Independence of perceptual and sensorimotor predictions in the size–weight illusion

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The smaller of two equally weighted objects is judged to be heavier when lifted. Here we disproved a leading hypothesis that this size–weight illusion is caused by a mismatch between predicted and actual sensory feedback. We showed that when subjects repeatedly lifted equally heavy large and small objects in alternation, they learned to scale their fingertip forces precisely for the true object weights and thus exhibited accurate sensorimotor prediction. The size–weight illusion nevertheless persisted, suggesting that the illusion can be caused by high-level cognitive and perceptual factors and indicating that the sensorimotor system can operate independently of the cognitive/perceptual system.

When lifting two objects of different volume but equal weight, people judge the smaller object to be heavier. This size–weight illusion, first documented by over 100 years ago[1,2], is both powerful and robust. The illusion does not lessen when the lifter is informed that the objects are equally weighted[3,4] and does not seem to weaken with repeated lifting[5,6]. The illusion is strongest when subjects grasp the objects so as to obtain haptic cues about size, but is still powerful when only visual information about size is available, as when lifting the objects by strings[7].

Although the mechanisms underlying the illusion remain a matter of controversy, a leading hypothesis is that the illusion stems from a mismatch between expected and actual sensory feedback related to object weight[8–10]. The idea is that the smaller of two equally weighted objects is judged to be heavier because it is heavier than expected. This sensory mismatch hypothesis can be cast in terms of current motor control theory[11–14]. During the lifting task, the central nervous system generates a prediction of sensory feedback based on an internal forward model of the object to be grasped and a copy of the motor commands (efferent copy[15]). The predicted sensory feedback (corollary discharge[16]) is then compared to the actual sensory feedback. The error signal from this comparison would then feed into neural circuits responsible for producing weight judgments. If subjects have an erroneous forward model of the object because of misleading visual cues, a mismatch between predicted and actual sensory feedback will arise. Support for the mismatch hypothesis comes from a study in which subjects were asked to lift a large can and a small can placed on the palm, and then report which felt heavier[9]. In individuals who experience the illusion, peak lift acceleration and height are reliably greater for the large object. However, reliable differences in peak lifting acceleration or height are not observed in those few individuals who do not experience the illusion.

People's expectations about object weight are observed in their motor output during the initial load phase of lifting during which vertical load force is increased before lift-off. When lifting objects held with the tips of the thumb and index finger on either side, it is necessary to increase horizontal grip force to prevent slip. During the load phase, grip force and load force are increased in parallel. The rates of change of grip force and load force, which are precisely scaled to the expected weight of the object[17,18], increase to a maximum and then decrease in anticipation of lift-off. These early peaks in the force rates are the result of feedforward or anticipatory control processes and thus index subjects' predictions of object weight. If people's predictions of object weight are faulty, then lift-off will occur either sooner than expected or not at all. Either event leads to reflex-mediated changes in force output within about 100 ms (refs. 18, 19). Thus, the motor system reacts rapidly to both the presence of unexpected sensory events and the absence of expected sensory events[20].

Previous work on precision lifting has identified a number of factors that influence predictive scaling of fingertip forces when lifting an object. These include visual and haptic information about object size[21–23] and shape[24,25], visual information about object weight distribution[26,27] and identity[28], and immediate sensorimotor memory obtained from previous lifts with the same object[17,18,24,25]. Here we were concerned with two of these factors: visual information about object size and sensorimotor memory. When people lift boxes of varying size but equal weight, the peak values of grip and load forces and force rates and vertical acceleration after lift-off increase with box size[21,23]. Sensorimotor memory is also a powerful predictor of anticipatory force control. When the weight of a repeatedly lifted object is unexpectedly increased or decreased, subjects generate inappropriate forces on the first trial after the switch but fully adapt to the new weight within a single trial[18]. Similar one-trial learning for unexpected changes in surface friction[18] and object shape[24] has been demonstrated.

Here we directly pitted visual size cues and sensorimotor memory against one another by asking subjects to repeatedly lift objects of unequal size but equal weight (Fig. 1) in alternation. We expected that subjects would initially scale their fingertip forces based on the visual size of the objects. However, we predicted that sensorimotor memory would eventually dominate

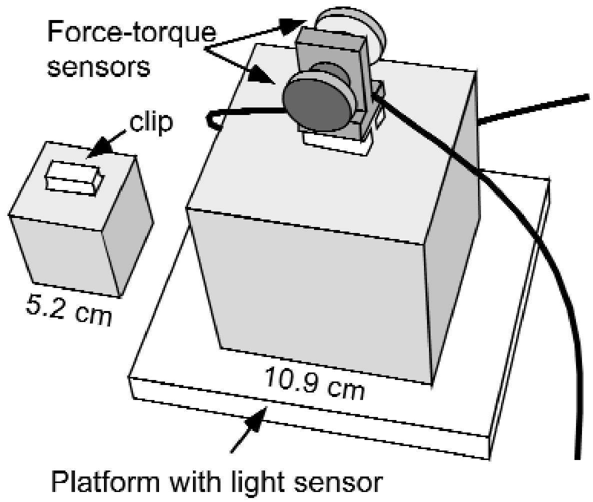

Fig. 1. Size–weight stimuli. Relative sizes of the large and small objects. Subjects lifted the objects by grasping a handle using a precision grip with the tips of the index finger and thumb on either side and separated by 5 cm. The handle was equipped with two force–torque sensors and could be quickly moved from object to object. Plastic contact disks (3 cm in diameter) were mounted on each sensor and covered in medium-grain sandpaper (number 220). The handle was attached by clips located on top and in the center of each object. A light-sensitive diode embedded into the center of the lifting platform recorded object lift-off.

and that, after some number of trials, subjects would correctly scale their fingertip forces to the true (equal) weights of the two stimuli. We also predicted, based on previous reports[5,6], that subjects would still experience the size–weight illusion after repeated lifting. Confirmation of these two predictions would provide direct evidence against the sensory mismatch hypothesis. Provided subjects continue to experience the size–weight illusion after repeated lifts, the sensory mismatch hypothesis predicts that fingertip forces will be scaled to the visual size of the objects and not to object weight. Refutation of the sensory mismatch hypothesis would support an explanation of the illusion based on higher-level cognitive and perceptual factors and would add to evidence that the cognitive/perceptual system can operate independently of the sensorimotor system[29–31]. The hypothesis that the cognitive/perceptual system is independent of the sensorimotor system also predicts that cognitive information given to subjects should have little influence on their predictive force control. We evaluated this broader hypothesis by including a condition in which subjects were verbally informed, before lifting, that the large and small objects were equal in weight.

Results

When asked to visually examine the stimuli before lifting and report which was expected to be heavier, participants were unanimous in reporting an initial expectation of the larger stimuli being heavier. After the set of 20 lifting trial pairs was completed, all participants reported a final sensation of the smaller stimuli being the heavier of the two and thus experienced the size–weight illusion. Moreover, results from a control experiment (described below) indicated that the strength of the illusion was as strong at the end of the lift series as at the beginning.

On the first trial, a representative subject overestimated the forces required for the large object and underestimated the forces required for the small object (Fig. 2, left). Compensatory, reflex-mediated force adjustments were observed in both cases. When lifting the large object, both grip and load force overshot their final levels, and lift-off occurred earlier than expected, shortly after the force rates peaked. The unexpected early lift-off led to a more rapid decrease in force rate some 100 ms later. When the small object was lifted, both grip force and load force increased and then leveled off in anticipation of lift-off. When lift-off did not occur as expected, the forces started to increase again until lift-off was achieved. In later lifting trials (Fig 2, right), the force

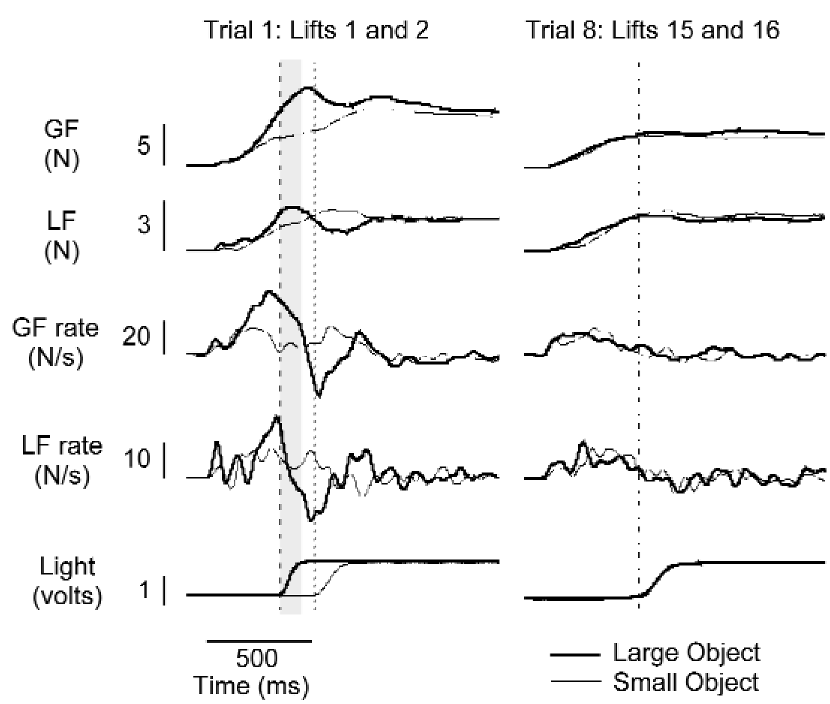

Fig. 2. Fingertip force records. Grip force (GF, in Newtons), load force (LF), grip and load force rates and light-sensitive diode recorded in the first trial (lifts 1 and 2; left) and the eighth trial (lifts 15 and 16; right). This subject lifted the large object (thick traces) and then the small object (thin traces) in each trial (pair of lifts). In all trials, subjects grasped the object and increased grip and load force together until lift-off (signaled by the light diode) occurred. In the first trial, peak grip and load force rates were scaled to object size, whereas by the eighth trial, the peak force rates were similar for the two objects and appropriately scaled to object weight. When the small object was lifted in the first trial, the initial increase in load force was insufficient to cause lift-off and load force increased again before lift-off (dotted line) occurred. When the large object was lifted in the first trial, the grip and load forces overshot their final levels and lift-off (dashed line) occurred earlier than expected. This led to a sharper decrease in force rates 100 ms later (right edge of gray bar). In the eighth trial, lift-off (dotted–dashed line) occurred at about the same time for both objects.

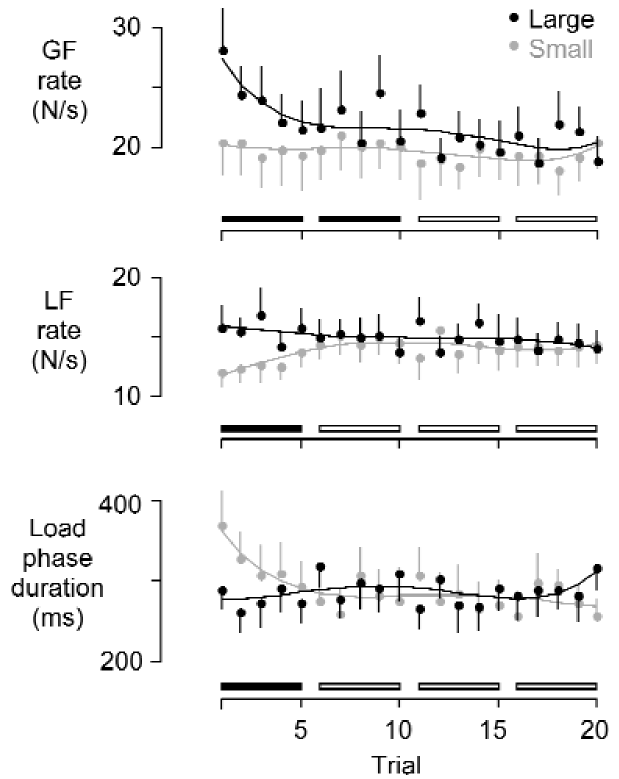

Fig. 3. Averaged lift parameters. Peak grip force rate (top), peak load force rate (middle) and load phase duration (bottom), as a function of trial. Each black (large object) and gray (small object) dot represents an average of 20 subjects (vertical lines, standard errors). Data from cued and non-cued conditions were combined. Fourth-order polynomial functions were fitted for each object to provide a visual impression of the adaptation over trials. Horizontal bars indicate, for each block of five trials, whether there was (filled) or was not (open) a reliable effect of object size on the dependent variable ($p < 0.05$).

and force rate functions for the small and large objects were very similar. Moreover, lift-off occurred at about the same time, well after the force rates peaked and when these rates had decreased close to zero. The small fluctuations in load force following lift-off were due to inertial loading; these were anticipated by parallel changes in grip force[32]. In contrast to the initial trials, grip and load force neither overshot nor undershot their final levels, and no corrective adjustments in force were observed. These results indicated that the subject learned to scale fingertip forces to the actual object weights and generated accurate sensory predictions.

To quantify the history of force adaptation, we divided the 20 lifting trials into 4 successive blocks of 5 trials and examined data averaged across all subjects (Fig. 3). In the first block of trials, greater peak grip (ANOVA, $F_{1,18} = 25.84$; $p < 0.001$) and load (ANOVA, $F_{1,18} = 35.11$; $p < 0.001$) force rates were observed when lifting of the large object was compared with that of the small object. As a consequence, shorter load phase durations were also observed (ANOVA, $F_{1,18} = 5.28$; $p = 0.034$). There was no effect of cue condition (cued versus non-cued) or interaction between cue condition and object size for any of the dependent variables ($p > 0.05$ in all cases). In the second block of five trials, peak grip force rate was greater for the large object (ANOVA, $F_{1,18} = 7.69$; $p = 0.013$) but there was not a reliable difference in peak load force rate (ANOVA, $F_{1,18} = 2.63$; $p = 0.122$) or load phase duration (ANOVA, $F_{1,18} = 0.20$; $p = 0.662$). Again, there were no significant effects of cue condition or interactions between cue condition and object size for any of the dependent variables ($p > 0.05$ in all cases). In the third and fourth blocks of five trials, no reliable effects of object size or cue condition were observed on any of the dependent variables ($p > 0.05$ in all six cases). These results confirmed that subjects initially based their sensorimotor predictions on the objects' visual size. However, after the first five to ten trials, subjects increased grip and load force at similar rates for the two objects, indicating that force output was scaled to true object weight, independent of the visual size of the objects.

Subjects were instructed to lift vertically and not to tilt the object to eliminate any object-size-dependent differences in torque or inertial moments that may have otherwise influenced grip force[26,27,33–35] and weight perception[36,37]. To test whether subjects complied with these instructions, we determined the peak absolute tangential torque generated at the index finger for each lift. The mean values for the large (10.03 ± 5.37 milliNewton meters, mNm) and small (7.79 ± 4.16 mNm) objects were not reliably different (ANOVA, $F_{1,19} = 0.24$; $p = 0.629$).

Although all subjects experienced the size–weight illusion, it was important to demonstrate that the strength of the illusion was not altered by repeated lifting. We compared two additional groups of subjects who provided weight estimates after either 1 or 20 lift trials. We used the absolute magnitude estimation procedure[38], in which subjects choose numbers representing the perceived weights of the size–weight stimuli. The ratio of the estimates for the small and large objects was taken as an index of illusion strength. The average ratios obtained after 1 (1.55 ± 0.80) and 20 (1.64 ± 0.45) lift pairs were not reliably different (ANOVA, $F_{1,18} = 0.09$; $p = 0.763$). Thus, the strength of the illusion was not affected by repeated lifts of the size–weight stimuli.

Discussion

According to the sensory mismatch hypothesis, the size–weight illusion arises from a discrepancy between actual and expected sensory feedback[8–10]. Our finding that subjects experienced the size–weight illusion while accurately predicting the fingertip forces required to lift the size–weight stimuli clearly refutes this hypothesis. We showed that, when repeatedly lifting small and large objects of equal weight, the motor system adapted such that anticipatory changes in fingertip force were precisely scaled to object weight. Such adaptation could be achieved by an updating of the forward models of the two stimuli based on the errors in sensory prediction. Once adapted, the forward models will generate accurate sensory predictions that in turn can be used to estimate the forces required to lift the stimuli[39–41].

We demonstrated that repeated lifting of the stimuli did not alter the strength of the size–weight illusion. This finding, which is consistent with previous reports[5,6], indicated that the size–weight illusion was truly independent of errors in sensorimotor prediction. Subjects provided similar weight estimates for the size–weight stimuli in the first and last lifting trials even though errors in sensorimotor prediction were observed in the first trial but not the last.

Fingertip forces were gradually scaled to the true object weights over 5–10 lifting trials. This gradual adaptation stood in marked contrast to the one-trial learning reported when subjects repeatedly lift a single object[18,24] and was probably due to three factors: conflicting visual information about object size, lifting the two objects (but not weights) on alternate trials and the uncommon densities of the objects[28]. Although sensorimotor memory and visual size both influenced predictive force control, at least initially, cognitive knowledge about object weight did not seem to influence force prediction. Verbal instructions about object weight had no bearing on fingertip force control.

Our finding that the size–weight illusion was not associated with errors in sensorimotor prediction argues for a purely cognitive/perceptual account. Support for this view comes from a study suggesting that domain-specific semantic knowledge can influence perceived weight[42]. Golfing enthusiasts and non-golfers were asked to compare the weights of real golf balls and practice golf balls that were altered to be equal in weight to the real balls. The golfers, who expected the practice ball to be lighter, reported that the practice ball was heavier. In contrast, the non-golfers, who held no such expectation, judged the balls to be equal in weight.

Although our results did not support the mismatch hypothesis at the sensorimotor level, they were consistent with the hypothesis applied at a purely cognitive or perceptual level. This argues for a separation of sensorimotor and cognitive predictions of object weight. This idea finds support from a growing body of literature emphasizing that visual information is processed in distinct neural pathways depending on whether the information is used to control actions or make perceptual judgments[29–31]. Although perceptual cues can influence force predictions during the inititial interaction with objects[21,22,43], after a period of ongoing interaction, immediate sensorimotor memory comes to guide such predictions, independent of perceptual cues. However, people may continue to make erroneous perceptual predictions about weight based on visual information about object size. Dissonance between these perceptual predictions and actual sensory feedback may underlie the size–weight illusion. This would indicate separate comparison processes for perceptual and sensorimotor predictions.

Methods

Twenty female and twenty male subjects 17–45 years of age participated in this study after providing informed consent. None of the subjects reported neurological or visual impairments. The subjects lifted a large box ($10.9 \times 10.9 \times 10.9$ cm^3) and a small box ($5.2 \times 5.2 \times 5.2$ cm^3), each constructed of balsa wood and weighted with lead shot, mixed in putty, located in the center. Subjects lifted the boxes by grasping a removable handle mounted on top by a plastic clip (Fig. 1). The handle was equipped with two six-axis force–torque sensors (Nano F/T; ATI Industrial Automation, Garner, North Carolina) that measured the forces and torques applied by the digits in three dimensions. The range and resolution of the sensors have been reported elsewhere[33]. The weight of each box, including the handle, was 3.82 Newtons (0.39 kg). The densities of the large box (0.3 kg per l) and small box (2.8 kg per l) straddled the density for most commonly manipulated objects (about 1 kg per l)[28].

Subjects grasped the handle with the tips of the thumb and index finger on the two opposing vertical contact surfaces. On hearing a tone, the subjects were required to grasp and lift the object about 5 cm above the support surface and then hold it in a stationary position until they heard a second tone 3 s after the first. They then replaced the object on the platform. The subjects were also asked to maintain a constant rate of lifting. A trial consisted of two lifts, one with the small object and one with the large object (order counterbalanced across subjects). Each subject completed 20 trials for a total of 40 lifts. Before the start of the lifting trials, participants were asked, "Which of these two boxes would you expect to be heavier?" After the last lifting trial, they were asked, "Which of these two objects felt heavier when you were lifting them?" Subjects were assigned randomly to either the non-cued or cued group, with 10 subjects in each group. Those in the cued group were told, "Although these objects differ in size, they have been specially constructed for this experiment to have equal weight."

Two additional groups of 10 subjects each were tested to determine whether the strength of the size–weight illusion changed as a result of repeated lifting. The two groups provided weight estimates for the two stimuli when lifting the small and large objects either for the first or twentieth time. We used the absolute-magnitude estimation procedure[38]. Each subject lifted one of the objects (order counterbalanced across subjects) and, after replacing the object on the platform, assigned a number of their choosing that best represented its weight. The subject then lifted the other object and again assigned a number representing its weight. The stimuli and lifting procedure were identical to those described above. The ratio of the numbers assigned to the small and large objects was used as an index of the strength of the size–weight illusion. A ratio greater than 1 would be expected under the illusion (that is, the small object should be assigned the greater number).

Signals from the two force–torque sensors and the light-sensitive diode were sampled at 400 Hz. We computed the load force, defined as the resultant force tangential to the grasp surface, and the grip force normal to the grasp surface. The torque acting in the plane of the contact surface and about the normal vector located at the center of normal force pressure was also computed[33]. To obtain grip and load force rates (first derivative of force with respect to time), the force signals were smoothed using a fourth-order, zero-phase lag, low-pass Butterworth filter (cutoff frequency, 14 Hz) and then were differentiated using a three-point central difference equation. Although we recorded forces and torques applied by both the index finger and thumb, for simplicity we only reported results pertaining to the index finger. However, because subjects lifted the objects vertically, very similar results were obtained for both digits. For each trial, we determined the peak grip and load force rates, the peak absolute tangential torque and the load phase duration (the time from when load force exceeded 0.2 N/s until lift-off). ANOVAs were used to assess the effects of object size and cue condition on these dependent variables at different points in the lift series. An alpha level of 0.05 was considered statistically significant.

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