed 20 cm from a start marker at the end of the table. Following this was the lifting task where the goal was to lift the object while minimizing object roll. Participants performed 10 lifts in total following which they were asked to again estimate the CM.

Hefting and CM estimation task. Results from our previous study [6] showed that hefting the individual parts of the object separately did not improve performance during initial trials. However, to ensure that participants had explicit knowledge of the density of the different weights, the hefting task was performed. Prior to estimating the CM of the object, the participant hefted the device, and the respective weights separately. Following this hefting procedure, the participant was presented with the device in the desired configuration. The participant was then asked to indicate where he/she thought the horizontal CM of the object was, by pointing with a pen on a ruler placed in front of the object. This CM estimation task was done to determine whether participants could use visual cues of object shape and density distribution to estimate the CM of the object. At the end of the 10 trials, the participant again estimated the CM of the object to test if experience lifting the object modified their CM estimation [9,13,14].

Lifting task. After the CM estimation task, the participant was asked to place their right hand (palm down) on the start marker. The task goal was to minimize object roll. The participant was instructed to lift the object in a smooth self-directed manner. For each trial, following an audio tone, the participant reached and grasped the object using his/her right thumb and index finger, anywhere on the respective grip surfaces, and lifted the object vertically upwards to the height of a 15-cm marker placed next to the object. The participant held the object at that height until presentation of a second audio tone (5s after first tone), after which he/she placed the object back on the table, and returned his/her hand to the start marker awaiting the start of the next trial.

Data Processing

Throughout the lifts, digit forces and torques applied to the grip surfaces recorded by the force transducers, and position data recorded by the electromagnetic sensor were sampled at 500
and 120 Hz, respectively, using custom written software in WinSC and then analyzed in WinZoom (Umeå University, Sweden). Data collected were filtered using a second-order low pass Butterworth filter with a cutoff of 6 Hz. Lift onset was defined as the point at which the vertical position of the object went above 1 mm and subsequently remained above this value. Object roll occurred in the parafrontal plane and all variables involved forces within this plane. The outcome measures included:

1. Peak object roll, defined as the angle of the object in the frontal plane. Peak object roll was recorded shortly (< 500 ms) after lift onset before somatosensory feedback resulted in corrective responses to counter object roll. Positive values represent counterclockwise roll (towards the thumb) and negative values represent clockwise roll (towards the index finger).

2. Digit load force (LF) at lift onset is the tangential component of the force produced by each digit measured in newton (N).
   a. Load force difference \( (LF_{\text{digit}}) = LF_{\text{thumb}} - LF_{\text{index}} \)
      Positive values indicate larger thumb than index finger load force while negative values indicate larger index finger than thumb load force.

3. Digit center of pressure (COP) is the measure of digit placement defined as the point of contact of each digit on the grip surface measured in millimeter (mm). This was computed using the formula:
   \[
   COP_{\text{digit}} = \frac{(TX_{\text{digit}} - (LF_{\text{digit}} \times \text{thickness of grip surface}))}{GF_{\text{digit}}}
   \]
   where \( TX \), digit torque in the frontal plane, is the torque generated by each digit on the grip surface measured in newton millimeter (Nmm). In this instance, the grip surface was the lever arm while the force transducer was the fulcrum. The thickness of the grip surface was 4 mm, and \( GF \), the digit grip force at lift onset, is the normal component of the force produced by each digit measured in newton (N).
   a. Center of pressure difference \( (COP_{\text{digit}}) = COP_{\text{thumb}} - COP_{\text{index}} \)
      Positive values indicate higher thumb than index finger COP while negative values indicated higher index finger than thumb COP.

4. Compensatory moment (Mcom) defined as the anticipatory moment generated by the digits in response to the representation of object CM measured in newton millimeter (Nmm). This was computed using the formula:
   \[
   M_{\text{com}} = \left( LF_{\text{digit}} \times \frac{d}{2} \right) + \left( GF_{\text{center}} \times COP_{\text{digit}} \right)
   \]
   where \( d \) is the width between both grip surfaces (80 mm). A positive Mcom represented a clockwise moment while a negative Mcom represented a counter-clockwise moment.

**Data Analysis**

Peak roll was used to determine accomplishment of task goal. Anticipatory planning of digit forces and placement were analyzed using the resultant Mcom, digit COP and digit load force at lift onset.

**Effect of shape and density cues on CM estimation.** We performed mixed ANOVAs with trial (before lift 1 and after lift 10) as the within-subjects factor and experimental
configuration (Experiment 1, 2, and 3) as the between-subjects factor, with the CM location (Experiment 1 and 2) and shape cue (Experiment 3) on the left and right, respectively.

**Effect of shape and density cues on anticipatory planning.** For Experiments 1 & 2, we performed mixed ANOVAs with trial (lift 1 and lift 10) as the within-subjects factor and CM location (left and right side) as the between-subjects factor on the peak roll, Mcom, COP difference, and load force difference. For Experiment 3, we performed mixed ANOVAs with trial (lift 1 and lift 10) as the within-subjects factor and shape cue (left and right side) as the between-subjects factor on each of each measure. Interaction effects were examined using tests of simple main effects. Bonferroni corrections were used where applicable. Significance was considered at the $p < .05$ level.

**Results**

**CM Estimation**

Participants in each of the experiments accurately estimated the CM location before and after lifting the object ($\pm$ 5 mm from the CM location, see **Fig 2**), with no significant differences in CM estimation before and after lifting and no interaction between trial and experiment configuration, $p > .05$ in all cases. Thus, participants were able to use visual density cues to estimate the CM location accurately for each of the object configurations.

**Experiment 1: Symmetrical shape and asymmetrical density cues**

**Fig 2** shows the object roll, Mcom, COP, and load force of a representative participant for the first and tenth lifts of the inverted T-shaped object with a left CM during Experiment 1. On the first lift, there was a large peak roll due to the negligible Mcom generated by the participant, which was insufficient to counter the torque of the object. The small Mcom was caused by the very small COP difference, with the thumb only slightly higher than the index finger, and symmetrical thumb and index finger load force. Comparatively, on the tenth lift, there was a small...
roll owing to the large Mcom generated. This Mcom was a result of both a higher thumb than index finger COP and a larger thumb than index finger load force.

As described below, and seen in Fig. 4, group means between the left and right CM locations and between trial 1 and trial 10 were generally consistent with this representative illustration. There was a trial x CM location interaction for peak roll, $F(1, 18) = 84.51, p < .001, \eta^2 = .82$, with larger rolls in the direction of the CM location at trial 1 than at trial 10 ($p's < .05$). Peak
Fig 4. Experiment 1 lifting task results. Group means (95% confidence interval) at trial 1 and trial 10 of peak roll, Mcom, COP difference, and load force difference in left and right CM conditions. Asterisks indicate p < .05.
roll at trial 1 was due to a lack of Mcom by participants (trial x CM location, $F(1, 18) = 159.06$, $p < .001$, $\eta^2_p = .90$). Specifically, there was no difference between the Mcom for the left and right CM location at trial 1 ($p > .05$), but at trial 10, an appropriate Mcom was generated (of opposing direction between CM locations, $p < .05$).

The lack of Mcom at trial 1 was a result of collinear digit placement and digit load forces. Specifically, there was a trial x CM location interaction for COP difference ($F(1, 18) = 14.98$, $p < .001$, $\eta^2_p = .45$), where participants did not exhibit different digit placements between the left and right CM locations at trial 1 ($p > .05$), but did so at trial 10 ($p < .05$). Similarly, there was a trial x CM location interaction for load force difference ($F(1, 18) = 27.45$, $p < .001$, $\eta^2_p = .68$), where participants did not partition load force according to CM location at trial 1 ($p > .05$), but did so at trial 10 ($p < .05$).

### Experiment 2: Asymmetrical shape and asymmetrical density cues

The previous experiment requiring manipulation of an object with an incongruent shape and density cue showed erroneous anticipatory planning of both digit placement and load forces. Here we tested whether congruent shape and density cues (i.e., an L-shaped object with a uniform density) would result in modulation of digit placement and forces to achieve an appropriate Mcom. **Fig 5** shows the object roll, Mcom, COP, and load force of a representative participant for the first and tenth lifts with the object’s CM on the left during Experiment 2. On the first lift, there was a large peak roll. This large roll was due to an insufficient Mcom generated by the participant. However, the Mcom generated was in the appropriate direction to counter object torque. There was a very small COP difference, with the thumb only slightly higher than the index finger, but the Mcom was the result of the larger thumb to index finger load force. The participant could infer object CM, and an Mcom in the appropriate direction was generated; however, this did not prevent object roll. Comparatively, on the tenth lift, there was a small roll owing to a large Mcom generated. This Mcom was a result of both a higher thumb to index finger COP and a larger thumb to index finger load force.

As described above, and seen in **Fig 6**, group means between the left and right CM locations and between trial 1 and trial 10 were generally consistent with this representative illustration. There was a trial x CM location interaction for peak roll ($F(1, 18) = 45.03$, $p < .001$, $\eta^2_p = .71$), with larger rolls in the direction of the CM location at trial 1 than at trial 10 ($p’s < .05$). Unlike in Experiment 1, the Mcoms were different (and in the correct direction) between the left and right CM locations on trial 1 ($p< .05$). However, the differences ($p< .05$) were larger at trial 10 (trial x CM location interaction, $F(1, 18) = 159.61$, $p < .001$, $\eta^2_p = .90$).

The lack of Mcom of appropriate magnitude to prevent large roll at trial 1 was a result of collinear digit placement. Specifically, there was a trial x CM location interaction for COP difference ($F(1, 18) = 12.34$, $p < .05$, $\eta^2_p = .41$), where participants did not exhibit different digit placements between the left and right CM locations at trial 1 ($p > .05$), but did so at trial 10 ($p < .05$). The load force partitioning between digits was different (and in the correct direction) between the left and right CM locations on trial 1 ($p< .05$), but the difference ($p< .05$) was larger at trial 10 (trial x CM location interaction, $F(1, 18) = 153.99$, $p < .05$, $\eta^2_p = .47$).

### Experiment 3: Asymmetrical shape and symmetrical density cues

Overall, the previous experiment requiring manipulation of an object with congruent asymmetrical visual shape and density cues resulted in the modulation of Mcom by modulating digit load force (but not digit placement). The resultant effect was insufficient to prevent object roll.
To determine whether the results of the prior two experiments (and prior studies) are the result of visual shape cues overriding weight distribution (density) cues, here we present subjects with an asymmetrically-shaped object with weight distribution cues indicating a centered CM. Fig. 7 shows the of object roll, Mcom, COP, and load force of a representative participant for the first and tenth lifts with the object’s CM on the left during Experiment 3. On the first
Fig 6. Experiment 2 lifting task results. Group means (95% confidence interval) at trial 1 and trial 10 of peak roll, Mcom, COP difference, and load force difference in left and right CM conditions. Asterisks indicate $p < .05$.

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and tenth lift, object roll was minimal, Mcom generated was small, and digit COP and load forces were collinear throughout.

As seen in Fig 8, the asymmetrical shape cue did not result in erroneous object roll ($p's > .05$) and participants generated minimal Mcom, with no Mcom differences between the
Fig 7. Representative plots, Experiment 3. Plots show trial 1 (left panel) and trial 10 (right panel) in the left shape cue condition. Vertical dotted lines indicate lift onset. Horizontal dotted lines in the second row show the target Mcom required to equal object torque. In the COP and load force rows, solid lines represent the thumb and dotted lines represent the index finger.

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left and right shape cues at both trials 1 and 10 ($p > .05$). The lack of Mcom difference was a result of nearly collinear digit placement and digit load forces for both left and right shape cues. Participants did not exhibit different digit placement and forces between left and right shape cues at both trials 1 and 10, with no significant interaction between trial and shape cue ($p > .05$).
Fig 8. Experiment 3 lifting task results. Group means (95% confidence interval) at trial 1 and trial 10 of peak roll, Mcom, COP difference, and load force difference in the left and right shape cue conditions.

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Discussion

The present study investigated the effect of congruent and incongruent visual cues of shape and weight distribution (density) on anticipatory planning of digit placement and forces. Our first hypothesis, testing whether shape and density cues differentially influenced digit placement and forces on initial trials, was partially supported. In line with our hypothesis, we found
differential modulation of digit placement and forces on initial trials, but only when shape and density cues were congruent. However, in contrast to our hypothesis, we found that load force, instead of digit placement, was modulated and contributing to an Mcom in the correct direction. In testing our second hypothesis, whether shape cues will override density cues when cues are incongruent, our results showed this to not be the case in all instances. Specifically, when shape and density cues were incongruent, subjects adopted collinear digit placement and forces. This resulted in an inappropriate Mcom in Experiment 1 (i.e., a symmetrical inverted T-shape with asymmetrical weight distribution), but led to an appropriate Mcom in Experiment 3 (i.e., a centered weight distribution). We discuss these findings in relation to previous work and possible motor planning mechanisms.

Incongruent cues lead to symmetrical digit placement and forces

Our previous work has identified a dichotomy between the ability to accurately estimate CM location and the use of that information to update or generate an internal model that would allow appropriate planning of digit forces [6]. Specifically, an object’s CM could be accurately estimated based on density cues, and subjects could use such density cues to scale the overall digit force, but only when the objects had consistent densities (i.e., they used higher forces on initial lifts with brass than plastic objects). However, on initial lifts with objects with inconsistent densities (i.e., CM location is off-centered), planning of digit forces did not result in generation of Mcom to counter object torque. Consistent with and adding to that finding, here we showed that this is not only present for the anticipatory planning of digit forces on initial trials, but also for the anticipatory planning of digit placement. Additionally, our results showed that the lack of force scaling on initial lifts reported in that study [6] was not due to proactive interference as the results were replicated in the present study using a between-subject design.

The results of Experiment 1 (symmetrical inverted-T shape with off-centered CM) indicated a possibility where the symmetrical shape cues, as opposed to the asymmetrical density cues, affected digit placement and forces (i.e., resulting in collinear positions and forces). It is unclear if the collinear pattern was due to the incongruent cues or preference for visual shape cues. To attempt to resolve between these possibilities, Experiment 3 involved lifts with an asymmetrical inverted-T shape with a centered CM. If visual shape cues were more robust in determining anticipatory planning, we would expect generation of an Mcom in the opposite direction of the longer arm. However, a lack of Mcom indicated that participants did not use the asymmetrical shape cue in the planning of the grasp task. There are two possible explanations for these findings from these two experiments. First, it could be that visual shape cues of symmetrical objects override other weight-distribution cues, whereas asymmetrical objects do not. This might be because we experience manipulations with many symmetrical objects in our daily lives, most of which have a symmetrical weight distribution (i.e., consistent material throughout). Second, when shape cues and density cues are incongruent, subjects might default to a behavior similar to when lifting symmetrically shaped objects where anticipatory planning of forces and placement are collinear. This would result in inappropriate Mcoms in Experiment 1, but appropriate Mcoms in Experiment 3. We cannot distinguish between these two possibilities. However, both possibilities also explain the failed transfer of digit placement and forces following object rotation and translation when the CM is off-centered but the object is symmetrical in appearance [10–12,15–19].

Congruent cues lead to differential digit force modulation

Consistent with previous findings using objects with congruent shape and density cues, congruent cues in Experiment 2 (i.e., asymmetrical shape and densities) resulted in the generation
of an Mcom that is in the appropriate direction required to reduce object roll [15]. Extending this finding, we have shown that the Mcom is a result of differential digit force modulation, and not digit placement modulation. This suggests that like visual size cues [20], visual shape cues with objects of consistent densities exert a powerful influence on grasp control during initial lifts. Thus, the findings of Experiment 3 are not due to subjects’ general inability to transform visual shape cues into a grasp performance, as they did so here, albeit when the object had a consistent density.

Digit placement is not partitioned regardless of visual cues

Our data show that on initial trials, even with knowledge of object CM through visual shape and density cues, the thumb and index finger are placed collinearly to each other on either side. This is in contrary to our hypothesis that digit placement would be partitioned, which was based on previous findings that finger placement was more robust during memory retrieval of prior lifts compared to digit forces [11], suggesting not only differential learning rates but separate control mechanisms. Here, we show that visual shape and density cues are insufficient to elicit digit placement partitioning on the first trial in a series of (blocked) trials. This suggests that, when implicit knowledge of object properties can be obtained through subsequent lifts, digit placement is a context-dependent learned strategy where digit placement is planned only after obtaining knowledge of object torque through prior experience. Prior to this, a default colinear placement pattern is used. This strategy could have been used to prevent erroneous Mcom from being generated. Because of the strong association between digit force and placement [3], altering digit placement would be associated with altering digit forces. Without specific sensorimotor memories of the object, varying both forces and placement would lead to a large probability of making errors. Digit placement that is not collinear would result in the system having to adjust for digit force partitioning through further force modulation. Digit placement does not change after contact is made with the object, as such, placing the digits non-collinearly would create greater biomechanical constraints if the placement were wrong. For example, if the thumb was placed higher than the index finger when the object CM was on the right side, the index finger would have to apply a much larger load force in order to prevent object roll. Thus, the internal model might be set up in a default manner where the digits are placed collinearly, resulting in Mcom generation that is entirely due to force modulation.

Another reason that could account for the little to no digit placement modulation in our study is that the torque used here is smaller than that used in previous work [14,15]. This could have contributed to participants resorting to a ‘digit force modulation’ only strategy, as opposed to a ‘digit force and position’ modulation strategy on the first lift. Nevertheless, our study suggests that when visual cues are incongruent, the complexity results in an error-based learning strategy where initial trials are used to gain implicit knowledge of object dynamics [21]. Thus, on initial trials, the default strategy of collinear digit forces and placement is used. When visual cues are congruent, with digit placement planned collinearly, digit forces are then anticipated and modulated in an attempt to generate an Mcom opposing object torque. It should be noted that predictability of an upcoming visual cue also may play a role in subjects’ ability or choice to modulate digit placement in response to that cue [2].

Possible cortical networks involved in planning of digit forces and placement

Studies that have used repetitive transcranial magnetic stimulation (rTMS) inducing temporary virtual lesions on specific cortical regions have identified a fronto-parietal network of regions involved in the visuomotor control of digit forces and placement (when they are collinear).
This network includes the anterior intraparietal area (AIP) [22], the dorsal and ventral premotor cortex (PMv) [23], and the primary motor cortex [24]. AIP and PMv have shown specifically to be involved in digit placement (with artificial lesions resulting in non-collinear digit placement). Furthermore, the above study [22] showed rTMS applied 270–220 ms before digit contact altered digit placement, whereas rTMS applied later, 170–120 ms before the digit contact, altered force scaling [22]. This suggests that AIP processes digit placement before force scaling. Thus, it supports our supposition that load force modulation (seen in Experiment 2) is based on collinear digit placement (because force scaling is processed after digit placement in AIP).

Regarding cortical networks that are involved in processing of visual cues of shape and density, sensory areas in the parietal and temporal cortices have been suggested to process visual cues of size and/or shape. Specifically, studies have pointed to AIP [25,26] and the superior parietal occipital cortex [27,28] in processing visual cues of object shape. These studies typically used objects with uniform densities. Moreover, these studies have assumed congruence between visual shape and density cues. To the best of our knowledge, the cortical regions involved in integration of object properties obtained through visual cues, such as shape and density, remains an untested question. Studies investigating potentially separate neural mechanisms responsible for processing visual cues of shape and density might give additional insights into how the system attempts to reconcile incongruent cues.

Conclusions
We investigated the effect of congruent and incongruent visual cues of object shape and weight distribution (density) on anticipatory planning of digit placement and forces. With congruence between visual cues of object shape and density, we showed differential modulation of forces and placement, specifically, modulation of load force but not placement. With incongruence between visual cues of object shape and density, we showed collinear application of digit placement and symmetrical partitioning of forces. This suggests that congruent and incongruent visual cues of shape and density have a differential influence on anticipatory planning of digit forces and placement. A continuum of visual cues, such as those alluding to shape and density, need to be integrated. Such integration becomes more challenging when cues are incongruent, in which case the system defaults to a collinear force and positioning pattern. This happens even when the shape cue warrants non-collinear force and position.

Supporting Information
S1 File. Individual data points for Experiment 1, 2, and 3.
(XLSX)

Author Contributions
Conceived and designed the experiments: MS AMG. Performed the experiments: TLM. Analyzed the data: TLM MM MS AMG. Wrote the paper: TLM MM MS AMG.

References

4. Buckingham G, Cant JS, Goodale MA. Living in a material world: how visual cues to material properties affect the way that we lift objects and perceive their weight. Journal of Neurophysiology. 2009 Dec 1; 102(6):3111–8. doi: 10.1152/jn.00515.2009 PMID: 19793879


APPENDIX C

RESEARCH ARTICLE

Generalization of Dexterous Manipulation Is Sensitive to the Frame of Reference in Which It Is Learned

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Abstract

Studies have shown that internal representations of manipulations of objects with asymmetric mass distributions that are generated within a specific orientation are not generalizable to novel orientations, i.e., subjects fail to prevent object roll on their first grasp-lift attempt of the object following 180° object rotation. This suggests that representations of these manipulations are specific to the reference frame in which they are formed. However, it is unknown whether that reference frame is specific to the hand, the body, or both, because rotating the object 180° modifies the relation between object and body as well as object and hand. An alternative, untested explanation for the above failure to generalize learned manipulations is that any rotation will disrupt grasp performance, regardless if the reference frame in which the manipulation was learned is maintained or modified. We examined the effect of rotations that (1) maintain and (2) modify relations between object and body, and object and hand, on the generalizability of learned two-digit manipulation of an object with an asymmetric mass distribution. Following rotations that maintained the relation between object and body and object and hand (e.g., rotating the object and subject 180°), subjects continued to use appropriate digit placement and load force distributions, thus generating sufficient compensatory moments to minimize object roll. In contrast, following rotations that modified the relation between (1) object and hand (e.g. rotating the hand around to the opposite object side), (2) object and body (e.g. rotating subject and hand 180°), or (3) both (e.g. rotating the subject 180°), subjects used the same, yet inappropriate digit placement and load force distribution, as those used prior to the rotation. Consequently, the compensatory moments were insufficient to prevent large object rolls. These findings suggest that representations of learned manipulation of objects with asymmetric mass distributions are specific to the body- and hand-reference frames in which they were learned.
Introduction

To skillfully manipulate objects with the fingertips requires the ability to adapt the fingertip forces to the constraints imposed by an object’s physical properties. This requires both the use of tactile feedback and feedforward (anticipatory) control, the latter of which takes advantage of the stable and predictable physical properties of objects. These feedforward control predictions are based on visual cues of the object’s properties and internal representations (sensorimotor memories) associated with the object [1,2,3]. Visual cues can provide direct information about object size [4,5,6], shape [7,8,9,10], and identity [1], but might also provide indirect information about weight and mass distribution, which can sometimes be imprecise. Since weight and mass distribution information is only available after object lift-off, internal representations formed during earlier experiences with the object are used to scale forces to the weight and mass distribution of the object [1,2,3].

To understand the nature of these internal representations, studies have used a paradigm in which the visual cues of the object are not salient [11,12,13,14,15,16,17,18]. This paradigm required subjects to grasp and lift with the index finger and the thumb a symmetrically shaped object, an inverted T-shaped object, with an asymmetric mass distribution (i.e. one side of the base of the inverted T-shaped object is heavier than the other side). The goal of the task was to minimize object roll. On their first object lift, subjects exerted symmetrical grip forces and symmetrical load forces by the index finger and the thumb, and thereby generated little or no compensatory moment counteracting the external torque caused by the asymmetric mass distribution, which resulted in a large object roll. However, subjects learned within just a few lifts to minimize object roll by applying more load force in the digit on the heavier side of the inverted T-shaped object. Subsequent studies removed digit placement constraints, whereby subjects could grasp and lift the inverted T-shaped object anywhere along two grasp surfaces [14,16,17,18,19,20]. Results of these studies showed that load forces were modulated in parallel with digit placement, i.e., higher digit placement on the heavier side of the object, with both digit positions and forces contributing to generating a compensatory moment to prevent roll.

Some studies have questioned the extent to which these internal representations generated within a specific object orientation are generalizable to novel orientations [11,12,13,15,18,20,21,22,23]. These studies typically required subjects to grasp and lift an object with an asymmetric mass distribution in one orientation, learn the manipulation, and then lift and grasp it in a novel orientation, e.g., following 180° rotation of the object. This rotation modifies both body and hand frames of reference from that to trials preceding the rotation. In other words, if the center of mass (CoM) is on the object’s left side before rotation, it would be toward the left side of the body and oppose the thumb during lifts with the right hand. Conversely, after rotating the object 180°, the CoM would oppose the index finger and be toward the right side of the body. After such object rotations, subjects failed to prevent object roll on their first attempt to grasp and lift the object due to inappropriate load force scaling [11,12,13,15,21] as well as inappropriate digit placement [18,20]. These findings suggest that internal representations of learned manipulations of objects with asymmetric mass distributions are specific to the frame of reference in which they were formed. However, it is unknown whether that frame of reference is specific to the hand, the body, or both, because rotating the object 180° modifies both the relation between the object and body and between the object and hand as described above.

An alternative, yet untested, explanation for the failure in transferring learned manipulation and therefore preventing roll might be that any modification in object orientation interferes with generalization of learned manipulation, regardless of whether the frame of reference is maintained or modified. In a pioneering study pointing to the complexity of mental rotation
Shepard and Metzler [24] found an increase in time in identifying two shapes as similar with an increase in the angular difference between the two shapes. Given the complexities involved in identifying object geometry after mental rotation of an object, any kind of rotation, even that which maintains the body and hand frames (e.g. 360° rotation of object, or subject, or both), might disrupt transfer of learned manipulation of the same object in a different orientation.

We addressed two overarching aims in a set of 8 experiments. First, we examined the effect of rotations that maintain the relation between the both the object and body and object and hand. Second, we examined the effect of rotations that modify both and either of these relations on the ability to transfer learned manipulation. Based on previous findings, we hypothesized that rotations that modify both the relation between the object and body, and between object and hand, will impair performance. Results from rotations that modify either the relation between the object and body, or between object and hand, will elucidate whether the reference frame used to learn object manipulation is specific to the body, the hand, or both. For example, impaired performance after a rotation that modifies only the object to hand relation and correct performance following a rotation that modifies the object to body relation would suggest that internal representations of objects with asymmetric mass distributions are specific only to the hand reference frame in which it was learned (and not the body reference frame). Alternatively, impaired performance induced by both of these rotation types would suggest that internal representations of objects with asymmetric mass distributions are specific to both body and hand reference frames in which they were learned. Finally, should performance be disrupted also in conditions that do not modify reference frames, this would suggest that the act of rotation is what disrupts performance, and not the change in reference frame.

Methods
Participants
Eighty-seven right-handed healthy adults (59 females; Median age: 27; Range: 20–34) with normal or corrected-to-normal vision participated across 8 experimental conditions. We included in the main analyses 10 subjects for each experimental condition, excluding 7 subjects (see below). All subjects gave written informed consent and the Teachers College, Columbia University Institutional Review Board approved the study procedures.

Materials and Procedures
Subjects were asked to grasp and lift an inverted T-shaped object (Fig 1A) with an asymmetric CoM using the tips of their right index finger and thumb, with the aim of preventing object roll [11,12,18,20,25].

Forces and moments exerted by the thumb and index finger were measured by two force/torque transducers (Nano 17, ATI Industrial Automation, NC). The transducers measured grip force, load force, and moment with resolutions of 0.05 N, 0.025 N, and 0.125 Nmm, respectively. The force transducers were attached parallel to each other on the vertical column of the inverted T-shaped object (made from Plexiglass). The force transducers were covered by two parallel Plexiglass grip surfaces (height: 7.0 cm; width: 1.9 cm; depth: 0.3 cm; distance between grip surfaces = 8.0 cm). Each of the Plexiglass grip surfaces was covered with a thin sheet of balsa wood to increase the friction between the digits and the object’s contact surfaces. At the base of the object, two black balsa wood surface covers visually concealed the asymmetrically distributed mass (a solid brass block; height: 2.5 cm; width: 7.0 cm; depth: 2.5 cm; mass: 405 g). Thus, the object was symmetrical in appearance (inverted “T”), but not in mass distribution. An electromagnetic position-angle sensor (Polhemus Fastrack; angular resolution: 0.025°, displacement resolution: 0.0005 cm) was attached at the top of the object to measure
Fig 1. A depiction of the visually symmetrical object with a visually concealed asymmetric mass distribution, and the experimental procedure for the 8 conditions. (A) Custom built inverted ‘T’-shaped object. A solid brass metal block was placed on either the left or right side on the base of the object.

The solid brass metal block was visually concealed with two balsa wood covers that were placed on the left and right side on the base of the object. Thus, the object was symmetrical in appearance but not in mass distribution. An electromagnetic position sensor was placed at the top of the vertical column to measure object roll. The grasp surfaces were attached to the force sensors that measured forces and centers of pressure of the thumb and index finger. Left
Generalization of Dexterous Manipulation

and right panels show front and side views of the object. (B) Experimental procedures for each of the 8 conditions during pre-rotation trials (with the center of mass on the left, see white dotted outline) and following a rotation, the post-rotation trials. The rotation either maintained hand and body reference frames (Condition 1–4) or modified hand and/or body reference frames (Conditions 5–8). Conditions that maintained hand and body reference frames involved a 360° object rotation (Condition 1), 360° subject rotation (Condition 2), 360° object and subject rotation (Condition 3), and a 180° object and subject rotation (Condition 4). Conditions that modified hand and/or body reference frames involved a 180° object rotation (Condition 5), 180° subject rotation (Condition 6), 180° hand rotation (Condition 7), and a 180° hand and subject rotation (Condition 8). A full circle arrow indicates a 360° rotation (by object and/or subject, dependent on condition), and a half circle arrow indicates a 180° rotation (by object and/or subject and hand, dependent on condition).

The object roll. The total mass of the object, including the force sensors, position-angle sensors, brass, and the balsa wood covers was 585 g. Fingertip force data were sampled at 500 Hz and position data were sampled at 120 Hz using SC/Zoom (Umeå University, Sweden).

Subjects sat comfortably in front of a height-adjustable table facing the object with their right elbow flexed approximately 90° in the parasagittal plane, with their right shoulder aligned with the midpoint of the object. The right hand was placed, palm facing down, at a marked start location, 24 cm from the midpoint of the object. Following an auditory cue, subjects were instructed to reach from the marked start location, grasp the grip surfaces with the tip of the thumb and the index finger, and lift the object at a natural speed to a height of an adjacent marker (10 cm). Following a second auditory cue (occurring 5 s after first auditory cue), subjects were instructed to replace both object and hand back to their respective start locations. Subjects were asked to minimize as best possible object roll. No instruction was given regarding the location of fingertip placement on the object.

There were two blocks of 16 trials, with a 20-s inter-stimulus interval between trials. Each block contained 8 pre-rotation trials, followed by a rotation of the object, subject’s hand, both object and subject, or both subject and subject’s hand (see below), and 8 post-rotation trials thereafter. Rotations were performed around the vertical axis of the object (Fig 1B). The CoM of the object was on a given side during the pre-rotation trials of the first block, and then on the other side during the pre-rotation trials of the second block. CoM location (left or right) in the first block was counterbalanced across subjects in each condition. Subjects were asked to indicate the heavier side of the object, left or right, prior to and following exposure to each rotation. Subjects (n = 7) that gave an incorrect response were excluded from the main analyses, but we compared their performance qualitatively to those that gave a correct response. Subjects experienced only one type of rotation, which prevented proactive interference or learning across conditions. Subjects experienced 1 of 8 experimental manipulations (n = 10 in each group; see Table 1 and Fig 1B) following pre-rotation trials:

**Conditions that maintain the relation between object and hand and between object and body.** In Condition 1 (360° rotation of the object), subjects were asked to observe the object being rotated by the experimenter 360°. The relation between the object and body, and between the object and hand, was unchanged following this rotation, with the CoM on the same side of the body and on the same digit side during pre- and post-rotation trials.

In Condition 2 (360° rotation of the subject), subjects were instructed to stand up and walk 360° around the table and return to their pre-rotation seated position. As in Condition 1, following this rotation, the body-to-object and hand-to-object relations were the same during pre- and post-rotation trials.

In Condition 3 (360° rotation of the object and subject), subjects were asked to observe the object being rotated 360° by the experimenter and to subsequently stand up and walk in the same direction around the table and return to their pre-rotation seated position. As with Conditions 1 and 2, the relations between object and body, and between object and hand, were the same during pre- and post-rotation trials.
Table 1. Description of each of the 8 experimental conditions.

<table>
<thead>
<tr>
<th>Condition</th>
<th>Description</th>
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<tbody>
<tr>
<td>1</td>
<td>360° rotation of the object</td>
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<tr>
<td>2</td>
<td>360° rotation of the subject</td>
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<tr>
<td>3</td>
<td>360° rotation of the object and subject</td>
</tr>
<tr>
<td>4</td>
<td>180° rotation of the object and subject</td>
</tr>
<tr>
<td>5</td>
<td>180° rotation of the object</td>
</tr>
<tr>
<td>6</td>
<td>180° rotation of the subject</td>
</tr>
<tr>
<td>7</td>
<td>180° rotation of the hand around the object</td>
</tr>
<tr>
<td>8</td>
<td>180° rotation of the hand and subject</td>
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</tbody>
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In Condition 4 (180° rotation of the object and subject), after observing a 180° rotation of the object by the experimenter, subjects were asked to stand up and walk 180° in the same direction around to the other side of the table, and be seated. As in Conditions 1 to 3, the object-to-body and object-to-hand relations during pre-rotation trials remained unchanged following rotation of both object and subject.

**Conditions that modify the relation either between object and hand, between object and body, or both.** In Condition 5 (180° rotation of the object), subjects were asked to observe the object being rotated 180° by the experimenter. This rotation modified the relation between the object and the subject’s body, and the relation between the object and the subject’s hand from that during pre-rotation trials. For example, for an object with a left CoM, the heavier side of the object is on the left side of the body and on the thumb side prior to object rotation. Following a 180° rotation of the object, the heavier side of the object is on the right side of the body and on the index finger side.

In Condition 6 (180° rotation of the subject), subjects were asked to stand up and walk 180° around to the other side of the table, and be seated facing the object from the other side of the table. Similar to the manipulation in which the object is rotated 180° (Condition 5), a 180° rotation of the subject modified the object-to-body and the object-to-hand relation from that during pre-rotation trials.

In Condition 7 (180° rotation of the hand around the object), subjects were asked to orient their hand 180° around the object and lift the object in this new hand configuration with the fingertips facing toward the body. This rotation modified the relation between the object and the hand, but maintained the relation between the object and the body, from that during pre-rotation trials. For example, for an object with a right CoM, the heavier side of the object is on the right side of the body before and after hand rotation, but on the index finger side before rotation and on the thumb side after rotation.

In Condition 8 (180° rotation of the hand and subject), unlike the pre-rotation trials in all other conditions, whereby subjects lifted the object with their hand with their fingertips facing away from the body, subjects lifted the object during pre-rotation trials with their hand rotated around the object (as in the post-rotation trials of Condition 7), with their fingertips facing the body. The rationale for this particular pre-rotation trial procedure was based on results from the condition with the 180° rotation of the hand. For this condition (180° rotation of the hand), we found non-collinear digit placement on the first post-rotation trial (i.e. the thumb position was higher than the index fingertip position), regardless of whether the CoM was on the left or
right side. We hypothesized that subjects partitioned their fingertips in this way due to the biomechanical constraints of the hand in this oriented position. With the digits facing the body and the wrist flexed, the non-physiological moment arms and/or the length of the finger flexors compared to their length-tension curve allows for supination to occur with greater ease than pronation. Supination would result in the thumb position being higher than index fingertip position. We tested this hypothesis by examining digit placement on the first pre-rotation trial when subjects had no explicit knowledge of the CoM location. Higher thumb than index finger placement on the first trial (compared to collinear digit placement seen when lifting a visually symmetrical object with the fingers facing away from the body) would support the hypothesis that subjects place their digits in this way due to biomechanical constraints. After the 8 pre-rotation trials, subjects were instructed to move 180°, toward the other side of the table, facing the object from the other side of the table, and lift the object with their fingertips facing away from the body. The procedure of the post-rotation trials was similar to that of the condition with the 180° rotation of the subject. Rotation of the subject and hand modified the body-to-object relation but not the hand-to-object relation from that during pre-rotation trials. For example, for an object with a right CoM, the right side of the body will be on the CoM side before rotation, and the left side will be on the CoM side after rotation, and the index finger will be on the CoM side before and after rotation.

Data Analyses
Time of lift onset was defined as the time point at which the vertical position of the object exceeded 0.1 cm and continued to increase thereafter.

We measured peak object roll (in degrees) on the frontal plane of the object occurring after object lift onset, with positive and negative values denoting rolls in the direction of the thumb and the index finger, respectively.

We recorded digit load force, the vertical force component parallel to the grip surface exerted on the thumb and the index finger to lift the object, and computed the difference between these load forces. A zero value indicates symmetrical load forces by the thumb and the index finger, a positive value indicates that the thumb exerted more load force than the index finger, and a negative value indicates that the index finger exerted more load force than the thumb.

We also calculated the vertical coordinate of the point of resultant digit force relative to the center of the force-torque transducers (center of pressure). Center of pressure for the thumb and the index finger was defined as the vertical distance of each digit from the center of the grip surface/transducer (in mm), using the formula: 

\[ \text{COP} = \frac{[Mx-(Ftan \times w)]}{Fnr} \]

where \( Mx \) is the moment about the x-axis (see Fig 1B), \( Ftan \) is the digit load force, \( w \) is the distance between the surfaces of the force/torque transducer and the grip surface (4 mm), and \( Fnr \) is the mean grip force component perpendicular to the grip surface by the index finger and the thumb. Positive and negative values denote higher and lower center of pressure relative to the center of each transducer. We report the vertical distance between the centers of pressure of the index finger and the thumb (center of pressure difference). A zero value indicates collinear digit center of pressure, a positive value indicates that the thumb’s center of pressure is higher than that of the index finger, and a negative value indicates that the index finger’s center of pressure is higher than that of the thumb.

Finally, we calculated the compensatory moment (N mm) using the formula:

\[ \text{Mom} = \frac{[(\Delta Ftan)^2 + Fnr^2]}{d^2} \]

where \( \Delta Ftan \) is the difference in load force between the thumb and the index finger, \( d \) is the grip width, and \( ACOP \) is the difference between the vertical coordinate of the thumb and index finger center of pressure. Positive and negative values denote compensatory moment generated in the direction of the index finger and thumb, respectively.
Grip force ($F_n$) can contribute to the compensatory moment, and thus roll, if the center of pressure difference between the thumb and the index finger is non-zero. However, we found no significant differences in grip force when comparing the trial preceding and following rotation for each of the conditions for left CoM and right CoM blocks, respectively (all $p$'s > 0.05).

Our main analyses focused on the effect of each rotation on object roll, compensatory moment, difference between the vertical coordinate of thumb and index finger center of pressure, and difference between the load force exerted by the thumb and index finger in each of the conditions for left and right CoM blocks, respectively. Therefore, we ran repeated measures analysis of variance (ANOVA) that examined the effect of trial (last pre-rotation trial, first post-rotation trial, and last post-rotation trial) on all the above variables. For significant main effects, we conducted Bonferroni-adjusted pairwise comparisons to examine differences between the first post-rotation trial and the last pre-rotation trial, and differences between the first post-rotation trial and the last post-rotation trial (setting the $p$ value at 0.016 to adjust for 3 comparisons). We used the non-parametric McNemar's test to examine the difference in direction of compensatory moment and the change in sign of center of pressure difference and load force difference between the last pre-rotation and the first post-rotation trial (see [18]). In addition, we qualitatively compared the extent to which subjects who gave incorrect responses in estimating the heavier side of the object performed differently to those that gave correct responses. Finally, to examine the extent to which learned manipulation transfer varies within conditions that modify object-hand-body relations (Conditions 5–8) and within those that do not modify these relations (Conditions 1–4), we compared roll on the first post-rotation trial within Conditions 5–8 and within Conditions 1–4, respectively, in each of the CoM blocks, using one-way ANOVAs.

Results

We will describe the effect of each rotation in each of the 8 conditions on object roll, compensatory moment, center of pressure difference between the thumb and the index finger, and load force difference between the thumb and the index finger on the first post-rotation trial. Rotations in Conditions 1–4 (360° rotation of object, subject, or both, and 180° rotation of object and subject) maintained the relation between object and body, and between object and hand, from that during pre-rotation trials. Rotations in Conditions 5 and 6 (180° rotation of object and subject, respectively) modified the relations between object and body and between object and hand from that during pre-rotation trials. The rotation in Condition 7 (180° rotation hand rotation) modified the relation between object and hand, but maintained the relation between object and body, from that during pre-rotation trials. Finally, the rotation in Condition 8 (180° rotation of subject and hand) modified the relation between object and body from that during pre-rotation trials, but maintained the relation between object and hand. As described below, subjects in conditions with rotations that maintained the object-body and object-hand relations (Conditions 1–4) continued, after rotation, to generate effective compensatory moments to minimize roll by appropriate digit placement and load force distributions. Subjects in conditions with rotations that modified the relation between object and hand and/or between object and body (Conditions 5–8) did not generate effective compensatory moments and made large rolls after rotations, due to using the same, yet inappropriate digit placement and load force distributions as those used on pre-rotation trials.

Maintaining the relation between object and hand and between object and body

Fig 2 shows object roll, compensatory moment, and center of pressure and load force differences between the thumb and the index finger from a representative subject exposed to a
rotation that did not modify the relation between object and body, and between object and hand from that in pre-rotation trials. Data are from the first and last pre-rotation trial with the subject lifting the object with a left CoM, and from the first post-rotation trial for Condition 3. On the first pre-rotation trial, having not experienced lifting the object, the subject lifted the object as if the CoM was centered in the visually-symmetric object. Specifically, the subject applied symmetrical load force in the thumb and the index finger and placed the thumb and the index finger collinearly. Consequently, the subject generated little or no compensatory moment, resulting in a large object roll to the left (the heavier side). This is the case for all
subjects across conditions. However, by the last pre-rotation trial, the subject exerted larger load force in the thumb than the index finger, and placed the thumb higher than the index finger, which led to an effective compensatory moment that counteracted the external moment created by the CoM (toward the index finger), and minimized roll. This is all consistent with previous work [11,12,15,18,20,26]. Similar to the last pre-rotation trial, on the first post-rotation trial, the subject asymmetrically partitioned load force and digit placement by the thumb and the index finger, and thereby generated an effective compensatory moment to minimize object roll.

Fig 3 shows that these findings were generally representative of all subjects in each of the four conditions (1–4) with rotations that did not modify the body-to-object and hand-to-object relations, and with the CoM of the object on the left and on the right. Other than very few exceptions that are described below, there were negligible differences in mean object roll, compensatory moment, digit center of pressure difference, and digit load force difference between the last pre-rotation trial and the first post-rotation trial, and between the first and the last post-rotation trial. There were no significant main effects of Trial (last pre-rotation, first post-rotation, last post-rotation trial) on object roll, compensatory moment, digit center of pressure difference, and digit load force difference in these conditions, except for the following: (1) object roll in Condition 2 (360° rotation of subject) when subjects lifted an object with a left CoM ($F(2, 18) = 5.56, p < 0.05, \eta_p^2 = 0.38$), with Bonferroni-adjusted pairwise comparisons showing a significant difference between the first and last post-rotation trial, likely reflecting improvement with continual practice; (2) object roll ($F(2, 18) = 5.96, p < 0.05, \eta_p^2 = 0.40$) and compensatory moment ($F(2, 18) = 6.11, p < 0.05, \eta_p^2 = 0.40$) in Condition 3 (360° rotation of subject and the object) in the right CoM block, with significant differences between the last pre-rotation trial and the first post-rotation trials (however, there were no differences between the first and the last post-rotation trials, and the compensatory moment on both last pre-rotation and first post-rotation trials was in the same appropriate direction) and (3) digit center of pressure difference in Condition 1, 360° rotation of the object with a right CoM, ($F(2, 18) = 4.26, p < 0.05, \eta_p^2 = 0.32$), but no significant differences between the first post-rotation trial and both last pre- and post-rotation trials. Despite these differences in roll and compensatory moment, McNemar’s tests showed no significant differences in direction for compensatory moment and in sign for center of pressure difference and load force difference ($p’s > 0.05$) between the last pre-rotation trial and the first post-rotation trial in Conditions 1 to 4. In summary, these conditions predominantly showed no main effects of Trial on roll, compensatory moment, center of pressure difference, and load force difference, and no differences in direction and sign on these variables between pre- and post-rotation trials. This suggests that the act of rotating the object, subject, or both while maintaining the relation between object and body, and between object and digits, as that from trials preceding the rotation, does not disrupt the ability to transfer manipulation learned across trials preceding the rotation.

Disrupting the relation between either object and hand or between object and body, or both

Fig 4 shows data from a representative subject on object roll, compensatory moment, and center of pressure and load force differences between the thumb and index finger on the first and last pre-rotation trial and on the first post-rotation trial. The CoM is on the right during pre-rotation trials and on the left after 180° rotation of object. The relations between the object and subject’s body and between the object and subject’s hand were modified by this rotation. Similar to that seen in Fig 2, the thumb and the index finger load force was symmetrical and the thumb and the index finger center of pressure was collinear during the first pre-rotation trial,
Fig 3. Group means (± 1 standard error) for Conditions 1–4 that maintain object-hand and object-body relations. (A) Object roll with positive and negative values indicating roll towards the thumb and the index finger respectively; (B) Compensatory moment (Mcom) with positive and negative values indicating moments generated away from the thumb and the index finger respectively; (C) Vertical distance between the thumb and the index finger center of pressure (ΔCOP) with positive values indicating higher thumb placement than index finger placement and negative values indicating higher index finger placement than thumb placement; (D) Difference in load force (ΔFtan) by the thumb and the index finger with positive values indicating more force by the
thumb than the index finger and negative values indicating more force by the index finger than the thumb. Data are shown for the first and last pre-rotation trial, and the first and last post-rotation trial, with the object’s CoM on the left (left panel) and on the right (right panel) during pre-rotation trials, for Condition 1 (360° rotation of object; clear), Condition 2 (360° rotation of subject; light gray), Condition 3 (360° rotation of object and subject; dark gray) and Condition 4 (180° rotation of object and subject; medium gray) and Condition 4 (180° rotation of object and subject; dark gray). The first pre-rotation trial for the left and right CoM blocks in each condition is only shown for half of the subjects (because half started the task with the object’s CoM on the left and right, respectively). Statistically significant differences between the first post-rotation trial and the last pre-rotation trial and between the first post-rotation trial and the last post-rotation trial are denoted with an asterisk (*p < 0.05).

thereby resulting in negligible compensatory moment and large object roll. In contrast, during the last pre-rotation trial this subject exerted larger load force in the index finger than the thumb and placed the index finger higher than the thumb. Thus, this subject generated a large

Fig 4. A representative subject’s performance traces by in a condition that modifies object-subject and object-body relations. (A) Object roll; (B) Compensatory moment (Mcom, solid line) and target Mcom (dotted line, plotted as same sign as Mcom for graphical purposes); (C) Center of pressure (COP) by the thumb (dotted line) and the index finger (solid line); (D) Load force (Ftn) by the thumb (dotted line) and the index finger (solid line). Data are shown for the first (left panel) and last pre-rotation trial (middle panel) with the object’s CoM on the right and, following a rotation that modifies both the relation between the object and body and object and hand (Condition 5), the first post-rotation trial (right panel). The vertical dotted line represents the lift onset time.
compensatory moment towards the thumb and minimized object roll accordingly. Ideally, to successfully minimize roll on the first post-rotation trial (with the CoM now shifted to the left), the subject should have applied larger load force and higher center of pressure by the thumb than the index finger, thereby generating a compensatory moment towards the index finger. In contrast to this ideal strategy, this subject continued to place his index finger higher than the thumb, and exerted larger load force by his index finger than the thumb on the first post-rotation trial. Thus, the compensatory moment was in the same, yet inappropriate, direction as that at the last pre-rotation trial, which resulted in large object roll. As described below, these findings were generally representative of subjects in conditions in which the rotation modified the relations between the object and body and/or between the object and hand, with a couple of nuances in digit placement that are described below. We report below group data from each of the conditions that disrupt the relation between object and hand and object and body (Conditions 5 and 6) and conditions that disrupt the relation between object and hand (Condition 7) and object and body (Condition 8).

Disrupting the relation between object and hand and between object and body. Fig.5 shows mean peak roll, compensatory moment, center of pressure difference and load force difference between the thumb and the index finger on the first and last pre-rotation and on the first and last post-rotation trials, with the CoM of the object on the left and right for Conditions 5 (180° rotation of object) and 6 (180° rotation of subject). Compared to the last pre-rotation trial and the last post-rotation trial, subjects typically produced a large object roll and little compensatory moment on the first post-rotation trial, both of which were in the direction of the CoM. For both conditions and with the CoM on either side, there were significant main effects of Trial on roll (Condition 5 left CoM: F(2, 18) = 44.98, p < 0.05, η² = 0.83, right CoM: F(2, 18) = 45.40, p < 0.05, η² = 0.84; Condition 6 left CoM: F(2, 18) = 35.77, p < 0.05, η² = 0.80, right CoM: F(2, 18) = 16.24, p < 0.05, η² = 0.64) and compensatory moment (Condition 5 left CoM: F(2, 18) = 87.40, p < 0.05, η² = 0.91, right CoM: F(2, 18) = 86.82, p < 0.05, η² = 0.91; Condition 6 left CoM: F(2, 18) = 77.42, p < 0.05, η² = 0.90, right CoM: F(2, 18) = 17.53, p < 0.05, η² = 0.66), with very large effect sizes. Bonferroni-adjusted pairwise comparisons showed significantly larger object roll on the first post-rotation trial than both the last pre-rotation trial and the last post-rotation trial in both conditions. In the condition with the 180° rotation of object (with a right CoM during pre-rotation trials), compensatory moment was significantly smaller on the first post-rotation trial than both last pre- and last post-rotation trials. In the conditions with 180° rotation of object (with a left CoM during pre-rotation trials) and subject (with left CoM and right CoM during pre-rotation trials), compensatory moment was significantly smaller on the first post-rotation trial than the last post-rotation trial, but not the last pre-rotation trial. In addition, there was no significant difference in direction of compensatory moment between the last pre-rotation trial and the first post-rotation trial (p > 0.05). These findings suggest that these rotations disrupted the ability of subjects to transfer learned manipulation from trials preceding the rotation to the first trial after the rotation. Fig.5 also shows that subjects continued to use the same, yet inappropriate, digit placement and force distributions on the first post-rotation trial as on the last pre-rotation trial, or tended to use collinear digit placement. There were significant main effects of Trial on digit center of pressure difference (Condition 5 left CoM: F(2, 18) = 18.45, p < 0.05, η² = 0.67, right CoM: F(2, 18) = 10.71, p < 0.05, η² = 0.54; Condition 6 left CoM: F(2, 18) = 6.13, p < 0.05, η² = 0.41, right CoM: p > 0.05). Bonferroni-adjusted pairwise comparisons showed that there were no significant differences between the last pre-rotation trial and the first post-rotation trial for all conditions. We found, however, significant differences in digit placement between the first and last post rotation trial (Condition 5, left and right CoM blocks). Finally, significant main effects of Trial on load force difference in all conditions with the CoM on either side (Condition 5 left
Fig 5. Group means (±1 standard error) for Conditions 5–6 that modify object-hand and object-body relations. (A) Object roll with positive and negative values indicating roll towards the thumb and the index finger respectively; (B) Compensatory moment (Mcom) with positive and negative values indicating moments generated away from the thumb and the index finger respectively; (C) Vertical distance between the thumb and the index finger center of pressure (ΔCOP) with positive values indicating higher thumb than index finger placement and negative values indicating higher index finger than thumb placement; (D) Difference in load force (ΔFtan) by the thumb and the index finger with positive values indicating more force by the thumb than the index finger.
and negative values indicating more force by the index finger than the thumb. Data are shown for the first and last pre-rotation trial, and the first last post-rotation trial, with the object's CoM on the left (left panel) and on the right (right panel) during pre-rotation trials, for Condition 5 (180° rotation of object; clear) and Condition 6 (subject 180° rotation of object; light gray). The first pre-rotation trial for the left and right CoM blocks in each condition is only shown for half of the subjects (because half started the task with the object’s CoM on the left and right, respectively). Statistically significant differences between the first post-rotation trial and the last pre-rotation and between the first post-rotation trial and the last post-rotation trial are denoted with an asterisk (p < 0.05).

CoM: (F(2, 18) = 23.00, p < 0.05, η² = 0.72; right CoM: (F(2, 18) = 13.92, p < 0.05, η² = 0.61; Condition 6 left CoM: (F(2, 18) = 9.41, p < 0.05, η² = 0.51; right CoM: (F(2, 18) = 32.49, p < 0.05, η² = 0.78) were due to differences between the first and last post-rotation trials (Conditions 5 left CoM and right CoM blocks, Condition 6, right CoM block). Taking center of pressure difference and load force difference results together, most of the main effects were due to significant differences between the first- and last post-rotation trials, with negligible differences between the last pre-rotation trial and the first post-rotation trial. This suggests that subjects adopted similar force and digit placement distributions on the first post-rotation trial as on the last pre-rotation trial, which were dissimilar to that used on the last post-rotation trial. Although in some cases there were negligible differences between the first and the last post-rotation trials, center of pressure difference and load force difference at the first post-rotation trial were in the same direction as those at the last pre-rotation trial in both conditions and CoM blocks (all p’s > 0.05). Together, these results suggest that rotating an object or subject in a way that modifies the relation between both object and body and object and hand, from that during pre-rotation trials disrupts the ability to transfer learned manipulation.

Disrupting the relation between object and hand while maintaining the relation between object and body. Fig 6 shows mean peak roll, compensatory moment, center of pressure and load force differences between the thumb and the index finger at the first and last pre-rotation trial, the first and last post-rotation trial, in both left and right CoM blocks for Condition 7 (180° rotation of hand). As the figure shows, on the first trial after hand rotation with the CoM on the left (index finger side), subjects placed the thumb higher than the index finger, and exerted more load force with the index finger than the thumb. The combined effect of these responses resulted in negligible compensatory moment and large object roll. This particular configuration of load force and center of pressure by the index finger and the thumb was also seen on the first post-rotation trial with the CoM of the object on right (thumb side). In both CoM blocks, compensatory moment was generated towards the index finger, which is the appropriate direction when the object’s CoM is on the right, but not the left. Nevertheless, as Fig 6 shows, subjects produced large rolls on this first post-rotation trial in both CoM blocks, albeit smaller when the CoM was on the right. We found significant main effects of Trial on roll for both left CoM (F(2, 18) = 30.90, p < 0.05, η² = 0.77) and right CoM blocks (F(2, 18) = 15.32, p < 0.05, η² = 0.63) with large effect sizes. Pairwise comparisons showed significant differences in roll between the first post-rotation trial and the last post-rotation trial in both CoM blocks, but a significant difference between the first and last post-rotation trial only for the left CoM block. This suggests that subjects minimized roll on the first post-rotation trial similarly to that on the last post-rotation trial in the right CoM block, but failed to do so in the left CoM block. We found significant main effects of Trial on compensatory moment when the object CoM was on the left (F(2, 18) = 36.09, p < 0.05, η² = 0.80) and right (F(2, 18) = 28.12, p < 0.05, η² = 0.76) with large effect sizes. Pairwise comparisons showed significant difference between the first and last post-rotation trial, but not the last pre-rotation trial, for the left CoM block, and a significant difference between the first post-rotation trial and last pre-rotation trial, but not the last post-rotation trial, for the right CoM block. Again, this indicates the compensatory moment on the first post-rotation trial was similar to that on the last post-rotation trial in the right CoM block, but not the left CoM block. In addition, a significant difference in
Fig 6. Group means (± 1 standard error) for Condition 7 that modifies the object-hand relation.
(A) Object roll with positive and negative values indicating roll towards the thumb and the index finger respectively. (B) Compensatory moment (Mcom) with positive and negative values indicating moments generated away from the thumb and the index finger respectively. (C) Vertical distance between the thumb and the index finger center of pressure (ΔCOP) with positive values indicating higher thumb than index finger.
placement and negative values indicating higher index finger than thumb placement, and (D) Difference in load force (ΔFtanj) by the thumb and the index finger with positive values indicating more force by the thumb than the index finger and negative values indicating more force by the index finger than the thumb. Data are shown for the first and last pre-rotation trial, and for the first and last post-rotation trial, with the object’s CoM on the left (left panel) and on the right (right panel) during pre-rotation trials. The first pre-rotation trial for the left and right CoM blocks is only shown for half of the subjects (because half started the task with the object’s CoM on the left and right, respectively). Statistically significant differences between the first post-rotation trial and the last pre-rotation and between the first post-rotation trial and the last post-rotation trial are denoted with an asterisk (p < 0.05).

direction between the last pre-rotation trial and the first post-rotation trial in the right CoM block (p < 0.05) but not in the left CoM block (p > 0.05) suggests that subjects transferred learned manipulation after hand rotation to a greater extent when the object’s CoM was on the right than the left. We found a significant main effect of Trial on load force difference for the left CoM block with a large effect size (F(2, 18) = 22.69, p < 0.05, η² = 0.72). Pairwise comparisons showed a significant difference between the last pre-rotation trial and the first post-rotation trial (and a significant change in sign, p < 0.05), and no significant main effect of trial on load force difference for the right CoM block (and no change in sign, p > 0.05). We also found significant main effects of Trial on center of pressure difference for the left (F(2, 18) = 5.58, p < 0.05, η² = 0.38) and right CoM blocks (F(2, 18) = 12.81, p < 0.05, η² = 0.59) with large effect sizes. In addition, pairwise comparisons showed a significant difference between the first post-rotation trial and the last pre-rotation trial for the right CoM block (and with the sign only changing for the right, but not left block), and no difference between the first and last post-rotation trial for both CoM blocks.

In summary, we show differing results for left and right CoM blocks. Subjects failed to minimize roll on the first post-rotation trial more so when lifting an object with a left than a right CoM when the hand is oriented around the object, all of which might be a function of the biomechanical constraints of the hand in this orientation. Higher positioning of the thumb than index finger instead of collinear digit placement on the very first pre-rotation trial with the hand rotated around the object (when subjects have no knowledge of the asymmetric CoM in the visually symmetric appearing object) would support the hypothesis that biomechanical constraints of the hand in this orientation contributes to this particular digit partitioning, and thus compensatory moment and object roll results obtained in Condition 7. We report our examination of this hypothesis in the next section.

Disrupting the relation between object and body while maintaining the relation between object and hand. In this condition (Condition 8), subjects lifted the object on the pre-rotation trials with the hand rotated around the object such that the fingertips faced the body, and following the pre-rotation trials, moved to the other side of the table and lifted the object such that the fingertips faced away from the body. The object CoM was on the same digit-side on pre and post-rotation trials. Fig 7 shows mean object roll, compensatory moment, center of pressure and load force by the index finger and the thumb, on the first and last pre-rotation trial, and on the first and last post-rotation trials of Condition 8. On the first post-rotation trial, compared to the last pre-rotation trial and the last rotation trial, object roll was larger and the compensatory moment was in the opposite (p’s < 0.05), and incorrect, direction in both CoM blocks. With significant main effects of Trial on roll (left CoM: F(2, 18) = 15.86, p < 0.05, η² = 0.64; right CoM: F(2, 18) = 43.51, p < 0.05, η² = 0.83) and compensatory moment (left CoM: F(2, 18) = 23.15, p < 0.05, η² = 0.72; right CoM: F(2, 18) = 21.78, p < 0.05, η² = 0.71), pairwise comparisons showed significant differences between the first post-rotation and both the last pre-rotation trial and the last post-rotation trial. Fig 7 shows positive center of pressure difference values in both left and right CoM blocks on the first and
Fig 7. Group means (± 1 standard error) for Condition 8 that modifies the object-body relation. (A) Object roll with positive and negative values indicating roll towards the thumb and the index finger respectively. (B) Compensatory moment (Mcom) with positive and negative values indicating moments generated away from the thumb and the index finger respectively. (C) Vertical distance between the thumb and the index finger center of pressure (ΔCOP) with positive values indicating higher thumb than index finger.
last pre-rotation trial, indicating higher thumb than index placement. The higher placement of the thumb than index finger on the first and last pre-rotation trial in the left CoM block, while the index finger is on the heavier side of the object, further supports the hypothesis for this particular digit placement configuration and hand orientation to be a function of the biomechanical constraints of the hand. We found significant main effect of Trial on center of pressure difference in the left (F(2, 18) = 7.40, p < 0.05, η² = 0.45) and right CoM blocks (F(2, 18) = 13.24, p < 0.05, η² = 0.66). However, there were no significant differences between the first post-rotation trial and both last pre-rotation trial and last post-rotation trial in the left CoM block. In the right CoM block, we found a significant difference between the first post-rotation trial and the last pre-rotation trial, and no difference between first and last post-rotation trials. Finally, load force difference, as shown in Fig 7, was typically smaller on the first post-rotation trial than the last post-rotation trial (both CoM blocks) and the last pre-rotation trial (left CoM block only). We found significant main effects of Trial on load force difference for both left (F (2, 18) = 7.93, p < 0.05, η² = 0.47) and right CoM blocks (F(2, 18) = 8.91, p < 0.05, η² = 0.50). Pairwise comparisons showed significant differences between the first post-rotation trial and the last post-rotation trial for the right CoM block, and a significant difference between the first post-rotation trial and the last pre-rotation for the left CoM block. Although there were some significant differences between the last pre-rotation trial and the first post-rotation trial in center of pressure difference (right CoM block) and load force difference (left CoM block), McNemar’s tests showed no significant change in sign between the last pre-rotation trial and the first post-rotation trial for either of these variables in either CoM blocks. Taken together, the results suggest that modifying the relation between the object and the body while maintaining the relation between the object and digits disrupts the ability to transfer manipulations learned in the trials preceding the rotation.

Comparing object roll following rotation in subjects who correctly and incorrectly estimated CoM-side of the object

As indicated above, we excluded 7 subjects who were unable to verbally indicate the side of the object that was heavier following the last pre-rotation trial. If we included these subjects, we could not have ruled out that failed learning transfer following rotation in any of the conditions was due to not having explicit knowledge of the CoM location. Surprisingly, the mean object roll on the first post-rotation trial by subjects within Conditions 1 to 4 who gave an incorrect estimate of CoM location in both left (n = 3; M = 2.27, SD = 1.91) and right CoM blocks (n = 3; M = -3.08, SD = .39) was within the standard deviation of the mean object roll by subjects within the same conditions who gave correct CoM-side estimates (Conditions 1–4: left CoM block: M = 2.62, SD = 2.64, right CoM block: M = -3.13, SD = 2.91), respectively. Similarly, object roll on the first post-rotation trial by the one subject in Condition 6 who gave an incorrect CoM-side estimate in the left CoM block (M = -15.03) was also within the standard deviation of the mean object roll by subjects in the same condition and block who gave correct
CoM-side estimates ($M = -10.52, SD = 5.86$). Thus, the inability to explicitly identify the heavier side seemingly did not affect task performance.

Comparing learning transfer within conditions that modify and within conditions that maintain relations between object, hand, and body

As the above results showed, any rotations that disrupted the relation between object and body, object and hand, and both, impaired the ability of subjects to successfully minimize roll on the first post-rotation trial whereas rotations that maintained these relations gave no such impairments. We compared object roll on the first post-rotation trial within Conditions 5–8, which modified the relation between object and hand, or object and body, or both. We also compared object roll on the first post-rotation trial within Conditions 1 to 4, which maintained the relations between object and hand and object and body. In both comparisons, we found no significant differences in object roll on the first post-rotation trials within Conditions 1 to 4 and within Conditions 5 to 8, for left and right CoM blocks, respectively (all $p’s > 0.05$). These findings suggest that disruption to any relation (object and body, object and hand, both) in which an object manipulation task is learned will give way to impaired performance of similar magnitudes.

Discussion

We examined the ability to minimize roll of an object with an asymmetric mass distribution during a grasp and lift task, followed by rotations that either maintained (Conditions 1–4) or modified (Conditions 5–8) the relation between the object and the body, hand, or both, from that preceding the rotation. This task required modulating compensatory moment, through a combination of asymmetric partitioning of digit position and load force by the thumb and the index finger, to minimize object roll. Subjects in Conditions 1 to 4 generated an appropriate compensatory moment to minimize roll on the last pre-rotation and on the first post-rotation trial. Therefore, there was a transfer in learned compensatory moment to minimize roll following rotations in Conditions 1 to 4. In contrast, and as hypothesized, following rotations in Conditions 5 to 8, there generally were large differences in the ability to transfer learned compensatory moment and therefore minimize roll on the first post-rotation trial. Specifically, subjects produced large object rolls compared to the last pre- and the last post-rotation trials.

Together, these findings extend those of previous studies in two important ways. First, successful transfer of learned manipulation following rotations in Conditions 1 to 4 suggests that failed transfer of learning following rotations in Conditions 5 to 8 is not an artifact of having visually observed and/or performed a rotation. Second, failed learning transfer also occurs (and of similar magnitude) when modifying either object-to-body or object-to-hand relations compared to modifying both relations. This suggests that modifying one reference frame is no more detrimental to grasp performance than another. As described below, these findings support the notion that internal representations of learned manipulations of objects with asymmetric mass distributions are specific to the context and reference frames in which they were learned and, therefore, that multiple representations exist for sensorimotor control of the hand [22,23].

Previous studies that investigated the effect on grasp performance of rotating objects with asymmetric mass distributions did not consider an alternative explanation for failed learning transfer. Specifically, given the complexities involved in mental rotation, any kind of rotation (even that which maintains body and hand frames) might disrupt the ability to minimize roll. Here we show that subjects could transfer learned manipulation following rotations that maintain hand and body frames relative to the object, even in conditions whereby the orientation of the object is changed from that prior to the rotation (180° rotation of object and subject).
These findings suggest that the rotation experienced or performed, which subjects were asked to attend to (by watching the object being rotated, or watching the object as they moved around it), did not disrupt their ability to successfully retrieve and use the internal representation formed during trials preceding the rotation. The fact that experiencing a rotation was not detrimental to grasp performance in Conditions 1 to 4 suggests that the disruption in grasp performance following rotations in Conditions 5 to 8 is unlikely a byproduct of observing or performing a rotation. Thus, our findings support the notion that internal representations of learned manipulations with objects with asymmetric mass distributions are specific to the hand and body frames (relative to the object) in which the manipulation was first learned.

The fact that in Conditions 5 to 8 subjects generally failed to counteract the external moment on the object and thus to prevent object roll in the direction of the CoM following 180° rotation of object, subject, hand, and hand and subject, are consistent with findings from previous object rotation and hand translation studies [11,12,13,15,18,20,21]. Specifically, this previous work and our findings showed that failure to prevent object roll on the first post-rotation trial is due to inappropriate scaling of forces [11,12,13,15,21] as well as inappropriate digit placement [18,20]. Inspection of digit and force partitioning by the thumb and the index thumb following rotations of object, subject, hand, and hand and subject (see Figs 4 through 7), as well as results from McNemar’s tests, indicate that subjects in these conditions typically followed the same, yet inappropriate, digit and force partitioning pattern following rotation as that prior to rotation. There were some exceptions, where subjects reverted to a ‘default’ digit force-position pattern following rotation, whereby the object was treated as having a symmetrically distributed mass, e.g. applying the same load force by index finger and thumb—see Fig 7, left CoM. The phenomenon of implementing the same motor output following a rotation perturbation is reminiscent of that seen in reaching studies. Specifically, after adapting to Coriolis forces [27] viscous forces [28,29,30,31], inertial loads [32], or rotations of visual feedback about the hand [33,34,35,36,37], subjects continued to use the same motor command and adopted the same movement strategies, thereby resulting in aftereffects. As has also been shown in visuomotor reaching studies [36], one might expect learning transfer to fall off continuously as a function of the magnitude of the rotation relative to the training direction (that is, if the same mechanism is shared across our task and learning of reaching movements). Our present findings suggest that such deterioration in learning transfer might be a function of the change in body-to-object relation associated with the increase in angle from the training direction. We did not test rotations less than 180° as they would necessitate maintaining the hand-object relation and/or placing the hand in a biomechanically awkward position after rotation. However, it should be noted that even after 360° rotations, subjects could successfully transfer learned manipulation. Thus, we conclude it is unlikely that our findings are dependent on the magnitude of the rotation relative to the trained direction.

Our findings support the conclusions of a study by [22] that examined how the experience with the dynamics of a specific hammer in one orientation generalized to other orientations. The aim of [22]’s study was to test two alternative hypotheses about whether the motor system used multiple representations of the dynamics associated with different tool orientations or, conversely, whether the motor system used a single general representation that applied to all virtual tool orientations. These authors argued that transfer of learning in one orientation to a novel orientation would support the notion of a single representation applying to all orientations, whereas limited transfer to a novel orientation would support the existence of multiple orientation-specific representations. Their results support the latter hypothesis as there was limited learning transfer when the hammer was presented in a novel orientation relative to the one subjects learned the manipulation in. In addition, and consistent with our findings, [22] showed that subjects were not using a default force pattern in this new orientation, but were
using the same force pattern as that used during the training orientation. Their results and ours suggest that internal representations of object manipulation are orientation specific, and that multiple representations exist for sensorimotor control, with the appropriate representation being selected based on the context in which the movement occurs [22,23,38,39,40]. Furthermore, when a mismatch occurs in the reference frame between the learned orientation (in which an object manipulation task is learned) and a novel orientation, the manner with which an object is first grasped in a novel orientation (with regards to forces and position) generally mimics the manner with which it was grasped in the preceding orientation. This is at least the case during the early stages of sensorimotor learning.

The nature of internal representations relating to previous experiences with objects with asymmetric mass distributions is not well understood. For example, it is unknown whether the reference frame of every formed representations in one orientation is, relative to the object, specific to the hand, the body, or both, because rotations used by studies to date (mostly 180° rotation of object) modified both relations between the object and body and between the object and hand. In the present experiments, we included conditions that either modified the relation between object and body, or between object and hand, or both, to determine if the same magnitude of disruption to grasp performance would occur in each of these conditions. This was found to be the case. From these findings, it could be that the internal representation is not only specific to the hand (and digits) with which the task was learned, but the representation is also specific to the body position (relative to the object) in which the task was learned. Disrupting either the relation between the object and digits, or between the object and body position, will give way to deteriorated grasp performance of similar magnitude. However, there might be another contributing factor that failed learning transfer in Condition 7 (hand rotation) and Condition 8 (hand and subject rotation), the conditions which disrupted either hand or body frames, respectively. Rotations in these conditions not only changed the hand position relative to the object (Condition 7) or the body position relative to the object (Condition 8). The rotations in these conditions also changed the hand position relative to the body (from the fingers pointing away from the body prior to rotation to the fingers pointing toward the body following rotation in Condition 7, and vice versa in Condition 8). Thus, another factor that could explain failed transfer of learned manipulation is that the learned representation is also specific to the hand position relative to the body position. If this is the case, then the learned representation, which is specific to the hand and body relation in which it was formed, cannot be used to successfully grasp the object when the map between hand and body changes.

A study by [15] included a condition similar to our Condition 7, which involved rotation of the hand around the object. They reported learning following rotation of the hand, which is in line with what we found in the right CoM block, but not the left CoM block. The results from Condition 7 (right CoM block) and that from [15] are in contrast to all other findings from conditions with rotations that modified hand and/or body frames from that prior to the rotation. When the object’s CoM was on the right, and following a rotation of the hand around the object, roll was in the direction of the CoM but not significantly larger than that on the last trial following rotation. In addition, unlike all other findings from conditions with modified hand or body frames (or both), compensatory moment was in the same direction at the first and last post-rotation trial. From inspection of Fig.6, it seems that this appropriate behavior on the first trial following rotation was a result of higher thumb than index finger placement when the hand was oriented around the object. The fact that the same digit partitioning was seen in both CoM blocks following hand rotation led to our hypothesis that such behavior could have been due to the biomechanical constraints imposed on the hand when placed in this particular orientation. Similar asymmetrical digit partitioning on the first trial of Condition 8 (when the hand was also oriented around the object) supported our hypothesis
that this particular digit placement configuration and hand orientation was a function of the biomechanical constraints of the hand. Interestingly, in both CoM blocks on the first post-rotation trial of Condition 7, subjects exerted more load force with the index finger than the thumb. This phenomenon, too, could be confounded by biomechanical factors, i.e. higher thumb than index placement might have to be accompanied by higher load force by the index finger than the thumb to prevent the object from slipping. The biomechanical constraints of the hand with the fingertips oriented toward the subject can similarly explain the results from [15] study. They combined findings from lifting an object with a left CoM and right CoM, respectively, such that it was not possible to see whether differences were seen between these different blocks. Nevertheless, since they do not report forces and did not measure digit position, it is unknown whether subjects exhibited the same digit force and position partitioning on the first post-rotation trial as what was shown here. Thus, we conclude that the likely contribution of biomechanical constraints of the hand in this orientation to behavioral results of our Condition 7 (appropriate behavior in the right CoM block but inappropriate behavior in the left CoM block), and of [15], cannot be ruled out.

Finally, the finding that subjects who were unable to articulate explicit knowledge of the CoM fared no worse in minimizing object roll than subjects who could do so is consistent with the proposition that consecutive exposure to manipulations of an object with a given CoM location allows for implicit learning about the magnitude and direction of the external torque caused by the added mass [18]. Furthermore, this result suggests that explicit knowledge of the object CoM was not necessary for successful grasp performance in this subset of subjects. However, it remains to be determined why this mismatch between implicit and explicit knowledge of object CoM occurred only in this subset of subjects.

In summary, our findings extend those of previous object rotation studies by showing failed transfer of learning following rotation is not simply an artifact of having visually observed or performed a rotation. Furthermore, our findings suggest that internal representations of an object with an asymmetric CoM are orientation-specific, and that there are multiple representations for manipulating these objects in multiple orientations. These internal representations can be retrieved and used to successfully manipulate an object only when the reference frame in which the manipulation was learned matches the reference frame in which the manipulation is performed, at least during the early stages of sensorimotor learning.

Supporting Information

S1 File. Individual data points for all subjects in each of the 8 conditions. (XLSX)

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Author Contributions

Conceived and designed the experiments: MM EK TLM MS AMG. Performed the experiments: MM EK TLM. Analyzed the data: MM EK TLM MS AMG. Wrote the paper: MM EK TLM MS AG.

References


APPENDIX D

Digit Position and Forces Covary during Anticipatory Control of Whole-Hand Manipulation

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Theoretical perspectives on anticipatory planning of object manipulation have traditionally been informed by studies that have investigated kinematics (hand shaping and digit position) and kinetics (forces) in isolation. This poses limitations on our understanding of the integration of such domains, which have recently been shown to be strongly interdependent. Specifically, recent studies revealed strong covariation of digit position and joint forces during the loading phase of two-digit grasping. Here, we determined whether such digit force-position covariation is a general feature of grasping. We investigated the coordination of digit position and forces during five-digit whole-hand manipulation of an object with a variable mass distribution. Subjects were instructed to prevent object roll during the lift. As found in precision grasping, there was strong trial-to-trial covariation of digit position and force. This suggests that the natural variation of digit position that is compensated for by trial-to-trial variation in digit forces is a fundamental feature of grasp control and not only specific to precision grasp. However, a main difference with precision grasping was that modulation of digit position to the object’s mass distribution was driven predominantly by the thumb, with little to no modulation of finger position. Modulation of thumb position rather than fingers is likely due to its greater range of motion and therefore adaptability to object properties. Our results underscore the flexibility of the central nervous system in implementing a range of solutions along the digit force-to-position continuum for dexterous manipulation.

Keywords: grasp control, anticipatory planning, whole hand manipulation, object manipulation, digit position, load force, kinematics, kinetics

INTRODUCTION

Successful object manipulation is thought to rely on the use of stored internal representations of an object’s properties (Johansson and Westling, 1988; Gordon et al., 1991a,b, 1993). These representations are updated through anticipatory feedback and feedback mechanisms (for a review Johansson and Flanagan, 2005). Most work informing the above theory studied either kinematics (hand shaping e.g., Jeannerod, 1984; Santello and Soechting, 1998; Santello et al., 2002; Assazini et al., 2016) and digit positioning e.g., Cohen and Rosenbaum, 2004; Lukos et al., 2007) or kinetics (fingertip forces e.g., Westling and Johansson, 1987; Salimi et al., 2000, 2003; Reilman et al., 2001; Patalay et al., 2004; Crajé et al., 2013).
these interdependent domains in isolation limits our understanding of their integration for planning and execution of object manipulation. For example, most studies on grasp kinetics focused how subjects modulate digit forces to object properties when grasping an object at fixed contact points. This task allows creating an internal representation of the forces, but only at those fixed contact points. Fu et al. (2010) addressed this limitation by studying planning of forces with unconstrained digit positions during two-digit object manipulation. The mass distribution was centered or off-centered and the task goal was to minimize object roll at lift onset. Visual cues of object properties were not salient (the object was symmetrically shaped but asymmetrical in mass distribution). Thus, internal representations formed during earlier experiences of the object were to be used to anticipatorily modulate position and forces. With unconstrained digit positions, subjects modulated both digit position and load forces to the object’s center of mass (CoM), e.g., higher load forces and digit positioning on the heavier object side. They found strong correlations between the vertical distance of thumb and index fingertip and forces on a trial-by-trial basis. Importantly, the compensatory moment (Mcom) counteracting the external torque of the CoM was statistically indistinguishable between the “unconstrained” and “constrained” grasp groups.

The authors argued that modulating digit forces in response to digit position minimized Mcom variability. Digit position and force modulation has been replicated in other two-digit manipulation studies (Zhang et al., 2010; Fu and Santello, 2014; Marneweck et al., 2015). Thus, constraining digit position, like most previous work, prevents fundamental features of dexterous grasp control: (1) modulating digit position to object properties and task demands, and (2) modulating digit forces to compensate for trial-to-trial digit position variability.

Whether these phenomena of digit position modulation and successive force modulation are a general feature of grasp control, and not specific to precision grasp control, is unknown. For example, in another commonly employed grasp type, whole-hand grasping, four-finger positioning might not be modulated to the same extent as the index finger during two-digit (precision) grasping, given the former’s constraints to change individual finger position relative to the thumb during whole-hand grasping (Santello et al., 2013). In precision grasping, it was proposed that the functional role of modulating position was minimizing force and effort (given its link with lower grip force; Fu et al., 2010). In whole-hand grasping, the availability of more digits might weaken the need to implement a criterion of grip force minimization since they can simply alter the force distribution between digits (e.g., change force sharing patterns). Thus, digit position and forces during whole-hand grasping might not be modulated to the same extent as that found during precision grasping. Reports of differential neural circuits between precision and whole-hand grasping (e.g., Begliomini et al., 2007) further supports the possibility for differential behavioral idiosyncrasies between such grip types, such as how force and position is utilized during anticipatory planning of object manipulation.

Here, we determined digit position and forces modulation during anticipatory control of learned whole-hand object manipulation (object roll minimization) of a box with a centered and off-centered CoM, respectively. To achieve the task goal of minimizing object roll at lift onset, by matching the expected CoM location (and thus counteracting the external torque), digit position and force modulation must be anticipatory (in this case, based on prior lifting experience with the object), because no feedback about the actual CoM location is available until after lift onset. First, we hypothesized that subjects would modulate digit position and load force to the object’s CoM prior to lift onset (i.e., before sensory feedback signaling mass and its distribution becomes available). However, we expected less modulation of position by the four fingers than the thumb, given their aforementioned biomechanical constraints. Second, we hypothesized a strong trial-to-trial covariation in position and force.

**MATERIALS AND METHODS**

**Subjects**

Twelve healthy adult subjects (eight females, age in years: Mean = 26, SD = 4) with normal or corrected-to-normal vision took part in the experiment. Subjects were right-handed (Oldfield, 1971) and reported no upper limb orthopedic impairments (or any other issue that might affect grasp performance). All subjects gave written informed consent to the study prior to testing in accordance with the Declaration of Helsinki. The experimental protocols were submitted to, and approved by, the Institutional Review Board at Teachers College, Columbia University.

**Materials and Procedures**

Subjects were asked to grasp and lift, using a whole hand grip, a rectangular box with a concealed CoM that was centered or off-centered (on the left or right side of the box; Figure 1). The aim of the task was to prevent object roll.

The surfaces of the rectangular box (height: 16.5 cm; width: 8 cm; depth: 8.5 cm) concealed the position of the added mass (see below). Thus, when the CoM was centered, the object was symmetrical in appearance and in mass distribution. When the CoM was off-centered, the object was still symmetrical in appearance, but not in mass distribution (Figure 1A). To vary the mass distribution, two lead blocks (each with a height of 5 cm, width of 8 cm, depth of 1 cm, and mass of 370 g) were placed on the left, center, or right side of the box (Figure 1B). The external torque created by a left or right mass distribution was ±21.74 Ncm.

The two lateral grip surfaces of the box were made of carbon fiber (height: 15.2 cm; width: 7.6 cm; thickness: 3 mm). The carbon fiber sheet was covered with a thin balsawood sheet (thickness: 2 mm) to cover the screws that attached the carbon fiber sheet to the force transducer. Sandpaper was affixed to the balsawood to increase the friction between the digits and the object’s contact surface. The front, back, and top side of the box were detachable as a unit from the grip surface sides to easily shift the CoM (Figure 1B).
A force/torque transducer (Mini 40, ATI Industrial Automation, NC, USA) was affixed to each of the grip surfaces. The transducers measured load force, grip force, and moments exerted by the digits with resolutions of 0.01 N, 0.02 N and 0.0125 Ncm, respectively. Note that the force/torque transducer on the finger side of the grip device measured the total grip and load forces exerted by all fingers, as well as the net moment of all fingers relative to the center of the sensor. An electromagnetic position-angle sensor (Polhemus Fastrack; angular resolution: 0.025°; displacement resolution: 0.0005 cm) was attached at the top of the box to measure object roll. The total mass of the box, with the force transducers, position-angle sensor, and lead blocks was 1270 g. Fingertip force data were sampled at 500 Hz and position data were sampled at 120 Hz using SC/Zoom (Umeå University, Sweden). Data collected were filtered using a second-order low pass Butterworth filter with a cut-off of 6 Hz, and the force/torque transducer data were synchronized by interpolating with position data offline.

A webcam was affixed to the edge of the table, 45 cm to the grasp surface of the box and in line with the center of the box, to record the position of the index, middle, ring, and little fingertips (resolution: 640 × 480; frame rate: 25 frames/s). This recording was done because individual position of the four fingertips could not be determined from the center of pressure (COP) recorded by the force transducer, which can only record the net COP of all four fingertips (see below). The thumb position was determined from the COP recorded by that transducer.

Subjects sat in front of a height-adjustable table facing the box with the right elbow flexed approximately 90° in the parasagittal plane. The right shoulder was aligned with the midpoint of the box. The right hand was placed palm facing down at a marked start location, which was 12 cm from the midpoint of the box. Following an auditory cue, subjects were instructed to reach from the marked start location, grasp the grip surfaces with the tips of the thumb and fingers of the hand, and lift the box at a self-selected speed to the height of an adjacent marker (10 cm). Following a second auditory cue, occurring 1.5 s after the vertical distance of the box exceeded 6 cm, subjects were instructed to replace both box and hand back to their respective start locations. Subjects were asked to minimize the roll of the box as best as they could. No instruction was given regarding fingertip position on the box.

There were three blocks of trials, each corresponding to the CoM on the left, center and right side (with the block order following a Latin Square sequence across subjects). When the CoM was on the left, subjects were to produce a supination moment to counter the external torque of the mass. When the CoM was on the right, subjects were to produce a pronation moment to counter the external torque caused by the added mass. For each block, there were five practice trials and 20 test trials with a 5-s inter-stimulus interval between trials (recorded from the second auditory cue). Practice trials were given to ensure correct execution of the task during the 20 test trials, which was the main focus of analyses. The number of practice trials was chosen based on previous studies with similar tasks that showed that subjects can learn an object roll minimization task within three trials (e.g., Fu et al., 2010).

**Data Analyses**

We quantified peak roll (in degrees) on the frontal plane of the box occurring after lift onset. Lift onset was defined as the time at which the vertical position of the object (as measured from the table surface) exceeded 1 mm and continued to increase thereafter. Subjects at times would exceed this 1-mm position criterion by means of a movement in a roll or pitch direction (with some part of the box not fully lifted from the table). However, we chose this stringent criterion for defining object lift onset to avoid as best possible any influence of feedback signaling mass and distribution on
our measures, which were primarily focused on anticipatory control of digit position and forces. Positive and negative values denote rolls in the direction of the thumb and fingers, respectively.

We recorded digit load force at lift onset, the vertical force component parallel to the grip surface, exerted on the thumb and on the four fingers, respectively. We computed the difference between these load forces (ΔFy), such that a zero value denotes symmetrical load forces exerted by the thumb and four fingers. A positive ΔFy value denotes that the thumb exerted more load force than the four fingers combined, whereas a negative ΔFy value denotes that the four fingers combined exerted more load force than the thumb.

The COP was computed for the thumb and the four fingers at lift onset. COP is defined as the vertical coordinate of the point of resultant force relative to the center of the force transducer:

\[ \text{COP} = \frac{(\text{Tx} - (\text{Fy} \times w))}{\text{Fx}}, \]

where Tx is the moment about the x-axis, Fy is the load force, w is the distance between the surfaces of the force/torque transducer and the grip surface (0.5 cm), and Fz is the mean grip force component perpendicular to the grip surface averaged across thumb and four fingers (Figure 1C). We took the difference between the COP of the thumb and the net COP of the four fingers (ΔCOP). A positive ΔCOP value denotes that the thumb COP was higher than the net COP of all fingers, whereas a negative ΔCOP value denotes that the net COP of the four fingers was higher than the thumb COP. Furthermore, the Moem (Ncm) was computed using the formula:

\[ \text{Moem} = (\text{ΔFy} \times d^2) + 1/2 \times Fz \times \Delta \text{COP}, \]

where \( d \) is the grip width (8 cm). Positive and negative Moem values denote Moem generated in the direction of the fingers and thumb, respectively.

As mentioned above, the COP of individual fingers could not be determined from the force and torque output of the force transducer (as was done for the position of the thumb). Thus, to determine the position of each fingertip, we used a webcam to record fingertip position on each test trial. Digit position data were extracted at two time points: at the first frame showing vertical motion of the box and at the frame 0.16 s before that. The vertical distance between the centroid of each fingertip and the center of the grip surface was measured using video-based movement analysis software (Dartfish Pro Suite 9.0TM, Fribourg, Switzerland), using the height of the box as the environmental reference point. There was no statistically significant difference in the position of the four fingertips extracted at the two frames (p's > 0.05), thus we used the frame 0.16 s before the object lift onset frame.

Our main focus was on examining the kinetics and kinematics of successful anticipatory control of whole-hand manipulation, and their possible relation. To do so, we used three-level one-way repeated measures analyses of variance (ANOVA) to compare the following variables averaged across 20 trials per subject across the three CoM conditions: peak object roll, Moem, ΔFz, ΔFy, and ΔCOP. Furthermore, we compared the extent to which digit position of the four fingers, as captured by our webcam data, varied across CoM conditions using a 4 × 3 repeated measures ANOVA (with Fingers and CoM as within-subject factors). For one subject, we removed one of the 20 trials (one CoM condition) because the force transducer was overloaded. For significant main effects, we performed Tukey post hoc tests. We report partial eta squared (\( \eta^2_p \)) as a measure of effect size. Finally, for each subject we calculated Pearson's correlations between ΔFy and ΔCOP (20 values for each CoM condition). A mean correlation coefficient \( r \) was then calculated for each CoM condition using Fisher's z transformation.

**RESULTS**

Figure 2 shows data from a representative subject who grasped and lifted the box on a test trial with a left, right and centered mass distribution, respectively. When manipulating the box with a centered mass distribution, the subject did not need to generate a Moem and therefore the box did not roll. When manipulating the box with an off-centered mass distribution, the subject had to generate an appropriate Moem in the opposite direction of box's CoM (e.g., clockwise/supination and counterclockwise/pronation when the mass was on the left and right side, respectively) to minimize object roll. Interestingly, for this subject the COP of the thumb was always higher than that of the net COP of the fingers, and the load force of the four fingers was always higher than that of the thumb, regardless of the box's mass distribution.

The above results were also generally found across all subjects (Figure 3). We found significant main effects of CoM (left, right, centered) on Moem (F(2,22) = 354.70, p < 0.05, \( \eta^2_p = 0.97 \)) and object roll (F(2,22) = 28.53, p < 0.05, \( \eta^2_p = 0.72 \)), and large effect sizes. Tukey post hoc showed significant differences in Moem and roll when comparing left, right and centered mass distributions.

Figure 4 shows that in all CoM conditions, subjects generally exerted higher load forces by the fingers than thumb. Nevertheless, there was a significant main effect of CoM (left, right, centered) on ΔFy (F(2,22) = 5.69, p < 0.05, \( \eta^2_p = 0.32 \)), with Tukey post hoc showing a significant difference between left and right CoM conditions. By the thumb and the net Fy by the fingers were also each, respectively, significantly modulated based on the CoM (thumb: F(2,22) = 5.44, p < 0.05, \( \eta^2_p = 0.33 \); fingers: F(2,22) = 3.54, p < 0.05, \( \eta^2_p = 0.24 \)) with Tukey post hoc showing significant differences between left and right CoM conditions.

Figure 4 also shows, consistent with the above data from a representative subject, that subjects generally tended to grasp the object with the thumb COP higher than that of the fingers in all CoM conditions. Nevertheless, we found a significant main effect of CoM (left, right, centered) on ΔCOP (F(2,22) = 10.51, p < 0.05, \( \eta^2_p = 0.49 \)), and Tukey post hoc showed a significant difference between the left and both right and centered CoM conditions. Interestingly, we observed a stronger COP modulation to object
CoM in thumb COP than in the net COP of the fingers (Figure 4B). This was further quantified by a main effect of CoM on thumb COP ($F_{(2,22)} = 4.79, p < 0.05, \eta^2_p = 0.30$) but not on fingers COP ($p > 0.05$). Tukey post hoc showed a significant difference between thumb COP from left and right CoM conditions. Furthermore, the individual position of the four
fingertips (as captured by the webcam) varied little across CoM conditions (Figure 5), with no main effect of CoM ($p > 0.05$) and no interaction between Finger and CoM ($p > 0.05$). Of note, there was no significant difference ($p > 0.05$) in mean grip force at lift onset of a box with a left, right, or centered mass distribution. There were also no significant effects of trial number on thumb COP (or any other measure; $p’s > 0.05$) in any of the CoM conditions. Together, these findings suggest that the modulation in $\Delta$COP to the object’s CoM was largely driven by changes in the thumb COP rather than the position of the four fingertips.

Our correlational analyses showed very strong, negative and significant correlations between $\Delta$Fy and $\Delta$COP in each condition (Figure 6; this figure also shows some exceptions to what was typically seen in load force difference and $\Delta$COP, e.g., see subject depicted in subfigure at top right, right panel, showing a positive load force difference and negative $\Delta$COP). The mean correlation coefficient $\tau$ (calculated after Fisher’s $r$-$z$ transformation) was 0.81 (95% CI: 0.57, 0.92), 0.86 (95% CI: 0.68, 0.94), and 0.86 (95% CI: 0.66, 0.94) for the left, centered and right mass distribution conditions, respectively. Altogether, these findings suggest that the strong covariation of both fingertip position (driven by the thumb) and load force contributed to successful whole-hand object manipulation.

**DISCUSSION**

This study measured the extent to which digit position and forces are modulated for anticipatory control of learned manipulation.
of objects using the whole hand. Our findings supported our first hypothesis that digit position and force are modulated based on object CoM, with digit position modulation being limited to thumb position, and little to no modulation of finger position. Our second hypothesis of strong trial-to-trial covariation between digit position and load force was also supported. To our knowledge, this study is the first to have measured digit force-to-position modulation and its covariation in a grip type other than a two-digit precision grip type. Our results suggest that digit force modulation to position—necessary by the need to perform a given manipulation in a consistent fashion despite trial-to-trial variability in digit placement—is a fundamental and ecological feature of grasp control regardless of the number of fingers involved in the grasp.

**Digit Force-to-Position Modulation in Whole-Hand Grasping and Manipulation**

In achieving the task goal of minimizing the roll of a box with an off-centered mass distribution, subjects could have utilized three possible solutions. First, and as has been shown in precision grasping (Fu et al., 2010; Zhang et al., 2010; Marnievec et al., 2015), subjects could have modulated both digit position and load forces, with higher digit positioning and larger forces on the heavier side of the object. Our results show that this solution was only partially implemented in our task (see third solution below). Second, subjects could have modulated forces only while using the same digit position regardless of object CoM. Studies on constrained grasping have shown that subjects can modulate digit forces at fixed digit placement when they are not given the option of modulating digit position (for a review, Zatsiorsky and Latash, 2008). In our unconstrained grasp scenario, however, subjects did modulate digit position and force. Third, subjects could have modulated digit position to the CoM mostly by the thumb and not the fingers, given the biomechanical limitations of all fingers to move relative to each other and the thumb in a whole-hand grasp. This third solution is consistent with our results, and provides the first description of unconstrained digit force modulation for whole-hand grasping and manipulation.

The greater modulation of the thumb position than fingers is likely due in part to the thumb's greater range of motion and degree of independence. Specifically, the thumb can abduct to a greater degree than the fingers (70° vs. 30° in the index finger; Marzke, 1994; Jones and Lederman, 2006). Another unique feature of the thumb, due to the articulation of the thumb metacarpal and the trapezium, is that it can rotate 45° around its longitudinal axis. The greater modulation of the thumb position than the fingers is also likely due to biomechanical limitation of all fingers to move independently from each other and from the thumb. Finally, it might be worth considering whether the position of the four fingers was modulated less than that of the thumb because there was less room along the grasp surface for the fingers to be modulated. We considered this during the design of the vertical dimension of the grasp surface. The grasp surface height was set to 15 cm, based on how much digit position has been shown to vary in previous 2-digit grip studies (e.g., ~1.5–2 cm) utilizing similar experimental paradigms, and given that the maximum finger span (distance between index and little finger tip) of an average hand does not exceed 15 cm. Therefore, it is unlikely that the height of the grasp surface played a significant role in the limited position modulation of the fingers compared to the thumb.

**Digit Force and Position Covariation in Whole-Hand Grasping and Manipulation**

Like that seen in precision grasping (Fu et al., 2010), the linear negative correlation between trial-to-trial distance between digit COP and load force difference was very strong. Thus, the coordination of COP and load force is indeed a critically important phenomenon for grasp manipulation, at least for two commonly employed grasp types, e.g., two-digit grasp (e.g., Fu et al., 2010) and whole-hand grasp (present work). Despite this trial-to-trial variability in forces and digit position (with variability in the latter seen mainly in the thumb), the M1cm required by our task goal (object roll minimization) was nevertheless attained. Our findings further support the explanation put forth previously (Fu et al., 2010) that subjects are able to compensate for trial-to-trial variability in digit positioning through anticipatory modulation of forces. Little to no modulation of finger positioning resulted in a net negative load force difference between the thumb and the fingers in all conditions (though of different magnitudes),
indicating the fingers always exerted more load force to account for modulation of the thumb position. A previous study has reported this same pattern, albeit during the static phase of lifting an object with a centered CoM using a whole-hand grasp at constrained contacts (Rollmann et al., 2001). They suggested that the load force by the four fingers had...
to compensate for the negative/downward load force in the thumb. Similarly, subjects in the present study could have increased load forces in their fingers to compensate for less load force in the thumb. Furthermore, since we did not constrain digit positioning, subjects placed their thumb at a position that might have spared them from the need to modulate thumb load force. A limitation of our study was that we could not measure individual forces exerted by each of the four fingers. Specifically, it is possible that the four fingers used an additional strategy to minimize object roll by redistributing forces among the four fingers and altering the force sharing pattern as shown in other studies of whole hand object manipulation at constrained contacts (e.g., Santello and Soechting, 2000; Rearrick and Santello, 2002; Zatsiorsky et al., 2003; Shim et al., 2005). Thus, the ability to redistribute forces among the four individual fingers might reduce the need or outweigh any additional gain of modulating digit positions.

Theoretical Considerations for Anticipatory Control of Object Manipulation

We currently understand anticipatory control of object manipulation to rely on visual feedback and on sensorimotor memories from prior interactions with the same or similar object (for a review, see Johansson and Flanagan, 2009). Specifically, anticipatory digit force control is based on comparing actual sensory consequences, obtained from feedback mechanisms, with sensory consequences that we expect based on upcoming motor actions, derived from feedforward mechanisms, at a series of crucial time events. In the event of a mismatch between the actual and planned sensory consequences, modulation of forces would be triggered, and the associated sensorimotor memory might be updated.

Most previous work informing this theoretical perspective has been studied using either kinematics (measuring hand shaping e.g., Amiunni et al., 2006 and digit positioning e.g., Cohen and Rosenbaum, 2004) or kinetics (measuring fingertip forces e.g., Bursztyn and Flanagan, 2008). Our work and that from a previous study (Fu et al., 2010) suggest an update to this theoretical perspective, with a specific inclusion of the evidently strong integration of kinematical and kinetical variables during the loading phase of motor control. That a stable Mcm is still reached, despite trial-to-trial variation in digit positioning supports the system’s ability to sense digit position during load phase and integrating this information very swiftly to modulate load forces accordingly prior to object lift onset. What might enable this rapid sensing of digit positioning prior to load force modulation before the object is lifted? Our findings of trial-to-trial variation in digit position (of the thumb) and forces suggest anticipatory modulation of forces would not only depend on sensorimotor memory of forces and digit positioning from previous grasping experience, but also on feedback from the actual positioning of the fingertips. Fu et al. (2010) proposed that such feedback of digit position is likely acquired before digit contact, and between digit contact and lift onset, via visual, tactile, and proprioceptive inputs. Subsequently, a comparison is made between the expected and actual feedback of digit position, with a mismatch resulting in a change in the planned digit forces. This means that the forces originally planned before contact (based on the anticipated CoM location from prior lifts) would require online monitoring following contact, and occurring possibly through an integration of proprioception, tactile and visual input, and correcting, to compensate for positioning variation. The mechanisms that allow such swift integration of digit position variability, and subsequent load force adjustment, prior to lift onset, remains to be elucidated. Nevertheless, a study by Davare et al. (2007) gives neurophysiological support for the proposition that forces are modulated in response to digit positioning during anticipatory planning of object manipulation. Specifically, they showed that repetitive transcranial magnetic stimulation (rTMS) applied over anterior intraparietal area (AIP) 270–220 ms before object contact disrupted digit positioning, whereas rTMS at a later time point, 170–120 ms before object contact, disrupted digit forces. Although our study designs varied (e.g., their design had no specific metric of task correctness such as object roll minimization in our design), both our results point to force modulation being planned in response to digit positioning during anticipatory planning of object manipulation.

Ruminating of the classic concept of “motor equivalence” (Lashley, 1930; Cole and Abbs, 1980), the ability to generate an appropriate Mcm despite trial-to-trial variation in digit position and force suggests the presence of a higher order motor plan or neural representation that codes the task goal independent of the variety of ways in which it can be reached. Our findings suggest that the natural variation of digit position, for which digit forces must compensate on trial-to-trial fashion, is a fundamental feature of grasp control regardless of the number of fingers involved in the grasp. These findings support humans’ ability to monitor online whether planned and actual digit position coincide, and to correct for a possible mismatch, by modulating load force. This phenomenon is critically important to ensure that the desired force and/torque magnitude is attained by the time manipulation can be initiated.

AUTHOR CONTRIBUTIONS

Designed the experiment: MM, TL-M, MS, AMG. Performed the experiment: MM, TL-M. Analyzed and interpreted the data: MM, TL-M, MS, AMG. Wrote and edited the manuscript: MM, TL-M, MS, AMG. Approved the final version of the manuscript: MM, TL-M, MS, AMG. Agreed to be accountable for all aspects of the work: MM, TL-M, MS, AMG.

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REFERENCES


Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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APPENDIX E

RESEARCH ARTICLE | Control of Movement

Hand forces and placement are modulated and covary during anticipatory control of bimanual manipulation

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Lee-Miller T, Santello M, Gordon AM. Hand forces and placement are modulated and covary during anticipatory control of bimanual manipulation. J Neurophysiol 121: 2276–2290, 2019. First published April 10, 2019; doi:10.1152/jn.00760.2018.—Dexterous object manipulation relies on the feedforward and feedback control of kinetics (forces) and kinematics (hand shaping and digit placement). Lifting objects with an uneven mass distribution involves the generation of compensatory moments at object lift-off to counter object torques. This is accomplished through the modulation and covariation of digit forces and placement, which has been shown to be a general feature of unimanual manipulation. These feedforward anticipatory processes occur before performance-specific feedback. Whether this adaptation is a feature unique to unimanual dexterous manipulation or general across unimanual and bimanual manipulation is not known. We investigated the generation of compensatory moments through hand placement and force modulation during bimanual manipulation of an object with variable center of mass. Participants were instructed to prevent object roll during the lift. Similar to unimanual grasping, we found modulation and covariation of hand forces and placement for successful performance. Thus this motor adaptation of the anticipatory control of compensatory moment is a general feature across unimanual and bimanual effectors. Our results highlight the involvement of high-level representation of manipulation goals and underscore a sensorimotor circuitry for anticipatory control through a continuum of force and placement modulation of object manipulation across a range of effectors.

NEW & NOTEWORTHY This is the first study, to our knowledge, to show that successful bimanual manipulation of objects with asymmetrical centers of mass is performed through the modulation and covariation of hand forces and placements to generate compensatory moments. Digit force-to-placement modulation is thus a general phenomenon across multiple effectors, such as the fingers of one hand, and both hands. This adds to our understanding of integrating low-level internal representations of object properties into high-level task representations.

INTRODUCTION

Successful grasping and dexterous object manipulation depend on feedforward (anticipatory) and feedback (online) mechanisms (Flanagan and Beldzner 2000; Johansson and Cole 1992; Johansson and Flanagan 2009; Westling and Johansson 1984). On initial lift, selection of digit forces for grasping and manipulation rely on visual cues and the retrieval of sensorimotor memories from previous grasping experiences to anticipate object properties such as its size, mass and weight distribution (Croqué et al. 2013; Gordon et al. 1991, 1993; Gordon and Salimi 2004; Jermakow and Johansson 1997; Salimi et al. 2003). Sensory feedback from subsequent object manipulation provides additional information about object properties and enables the updating of the internal representation of object dynamics to anticipate sensory consequences (Flanagan et al. 2003; Johansson and Westling 1987, 1998).

Earlier studies on the grasping and lifting of novel objects with an asymmetrical weight distribution, i.e., the center of mass is not in line with the midpoint between the grasping digits, examined fingertip force control (Bursztyn and Flanagan 2008; Gordon and Salimi 2004; Salimi et al. 2000) and grasp kinematics (Lukos et al. 2007) separately. However, by constraining digit placement while measuring forces, the internal representations are also constrained to the contact point. More recently, studies examining both kinetics and kinematics have shown that digit forces and placement are modulated to generate compensatory moments to prevent the object from rolling (Fu and Santello 2015; Fu et al. 2010; Shibata and Santello 2017; Zhang et al. 2010). In a two-digit precision grip task, compensatory moment is generated through the modulation of digit forces and placement such that the vertical load force is larger and/or the location of the digit is higher on the object side corresponding to the center of mass (Fu et al. 2014; Fu and Santello 2014; Lukos et al. 2008; Marneweck et al. 2015). Moreover, it has been found that during stable performance, digit forces and digit placement covary such that, despite trial-to-trial variability of force and placement, compensatory moment remains relatively stable (Fu et al. 2010; Naceri et al. 2014; Shibata et al. 2014). Specifically, when contact is made anywhere on an object’s graspable surface, feedback about digit placement is thought to be used to modulate anticipatory digit forces accordingly (Fu et al. 2010). Overall, in the absence of asymmetrical cues, such as on the first manipulation of a visually symmetrical object, equal digit forces and collinear placements are used (Lukos et al. 2007; Salimi et al. 2000). Once sensory cues about the asymmetrical center of mass are obtained, different digit forces are applied...
and placement begins to be modulated noncollinearly. This is possibly done to minimize the cost function related to comfort (Rosenbaum et al. 1996; Zhang and Rosenbaum 2008). On subsequent lifts, while digit forces and placement are modulated noncollinearly, force-to-placement covariation enables stable compensatory moment generation despite trial-to-trial variability. This suggests that there is a high-level representation of the object torque (task goal) that is used to control anticipatory planning.

Previous studies have shown similar modulation of forces and placement using three-digit (Albert et al. 2009; Fu et al. 2011; Fu and Santello 2012) and whole hand (Marnowek et al. 2016) grips. Aside from unimodal grasping, manipulation can also be performed with two hands. The extent to which task representations are restricted to unimodal (where digits cooperate with each other) or bimodal (digits of one hand working with digits of another) tasks is not known. Previous studies have shown that fingertip forces differ between unimodal and bimodal tasks but that these differences are dependent on the task requirements (Dimidiou and Buckingham 2018; Gomiak et al. 2009). It has also been shown that bimodal coordination is sensitive to the task goal (Diedrichsen and Gaisl 2009; Diedrichsen 2007; Manden 1981). If the internal representations of forces and placement (low level) are integrated into task representations (high level), bimodal manipulation would be characterized by stable trial-to-trial compensatory moments despite variable hand forces and placements. Thus, this study would add to the current understanding of bimanual actions by showing that the behavior of force and placement modulation and covariation seen in unimodal grasping can also be seen during unconstrained bimanual lifting. However, the much larger forces, exerted over a larger surface than fingertips, potentially generated by two hands may allow the requirement to modulate hand placement.

In the present study we addressed whether participants could generate an anticipatory compensatory moment to counter object roll, and if hand forces, center of pressure, and placement were modulated, in a bimanual lifting task with symmetrical (centered) or asymmetrical (off-centered) object center of mass. Over two experiments, 2 participants lifted a visually symmetrical box with each hand on the corresponding side of the box. In experiment 1, we determined whether participants are able to generate a compensatory moment in opposition to object torque and if hand forces and center of pressure are modulated. Anticipatory planning of forces was examined by analyzing hand forces, center of pressure and placement at lift onset, i.e., before explicit sensory information of object torque can be obtained, and rates of force development (Fu and Santello 2014; Johansson and Westling 1984). The larger surface of the hand might make it impractical to equate center of pressure with hand placement. Compensatory moment generation during bimanual manipulation could thus involve hand force modulation with either collinear or noncollinear hand center of pressure and hand placement (similar to two-digit unconstrained grasping). Thus, in experiment 2, we repeated the experiment while also measuring the kinematics of hand placement under motion capture to determine the extent of hand position modulation. We addressed whether in a bimanual palmar hand task the hands would act in a similar way to the thumb and index finger in a two-digit precision grip task. We hypothesize that participants would maintain successful performance by generating a desired compensatory moment through the

modulation of (1) hand forces and center of pressure, and (2) hand forces and placement, with covariation of forces to center of pressure and placement similar to two digit and whole hand grasping. Thus anticipatory control would be accomplished by (1) applying a larger load force and/or higher center of pressure (experiment 1) or hand placement (experiment 2) on the heavier side of the box at lift onset, and (2) higher peak load force rates, for the hand on the heavier side, before lift onset. Covariations of forces and placement would show higher order representations of task goal (compensatory moment) as opposed to low-level control of forces and placement.

**MATERIALS AND METHODS**

**Participants**

Ten healthy adults (median age: 23 yr, range: 18–33 yr; 4 women) participated in experiment 1, and 10 healthy adults (median age: 23.5 yr, range: 22–31 yr; 5 women) participated in experiment 2. Participants were right-handed, had normal or corrected-to-normal vision, and had no upper limb orthopedic impairments. Written informed consent was obtained before participation in compliance with the Declaration of Helsinki. The study was approved by the Teachers College, Columbia University Institutional Review Board.

**Apparatus**

A custom-made device, designed to resemble a box (30 × 42 × 15 cm), was used to measure the forces and torques of the left and right hand (Fig. 1). The sides of the device were made of carbon fiber plates with 120-grit sandpaper on the lateral grip surfaces (30 × 15 cm, thickness 5 mm). These were attached to two multiaxis force sensors (Mini 40 Force/Torque transducer; ATI Industrial Automation). The force sensors measured the applied grip force, load force, and torques (resolution = 0.01 N, 0.005 N, and 0.0125 Nm, respectively) of the left and right hand. An electromagnetic sensor (Polhemus Fastrack, 0.005 mm of range, and 0.025° resolution) was mounted inside the device to measure vertical position and roll of the box. A movable load weight was placed on either the left, center, or right side of the device (inside the box) to generate the torque in the left, center, and right conditions. During experiment 2, hand placements were recorded using an eight-camera three-dimensional motion capture system (Vicon Workstation 612, Lake Forest, CA).

**Procedure**

Participants were seated in front of a height-adjustable table, with their elbows flexed 90° in the parasagittal plane, the object directly in front of them on the table, and their hands on their laps. Before the start of the experiment, participants held an object of similar size and weight to get an approximation of the weight of the object without any cues of object center of mass. The task goal was to lift the object while minimizing object roll. Participants were instructed to lift the object in a smooth, self-directed manner. For each trial, following an audio tone, participants reached and grasped the object on the lateral surface using both their hands, anywhere on the respective grip surfaces, and lifted the object vertically upwards using their palms and fingers. Participants were instructed to lift the object to a height of 10 cm, up to a reference marker placed next to the object. Participants held the object at that height until presentation of a second audio tone (5 s after first tone), after which they placed the object back on the table and returned their hands to the start point or across the start of the next trial. Participants then performed 5 practice lifts followed by 20 experimental lifts in either the left, centered, or right condition. Participants performed the 25 lifts in all three conditions blocked, the
order of conditions was counterbalanced across subjects, and a rest period was given before each condition.

In experiment 1, hand placement was measured using hand center of pressure. However, as mentioned above, the larger surface of the hand allows the center of pressure to vary while keeping hand placement the same. Thus experiment 2 was conducted to determine actual anatomical hand placement. In experiment 2, before the object was lifted, markers were placed on the participants' hands. Markers were placed on the tips of the fingers and thumbs, the metacarpophalangeal joints of the index and little finger, and radial and ulnar styloid of the wrist, and the experimental procedures were repeated for 10 additional subjects.

Data Processing

Throughout the lifts, hand forces and torques applied to the grip surfaces recorded by the force transducers, and position data of the box recorded by the electromagnetic sensor were sampled at 500 and 120 Hz, respectively, with the use of custom-written software in WinSC (Umeå University, Umeå, Sweden). Hand placement data were sampled at 120 Hz. Data collected were filtered using a second-order low pass Butterworth filter with a cutoff frequency of 6 Hz. To examine anticipatory planning, measures were recorded at lift onset before performance-specific feedback mechanisms influence grasp control. To further examine anticipatory planning, peak force rates before lift onset were collected (Perissberg et al. 1992; Fu and Santello 2014; Gordon et al. 1993; Johansson and Westling 1984). Lift onset was defined as the point at which the vertical position of the object went above 1 mm and subsequently remained above this value. Object roll occurred in the frontal plane and all variables involved forces within this plane. The outcome measures included the following:

1) Peak object roll is defined as the angle of the object in the frontal plane. Peak object roll was recorded shortly (~250 ms) after lift onset. This variable denotes the extent to which subjects accomplished the task goal (object roll minimization) and whether participants were able to counter object torque before it affected performance. Positive values represent counterclockwise roll (toward the left), and negative values represent clockwise roll (toward the right).

2) Load force (LF) at lift onset is the tangential component of the force produced by each hand measured in Newton (N).

a) Load force difference (LF_{left} - LF_{right}), Positive values indicate larger left than right hand load force while negative values indicate larger right than left hand load force.

b) Peak LF rate is the peak of the first derivative of LF before lift onset.

3) Grip force (GF) at lift onset is the average normal component of the force produced by each hand measured in Newton (N).

a) Peak GF rate is the peak of the first derivative of GF before lift onset.
4) Center of pressure (COP) is the vertical coordinate of the point of application of the hand on the grip surface and represents the sum of all the hand forces acting on the grip surface. It is measured in centimeters (cm). This was computed using the formula (Fu et al. 2010; Zhang et al. 2010): \( \text{COP}_{\text{hand}} = \frac{\text{FL}_{\text{hand}}}{\text{TF}_{\text{hand}}(\text{w} + \text{h})} \), where \( \text{TF}_{\text{hand}} \) is the thickness of the friction surface, and \( \text{w} \) and \( \text{h} \) are the width and height of the object, respectively. The COP was determined on the grip surface using a Newton sensor (Ncm). The thickness of the grip surface was 0.5 cm.

5) Compensatory moment (Mom) is defined as the anticipatory torque generated by the hands, in response to object torque, measured in Newton centimeter (Ncm). This was computed using the formula (Fu et al. 2010; Zhang et al. 2010): \( \text{Mom} = \frac{\text{FL}_{\text{obj}}(\text{w} - \text{d})}{\text{TF}_{\text{hand}}} \), where \( \text{d} \) is the width of the box (4 cm). A positive Mom denotes a clockwise moment while a negative Mom denotes a counterclockwise moment.

6) **Experiment 2**: hand placement (HP) is the vertical coordinate of the first metacarpophalangeal joint of each hand on the grip surface.

7) **Hand placement difference (HPD)**: \( \text{HPD} = \text{HP}_{\text{left}} - \text{HP}_{\text{right}} \).

**Data Analysis**

Peak roll was used to determine accomplishment of task goal. Anticipatory planning of hand forces and placement were analyzed using the resultant Mom, \( \text{FL}_{\text{obj}} \), COP, \( \text{FL}_{\text{obj}} \), and HPD at lift onset, as well as peak GF and LF rates. We performed a three-level (left, centered, right) one-way repeated measures ANOVA to compare the task. Significance was considered at \( P < 0.05 \). For all comparisons, the Bonferroni corrections were used where applicable. Significance was considered at the \( P < 0.05 \) level. To examine the possible relation between LF, COP, and HPD, we performed linear regression analysis to obtain the Pearson's correlation coefficient between \( \text{FL}_{\text{obj}}, \text{COP}, \text{FL}_{\text{obj}}, \text{HPD}, \text{COP}_{\text{adv}} \), and \( \text{HPD}_{\text{adv}} \) (20 values for each condition) at lift onset. Fisher's r-to-z transformation was then used to calculate the mean correlation coefficient \( r \).

**RESULTS**

**Experiment 1: Successful Manipulation Through Generation of Mom**

Figure 2 shows the object roll, Mom, LF, COP, GF, and force rates of a representative participant after 5 practice trials in the left, centered, and right condition of mass (CoM) conditions during experiment 1. For the left and right mass distributions, to prevent object roll, participants had to generate Mom in the opposite direction of the object torque (clockwise for left CoM, counter-clockwise for right CoM). This was done through the modulation of LF and COP where, from lift onset, hand LF and COP were higher on the side opposite the object CoM. Additionally, peak GF and LF rates occurred before lift onset with peak LF rates differing between the left and right hand. For the centered mass distribution, the lack of inherent object torque did not require the participants to generate any Mom to perform roll. As a result, LFs were equal and COPs were collinear at lift onset. For all three conditions, GF was generated to successfully lift the object and the rates of GF development were similar for the two hands for each condition.

**Group means between the three CoM conditions were generally consistent with this representative illustration indicating that the sensorimotor control was influenced by object torque (Fig. 3).** All participants were able to minimize object roll below 1° from large object rolls on the first trial (approximately \( 7° \)). Repeated measures ANOVA showed a significant effect of CoM on peak roll \( F(2,18) = 17.27, P < 0.001, \eta^2_p = 0.73 \). Post hoc tests revealed that peak roll for the left condition differed from that of the right condition \( F(2,18) = 12.77, P < 0.001, \eta^2_p = 0.59 \). Figure 3B shows that Mom was applied in the appropriate direction to counter object roll for the left and right CoM conditions and near zero for the centered CoM condition. The generation of Mom was due to modulation of LF and COP of both hands. Results showed a statistically significant effect of CoM on \( \text{FL}_{\text{obj}} \) \( F(2,18) = 63.37, P < 0.001, \eta^2_p = 0.99 \) and \( \text{COP}_{\text{adv}} \) \( F(2,18) = 47.88, P < 0.001, \eta^2_p = 0.81 \) between the two hands. For the left CoM condition, LF of the left hand was larger than LF of the right while the opposite (LF of right hand larger than left) was seen for the right CoM condition \( (3C) \). From Fig. 3C, for the centered CoM condition, LF of the left and right hand was similar as seen from the almost zero \( \text{FL}_{\text{adv}} \). COP showed similar differences as LF between the hands across all conditions \( (3G) \). Additionally, GF was applied to successfully lift the object. Results showed a significant effect of CoM on GF \( F(2,18) = 5.31, P < 0.05, \eta^2_p = 0.37 \). Figure 3E shows that GF of both hands
Fig. 2. Representative plots for experiment 1. Plots show a representative trial for the left, centered, and right center of mass condition. Vertical dotted lines indicate left onset. Horizontal dotted lines in the second row show the target compensatory moment (Moem) Moem required to equal object torque. Other than roll and Moem, solid lines represent the left hand and dotted lines represent the right hand. LF, load force; GF, grip force; COP, center of pressure.
hands was slightly higher when the CoM was on the right than centered. Analysis of peak GF rates showed that there was no statistically significant difference between the CoM conditions ($P = 0.598$, $\eta^2_p = 0.05$) while there was a significant effect of CoM on peak LF rate difference between the left and right hands [$F(2,18) = 225.70$, $P < 0.001$, $\eta^2_p = 0.96$]. Similar to LF difference, peak LF rates were higher for the left hand and higher for the right hand in the left and right CoM conditions respectively, with no difference for the centered CoM condition (Fig. 3D).

**Covariation of hand forces and HP**: Linear regression analyses performed on $LF_{diff}$ and $COP_{diff}$ at lift onset showed a strong negative correlation between $LF_{diff}$ and $COP_{diff}$. With the use of Fisher’s $z$ transformation, average Pearson’s correlation coefficient for each condition fell between $-0.78$ to $-0.91$ ($P < 0.05$).

Notably, correlation coefficient for the centered CoM was higher ($-0.91$) than the left ($-0.79$) and right ($-0.85$) CoM. Even though the average correlation between $LF_{diff}$ and $COP_{diff}$ across participants shows this negative covariation, some individual differences exist. Figure 4 shows the covariation of $LF_{diff}$ and $COP_{diff}$ of individual participants for all conditions in experiment 1. For the left CoM condition, appropriate Mcom generation was achieved generally by positive $LF_{diff}$ and $COP_{diff}$ (Fig. 4, A–J). One participant (Fig. 4B) applied smaller values of $LF_{diff}$ but larger values of $COP_{diff}$ than the rest of the participants while three participants (Fig. 4, D, E, and G) applied larger $LF_{diff}$ and smaller $COP_{diff}$ such that in some trials negative $COP_{diff}$ was used. The participant in Fig. 4H showed no correlation between $LF_{diff}$ and $COP_{diff}$. The right CoM condition showed similar
results but with \( \text{LF}_{\text{HPR}} \) and COP\(_{\text{HPR}} \) in opposite directions. Importantly, participants did not favor the same strategy for the left and right conditions. For the centered CoM condition, almost all participants applied small \( \text{LF}_{\text{HPR}} \) and \( \text{COP}_{\text{HPR}} \) thus resulting in clusters around the zero point.

**Experiment 2: Generating Mcom Through Hand Force and HP Modulation**

The results of **experiment 1** showed that the CoM varied as a function of CoM location; i.e., it was higher on the side of the CoM. However, unlike in two-digit grasping, hand location cannot be directly inferred from COP since there is no one-to-one relation between COP and the hand. Specifically, for two-digit grasping, the COP can be associated with the finger-tip location. In contrast, when the whole hand is in contact with the grip surface, COP cannot be univocally associated with the digit and/or palm position due to the larger number of contacts. Thus, to determine whether subjects modulate both HP and forces, **experiment 1** was repeated with 10 different subjects with the additional use of motion capture to determine HP. Group means show similar results to **experiment 1** (Fig. 5).

Repeated measures ANOVA showed a significant effect of CoM on peak roll \( F(2,18) = 6.61, P < 0.05, \eta^2 = 0.42 \), where the peak roll for the left condition differed from that of the right (Fig. 5A). After a significant effect of CoM on Mcom \( F(1,11.13,18) = 1126.91, P < 0.001, \eta^2 = 0.99 \), post hoc tests revealed that Mcom was applied in the appropriate directions to counter object roll (Fig. 5B). Similarly, results showed...
a significant effect of CoM on LF
\( F(1, 247, 18) = 701.90, P < 0.001, \eta_p^2 = 0.99 \)
and COP \( F(2, 128) = 81.45, P < 0.001, \eta_p^2 = 0.90 \).
Post hoc tests revealed that LF and COP differed across all conditions. The LF and COP of the left hand were larger and higher than the right hand for the left CoM condition and collinear for the centered condition, while the right hand had larger LF and higher COP than the left hand for the right condition (Fig. 5, C and G). There was a significant effect of CoM on GF \( F(2, 18) = 5.45, P < 0.05, \eta_p^2 = 0.38 \), with post hoc tests revealing that GF of both hands was slightly larger when the CoM was on the left compared with the center (Fig. 5E). Analysis of peak GF rates (Fig. 5F) showed that there was no statistically significant difference between the CoM conditions \( (P = 0.384, \eta_p^2 = 0.10) \) while there was a significant effect of CoM on peak LF rate difference between the left and right hands \( F(1, 284, 11.56) = 92.93, P < 0.001, \eta_p^2 = 0.91 \).

Post hoc tests revealed that peak LF rate difference differed across all conditions similar to results from experiment I (Fig. 5D).

Group means of HP revealed similar HP partitioning. Results showed a significant effect of CoM on HP \( F(2, 18) = 52.97, P < 0.001, \eta_p^2 = 0.86 \). In Fig. 5H, similar to the LF and COP, for the left CoM condition, the left hand was placed higher than the right hand. For the centered CoM condition, the left and right hand were placed in similar locations on their respective surfaces. For the right CoM condition, the right hand was placed higher than the left hand. Comparing between individual hand COP and HP, results
showed a significant effect of type for the left hand \[ F(1,19) = 5.88, P < 0.05, \eta^2 = 0.46 \], with COP higher than HP across all CoMs. For the right hand, results showed a significant interaction \[ F(1,15,10.82) = 17.69, P < 0.001, \eta^2 = 0.66 \]. Post hoc tests revealed that COP was higher than HP of the right hand for the centered and right CoM (P < 0.05).

**Finger spacing, wrist deviation, and HP in the y-direction.** Results indicate that participants performed the task with similar finger spacings, wrist deviations, and similar placement of the left and right hand in the y-axis (Table 1). Results from our analysis of finger spacing showed that finger spacing between the fingers was kept constant across the conditions for both hands (P > 0.05). Results from our analysis of radial and ulnar deviation of the wrist showed that wrist deviation did not change across the conditions for both the left and the right hand (P > 0.05). Examining HP in the y-axis, results showed that HP in the y-axis between the left and right hand did not differ across trials for all conditions (P > 0.05).

**Covariation of hand forces and HP.** Linear regression analyses on LF and COP at lift onset showed similar results to experiment 1. Pearson’s correlation results showed a strong negative correlation between LF and COP. Fisher’s z transformation showed that the average correlation coefficient for each condition fell between −0.76 to −0.93 (P < 0.05). As it was in experiment 1, correlation coefficient for the centered CoM was higher (−0.93) than the left and right CoM (−0.76). Similar to the overall negative covariation of LF and COP across participants with some variations of the strategies used in experiment 1, there was a negative covariation between LF and HP at lift onset in experiment 2. Specifically, correlation coefficients between −0.50 and −0.66 were seen across participants as seen in Fig. 6, which shows the individual correlation plots of LF and HP across the 20 trials. Some participant-to-participant preferences can be seen where some participants would rely on LF or HP modulation more than other participants. For the left CoM condition, one participant used smaller values of LF than HP, and with larger values of HP than LF (Fig. 6G). For the right CoM condition, some participants relied more on LF than HP, as seen by less negative HP values with positive values of HP on some trials (Fig. 6A, A and E-J). Analysis of COP and HP showed a positive correlation between 0.64 to 0.79. Correlation analysis between GF and other variables indicated zero to weak covariation.

**Learning Mcom for Object Roll Minimization.** Object roll minimization through the generation of Mcom was learned equally well within the practice trials by participants in both experiment 1 and 2. We found no significant difference between experimental group and trial or CoM. Thus we grouped the two experiments together and looked at learning within the five practice trials. Figure 7A shows the Mcom and resultant peak roll across all 25 trials (5 practice, 20 experimental). Results showed a significant interaction between the effects of CoM and trial for Mcom \[ F(2,47,46.96) = 74.53, P < 0.001, \eta^2 = 0.81 \] and peak roll \[ F(3,78,53.33) = 54.52, P < 0.001, \eta^2 = 0.65 \]. Post hoc tests revealed a significant difference between trials 1 and 2 for the left and right CoM but not between subsequent trials. In trial 1, participants generated small Mcoms \[ \text{means} \pm SD = 80.37 \pm 76.47 \text{Ncm (left)}, 26.32 \pm 89.49 \text{Ncm (centered)}, -19.12 \pm 54.10 \text{Ncm (right)} \] compared with the target Mcom of 200 Ncm. This resulted in large peak rolls for the left and right CoM conditions \[ \text{means} \pm SD = 5.55 \pm 3.46^\circ \text{(left)}, -1.11 \pm 4.38^\circ \text{(centered)}, -5.71 \pm 2.84^\circ \text{(right)} \]. By trial 2, Mcom was generated in the appropriate directions \[ \text{means} \pm SD = 199.06 \pm 31.71 \text{Ncm (left)}, 6.93 \pm 13.57 \text{Ncm (centered)}, -189.03 \pm 35.21 \text{Ncm (right)} \]. Peak roll was thus minimized by trial 2 \[ \text{means} \pm SD = -0.13 \pm 1.86^\circ \text{(left)}, -0.77 \pm 1.19^\circ \text{(centered)}, -0.91 \pm 1.92^\circ \text{(right)} \]. There was no difference between trials for the centered CoM as there was no object torque and thus no need to generate Mcom for this condition. In general, participants learned to generate the appropriate Mcom to counter object roll very early in the practice phase.

**DISCUSSION.** The present study examined the motor planning of object manipulation through the modulation and covariation of hand forces and placement during bimanual lifting of an object with an asymmetrical center of mass. Our results showed that successful performance (lifting the object while preventing

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**Table 1. Analysis of finger spacing, wrist deviation, and hand placement in the y-axis for the left and right hand.**

<table>
<thead>
<tr>
<th>Finger Spacing, Wrist Deviation, and Hand Placement</th>
<th>Center of Mass</th>
<th>P Value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Left</td>
<td>Centered</td>
</tr>
<tr>
<td>Finger spacing, cm</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Left hand</td>
<td>4.0 ± 0.6</td>
<td>4.2 ± 0.4</td>
</tr>
<tr>
<td>Index-middle finger</td>
<td>3.8 ± 0.5</td>
<td>3.8 ± 0.2</td>
</tr>
<tr>
<td>Middle-ring finger</td>
<td>3.7 ± 0.2</td>
<td>3.6 ± 0.2</td>
</tr>
<tr>
<td>Ring-little finger</td>
<td>3.6 ± 0.3</td>
<td>3.4 ± 0.3</td>
</tr>
<tr>
<td>Right hand</td>
<td>4.2 ± 0.5</td>
<td>4.3 ± 0.5</td>
</tr>
<tr>
<td>Index-middle finger</td>
<td>3.6 ± 0.2</td>
<td>3.7 ± 0.2</td>
</tr>
<tr>
<td>Middle-ring finger</td>
<td>3.4 ± 0.2</td>
<td>3.4 ± 0.2</td>
</tr>
<tr>
<td>Ring-little finger</td>
<td>3.5 ± 0.2</td>
<td>3.5 ± 0.2</td>
</tr>
<tr>
<td>Wrist Deviation, cm</td>
<td>0.9 ± 0.3</td>
<td>0.7 ± 0.3</td>
</tr>
<tr>
<td>Right hand</td>
<td>0.9 ± 0.3</td>
<td>0.9 ± 0.3</td>
</tr>
<tr>
<td>Hand placement in y-axis difference, cm</td>
<td>0.24 ± 0.17</td>
<td>0.17 ± 0.15</td>
</tr>
</tbody>
</table>

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object roll) was accomplished by generation of a compensatory moment through the unequal modulation of hand forces and noncollinear placement. As in two-digit and whole hand grasp, there was a covariation of effector (in this case hand) placement and forces. That a stable compensatory moment could be attained despite trial-to-trial covariation of forces and placements shows the integration of these representations into a high-level task representation. To our knowledge, this study is the first to show the modulation and covariation of forces and placement during bimanual manipulation. Our previous studies have shown that a similar force and placement strategy is seen in two-digit (Fu et al. 2010; Lee-Miller et al. 2016), three-digit (Fu et al. 2011), and whole hand (Marneweck et al. 2016) manipulation thus representing a general feature of object manipulation across multiple effectors and degrees of freedom. These results are discussed in line with our current understanding of sensorimotor integration and potential neural mechanisms of control.

**Generation of Compensatory Moment to Counter Object Torque**

In the present study, large rolls were seen on initial trials due to the inappropriate generation of compensatory moments to counter object torque. On the second consecutive lift and thereafter, an appropriate compensatory moment was applied through load force and hand placement modulation (Fig. 7A). This learning is similar to unimanual grasping, where an
appropriate compensatory moment sufficient to counter object torque was established on the third or fourth consecutive lift (Fu et al. 2010, 2011). The additional degrees of freedom in bimanual grasping may have resulted in a slower learning rate. However, the similar rate of learning between unimanual and bimanual grasping is an interesting finding and could reflect the flexibility of the sensorimotor system to integrate task solutions across effectors.

Anticipatory planning was determined by observing the measures at lift onset before performance-specific feedback mechanisms influence grasp control. Additionally, the difference at each effector between peak load force rates occurring before lift onset across the conditions further indicates the anticipatory planning of forces for establishing a compensatory moment (Fu and Santello 2014; Johansson and Westling 1984). Along with hand load forces and placement, grip force is another measure that could influence the compensatory moment. Similar to previous studies using two-digit precision grip tasks (Salini et al. 2000; Zhu et al. 2010), our findings show that hand grip force is similar regardless of asymmetrical center of mass location but slightly higher than when the center of mass was centered. That grip forces of either hand were similar, despite differing load forces, is in line with previous studies showing intermanual coordination of grip forces, scaled to load force generated by either the left or right hand (Bracewell et al. 2003; Serrien and Wiesendanger 2001; White et al.
It is likely that the higher grip force for the asymmetrical centers of mass was necessary to prevent slippage or damage to the object (Edin et al. 1992; Gordon et al. 1993; Johansson and Cole 1992). Additionally, the off-centered location of the center of mass could have resulted in an uneven distribution of the torsional load on one hand thus requiring larger grip forces overall (Jenmalm et al. 2000; Johansson et al. 1999; Salimi et al. 2000).

We have shown that motor adaptation to manipulate an object with an asymmetrical center of mass is a general feature across multiple effectors. This adaptation to a novel object using different combinations of effector forces and placement to generate similar compensatory moments is consistent with the concept of motor equivalence (Fu et al. 2011; Fu et al. 2010). Motor equivalence refers to the ability to use different or varying effector degrees of freedom to perform the same task (Bernstein 1966; Lashley 1950; Weng 2000). The concept of motor equivalence has been observed when a distal thumb-index finger contact site can be achieved despite variable joint angles and trajectories (Cole and Abbs 1986). Further studies could look at the generalizability of the learned adaptation and whether learning of the task unimanually can be transferred to bimanual grasping and vice versa.

Covariation of Hand Forces and Center of Pressure in Bimanual Manipulation

Once a noncollinear strategy was determined, planning and/or execution errors that lead to noise in the system could be compensated by force-to-placement covariation. Overall, our linear regression analyses showed that successful completion of the task resulted in a correlation between load force difference, center of pressure difference, and hand placement difference (which together were positively correlated), showing a tighter coupling between load force difference and center of pressure difference than between load force difference and hand placement difference. It is also interesting to note that strategies varied across participants (Figs. 4 and 6) with some participants moving towards placing their hands further apart vertically to minimize forces, whereas others kept their hands relatively collinear using larger forces. Despite participant preferences, the overall negative covariation of hand load forces and center of pressure is a common feature of the unconstrained paradigm and allows trial-to-trial variability of load force and center of pressure while maintaining a stable compensatory moment. For the hand, the center of pressure is equivalent to the net point of force application from the placement of the palm and digits. Thus center of pressure modulation would be possible even if the hands are placed collinearly. If so, the generation of compensatory moment would be driven by the covariation of load forces and center of pressure alone. Our findings of hand placement modulation and covariation with load force (Figs. 4 and 6) show that the hands were physically placed at different points (noncollinear) across conditions. Thus hand placement was integrated into the task representation to influence compensatory moment generation. If a force contact with the object is made, sensory information of the contact points is used to control and update digit forces to generate the appropriate compensatory moment (Davare et al. 2019; Fu et al. 2010; Mojolahedi et al. 2015). These studies employed two-digit grasping with the forces of each digit being exerted at the digit center of pressure. Thus, once contact is made, digit center of pressure can only vary slightly by the rolling of the digits on the grasp surface. Therefore, a comparison of feedback of the actual versus expected digit center of pressure would trigger updates to the digit forces before executing object lift (Fu et al. 2010). For the whole hand case, the overall hand center of pressure comprises the individual digit and palm centers of pressure. Hand center of pressure can vary much more depending on the relative contributions of the individual digit and palm centers of pressure. We examined the changes in hand center of pressure from contact to after lift onset for all centers of mass (Fig. 7B). Center of pressure of the right hand fluctuated from contact to lift onset, stabilizing thereafter for the left and centered conditions. Center of pressure of the left hand appeared to only fluctuate during the right center of mass condition. Additionally, this fluctuation stabilizes only at lift onset. These observations suggest that feedback on hand placement is used to update hand forces and make adjustments to hand center of pressure to generate the appropriate compensatory moment. Previous studies examining responses to perturbations of one hand during a bimanual task have shown corrective responses in the other hand within a single trial (Dimitriou et al. 2012) or both hands (Diedrichsen 2007). This suggests that feedback-driven responses of one limb to task-relevant perturbations can be elicited in the other limb from online sensory information.

Previous studies into bimanual coordination examined the influence of task goals, maintaining object position versus maintaining object length, and showed that the direction of responses was determined by the desired outcome of the task (Diedrichsen and Gurfinkel 2009). Additionally, control of forces has been shown to be dependent on the object properties, with smaller forces applied to fragile objects (Gomiak et al. 2010). Other studies have shown a similar task dependent characteristic of bimanual coordination (Dimitriou and Buckingham 2018; Mursadi et al. 1981; Ourrani et al. 2013). Taken together with these studies, our results show that the coordination of bimanual hand forces and placement occurs as a result of the task-specific requirements of compensatory moment generation.

Possible Neural Networks Involved in Effector Force and Placement Modulation and Covariation

The paradigm used in the present study alludes to a wide network of neural structures involved in motor learning and control (for review, see Wolpert et al. 2011). In this paradigm, such networks involving numerous cortical areas have been suggested for unimanual tasks (Fu et al. 2010, 2014; Santello et al. 2013). A distinction should be made between bimanual tasks that involve two unimanual tasks (Hughes and Fränz 2008; Theorin and Johansson 2007; Witney 2004) and bimanual movements that cannot be distinguished into unimanual ones, such as the present study and the inherent complexities (Duque et al. 2010). Additionally, aside from neural control, the modulation of forces could have made use of the biomechanical affordances of the hands to attain some mechanical advantage (Shim et al. 2004). Based on this viewpoint, compensatory moment generation would be a result of the coordination of hand moments to minimize effort. Further
studies could explore the mechanical aspects of this type of bimanual control. The neural underpinnings of bimanual control are less understood than unimanual grasping (Le and Niemeier 2013) but suggest that a neural network exists for bimanual coordination (Gerloff and Andres 2002; Kantak et al. 2017; Santello et al. 2013; Therion and Johansson 2007; Vinjamuri et al. 2006). Together with previous studies, the present findings suggest that the modulation and covariation of forces and placement are general features that exist across multiple effectors (two-digit, three-digit, whole hand, bimanual).

The posterior parietal cortex (PPC) is involved in the sensory control of reach to grasp movements [for review, see Culham and Valyear (2005)]. The PPC has been shown to be involved in the coordination of fingertip forces (Ehrsson et al. 2003; Jenmalm et al. 2006) and the integration of multisensory input (Avillac et al. 2005). Similarly, the anterior intraparietal area within the PPC is involved in hand shaping for two-digit precision grasps (Davare et al. 2007; Tunik et al. 2008), whole hand grasping movements (Baumann et al. 2009; Frey et al. 2005), and bimanual grasping specifically in the formation of maximum grip aperture between the hands (Le et al. 2014). It has been suggested that different points on an object are used in the learning of object manipulation, especially when the dynamics associated to the points differ (Heald et al. 2018). In the present study, because of the asymmetrical center of mass, grasp placement on points of the left and right grasp surface afford different dynamics, such as applying more load force on the heavier side. Thus choosing grasp control points dictates how forces are distributed across digits of one hand in unimanual grasp and digits/hands in bimanual grasps. Interhemispheric studies have shown that there is a right hemisphere dominance, via the right anterior intraparietal, in choosing grasp points (Le and Niemeier 2013). Once contact is made, sensory of effector contact points has recently been suggested to involve the inferior parietal lobule via tactile afferents to the somatosensory cortex (Toma et al. 2019). Thus, building on our previous study (Fu et al. 2011), we suggest that the PPC could be involved in the transformation of effector-specific force and placement modulation to higher level task representations of compensatory moment after sensorimotor experience with the object. Indeed, studies have shown that areas within the PPC have functions that are not effector specific (Heed et al. 2011; Vangheluwe et al. 2006).

Studies have indicated that the ventral premotor cortex is an important area in fingertip force control during two-digit precision grip tasks (Ehrsson et al. 2001), while virtual lesions of the ventral premotor cortex show its involvement in hand shaping (Davare et al. 2006). However, when comparing two-digit precision and whole hand "power" grip tasks, functional magnetic resonance imaging has shown that ventral premotor cortex was involved in precision but not whole hand tasks (Ehrsson et al. 2000). Thus, although the premotor cortex is related to bimanual coordination [for review, see Swinnen and Wenderoth (2004)], further research is needed to elucidate its involvement in force and placement control aside from precise grasp feedback of digit placement after contact may be used to modulate digit forces (Davare et al. 2019; Fu et al. 2010; Mojtabah et al. 2015). Recently, with the use of a two-digit manipulation task, it was suggested that different circuits are involved when the choice of contact was either constrained or unconstrained (Marneweck et al. 2018). Specifically, cerebellar lobules IV-V were involved in the online control of digit forces to digit placement variability. The cerebellum has been also shown to be involved in anticipatory adjustments during bimanual unloading tasks (Diedrichsen et al. 2005). Thus the cerebellum could be involved in the general feature of force to placement modulation by controlling the modulation of effector forces after feedback is obtained about effector placement on contact. Whether or not these overlapping circuits are able to facilitate transfer and generalizability of effectors into high-level representations remains to be determined.

Conclusions

We have shown that the dexterous bimanual grasping and lifting of a box with an asymmetrical center of mass is accomplished through the anticipatory planning of a moment that opposes the intrinsic object torque. This compensatory moment is achieved by modulating hand forces and placement such that the hand placed on the heavier side has larger forces and higher placement than the hand on the lighter side. The modulation of hand forces and placement co-varied to allow stable trial-to-trial compensatory moments despite varying forces and placements, similar to two-digit, three-digit, and whole hand grasping. We conclude that these features are similar across multiple effectors and grasp types and therefore are likely to represent a general feature of motor adaptation.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

T.L.M., A.M.G., and M.S. conceived and designed research; T.L.M. performed experiments; T.L.M. analyzed data; T.L.M., A.M.G., and M.S. interpreted results of experiments; T.L.M. prepared figures; T.L.M. drafted manuscript; T.L.M., A.M.G., and M.S. edited and revised manuscript; T.L.M., A.M.G., and M.S. approved final version of manuscript.

REFERENCES


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