















between perception and action. This latter result confirms that heaviness perception relies on prior knowledge of mass-volume relationship, and that anticipatory grip control can be performed independently of the visual inputs.

## Size-weight illusion

Our experiments differed in significant ways from earlier studies of the size-weight illusion (Kawai et al., 2007; Stevens and Rubin, 1970). They were performed in a dark room, with phosphorescent objects, providing the subjects with visual stimuli by and large reduced to retinal size. The carriage added its mass to that of the interchangeable objects, but was not visible. The only effect was to modify the apparent density of the stimuli. We employed a single-stimulus method, which eliminates the need to rely on references. Despite these differences, we observed the typical features of the SWI, namely that heaviness rating increases with mass and decreases with volume.

## Inertia perception and size-inertia illusion

Earlier experiments on inertia perception and on the size-inertia illusion were performed in parabolic flights (Kingma et al., 1999; Ross, 2008) as well as in laboratories on Earth (Bergmann Tiest and Kappers, 2010; Crawford and Kama, 1961; Plaisier and Smeets, 2012). A novel experimental methodology was used in our experiments. Most notably, our study differed from the experiments conducted by Bergmann Tiest and Kappers (2010) and Plaisier and Smeets (2012) in the manner an object’s inertia was made available to the participants. Unlike previous studies, where stimulus objects were suspended by a pair of wires, a non-contact air bearing slide was used. This ensured much greater accuracy in the delivery of the stimuli. For comparison, consider that a suspended object gives a ratio of potential energy to kinetic energy of about 0.9. Taking a peak velocity of 1.0 m/s, a travel distance of 0.5 m, and a wire length of 2.3 m, as in (Plaisier and Smeets, 2012), a sliding object gives a ratio of about 0.02 for a tilt angle error of  $0.1^\circ$ , *ceteris paribus*. Moreover, the air bearing slide precluded any object twisting that could introduce spurious inertial cues. It also allowed for precision grip force measurement and guaranteed a reliable decomposition of the mechanical interaction forces into load and grip components, that is the working and the non-working forces.

We could nevertheless confirm the main observation that inertia discrimination is poorer than weight discrimination by a factor of about two (Bergmann Tiest and Kappers, 2010; Ross and Reschke, 1982), as quantified by the Weber fraction, and that a size-inertia illusion of similar magnitude to the size-weight illusion was observed. In contrast, we did not observe that object mass perceived through inertia was about half as large as when perceived through weight. This difference can be explained by noting that our measure of heaviness sensation coincides with a maximum likelihood estimator of the probability of deeming an object ‘heavy’, and that our psychophysical method was self-consistent for each experimental condition, which was not the case in previous studies.

## Perceptual invariance to mechanical work

As noted in Materials and Methods, the mechanical work required to move a given object differs by three orders of magnitudes between the inertia and the gravity conditions. Nevertheless, a similar effect of visual size on heaviness rating was observed between the two conditions. This result agrees with the observation of Kawai et al. (2007) that the SWI is observed for a very wide range of masses, from 30 g to 6 400 g, which lends support to the notion that a possible neural mechanism supporting the perception of mass is mediated by a normalization process. In this mechanism, the responses of neurons are scaled by a factor resulting from summed activity of a pool of neurons. This type of neural processing is thought to be common in multiple sensory systems (Carandini and Heeger, 2011).

It is also interesting to consider the size-mass illusions in a statistical perspective to better understand the observed perceptual invariance. The reliability of haptic mass cue in the inertia condition is half as large as in the gravity condition (Bergmann Tiest and Kappers, 2010; Ross and Reschke, 1982). However, in our study, the reliability of visual mass cue, given by the object’s size and apparent density, was not changed between the two experimental conditions, the stimulus objects being the same. From a simple linear cue combination model perspective (Landy et al., 2011), where an observer weighs each cue according to its reliability, one would



predict that size should have a larger effect on heaviness rating in the inertia condition. This suggests that another statistical parameter should be considered to understand the observed compensatory effect.

## Minimal description of anticipatory motor behavior

We considered the same parameters as in several studies about anticipatory motor control in the context of the SWI (Buckingham and Goodale, 2010; Flanagan and Beltzner, 2000; Grandy and Westwood, 2006). We showed that the load phase duration and the peak of load force rate are not independent, and both depend on  $\alpha$ , the overall slope of the monotonically increasing load force trajectory during preparatory loading. We further observed that the peak of the grip force rate was proportional to the peak of the load force rate. These factors suggest that a single parameter is sufficient to account for the anticipatory behavior of a simple grasp.

For a more accurate account of the grip behavior, one could consider cubic approximations for  $F_L(t)$  during the load phase, two being the smallest degree of representation for  $\dot{F}_L(t)$  in the calculation of a peak for  $\dot{F}_L(t)$ . We did perform such regressions on the entire collection of fingertip force traces, as shown in Figure 3F-H. Interestingly, we observed that the second- and third-order regression parameters were linearly related to the first-order parameter, which confirms our hypothesis that anticipatory gripping behavior can be well modeled by a single parameter, the slope of the linear regression,  $\alpha$ . The data shown in Figure 3F were fitted with a cubic regression of the form,  $a_0 + a_1x + a_2x^2 + a_3x^3$ . We imposed the first-order regression parameter,  $a_1$ , to be positive in order to avoid ambiguous optimization. In the gravity condition, linear regressions between  $a_2$  and  $a_1$ , and between  $a_3$ , and  $a_2$ , gave  $a_2 = 0.4 a_1 - 2.2$  ( $r^2 = 0.5$ ;  $p = 0.00$ ) and  $a_3 = -0.5 a_2 + 0.3$  ( $r^2 = 0.9$ ;  $p = 0.00$ ). A similar analysis can be performed for the results of the inertia condition.

## Fingertip forces while lifting vs. sliding

The anticipatory behavior of grip control exhibited similar dependencies in the two experimental conditions, but some differences can be pointed out. To clarify these differences, we compared the values of the slope,  $\alpha$ , between the two conditions (see Figure 4C). The values of  $\alpha$  was calculated by averaging the measured values for each stimulus object, over all participants. The magnitude of  $\alpha$  in the gravity condition was four times larger than in the inertia condition. This result confirms that grip strength order of magnitude was significantly different between the two conditions, reflecting the difference in the mechanical conditions. We further note that the range of  $\alpha$  is about twice larger in the gravity condition than in the inertia condition. Moreover, for each stimulus object, we computed the ratio of the standard deviation of  $\alpha$  in the inertia condition to the standard deviation of  $\alpha$  in the gravity condition, and obtained a value of  $2.2 \pm 0.5$ . Interestingly, this ratio corresponds to the ratio of the Weber fractions in the two conditions, which suggests the origin of the ratio between an inertia percept and a weight percept (Bergmann Tiest and Kappers, 2010; Ross and Reschke, 1982).

There was little evidence that the motor behavior of the participant had a predictive character from one trial to the next. However, one can wonder whether there was any prediction at a more global level, between consecutive experimental conditions. To this end, the slope,  $\alpha$ , was computed for two subgroups of participants, those who started with the gravity condition and those who started with the inertia condition (see Figure 4D). Interestingly, the participants who started with the inertia condition tended to use a stronger grip in both conditions. As the two experimental conditions were performed for all subjects over two consecutive days, these results suggest that a longer term memory was stored by the sensorimotor system. A further study would be necessary to better understand this phenomenon.

The apparatus made it possible for participants to apply a non-working force component other than a grip force. We measured this component for a representative participant in the gravity condition, and plotted its temporal trajectory in the load phase, as represented in Figure 3B. This force was small compared to the grip force, which confirmed that the grip force was the main contributor to the non-working forces. Moreover, the values measured for the grip force parameters, load phase duration and peaks of grip and load force rates, are typical of the values reported in the literature (Buckingham and Goodale, 2010; Flanagan and Beltzner, 2000; Grandy and Westwood, 2006), confirming that the sliding mechanism did not modify substantially the behavior of the participants.

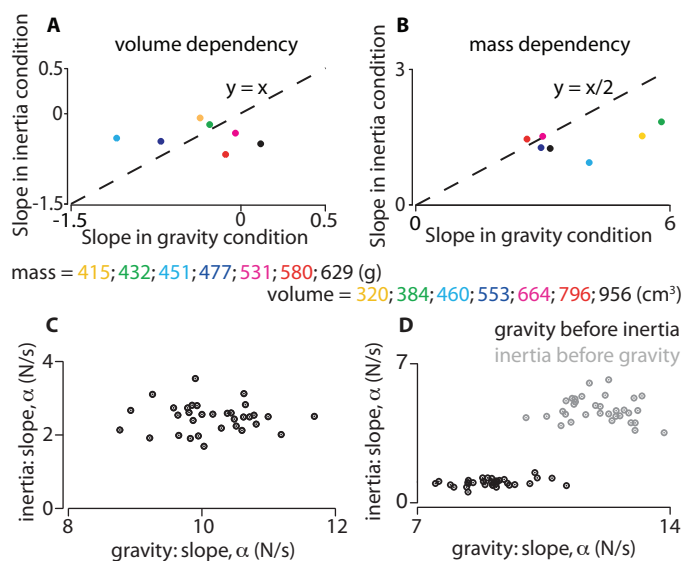


Figure 4: Comparison of results between the gravity condition and the inertia condition. For each panel, the horizontal and vertical axes correspond to the values measured in the gravity condition and in the inertia condition respectively. Panels A and B show the values of the slope of the linear regression performed on each curve individually of Figure 2A-D. Panel A corresponds to the analysis of the dependency of heaviness rating on size (Fig 2A and C), and Panel B corresponds to the analysis of the dependency of heaviness rating on mass (Fig 2B and D). The dashed lines in Panels A and B represent respectively the equations,  $y = x$ , and  $y = x/2$ . Each color indicates a given parameter reported at the bottom of the corresponding panels. In panel C, black dots represent the slope  $\alpha$  for each mass-volume stimulus pair, averaged over all participants. In panel D, the same analysis as in panel C was performed, but for two subgroups of participants: those who started with the gravity condition and those who started with the inertia condition. The black dots correspond to the first group and the grey dots to the second.

## Dissociation of perception and action

Our findings confirm and generalize the hypothesis that there is a fundamental dissociation between heaviness sensation and anticipatory grip behavior. Importantly, we generalized this hypothesis to the effect of inertia cues, using a wide range of de-correlated stimulus masses and volumes. In both experimental conditions, whereas heaviness rating was monotonously related to stimulus mass and volume, anticipatory control of fingertip forces was independent of both mass and volume. The data nevertheless revealed several differences with previous observations in similar studies (Buckingham and Goodale, 2010; Flanagan and Beltzner, 2000; Grandy and Westwood, 2006).

In these studies, it was observed that while overall fingertip forces were not affected by size cues, such was not the case during the initial lifts, suggesting a fast adaptation mechanism in the motor system to the true object weight. We analyzed whether the same adaptation phenomenon could be observed. In the gravity condition, for each stimulus and participant, the slope,  $\alpha$ , of the linear regression corresponding to the first and the last trials was computed. Figure 5A-D show the average and the standard-deviation of the results over all participants. Despite a small trend at the global level, there is no significant change in the dependencies of the fingertip forces between the first and the last trials, suggesting that the protocol was effective at preventing the participants from predicting the true stimulus weight after the first lifts, and that there was no predictive behavior, even in the first lifts.

Johansson and Westling (1988) showed that the weight of lifted objects can affect the grip force adjustment during subsequent lifts. This observation was confirmed recently by Loh et al. (2010), who showed that a lifted weight can affect the corticospinal excitability. In these studies, however, a maximum of three different stimuli were used. Here, we tested whether such an effect was observed with thirty-three stimuli. We also investigated the assumed predominance of the mechanical cues compared to the visual cues. To this end, the correlation between  $\alpha$  and the stimulus weight of the preceding lift was compared to the correlation of  $\alpha$  with the stimulus volume of the current lift, as shown in Figure 5E. There was no significant difference between

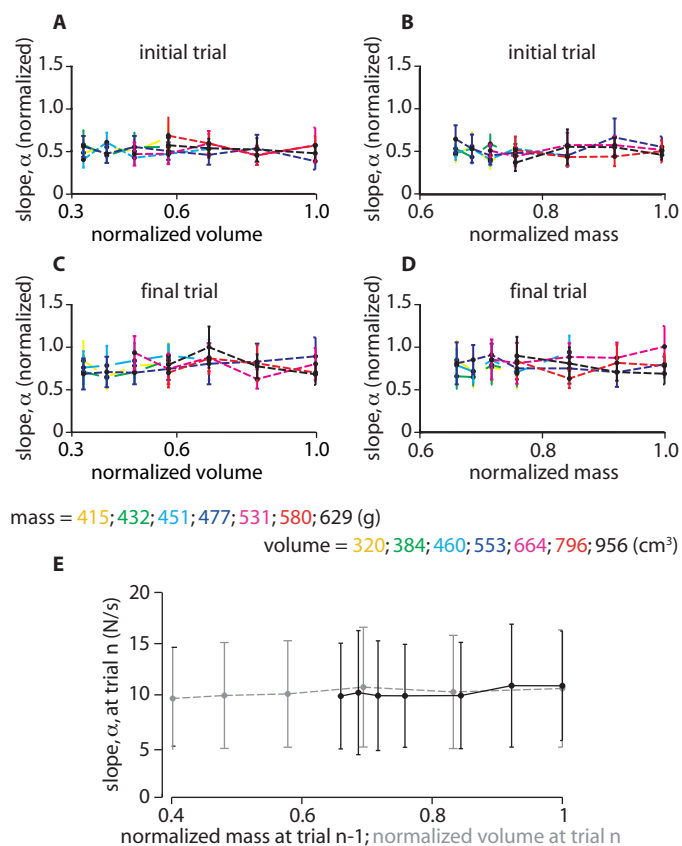


Figure 5: Adaptation of motor prediction over trials in the gravity condition. Panels A and B show the dependency of the normalized slope,  $\alpha$ , on normalized size and mass for the first trial the given stimulus was presented to participants. Panels C and D report the results for the same parameters for the last trial the given stimulus was presented to participants. The black dots indicate the average measurement, the vertical lines indicate the standard deviation of the measurement, and the dashed lines relate the data points with a fixed parameter. Each color indicates a given parameter reported at the bottom of the corresponding panels. Panel E shows the comparison between the effect of preceding lifted weight and current object volume on motor prediction in the gravity condition. The black dots correspond to the effect of previous lifted weight, and the grey dots correspond to the effect of current object volume. The dashed lines relate the data points of corresponding analysis. Stimulus mass and volume were normalized, but not the slope of the linear regression of the load force trajectory,  $\alpha$ .

the two correlations, and the grip force prediction was similarly impacted by the previous lifted weight and by the current size. A quantitative analysis using a linear regression confirmed this observation. This result confirms the necessity of using large sets of mass-size pairs in precision grip control studies, effectively reducing the effect of “sensorimotor memory” during anticipatory motor behavior in an effort to study of each lift as an independent event.

Using functional magnetic resonance imaging, Chouinard et al. (2009) suggested that anticipatory motor control, presumably based on object weight and size, was processed by sensory and primary motor areas, while heaviness sensation, presumably based on apparent density, was processed by the ventral motor area. Accounting for the results of Chouinard et al. (2005) and Loh et al. (2010) confirming the role of the primary motor area in storing weight information, the small number of stimuli employed in the experimental paradigm of Chouinard et al. (2009) could not disentangle the role of visual size from that of motor memory. It follows that our paradigm, which minimizes the role of motor memory, could be advantageously adapted to the investigation of the neural pathways involved in size-mass illusions. Additionally, it would be relevant to investigate the dissociation of perception and action in the temporal domain, using for instance electro- or magnetoencephalography, to better understand the difference in timescale of adaptation between perception and action.

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## Disclosures

The authors declare no conflict of interest, financial or otherwise.

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