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RESEARCH ARTICLE

The intermanual transfer of anticipatory force control in precision grip lifting is not influenced by the perception of weight

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Abstract Passing objects from one hand to the other occurs frequently in our daily life. What kind of information about the weight of the object is transferred between the holding and lifting hand? To examine this, we asked people to hold (and heft) an object in one hand and then pick it up with the other. The objects were presented in the context of a size–weight illusion: that is, two objects of different sizes but the same weight were used. One group of participants held one of the objects in their left hand and then picked it up with their right. Another group of participants simply picked up the objects from a table. Thus, the former group had on-line information about the weight of the object, whereas the latter did not. Both groups showed a strong and equivalent size–weight illusion throughout the experiment. At the same time, the group that lifted the objects from the hefting hand applied equal grip force to the small and large object right from the start; in contrast, the group lifting the objects from the table, initially applied more grip force to the large than to the small object before eventually applying the same force to both. In two additional groups, a delay period was imposed between the lifting of the first and the second hands. The force parameters employed by these last two groups were virtually identical to those used by the group that lifted the object directly from the other hand. These results suggest that the initial calibration of grip force uses veridical information about the weight of the object provided by the other hand. This veridical information about weight is available on-line and is retained in memory for later access. The perceived weight of the object is basically ignored in forming grasping forces.

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Introduction

When lifting an object, people scale their fingertip forces in anticipation of the expected or predicted weight of the object (Johansson and Westling 1988). Specifically, when using a precision grip with the tips of the index finger and thumb on either side, vertical load force and horizontal grip force are increased more rapidly when lifting an object that is expected to be heavier compared to when lifting an object that is expected to be light. When lifting an object for the first time, predictions about weight are based on sensed properties of the object including its identity (Gordon et al. 1993) and size (Gordon et al. 1991a, b). When such cues are misleading or unavailable, errors in force scaling may occur when first lifting the object. However, within a few repeated lifts of the same object, accurate anticipatory force scaling is typically observed (Johansson and Westling 1988; Gordon et al. 1993), and it has been suggested that this rapid adaptation results from updating an internal representation or model of the physical properties of the object (Johansson and Westling 1988; Flanagan and Wing 1997; Flanagan et al. 2006).

Johansson et al. (1984) referred to the knowledge of object properties gained from previous lifts as *sensorimotor memory*. This has proven to be a good choice because recent studies, exploiting the size–weight illusion, have shown that people maintain independent and distinct sensorimotor and perceptual representations of object weight (Flanagan and Beltzner 2000; Grandy and Westwood 2006). In the classic "size–weight" illusion, the smaller of two equally weighted objects is typically perceived as being heavier (Charpentier 1891; Murray et al. 1999). When repeatedly lifting such objects, participants initially apply more force to the large object than to the small one. However, after only a few trials they fine-tune their forces to the actual weight of the objects (Flanagan and Beltzner 2000; also see Grandy and Westwood 2006). Even when a delay as long as 24 h is introduced between two series of lifting trials, participants will still apply the correct grip and load forces after the delay, indicating that some memory of earlier sensorimotor information is retained (Flanagan et al. 2001). Remarkably, even though the motor system learns to apply the appropriate forces, participants continue to show the size–weight illusion, and report an illusion that is just as robust at the end of the experiment as it was at the outset.

In everyday tasks, we often lift objects successively with different hands or transfer an object from one hand to another. Here the question arises as to whether the control of each hand is based on distinct internal models of the properties of the object or a common internal model shared by both hands. If the hands share a common internal model, efficient and complete intermanual transfer of object properties is expected. Recent studies have shown that adaptation to novel and complex loads applied to the hand during goal-directed reaching shows no (Malfait and Ostry 2004) or limited (Criscimagna-Hemminger et al. 2003) transfer between hands. In contrast, Gordon et al. (1994) showed good intermanual transfer of weight information when lifting mass loads with a precision grip in the absence of visual or haptic cues about object weight. The latter result suggests that, for familiar loads, parametric information about the load (e.g., weight) gained when lifting an object with one hand can be used when subsequently lifting it with the other hand. Excellent intermanual transfer of weight information has also been demonstrated in voluntary unloading tasks where a load acting on one hand is lifted by the other hand and the participant attempts to keep the unloaded hand from moving (Dufosse et al. 1985; Kaluzny and Wiesendanger 1992; Massion 1992). In such tasks, good performance requires that information about the load is available to the lifting hand and also requires good temporal coordination between the actions of the two hands (cf. Diedrichsen et al. 2003).

Although the weight of evidence favors the notion that information about object weight is transferred from one hand to another, it is an open question whether this information is linked to the perceived weight of the objects (i.e., the perceptual representation of weight) or the representation of object weight used for motor control (i.e., the sensorimotor representation of weight). The aim of this study was to answer this question. To do so, we used size–weight stimuli (i.e., small and large equally weighted cubes) so that we could dissociate actual and perceived weight in four different lifting conditions.

To pit the perceptual representation of weight against the sensorimotor representation of weight, participants in the palm group (PAL) held either the small or large cube in the palm of their left hand. The cube was placed there by the experimenter and participants were asked to heft the object up and down a few times in order to gain experience of the weight of the object. They were then instructed to pick up the object using their right hand by grasping, with a precision grip, a small handle mounted on the top of the object. When applying initial grip and load forces to the object with the right hand, the motor system could base its computations on either the perceived weight of the object, in which case more force would be generated for the small object, or sensorimotor information obtained when hefting the object with the left hand. In the latter case, we would expect either equal forces to be generated for the two cubes or slightly greater force to be generated for the larger cube depending on how rapidly the motor system adapts (see Flanagan et al. 2006 for a review of force adaptation in precision lifting).

To test whether the motor system made use of on-line sensorimotor information from the left hand (i.e., tactile and proprioceptive afferents and efference copy of motor commands) or sensorimotor memory established during hefting, a delay palm group (DPAL) was included. After participants in the DPAL group hefted the object with the left hand, the experimenter removed the object from their left palm and placed it on a table in front of them. After a 10-s delay period, participants were instructed to use their right hand to pick up the object by grasping the handle with a precision grip. If sensorimotor memory of object weight transfers between the two hands, then force scaling in this group should be as accurate as in the PAL group.

To examine whether intermanual transfer, where the object was lifted successively by the two hands with the same posture (precision grip), differed from intermanual transfer where the object was hefted by one hand and then lifted by the other, a third group of participants (delay table group, DTAB) were instructed to pick up one of the objects from a tabletop, first with their left hand and then, after a 10-s delay, with their right hand.

Finally, to replicate findings in earlier studies (Flanagan and Beltzner 2000; Grandy and Westwood 2006) and establish baseline performance without intermanual transfer, a fourth group of participants (Baseline group) were asked to pick up the same pair of objects from a table repeatedly and alternately with their right hand and with a delay of approximately 10 s between lifts. Based on previous studies (Flanagan and Beltzner 2000; Grandy and Westwood 2006), we expected that, on the initial lifts, participants would apply more force to the large object than to the small one, presumably because they were using a model in which large objects are assumed to weigh more than small ones.

Materials and methods

Participants

Four groups of healthy right-handed participants with normal or corrected-to-normal vision were recruited from the UWO campus. PAL group, 9 females and 7 males, aged 19–35 years (mean = 23.7, SD = 4.96 years), lifted the target object from the palm of their left hand using their right hand after hefting with their left hand for approximately 5 s. DPAL group, 4 females and 8 males, aged 17–30 years (mean = 19.4, SD = 3.9 years), initially held the object on their left palm for 5 s. The experimenter then removed the object and placed it on the tabletop. After a 10-s delay, the participant lifted the same object from the tabletop with their right hand. DTAB group, 8 females and 4 males, aged 17–24 years (mean = 18.4, SD = 1.88 years), initially lifted the target object from the tabletop with their left hand and held it for 5 s before replacing it back to the tabletop. After a 10-s delay, the participant lifted the same object from the tabletop with their right hand. Finally, Baseline group, 9 females and 7 males, aged 16–37 years (mean = 26.4, SD = 6.23 years), lifted the target objects from a tabletop with their right hand only. All participants gave written informed consent. Their handedness was assessed with Edinburgh handedness inventory (Oldfield 1971). The study was approved by the Psychology Research Ethics Board of the University of Western Ontario.

Materials

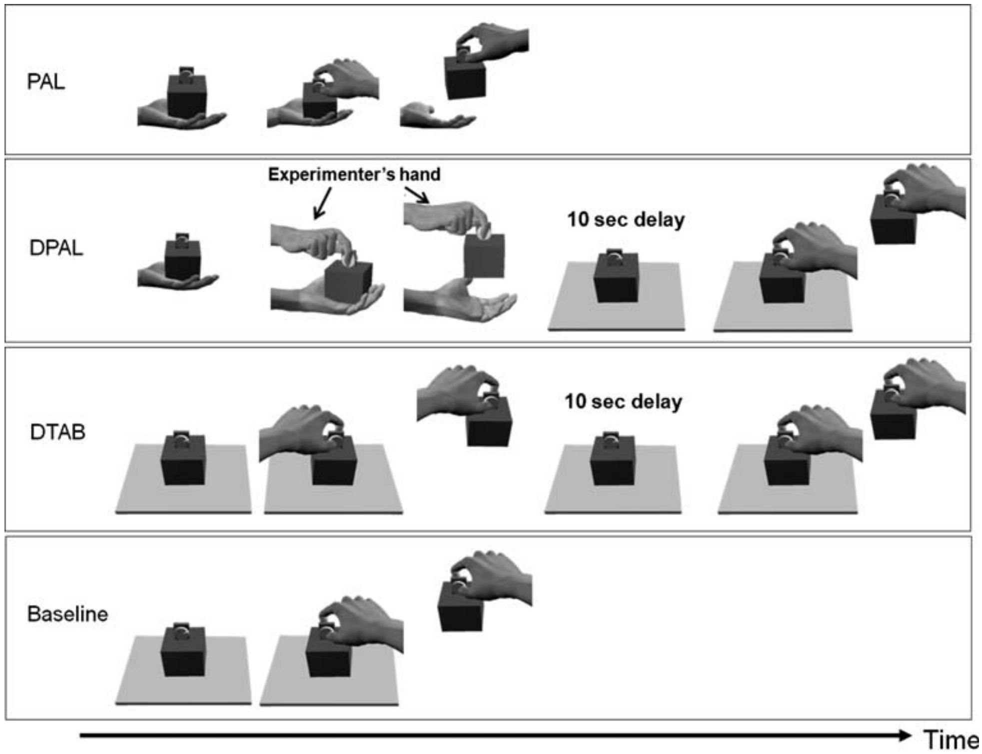
The participants lifted two black boxes of the same weight (0.28 kg) but different sizes (big: $10.9 \times 10.9 \times 10.9$ cm^3, density 0.22 kg/l; small: $5.2 \times 5.2 \times 5.2$ cm^3, density 2.01 kg/l). The weight of the box was adjusted by carefully inserting lead shots and sponges so that its center of mass matched the geometric center of the box. The volume and weight of these boxes were designed to approximate the objects used by Flanagan's group (Flanagan and Beltzner 2000; Flanagan et al. 2001) to enable comparison between studies. A pair of 6-axis force-torque sensors (Nano 17 F/T; ATI Industrial Automation, Garner, North Carolina), which measured the 3D forces and torques, was mounted to a bridging handle on each box. The range and resolution of this device has been documented by Kinoshita et al. (1997). The force transducers were screwed onto an aluminum handle which could be easily mounted and dismounted. The force transducers and the handle together weighed 0.05 kg, so, when mounted to the boxes, each device weighed 0.33 kg (3.23 N). Two cylinders of the same volume (73.5 cm^3) and weighing 3.06 N and 4.04 N, respectively, were used for training. Cylindrical rather than cubical objects were used in the training phase to minimize the possibility that, when performing the task during the experimental phase, the participants would adopt a default strategy established during the training phase. A digital I/O card sampled the output of the force transducers at a rate of 1,000 Hz. The force along the axis orthogonal to the grip surface (F_z) is the grip force, and the vector addition of forces tangential to the grip surface is the load force $\left(LF = \sqrt{F_x^2 + F_y^2}\right)$. All participants lifted the boxes with their right hand. The entire experiment was controlled and monitored by two different PCs, with custom software programmed in Microsoft Visual C++ and the Psychophysics toolbox extensions for Matlab (Brainard 1997; Pelli 1997).

Procedures

Each participant was seated in front of a table. Every experiment started with a training phase during which the participant practiced lifting for at least ten trials with the cylindrical objects. Once a participant could follow his/her respective instructions and lift the objects vertically and steadily, as indicated by smooth force trajectories plotted on a monitor after every trial, the experimenter switched the cylinders to the cubes and started the experimental phase. All participants were aware that they were lifting the same pair of cubic objects throughout the experimental phase. All aspects of the procedure, except for the objects, were the same in the training and the experimental phases.

For the PAL group (Fig. 1, first row), the object was initially placed on the palm of the left hand and the participant was instructed to "heft" the object by moving that hand up and down a few times (approximately 5 s). A tone from the PC speaker (time zero) then signaled the participant to lift the object by grasping the handle with the

Fig. 1 Order of events in a trial for different groups. A trial starts from the leftmost event and progresses rightwards. All pictures of hands indicate the participant's hand unless otherwise noted



thumb and index finger of the right hand using a precision grip. The participant lifted the object and held it at a height of approximately 5–10 cm from the palm until a tone from the PC speaker (time 3,000 ms) signaled him/her to rate the heaviness of the object by reporting an integer; the heavier the object, the larger the number. No constraints on the range of this integer were provided, and participants were allowed to use a range they found comfortable (Zwislocki and Goodman 1980). The participant then put the object back to where it was at the beginning of the trial.

Participants in the DPAL group (Fig. 1, second row) also hefted the object with their left hand at the beginning of a trial (for approximately 5 s) but then the experimenter removed the object from the participant's palm and placed it on the table. After a 10-s delay period, a tone from the PC speaker (time zero) signaled the participant to lift the object from the table with their right hand using a precision grip. The remaining events in a trial for the DPAL group after the delay period were the same as those for the PAL group.

DTAB group (Fig. 1, third row) lifted the object from the table with their left hand using a precision grip and held it for 5 s at the beginning of a trial, and then replaced the object back to the table. After a 10-s delay period, a tone from the PC speaker (time zero) signaled the participant to lift the object from the table with their right precision grip. The remaining events in a trial for the DTAB group after the delay period were the same as those for the PAL and DPAL groups.

For the Baseline group (Fig. 1, bottom row), one of the objects was initially placed on a plastic panel that sat on the table. Similar to the PAL group, a tone signaled the participant to lift the object and hold it at a height of approximately 5–10 cm from the panel until another tone from the PC speaker signaled him/her to replace the object and rate its heaviness.

All participants were able to lift the object in the instructed manner before starting the experimental trials. Each participant was given 20 trials in pseudorandom alternation in which pairs of trials consisting of a big object followed by a small object or vice versa were presented. There was a 10-s delay between trials for all lifting groups. The alternation of big and small objects optimized the conditions for obtaining a size–weight illusion. The participants were aware that they were lifting and weighing the same two objects throughout the experiment.

Data analysis

The perceptual estimation of weight on each trial was normalized to a z-score distribution that used each participant's own mean and standard deviation across all trials. The force measurement was resampled at 500 Hz and filtered with a 4th order, zero-phase lag, low-pass Butterworth filter (cutoff frequency = 14 Hz). The mean of the two grip forces and the sum of the two load forces, measured from the index and the thumb, were used in the

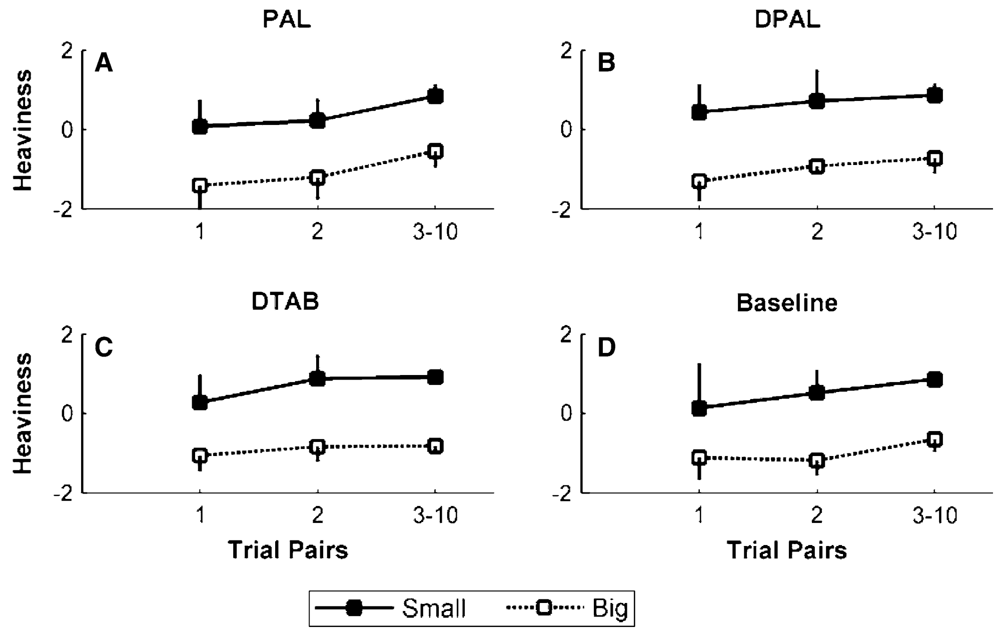


Fig. 2 Normalized perceived heaviness in each lifting group. **a** PAL group; **b** DPAL group; **c** DTAB group; **d** Baseline group. The *open squares* represent the big object, and the *filled squares* represent the small object. The *error bars* represent standard error

analysis. To obtain grip and load force rates, the force data were differentiated using a 5-point central difference equation.

The dependent measures were the same as those adopted in Flanagan and Beltzner (2000), including peak grip force, peak grip force rate, peak load force, peak load force rate, and load phase duration. Because these force parameters quickly adapted to a stable level appropriate for the real weight of the target objects during the first couple of trial pairs, data from each individual trial pair were presented for only trial pair 1 and 2, and data from trial pair 3 to 10 were averaged to simplify data presentation.

All dependent measures were subject to a 4 Group (PAL/DPAL/DTAB[1]/Baseline) $\times$ 2 object size (Big/Small) $\times$ 3 trial pairs (1, 2 and the average of 3–10) mixed design ANOVA. Group was a between-participants factor, and the other factors were within-participants factors. Tukey's HSD was used for pairwise comparisons within each lifting group. To more closely examine how well object weight information was transferred between hands, lifting dynamics of both hands ($DTAB_L$ and $DTAB_R$ in Figs. 3, 5) from the DTAB group were subject to an additional repeated-measure ANOVA, with hand (left/right), object size (Big/Small), and trial pairs (1, 2 and the average of 3–10) as three factors. The DTAB group was the only group with procedures appropriate for this analysis. The significance level (*alpha*) for all statistical tests was set at 0.05.

[1] Data from the right hand ($DTAB_R$ in Figs. 3–5) were analyzed here.

Results

Perceptual reports

The three-way mixed design ANOVA revealed a significant main effect of object size, $F(1, 52) = 638.9$, $P < 0.0001$. The signature pattern of the size–weight illusion was present, wherein participants consistently reported that the small object was heavier than the big object (Fig. 2). The main effect of trials was also significant, $F(2, 104) = 27.8$, $P < 0.0001$ and there was no interaction between trials and object size, $F(2, 104) = 1.1$, $P = 0.35$, indicating that the perceived heaviness of both objects increased as the trials proceeded (see similar results in Grandy and Westwood 2006). The fact that there was no interaction between Group and either Object Size or Trial Pairs (and no three-way interaction) indicates that all groups of participants perceived the size–weight illusion in the same fashion throughout the experiment.

Lifting dynamics

Ensemble averages of grip and load forces and the corresponding force rates for each group are illustrated in Fig. 3. Each panel shows the force or force rate traces of the first trial pair and the average of the third to the tenth trial pairs. Figure 4 illustrates hypothetical results for the peak values of these forces and force rates. We predicted a three-way Group $\times$ Object Size $\times$ Trial Pairs interaction. With the

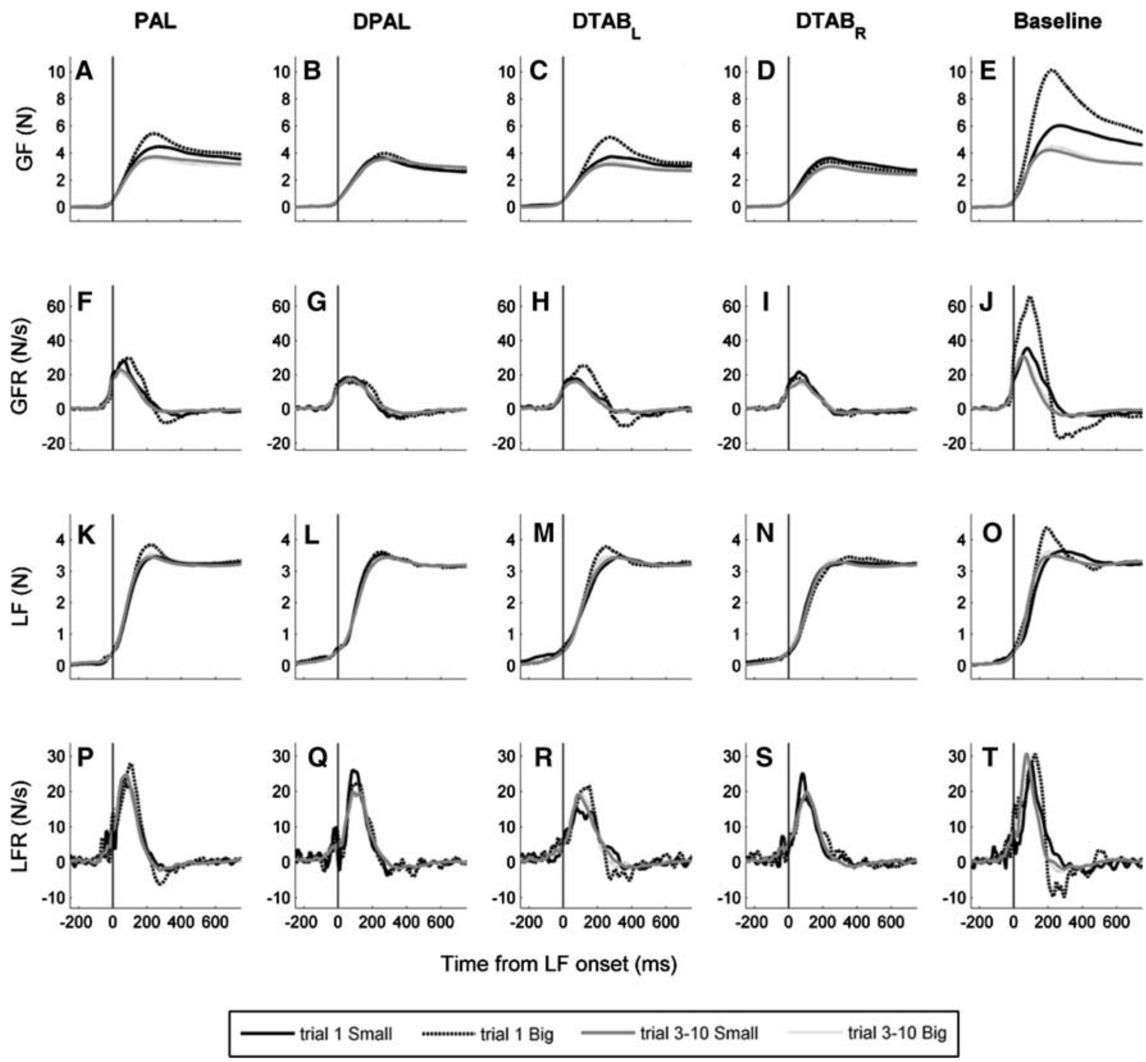


Fig. 3 Group average of force trajectories in each lifting group. Each individual's force trajectory from the same trial pair was aligned at the load force onset and encompassed the time span from 200 ms before to 800 ms after load force onset (time 0). Because of their similarity, the group-average trajectories from the third to tenth trial pairs were collapsed. **a–e** Peak grip force (PGF); **f–j** peak grip force rate (PGR); **k–o** peak load force (PLF); **p–t** peak load force rate (PLR). $DTAB_L$ trajectories from the left hand of the DTAB group, $DTAB_R$ trajectories from the right hand of the DTAB group

exception of the PAL group, we predicted that greater peak forces and peak force rates would be applied to the big object than the small one on the first trial. This effect was not predicted for the PAL group because we expected sensorimotor information about object weight to be transferred across hands. In the DPAL and DTAB groups, we predicted that this information would not be available due to the delay. Actual peak force and force rate values are illustrated in Fig. 5.

Peak grip force

The Group × Object Size × Trial Pairs interaction was significant, $F(6, 104) = 4.8$, $P < 0.001$. In contrast to the predicted data pattern (Fig. 4), this interaction was due to the fact that participants in the Baseline group, who lifted objects from the table, applied greater grip force to the big object (10.8 N) than they did to the small object (6.4 N) on the first pair of trials ($P < 0.01$), but participants in the PAL, DPAL, and DTAB groups, who first experienced the object with their left hand before the right hand lifted it for the first time, applied similar grip forces to both objects (all Ps > 0.1; Fig. 5a, b, d, e). On subsequent trials, all groups applied similar forces to both objects (all Ps > 0.05). All of the lower order effects were significant: Object Size: $F(1, 52) = 15.1$, $P < 0.001$; Trial Pairs: $F(2, 104) = 14.4$, $P < 0.001$. Group: $F(3, 52) = 145.8$, $P = 0.001$; Object Size × Trial Pairs interaction, $F(2, 104) = 6.6$, $P < 0.01$; Group × Trial Pairs interaction, $F(6, 104) = 5.4$, $P < 0.001$; Group × Object Size interaction, $F(3, 52) = 7.1$, $P < 0.001$.

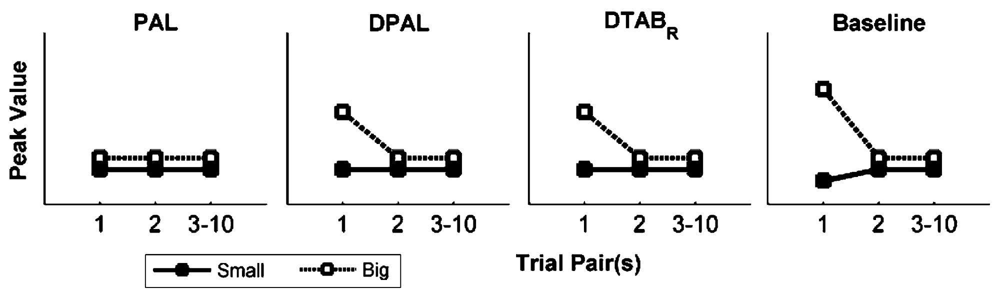


Fig. 4 Hypothetical results of the peak lifting dynamics in each lifting group. The *open squares* represent the big object, and the *filled squares* represent the small object. All groups except for the PAL group are predicted to show greater forces and force rates on the first trial pair

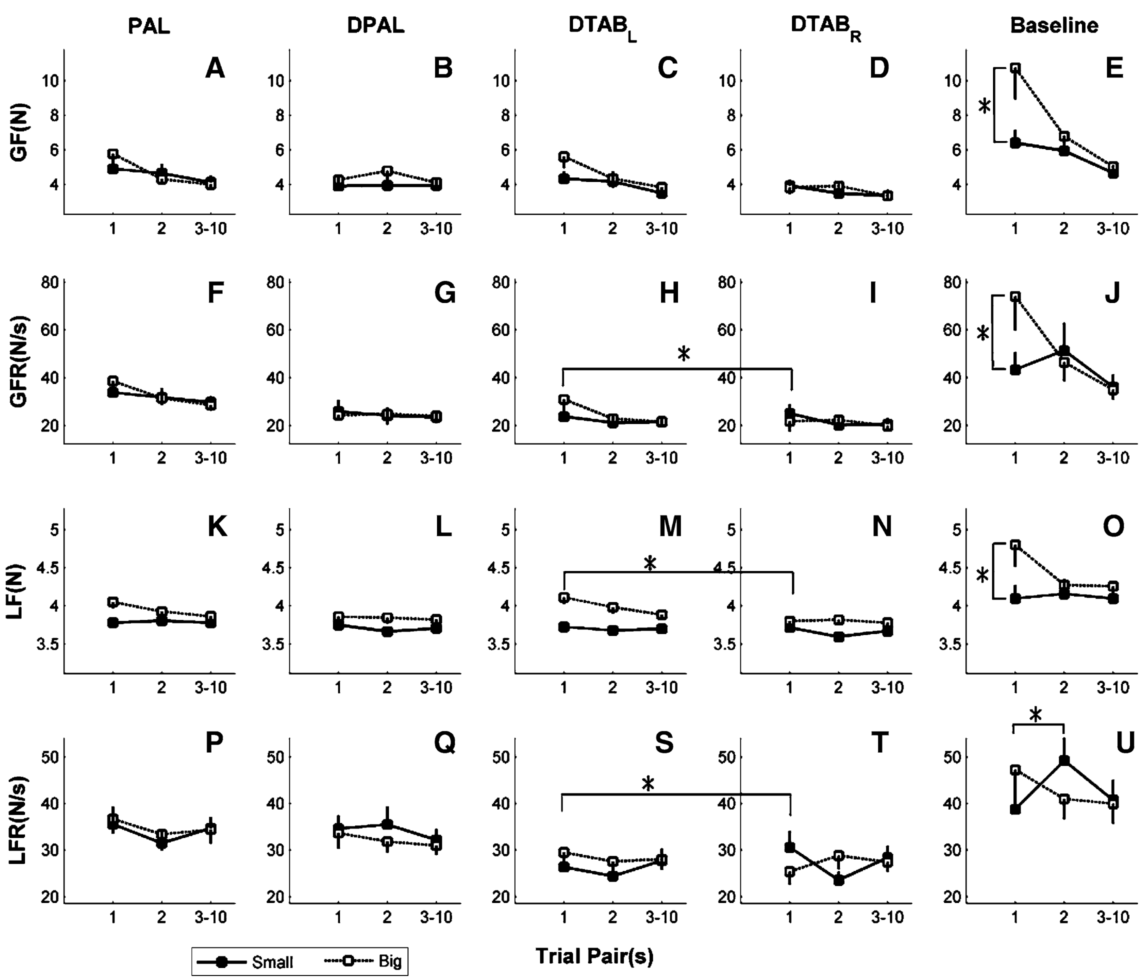


Fig. 5 Peak lifting dynamics in each group. The *asterisks* indicate significant differences (at least $P < 0.05$) either between force parameters applied to big and small objects in the same trial pair (the Baseline column), or between force parameters applied by left and right hands on the same object and same trial pair (DTAB$_L$ and DTAB$_R$ columns). The *error bars* represent standard error

Peak grip force rate

Similar to peak grip force, the three-way interaction was also significant, $F(6, 104) = 6.47$, $P < 0.0001$. Again, for participants in the Baseline group, higher peak grip force rates were observed for the big object than the small object on the first pair of trials ($P < 0.0001$), but this was not the case for the participants in all the other groups (Fig. 5f, g, i, j). Other significant effects include: Object Size × Trial Pairs, $F(2, 104) = 5.3$, $P < 0.01$; Group × Trial Pairs, $F(6, 104) = 2.9$, $P < 0.01$; Group × Object Size interaction, $F(3, 52) = 4.7$, $P < 0.01$; Group, $F(3, 52) = 6.2$, $P < 0.01$; Trial Pairs, $F(2, 104) = 8.2$, $P < 0.001$.

Peak load force

Similar to what was found for peak grip force and peak grip force rate, the ANOVA revealed a significant three-way interaction, $F(6, 104) = 3.9$, $P < 0.01$. This was because participants in the Baseline group applied more load force on the big object (5.8 N) than on the small object (4.9 N) at the first Trial Pair ($P < 0.05$), whereas participants in the other groups applied equivalent load force on both objects at the first Trial Pair. In the remaining trials, all groups applied the same load force to both objects throughout the remaining trials (Fig. 5k, l, n, o). Other significant effects in this analysis included: Object Size × Trial Pair interaction, $F(2, 104) = 4.1$, $P < 0.05$; Group × Object Size interaction, $F(3, 52) = 3.9$, $P < 0.05$; Object Size, $F(1, 52) = 60.1$, $P < 0.0001$; Group, $F(3, 52) = 6.9$, $P < 0.001$; Trial Pair, $F(2, 104) = 5.9$, $P < 0.01$.

Peak load force rate

The three-way interaction was significant, $F(6, 104) = 4.4$, $P < 0.001$. However, contrary to the other dependent measures, the three-way interaction here is due to a significant difference between the first and the second trial in the Baseline group when lifting the small object ($P < 0.05$), but no such difference was observed when lifting the big object. This suggests that, in the second trial with the big object, participants decreased load force, at least in part, by decreasing the time period over which load force increased. A significant effect of Group, $F(3, 52) = 4.2$, $P < 0.05$ (Fig. 5p, q, s, t) was also observed but no other effects for the peak load force rate approached significance.

Although the difference between the peak load force rate applied to the big and the small objects did not reach significance on the first Trial Pair ($P = 0.17$), when we included only the first Trial Pair in the analysis, there was a marginally significant interaction between Object Size and Group, $F(3, 52) = 2.76$, $P = 0.051$. Thus, across the four different dependent measures analyzed, we consistently observed that only participants in the Baseline group applied greater forces and increased these forces more rapidly for the big object compared to the small one when they lifted these objects with their right hand for the first time.

Within-subject comparison of the DTAB group

The comparison between the lifting dynamics of the left hand (Fig. 5c, h, m, r; $DTAB_L$) and right hand (Fig. 5d, i, n, s; $DTAB_R$) of the DTAB group is of particular interest because it would reveal how good the intermanual transfer is within the same person. All four dependent measures of lifting performance from both hands of the DTAB group were subject to three-way repeated-measure ANOVAs (Hand × Object Size × Trial Pair). Significant or marginally significant three-way interactions were observed for peak load force, $F(2, 22) = 3.07$, $P = 0.07$ and peak load force rate, $F(2, 22) = 4.24$, $P < 0.05$, and peak grip force rate, $F(2, 22) = 2.90$, $P = 0.08$, but not for peak grip force, $F(2, 22) = 1.67$, $P = 0.21$.

To further explore the significant three-way interactions, data from each object size were subjected to two-way (Hand × Trial Pair) ANOVAs. For the small object, no significant hand-related effects were observed for peak load force, peak load force rate, and peak grip force rate (all Ps > 0.05). For the big object, the Hand × Trial Pair interaction was significant for peak load force rate, $F(2, 22) = 5.42$, $P < 0.05$, marginally significant for peak load force, $F(2, 22) = 2.97$, $P = 0.07$, and significant for peak grip force rate, $F(2, 22) = 6.58$, $P < 0.01$. Post-hoc pairwise comparisons showed that these effects were mainly due to the greater force and force rates applied by the left hand than by the right hand on the first trial (peak load force: 4.11 vs. 3.80 N for the left and right hand, respectively, $P < 0.001$; peak load force rate: 29.52 vs. 25.39 N/s, $P < 0.05$; peak grip force rate: 30.95 vs. 21.79 N/s). None of the peak load force, peak load force rate and peak grip force rate differed between the two hands on any of the other trial pairs (all Ps > 0.10). Thus, the analysis on three out of four lifting dynamics showed that the two hands actually only lifted the big object differently on the first trial, likely due to the wrong expectation of weight when grasping the big object for the first time.

To summarize, the size–weight illusion persisted throughout the experiment for all groups such that participants always felt the smaller object to be heavier than the larger one, even though they were of the same weight. Nevertheless, despite the presence of the size–weight illusion, accurate intermanual transfer of the actual grip and load forces was observed. In other words, intermanual transfer of anticipatory force control reflects the sensorimotor rather than the perceptual representation.

Discussion

Previous work has established that information about object weight is transferred across the hands when successively lifting objects with each hand (Gordon et al. 1994). In addition, recent experiments have shown that the brain maintains two independent representations of object weight—a perceptual representation that is influenced by the size of objects (as revealed by the size–weight illusion) and a sensorimotor representation that is not. The aim of the current study was to establish which of these two representations of weight is transferred across hands when lifting objects.

For participants in the PAL and DPAL groups, who initially hefted the object in the left hand, either of these representations of weight could have been used when first lifting the object with the second, right hand. The fact that there was no difference in the grip and load forces applied to the big and small objects on the initial right hand trials suggests that an accurate sensorimotor representation of object weight, established during hefting, was available to the right hand when first lifting the object. This result clearly shows that the right hand did not make use of the perceptual representation of object weight (i.e., the perceived heaviness of the object) when first lifting the object.

When using the right hand to directly lift the object from the palm of the left hand, participants in the PAL group could have used on-line sensorimotor information from the left hand to control the forces generated by the right hand. Alternatively, they could have used sensorimotor memory (i.e., a stored sensorimotor representation) of object weight established while hefting the object with the left hand. If participants relied entirely on on-line sensorimotor information, then inaccurate force scaling should have been observed when a delay between hefting with the left hand and lifting with the right was present (as in the DPAL group). As it turned out, this was not the case. Instead, the force applied to the object with the right hand by participants in the DPAL group did not differ from those used by participants in the PAL group. In other words, it seems that the sensorimotor information from the left hand remained in sensorimotor memory and was later used to scale the grip and load forces in the right hand. Although it is possible that on-line sensorimotor information was used by the PAL Group, the fact that there was no difference in the forces applied by the PAL and DPAL groups suggests that sensorimotor memory is just as accurate as on-line information. Would a longer delay have revealed incomplete transfer? How long would it take for the sensorimotor information of object weight to decay significantly after one lifted that object? Although a 10-s delay between trials in DPAL and DTAB groups may seem trivial, longer periods of delay may not change the results. Flanagan et al. (2001) observed long lasting memory for object weight and it is thus possible that perception based memory may not be used even with long delays.

The observation that the 10-s delay did not bias the grip force toward the perceptual representation stands in contrast with the results from experiments that have looked at the effect of delay on the kinematics of grasping. After a 4-s delay, the scaling of grip aperture reflects the perceived rather than the real size of the goal object (Hu and Goodale 2000). This difference in the effects of delay is consistent with the notion that the computation of the trajectory of the grasping hand as it approaches the goal object depends on processes with quite different temporal constraints (and neural substrates) than those involved in the computation of the initial forces that are applied when objects are finally grasped and/or lifted (Brenner and Smeets 1996; Milner and Goodale 2006).

We obtained similar results for participants in the DTAB group, who lifted with the left hand using a precision grip, and participants in the DPAL group who hefted with the left hand. That is, both groups exhibited accurate force scaling with the right when first lifting with the right hand following a delay period after hefting or lifting with the left hand. This result further supports the idea that sensorimotor memory of object weight is transferred from the left to the right hand and also indicates that an accurate memory can be formed from both hefting the object with the left hand and lifting it with a precision grip.

The performance of participants in the Baseline group, who lifted the objects from the table with the right hand without previously lifting or hefting them with the left hand, showed similar force profiles to those found in previous studies that have examined grip and load forces in the context of a size–weight illusion (Flanagan and Beltzner 2000; Flanagan et al. 2001). As expected, these participants generated greater grip and load forces when lifting the large cube compared to the small cube. This group provides an important control in demonstrating that we were able to reveal expected differences in force output for the two cubes using our stimuli and data analysis procedures. One may wonder why the performance differed so much between the Baseline group and the left hand condition of the DTAB group ($DTAB_L$), given that the only difference in experimental settings of these two conditions was the lifting hand. It has been shown that the dominant hand produces greater voluntary finger force than the non-dominant hand (Henningsen et al. 1995). In addition, Henningsen et al. (1995) suggests that the linkage between visual information and force control is more efficient for the dominant than the non-dominant hand. It is likely that the dominant hand may be more prone to the initial expectation of weight based on visual size information than the non-dominant hand and thus resulted in the difference between the Baseline and the $DTAB_L$ conditions. Further studies are required to clarify whether the efficiency of visuomotor linkage influences how the motor system estimate grip and load force based on the visual size of objects.

Our results clearly show that veridical or accurate information about object weight is transferred across the hands because participants generate appropriate fingertip forces. We refer to this information as a sensorimotor representation of weight and distinguish it from a perceptual representation. This distinction is based on the assumption that participants experience the size–weight illusion regardless of the mode of lifting or the hand employed. The size–weight illusion does not depend on the mode of lifting, is experienced even when the objects are supported passively on the hand, and is robust when the two objects are lifted simultaneously by different hands (Charpentier 1891; Murray et al. 1999). Importantly, we confirmed these previous findings in a pilot experiment in which participants gave two reports of perceived heaviness, one during hefting the object in the left palm, the other after lifting with the right hand. Similar weight estimates were reported for both hands. This indicates that participants did not generate right hand forces based on the perceived weights of the objects gained from left hand hefting. If they had, we would have observed greater forces when lifting the small object. Consequently, we believe that our conclusion—that right hand forces are based on sensorimotor representations established by left hand lifting—is entirely reasonable and supported by the results. Moreover, this conclusion is clearly distinct from the conclusions drawn by Flanagan and Beltzner (2000) who did not address the issue of transfer across hands.

Because we are arguing for the intermanual transfer of the sensorimotor representation, a theoretical issue naturally follows: what do we mean by "sensorimotor representations" and "transfer"? Several different terms have been put forward when referring to sensorimotor representations of weight (including internal model and sensorimotor memory) and some authors have argued in favor of the idea that people remember actions (e.g., fingertip forces or motor commands) rather than object properties (e.g., Quaney et al. 2003). However, we believe that the weight of evidence favors the notion that people do remember or store information about object properties (in this case weight) in memory and use this to guide future motor commands (Flanagan et al. 2006). This may not mean that a specialized "transfer mechanism" is required. Instead, we prefer the idea that there is a sensorimotor memory of object weight that can be accessed by both hands.

In our study, participants in the PAL, DPAL, and DTAB groups adapted their force output very quickly such that a single experience of the object with the left hand (i.e., a period of hefting or a precision grip lift) resulting in accurate force control on the very first lift of the right hand. That is, no differences in force output were observed between the small and large cube on the first lift of the right hand. Participants in the Baseline group, who lifted the objects with only their right hand, also adapted to the actual weight quickly after the first trial. This contrasts with the slightly slower adaptation observed in previous studies using abnormally dense objects (Gordon et al. 1993; Flanagan and Beltzner 2001; Grandy and Westwood 2006). In the previous studies, participants applied greater force to the larger object compared to the smaller one for approximately five trials before they applied the same force on both objects. This suggests that object size can continue to influence the predicted weight of the object used by the motor system for several trials despite afferent and efferent feedback about the true weight of the object. One difference between the current study and previous ones is that a training phase was included here where subjects lifted two cylindrical objects of equal size but different weight. By dissociating size and weight, perhaps the training phase slightly weakened the weighting subjects gave to visual cues in comparison to sensorimotor memory such that quicker adaptation was observed.

It is conceivable that participants adopted default grip and load forces at the beginning of the experimental phase based on the weights of the cylindrical objects used in training. Because the cylindrical objects were similar in weight to the cubical objects used in the experimental phase, such default forces would be reasonably accurate. However, our results argue against the possibility that participants used default grip and load forces in the experimental phase. In the Baseline condition, participants employed very different forces for the small and large objects in the first trial whereas, in the other conditions, participants employed far more similar forces for the two objects. Importantly, all groups received the same training and therefore it seems unlikely that the training resulted in a default strategy.

We found that magnitude estimates of heaviness increased over trials for both objects. A similar result was reported by Grandy and Westwood (2006) who suggested that this increase might be due to fatigue. However, given the relatively few number of trials performed by each participant in our study, this explanation can be questioned. In any event, we would emphasize that the magnitude of the size–weight illusion was quite constant throughout the experiment and did not vary significantly with repeated lifting.

The results of the present study add to a growing body of evidence that the neural systems controlling the application of grip and load forces in manual prehension are quite separate from those mediating the perception of weight (Flanagan and Beltzner 2000). The motor system, once it has interacted with an object a few times, bases its computations entirely on the weight of that particular object and does not take into account the object's density or its relative weight with respect to other objects. In contrast, the perception of the object's weight remains highly contextual and is influenced by the object's apparent density and weight with respect to other objects (Flanagan and Beltzner 2000; Flanagan et al. 2001; Grandy and Westwood 2006). In other words, perception, which has to represent a vast array of objects, works with relative rather than real-world metrics. However, relative metrics are of little use to the motor system, which has to adjust its outputs to conform to the requirements of real-world physics. The present experiment demonstrates that these two systems can operate at the same time and generate quite different outputs that are (ultimately) derived from the same objects—and that this independence is maintained even when information has to be transferred from one hand to the other.

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