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Published in:
Vision Research

DOI:
10.1016/j.visres.2015.02.005

Publication date:
2015

Document Version
Early version, also known as pre-print

Link to publication in Heriot-Watt University Research Portal

Citation for published version (APA):
The impact of unilateral brain damage on weight perception, sensorimotor anticipation, and fingertip force adaptation

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Keywords: Brain damage; object lifting; grip force; load force; material weight illusion, size weight illusion

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Abstract

Damage to the left parietal cortex can lead to apraxia – a selective deficit in tool use and action planning. There is conflicting evidence as to whether this disorder affects more fundamental motor parameters, such as applying the appropriate forces to lift objects based upon how heavy they look. Here we examined how individuals with left and right-lateralized brain damage lift and perceive the weight of objects of the same mass which vary in their size and material properties. No clear differences emerged between the groups in terms of how visual material properties affected their perceptions of object weight or their initial application of grip and load forces. There was, however, some evidence that unilateral brain injury impaired the use of size cues for the parameterization of grip forces.
Introduction

A large body of evidence has indicated that our conscious perception of an object’s weight does not accurately reflect its physical mass. This discrepancy between experience and veridical reality is readily demonstrated through various weight illusions, where objects of identical mass feel different weights to one another due to variations in other physical properties. In the most famous of these, the size-weight illusion (SWI), small objects feel heavier than large objects which have been adjusted to have the same mass (Charpentier, 1891; Murray, Ellis, Bandomir, & Ross, 1999). Similarly, in the material-weight illusion (MWI), objects which appear to be made from low-density materials are judged as feeling heavier than objects of the same mass which appear to be made from high-density materials (Ellis & Lederman, 1999; Seashore, 1899). These illusions are persistent, cognitively impenetrable, and appear to be a consequence of how we integrate our prior expectations with sensory input (i.e., the heavy-feeling objects feel heavy because lifters expected them to be lighter than they actually are – for review see Buckingham, in press).

Expectations of object heaviness do not just affect perceptual judgements, but also influence the way that lifters interact with objects. Due to the predictive way in which objects are lifted, the rates at which the initial grip and load forces are applied during a lift will reflect how heavy and object looks rather than its actual mass. Thus an individual will initially lift a large object with a higher rate of force than they would use to lift an identically-weighted small object (Flanagan & Beltzner, 2000; Gordon, Forssberg, Johansson, & Westling, 1991), and they will initially lift a heavy-looking object with a higher rate of force than they would use to lift a light-looking object of the same mass (Baugh, Kao, Johansson, & Flanagan, 2012; Buckingham, Cant, & Goodale, 2009). In contrast to the persistence with which expectations influence a lifter’s perception of heaviness, the gripping and lifting forces are rapidly modified with practice. Thus, only for the first few trials will individuals grip and lift the various illusion-inducing objects with different forces from one another, before adjusting their forces to reflect the stimuli’s actual and identical masses (Buckingham et al., 2009; Flanagan & Beltzner, 2000). These effects are known as sensorimotor prediction and sensorimotor adaptation, respectively. This divergence between how illusion-inducing objects are perceived and acted upon has been taken to indicate that there are distinct neural representations maintained for conscious weight perception and predictive fingertip force control (Chouinard, Large, Chang, & Goodale, 2009; Flanagan, Bittner, & Johansson, 2008). However, there has been little support for this proposition from work with various neurological patient groups (Li, Randerath, Goldenberg, & HermSDörfer, 2011; Rabe et al., 2009).

The left cerebral hemisphere is an obvious candidate for the neural locus of predictive fingertip force control based on learned object properties such as size and material. The left hemisphere, in particular regions in the parietal cortex, has been associated with action planning and tool use in a number of studies (e.g., Valyear, Cavina-Pratesi, Stiglick, & Culham, 2007). Furthermore, damage to the left parietal cortex is thought to be the primary cause of deficits with tool use which are a particularly important manifestation of limb apraxia (Buxbaum, 2001; Goldenberg, 2014). Of particular relevance to the current work, it has been proposed that apraxia represents a specific impairment to the use of internal representations required for planning interactions with tools (Buxbaum, Johnson-Frey, & Bartlett-Williams, 2005). However, in spite of the clear conceptual link from this literature to the predictive way objects are lifted in weight-illusion paradigms, there has been no evidence for any such deficits in patients with left brain damage. The most comprehensive
study examined groups of patients with varying degrees of apraxia following unilateral damage to the left hemisphere and compared their fingertip forces and weight perception with non-apraxic patients with left and right brain lesions, as well as a control group (Li et al., 2011). The authors noted that individuals with apraxia showed a similar degree of size-based fingertip force scaling to the other groups, suggesting that the predictive application of fingertip force behaviour is neither lateralized to the motor-dominant left hemisphere (see also Buckingham, Ranger, & Goodale, 2012) nor related to the tool-used deficits seen in individuals with apraxia.

The findings outlined above would seem to indicate that the deficits in tool use/pantomime seen in apraxic patients are unrelated to sensorimotor prediction when lifting objects. A recent study by (Eidenmüller, Randerath, Goldenberg, Li, & Hermsdörfer, 2014) suggests that at least some forms of apraxia may disrupt the natural application of forces that individuals use to lift a range of familiar objects. In their study, individuals with left and right unilateral brain damage lifted a variety of everyday objects such as bottles of milk and packets of cigarettes while their gripping forces were measured with finger-mounted sensors. Typically, an unimpaired lifter’s grip forces will show a precise anticipation of a familiar object’s mass (Hermsdörfer, Li, Randerath, Goldenberg, & Eidenmüller, 2011). However, individuals with left brain damage (LBD) had clear impairments in their fingertip force scaling, showing far weaker associations between grip force rate and object heaviness than age-matched controls and patients with damage to their right hemisphere. Instead, the left brain damaged patients tended to grip the heaviest objects with approximately the same rate of force as the lightest objects. The deficit was most prominent in patients with visuo-motor apraxia as measured by the imitation of meaningless gestures. Similar findings have been reported in a group of six LBD patients when the vertical lifting forces were examined as a measure of weight anticipation during lifts of everyday objects (Dawson, Buxbaum, & Duff, 2010). Thus, in contrast to the research on how size affects anticipatory fingertip force control (Li et al., 2011), it appears that the fronto-parietal networks which have been implicated in successful praxis may be also critical for sensorimotor prediction based on object identity. These findings could be interpreted as an involvement of left hemisphere networks in independent processing of tool and object related information, which may in turn code the implicit knowledge of the forces required to lift a familiar object as well as one’s understanding of how to use a particular tool.

The divergent findings of the object lifting studies in patients with LBD to date appears to indicate that object size influences fingertip force control in a way which is independent from how object identity influences how we grip and lift objects. Although there is no clear empirical evidence for this proposition, there are some findings consistent with this proposal in the object lifting literature. For one, the influence of size on fingertip forces appears to be particularly persistent, far more so than object identity or material properties. In most SWI studies, lifters will take several trials to adapt their fingertip forces to the objects’ actual masses (e.g., Buckingham & Goodale, 2010; Chouinard et al., 2009; Flanagan & Beltzner, 2000; Grandy & Westwood, 2006), whereas studies where lifters who encounter unexpectedly-weighted objects without variations in size show extremely rapid, single-trial, adaptation (Buckingham et al., 2009; Gordon, Westling, Cole, & Johansson, 1993). If size cues are sufficiently salient and persistent to hinder the rapid adaptation to object mass, they may be resistant to the effects of LBD and apraxia which seem to hinder predictive grip force application with real-world objects.
To better determine if and how left brain damage influences the predictive application of fingertip forces, we examined object lifting behaviour in variety of contexts. Groups of patients with left and right unilateral brain injury lifted and judged the weight of (1) cubes with a normal size-weight relationship, (2) identically-weighted cubes with different volumes which typically induce the SWI, and (3) identically-weighted cubes of the same volume which varied in their apparent material properties to induce the MWI. In this latter case, when these objects are lifted, unimpaired lifters will lift the heavy-looking objects with more force than the light-looking objects, and judge the heavy-looking object as feeling lighter than the one which appear to be less heavy (Buckingham et al., 2009; Buckingham, Ranger, & Goodale, 2011). If the ability to use tools is related to the ability to the utilization of representations of object properties, lifters with LBD and apraxia are likely to show impaired predictive application of fingertip forces based on material properties, which should contrast their performance in the SWI condition.

Materials and methods

In the current work, thirteen patients with left brain damage (LBD, 7 male, mean age = 56.7 years ± 15.9), eleven with right brain damage (RBD, 6 male, mean age = 59.3 years ± 9.4), and fourteen neurologically-intact control subjects (CTR, 6 male, mean age = 57.3 years ± 8.4) were tested. Demographic and clinical information for the individuals in the LBD and RBD groups can be found in table 1. All participants were recruited from Munich, and testing was undertaken in the native language (German). All participants gave informed consent prior to testing, and all procedures were run in accordance with The Code of Ethics of the World Medical Association (Declaration of Helsinki) and approved by the local ethics board at the Medical Faculty of the Technische Universität München.

Insert table 1 here

A variety of objects were lifted in three conditions – Natural, SWI and MWI. In the Natural condition, participants lifted naturally-weighted large and small wooden cubes. The large cube was 10×10×10cm, and weighed 700g, whereas the small cube was 5×5×5cm and weighed 90g. In the SWI condition, participants lifted identically-weighted large and small metal cubes. In this condition, the large cube was 10×10×10cm, and weighed 700g, whereas the small cube was 5×5×5cm and also weighed 700g. In the MWI condition, participants lifted identically-weighted large cubes which appeared to be made from aluminium and expanded polystyrene. Both cubes in this condition were 10×10×10cm and weighed 700g. In the SWI and MWI conditions, where adjustments were made to the natural weight of the stimuli, objects were hollowed out and filled with lead. Care was taken to ensure that all objects were centrally weighted. Further details about the construction of these stimuli can be found in Buckingham & Goodale (2013). Finally, a 540g grey plastic cylinder (diameter 7.5cm, height 8cm) served as a neutral object for the washout trials. All objects were fitted with a mount in the centre of the top surface in order to facilitate the rapid attachment and removal of a 140g handle. The contact surfaces of the handle were covered with sandpaper, allowing participants
to grip all the objects with a grip utilising the thumb, index finger, and middle finger. The custom-made handle contained three force sensors, two of which recorded the forces lateral (left and right grip forces, 0-80 N, accuracy ±0.1N) to the handle’s surface and one of which recorded the vertical load force (0-60N, accuracy ±0.1N) each with a sampling frequency of 100 Hz (for details see Li et al., 2011).

Participants were seated in front of a table and lifted objects in three sequential conditions, preceded and separated by washout trials with a neutral object. LBD and RBD patients lifted with the hand ipsilateral to their lesion, and all subjects in the CTR group lifted with their left hand. First, participants lifted the neutral object six times in a row. Then, participants lifted the large and small wooden cubes in alternation six times apiece (the Natural condition). Following another six lifts of the neutral objects, participants then lifted the large and small metal cubes in alternation six times apiece (the SWI condition). Finally, following another six lifts of the neutral object, participants lifted the aluminium and polystyrene cubes in alternation six times apiece (the MWI condition). The first object to be lifted in each condition was counterbalanced across participants. Prior to each condition, participants were asked to verbally indicate which object out of the pair they expected to be the heaviest. They were also asked to give a verbal indication of which object felt heaviest after the 3rd pair of lifts and after the final pair of lifts. Both of these post-lift ratings were averaged within subject to yield a proportional value representing how many perceptual reports on average stated they experienced the various weight illusions. In all cases, participants were permitted to report that the objects felt equally heavy if necessary. One patient in the LBD group was severely aphasic and, despite completing the lifting trials, was unable to give a verbal report of how heavy the objects felt.

The force transducers recorded the lateral grip forces and the vertical load forces for a total of 5.5 seconds after participants were told to initiate their lift. The averaged grip force and the load force were differentiated to yield grip force rate (GFR) and load force rate (LFR). Non-parametric kernel estimates were used to smoothen the data as well as to calculate time derivatives with an effective cut-off frequency of 12 Hz (Marquardt & Mai, 1994). The difference between the peak GFR and peak LFR used to lift the objects in each pair (heavy-looking object – light-looking object) yielded the GFR<sub>diff</sub> and LFR<sub>diff</sub> measures. The GFR<sub>diff</sub> and LFR<sub>diff</sub> on the first lift in each condition served as our measure of sensorimotor prediction based each object’s appearance, and the GFR<sub>diff</sub> and LFR<sub>diff</sub> averaged across the lifts 3-5 in each condition was taken to indicate the degree of fingertip force adaptation in each condition. Lifts 3-5 were chosen for this latter measure because, in multiple cases, the force data from final trial pair was lost due participant fatigue in the LBD and RBD groups. Other missing values (3.3% of the CTR data, 7.1% of the LBD data, and 7.2% of the RBD data) were filled with the series mean.
Results

Perceptual reports

There were no obvious differences between the groups in terms of their expectations of heaviness or their subsequent perceptions of heaviness in any of the conditions.

Prior to lifting the differently-sized, differently-weighted wooden cubes in the natural condition, 75% of those in the LBD group, 90.9% of those in the RBD group, and 100% of those in the CTR group showed intact expectations for size, stating that they predicted the large wood cube would be heavier than the small wood cube. The majority of participants reported accurate weight perception, with 79.2% of the LBD, 100% of the RBD and 100% of CTR reports indicating that they perceived the large wood cube to be heavier than its smaller and lighter counterpart.

Prior to lifting the differently-sized, identically-weighted cubes in the SWI condition, 83.3% of the LBD group, 70% of the RBD group and 100% of the control group again showed intact expectations for size, stating that they expected the large metal cube to be heavier than the small metal cube. After lifting, 83.3% of the LBD, 75.3% of the RBD, and 95.8% of the CTR perceptual reports given by the participants indicated that they experienced the SWI, stating that the small cube felt heavier than the large cube.

Prior to lifting the identically-sized and-weighted cubes with different material properties in the MWI condition, 83.3% of the LBD group, 100% of the RBD group, and 100% of the CTR group showed appropriate expectations for object material properties, stating that they expected the aluminium cube to be heavier than the polystyrene cube. After lifting, and in contrast to the SWI condition, relatively few individuals experienced the MWI, with only 37.5% of the LBD, 59.1% of the RBD, and 35.1% of the CTR perceptual reports stating that the polystyrene cube felt heavier than the aluminium cube.

Fingertip forces

The primary measures of sensorimotor prediction and adaptation reported in this study are the GFR_{diff} and LFR_{diff} – the peak grip and load force rate used to lift the light-looking cube subtracted from the peak grip and load force rate used to lift the heavy-looking cube in each condition. This measure was examined on trial 1 and across the averages of trials 3-5. A positive GFR_{diff} and LFR_{diff} which is significantly different from 0 during the initial trials in any of the conditions would indicate adequate sensorimotor prediction. By contrast, a GFR_{diff} and LFR_{diff} which significantly differed from 0 on later trials would indicate good sensorimotor adaptation in the Natural condition (where the objects had different mass), but poor adaptation in the SWI and MWI conditions (where objects had the same mass).

First, the groups were examined with individual one-sample t-tests to determine if the GFR_{diff} differed significantly from zero on the first trial, as an index of sensorimotor prediction (Figure 2A). As expected, on trial 1 the CTR group showed clear sensorimotor prediction in the Natural (t(13) =
Next, each of the groups were examined with individual one-sample t-tests to determine if the GFR_{diff} differed significantly from 0 on the later trials, as an index of sensorimotor adaptation (Figure 3A). Although the GFR_{diff} in the CTR group did not differ from 0 in the SWI condition (t(13) = 1.44, p=.17), and showed a robust difference in the Natural condition (t(13) = 5.14, p<.001), indicating adequate sensorimotor adaptation, they did not appear to adapt their forces in the MWI condition (t(13) = 2.70, p<.05). By contrast, the LBD group showed good evidence of sensorimotor adaptation, lifting on later trials with a GFR_{diff} which did not differ from zero on both the SWI (t(12) = 1.14, p=.27) and MWI conditions (t(12) = 1.80, p=.10), and a GFR_{diff} which was significantly larger than zero in the Natural condition (t(12) = 3.64, p<.005). Finally, the RBD group showed sensorimotor adaptation in the Natural condition (t(10) = 3.87, p<.005) and the MWI condition (t(10) = 1.9, p=.09), but poor adaptation in the SWI condition (t(10) = 2.33, p<.05). A one way ANOVA for the sensorimotor adaptation scores revealed no differences between the groups in either the SWI (F(2,35) = 0.58, p=.56), MWI (F(2,35) = 0.21, p=.82), or Natural (F(2,35) = 2.3, p=.11) conditions for the GFR_{diff} scores.

In terms of LFR_{diff} on the later trials (Figure 3B), the CTR group showed normal adaptation to the objects’ different weights in the Natural condition (t(13) = 7.71, p<.001), and the objects’ identical weights in the SWI condition (t(13) = 1.97, p=.07), but poor adaptation in the MWI condition (t(13) = 2.59, p<.05). The LBD group showed good sensorimotor adaptation in the Natural (t(7) = 6.19, p<.001) and MWI (t(7) = 1.29, p=.24) conditions, but poor adaptation in the SWI (t(7) = 2.97, p<.05).
Finally, the RBD group showed good adaptation in the Natural (t(9) = 3.56, p<.01) and MWI (t(9) = 1.12, p=.29) and SWI (t(9) = 1.88, p=.09) conditions. A one way ANOVA for the sensorimotor adaptation scores revealed no differences between the groups in the SWI (F(2,29) = 1.22, p=.31), MWI (F(2,29) = 0.21, p=.98), or Natural (F(2,29) = 0.23, p=.80) conditions for the LFR <sub>diff</sub> scores.

Insert figure 3 here

Discussion

The goal of this study was to determine if damage to the motor-dominant left hemisphere affects fingertip force control and weight perception. To this end, we examined how individuals with unilateral brain injury interacted with object pairs which varied in either their mass, volume or apparent material properties. In each of these three conditions, participants lifted pairs of objects, one of which appeared to be heavier than the other. Prior to lifting, participants reported which of the objects they expected to be heavier, and twice during each condition they reported which object felt heavier. The rate at which grip and load forces were applied to each object was measured on every trial, and the difference between the forces used to lift the heavy-looking and light-looking object in each pair served as a metric of different aspects of sensorimotor performance.

In the first condition (Natural), participants lifted large and a small wooden cubes with the same density and, as a consequence, different weights from one another. The majority of participants in all groups expected the large cube to weigh more than the small cube, and (unsurprisingly) subsequently judged the large cube as feeling heavier than the small cube. This condition, while of little theoretical interest to the experimental question, does serve to show that participants were, on the whole, able to understand the concept of heaviness and accurately report real weight differences. However, in terms of the grip forces applied to the objects, there were indications that the LBD and RBD groups were impaired in their initial sensorimotor prediction, failing to lift the heavy-looking cube with more force than the light-looking cube. This contrasted with the behaviour of the control subjects, who applied more force to the large cube than the small cube, as indicated by GFR <sub>diff</sub> which was significantly greater than zero. Interestingly, neither the LBD nor RBD groups showed any difficulties scaling their load force rates to object size, suggesting that any deficit in force scaling may be restricted to the gripping forces. In both grip and load forces, all groups in this condition showed similar patterns of sensorimotor adaptation, learning to apply grip force at a greater rate to the heavy cube than to the light cube.

In the SWI condition, participants lifted large and small metal cubes which had the same mass as one another. As in the first condition, the majority of participants in all groups expected the large cube to outweigh the small cube, and in the majority of cases reported experiencing a SWI (i.e., that the small cube felt heavier than the large cube). It is worth noting that the clear presence of the size weight illusion in the LBD group compliments earlier work showing an intact SWI in individuals with left brain damage and apraxia (Li et al., 2011). Similarly, and also in agreement with Li and colleagues (2011), the LBD and RBD groups showed accurate sensorimotor prediction of load forces based on object size, indicating that unilateral brain damage does not impair the use of size as a cue to weight. By contrast, there was some evidence that unilateral brain injury selectively impairs the scaling of grip forces to size cues, as neither the LBD nor RBD group showed significant sensorimotor
prediction in the SWI condition. However, it is worth highlighting that none of the groups differed from one another when directly compared on either measure. In terms of fingertip force adaptation, the LBD group showed difficulties adapting their load forces, whereas the RBD group showed difficulties adapting their grip forces.

In the MWI condition, participants lifted identically-sized and –weighted cubes which appeared to be made from metal and polystyrene. The majority of participants in all groups expected the metal cube to outweigh the polystyrene cube. However, despite the fact that these cubes have been shown to induce a MWI in normal populations (Buckingham et al., 2009, 2011; Buckingham & Goodale, 2013), there was little evidence of such an effect here. Only the RBD group reported experiencing the MWI a substantial proportion of the time, whereas other groups tended to report either that the objects felt the same weight as one another or, less frequently, that the metal cube felt heavier than the polystyrene cube. In terms of lifting behaviour, however, all of the groups showed robust sensorimotor prediction of grip forces to objects’ material properties, and only the RBD group showed an impairment in prediction with their loading forces. In this case, it is unclear whether this lack of prediction in the RBD group stems from a particular deficit in utilization of object properties, or merely from the high variability seen in this measure.

The main aim of this study was to examine how visual material cues influenced the application of fingertip forces when lifting objects in patients with damage to the left hemisphere. Previous work has demonstrated that, while these patients have no deficits in using size cues to scale their gripping (Li et al., 2011), they are impaired at using object identity to guide the application of fingertip forces (Eidenmüller et al., 2014). Conceptually, the apparent material of an object appears to bridge the gap between these two paradigms, and examining object lifting performance in this patient group would have enhanced our understanding of the extent and root cause of the difficulties that individuals with apraxia experience with tool use. If patients in the LBD group showed a familiar object-like impairment in their sensorimotor anticipation of material properties, it would suggest that size cues to object weight are a unique and special property which is largely conserved in the sensorimotor system following this type of brain injury. If, however, patients with LBD were not impaired in using materials properties to guide their initial forces, it would suggest that object identity is processed separately from more general size and material cues to weight. Our data appear to support this latter view, as both of our patient groups lifted the metal cube with a higher rate of force than the polystyrene cube on the first trial. Thus, our findings provide tentative evidence that unilateral brain injury does not affect how visual material cues are used to guide gripping and loading forces, suggesting that object identity is either less robust to brain injury than material cues (perhaps due to differences in how difficult it is to identify an individual object as opposed to identifying a block of homogenous material), or processed by alternate regions of the sensorimotor system. Further work examining how sensorimotor memory for object identity and material properties interact with one another in patients with unilateral brain damage is necessary to disentangle these possibilities.

Beyond the main aim of the study, two findings from the current work were sufficiently unexpected to require further discussion. The first, the lack of a robust MWI effect, may stem from the method of reporting employed in the current work, as it is likely that our simple method of perceptual reports is substantially less sensitive than the numerical ratings used in previous works (Buckingham et al., 2009, 2011; Buckingham & Goodale, 2013). Furthermore, the lack of a MWI, especially in our
control group, may be a consequence of the age of the sample in our current work. The MWI studies using these stimuli listed above have focussed on university-aged participants. To our knowledge, no body of work has investigated how weight illusions alter over the course of one’s lifespan, and our findings provide some indications that this might be an interesting topic for further study.

The second point worth examining from the current body of work is the lack of sensorimotor prediction for grip force rates based on object size. The previous work on this topic (Li et al., 2011) suggested that it was likely that both the LBD and RBD groups would show intact sensorimotor prediction. Indeed, both groups lifted the large cube with a higher rate of load force than the small cube. However, this pattern failed to emerge with the grip force rate – both groups lifted the differently-sized objects with similar rates of grip force on the first trial. Similar patterns of data were seen in the natural condition – the LBD and RBD groups lifted the large and small cubes with similar grip forces, but disparate load forces. It seems unlikely that this lack of grip force scaling to object size cues is a consequence of a default grip force, as this would not explain why these individual scaled their grip forces to object material properties just as well as the control subjects did. Instead, it seems that unilateral brain damage may lead to a selective impairment in the parameterization of grip forces for object size cues. Li et al. (2011) report similar conclusions in a sub-sample of their LBD individuals, suggesting that those with the largest occipito-parietal lesions showed the greatest impairments of grip force scaling. This finding is also consistent with an earlier single case study reporting a patient with a left parieto-occipital lesion who also showed no scaling of grip forces according to size (Li, Randerath, Goldenberg, & Hermsdörfer, 2007). Interestingly, the opposite pattern was found in a study of lifting SWI-inducing objects in patients with cerebellar diseases, who showed normal anticipation of size for the grip forces, but reduced anticipation for the load forces (Rabe et al., 2009).

To sum up, the current work aimed to investigate whether individuals with unilateral brain damage were impaired in using apparent material properties to anticipate the mass of objects when lifting them. We found no evidence that unilateral brain damage affected the anticipatory control of objects based upon their material properties. We did, however, find deficits in how individual with brain injury scale their grip forces, but not load forces, to size cues Future work will build on these findings to examine how different types of brain injury affects the integration of long-term prior expectations of object weight derived from various visual cues with short-term feedback from recent object interactions.

Acknowledgements

This project was funded with a grant to support the initiation of international collaboration from the Deutsche Forschungsgemeinschaft (DFG). We thank Prof. G. Goldenberg, head of the Clinic for Neuropsychology at Hospital München-Bogenhausen for his support providing us with access to the patients tested in this study.
References


Figure captions

Table 1. Demographic for all groups, and available clinical information for the LBD and RBD groups. Aphasia tested with the Aachen Aphasia test (Huber, Poeck, & Willmes, 1984). Hand and finger imitation tests developed by G. Goldenberg (G Goldenberg & Hagmann, 1997).

Figure 1. The stimuli used across the conditions (left panels), and the handle containing the force transducers attached to the large aluminium cube (right panel).

Figure 2. The (A) GFR_{diff} and (B) LFR_{diff} used for the first lift the object pairs in each condition. This measure is an index of effective sensorimotor prediction based on the visual properties of the objects, with significant differences suggesting good sensorimotor prediction. Error bars indicate standard error of the means. * indicates a significant difference from zero at p ≤ .05.

Figure 3. The (A) GFR_{diff} and (B) LFR_{diff} used in the later lifts of the object pairs in each condition. This measure provides an indication of the efficiency of sensorimotor adaptation, with significant differences in the natural condition indicating good adaptation, but significant differences in the illusion conditions indicating poor adaptation. Error bars indicate standard error of the means. * indicates a significant difference from zero at p ≤ .05.