Observing object lifting errors modulates cortico-spinal excitability and improves object lifting performance

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Abstract

Observing the actions of others has been shown to modulate cortico-spinal excitability and affect behaviour. However, the sensorimotor consequences of observing errors are not well understood. Here, participants watched actors lift identically-weighted large and small cubes which typically elicit expectation-based fingertip force errors. One group of participants observed the standard overestimation and underestimation-style errors that characterise early lifts with these cubes (Error Video – EV). Another group watched the same actors performing the well-adapted error-free lifts that characterise later, well-practiced lifts with these cubes (No Error Video – NEV). We then examined actual object lifting performance in the subjects who watched the EV and NEV. Despite having similar cognitive expectations and perceptions of heaviness, the group that watched novice lifters making errors themselves made fewer overestimation-style errors than those who watched the expert lifts. To determine how the observation of errors alters cortico-spinal excitability, we measured motor evoked potentials in separate group of participants while they passively observed these error and no-error videos. Here, we noted a novel size-based modulation of cortico-spinal excitability when observing the expert lifts, which was eradicated when watching errors. Together, these findings suggest that individuals' sensorimotor systems are sensitive to the subtle visual differences between observing novice and expert performance.

Keywords: Object lifting; size-weight illusion; action observation; motor learning; grip force error

Introduction

Before picking up an object, individuals will implicitly estimate its weight based on its visual properties, and these expectations of heaviness drive the way that they lift objects. This means that when lifting something for the first time, a lifter's fingertip forces reflect their initial predictions about an object's weight, rather than the actual mass of the object (Gordon et al., 1991). The feed-forward nature of human lifting behaviour often results in grip and load force errors, which can be especially dramatic when objects have an unusual weight for their appearance (e.g., Buckingham, Cant, and Goodale, 2009; Johansson and Westling, 1988). These errors do not generally persist and individuals are rapidly able to overcome their expectations of heaviness, tuning their fingertip forces to the actual, rather than expected, weight of the object(s) being lifted (Flanagan and Beltzner, 2000; Grandy and Westwood, 2006; Mon-Williams and Murray, 2000). In other words, when lifting objects repeatedly, individuals rapidly and implicitly learn to lift them with the appropriate level of grip and load forces for their actual weight.

Despite the widely-held assumption that fingertip force adaptation is mediated solely by fast-adapting Type-2 afferents in the fingertips (Johansson and Flanagan, 2009), it has recently been demonstrated that vision plays a crucial role in this form of motor learning. When they are deprived of vision individuals show deficits in their ability to correct their fingertip force errors, continually lifting objects with forces that reflect how heavy the objects look, rather than how heavy the objects actually are (Buckingham and Goodale, 2010a; Buckingham, Ranger, and Goodale, 2011). These findings indicate that individuals receive valuable information describing the direction and magnitude of a lifting error from visual kinematic cues.

Consistent with this proposal, a variety of studies have demonstrated that humans are surprisingly adept at acquiring useful information, such as object weight, from the observed visual kinematics of others' lifts (Bingham, 1987; Hamilton et al., 2007). Not only are individuals able to use these kinematic cues, but there is emerging evidence that the link between acting and perceiving is an automatic one. Hamilton and colleagues (Hamilton et al., 2004) demonstrated that our perception of an actor's lift is modulated by the weight of an object the observer is holding (interestingly, in the opposite direction from what might be expected – holding a light box made the observed lift appear comparatively effortful, and vice versa). Furthermore, individuals implicitly use kinematic cues observed in other lifters when lifting objects which have an unpredictable weight (Meulenbroek et al., 2007). Perhaps the strongest argument for an automatic link between visual kinematics and action production in the context of object lifting comes from a recent series of action observation studies showing that the sensorimotor system appears to encode the force requirements of an observed lift. Using transcranial magnetic stimulation (TMS) to evoke motor potentials (MEPs) in a passive observation task, Alaerts et al., (2009) demonstrated that merely watching a video of someone else lifting a heavy object elicits a larger MEP than is elicited while watching a similar video of a lighter object. Subsequent studies have revealed that this force-related modulation of cortico-spinal excitability was caused by differences between the kinematics of the effortful (heavy objects) and easy (light objects) lifts, rather than semantic or material-based visual cues to object (Alaerts, Swinnen, and Wenderoth, 2010; 2010; Senot et al., 2011). The effects of observing the actions of others are not limited to the modulation of cortico-spinal excitability. A recent study has shown that the forces involved in lifting can be modulated by observing others, elegantly demonstrating that, compared to viewing an object being lightly touched, watching an actor firmly pinching a target object will increase the gripping force subsequently used to lift that object (Uçar and Wenderoth, 2012).

These studies tend to be interpreted within the broader context of the putative human mirror neuron system (Gallese et al., 2011; Mukamel et al., 2010). The overlapping neuronal populations and cortical regions in human and non-human primates has been taken by some as a mechanism for observational learning, by means of implicit neural simulation of the observed action (Calvo-Merino et al., 2005; Jeannerod, 2001). However, the concept of mirror neurons, as typically discussed, offers no insight into how the sensorimotor system reacts to the observation of the commonplace errors that must drive motor learning. This question needs to be addressed at both the level of behaviour and cortico-spinal excitability. In terms of behaviour, it would presumably be maladaptive for the sensorimotor system to copy the motor output of an observed error. Although very few empirical studies have examined the consequences of error observation in any context whatsoever, some recent hints have emerged that individuals can improve their subsequent performance by observing errors. (Mattar and Gribble, 2005) had participants reach toward a visually-defined target in a novel force-field – a task that normally requires a substantial amount of learning. They noted that after observing videos of others performing an aiming task, participants performing the same task learned to overcome the dynamics of the force-field more rapidly. Furthermore, observing a different force-field from the one they eventually had to deal with substantially slowed their rate of adaptation, hinting at an automatic observational learning effect (see also Brown et al. 2009). Crucially, Brown and colleagues parametrically varied the degree of error in these videos, noting that participants were able to benefit more from observing larger errors than smaller ones (Brown et al., 2010). This finding was, of course, not an unexpected result given that the correct performance in the task relied exclusively on vision, and the errors provide the only visual indications of the situational dynamics. This work does, however, provide some preliminary hints that there may be a specific and important role for error observation in subsequent behavioural outputs, leading us to predict that observing lifting errors will improve subsequent lifting performance more than observing well-practiced lifts. The role of errors in driving cortico-spinal excitability is less clear, with no work examining MEPs during the observation of motor errors. As there are indications that observing errors may help improve subsequent performance, it is possible that the errors are encoded by the sensorimotor system to drive the subsequent corrective behavioural response. If the low-level motor resonance within the sensorimotor system slavishly mimics what is observed, such a mirroring response would manifest as a large MEP for an overestimation of force and a small MEP for an underestimation of force. However, as errors appear to drive improved behaviour (i.e., in directional opposition to the initial error), the MEPs might in fact oppose the pattern of resonance normally evoked by lifting forces – a large MEP to counteract an erroneous underestimation of force and a small MEP to counteract an erroneous overestimation of force.

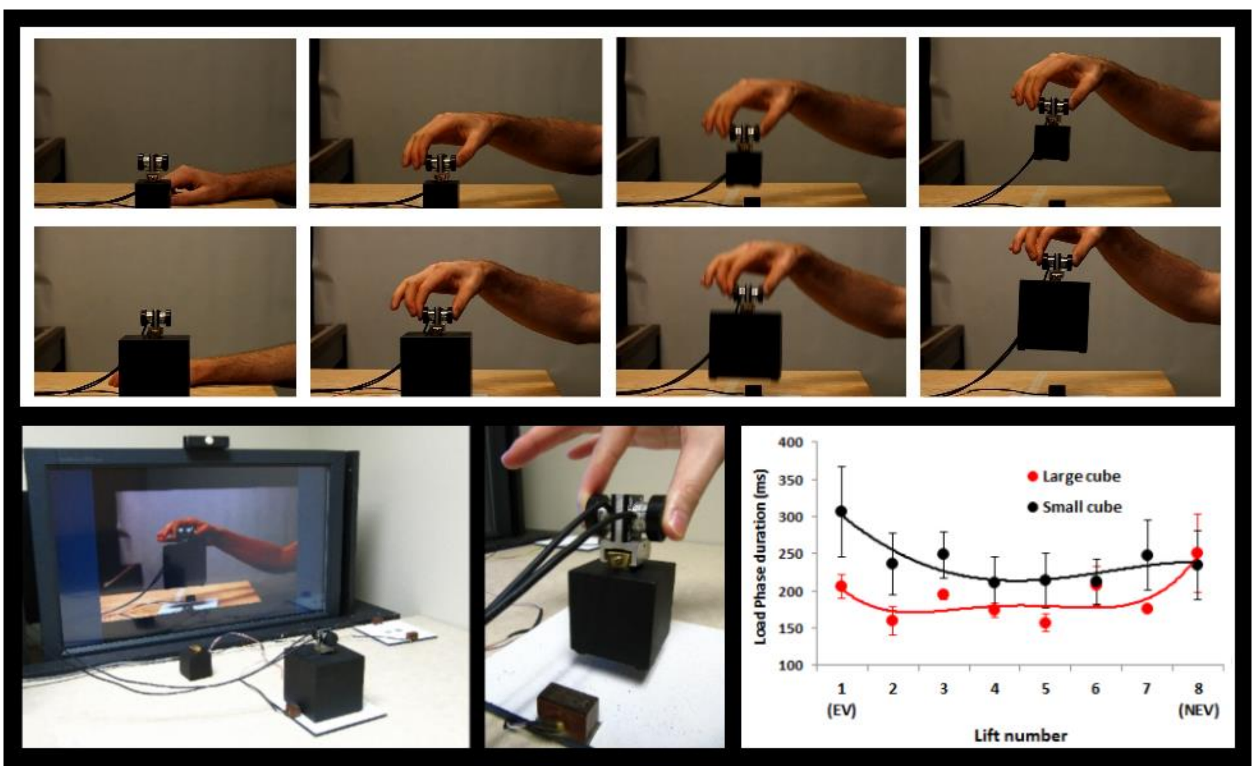
The goal of the current work was to examine the consequences of observing errors, within the simple motor learning framework of fingertip force adaptation during object lifting. To this end, we examined the sensorimotor consequences of watching the visual consequences of overestimations and underestimations of lifting forces (the error video - EV) as compared to well-adapted object lifting performance (the no error video - NEV) at the behavioral and cortico-spinal level. If errors are in fact crucial cues for observational learning, it is likely that observing them will (1) improve fingertip force adaptation and (2) modulate cortico-spinal excitability in a way that is specific to the overestimation or underestimation nature of the error.

Method

Video stimuli

A 66 cm screen monitor at a resolution of 1024 x 768 was used to display a short video to participants, depicting five different actors (3 male, 2 female, mean age = 24.6 years ± (SD) 0.9) repeatedly lifting a small cube (5 cm × 5 cm × 5 cm) and large cube (10 cm × 10 cm × 10 cm) in alternation. Unbeknownst to the participants (or the actors in the videos), the cubes had been adjusted to have identical weights (700g). These stimuli typically elicit the size-weight illusion, along with a stereotyped pattern of fingertip force rate errors during initial lifts (i.e., excessive force for the large cube, and insufficient force for the small cube), followed by a rapid adaptation of fingertip force rates to the actual, and identical, weights of the cubes (see Buckingham and Goodale, 2010b) for details).

Two types of video montages were created (Figure 1): Error Videos (EV) and No-Error Videos (NEV). We quantified the videos' kinematics by calculating the average load phase duration (averaged from only four actors, as the liftoff data from a 5th actor was lost due to collection errors). Load phase duration was defined as the time which elapsed between the initial application of load force to the object-mounted force transducers (when the force reached a threshold of >10% of the maximum overall value) and the point of object liftoff (as measured by lift off pad detailed below). The EV montages were comprised solely of repeats of actors' first lifts of the small and large cubes (Figure 1). The other video montage – the NEV – was built up from repeated presentations of same actors' 8th lift of each cube, well-practiced lifts where the actors' fingertip forces were adapted to the actual (identical) weight of the objects (Figure 1). The actors were unaware of the cubes' adjusted equal weights, and the lifting dynamics in these videos were completely natural and not coached.



In spite of the presence or absence of lifting errors, the EV and NEV montages were visually very similar (see Supplementary Videos 1 and 2). All videos were recorded from the actors' left sides, and showed the inner right forearms of the actors as they gripped the handle and lifted each cube. Each of these videos was approximately two minutes long, and contained a total of 20 lifts. To counter potential order effects with regard to which cube was lifted first, two variants of the EV and NEV montages were created – one where the large cube was lifted before the small cube (watched by half of the participants), and another where the small cube was lifted before the large cube (watched by the other half of the participants).

Behavioural experiment – lifting after observing others' lifts

Forty-four self-reported right-handed students from the University of Western Ontario took part in the behavioural experiment. Three participants were removed as outliers (with the force rates on multiple trials > 2 SD above the mean), leaving a sample of 41 [6 male, 35 female; mean age = 20.2 years ± (SD) 2.3]. Participants had normal or corrected-to normal vision and were naïve to the experimental hypothesis. Testing procedures were approved by the University of Western Ontario Research Ethics Board, and prior to testing, all participants gave written informed consent.

Fingertip forces were measured by a small handle with opposing grip pads that facilitated a precision grip with the thumb and forefinger, which contained a pair of six-axis force-torque sensors (Nano17 F/T; ATI Industrial Automation, Garner, NC). To minimize the possibility of slippage during a lift, the surface of the grip pads were covered with rough sandpaper to provide friction. The cube was placed on a lift-off pad on the table in front of the subject. The pad contained light sensors that projected a small beam of light 3 mm above and parallel to the surface of the table. These sensors provided a time stamp for object lift-off: when the cube was stationary on the table, the beam of light was broken; when the cube was lifted, the beam of light was unbroken.

This experiment consisted of two stages: an observation stage and a lifting stage. In the observation phase, participants sat on a height-adjustable chair in front of a table and watched one of the videos described above. As lifters' fingertip forces have been shown to rapidly adapt with these stimuli (Buckingham and Goodale, 2010b), this task utilized a between-participants design. Thus, participants were randomly assigned to either the EV group (n=21) or NEV group (n=20). Again, the video presentation and lifting order (i.e., whether the large cube was lifted before or after the small cube) was counterbalanced across the groups, and congruent within participants (participants who watched the small cube being lifted first, themselves lifted the small cube first).

In the lifting stage of the experiment (i.e., after watching the video), participants simply lifted the cubes that they had just watched the actors lift in the video. Participants wore opaque LCD shutter goggles to ensure that they received no clues as to the cubes' weights between trials. Trials were initiated with a computer-generated auditory cue, at which point the goggle lenses became transparent and the participants gripped the handle with the thumb and forefinger of the right hand. Just as they had seen the actors do in the video, participants lifted the cube approximately five cm off the table in a smooth, controlled fashion and held it steady at the peak of the lift. Four seconds later, a second auditory tone signaled the end of the lift, and participants gently lowered the cube to the liftoff pad. These procedures were repeated, alternating between lifts of the small and large cubes on a trial-by-trial basis for a total of 30 lifts (15 lifts of each). Before watching the videos or lifting any of the cubes, participants were given five practice trials using non-experimental stimuli (blue cylinders), to ensure they were lifting in an appropriate fashion.

The force transducers recorded fingertip forces in the x, y, and z dimensions at 1000 Hz. The average of the forces tangential to the surface of the grasp pads at each time point was defined as the grip force, whereas the sum of the remaining forces (consisting mostly of those forces opposing gravity) at each time point was defined as the load force. The rates of change of these values were calculated with a 5-point central difference equation, and the peak value was taken to represent our primary dependent variable of sensorimotor prediction – peak load force rate (LFR). Additionally, to determine whether lifting observation influenced individuals' perceptions of heaviness we examined the expected weight before, and perceived heaviness after participants had lifted the cubes. To this end, after watching the video, participants gave a number between one (lightest) and one-hundred (heaviest) representing how much they expected each cube to weigh. Then, after the lifting phase of the experiment, participants used the same scale to assign a number to how heavy each cube felt to them. All statistical analyses (outlined in the various results sections) were performed with IBM SPSS Statistics version 20.

TMS experiment - Motor potentials evoked during passive observation of lifts

Nineteen self-reported right-handed staff and students from the University of Western Ontario took part in the TMS experiment. One participant was removed due to difficulties in reliably localising their hand area, leaving a sample of 18 [12 male, 6 female; mean age = 27.4 years ± (SD) 7.0]. Participants had normal or corrected-to normal vision and were naïve to the experimental hypothesis. None of the participants in the TMS experiment has taken part in the earlier behavioural experiment. Testing procedures were approved by the University of Western Ontario Research Ethics Board, and prior to testing, all participants gave written informed consent.

Cortical stimulation was applied with a Magstim air-cooled double 70mm (figure-8) coil via Magstim Rapid 2 stimulator. EMG activity was recorded using surface electrodes (Delsys). Electrodes consisted of three 1 × 10 mm parallel silver bars placed 10 mm apart, which were housed in a compact case containing a 10 × preamplifier. Electrodes were placed to record the activity of the key muscle groups involved in a one-handed precision grip and lift: the right hand adductor pollicis brevis (ADPB) and flexor pollicis brevis (FPB), the wrist flexor (WF), and wrist extensor (WE) muscle groups. The skin around these muscles was cleaned and abraded with alcohol, and the electrodes were attached with adhesive backing and, where necessary, medical tape. Electrode placement was verified using a number of test maneuvers including movement and isometric force tasks (Gribble and Ostry, 1998). EMG signals were amplified by a factor of 1000 and digitally sampled at 4000 Hz. The ‘hand knob’ region of the left primary motor cortex (M1) was localized based on anatomical landmarks in each individual with a previously-acquired anatomical 3T Siemens MRI scan, and the focal TMS was guided using Brainsight (Rogue Research Inc.). The TMS was applied focally to the hand region of M1 to evoke motor potentials which were measured from the four muscles outlined above. In the setup phase, the experimenters refined the stimulation location by grid-searching around the anatomically-localized hand-knob region (average XYZ Talairach coordinates: -30.3, -29.6, 55.7) until a cortical area was identified which elicited a visible twitch in the participants hands and consistent MEPs in the relevant hand and arm muscles (average XYZ Talairach coordinates: -50.9, -24.5, 73.9) . The intensity of the stimulator was then reduced until a TMS pulse elicited no movement, but continued to elicit a visible MEP (i.e. easily distinguishable from baseline in a graphic plot of the electrode activity for 500ms after the TMS pulse was triggered) in any of the recorded muscles on 7 out of 10 stimulations while at rest.

In this task, which aimed to replicate the general procedure of Alaerts et al., (2010), participants watched the videos while receiving single-pulse TMS over the hand area of the left M1. Participants sat in front of the video monitor with their head in a chin rest and their arm relaxed on the table in a partially supine posture. Single pulse TMS was applied at a random point during the lift by one of the experimenters pressing a foot pedal. This experimenter stood behind the participant watching the video, to ensure a pulse was applied on each observed lift. A second experimenter, who was blind to the experimental condition, held the coil unsupported over the region identified in the setup phase (i.e., the hand-knob region of M1). Each participant viewed the same EV and NEV montages two times, with the presentation order counterbalanced across participants. As each video contained 20 lifts, participants received 80 TMS pulses over the course of the experimental trials. The signals from the electrodes over the first 250ms after the TMS pulse (a broad window containing any MEPs) were stored on an external laptop for offline analyses. MEPs with a peak value > 2SD above the mean within each subject were defined as outliers and removed. These signals were amplified, band-pass filtered between 10 and 500 Hz, rectified, and then normalized to be a proportion of each individual subject's highest MEP for each individual muscle.

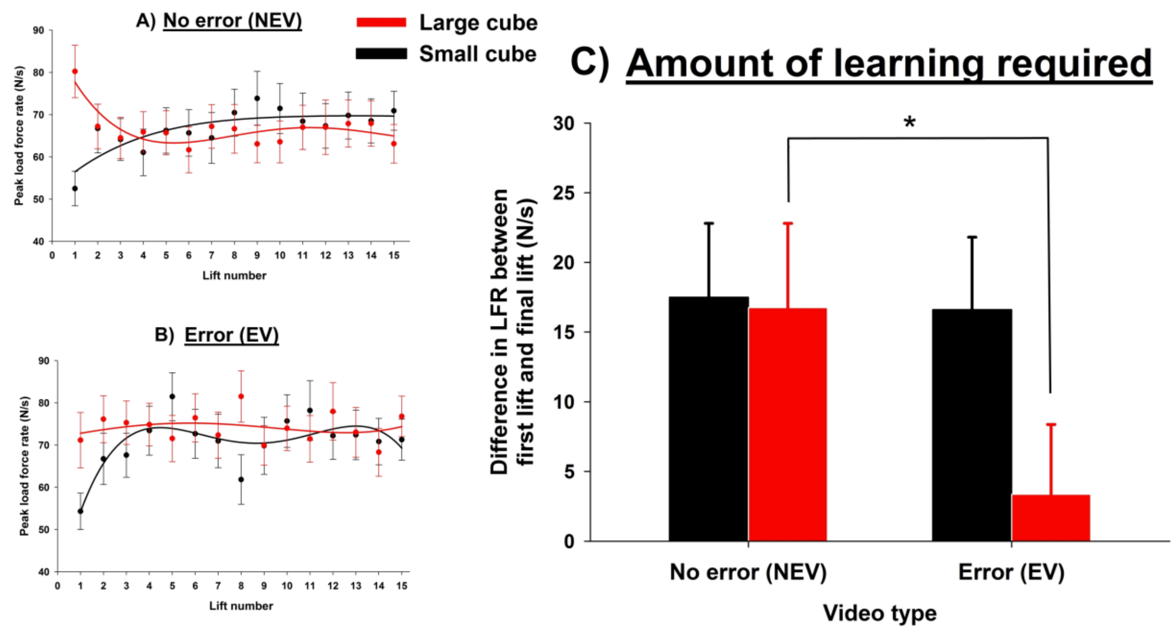
Results

Behavioural experiment – lifting after observing others' lifts

After watching the video, but prior to actually lifting the cubes, participants verbally reported that they expected the large cube to weigh more than the small cube (Table 1). This expectation did not differ between the EV and NEV groups (Table 1), indicating that participants gained no conscious awareness of the cubes' identical weights from the videos alone. After the lifting portion of the experiment was completed, participants experienced a robust size-weight illusion, reporting that the small cube felt heavier than the large cube (Table 1). Therefore, as with the initial expectations of heaviness, the magnitude of the illusion was similarly unaffected by whether participants had watched the EV or the NEV. Neither the pre-liftoff expectations nor the post-lifting ratings of heaviness correlated with the average LFR or the LFR applied on the first trial for each object in either group (Supplementary Table 1).

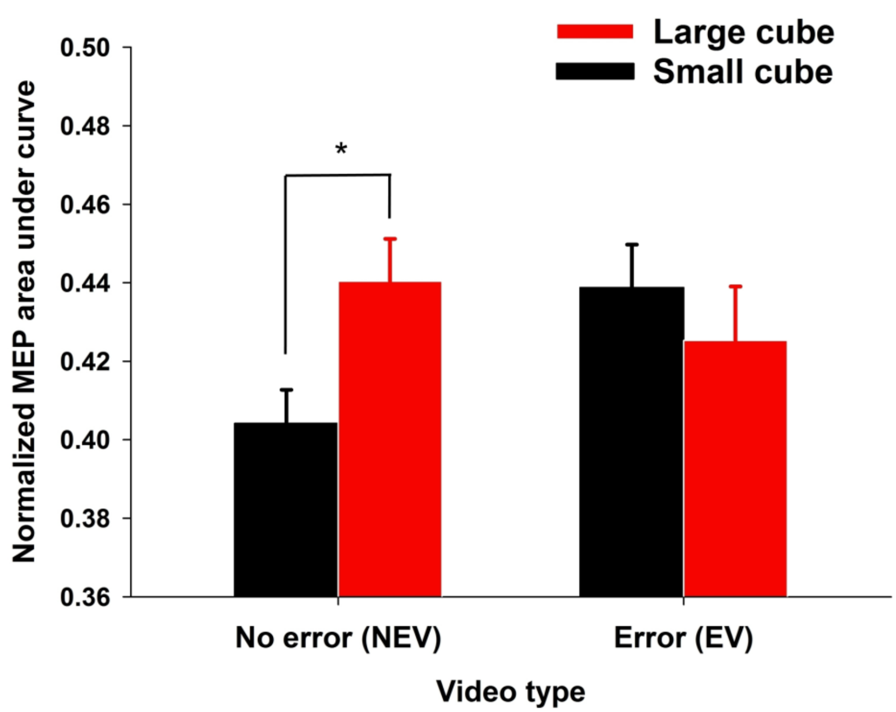
	Expected heaviness before lifting (mean ± standard error)		Within subject t tests (large vs. small)	Perceived heaviness after lifting (mean ± standard error)		Within subject t tests (large vs. small)
	Large cube	Small cube		Large cube	Small cube	
Error Video (EV)	63.1 ± 3.3	37.7 ± 5.3	p=.001	41.7 ± 4.7	65.6 ± 3.6	p<.001
No Error Video (NEV)	59.8 ± 5.0	32.3 ± 5.4	p=.003	31.7 ± 4.7	60.3 ± 4.6	p<.001
Between subject t tests (EV vs. NEV)	p=.57	p=.48		p=.14	p=.37	

In contrast to the cognitive measures, a clear difference emerged between the sensorimotor predictions made by the EV and NEV groups when they lifted the large and small cubes. Participants who watched the NEV lifted the cubes initially with the usual pattern of overestimations and underestimations seen for these objects (e.g., Buckingham and Goodale, 2010b). After a few trials, however, and in line with previous research (Flanagan and Beltzner, 2000) these errors were rapidly corrected, with the lifting forces rapidly reaching an asymptote (Figure 2A). In contrast, participants who watched the EV appeared to require very little adaptation of their forces when lifting the large cube – they lifted the large cube with approximately the same rate of force throughout the entire experiment (Figure 2B). In other words, participants who watched the EV made almost no overestimation-style errors. In order to quantify the benefit that is gained from watching the EV over watching the NEV, we created a simple metric of the total amount of fingertip force adaptation required for each cube in each condition over the course of the experiment by calculating the difference between the force rates on trial 1 (the initial error) and trial 15 (the final and presumably most well-adapted value). First, we examined this values in a mixed-design 2 (cube size) x 2 (video) ANOVA, and followed this omnibus test up with post hoc Bonferroni-corrected independent samples t-tests. From the ANOVA, we observed a significant main effect of size ($F(1,38) = 33.20$, $p<.001$) and a significant interaction between video and size ($F(1,38) = 6.06$, $p<.05$). Post hoc analyses confirmed that, although there were no differences between the groups with regard to their lifts of the small cube ($t(39) = 0.12$, $p=.91$; Figure 2C), the EV group did indeed outperform the NEV group when lifting the large cube ($t(39) = 2.57$, $p<.05$; Figure 2C). Thus, participants were, to a degree, able to learn from the mistakes of others to improve their lifting performance.



TMS experiment - Motor potentials evoked during passive observation of lifts

We followed up our behavioural experiment with a TMS study to determine the neural effects of observing the error-filled and error-free video stimuli. In this task, cortico-spinal excitability during the observation of these lifts was determined by examining the magnitude of MEPs elicited by TMS in observers who were watching lifts of identically-weighted large and small cubes. In the error video (EV) condition, participants watched actors overestimating the weight of the large cube and underestimating the weight of the small cube; in the no error video (NEV) condition, participants observed actors lifting the cubes with identical forces. For our initial exploratory analysis, we examined the MEPs from four hand and arm muscles in a MANOVA for the condition most comparable to the prior object lifting observation studies - comparing the NEV lifts of the large and small cubes (Alaerts et al., 2009). In this omnibus test we noted significantly higher MEPs when participants observed lifts of the large cube as compared to when they watched lifts of the small cube ($F(1,17) = 6.07$, $p<.05$). Of the four muscles recorded from, inspection of the data showed that this size-based cortico-spinal modulation was driven largely by the adductor pollicis brevis (ADPB), shown in Figure 3 (details of electrode positioning and MEP magnitudes for all muscles' can be found in the Methods and Supplementary Figure 1, respectively). To examine the modulatory effects in the ADPB alone, the large and small cube MEP magnitudes in the various conditions were examined in a 2 (cube size) × 2 (video type) ANOVA with repeated measures. As with the multivariate test, there were no main effects of video condition ($F(1,17)$ $= 0.4$, $p=.53$) or cube size ($F(1,17) = 1.54$, $p=.23$). There was, however, an indication of an interaction between video condition and cube size that did not reach statistical significance (F(1,17) = 3.47, p=.08), which we examined with Bonferroni corrected paired-sample post hoc t-tests. These analyses confirmed that, when observing lifts that did not contain errors (NEV condition), participants' MEPs were significantly larger when observing the large cube than when observing the small cube (t(17) = 3.02, p<.05, Figure 3A). However, this 'size effect' was completely eradicated when watching errors (t(17)=0.69, p=.50; Figure 3B), and there was no hint of any size-based modulation of cortico-spinal activity for watching overestimations of the large cube as compared to underestimations of the small cube. As there were no differences in the background EMG between any of the conditions (all p values > .17, see Supplementary Figure 2), these effects are likely to have been caused by differences in cortio-spinal excitability induced by the various observation conditions.



General discussion

In the current work, we examined the effect that the observation of object lifting errors has on individuals' lifting performance and cortico-spinal excitability. Separate groups of participants watched videos of actors lifting the identically-weighted large and small wooden cubes that typically elicit size-weight illusions and fingertip force errors. One (the Error Video - EV) showed naïve actors making typical overestimation- and underestimation-style errors made when lifting these cubes, and the other (the No Error Video - NEV) showed the same naïve actors lifting the cubes with very similar, well-adapted forces. Participants who observed both of the cubes being lifted with the same force as one another (i.e., without errors – NEV) tended to lift the cubes with incorrect fingertip forces (i.e., excessive force for the large cube and less force for the small cube). Participants who observed the error-filled lifts (EV), however, were far less prone to overestimating the weight of the large cube than their counterparts, suggesting they were learning through observing these errors. We also examined cortico-spinal excitability when another group of participants who passively observed error-filled and error-free lifts. When participants observed the cubes being lifted with the same force as one another (i.e., without errors), a robust size-based cortico-spinal modulation was evident: larger MEPs were elicited when participants observed lifts of the large cube than when they observed lifts of the smaller cube. When participants watched these same cubes being lifted with fingertip force errors, however, this size-based cortico-spinal modulation was completely eradicated; approximately equal magnitude MEPs were elicited whether participants watched errors based on overestimations of the large cube or errors based on underestimations of the small cube. In isolation, the behavioural and cortico-spinal findings make substantial contributions to their respective literatures, and together may point toward a low-level mechanism linking observational learning to fingertip force adaptation.

In our behavioural experiment, participants who watched the error video made significantly fewer overestimation-style errors than participants who watched the no-error video. In short, the current study is a striking demonstration of the powerful effect that information derived through visual observation can have on a task that is heavily dependent on haptic feedback (Johansson and Flanagan, 2009). Not only do these findings highlight the sensitivity of the human sensorimotor system to subtle visual cues (Buckingham et al., 2011), they also highlight the stark differences between the sensorimotor system and conscious expectations of heaviness. Neither the error nor the no-error video groups gained any conscious insight into the actual (identical) weight of the cubes from watching the videos, and their subsequent size-weight illusion was similarly unaffected. The fact that only the observers' load force rate scaling was influenced by watching others lift further suggests a low-level, non-cognitive mechanism, is underpinning these behavioural findings. These behavioural findings confirm and extend the idea that separate internal representations underpin the way we lift objects and the way we experience how heavy they feel (Chouinard et al., 2009; Flanagan and Beltzner, 2000; Flanagan et al., 2008).

It is worth taking time to discuss why those who watched the error videos outperformed their counterparts when lifting the large cube but not the small cube. We suspect that this interesting difference between overestimations and underestimations stems from the reliability of information available when watching the kinematic consequences of overestimations. Overestimation errors are characterized by rapid movements, large accelerations, and extremely short loading phase durations – kinematics that happen to be particularly visually salient. Furthermore, the load phase duration of actors' overestimation-style lifts had a far lower standard deviation than any of the other lifts which participants viewed; in other words, these lifts were more consistent. This relative saliency and consistency could allow the appearance and magnitude of an overestimation error to be readily identified and subsequently corrected. Underestimations of forces are, by contrast, defined by a mismatch between the expected and actual liftoff time (Johansson and Flanagan, 2009), which merely results in the object not moving. As an unmoving object is not a de facto cue to error, and as observers do not know when the actors expected liftoff to occur, underestimations may not have been consistently identified as errors, and consequently were not utilized to pre-adapt the lifts of the small cube. Future work could directly assess this proposition by examining fingertip forces after explicitly informing observers about the error-filled or error-free content of the videos they are observing.

In contrast to the straightforward outcomes of the behavioural experiment, our study examining cortico-spinal excitability during passive observations of lifts yielded a more complex pattern of results. We shall first examine the implications of the MEP data in the no-error video condition in the context of the lifting observation studies undertaken by Alaerts and colleagues (Alaerts et al., 2010, 2009). These authors demonstrated that observing error-free lifts of heavy-looking stimuli evokes larger motor potentials than observing lifts of light-looking stimuli. Subsequent research demonstrated that this effect appears to be driven by kinematic differences in the way that light and heavy objects are lifted, rather than differences in how heavy they look simply on the basis of their apparent static weight (Alaerts et al., 2009; Senot et al., 2011). In the current work, when comparing the EV to the NEV when object size was held constant, we noted that the EV and the NEV elicited similar MEPs for the small cube ($t(17) = 0.66$, $p=.52$). There was a trend for the EV to elicit a smaller MEP than the NEV when watching lifts of the large cube, but this comparison did not reach statistical significance ($t(17) = 1.99$, $p=.06$). In contrast, the current work appears to demonstrate that object size has a greater effect on cortico-spinal excitability than object kinematics: when participants in our experiment observed the no-error videos (NEV condition), they showed a greater level of cortico-spinal excitability watching lifts of a large cube as compared to when they watch lifts of an equally-weighted small cube even though the kinematics of these lifts were virtually identical (see Materials and Methods section). It is possible that the discrepancies between our work and the findings of Alaerts et al. (2009) may stem from differences in how the optimal hand area in primary motor cortex was defined between the studies.

This departure from prior literature may be due to the fact that participants observed actors performing lifts in the context of a situation in which object size was the only (misleading) cue to weight. Previous attempts to disentangle static and kinematic visual cues to weight have manipulated either actual object mass or a variety of different visual cues to weight (e.g., the presence or absence of a visible weight, the amount of water/sand in a bottle, or the label on an object); to our knowledge, our MEP task is the only action observation study to manipulate the visual size of the object. We suspect that this novel size-based cortico-spinal modulation stems from the reliability of volume, as inferred by visual size, as a cue to weight in our environment. This ‘size effect’ is consistent with our previous suggestions that visual size may be such a powerful cue to object weight that stimulus volume may have an automatic modulatory effect on the sensorimotor system (Buckingham and Goodale, 2010b). It remains to be seen whether other cues to weight (e.g., material) have similar low-level modulatory effects.

It is within the context of the size-based cortico-spinal modulations that we must examine the MEPs which were elicited when viewing errors. There was no difference between the magnitudes of the MEPs elicited when participants watched lifts of large and small cubes in the error video condition, suggesting that the typical cortico-spinal modulations elicited when viewing error-free lifts were eradicated. To reconcile our data with findings of past research on this topic, we suggest that a different, opposing, effect is counteracting the usual size-based modulation of cortico-spinal excitability that has been observed with no-error videos. Theoretically, this effect could have arisen from differences in the actors’ kinematics in the error videos when they lifted the large cubes as compared to when they lifted the small cubes. From the perspective of an observer, overestimations of force tend to result in easier-looking lifting kinematics (i.e., the large cube was lifted with rapid accelerations and short load phase durations). By contrast, the underestimations of force that were applied to the small cube give it the kinematics of a heavier object (see Supplementary Video 1). It has been convincingly demonstrated that observing such easy- and difficult-looking lifting kinematics can in fact modulate cortico-spinal activity such that observing lifts that look effortful will elicit larger MEPs than observing easy-looking lifts (Senot et al., 2011). It is likely that these kinematic-based modulations in cortico-spinal excitability oppose the size-based effects seen in the no error video, leading to the similar MEPs when watching error-filled lifts of large and small cubes (see also Obhi and Hogeveen, 2010).

Our MEP findings demonstrate that the cortico-spinal excitability during observation of a lift is a joint function of visual information about (1) the size of the object to be lifted, and, if available, (2) the weight of an object gleaned from observing kinematics of an individual lifting the same object. These ideas are consistent with the additive combination mechanism which has been proposed by (Loh et al., 2010), who demonstrated that an individual's pre-existing internal models of heaviness (i.e., sensorimotor memories from previous lifts) are combined with static visual cues to object mass prior to lifting – a process which evolves over a course of several hundred milliseconds. Our findings argue for the inclusion of observed kinematic information from prior lifts (evidently a reliable source of possible weight information for the sensorimotor system in this simple model). In support of this idea, (Alaerts et al., 2011) have shown that, in a blocked design, visual information about object weight from previously observed lifts drives cortico-spinal excitability before visual information about object weight in an upcoming observed lift is available. These low-level modulations may even serve a behavioural function, given the growing experimental evidence for a link between cortico-spinal excitability and motor output (Bagce et al., 2013; Klein-Flügge et al., 2013; Orban de Xivry et al., 2013). In the context of object lifting, Loh et al., (2010) have provided strong evidence that cortico-spinal excitability is related to fingertip force scaling by demonstrating that, in the same individuals, the ratio between MEPs before lifting for heavy and light objects correlates with the ratio for the force rates used to lift the same heavy and light objects. Thus, the cortico-spinal consequences of observing an error (even an error made by oneself) could automatically drive the correction of that error for future lifts, contributing to processes underpinning fingertip force adaptation and perhaps motor learning in general. If so, observation of one's own actions may a critical cue for error-based learning, possibly accounting for our recent findings that lifting without visual feedback impairs fingertip force adaptation (Buckingham and Goodale, 2010a; Buckingham et al., 2011). Thus, one role of the sensorimotor system is to gather evidence about the likely requirements of an upcoming motor plan from a variety of sources to drive successful behaviour. Although the current dataset is not able to directly speak to this question, as the TMS pulses were not time-locked to kinematic events in the video. we hope to explicitly test this prediction in future research by measuring lifting behaviour and cortico-spinal excitability at various time points throughout montages of observed lifts, when only a fraction of the kinematic error information is available (cf. Alaerts et al., 2011).

The current findings also provide an interesting new take on theories regarding the ‘action observation system’, where motor skills activate the same neural circuitry in left premotor cortex as observing the same action (Malfait et al., 2010; Mukamel et al., 2010). This link is normally considered to be an automatic mirroring relationship, implicitly preparing the observer to mimic the observed act. Our cortico-spinal and behavioural findings both point toward an automatic link between observation of an action and sensorimotor output. However, our findings clearly refute the suggestion that the sensorimotor system simply mirrors observed behaviour (Meulenbroek et al. 2007). Rather, our findings point toward a more complex relationship between the observer's prior knowledge and the dynamics of the observed task in relation to their own kinematic experiences. An observer’s perceptual expertise with the visual kinematics of biological motion combines with their prior expectations of how heavy and light objects are usually lifted to provide a context for the observed action. In the case of object lifting, when stimulus properties are observed in conjunction with incompatible lifting kinematics (e.g., a heavy-looking object being lifted with light-looking kinematics), the relationship between observation and behaviour becomes contrastive rather than integrative (Hamilton et al., 2004; Meulenbroek et al., 2007). It is feasible that, across a wide range of actions, (1) a lifetime’s worth of visual experience of one’s own kinematics and (2) an understanding of the statistics of the environment allows observed movements to be categorized as optimal or suboptimal, driving subsequent behaviour.

To sum up, this work has demonstrated that (1) observing object lifting errors improves subsequent object lifting performance when compared to observing error-free performance, and (2) this behavioural improvement is accompanied by sensorimotor modulations at the level of cortico-spinal excitability when observing these lifts. Not only do these findings shed light on the interactions that occur prior to sensorimotor prediction in the context of object lifting, but they pose larger questions about how we can best learn new motor skills. Extending the current findings to the topic of motor learning in general, one might predict that those who are learning new skills could profit more from watching others make mistakes than they would from watching experts - a conclusion which has exciting implications for the teaching of visuo-motor skills.

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<u>Figure captions</u>

Figure 1. The error and no-error videos watched by participants in both tasks (top panel), the experimental setup for the behavioural task (lower left panel and middle panel). The lower right panel shows the average loading phase durations of the actors lifting in the videos. The error video (EV) comprised a montage of lifts from the 1st trial, whereas the no-error video (NEV) comprised a montage of lifts from the 8th trial.

Table 1. Participants' expectations of heaviness before lifting and their perceptions of heaviness after lifting in the behavioural experiment, as a function of the size of the cube they were lifting (the within-subject comparison) and the video they watched (the between-subject comparison).

Figure 2. The peak load force rates used to lift the identically-weighted the large and small cubes on each trial for (A) the NEV group and (B) the EV group. These data are fit with a 4th order polynomial to better visualize the linear trends, and error bars show between-participants standard error of the means. The differences between the EV and NEV groups (C) were quantified by comparing the amount of adaptation that took place across the entire experiment (as indexed by the difference between the initial force errors on trial 1 and the final adapted forces on trial 15). Data are plotted on the positive axis for overestimations and underestimations. * indicates an alpha of .05.

Figure 3. The normalized MEP area under the curve for the motor potentials recorded from the adductor pollicis brevis (ADPB) while watching error and no-error lifts of the identically-weighted small and large cubes. Error bars show between subject standard error of the means. * indicates an alpha of .05. Error bars show normalized within-subject standard error of the means for each condition.

Supplementary Figure 1. The motor potentials evoked in each of the four recorded muscles, displayed on a common scale for comparison purposes. All significant differences between large and small cubes are displayed, with error bars showing normalized within-subject standard errors. * indicates an alpha of .05.

Supplementary Figure 2. The background EMG for each of the four recorded muscles for all conditions, displayed as a percentage of the peak MEP for a particular trial. Background EMG scores were derived from the mean of the final 50ms of the 250ms EMG recording, synchronised to the onset of the TMS pulse. Error bars show standard error of the mean. No significant differences between the level of background EMG in any of the conditions were observed.

Supplementary Table 1. Pearson's correlations between initial expectations of heaviness and sensorimotor prediction, as well as between perceived heaviness and sensorimotor prediction for the EV and NEV groups in the behavioural experiment. Following corrections for multiple comparisons, none of these correlations reached the level of statistically significance.

Supplementary Video 1. The video that participants observed during the Error Video (EV) condition. Actors in the video are making the characteristic overestimation and underestimation style errors when lifting the identically-weighted large and small cubes.

Supplementary Video 2. The video that participants observed during the No Error Video (NEV) condition. Actors in the video are applying approximately identical forces to the identically-weighted large and small cubes.