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Distinct contributions of explicit and implicit memory processes to weight prediction when lifting objects and judging their weights: an aging study

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Trewartha KM, Flanagan JR. Distinct contributions of explicit and implicit memory processes to weight prediction when lifting objects and judging their weights: an aging study. *J Neurophysiol* 116: 1128–1136, 2016. First published June 15, 2016; doi:10.1152/jn.01051.2015.—Weight predictions used to scale lifting forces adapt quickly when repeatedly lifting unusually weighted objects and are readily updated by explicit information provided about weight. In contrast, weight predictions used when making perceptual judgments about weight are more resistant to change and are largely unaffected by explicit information about weight. These observations suggest that distinct memory systems underlie weight prediction when lifting objects and judging their weights. Here we examined whether these weight predictions differ in their reliance on declarative and nondeclarative memory resources by comparing the adaptability of these predictions in older adults, who exhibit relatively impaired declarative memory processes, to those in younger adults. In the size condition, we measured lift forces as participants repeatedly lifted a pair of size-weight inverted objects in alternation. To assess weight judgments, we measured the size-weight illusion every 10 lifts. The material condition was similar, except that we used material-weight inverted objects and measured the material-weight illusion. The strengths of these illusions prior to lifting, and the attenuation of the illusions that arise when lifting inverted objects, were similar for both groups. The magnitude of the change in the illusions was positively correlated with implicit memory performance in both groups, suggesting that predictions used when judging weight rely on nondeclarative memory resources. Updating of lifting forces also did not differ between groups. However, within the older group the success with which lifting forces were updated was positively correlated with working memory performance, suggesting that weight predictions used when lifting rely on declarative memory resources.

explicit memory; implicit memory; weight predictions; weight illusions; aging

NEW & NOTEWORTHY

Distinct memory processes underlie weight predictions used when lifting objects and making perceptual judgments about weight. However, the nature of these memory processes has yet to be revealed. By comparing the adaptability of weight predictions in younger and older adults our findings demonstrate that distinct neural mechanisms for declarative and nondeclarative memory processes are recruited when predicting object weight for the purpose of lifting objects and judging object weight, respectively.

TO LIFT AN OBJECT SMOOTHLY and efficiently, people must make accurate predictions about its weight. Two complementary memory systems support such predictions when lifting. When lifting an object for the first time people can rely on learned associations, or priors, relating material and size to weight (e.g., Baugh et al. 2012; Buckingham et al. 2009; Flanagan et al. 2008; Flanagan and Beltzner 2000; Gordon et al. 1991, 1993; Grandy and Westwood 2006). However, once an object has been lifted, people can also rely on memory of the weight of that specific object to predict its weight in subsequent lifts (Flanagan et al. 2006; Johansson and Cole 1992; Johansson and Flanagan 2009). Such object-specific memory is particularly important when lifting unusually weighted objects, the weights of which are poorly predicted by existing priors, and supports fairly fast updating of lift forces across lifts. When individuals repeatedly lift objects that violate size-weight or material-weight expectancies, they learn to accurately scale their vertical load forces to the actual weight of the objects within 5–40 lifts, depending on the strength and nature of the violation and the number of objects involved (Flanagan et al. 2001, 2008; Flanagan and Beltzner 2000; Gordon et al. 1991, 1993; Grandy and Westwood 2006; Johansson and Cole 1992).

Weight predictions are not only used when lifting objects; they also bias perceptual judgments about weight. Thus people judge the smaller of two equally weighted objects to be heavier because it is heavier than expected. Likewise, if an object appears to be made of a lighter material (e.g., Styrofoam), it will be perceived as heavier than an equally weighted object that appears to be made of a heavier material (e.g., metal). Weight predictions used when judging weight have been shown to be independent of weight predictions used when lifting; when repeatedly lifting equally weighted large and small cubes in alternation, accurate force scaling is observed within 10 lifts whereas the size-weight illusion is unaffected after 40 lifts (Flanagan and Beltzner 2000; Grandy and Westwood 2006). However, with more extensive experience lifting size-weight inverted objects, the illusion can be altered and eventually reversed (Flanagan et al. 2008). On the basis of these results, it has been suggested that weight predictions in the size- and material-weight illusions are based on well-established priors about size- and material-weight relationships, which are generally resistant to change but can be altered through experience (Baugh et al. 2012; Flanagan et al. 2008).

Although the work reviewed above suggests that the memory processes underlying weight predictions used when judging weights and lifting objects are distinct, the precise nature of these memory processes has yet to be determined. The present

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study was designed to investigate the potential roles of nondeclarative and declarative memory resources in predictions of weight used for perception and action, respectively.

There are several reasons why we might expect weight predictions used when judging weight to be supported by nondeclarative, or implicit, memory systems. First, weight illusions are known to be cognitively impenetrable. Thus people experience the size- and material-weight illusions even when they are explicitly told that the objects actually have the same weight (Buckingham 2014; Flourney 1894; Nyssen and Bourdon 1955). Moreover, changes in these illusions, brought about through experience in lifting unusually weighted objects, appear to occur without the conscious intention to learn new associations between size and weight (Flanagan et al. 2008). These observations suggest that the memory systems involved in the prediction of object weight, in the context of judging weight, function outside of conscious awareness and do not depend on intentional processes.

By contrast, the ability to scale lifting forces when lifting unusually (or arbitrarily) weighted objects likely relies on explicit memory resources that allow people to intentionally form associations between object weight and other object properties such as color, size, and material composition (Ameli et al. 2008). Moreover, telling someone that a particular object is very heavy or very light will clearly influence the force he/she applies when subsequently lifting it. Thus it seems likely that learning to predict the weights of unusually weighted objects when lifting them involves associative memory resources. Moreover, given the short timescale within which participants can learn to scale lifting forces for unusually weighted objects, working memory resources linked to associative memory formation presumably play a key role.

The present study employed two approaches to investigate the nature of the memory systems underlying weight judgments and the updating of lifting forces. The first approach was to compare the adaptability of weight predictions, used to judge weight and scale lift forces, between groups of younger adults and healthy older adults, who differ substantially in declarative memory resources, including working memory and associative memory, but differ less in nondeclarative memory resources (Craik 2000; Hoyer and Verhaeghen 2006). The second, complementary approach was to investigate whether individual differences in the performance of nondeclarative and declarative memory tasks correlate with the adaptability of these different weight predictions.

We examined the memory processes underlying weight predictions by having participants lift size-weight and material-weight inverted objects in two separate experiments. We assessed the magnitude of the weight illusions in both experiments before experience with the inverted objects and after every 10 lifts of those objects in order to track changes in the illusion due to experience. We also recorded lifting forces in order to track how quickly younger and older adults scaled lifting forces when lifting the weight-inverted objects. We tested the hypothesis that nondeclarative memory processes underlie weight predictions used when judging weight. Given that older adults have relatively preserved implicit memory, we predicted that younger and older adults exhibit size- and material-weight illusions that are similarly strong initially and are updated at similar rates with experience in lifting unusually weight objects. We also predicted that, for both groups, changes in the illusions through experience would be correlated with scores on an independent implicit memory task. We also tested the hypothesis that declarative memory processes underlie weight predictions used for lifting. One prediction is that older adults exhibit impaired force scaling since they have known declines in declarative memory processes. A second possibility is that within the older adults lifting performance is correlated with performance on an independent explicit working memory task. We recently reported such a correlation in a force-field adaptation reaching task (Trewartha et al. 2014) where individual differences in working memory performance, rather than age per se, were the determining factor in motor learning impairments in older adults. Should we find a similar result for the updating of lifting forces used for object manipulation, it would suggest that similar underlying memory resources may be involved.

METHODS

Participants

Twenty-five younger adults (mean = 21.5, SD = 3.5; 18 women, 7 men) and nineteen older adults (mean = 64.7, SD = 6.1; 13 women, 6 men) were recruited to participate in this experiment. The younger adults were recruited from the undergraduate and graduate student populations at Queen's University, Kingston, ON, Canada, and the older adults were recruited from the Kingston community. Importantly, the older adults were all very high-functioning adults living independently. A health questionnaire was administered to the older adults to ensure that they were in good self-reported health with no significant medical and neurological conditions and had normal or corrected to normal vision. All participants self-identified as right handed. A Queen's University ethics committee approved the protocol, and all participants provided written informed consent. Participants completed a battery of neuropsychological tests to ensure that they were functioning normally for their age group. Those tests included the Stroop test (adapted from Spreen and Strauss 2001), the letter-number sequencing subtest of the Weschler Adult Intelligence Scale (WAIS; Weschler 1997), and the Trails A and B (adapted from Reitan 1958 and implemented with the End-Point KINARM, BKIN Technologies, Kingston, ON, Canada). Typical age differences were observed between younger and older adults for all of the neuropsychological tests (Table 1).

Table 1. *Means and SEs of neuropsychological tests and t-test results of age group comparisons for each test*

Age Group	Age, yr	Letter-Number Sequencing	Stroop Interference Score	Trails Difference Score
Younger adults	21.5 (±3.5)	13.04 (±0.58)	0.65 (±0.03)	8.4 (±6.5)
Older adults	64.7 (±6.1)	10.7 (±0.52)	0.54 (±0.03)	24.4 (±25.2)
Age difference		$P < 0.01$	$P < 0.01$	$P < 0.01$

Mean scores are presented with SEs in parentheses for the number of sequences remembered correctly (max. 21) in the Weschler Adult Intelligence Scale (WAIS) Letter-Number Sequencing subtest, the ratio between the seconds per item completed on the Congruent and Incongruent versions of the color Stroop test, and the difference in time (s) to complete versions B and A of the Trail Making test (Trails).

Materials

Participants were seated in a comfortable chair in front of a tabletop. A Plexiglas platform containing two force/torque sensors (Nano 17 F/T sensors; ATI Industrial Automation, Garner, NC), which effectively acted as weight scales, was located on the tabletop. Each sensor was capped with a circular (diameter 3 cm) flat cap upon which objects were placed. These sensors allowed us to measure the vertical load forces applied during lifting (sampled at 1,000 Hz). Between the participant and the force platform was a movable screen that could be drawn to prevent the participant from viewing the platform while the experimenter moved objects to and from the force platform.

For the size condition, we constructed a small (51 mm high × 51 mm in diameter) heavy (720 g) cylinder and a large (82 mm high × 82 mm in diameter) light (190 g) cylinder (see Fig. 1*A*). To test the size-weight illusion we also constructed a small and an equally weighted (455 g) large cylinder, equal in shape and volume to the small and large weight-inverted objects, respectively. The outer surface of all four cylinders was made of hard white plastic, and the mass was evenly distributed within each cylinder. For the material condition four cylinders of identical volume (70 mm high × 70 mm in diameter) were created. Two of these objects were covered in a Styrofoam veneer, and two were covered in a brass veneer. The foam and brass material-weight illusion objects each weighed 455 g, whereas the inversely weighted foam and brass objects weighed 720 g and 190 g, respectively.

Procedure

Object lifting task. All participants completed both the size and material conditions, counterbalanced across participants, and the procedure was the same for both conditions. To assess the size- and material-weight illusions we used the absolute-magnitude estimate procedure (Flanagan et al. 2008; Flanagan and Beltzner 2000; Zwislocki and Goodman 1980). Participants first lifted one of the two equally weighted objects off the force platform (e.g., the smaller weight illusion object) and, after replacing the object on the platform, assigned a number to represent the weight of the object. They were instructed to use any number of their choosing. They were then asked to repeat this estimation procedure for the second object (e.g., the larger weight illusion object).

To quantify the strength and direction of the illusion, we first determined the percent increase from the smallest- to the largest-magnitude estimate and assigned a positive value (multiply by 1) if the small or foam object was perceived as heavier or a negative value (multiply by −1) if the large or brass weight illusion object was judged to be heavier. If the same value was assigned to both objects, a zero value was recorded for the percent change score. Thus positive values would be expected under the standard illusions.

An initial weight illusion assessment was obtained prior to any experience with the inversely weighted objects. Subsequently, the illusion was assessed after each block of 10 lifts of each of the two inversely weighted objects in order to track changes in the magnitude of the illusion related to experience with the inversely weighted objects. For both younger and older adults the duration of the illusion assessment trial was ~1 min. In each condition the participant completed four blocks, and thus the illusion was assessed a total of five times.

In each block participants lifted the inversely weighted objects in alternation for a total of 10 lifts of each object (20 lifts total). Participants were instructed to grasp the object using a precision grip with the tips of the thumb and forefinger of the right hand on the sides of the object. Each trial began with an auditory tone cuing participants to reach out and grasp the object. They were asked to pause briefly, then lift the object in the air and hold it aloft until a second tone cued them to replace it on the force sensor. The brief pause prior to lifting ensured that a clean signal was obtained from the force sensors to facilitate analysis of load forces. In *blocks 1* and *2* participants lifted the heavy object first (small or foam depending on the condition) off the left and right force sensors, respectively. In *blocks 3* and *4* participants lifted the light object first (large or brass depending on condition) off the left and right sensors, respectively.

When lifting an object just off a surface, as in our task, people increase load force to a target level slightly exceeding the predicted weight of the object (Flanagan and Beltzner 2000; Johansson and Westling 1988). This involves first increasing and then decreasing the rate of change of load force such that the peak rate of change of load force typically occurs when the load force is approximately half the predicted weight. We refer to this peak rate of change of load force as the first peak in load force rate because when the object is heavier than expected additional increases in load force, associated with additional peaks in load force rate, are observed. To measure how well participants scaled their lifting forces when lifting the inversely weighted objects, we determined the load force produced at the first peak in load force rate, which we denote as $\mathrm{LF}_{\mathrm{1st\ peak\ rate}}$ (Flanagan et al. 2008). When the object is lighter than expected, liftoff can occur before the load force reaches half the predicted weight. Therefore, we focused our analysis on the heavy small object and the heavy foam object, for which we could obtain accurate measures. We have previously shown that, when lifting unexpectedly heavy and light objects in alternation, predictions about both weights adapt in parallel (Flanagan and Beltzner 2000).

Figure 1*B* shows load force and load force rate as a function of time for two representative trials involving a heavy weight: one from an early trial in the first block and another late trial in the last block. For each trial, the open circle denotes the load force at the time of the peak load force rate during the initial increase in load force ($\mathrm{LF}_{\mathrm{1st\ peak\ rate}}$). During early lifts, participants underestimated the weight, which triggers a reflexive response involving repeated increases in load force until the object lifts off the surface (Johansson and Westling 1988). During later trials the object lifts off after a single increase in load force, indicating that participants have adapted their lifting forces to the weights of the objects. To determine whether aging is associated with changes in force scaling, we compared the rate at which younger and older adults adapted their load forces across the experiment.

Cognitive tasks. EXPLICIT MEMORY TASK. In our previous research we observed that age-related changes in performance of a spatial paired-associate working memory task correlated with declines in sensorimotor adaptation in a reaching task (Trewartha et al. 2014). In the present study we assessed whether a similar relationship would exist with the scaling of lifting forces, using the same spatial paired-associate working memory task (Fig. 2*A*). At the start of each trial, target regions (80 mm^2) were presented on a vertical computer screen with a black background. These regions were located radially 420 mm from a central home position. Initially, the target regions were filled with a white mask. During the learning phase of the trial, the mask was removed from each target region one at a time. Each mask was removed for 1,000 ms, with an interstimulus interval (ISI) of 1,000 ms, in an order that was randomized for each memory set (see below). Removal of each mask revealed either an empty target region (unfilled white square) or one of 10 colored shapes, constructed by combining squares, circles, rectangles, and triangles, that served as memory test stimuli. Participants were instructed to remember the stimulus associated with each location. In the test phase that immediately followed, participants watched the central home position as one of the stimuli that had been exposed during the learning phase was presented. Participants were required to select the spatial target location where they remembered seeing that stimulus by clicking on the location with a mouse. After their selection was made the next stimulus was revealed at the central position, and this process continued until each stimulus that had been revealed in the learning phase was presented in the test phase. No feedback was provided about selection accuracy. The difficulty of the task was increased across the session by increas-

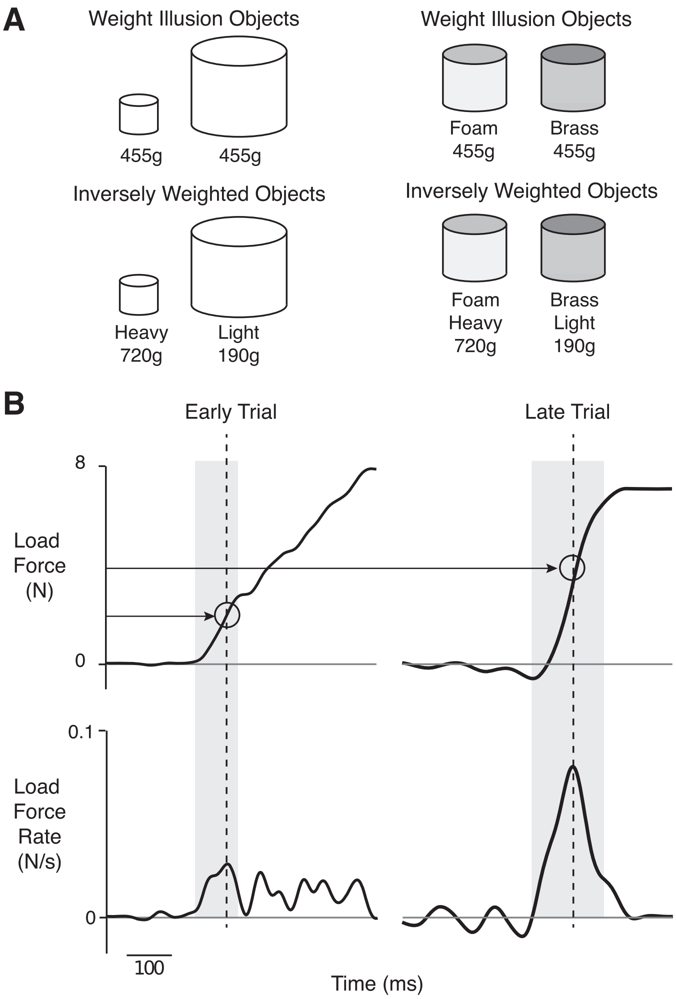

Fig. 1. Stimuli and example forces. *A*: equally weighted objects for testing weight illusions and inversely weighted objects. Participants lifted the objects using a precision grip with the tips of the index finger and thumb of the right hand on either side. Each object was lifted off a force sensor and replaced on the same sensor. *B*: individual load force and load force rate records from exemplary early and late lifts of the small heavy object. Vertical dashed lines mark the time of the initial peak in load force rate. Horizontal arrows mark the load force at the time of the initial peak in load force rate. Gray regions capture the initial increase in load force during the lift.

ing the size of the memory set. In the initial set, only one stimulus was presented at one of the locations and the other five locations were empty. The task advanced to the next set size if the participant correctly identified all of the memory items. If an error was made, the set size was repeated until the participant reached perfect performance or until the number of repetitions without success reached a maximum limit of 10. The set sizes ranged from one to six stimuli, and the task was continued until participants reached perfect performance on all six set sizes or until the maximum trial repetition limit was reached on a given set.

For each participant, we determined the percentage of correct responses across all test phases as well as the average reaction time of all test phase responses (i.e., correct and incorrect). The former provided a robust measure of explicit memory accuracy because participants with poorer explicit memory generated a greater number of repetitions, especially on the larger set sizes.

IMPLICIT MEMORY TASK. To test our hypothesis that weight predictions used when judging weight rely on nondeclarative memory resources, we used a word priming task that we have used previously as an index of implicit memory (Trewartha et al. 2014). In the learning phase, 40 words were presented in the center of a vertical computer screen in 60 pt white text on a black background. The words were presented one at a time for 2,000 ms, with an ISI of 500 ms, and participants were asked to read each word silently but were not given explicit instructions to remember them. In the subsequent, but unexpected, test phase a random selection of 30 of the learning phase words was presented along with 30 new words in a random order. For each trial, one of the words was presented in the center of the screen, covered by a solid gray mask comprised of overlapping gray dots (circles with a radius of 14 mm). The dots were removed at a rate of 90 dots/s, slowly dissolving the mask to reveal the hidden word. Participants were required to press the spacebar as soon as the word could be identified, regardless of how much of the word was visible. Upon pressing the spacebar, participants typed the word that they thought they identified and then automatically advanced to the next trial.

For each participant we determined the accuracy and reaction time for every response. To provide a general measure of implicit memory performance, we calculated a facilitation score for correct trials, defined as the percent difference in the average reaction time for old and new items. Specifically, we subtracted the reaction time for old items from the reaction time for new items and divided by the reaction time for old items. This percentage score represents the advantage of being primed with the words that were presented in the learning phase (i.e., the old words), expressed as a percent reduction in reaction time. One older adult and one younger adult did not complete the implicit memory task because of technical difficulties. However, it is important to note that none of the findings differed if those participants' data were removed from the analyses, so their data are included in the results reported below.

Data Analysis

Weight illusions. For each condition the illusion was assessed prior to any experience with unusually weighted objects to test whether long-term priors themselves are similar in younger and older adults. We also assessed the illusions after every 10 lifts of the unusually weighted objects to determine whether the learning processes associated with updating priors are also preserved in aging. To assess these questions we compared the strength of the size- and material-weight illusions across the experiment in an age group × condition (size-weight vs. material-weight) × block ANOVA. All pairwise comparisons are reported with a Bonferroni correction.

We also tested the hypothesis that experience-driven changes in weight illusions would be correlated with performance on the implicit memory task. To investigate this relationship, we calculated a weight illusion updating score by taking the difference between the first and last weight illusion assessments and averaging these scores for the size-weight and material-weight objects. This approach provided a general measure of experience-driven changes in weight illusions that was not specific to either the size- or material-weight illusion. As we have reported previously, these judgments can be quite variable (e.g., Flanagan et al. 2008), so our approach also provided increased power by producing stable estimates of the underlying ability within individuals.

Lifting forces. To quantify the extent to which individuals learned to scale their lifting forces to the unusually weighted objects, we focused on the $\mathrm{LF}_{\mathrm{1st\ peak\ rate}}$ for the heavy small and foam objects, consistent with previous research (e.g., Flanagan et al. 2008). This approach ensured accurate measurement of the initial peak in load force rate because measurements using the lighter objects are less reliable. To assess any differences in the rate of learning to scale lifting forces, for each participant and condition we calculated the average $\mathrm{LF}_{\mathrm{1st\ peak\ rate}}$ in each block of 10 trials and compared these averaged scores in an age group × condition × block ANOVA.

We also tested the hypothesis that the ability to scale lifting forces to unusually weighted objects is related to individual differences in

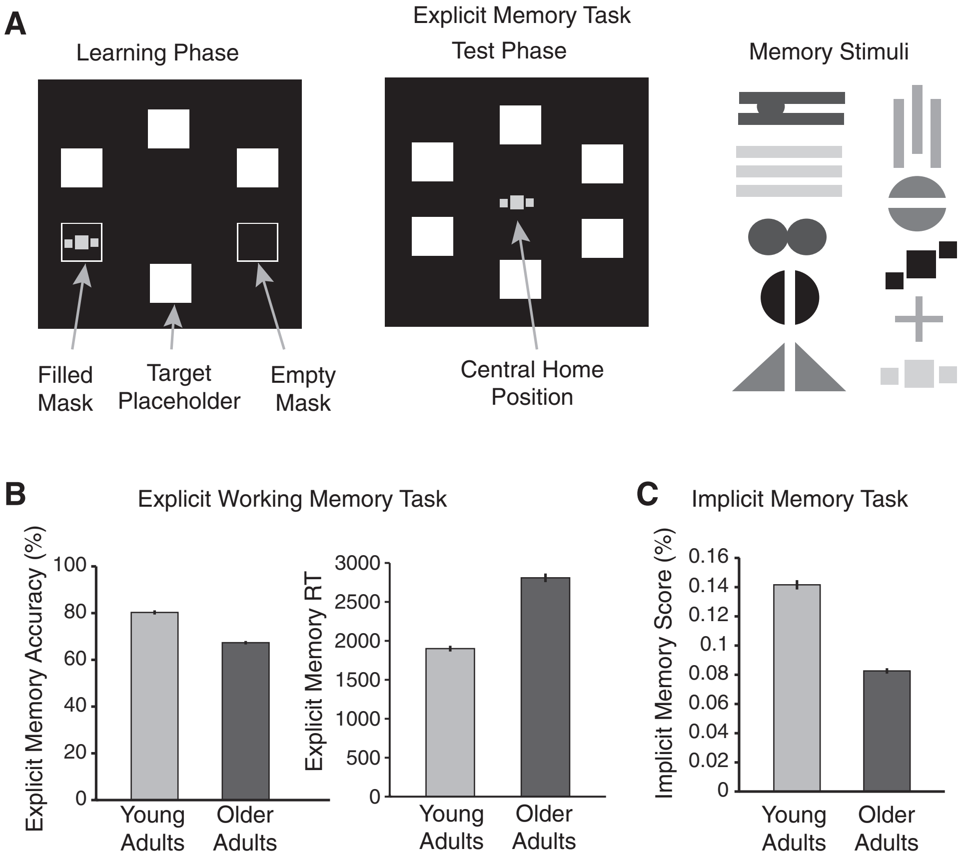

Fig. 2. Stimuli and results of the memory tasks. *A*: illustration of the spatial paired-associate learning task used to assess explicit memory. During the learning phase (*left*) masks at each target location are removed one at a time, revealing either an empty square or one of the memory stimuli (*right*). During the test phase (*center*) the memory stimuli are presented one at a time at the central home position and the participant selects the target location he/she remembers being associated with the stimulus. *B*: average accuracy and reaction time (RT) in the spatial paired-associate memory task. *C*: average facilitation scores on the word priming (implicit memory) task for younger and older adults. In *B* and *C* error bars represent ±1 SE.

working memory resources in aging. To provide a general measure of individual force scaling ability we calculated difference scores between $\mathrm{LF}_{\mathrm{1st\ peak\ rate}}$ for the first and the last lifts of the small and foam objects and averaged those scores. Correlations were then calculated between these force scaling scores and scores on the explicit working memory task in both groups of participants.

RESULTS

Cognitive Tasks

There were significant differences between younger and older adults on the explicit working memory task and significant differences on the implicit memory task. Older adults performed worse than younger adults on the spatial paired-associate working memory task (Fig. 2*B*), in terms of both accuracy [$t(42) = 4.68$, $P < 0.001$] and reaction time [$t(42) = -4.09$, $P < 0.001$]. Older adults also exhibited a smaller word priming score [$t(40) = 2.86$, $P < 0.01$] than younger adults on the implicit memory task (Fig. 2*C*). These findings are consistent with our previous observations (Trewartha et al. 2014) and provide motivation to explore the relationship between individual differences in memory abilities and predictions of object weight used for weight judgments and the scaling of lifting forces.

Weight Illusions

To test whether weight predictions used for judging weight, and the learning processes associated with updating of these predictions, are relatively maintained in aging, we measured the strength of the size- and material-weight illusions. There was no main effect of age group ($P > 0.11$), indicating that, overall, the illusion magnitudes did not differ between groups (Fig. 3*A*). There was a significant main effect of block [$F(4,39) = 11.1$, $P < 0.001$]. Pairwise comparisons revealed that the illusion was larger in the first assessment compared with the other four ($P < 0.05$) and larger in the second assessment compared with the final three ($P < 0.05$) for both groups and in both conditions. Importantly, pairwise comparisons also revealed that the strength of the illusion did not differ significantly between groups during the baseline assessment for either the size-weight ($P = 0.22$) or material-weight ($P = 0.83$) condition. A main effect of condition indicated that the illusion was larger in the size-weight condition compared with the material-weight condition [$F(1,42) = 50.3$, $P < 0.001$]. Finally, there was a significant interaction between condition and block [$F(4,39) = 5.4$, $P < 0.001$], but no other interactions were significant ($P > 0.18$). Interestingly, post hoc comparisons revealed that in the material-weight condition the magnitude of the illusions was attenuated significantly after only 10 lifts of the inversely weighted objects ($P < 0.01$), whereas the size-weight illusion was not significantly reduced after 10 lifts ($P > 0.9$); rather, it was not significantly reduced until after 20 lifts of the inversely weighted objects ($P < 0.01$). Together these findings indicate that the attenuation of the size- and material-weight illusions after experience with the inversely weighted objects was similar between younger and older adults.

To explore whether implicit memory resources underlie weight predictions used when judging weight, we tested the hypothesis that experience-driven changes in the illusion are

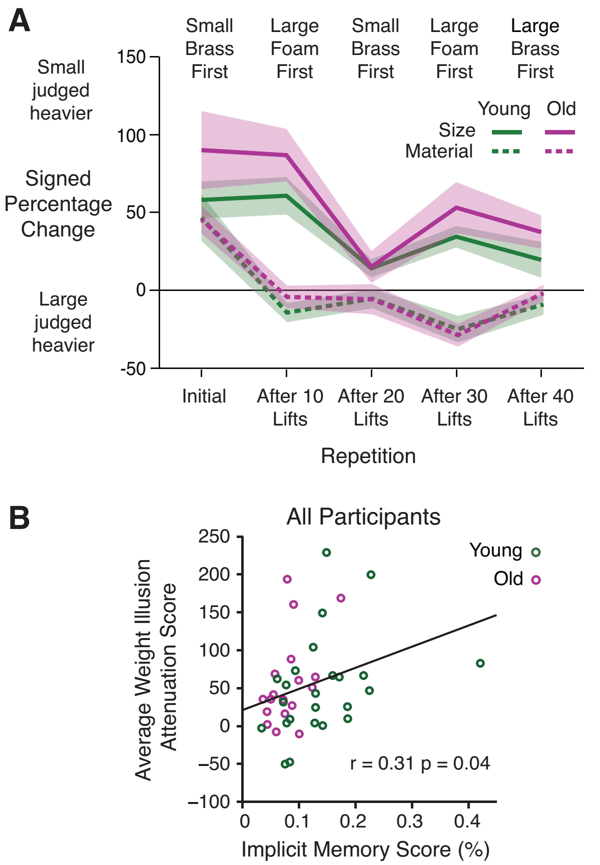

Fig. 3. Weight judgment results. *A*: strength and direction of the size-weight and material-weight illusions for younger and older adults at baseline and after every 10 lifts of the inversely weighted objects in each condition. The object that was lifted first on each weight-illusion assessment trial is labeled at *top*. Shaded regions represent ±1 SE. *B*: correlation across all participants between facilitation scores on the implicit memory test and the average change in the magnitude of the weight illusion for the size-weight and material-weight conditions. Data points are color coded to indicate which points belong to younger and older adults.

correlated with implicit memory performance. There was a significant positive correlation between implicit memory scores and weight illusion updating scores within the older adult group ($r = 0.48$, $P < 0.05$) and a trend toward a positive correlation in the younger adult group ($r = 0.36$, $P = 0.08$). When all participants were included in a single analysis, there was also a significant correlation ($r = 0.31$, $P < 0.05$) between implicit memory scores and weight illusion updating (Fig. 3*B*). Importantly, weight illusion updating scores did not correlate with explicit working memory scores in older adults ($r = -0.09$, $P = 0.71$) or younger adults ($r = -0.06$, $P = 0.79$) or across all participants ($r = -0.04$, $P = 0.81$) and did not correlate with chronological age in older ($r = 0.08$, $P = 0.75$) or younger ($r = -0.14$, $P = 0.51$) adults. These findings provide evidence that the updating of perceptual judgments about weight is associated with implicit memory resources in a way that is similar for younger and older adults.

Lifting Forces

To examine whether the updating of lifting forces declines with aging, we measured the lifting forces participants applied when lifting the inversely weighted objects. Figure 4*A* shows, for both the size- and material-weight conditions, $LF_{1st\ peak\ rate}$ as a function of lift number for the younger and older adults. The age groups did not differ overall in lifting forces ($P > 0.8$). There was a main effect of block [$F(3,40) = 14.6$, $P < 0.001$], as both groups learned to scale their lifting forces across the experiment in both conditions (Fig. 4*B*). In addition, the interaction between age group and condition was almost significant [$F(1,42) = 4.0$, $P = 0.052$]; older adults applied greater forces in the size-weight compared with the material-weight condition ($P = 0.051$), whereas younger adults did not differ between conditions ($P > 0.4$). Importantly, no other interactions were significant ($P > 0.19$), indicating that the groups were similarly able to adjust their lifting forces to the weights of the objects in both the size-weight and material-weight conditions.

To explore the possibility that the ability to scale lifting forces to unusually weighted objects is associated with individual differences in explicit working memory resources in aging, we correlated performance on the spatial paired-associate working memory task with force scaling in the older adults. Within the older adults this averaged adaptation score was significantly correlated ($r = 0.54$, $P < 0.05$) with accuracy scores on the spatial paired-associate learning task such that older adults who performed poorly on the explicit working memory task exhibited poorer force scaling (Fig. 5*A*). However, the averaged adaptation scores were not correlated with chronological age ($r = 0.13$, $P = 0.60$) or scores on the implicit memory task ($r = 0.17$, $P = 0.51$) within the older adult group. Among younger adults, who exhibited very good working memory performance with little variability between individuals, the averaged adaptation score did not correlate ($r = -0.16$, $P = 0.45$) with working memory performance (Fig. 5*B*). In addition, the averaged adaptation score did not correlate with the implicit memory score ($r = 0.05$, $P = 0.81$) or chronological age ($r = -0.09$, $P = 0.68$) within the younger adult group. These findings suggest that impairments in force scaling in later adulthood are associated with individual differences in working memory resources, rather than aging per se. Importantly, this observation provides evidence that declarative memory resources underlie weight predictions used when lifting objects.

DISCUSSION

The aim of this study was to investigate the role of nondeclarative and declarative memory resources involved in the updating of object weight predictions in two distinct contexts: judging object weight and scaling of lift forces when lifting objects. We compared younger adults to healthy older adults, who are known to have significant declarative memory impairments but relatively spared nondeclarative memory. We found that aging per se did not affect the adaptability of weight predictions used when judging weight or when scaling lifting forces. Older and younger adults did not differ in the magnitude of their initial size- and material-weight illusions during a baseline assessment and also did not differ in their updating of weight judgments, as evidenced by similar attenuation of the size- and material-weight illusions through experience with inversely weighted objects. Older and younger adults were also equally able to scale their lifting forces to efficiently lift inversely weighted objects, indicating that the ability to update

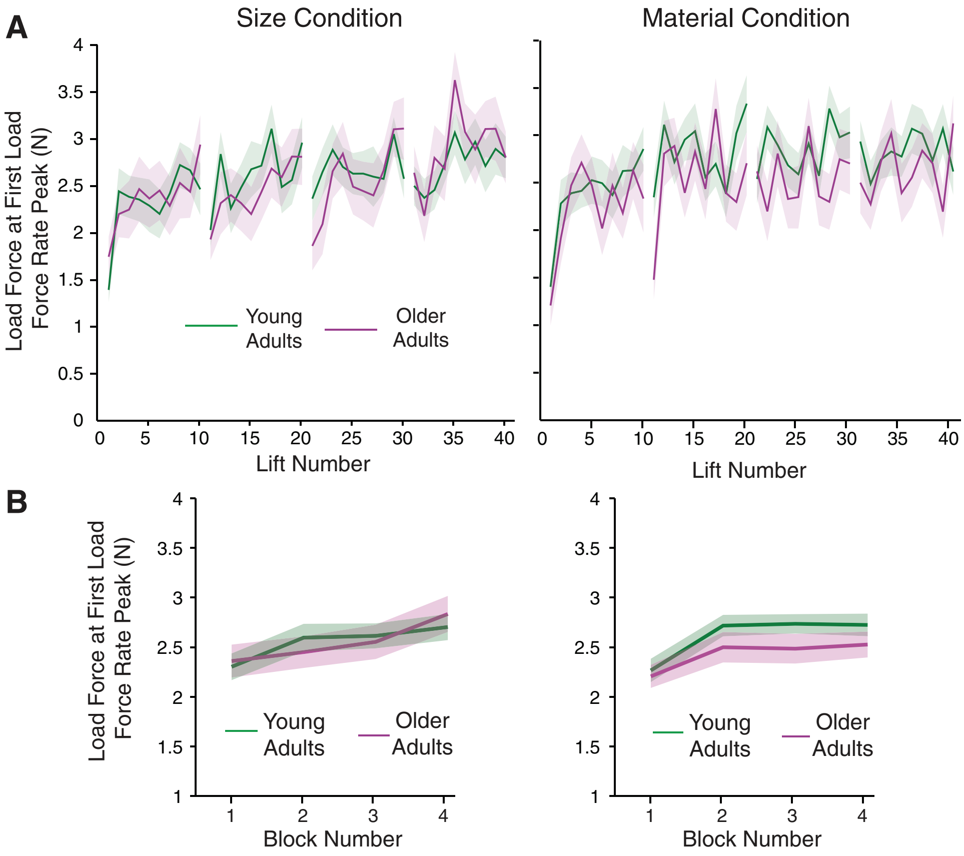

Fig. 4. Lifting performance. *A*: load force at the time of the initial peak in load force rate across all lifts of the heavy small (*left*) and foam (*right*) objects for younger and older adults. *B*: summary plots of the load force at the time of the initial peak in load force rate averaged across each block of 10 lifts in the size (*left*) and material (*right*) conditions for younger and older adults.

object-specific memory is relatively preserved in healthy aging. However, a second key finding was that within the older adults the ability to scale lifting forces was related to individual differences in explicit working memory performance such that older adults with poor working memory also exhibited poor force scaling. Finally, the extent to which weight judgments were updated through experience (i.e., the magnitude of the attenuation of the weight illusions) was correlated with performance on an implicit memory task across all participants. Together these findings indicate that weight predictions used when judging weight rely on nondeclarative memory resources, whereas weight predictions used to scale lifting forces are highly explicit, relying on declarative memory resources.

The present results are consistent with the idea that two complementary memory systems can be used to predict object weight. One system, used when judging weight, is based on well-learned priors linking weight to other object properties, including size and material, that can be directly appreciated via vision or touch. Predictions based on these priors can presumably also be used for force scaling when lifting objects that have not been previously lifted. Although these priors, as measured by weight illusions, can be modified quite quickly under appropriate experimental conditions (as in the present study), they are generally resistant to change (Flanagan et al. 2008; Flanagan and Beltzner 2000). This stability is important, as it enables us to reliably tag particular objects as being “heavy” or “light” relative to expected weight (see Baugh et al. 2012). The other memory system involves associative memory processes used to learn the weights of specific objects through direct experience of lifting them. In general, this object-specific memory enables us to rapidly adapt our lifting forces and is particularly important when lifting unusually weighted objects.

Our finding that implicit memory resources underlie weight predictions used for judging weight is consistent with the cognitive impenetrability of weight illusions. Previous research has shown that people experience the size-weight illusion even when they are informed that the small and large objects have the same weight (Buckingham 2014; Flourney 1894; Nyssen and Bourdon 1955). Moreover, people can learn to scale their lifting forces to the equal weight of the small and large objects, while at the same time maintaining a weight illusion (Flanagan and Beltzner 2000; Grandy and Westwood 2006). The hypothesis that implicit memory resources underlie weight predictions used when judging weight is consistent with our finding that healthy older adults, who exhibit relatively spared implicit memory, are similar to younger adults in terms of the strength of weight illusions. This hypothesis is also supported by our finding that the extent to which weight illusions are adapted through experience is correlated with performance on an independent implicit memory task across all participants. These findings support the notion that weight predictions used for judging weight operate outside of conscious awareness.

The leading explanation of weight illusions, which may be referred to as the expectancy hypothesis, posits that the illusions arise because object weight is judged relative to expected weight based on priors linking object size and apparent material to weight (Flanagan et al. 2008; Ross 1969). This explanation is supported by studies showing that experience of lifting size-weight inverted objects can attenuate (Nakatani 1985) and eventually invert (Flanagan et al. 2008) the size-weight illusions by altering expec-

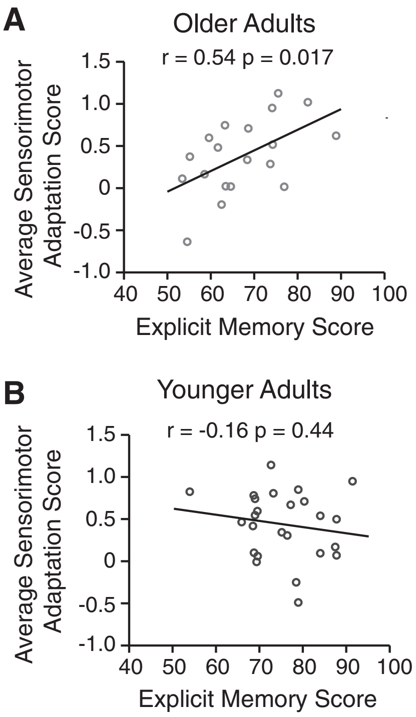

Fig. 5. Correlation between explicit memory and lifting performance. *A* and *B*: correlations between scores on the spatial paired-associate (explicit) memory task and the average difference between the first and last lifts of the heavy small and foam objects in terms of the load force at the time of the initial peak in load force rate for older (*A*) and younger (*B*) adults.

tations about object weight that are independent of predictions about weight used in lifting. Our findings demonstrate that such expectancies about object weight are altered implicitly, outside of conscious awareness. Further evidence in favor of the expectancy hypothesis comes from the observation that the size-weight illusion, based on the powerful prior that large objects should weigh more than smaller but otherwise similar objects, is more robust than the material-weight illusion, based on the arguably weaker prior linking surface material to weight (Buckingham et al. 2009; Buckingham and Goodale 2010, 2013). Interestingly, we found that the size-weight illusion was more resistant to change than the material-weight illusion in both younger and older adults, suggesting that size may induce stronger and less malleable expectancies about object weight than apparent material composition.

In contrast to the role of implicit memory in weight predictions used when judging weight, our results suggest that explicit memory resources underlie weight predictions used to scale lifting forces, allowing us to form associations between weight and particular identifiable objects. When healthy individuals lift objects repeatedly they use these associations to make predictions about the weight of the object, with accurate predictions leading to smooth and dexterous performance (Flanagan et al. 2006, 2008; Flanagan and Beltzner 2000; Gordon et al. 1991, 1993; Johansson and Westling 1988). Given that aging is associated with declines in associative memory (e.g., Naveh-Benjamin 2000), one might predict that object-specific memory used in object manipulation tasks also declines. Our data do not support this prediction. Instead, in the context of learning to lift two unusually weighted objects over repeated alternating lifts, older adults were able to scale lifting forces to a similar extent as younger adults. However, evidence for the role of declarative memory in weight predictions used to scale lifting forces came from individual differences in explicit memory resources. Within the older adult group performance on a spatial paired-associate working memory task was correlated with the extent to which participants learned to scale their lifting forces for the small heavy and foam heavy objects. That is, the ability to update object-specific memory during lifting is associated with individual differences in explicit working memory resources. This observation is quite similar to a recent study in which we reported a relationship between individual differences in explicit working memory and sensorimotor adaptation in a reaching movement task in older adults (Trewartha et al. 2014).

Although the present experiment relies on correlation analyses that do not demonstrate a causal relationship, the present findings establish a dissociation between weight predictions used for judging weight and weight predictions used when scaling lifting forces on the basis of the contribution of implicit and explicit memory resources, respectively. The ability to adapt weight predictions used for judging weight was found to be correlated with implicit but not explicit memory performance, whereas adaptation of weight predictions used when lifting objects was correlated with explicit but not implicit memory performance. A similar dissociation has been identified for learning processes involved in sensorimotor adaptation during reaching movements (McDougle et al. 2015; Taylor et al. 2014). In this work distinct learning processes operating on different timescales were identified: a fast process associated with explicit learning and a slow process associated with implicit learning. The present findings are broadly consistent with this idea of explicit and implicit learning mechanisms with different temporal properties, as weight predictions used for judging weight are adapted more slowly than weight predictions used to scale lifting forces.

The finding that, at the group level, older adults did not differ from younger adults in their ability to scale lifting forces seems to contradict previous work demonstrating that older adults exhibit a diminished ability to scale grip forces when lifting objects that differ in surface texture (Kinoshita and Francis 1996) and with evidence that older adults exhibit minimal scaling of fingertip forces in response to arbitrary color cues (Cole and Rotella 2002). However, those results were observed in groups of participants who were much older (mean = 86 yr old for Kinoshita and Francis 1996, mean = 77 yr old for Cole and Rotella 2002) than the present older adults, who were relatively young for an older adult sample (65 yr old on average). Thus general age-related impairments in the ability to scale lifting forces may not be evident until a more advanced age than the present sample of older adults. Impairments in the scaling of grip forces to changes in surface texture with aging are related to increased safety margins whereby older adults apply higher grip forces than necessary to prevent an object from slipping, regardless of surface texture (e.g., Cole et al. 1999; Kinoshita and Francis 1996). These increased safety margins have been explained in terms of declines in the functioning of cutaneous mechanoreceptive afferents with aging that prevent proper encoding of friction (Cole et al. 1999) rather than associative memory impairments.

Although we did not observe group differences between younger and older adults in the scaling of lifting forces, within the older adult group force updating was linked to explicit, associative memory resources. This finding is broadly consistent with the observation that older adults are impaired when scaling fingertip forces based on arbitrary color cues (Cole and Rotella 2002). The inability to use arbitrary color cues is likely due to age-related changes in associative memory that prevent them from linking visual object identity to fingertip forces required for efficient lifting. Thus age-related declines in explicit/associative memory resources, rather than age per se, are likely responsible for impairments in force scaling in older adults. This interpretation is consistent with a broader literature suggesting that motor control is cognitively demanding for older adults, and that experimentally limiting the availability of cognitive resources when performing motor tasks drastically exaggerates age-related motor impairments (see Seidler et al. 2010 for review). Thus, under conditions that impose more severe working memory demands, even high-functioning older adults may show impaired object-specific memory during object lifting because of overburdened working memory resources.

In summary, the present study reveals that two complementary memory systems underlying weight predictions used for weight judgments and object lifting can be dissociated in terms of their reliance on implicit and explicit memory resources, respectively. Moreover, we showed that aging per se does not impact the adaptability of weight predictions used for weight judgments or the scaling of lifting forces. Instead, the adaptability of those weight predictions is determined by individual differences in available implicit and explicit memory resources.

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DISCLOSURES

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

AUTHOR CONTRIBUTIONS

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

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