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Material evidence: interaction of well-learned priors and sensorimotor memory when lifting objects

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Baugh LA, Kao M, Johansson RS, Flanagan JR. Material evidence: interaction of well-learned priors and sensorimotor memory when lifting objects. *J Neurophysiol* 108: 1262–1269, 2012. First published June 13, 2012; doi:10.1152/jn.00263.2012.—Skilled object lifting requires the prediction of object weight. When lifting new objects, such prediction is based on well-learned size-weight and material-density correlations, or priors. However, if the prediction is erroneous, people quickly learn the weight of the particular object and can use this knowledge, referred to as sensorimotor memory, when lifting the object again. In the present study, we explored how sensorimotor memory, gained when lifting a given object, interacts with well-learned material-density priors when predicting the weight of a larger but otherwise similar-looking object. Different groups of participants 1st lifted 1 of 4 small objects 10 times. These included a pair of wood-filled objects and a pair of brass-filled objects where 1 of each pair was covered in a wood veneer and the other was covered in a brass veneer. All groups then lifted a larger, brass-filled object with the same covering as the small object they had lifted. For each lift, we determined the initial peak rate of change of vertical load-force rate and the load-phase duration, which provide estimates of predicted object weight. Analysis of the 10th lift of the small cube revealed no effects of surface material, indicating participants learned the appropriate forces required to lift the small cube regardless of object appearance. However, both surface material and core material of the small cube affected the 1st lift of the large block. We conclude that sensorimotor memory related to object density can contribute to weight prediction when lifting novel objects but also that long-term priors related to material properties can influence the prediction.

object lifting; sensorimotor integration; sensorimotor memory; weight prediction

IN OUR DAILY LIVES, WE ARE required to lift a wide array of objects that differ in size and material. To lift an object efficiently, an accurate prediction of the object weight is essential (Flanagan et al. 2006; Johansson and Flanagan 2009a; Johansson and Westling 1988; Wolpert and Flanagan 2001). For instance, when lifting an object 1 or 2 cm off a surface, people typically smoothly increase vertical load force to a level that just exceeds the predicted weight of the object. When this prediction is accurate, the object is lifted smoothly and efficiently.

When lifting a particular object for the first time, people are generally quite accurate at predicting its weight based on its size (Flanagan and Beltzner 2000; Gordon et al. 1991a,b; Mon-Williams and Murray 2000) and material (Buckingham et al. 2009; Gordon et al. 1993). Such predictions are based on long-term size-weight and material-density priors. These priors also underlie the size-weight illusion (Charpentier 1891; Flanagan and Beltzner 2000; Flanagan et al. 2008; Grandy and Westwood 2006; Ross 1969) and material-weight illusion (Buckingham et al. 2009; Ellis and Lederman 1999; Seashore 1899; Wolfe 1898). That is, people judge the smaller of two equally weighted objects to be heavier because it is heavier than expected. Similarly, when lifting two equally weighted and sized objects that appear to be constructed from materials with differing density, people will judge the apparently less dense object to be heavier because it is heavier than expected. These size-weight and material-density priors are resistant to change because they are based on stable and well-established correlations that broadly generalize across behavior situations and tasks (Flanagan et al. 2008). Thus short-term interactions with objects that violate the normal mapping between size and weight or between material and density have little effect on the size-weight and material-weight illusions, respectively (Buckingham et al. 2009; Flanagan and Beltzner 2000; Flanagan et al. 2008; Grandy and Westwood 2006).

Despite our general proficiency at predicting the weight of a newly encountered object based on its size and material, there are times when these predictions can be erroneous. In these circumstances, people are capable of using knowledge obtained from previous lifts of the object, known as sensorimotor memory, to adapt their lifting force in subsequent lifts of the same object (Flanagan et al. 2006; Johansson and Cole 1992; Johansson and Flanagan 2009a). A recent study by Cole (2008) suggests that people store information about object density, rather than weight per se, in sensorimotor memory. Cole (2008) asked participants to lift a large brown bottle 20 times. After a brief delay, participants lifted a slightly smaller bottle of similar visual appearance. Although participants were explicitly unaware of the reduction in bottle size, they nevertheless scaled their lifting forces appropriately to the smaller bottle. This result suggests that people combine sensorimotor memory of object density with an analysis of object size to predict the weight of previously lifted objects or, more precisely, objects they believe they have previously lifted. At present, it is not known whether sensorimotor memories are linked to specific objects that have been lifted, as it is often assumed (Flanagan et al. 2008), or if experience generalizes to new objects that are similar in appearance (e.g., shape and surface material) to a previously lifted object but clearly larger or smaller. On the one hand, if an individual lifts a small object (Fig. 1, small filled circle) that is lighter (i.e., less dense) than predicted based on its size and apparent material (Fig. 1, small empty circle), that individual may assume that a similar-looking but larger object will

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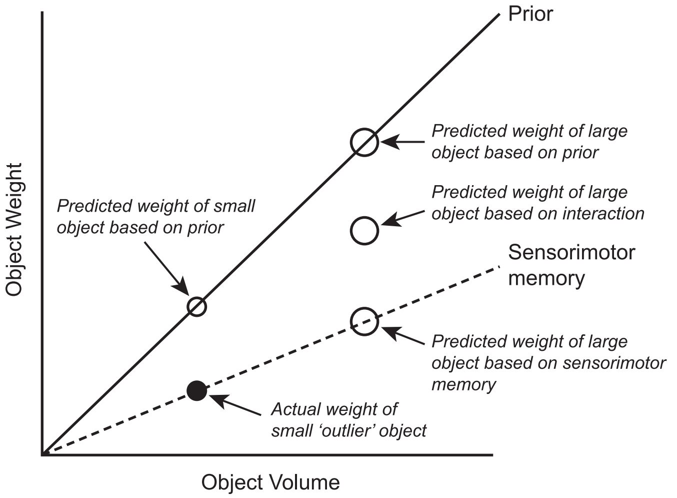

Fig. 1. Roles of priors and sensorimotor memory in weight prediction. The figure depicts a situation in which a participant lifts a small "outlier" object (small filled circle) that is much lighter than the predicted weight based on its size and apparent material (the prior; small empty circle) and then lifts a much larger object that is similar in apparent material. It is unclear what information that motor system will use to predict the weight of the larger object. Three scenarios are illustrated (large empty circles). First, weight prediction is based on the prior, ignoring the density of the smaller object. Second, weight prediction is based on sensorimotor memory of the density of the smaller object, ignoring the prior (i.e., well-learned associations between material and density). Third, the motor system uses information from both sources in extrapolating to the larger, newly encountered object, such that weight prediction is based on an interaction between the prior and sensorimotor memory.

have the same density as the small object and therefore be predicted to be also unusually light (Fig. 1, lower large empty circle). In other words, they may use sensorimotor memory of the density of the small object when lifting the large object. On the other hand, such use of sensorimotor memory may be limited to the specific circumstances in which the memory was formed, in which case the individual may resort to using stable, well-learned priors to predict weight when lifting the larger object (Fig. 1, upper large empty circle). For example, after lifting an unusually heavy glass of water, it would make little sense to extrapolate this unusual experience to all glasses of water lifted in the future. A third possibility is that participants rely on a combination of both short-term sensorimotor memory and long-term priors when extrapolating to the larger object (Fig. 1, middle large empty circle).

The aim of the current study was to investigate how sensorimotor memory of the density of an object interacts with well-established material-density priors when predicting the weight of a larger object appearing to be made of a similar material. To address this issue, participants were first asked to lift a small cube that had the visual appearance of wood, a relatively low-density material, or brass, which has a much higher density. Unknown to the participant, the inner core (either wood or brass) of each of these objects was manipulated to be either consistent or inconsistent with the outer appearance of the object. After several repeated lifts of the small cube, participants were then asked to lift a larger brass-filled cube with an outer visual appearance that matched the surface material of the smaller cube they had previously lifted.

We hypothesized that the density of the small cube, lifted by participants first, would influence the subsequent weight prediction of the large cube. Specifically, we predicted that individuals who first lifted the higher density small cubes, regardless of the covering material, would lift the larger cube with greater force than those individuals who lifted the less dense small cubes. We also hypothesized that the visual appearance of the larger cube would influence weight predictions as well. Specifically, we predicted that greater forces would be used to lift the large brass-covered cube than the large wood-covered cube, independent of the density of the smaller cube. Confirmation of these two predictions would indicate that people rely on both sensorimotor memory of object density and well-learned material-weight priors when lifting new objects that appear to be similar to a previously lifted object of a different size.

MATERIALS AND METHODS

Participants. The Queen's University General Research Ethics Board approved all experimental procedures. Fifty-one participants (22 males, age 18–27 yr, mean = 20 yr) were recruited from the population of undergraduate and graduate students at Queen's University and received $5 CAD compensation each for participating. All participants were right-handed and performed the experiment with the dominant hand, as assessed by a modified Edinburgh handedness inventory (Oldfield 1971). Participants were randomly assigned to one of the four experimental conditions (see below).

Apparatus. Six objects were used in this experiment. These included four small (27 cm^3) cubes that varied in both the material of the inner core (brass or wood) and the material of the outer surface (brass or wood). The brass-core cubes had a density of 8.4 g/cm^3, whereas the wood-core cubes had a density of 0.8 g/cm^3. Two large cubes (140 cm^3), both of which had brass cores (density of 8.4 g/cm^3), were also used. One of the large cubes had the outer appearance of wood, and the other had the outer appearance of brass.

In each trial, participants lifted an object from a tabletop platform (Fig. 2*A*) instrumented with force sensors (Nano 17 F/T sensors; ATI Industrial Automation, Garner, NC) and then replaced the object in the same location. The platform contained four sensors, but only the two nearest the participant were used. The force sensors were capped with flat circular disks with a diameter of 3 cm. These force sensors allowed for the precise measurement of the vertical load force applied to the object during lifting up until the point the object was lifted off the supporting disk.

Procedure. Participants were randomly assigned to one of four groups. Two of the groups lifted small cubes that were congruent in their fill and covering. Thus one of these groups ($n = 12$) lifted the brass-covered object with a brass core and the other group ($n = 13$) lifted the wood-covered object with a wooden core. The other two groups lifted small cubes that were incongruent in their fill and covering material. Thus one of these groups ($n = 12$) lifted the small brass-covered cube with a wood core, and the other group ($n = 13$) lifted the small wood-covered cube with a brass core. Each group of participants lifted the small cube 20 times, with a short pause after 10 lifts. The participants then completed 10 lifts of the large cube that had the same covering as the small object they had lifted.

Participants received both verbal instructions and a demonstration by the experimenter as to how to perform the lifting motion. Participants were asked to lift the test object ~2 cm off the tabletop, hold it in midair for 1 s, and then return it to its original location. At the start of the session, the small and large cubes were placed on two sensors closest to the participant (Fig. 2*A*), and the positioning of the two objects (i.e., which sensors they were placed on) was counterbalanced across participants within each group. Both the small cube and large cube were visible to the participant at all times during the experiment. The object to be lifted on a given trial was identified to the participant by a small circle of light, projected from above, onto the top face of the cube.

After completing the lifts of the large cube, each participant performed a material-weight illusion test using the absolute-magnitude-estimation procedure (Flanagan and Beltzner 2000; Zwislocki and Goodman 1980). The participant lifted the equally weighted

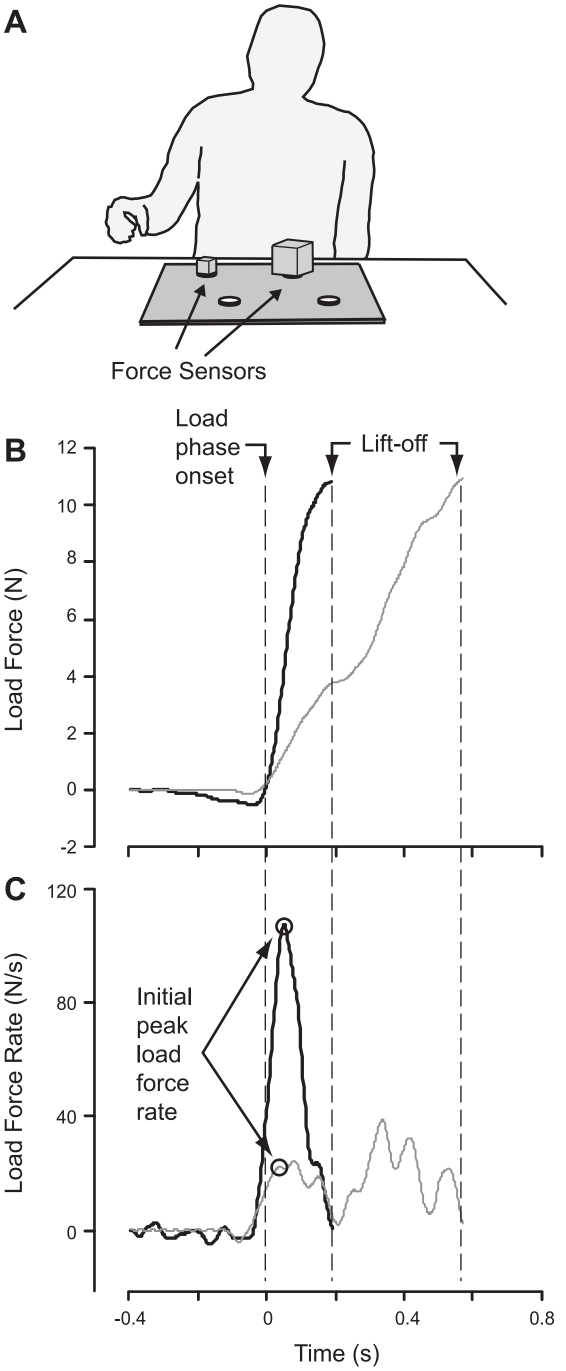

Fig. 2. Apparatus and data analysis. *A*: while seated, participants lifted and replaced 1 of 2 objects located on force sensors embedded in a platform. The platform contained 4 sensors, but only the 2 nearest the participant were used. A data projector, located above the participant, was used to indicate which object to lift on a given trial. *B*: load-force functions from 2 lifts of a large, heavy object. In 1 lift (thin gray curves), the initial increase in load-force undershot object weight, and, in the other lift (thick black curves), the initial increase in load force accurately reached the weight. Note that load force could not be recorded after lift-off, and therefore the curves only show load force up until lift-off. *C*: corresponding load-force rate functions. Note that the initial peak in load-force rate scaled with the initial increase in load force, which depends on predicted object weight.

brass- and wood-covered large cubes and was asked to assign a numerical value for the weight of each cube. Each cube was lifted once, and the order in which the two cubes were lifted was counterbalanced across participants within each group.

Data analysis. Vertical forces from the force sensors were sampled at 500 Hz. The raw force signals were low-pass filtered using a 4th order, zero-phase lag Butterworth filter with a cutoff frequency of 14 Hz. A signal representing the vertical force applied to the object by the hand (i.e., the vertical lifting or load force) was obtained by subtracting the vertical force that accounted for the weight of the object when fully supported by the transducer from the recorded signal. The processed signal was then differentiated with respect to time using a 1st order central difference equation to obtain the rate of change in load force, or load-force rate. For each lift, we determined the first peak in load-force rate during the load phase and the load-phase duration. The start of the load phase was defined as the time when load force first exceeded 0.1 N. Thus the first peak in load-force rate (a maxima followed by a decrease) had to occur after the load force exceeded 0.1 N. A threshold of 0.1 N was selected as load-force values early in the lift below this value would not be attributable to obvious attempts to lift the object but rather to initial finger placement on the block. The end of the load phase was defined as the time, just before object lift-off, when load force reached within 0.1 N of the weight of the object (Fig. 2, *B* and *C*). Because objects were being lifted off of the force sensor, we could not record load force after lift-off. This is not a problem for assessing predicted weight because the initial peak rate of change of load force occurred well before lift-off in all of the trials we analyzed (see RESULTS).

People tend to lift objects of varying weight in about the same amount of time. To accomplish this consistency, they scale the load-force rate, before object lift-off, to the expected weight of the object. In addition, when the instructed lift height is small, people typically reduce the load-force rate so that it approaches zero at the expected lift-off time. Therefore, the peak rate of change of load force during the initial increase in load force, which we will refer to as the initial peak load-force rate (Fig. 2*C*), provides an index of predicted weight (Flanagan and Beltzner 2000; Flanagan et al. 2008; Johansson and Westling 1988). If the object is heavier than predicted, object lift-off will not occur at the expected time (Fig. 2*C*, gray curves). The resulting absence of expected sensory information signaling lift-off triggers a reactive response characterized by pulsatile increases in load force until sensory information signaling lift-off is received (Johansson and Westling 1988). Therefore, the duration of the load phase also provides a measure of weight prediction. When object weight is greater than predicted, the load-phase duration is prolonged.

In most object-lifting studies, both vertical load force and horizontal grip force have been measured, typically by having participants lift via a handle instrumented with force sensors. Because in the current study participants lift objects off force sensors, only load force was measured. Importantly, load force provides a more accurate estimate of expected weight than grip force because the required load force depends only on object weight, whereas the required grip force depends on object weight as well as the frictional status of contacts between the object and the digits (Johansson and Westling 1984). One advantage of the current approach is that participants directly manipulate the objects and therefore obtain natural haptic cues about size and tactile cues about surface material (Flanagan et al. 2008).

Data analysis was focused on the 1st lift of the large cube as these lifts provided the opportunity to assess how sensorimotor memory, obtained from lifting the small cube, and material density priors, associated with the covering material of the large cubes, contributed to weight prediction. We also analyzed the 10th lift of the small cubes and the 10th lift of the large cubes to establish that, with repeated lifts of a particular object, participants are able to predict object weight correctly based on sensorimotor memory of previous lifts. We focused this analysis on lifts performed with the two brass-filled cubes because the very small (~0.2 N) forces required to lift the small wood-filled cubes prevented robust measures of the lift parameters, as initial finger placement on the block resulted in load forces that were often indistinguishable from those associated with the subsequent lift.

We assessed the strength and direction of the material-weight illusion using a signed percentage change score (Flanagan et al. 2008) derived from the numerical values assigned to the weights of the two cubes during the material-weight illusion test. Specifically, we determined the percentage increase from the smallest to the largest numerical values and assigned a positive value to this number if the wood-covered object was perceived as heavier (as expected) and a negative value to this number if the brass-covered object was perceived as heavier. Importantly, the material-weight illusion, like the size-weight illusion, is resistant to change following a small number of lifts (e.g., 40) of objects that violate the expected relation between apparent material and weight (Buckingham et al. 2009; Flanagan and Beltzner 2000). Thus testing the material-weight illusion at the end of the experimental session still allowed us to assess participants' expectations about weight based on apparent material.

RESULTS

Prediction of object weight during lifting. We expected that following repeated lifts of the small cubes, participants in all groups would learn to predict adequately the weight of the object. That is, we expected that participants would learn to scale appropriately the force output to the weight of the small cube such that the cover material would not significantly influence the force output. We focused this analysis on lifts performed with the two brass-filled cubes because the very small forces required to lift the small wood-filled cubes prevented robust measures of the lift parameters. Figure 3*A* shows that by the 10th lift, participants smoothly increased load force up to the weight of the object. No significant difference was observed in the initial peak load-force rate [$t(23) = 1.11$, $P = 0.281$] between the brass-covered and wood-covered cubes (Fig. 3*B*). Furthermore, no significant difference was observed in load-phase duration [$t(23) = -0.652$, $P = 0.521$] between the brass- and wood-covered cubes (Fig. 3*C*).

To assess the possible interaction between sensorimotor memory and well-established material-density priors on weight prediction, we examined lift performance on the first lift of the large cube, which had a brass core and a cover that matched that of the small cube previously lifted. Participants who previously lifted one of the two brass-filled small objects showed larger and more rapid initial increases in load force (Fig. 4*B*) compared with participants who previously lifted one of the two wood-filled small objects (Fig. 4*A*). In addition, participants who previously lifted small and large brass-covered objects showed larger and more rapid increases in load force (solid traces) compared with participants who had lifted small and large wood-covered objects (dashed traces). In most trials, the initial increase in load force was insufficient to lift the object, and additional increases in load force were required to achieve lift-off. However, participants who previously lifted the brass-filled and brass-covered small cube (and who then lifted the brass-covered large object) generated initial increases in load force that tended to reach a level that was close to the weight of the brass-filled large object (solid traces in Fig. 4*B*).

To assess statistically the interaction between sensorimotor memory and material-weight priors on weight prediction, we performed two 2 (cover) × 2 (fill) ANOVAs examining both the initial peak in load-force rate and the load-phase duration for the first lift of the large cube. This analysis revealed significant main effects of fill material on both initial peak load-force rate [$F(1, 46) = 33.90$, $P < 0.001$] and load-phase duration [$F(1, 46) = 24.94$, $P < 0.001$]. Participants who had initially lifted one of the small brass-filled cubes lifted the cover-matched large cube with a greater initial peak load-force rate than the participants who had initially lifted one of the small wood-filled cubes (Fig. 5*A*). Similarly, participants who first lifted one of the small brass-filled cubes lifted the cover-matched large cube with a substantially shorter load-phase duration than participants who had first lifted one of the small wood-filled cubes (Fig. 5*B*). The analysis also revealed significant main effects of cover material on both initial peak load-force [$F(1, 46) = 6.90$, $P = 0.018$] and load-phase duration [$F(1, 46) = 7.56$, $P = 0.010$]. Participants who first lifted one of the small brass-covered cubes lifted the cover-matched large cube with a greater initial peak load-force rate than participants who had initially lifted one of the small wood-covered cubes (Fig. 5*A*). Moreover, the increase in force produced by participants who first lifted the wood-covered brass-filled cube

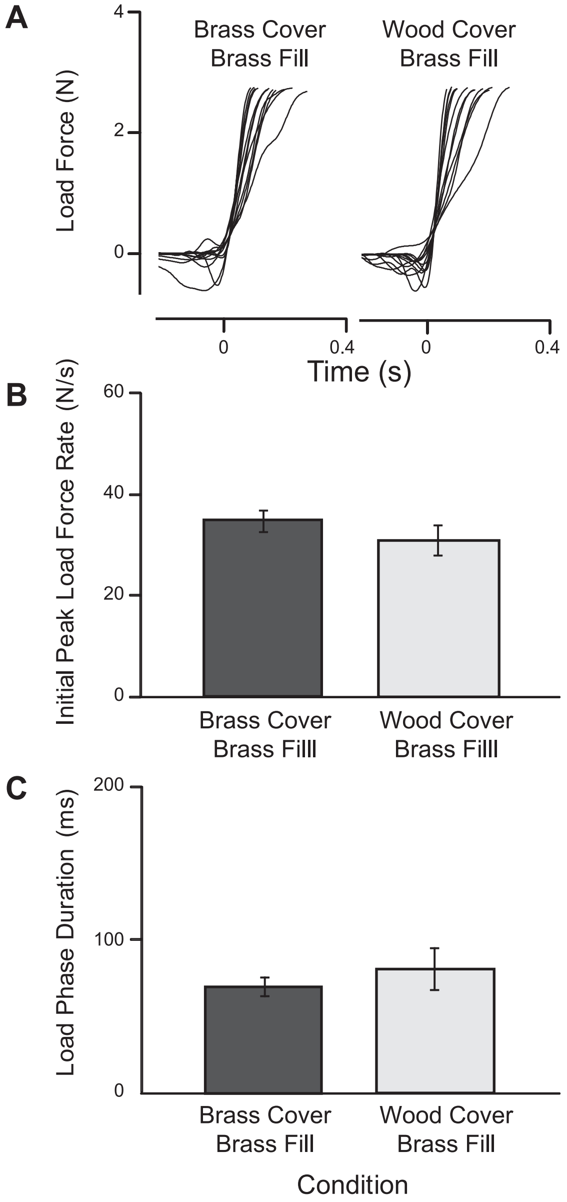

Fig. 3. Lift performance on the 10th lift of the small brass-filled cubes. *A*: load-force records as a function of time from the 10th lift of the small brass-covered or wood-covered cube. Records from all participants are shown. *B* and *C*: mean initial peak load-force rate (*B*) and load-phase duration (*C*), averaged across participants, of the 10th lift of the small brass-filled objects. The vertical lines represent ±1 SE.

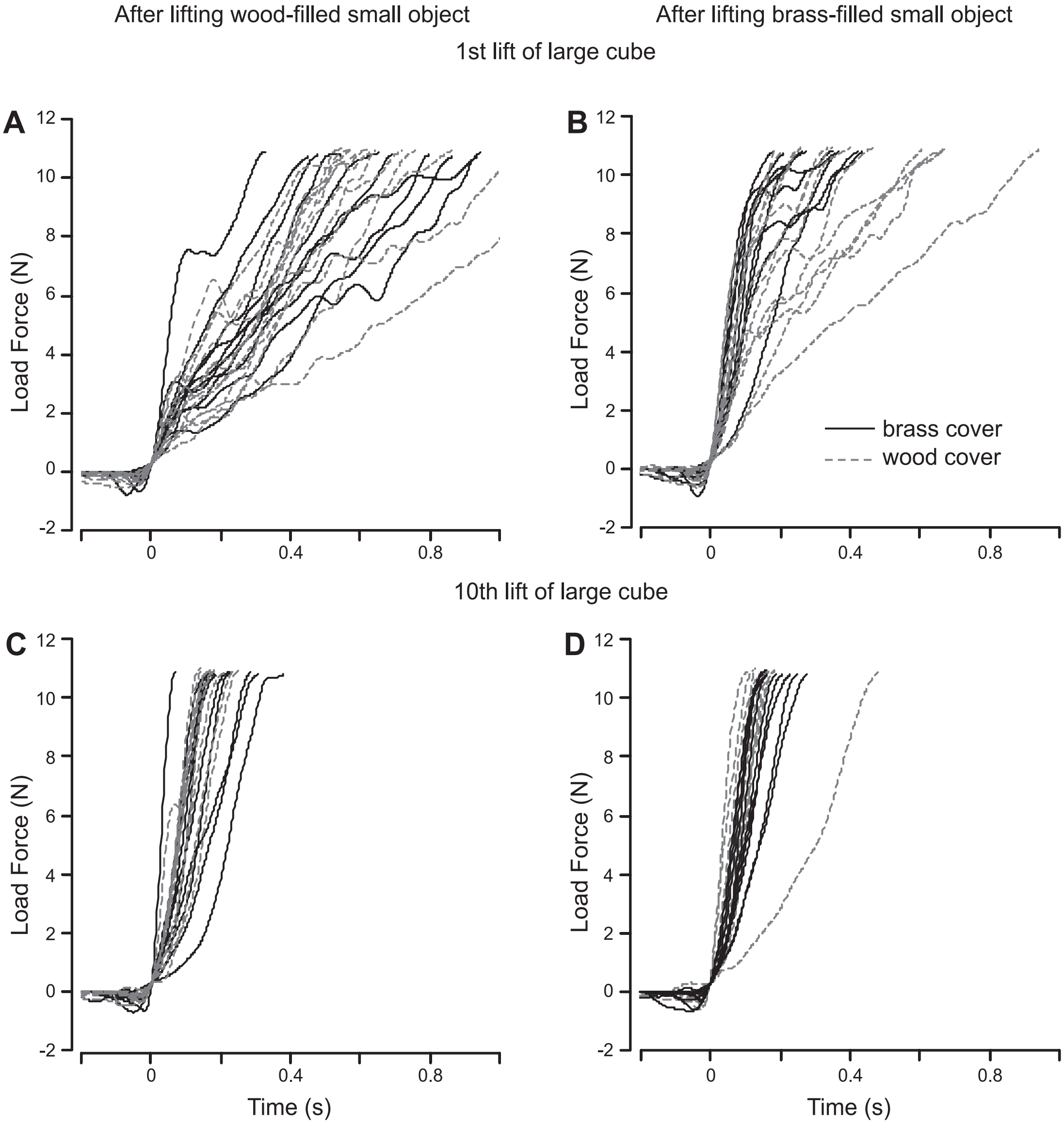

Fig. 4. Vertical load-force records from the 1st and 10th lifts of the large cube that was either covered in brass (solid black lines) or wood (gray dashed lines). *A*: records from the 1st lift of the large object by participants who previously lifted a wood-filled small object. *B*: records from the 1st lift of the large object by participants who previously lifted a brass-filled small object. *C* and *D*: records from the 10th lift of the large cube by the participants in *A* and *B*, respectively. *A*–*D*: solid lines show load-force records from participants who previously lifted a small object covered in brass, and dashed lines show load-force records from participants who previously lifted a small object covered in wood.

clearly exceeded the weight that would have been expected for a large wood cube (based on density extrapolation from the small wood-filled cubes to a larger size). Regarding the load-phase duration, participants who first lifted one of the small brass-covered cubes lifted the cover-matched large cube more quickly (i.e., with a shorter load-phase duration) than those who lifted one of the small wood-covered objects (Fig. 5*B*). There were no significant interactions between cover material and fill material for either the initial peak load-force or the load-phase duration (P = 0.725 and 0.356, respectively).

Adaptation to object weight during lifting and the material weight illusion. All participants adapted their lifting forces to the actual weight of the large cubes (Fig. 4, *C* and *D*). After 10 lifts of the large block, there were no significant effects of fill or cover on either initial peak load-force (P = 0.176 and 0.898) rate or load-phase duration (P = 0.313 and 0.188) and no significant interactions in either measure (P = 0.808 and 0.911; Fig. 5, *C* and *D*). At the end of the experiment, the material weight illusion was quantified using the signed percentage change score. To assess the presence of a material weight illusion, a 1-way ANOVA by experimental condition was performed. A significant intercept [$F(1, 47) = 20.381$, $P < 0.001$] verified participants experienced a material weight illusion, and a nonsignificant effect of condition revealed the illusion was statistically equivalent in all 4 participant groups. On average, participants reported that the wood-covered cube was 22% heavier than the equally weighted brass-covered cube.

DISCUSSION

Accurate prediction of object weight is an essential component of skilled and dexterous object manipulation (Flanagan et

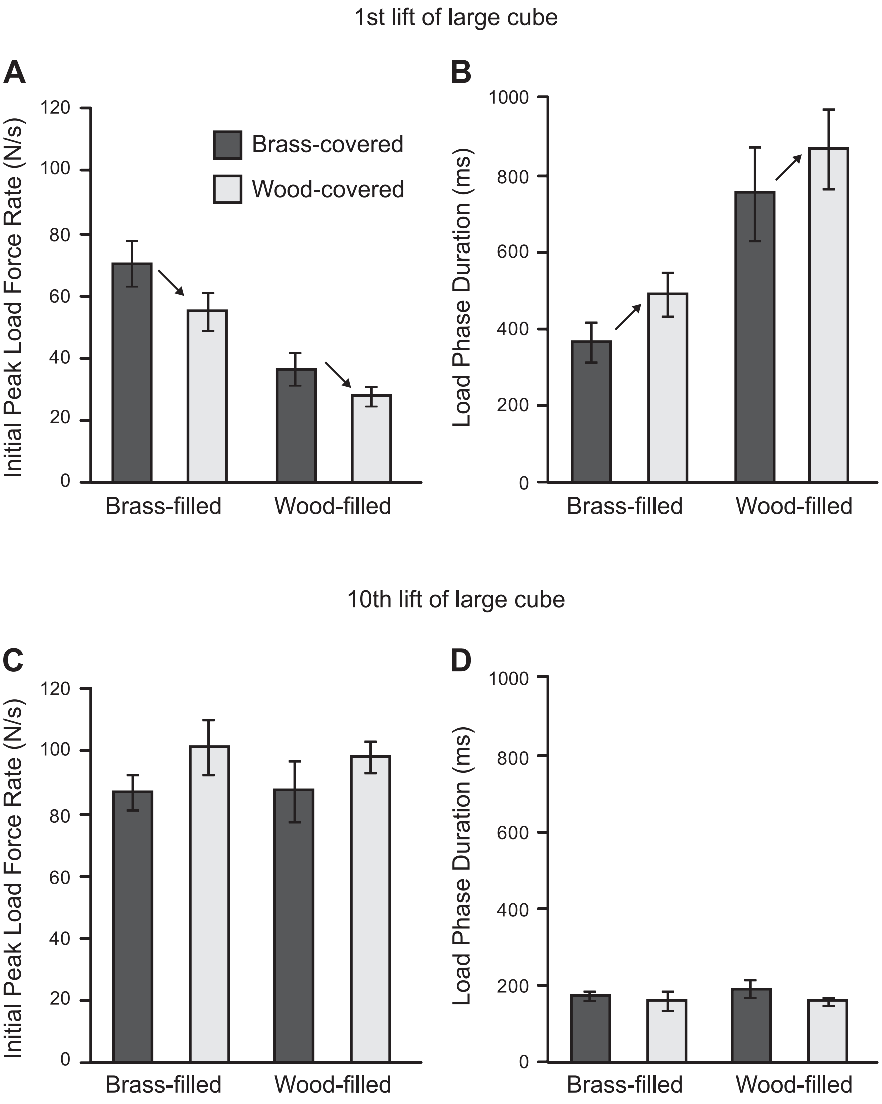

Fig. 5. Mean initial peak load-force rate (*A* and *C*) and load-phase duration (*B* and *D*), averaged across participants. *A* and *B*: 1st lift of the large cube. *C* and *D*: 10th lift of the large cube. The vertical lines represent ±1 SE. Arrows indicate the effect of well-established material-density priors on weight prediction on the 1st lift of the large cube.

al. 2006; Johansson and Flanagan 2009b; Johansson and Westling 1988; Wolpert and Flanagan 2001). When lifting an object for the first time, people can exploit well-learned associations to predict weight based on material (Buckingham et al. 2009; Gordon et al. 1993) and size (Flanagan and Beltzner 2000; Gordon et al. 1991a,b,c; Grandy and Westwood 2006; Mon-Williams and Murray 2000). Such prediction may be achieved through the use of well-established material-density priors combined with an assessment of the size of the object (Cole 2008). Information about size can be extracted both visually (Gordon et al. 1991c) and haptically (Gordon et al. 1991b). Information about material can presumably also be extracted through vision and haptics. Although the role of haptic material cues has been examined for grip-force scaling (Johansson and Westling 1984, 1987; Westling and Johansson 1987), to our knowledge no one has explicitly examined the role of haptic material cues in load-force scaling during lifting and/or the material-weight illusion.

There are inevitably instances when predictions about object weight based on material and size are erroneous. In such cases, mismatches between predicted and actual sensory events related to lift-off occur and trigger suitable corrective actions (Johansson and Westling 1988). Concurrently, people learn from these errors such that they more accurately scale the forces applied to the object when lifting it again. The knowledge gained from recent previous lifts has been referred to as sensorimotor memory and, in the case of objects that are poorly predicted by size and material, presumably involves learning an arbitrary association between a specific object and its density. In the present study, we found that when participants repeatedly lifted an object for which the weight was erroneously predicted initially, they learned to scale their lifting forces appropriately. This was evident when examining the 10th lifts of the small and large brass-filled cubes. Thus they relied on sensorimotor memory to create an arbitrary association between object identity and density. Such learning can be long lasting. After lifting an unusually weighted object, people demonstrate accurate scaling of load (and grip) forces when lifting the same object 1 or even several days later (Flanagan et al. 2001, 2008; Gordon et al. 1993). When lifting objects without strong material and size cues, force adaptation typically occurs within a single lift (e.g., Johansson and Westling 1988). However, when size and material cues provide misleading information about weight, a number of lifts are required before forces are accurately scaled to object weight (Buckingham et al. 2009; Flanagan and Beltzner 2000; Flanagan et al.

2008; Gordon et al. 1993). During the adaption period, weight prediction is presumably based on a combination of sensorimotor memory and long-term priors.

The central aim of the current study was to examine the roles of sensorimotor memory and well-established material-density priors when lifting a new object that is clearly larger but otherwise similar to a previously lifted object. We found that sensorimotor memory had a strong influence on participants' weight predictions. For example, when participants had repeatedly lifted the small wood-covered brass-filled cube, which was much denser than initially expected, and then lifted the large wood-covered cube, they scaled their lifting force for a high-density object when first lifting the large cube rather than a low-density (i.e., wood-filled) object. That is, their initial increase in load force when first lifting the large wood-covered cube was much larger than that produced by participants who initially lifted the small wood-covered, wood-filled cube. However, the increase in load force in the first lift of the large cube was not as strong as when participants had repeatedly lifted the small brass-covered, brass-filled cube and then lifted the large brass-covered cube. This effect of surface material, independent of weight or density, indicates that material-density priors also influenced the prediction of weight when lifting the large cube. Because participants were lifting objects off of force sensors, we chose to make the critical test object always larger and heavier than the objects used in the first block. This effectively ensured that a participant's predicted weight of the test object was either equal to or less than the actual weight, allowing accurate load-force measurements to be obtained from the sensor before object lift-off occurred. However, had we made the critical test object smaller than the objects used in the first block, we would expect that both sensorimotor memory and material-density priors would have the same roles in object weight prediction as what we observed for the larger cubes.

Although the combination of sensorimotor memory with material priors may often result in improved prediction of object weight and hence lifting performance, this will not always be the case. For example, in the present study, a more accurate lift of the large wood-covered, brass-filled cube would have been achieved simply by extrapolating density information obtained from the small cube to the large cube. It is possible that, through experience, people learn to combine optimally sensorimotor memory (a form of sensory evidence) and priors, as has been shown in other motor tasks (Körding et al. 2004; Körding and Wolpert 2004).

The test of the material-weight illusion, performed at the end of the experimental session, indicated that participants in the different experimental groups began the study with similar long-term priors about the densities of the surface materials used in this experiment (i.e., brass and wood). Participants judged the wood-covered cube to be heavier than an equally weighted and equally sized brass-covered cube, as expected, and no significant differences among groups in the strength of the material-weight illusion were observed. This finding indicates that participants expected the wood-covered cube to be of lower density than the brass-covered cube. It may be noted that the size of the material-weight illusion was similar for all groups, even though participants in two of the groups lifted objects that violated the normal mapping between apparent material and weight. This result is not surprising because previous research has shown that the material-weight illusion (Buckingham et al. 2009), like the size-weight illusion (Flanagan and Beltzner 2000; Grandy and Westwood 2006), is not affected by short-term interactions with objects that violate long-term priors. Extensive lifting of size-weight inverted objects (e.g., over 1 wk of ≥200 lifts a day) is required for participants to exhibit an inversion of the size-weight illusion (Flanagan et al. 2008).

The current study provides further evidence of the independent effects of sensorimotor memory and material-density priors in the scaling of fingertip forces, as each source of information can have dissociable effects on the prediction of object weight. This conclusion is further strengthened by recent work examining separable neural mechanisms underlying the different types of processes used in weight prediction. For example, recent work utilizing repetitive transcranial magnetic stimulation (rTMS) to investigate the cortical regions contributing to weight prediction revealed rTMS applied to dorsal premotor cortex disrupts arbitrary associative memory for weight, whereas rTMS applied to primary motor cortex disrupted sensorimotor memories (Chouinard et al. 2005). Additional support comes from functional magnetic resonance imaging studies that have all pointed toward the right inferior parietal cortex, cerebellum, and right inferior frontal cortex as being involved in the updating of sensorimotor memory representations (Jenmalm et al. 2006; Schmitz et al. 2005).

The current study is the first to demonstrate how sensorimotor memory pertaining to object density interacts with our well-established material-density priors. Our results indicate that people rely on a combination of these two kinds of information when making weight predictions about newly encountered objects. We suggest that when participants encounter an object for which long-term priors result in an erroneous prediction of weight, the specific object is flagged by the sensorimotor system as an "outlier," and future interactions with this same object are guided primarily by the more accurate predictions based on sensorimotor memory, which can be long-lasting (Flanagan et al. 2008). When individuals need to extrapolate to a newly encountered object that is similar to one previously identified as an outlier, we suggest that the relative impact of long-term priors vs. sensorimotor memory depends on the extent of similarity between the previously encountered outlier and the newly encountered object. However, further study is required both to quantify fully the relation between long-term priors and the putative outlier system and to specify conditions in which priors are modified or new priors are created. Finally, we suggest that the combination of long-term priors and an outlier system may provide an efficient means of remembering object weights. That is to say, under such a system there is no need to store all weights of a particular family of objects for which the weight can be well-predicted by size-weight and material-weight priors. Rather, we must only store the weight of objects that are not well-predicted by these priors, a much less common occurrence.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

L.A.B., M.K., R.S.J., and J.R.F. conception and design of research; L.A.B. and M.K. performed experiments; L.A.B., M.K., and J.R.F. analyzed data; L.A.B., M.K., R.S.J., and J.R.F. interpreted results of experiments; L.A.B. and J.R.F. prepared figures; L.A.B. and J.R.F. drafted manuscript; L.A.B., R.S.J., and J.R.F. edited and revised manuscript; L.A.B., M.K., R.S.J., and J.R.F. approved final version of manuscript.

REFERENCES

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. *J Neurophysiol* 102: 3111–3118, 2009.

Charpentier A. Analyse experimentale quelques elements de la sensation de poids [Experimental study of some aspects of weight perception]. *Arch Physiol Norm Pathol* 3: 122–135, 1891.

Chouinard PA, Leonard G, Pauls T. Role of the primary motor and dorsal premotor cortices in the anticipation of forces during object lifting. *J Neurosci* 25: 2277–2284, 2005.

Cole KJ. Lifting a familiar object: visual size analysis, not memory for object weight, scales lift force. *Exp Brain Res* 188: 551–557, 2008.

Ellis RR, Lederman SJ. The material-weight illusion revisited. *Percept Psychophys* 61: 1564–1576, 1999.

Flanagan JR, Beltzner MA. Independence of perceptual and sensorimotor predictions in the size-weight illusion. *Nat Neurosci* 3: 737–741, 2000.

Flanagan JR, Bittner JP, Johansson RS. Experience can change distinct size-weight priors engaged in lifting objects and judging their weights. *Curr Biol* 18: 1742–1747, 2008.

Flanagan JR, Bowman MC, Johansson RS. Control strategies in object manipulation tasks. *Curr Opin Neurobiol* 16: 650–659, 2006.

Flanagan JR, King S, Wolpert DM, Johansson RS. Sensorimotor prediction and memory in object manupulation. *Can J Exp Psychol* 55: 87–95, 2001.

Gordon AM, Forssberg H, Johansson RS, Westling G. Integration of sensory information during the programming of precision grip: comments on the contribution of size cues. *Exp Brain Res* 85: 226–229, 1991a.

Gordon AM, Forssberg H, Johansson RS, Westling G. The integration of haptically acquired size information in the programming of precision grip. *Exp Brain Res* 83: 483–488, 1991b.

Gordon AM, Forssberg H, Johansson RS, Westling G. Visual size cues in the programming of manipulative forces during precision grip. *Exp Brain Res* 83: 477–482, 1991c.

Gordon AM, Westling G, Cole K, Johansson RS. Memory representations underlying motor commands used during manipulation of common and novel objects. *J Neurophysiol* 69: 1789–1796, 1993.

Grandy MS, Westwood DA. Opposite perceptual and sensorimotor responses to a size-weight illusion. *J Neurophysiol* 95: 3887–3892, 2006.

Jenmalm P, Schmitz C, Forssberg H, Ehrsson HH. Lighter or heavier than predicted: neural correlates of corrective mechanisms during erroneously programmed lifts. *J Neurosci* 26: 9015–9021, 2006.

Johansson RS, Cole KJ. Sensory-motor coordination during grasping and manipulative actions. *Curr Opin Neurobiol* 2: 815–823, 1992.

Johansson RS, Flanagan JR. Coding and use of tactile signals from the fingertips in object manipulation tasks. *Nat Rev Neurosci* 10: 345–359, 2009a.

Johansson RS, Flanagan JR. Sensorimotor control of manipulation. In: *Encyclopedia of Neuroscience*, edited by Squire L. Oxford, UK: Academic Press, 2009b, p. 593–604.

Johansson RS, Westling G. Coordinated isometric muscle commands adequately and erroneously programmed for the weight during lifting task with precision grip. *Exp Brain Res* 71: 59–71, 1988.

Johansson RS, Westling G. Roles of glabrous skin receptors and sensorimotor memory in automatic-control of precision grip when lifting rougher or more slippery objects. *Exp Brain Res* 56: 550–564, 1984.

Johansson RS, Westling G. Signals in tactile afferents from the fingers eliciting adaptive motor-responses during precision grip. *Exp Brain Res* 66: 141–154, 1987.

Körding KP, Ku SP, Wolpert DM. Bayesian integration in force estimation. *J Neurophysiol* 92: 3161–3165, 2004.

Körding KP, Wolpert DM. Bayesian integration in sensorimotor learning. *Nature* 427: 244–247, 2004.

Mon-Williams M, Murray AH. The size of the visual size cue used for programming manipulative forces during precision grip. *Exp Brain Res* 135: 405–410, 2000.

Oldfield RC. The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia* 9: 97–113, 1971.

Ross HE. When is a weight not illusory? *Q J Exp Psychol* 21: 346–355, 1969.

Schmitz C, Jenmalm P, Ehrsson HH, Forssberg H. Brain activity during predictable and unpredictable weight changes when lifting objects. *J Neurophysiol* 93: 1498–1509, 2005.

Seashore CE. Some psychological statistics. 2. The material-weight illusion. *University of Iowa Studies in Psychology* 2: 36–46, 1899.

Westling G, Johansson RS. Factors influencing the force control during precision grip. *Exp Brain Res* 53: 277–284, 1984.

Westling G, Johansson RS. Responses in glabrous skin mechanoreceptors during precision grip in humans. *Exp Brain Res* 66: 128–140, 1987.

Wolfe HK. Some effects of size on judgments of weight. *Psychol Rev* 5: 25–54, 1898.

Wolpert DM, Flanagan JR. Motor prediction. *Curr Biol* 11: R729–R732, 2001.

Zwislocki JJ, Goodman DA. Absolute scaling of sensory magnitudes: a validation. *Percept Psychophys* 28: 28–38, 1980.