

Perception-Action Dissociation Generalizes to the Size-Inertia Illusion

Running title: Perception-Action Dissociation in Size-Mass Illusions

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Abstract

Two objects of similar visual aspects and of equal mass, but of different sizes, generally do not elicit the same percept of heaviness in humans. The larger object is consistently felt to be lighter than the smaller, an effect known as the 'size-weight illusion'. We investigated whether the same effect can be observed if the mass of an object is available to participants through inertial rather than gravitational cues. We compared the responses of ten participants in two experimental conditions, where they manipulated objects supported by a frictionless, air bearing slide that could be oriented vertically or horizontally. We also analyzed the participants' anticipatory motor behavior by measuring the grip force prior to motion onset. We found that the perceptual illusory effect was qualitatively the same in the two conditions and observed that both visual size and haptic mass had a negligible effect on the anticipatory gripping control of the participants in the gravitational and inertial conditions, despite the enormous differences in the mechanics of the two conditions.

Key words: mass perception; motor programming; precision grip; sensorimotor integration; human

Introduction

When asked to compare the weight of two visually similar objects of the same mass but of different sizes, most people report that the larger object is lighter than the smaller. This remarkably robust visuo-haptic effect is known as the size-weight illusion (Charpentier, 1891; Ellis and Lederman, 1998; Murray et al., 1999). It has been studied quantitatively by presenting collections of stimulus objects with de-correlated masses and sizes to groups of participants (Cross and Rotkin, 1975; Kawai et al., 2007; Masin and Crestoni, 1988; Stevens and Rubin, 1970). As a whole, these studies suggest that heaviness percept can be described by a function of both mass and volume. Recently, it was found that a similar illusion is observed for inertia (Plaisier and Smeets, 2012), a 'size-inertia illusion' of magnitude similar to that of the size-weight illusion. In this study, four objects were suspended from a long wire, and participants were asked to push an object and rate the perceived heaviness. This finding suggests that the size-inertia illusion and the size-weight illusion are instances of a larger family of illusions, the 'size-mass' illusions, since mass is an invariant attribute of a solid object that does not depend on the constraints that govern its movements.

Analyses of the size-weight illusion frequently suggest the occurrence of a mismatch between the effort applied to lift an object, predicted on the basis of visual appearance, and the actual mechanical sensory outcome experienced while lifting the object. It is the so-called sensory mismatch hypothesis (Davis and Roberts, 1976; Granit, 1972; Ross, 1969). This hypothesis was recently challenged, with the observation that grip forces rapidly adapt to the true object weight while perception persists to be biased by size through many trials (Buckingham and Goodale, 2010; Flanagan and Beltzner, 2000; Grandy and Westwood, 2006). These authors propose that a dissociation between perception and action takes place in the brain, analogously to the dissociation that takes place between the dorsal and ventral visual pathways (Goodale and Milner, 1992; Milner and Goodale, 2006). Under this framework, the results of the sensorimotor size-weight studies suggests the existence of two neural pathways, one that processes size cues influencing perceptual reports, and one that is responsible for grip

control. More recently, several authors expressed reservations regarding the applicability of the visual system model to grip control (Schenk and *Journal of Neurophysiology* 111(7):3409-3416 2006), highlighting that in Flanagan and Beltzner (2000)'s study, visual size cues are shown to directly affect motor programming in the first lifts, without conscious inference.

The dissociation between perception and action observed in the size-weight illusion studies can also be thought to reflect a dominance of sensorimotor memory over on-line visual analysis. During any given lifting task, the size information that could contribute to the anticipatory preparation of a grip would be dominated by mechanical information memorized from previous lift experiences. If a large set of de-correlated stimuli are presented to observers over a short time period, would the fingertip forces then vary according to object size? This hypothesis can be tested experimentally. In previous size-weight studies investigating perception-action dissociation, a maximum of only three different objects were used. If the set was made sufficiently large, the memory of object weight becomes less reliable, and one would predict that fingertip forces would adjust to stimulus size, since no other information is available.

The size-inertia illusion is an intriguing counterpart to the size-weight illusion in the sense that the two elicit comparable perceptual outcomes, as shown by Plaisier and Smeets (2012), but in considerably different mechanical conditions. The fingertip forces required to displace a mass in weightlessness are several orders of magnitude smaller than the ones required to lift the same mass under normal gravity. How would fingertip forces adjust to mass and volume in the size-inertia illusion? It could be predicted that these forces would scale with object size since inertial cues are too weak to induce significant sensorimotor memory. Although some features of motor behavior, such as the peak velocity, were measured in the context of the size-inertia illusion (Kingma et al., 1999; Plaisier and Smeets, 2012), the anticipatory motor behavior was not investigated in this context. Additionally, these previous studies did not involve more than four stimulus objects.

In order to test the motor dissociation hypothesis, we conducted size-weight and size-inertia experiments with a large set of stimuli having de-correlated weights and sizes in wide ranges of values. We constructed an experimental station that permitted observers to experience these stimuli in rapid succession, both with and without the effect of gravity. This was accomplished through the use of a frictionless motion guidance technique achieved by a non-contact air bearing. The set-up was further configured so that the same precision grip could be employed in all conditions and we employed a single-stimulus psychophysical testing method which enabled the observers to respond to a large number of randomized stimuli in a short period of time.

Materials and Methods

Experimental Station

An air bearing slide (Model RAB1; Nelson Air Corp.; Milford, NH) was comprised of a 40 cm rail guiding a free-moving carriage with negligible friction. The slide could be positioned horizontally on a sturdy table, Figure 1A, creating an 'inertia condition', or vertically, Figure 1B, creating a 'gravity condition'. These two experimental conditions produced radically different mechanical situations. The mechanical work required to move an object in the gravity condition (500 mJ of potential energy, 500 g mass and 10 cm height) was three orders of magnitude larger than in the inertia condition (0.6 mJ of kinetic energy for an extremal speed of 5 cm/s). An L-shape bracket connected the handle to the stimulus object, see Figure 1A–C. A pinch gripping interface was attached to the long end of the bracket such that the same grip was employed in the inertia and in the gravity condition, see Figure 1C. The mass of the moving parts was 325 g. Two push-buttons were positioned on either side of the station to let the participant record their judgements. A contact switch reported the initial and final times of the stimulus motion. The interaction forces on each plate of the grip handle were measured by two six-axis force-torque sensors (Nano F/T, ATI Industrial Automation; Apex, NC).

Stimuli

The thirty-three stimuli were thin-walled, hollow, wooden cylindrical objects filled with a variable mixture of foam and lead beads. The aspect ratio of the cylinders were the same as in the study of Stevens and Rubin (1970) (height ÷ circumference = 1.8). There were seven different volumes and seven different masses, see Table 1, where the masses represent the total mass displaced by the participants. The objects were sprayed with a phosphorescent paint so that they could glow in the dark, as shown in Figure 1D. The experiment was

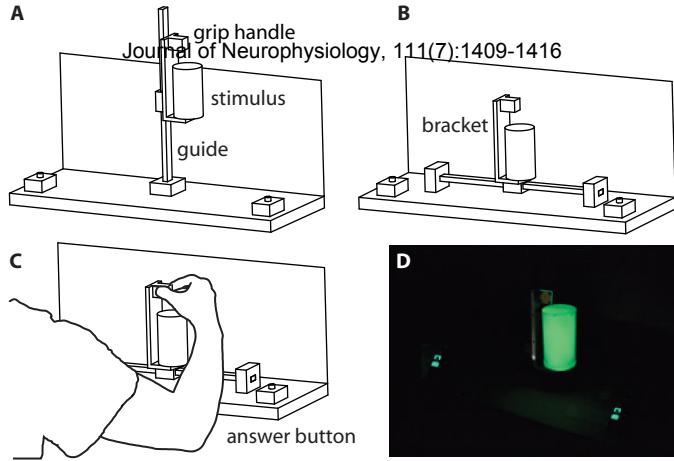


Figure 1: Experimental station. A) L-Shaped bracket vertically guided without friction by an air bearing system. Participants reported their judgements via two push buttons. B) Setup configured for the inertial cue condition. C) A grip handle enabled participants to lift the stimuli with a standardized pinch grip in the two condition. D) The viewing conditions were such that participants could not see the guiding mechanism but could see the stimulus object, the grip handle and the answer buttons.

performed in a darkened room to eliminate contextual information, yet the participants could see clearly the stimuli, the grip handle, and the answers buttons.

Psychophysical methods

Ten right-handed adults participated to the experiment (one male, nine females, ages ranging from 19 and 38, with a mean of 24). Participants were healthy with normal vision, or corrected-to-normal vision. They were naive to the experimental hypotheses, and had not taken part in any previous similar studies. The testing procedures were approved by the “Comité de protection des personnes Ile-de-France II” permit 2011-06-16 (IRB registration 1072), and participants gave their written informed consent prior to testing. The participants were instructed to grip the handle between their index and thumb fingers when prompted by a light indicator. All participants performed two tasks, corresponding to the two configurations of the slide. Half of participants began with the horizontal condition and half with the vertical condition.

In the vertical configuration, the task was similar to that employed in similar studies (Buckingham and Goodale, 2010; Flanagan and Beltzner, 2000; Grandy and Westwood, 2006). Importantly, participants were instructed to lift the object at constant velocity. In the horizontal configuration, it was specified to the participants that they should not move the stimulus at constant velocity and employ a spontaneous sensorimotor behavior. To the end, they moved the object back and forth guided by two phosphorescent stripes indicating the ends of its travel and then returned it to its initial position. After each trial, the participants reported whether the object felt either ‘heavy’ or ‘light’. This method was inspired by that developed by Morgan et al. (2000), who showed that it gives discrimination thresholds equivalent to those of the standard method of constant stimuli.

For each experimental configuration (vertical or horizontal), 170 trials were performed per participant. Each stimulus, characterized by its mass and volume, was presented on average five times per participant. For each configuration, the experiment was divided into 10 sessions. In each session, 17 different stimuli were randomly selected among the 33 available stimuli and presented to the participants in a randomized order drawn from a uniform distribution. Before each session of both experimental conditions, the stimuli having the lowest and the largest mass, but of median volume, were presented to the participants, who were informed that these were the lightest and heaviest stimuli. This procedure was intended to clarify for participants the answers ‘heavy’ and ‘light’.

Data analysis

Journal of Neurophysiology, 111(7):1409-1416

Heaviness ratings. When exposed to a stimulus of mass, m , and volume, v , the trial heaviness rating, h_i , was a quantity taking a value of 1 when the participant response was ‘heavy’ and of 0 when the response was ‘light’ for a given trial, i . Data from all participants were collected into a single dataset, where participant specificity was not taken into account. The population heaviness rating, \bar{h} , was defined to be the sample mean, $\bar{h} = 1/N \sum_{i=1}^n h_i$, of the ratings h_1, h_2, \dots, h_N , with N the number of times a stimulus object of mass m and volume v was presented.

The method is justified by the fact that the sample mean of the ratings coincides with the maximum likelihood estimator, \hat{p} , of the probability, p , of an ideal observer to answer ‘heavy’ when exposed to a stimulus of a given mass, m , and volume, v , in a given condition (an ideal observer is sensitive only to these variables). The trial heaviness ratings, h_1, h_2, \dots, h_N , reported by the ideal observer can be viewed as independent observations drawn from a Bernoulli distribution, which is characterized by the probability mass function, $f(h|p) = p^h(1-p)^{1-h}$. It is a standard result that the maximum likelihood estimates, \hat{p} , coincides with the sample mean as can be verified by maximizing the log-likelihood function, $\log \mathcal{L}(p|h_1, h_2, \dots, h_N) = 1/N \sum_{i=1}^N \log f(h_i|p)$, with respect to the probability p .

The Weber fraction for mass discrimination was measured from the population response. The relationship of heaviness ratings to mass, for the median volume (dark blue curve in Figure 2B and D), was fitted with a sigmoid function, $1/2(1+\text{erf}(x-\mu)/(\sigma\sqrt{2}))$, where μ and $\sigma\sqrt{2}$ are constants that represent the point of subjective equality and the just noticeable difference. The Weber fraction was defined to be the ratio, $2\sigma\sqrt{2}/(\mu + \sigma\sqrt{2})$, following Ross and Brodie (1987).

Grip force. The signals from the force transducers were sampled at a frequency of 1000 Hz. Following standard definitions, the ‘grip force’ was determined by the magnitude of the components of the two interaction forces normal to the two handle surfaces and the ‘load force’ was defined by the magnitude of the tangential force components. The straight line motion of stimulus objects, imposed by the slide, made unambiguous the decomposition of grasping forces into load (working forces) and grip (non working forces) components, appealing directly to the principle of conservation of mechanical energy. The temporal rate-of-change of these forces were calculated by smoothing the signal with a fourth-order, zero-phase lag, low-pass Butterworth filter with a cutoff frequency of 14 Hz, and then differentiating it using a 5-point central difference equation. Referring to Figure 3A, the load phase duration, τ , was defined to be the time interval starting when the load force and the load force rates both last exceeded zero before liftoff and ending at the instant of liftoff. In other words, the load force and load force rates were both strictly positive during the load phase. The instant of liftoff was given by the contact switch. The peaks of the load and grip force rates, p_L and p_G , occurred during this time interval. A peak was determined by finding the global maximum of the considered parameter over the load phase. For each trial, the time-course of the load force, $F_L(t)$, monotonically increased during the load phase and was fitted by a linear regression of the form, $\alpha t + \beta$.

It is worth considering how the grip parameters, τ and p_L , scale with the regression parameters, α and β . In the early stage of a grip, the load force follows, $F_L(t) \approx \alpha t$, since β can be set to zero with proper determination of the origin, noting that the load phase is short compared to the entire trial duration by a factor of at least one thousand. It follows that the peak of the load force rate must scale like $p_L \propto \alpha$. After liftoff, the law of dynamics, $m\ddot{x} = -F + F_L \approx -F + \alpha t$, governs the motion of a stimulus object of mass, m , located at position, x , where F represents a force that would maintain the object at rest in the absence of the hand force. The force, F , is the object weight, mg , in the gravity condition or a small contact force (necessary to engage the switch) in the inertia condition, F_0 . The time of lift-off is when $\dot{x} > 0$. Solving the dynamics with these boundary conditions gives an estimate of how the load phase duration varies with α . All calculations done, it is found that $\tau \propto F/\alpha$.

Results

Perception of heaviness

The heaviness ratings, \bar{h} , see Table 1, were plotted against the volume, v , of the stimulus for fixed masses, see Figure 2A,C, and against the stimulus masses, m , for fixed volumes, see Figure 2B,D. The results are reported

in terms of normalized quantities for mass and volume, obtained by dividing the physical values by their largest value. The results in Figure 2A,B show *Journal of Neurophysiology* t116(7):1408-1416 results of earlier reports of the SWI. Moreover, as it can be noted in Figure 2A,C, the results in the inertia condition are overall qualitatively similar to the results in the gravity condition, which confirm and generalize the observations of Plaisier and Smeets (2012).

Table 1: Data from the analysis of perception and action. Normalized ratings of heaviness of stimulus objects varying in mass and volume in the gravity condition (left columns) and in the inertia condition (right columns) and normalized values of the coefficient α reflecting anticipatory behavior.

		volume (cm^3)						
		320	384	460	553	664	796	956
mass (g)	629	heaviness		1.0 0.9	1.0 0.8	1.0 0.7	1.0 0.6	
	580	ratings, \bar{h}		1.0 0.6	1.0 0.6	0.9 0.5	0.9 0.3	
	531			0.9 0.6	0.8 0.6	0.8 0.7	0.8 0.5	0.7 0.3
	477	0.7 0.6	0.7 0.6	0.5 0.5	0.5 0.5	0.5 0.3	0.3 0.3	0.2 0.2
	451	0.5 0.5	0.4 0.5	0.3 0.4	0.2 0.4	0.1 0.3		
	432	0.3 0.6	0.2 0.4	0.3 0.5	0.2 0.4			
	415	0.2 0.4	0.2 0.4	0.1 0.4	0.1 0.4			
mass (g)	629	fingertip		0.9 0.9	0.9 0.7	0.9 0.7	0.8 1.0	
	580	forces, α		0.9 0.7	0.9 0.7	0.9 0.8	0.9 0.6	
	531			0.9 0.6	0.8 0.8	1.0 0.7	0.8 0.8	1.0 0.6
	477	0.9 0.7	0.8 0.5	0.8 0.6	0.8 0.6	0.8 0.8	0.9 0.6	
	451	0.8 0.8	0.9 0.7	0.9 0.7	0.8 0.5	0.9 0.7		
	432	0.9 0.6	0.8 0.8	0.8 0.9	0.8 0.7			
	415	0.9 0.5	0.8 0.7	0.8 0.7	0.9 0.7			

The data shown in Figure 2 were fitted with linear regressions of the form, $ax + b$. The resulting mean values \pm SD were as follows. In the gravity condition, the relationship between \bar{h} and v gave $a = -0.5 \pm 0.4$ and $b = 0.8 \pm 0.3$ with a coefficient of determination $r^2 = 0.7 \pm 0.3$ and a p-value $p = 0.12 \pm 0.21$. The relationship between \bar{h} and m gave $a = 3.9 \pm 1.3$ and $b = -2.4 \pm 0.8$ ($r^2 = 0.9 \pm 0.1$; $p = 0.03 \pm 0.04$). In comparison, in the inertia condition the relationship between \bar{h} and v gave $a = -0.5 \pm 0.2$ and $b = 0.8 \pm 0.3$ ($r^2 = 0.8 \pm 0.3$; $p = 0.1 \pm 0.14$). The relationship between \bar{h} and m gave $a = 1.4 \pm 0.3$ and $b = -0.6 \pm 0.2$ ($r^2 = 0.8 \pm 0.1$; $p = 0.08 \pm 0.07$). This analysis confirms quantitatively that the magnitudes of the two illusions are similar. There are discrepancies, however. First, the variability of the linear regression slope, a , in the gravity condition is about twice as large as in the inertia condition, Figure 4A,B. Second, for the larger masses, the size effect on heaviness perception is more predominant in the inertia condition than in the gravity condition. These discrepancies can be explained by the fact that the range of heaviness ratings in the inertia condition was about half as large as in the gravity condition (Bergmann Tiest and Kappers, 2010; Ross and Reschke, 1982). The latter observation was confirmed more quantitatively by measuring the Weber fractions (see Materials and Methods). The Weber fraction for mass discrimination was 0.15 in the gravity condition and 0.55 in the inertia condition, with a ratio of 2.7 between the two values, which indeed was that found by Ross and Brodie (1987).

Gripping behavior

We first considered the parameters analyzed in similar studies, namely the load phase duration, τ , and the peaks of load and grip force rate, p_L and p_G . However, τ and p_L are both related to the slope, α , of the load phase force trajectory, $F_L(t)$; $\tau \propto F/\alpha$ and $p_L \propto \alpha$. The validity of these relationships was confirmed by our data, particularly in the gravity condition, see Figure 3C,D, where the load phase duration, τ , is expressed as a function of the fraction mg/α . In the inertia condition, there was a clear linear dependence of p_L on α , but naturally no such correlation between τ and F_0/α could be expected since the contact force necessary to engage the switch, $F = F_0$, is negligible, making τ practically independent of α . As a result, the time course of the fingertip forces in the load phase were analyzed in terms of a single parameter, α , see Table 1.

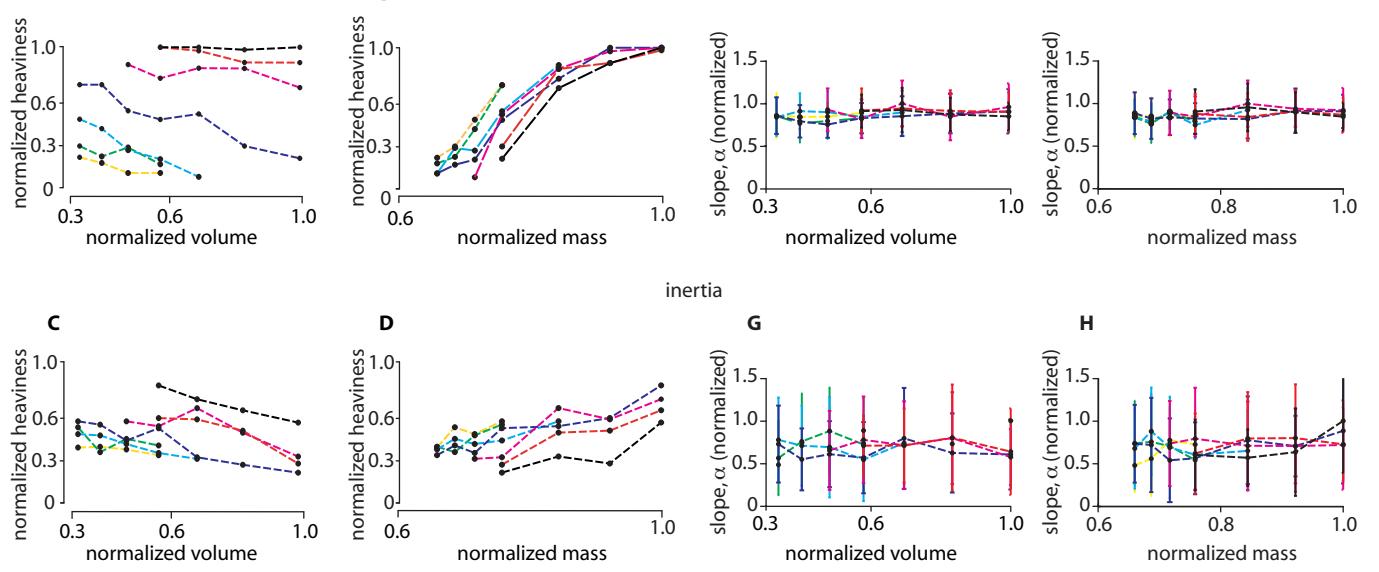


Figure 2: Quantitative analysis of perception-action dissociation. The top panels (panels A, B, E, F) represent the results in the gravity condition. The bottom panels (panels C, D, G, H) represent the results in the inertia condition. Panels A-D show the dependency of the normalized heaviness rating on normalized size and mass. Panels E-H show the dependency of the normalized slope of the linear regression of $F_L(t)$, α , on normalized size and mass. The black dots indicate 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.

In the gravity condition, regressions between τ , and α , and between p_L , and α , gave $\tau \approx 1.1 mg/\alpha + 4.7$ ($r^2 = 1.0$; $p = 0.01$) and $p_L \approx 0.4 \alpha$ ($r^2 = 0.8$; $p = 0.00$), as shown in Figure 3C,D. The peak of the grip force rate, p_G , was observed to be linearly correlated with the peak of load force rate, p_L , $p_G = 3.6 p_L - 7.7$ ($r^2 = 0.5$; $p = 0.00$), as shown in Figure 3E. In the inertia condition, the regression between p_L , and α , gave $p_L \approx 1.2 \alpha + 5.8$ ($r^2 = 0.6$; $p = 0.00$), and the regression between τ , and α , gave $\tau \approx 0.01 \alpha + 0.13$ ($r^2 = 0.1$; $p = 0.14$). We also observed a correlation between p_G and p_L , whose regression gave $p_G \approx 1.6 p_L + 13$ ($r^2 = 0.1$; $p = 0.00$).

There was no clear correlation between α and mass or between α and volume, as shown in Figure 2E-H. This observation was confirmed by a correlation analysis. In the gravity condition, the sample correlation coefficient was $r = 0.1 \pm 0.4$ and the p-value was $p = 0.58 \pm 0.28$, when correlating the normalized slope, α , to the normalized mass, m . Correlating the normalized slope, α , and the normalized volume, v , gave $r = 0.0 \pm 0.6$ and $p = 0.48 \pm 0.34$. Similarly, in the inertia condition, we obtained $r = 0.1 \pm 0.7$ and $p = 0.26 \pm 0.14$ when correlating α to m , and obtained $r = 0.1 \pm 0.4$ and $p = 0.60 \pm 0.21$ when correlating α to v . It is important to note that during the load phase, which is prior to the object motion, the load force is not directly related to the object mass since the object is still at rest. Nevertheless, in the gravity condition, object mass imposes a constraint on the load force as lift-off occurs when the load force counterbalances the object weight, as pointed out in Materials and Methods. If the regression parameter, α , is mass-independent, as observed in our study, then the load phase duration, τ , is dependent on mass, and conversely, if τ was mass-independent then α would be dependent on mass.

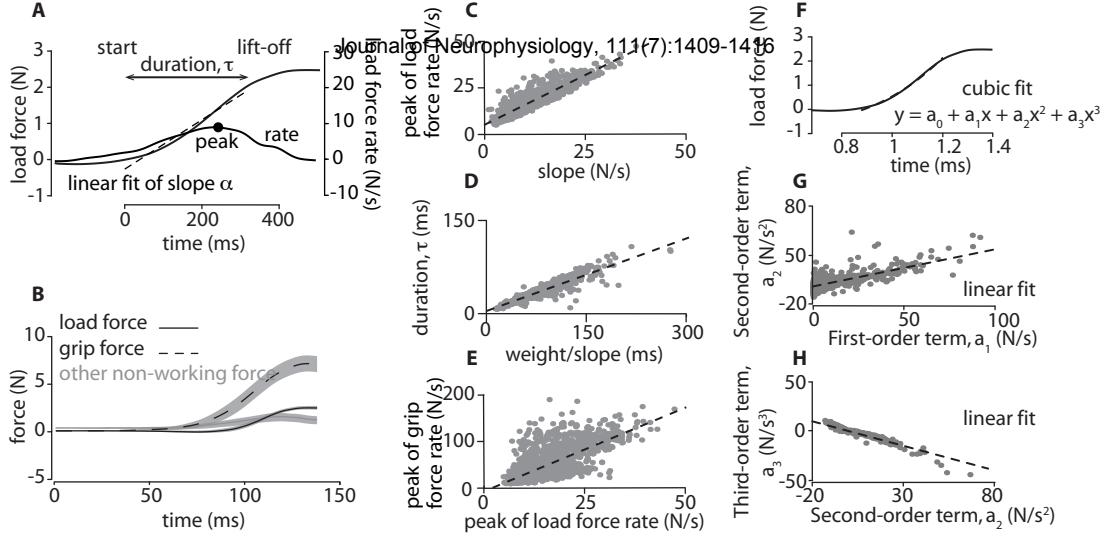


Figure 3: Parametrization of precision grip forces. All the results shown here were measured in the gravity condition. Panel A shows the motor parameters considered in our study. The solid black lines represent the average time course of load force, $F_L(t)$, for a representative participant, and the time course of load force rate, $\dot{F}_L(t)$, calculated from the average trajectory. The average was performed by synchronizing the lift-off of all trajectories. The start time of a trajectory was set as the time when both load force and load force rate exceeded the zero value. The dashed black lines represent the linear regression of $F_L(t)$, performed in the load phase of duration τ . The slope of the fitted line corresponds to the regression parameter, α . The black dot indicates the peak of $\dot{F}_L(t)$, noted p_L . Panel B shows the different contributions to the precision grip force. The solid and dashed black lines represent respectively the load force and the grip force. The solid gray line represents a non-working force other than the grip force. All the represented forces were averaged over all participant's lifts. The shaded area centered around each curve represents the standard-deviation of the corresponding force over all participant's lifts. Panels C, D, and E show the relationships between the different precision grip parameters considered in this study. Each gray dot represents the measurement for a given trial. The dashed black lines represent the linear regression of these relationships. Note that τ is plotted against the fraction mg/α in Panel D, which leads to a linear prediction. Panels F, G, and H show the cubic description of the load force. Panel F shows the result of a cubic regression on the representative trace of the load force, $F_L(t)$. The dashed black line represents the cubic regression of the represented trajectory over the load phase, $F_L(t) = a_0 + a_1 t + a_2 t^2 + a_3 t^3$, where a_0 , a_1 , a_2 , and a_3 are constant parameters called respectively zeroth-order, first-order, second-order, and third-order terms of the regression. Panels G and H show the relationships between the regression parameters. Each gray dot represents the measurement for a given trial. The dashed black lines represent the linear regression of these relationships. Note that the first-order regression parameter, a_1 , was constrained to be positive.

Discussion

We sought to investigate whether the pattern of perception-action dissociation, observed in the context of the classic size-weight illusion, could be generalized to the size-mass illusions, and in particular the size-inertia illusion, using a wide range of stimuli with de-correlated masses and sizes. For that, we created a device that enabled the use of a consistent grip across numerous stimuli and that established unambiguously the decomposition of fingertip forces into load (working forces) and grip (non-working forces) forces. The object stimuli were the same in the two conditions but the participants were exposed to radically different mechanical constraints. We found that a similar pattern of perception-action dissociation was observed in the two conditions. Whereas heaviness ratings depended on mass and on size similarly in the gravity condition and in the inertia condition, fingertip forces were independent of both mass and size. Additionally, we proposed that a single number could report the fingertip force parameters. Our study emphasized that when the testing conditions interfere with the short-term sensorimotor memory, achieved by de-correlating mass and volume, motor control is no longer predictive of the object's mass, but is also not dependent on visual size. This result suggests that the motor system relies strongly on the sensorimotor memory for anticipating action. Our study also highlighted that the magnitude of the mechanical cues, gravity vs. inertial forces, is not critical for observing a dissociation

between perception and action. This latter result confirms that heaviness perception relies on prior knowledge of mass-volume relationship, and the *Journal of Neurophysiology* 111(7):1409-1416 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°, 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 order 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 account for 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 α , 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, α . 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 $a_2 = 0.4a_1 - 2.2$ ($r^2 = 0.5$; $p = 0.00$) and $a_3 = -0.5a_2 + 0.3$ ($r^2 = 0.9$; $p = 0.00$). 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, α , between the two conditions (see Figure 4C). The values of α was calculated by averaging the measured values for each stimulus object, over all participants. The magnitude of α 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 α 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 α in the inertia condition to the standard deviation of α in the gravity condition, and obtained a value of 2.2 ± 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, α , 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.

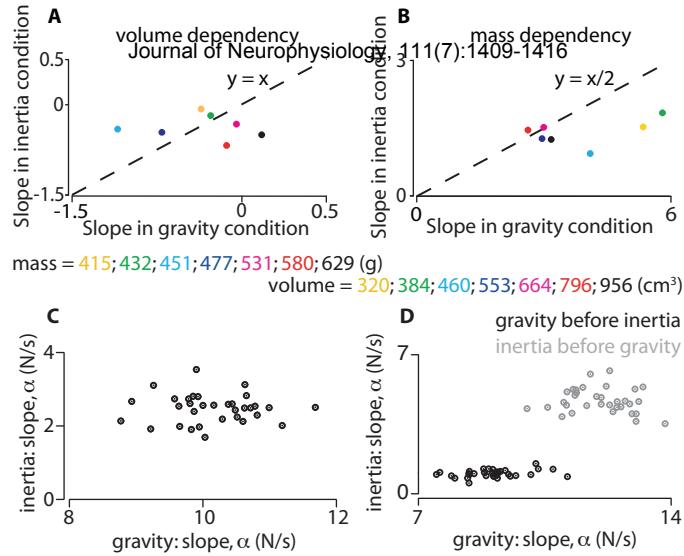


Figure 4: Comparison of results between the gravity condition and the inertia condition. For each panel, the horizontal and vertical axes correspond to the values measured in the gravity condition and in the inertia condition respectively. Panels A and B show the values of the slope of the linear regression 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 α 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, α , 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 α and the stimulus weight of the preceding lift was compared to the correlation of α with the stimulus volume of the current lift, as shown in Figure 5E. There was no significant difference between

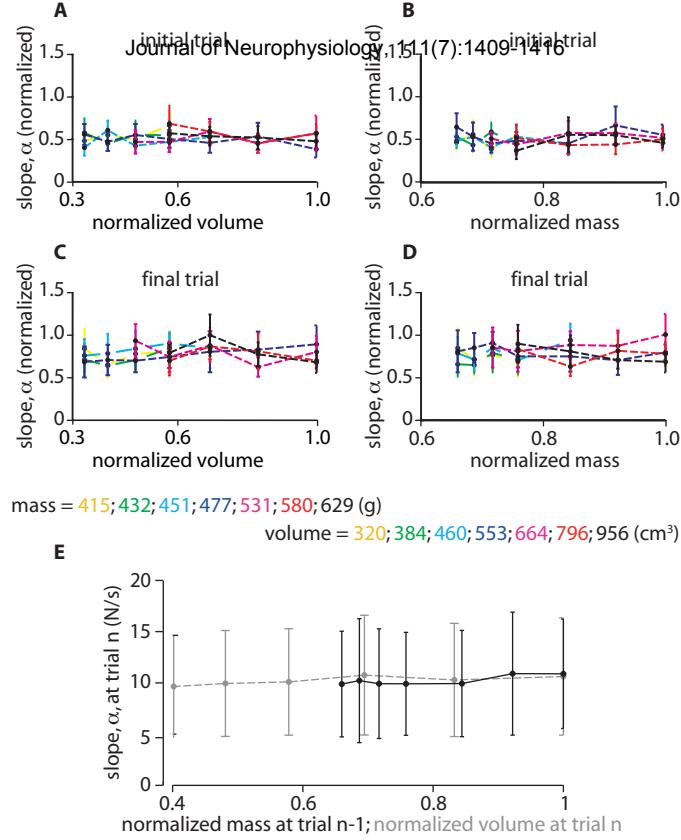


Figure 5: Adaptation of motor prediction over trials in the gravity condition. Panels A and B show the dependency of the normalized slope, α , on normalized size and mass for the first trial the given stimulus was presented to participants. Panels C and D report the results for the same parameters for 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, α .

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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