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Systematic underestimation of human hand weight

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According to Newton's laws, the weight of a body part is equal to its mass times gravitational acceleration. Our experience of body part weight, however, is constructed by the central nervous system. No sensory receptors directly specify the weight of body parts, and the factors influencing perceived weight remain unknown. The perceived weight of held objects has been linked to sensations of the magnitude of central motor commands sent to the muscles, what Helmholtz called the effort of will and has subsequently been called the sense of effort1. The link between the sense of effort and the perceived weight of objects is shown by studies demonstrating that held weights feel heavier when muscles are weakened by fatigue¹, anaesthesia2, and following brain damage³. Similar drive to muscles is required to counteract the force of gravity on the limbs themselves, though few studies have investigated the perceived weight of body parts4. Stroke patients with hemiplegia frequently comment that their limbs feel heavy5, an effect linked to fatigue in the affected limb⁶. Similarly, amputees commonly complain of the weight of prosthetic limbs7, despite these typically weighing less than actual limbs. Here we report that healthy adult humans systematically underestimate hand weight. We used a psychophysical matching task to measure the experience of hand weight, which was underestimated on average by 49.4%. We further found that experimental induction of hand fatigue causes a systematic increase in perceived hand weight. Our results demonstrate that humans fail to experience the full weight of

Participants first let their left hand hang freely, with their forearm

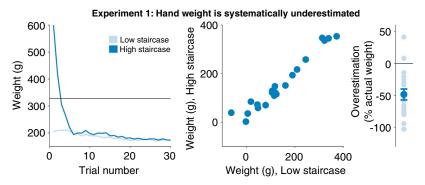
their body.

supported. The hand was then supported, and weights were suspended from a wristband. Participants judged whether each weight was heavier or lighter than perceived hand weight (see Supplemental experimental procedures in Supplemental information for details). A psychophysical staircase procedure was used to estimate perceived hand weight (results in Figure 1). There was clear convergence between the high and low weight staircases, which were strongly correlated, *r*(18) = 0.975, p < 0.0001, showing high reliability of hand weight estimates. Most critically, there was substantial underestimation of hand weight, on average by 49.4% of actual weight, t(19) = -5.75, p < 0.0001, d = 1.285.

In stroke patients, experiences of limb heaviness are linked to higher levels of fatigue⁶. In Experiment 2,

we therefore investigated whether experimental induction of hand fatigue would increase the perception of hand weight. Perceived hand weight was measured before and after 10 minutes of fatigue-inducing exercise. As in Experiment 1, there was clear underestimation of hand weight both at pre-test (M: -43.9%), t(19) = -5.57, p < 0.0001, d = 1.245, and at post-test (M: -28.8%), t(19) = -3.15, p < 0.01, d = 0.704. Critically, the magnitude of underestimation was reduced after fatigue-inducing exercise, t(19) = 3.10, p < 0.01, $d_{z} = 0.693$. Across participants, the increase in perceived hand weight after exercise was correlated with the increase in self-reported fatigue, r(18) = 0.464, p < 0.05.

The paradigm used in Experiments 1 and 2 involved comparing hand weight experienced at the start of each block to another weight



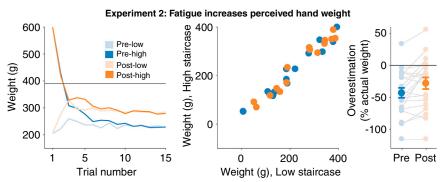


Figure 1. Experimental results.

Top row: Results from Experiment 1. Grand average psychophysical staircases starting from low (200 g) and high (600 g) weight initial estimates quickly converged on a common estimate of perceived hand weight (top left). The black horizontal line indicates the mean weight of the actual hand. Across participants, estimates from the two staircases were strongly correlated, indicating high reliability (top centre). Hand weight was systematically underestimated, on average by 49.4% of actual weight (top right). Bottom row: Results from Experiment 2. The low and high staircases again converged on common estimates of hand weight, both before and after fatigue-inducing exercise (bottom left). Estimates of hand weight were strongly correlated between the two staircases (bottom centre). There was again clear underestimation of hand weight at both time points. The magnitude of underestimation, however, was reduced following exercise (bottom right).



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presented on each trial. While periodic 'top up' presentation of hand weight was presented, there were nevertheless differential memory demands for hand and object weight. We thus conducted a third experiment in which five seconds of exposure to both hand weight and object weight were presented on each trial, with the order counterbalanced. Again, clear underestimation of hand weight was observed (*M*: -33.4%), t(19) = -4.51, p < 0.001, d = 1.009 (Figure S1 in Supplemental information).

The everyday experience of our body's weight as a result of gravity provides an interesting contrast to experiences of weightlessness in outer space. Astronauts themselves have been struck by the reemergence of the experience of body weight when they return to Earth. Our results show that the ordinary experience of body weight here on Earth - weightedness - can be precisely measured, but also that it dramatically underestimates the actual weight of the hand. People experience their hand as weighing much less than it actually weighs. This finding mirrors results from several other domains showing that healthy humans systematically misrepresent the physical characteristics of their own bodies8.

Experiences of body weight are qualitatively different than experiences of the weight of held objects. In daily life, the weight of our arms is not salient, though if you have tried lifting someone else's arm it is strikingly heavy. This is consistent with recent results from a leg amputee who showed a large reduction in the experienced weight of his prosthetic leg when it became more strongly embodied through the delivery of sensory feedback by intra-neural stimulation9. Conversely, the experienced heaviness of the affected limb in stroke patients with hemiparesis may be related to alterations in the experience of embodiment, such as somatoparaphrenia, supernumerary phantom limbs, and misoplegia. This suggests that embodiment is linked to an active suppression of the experienced weight of the embodied limb. Suppression of the experienced weight of body parts may thus be

intimately linked to the association of the body to the self. This may also explain why sensorimotor incongruence, which disrupts the self-attribution of seen body parts can produce experiences of limb heaviness¹⁰.

Underestimation of hand weight may have adaptive consequences for perception of object weight. Suppose that we hold an object in each hand, one weighing 500 g and the other weighing 400 g, a ratio of 1.25. Assuming that each arm weighs 3 kg, the total weight supported against gravity is 3.5 and 3.4 kg for the two arms, a ratio of just 1.03. According to Weber's law the ability to discriminate weights depends on their ratio, which is dramatically reduced by the inclusion of arm weight. Perceptually subtracting arm weight from this comparison can thus greatly enhance discrimination ability, functioning like the 'tare' button on a scale which resets the current reading

We believe that weight underestimation is a mechanism for the nervous system to modulate motivation for action and to signal the need for rest. Idioms like "my eyelids are getting heavy" suggest an association between altered experience of body part weight with fatigue and an associated motivation to rest. By making actions feel effortless, weight underestimation may encourage activity. Conversely, the reappearance of body weight with fatigue may produce the opposite effect.

SUPPLEMENTAL INFORMATION

Supplemental information includes description of experimental procedures, additional results, and one figure and can be found with this article online at https://doi. org/10.1016/j.cub.2023.05.041.

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AUTHOR CONTRIBUTIONS

E.R.F. and M.R.L. conceived the study and designed the experiments. All authors constructed equipment. J.J. and D.C. collected the data. All authors analysed the data. E.R.F. and M.R.L. wrote the paper. All authors approved the final version of the paper.

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