Year: 2012

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Introduction

Object manipulation requires the appropriate scaling of the hand aperture to the size of the object and the generation of lift and grip forces according to object weight. To estimate object properties and to issue appropriate motor commands in light of sensory and motor system noise, the central nervous system (CNS) combines afferent sensory cues with previous knowledge about object features. Recently, Bayesian Decision Theory has been applied to formalize processes of cue and sensorimotor integration (Körding and Wolpert 2006; Van Beers et al. 2002). According to this view, the nervous system combines prior knowledge about object properties gained through former experience ("the prior") with current sensory cues ("the likelihood"), to generate appropriate object property estimations ("the posterior") for action or perception.

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In most cases, the combination of *prior* and *likelihood* leads to an appropriate perception and behavior, but perception can be "misleading," if the *prior* is weighted higher than the *likelihood*, thus giving rise to a perception that does not correspond to the actual physical properties of the object. The *size–weight illusion* (SWI), first described by Charpentier (1891), represents such a case. The SWI arises when an individual lifts two objects of equal weight, but of different size, and perceives the smaller object as heavier. The illusion is robust (Chouinard et al. 2009; Dijker 2008; Flanagan et al. 2008; Flanagan and Beltzner 2000; Grandy and Westwood 2006; Kawai 2002, 2003; Murray et al. 1999), and the effect does not cease when the lifter is made aware that both objects have the same weight (Flanagan and Beltzner 2000). The SWI is believed to be a primarily haptic phenomenon as vision does not substantially contribute to the effect (Ellis and Lederman 1993).

There is evidence that perceptual and motor systems are differentially affected by the SWI. When people were asked to lift objects in an SWI context, they learned within the first 10 trials to scale their grip force according to the actual weight of the object, even though they still perceived the smaller object as heavier (Flanagan and Beltzner 2000). A subsequent study showed that experience reduces the prevalence of the SWI (Flanagan et al. 2008). Participants had trained up to 11 days to lift blocks with weights that varied inversely with volume. In addition to the rapid motor adaptation, they learned to predict the correct weights within about 240 lifts indicating that the perceptual system does adapt to weight cues, albeit at a slower pace than the motor system. Recent evidence suggests that these differences of the perceptual and motor system may be based on different mechanisms for integrating *prior* and *likelihood* (Brayanov and Smith 2010). The sensorimotor system is believed to function in a Bayesian manner when integrating probabilities subsequently used for motor commands. In contrast, the perceptual system integrates the *prior* and *likelihood* in an anti-Bayesian manner, overstating the value of unexpected sensory information (We will consistently use the term *prior* to refer to prior perceptual experience).

The size–weight illusion paradigm has been extensively studied to gain insight into the mechanism of cue integration for the perception of heaviness. However, to our knowledge, no study has investigated how the brain estimates object size based on expectations about weight. Thus, the aim of the present study was to investigate whether size perception is based on similar processes of *prior* and *likelihood* integration as the perception of heaviness. An experiment was designed in which participants lifted boxes of equal size but different weights, testing whether this would induce a *weight–size illusion* (WSI). We then sought to determine the differential effect of such an illusion on sensorimotor control using a size

matching task. Finally, to obtain a standard of comparison that allowed us to assess the frequency and magnitude of a weight–size illusion, the same participants also lifted objects in a size–weight illusion context.

Methods

Participants

Twenty-one adults (11 ♂, 10 ♀; mean age 22.7 ± 3.3 years), naïve to the purpose of the study and with no history of neurological impairments, participated in this study. 18 out of 21 subjects were right-handed, according to the Edinburgh Handedness Inventory (Oldfield 1971). All subjects gave voluntary informed consent prior to participating. The study was approved by the Institutional Review Board of the University of Minnesota.

Stimuli and procedure: size–weight illusion experiment

Stimuli

Fifteen rigid plastic boxes of equal height (6 cm) and width (4 cm) but varying length (3–10 cm in 0.5 cm increments) were used (for the purpose of this paper, we use the term "size" to refer to the length of the box). The size 6.5 cm box served as the *standard* stimulus. The remaining 14 boxes served as *comparison* stimuli. The weight of all *comparison* stimuli and the *standard* stimulus was 350 g. Five additional boxes weighing 200, 250, 300, 400, or 450 g all with a fixed length of 6.5 cm were used as distracters.

Procedure

Participants were seated on an adjustable chair in front of a table. The upper arm on the non-dominant side was held in a neutral position with the elbow flexed at 90° and the hand placed on the edge of the table. The non-dominant hand was used to execute all lifts. The *standard* or the *comparison* box was then placed in front of the participant's resting hand by the experimenter. After an auditory signal ("Lift"), the participant grasped the box along its length axis, which varied between boxes, using a precision grip (tips of the thumb and the index finger). The arm movement consisted of elbow flexion and extension in the sagittal plane. Participants were instructed to lift vertically and not to tilt the object. This eliminated any object size-dependent differences in torque or inertial moments, which may influence weight perception (Flanagan and Beltzner 2000). Participants were instructed to perform the lift to a height of about 10 cm above the table, then to hold the box

in this position for 2 s (hold phase) while rendering a verbal judgment about its perceived heaviness. Vision was occluded throughout the experiment. In advance of the experiment, participants performed practice lifts to experience grasping without vision.

Judgments were based on the magnitude estimation procedure (Stevens 1953; Zwislocki and Goodman 1980), where participants voice a number that best represents the perceived weight of the box. No constraints were placed on the value of the first number, stating the magnitude of the first perceived weight. However, the numbers stated in subsequent trials had to be proportional to the increase or decrease in perceived object weight (e.g., if the initial weight was judged as "5," a weight perceived as twice as heavy needed to be judged as "10"). All participants underwent a short training exercise and practice session before the start of the trials to ensure that they understood the procedure. After the rating, the box was placed back on the table and the hand returned to the starting point. As soon as the box was replaced, the experimenter exchanged the previous test box with a new box. The time interval between stimuli presentation was held constant. For each trial, the number value assigned by the participant to the comparison box could have been smaller (i.e., perceived as lighter), larger (i.e., heavier), or the same as the number assigned to the *standard* box.

Each trial consisted of two lifts, one using the 6.5 cm standard box and one using a *comparison* box. The order of lifts was pseudorandom and assured that subjects never lifted the same object more than twice in a row. Each of the 14 *comparison* boxes was compared four times to the *standard* object. The mean of the numbers assigned for the four trials represents the perceived magnitude estimation (PME) for a given *comparison* box. In addition, five randomly placed distracter trials, with boxes of different weights, were included in the testing sequence but were not used in further analysis. Thus, each subject executed 61 trials resulting in a total of 122 lifts. Participants were given two breaks to maintain their concentration level.

Stimuli and procedure: weight–size illusion experiment

Stimuli

While the SWI experiment used boxes of varying length, but constant weight, this experiment used a set of eleven boxes of different weights, but of constant length. Their weight ranged from 100 to 600 g in 50 g increments with the 350 g box serving as *standard* stimulus. The remaining ten boxes served as *comparison* stimuli. The length of each box was fixed at 6.5 cm, which was the size of the standard box used in the SWI experiment.

Five additional boxes were used as distracters, varying in length (5, 5.5, 6, 7, and 7.5 cm) but with an identical weight of 350 g. All of the boxes had the same height and width (6 × 4 cm).

Procedure

Participants performed the same lifting movements as in the SWI experiment with their non-dominant hand, but were asked to make magnitude estimations about the perceived size instead of the weight of the box. In addition to giving a verbal judgment, participants were asked to match the perceived size of the box with the index finger and the thumb of their dominant hand as if they would grasp the same box. This hand aperture (HA) gesture was executed while the non-dominant hand held the object, assuring that differences in memory processing could not account for possible differences in size perception.

Hand apertures were recorded using an optoelectronic motion capture system (Peak Motus) with a 120-Hz sampling frequency. Each recording lasted 5 s. Infrared reflective markers were attached to the tips of index finger and thumb. Before each data collection, a baseline recording was collected in which the participants were asked to hold the *standard* box along its length dimension (6.5 cm) using the thumb and index finger of their dominant hand. This procedure was performed to determine the distance between finger and thumb markers during holding, which allowed us to account for individual differences in finger size.

Each trial consisted of two lifts (*standard* and *comparison* box) for a total of 40 trials (four trials for each *comparison* box). Order of the presentation (*comparison* or *standard*) was pseudorandom. Five additional distracter trials, with boxes of varying length, were randomly inserted into the trial sequence, which were not investigated afterward. Vision was occluded at all times and two breaks were provided to assure continued attention. All participants completed the SWI and the WSI experiment at a maximum of 10 days apart (range: 1–10 days; mean: 4.6 ± 2.3 days). The testing order was counterbalanced across all subjects.

Measurements

Measuring the frequency of the size–weight illusion

To obtain a measure of how susceptible an individual was to perceive an illusion, we followed the procedure described by Kawai et al. (2007) and first computed the percentage of possible responses (e.g., heavier, similar, and lighter) for each size (e.g., 50 % heavier, 25 % lighter, and

25 % same for the 5.5 cm box). These individual percentages were then averaged across subjects (i.e., mean of % heavier, mean of % lighter, and mean of % same) for each comparison box (see Fig. 1). To obtain a measure of the frequency of the illusion for each subject, their respective percentage responses "heavier" and "lighter" were computed and subsequently averaged (see Fig. 2). In other words, an individual's frequency of the occurrence of an illusion reflected how often the participant did not respond "same," which would have been the correct answer. For simplicity and in accordance with Kawai et al. (2007), we use the term *frequency of the illusion* rather than the "frequency of the occurrence of the illusion" in this paper.

Measuring the frequency of the weight–size illusion

To obtain the frequency of the occurrence of the WSI as a function of object weight, we employed the same procedure as described above. However, here the subjects' responses were categorized as either *shorter* (number assigned to the *comparison* box was smaller than the *standard* box) or *longer* (number assigned to the *comparison* box was larger than the *standard* box).

Magnitude difference

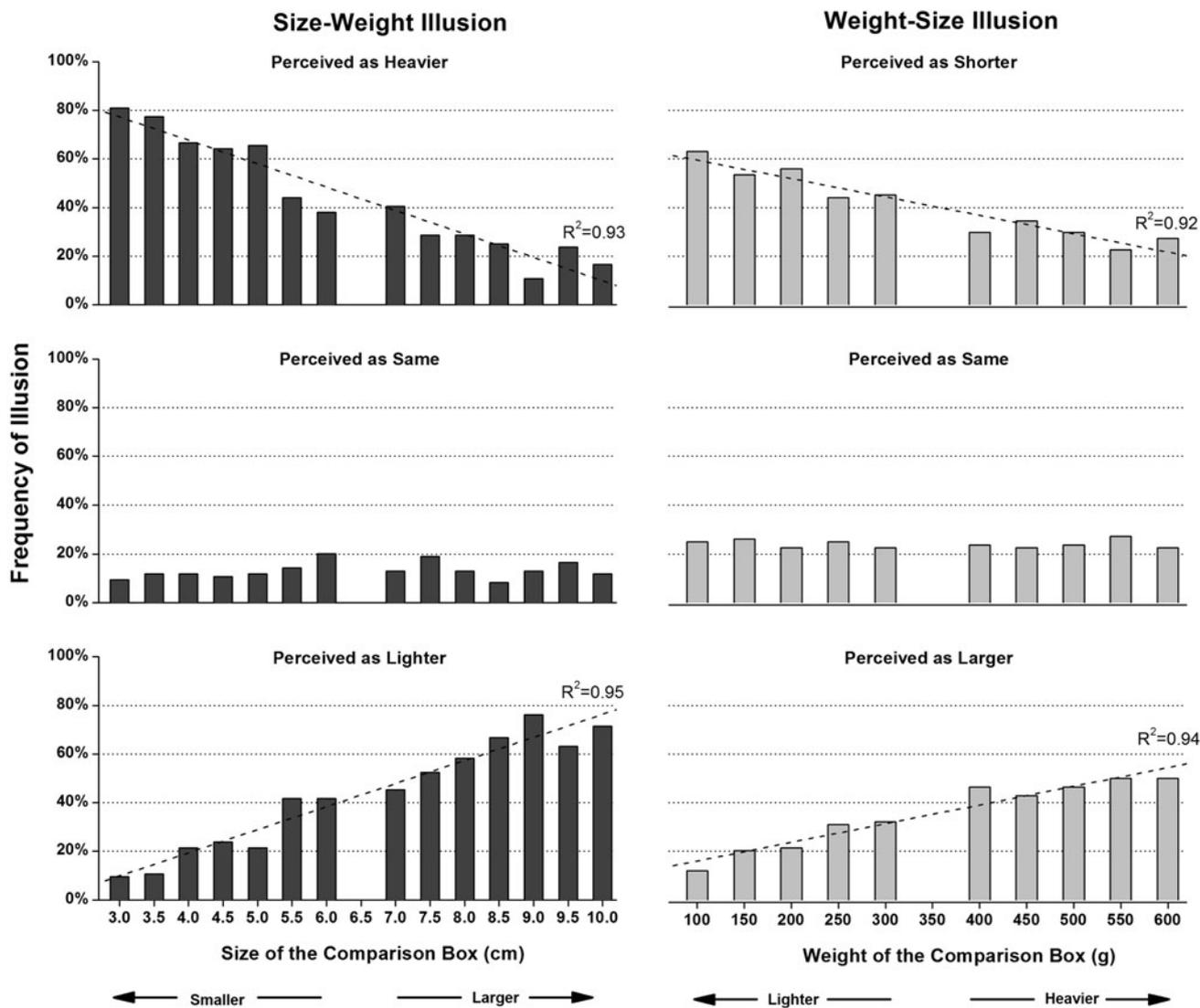To correct for scaling shifts during the experiment, a perceived magnitude difference (PMD) between the

Fig. 1 Frequency of the size–weight illusion (SWI) and weight–size illusion (WSI) for each *comparison* box. *Each bar* represents the mean percentage of all participants' responses for each *comparison* box based upon their verbal magnitude estimation of either weight or size. *SWI* The shorter *comparison* boxes ranged from 3 to 6 cm and the larger ranged from 7 to 10 cm. The 6.5 cm box served as the *standard*. The weight for all boxes was 350 g. *WSI* The lighter *comparison* boxes ranged from 100 to 300 g and the heavier from 400 to 600 g. The size for all boxes was fixed at 6.5 cm. The 350 g box served as the *standard*
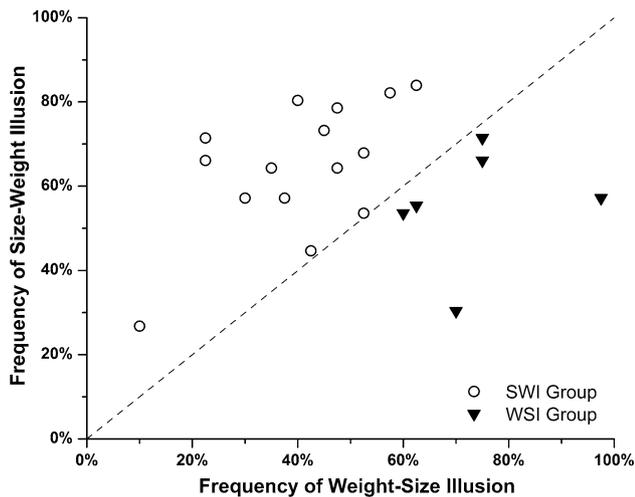
Fig. 2 Frequency of the size–weight illusion (SWI) and weight–size illusion (WSI) by participant. Each data point represents the observed frequency of the WSI and SWI for each participant. The *dashed line* indicates the line of equality, where both illusions occurred at equal frequency. Data points above the line of equality indicate that the participant was more susceptible to the SWI, while data points below the line of equality reflect a higher susceptibility to the WSI

comparison and the standard box in each trial was computed as follows:

$$PMD = [(PME\ comparison\ box - PME\ standard\ box)/ \\ PME\ standard\ box] * 100\ \%,$$

This conversion not only allows for comparison between first and last trials within each participant's data but also across participants. This ratio was further used to describe the strength of the illusions.

Hand aperture measures

The hand aperture data analysis was performed using customized software routines in MATLAB 7.0 Technical Programming Language. The raw time-position data of the markers were filtered offline using a fourth-order low-pass Butterworth filter with a cutoff frequency of 4 Hz. From the 5 s recorded, the last second of the filtered time-position data (120 data points) was used to calculate the mean distance between the two markers, because the last second of holding the hand gesture most accurately reflected the final size judgment. If the last second was unusable due to dropping the scaling hand during the hold phase, a manually defined window of 120 data points was chosen to derive an aperture measure. The hand aperture displayed for each box was then calculated as follows, taking the calibration aperture (baseline recording) into account:

$$HA = HA\_Box - (Calibration\ Distance - 6.5cm),$$

with 6.5 cm indicating the size of the *standard* box, HA_Box = hand aperture for the tested box and Calibration Distance = size of the standard box + the dimension of the marked finger tips. The hand aperture data for each *comparison* stimuli and for the *standard* box were averaged for each participant across all trials. In addition to the HA, a hand aperture difference (HAD) was calculated for each *comparison* box using the following formula:

$$HAD = [(mean\ HA\ comparison\ box - mean\ HA\ standard\ box)/ \\ mean\ HA\ standard\ box] * 100\%$$

Normalization of data

Data from the two experiments could not be compared directly due to different units of the steps between the *comparison* boxes for the two experiments (cm vs. g). In order to make the two experiments comparable, each *comparison* box was labeled with a digit. The digit represented the number of steps the *comparison* box was apart from the *standard* box. Negative digits were assigned for *comparison* boxes, which were either smaller (SWI) or lighter (WSI). *Comparison* boxes, which were larger (SWI) or heavier (WSI) than the *standard* box, were given a positive digit. For the SWI, the positive labels for the larger boxes were: $1 = 7.0$, $2 = 7.5$, $3 = 8$, $4 = 8.5$, $5 = 9$, $6 = 9.5$, and $7 = 10$ cm. The smaller boxes were labeled as follows: $-1 = 6$, $-2 = 5.5$, $-3 = 5$, $-4 = 4.5$, $-5 = 4$, $-6 = 3.5$, and $-7 = 3$ cm. The same digits were used for the Experiment 2 (WSI). Heavier *comparison* boxes were therefore labeled as $1 = 400$, $2 = 450$, $3 = 500$, $4 = 550$, $5 = 600$ g and -1, -2, -3, -4, and -5 were the labels for the 300, 250, 200, 150, and 100 g, respectively. Thus, a change from 0.5 cm in the WSI was weighted as a 1 and was thus considered equal to a 50 g change in the SWI.

Data reduction and correction

The first three complete records of hand apertures for each *comparison* box and the first 30 records for the *standard* box were used for further analysis (first valid 75 % of the recordings). If the minimum of three apertures for each *comparison* box was not obtained during the last second of recording, they were manually adjusted. Out of 1,140 valid apertures, 14 recordings were manually adjusted (1.2 % of the data). Due to technical problems with the motion capture system, hand aperture data of two participants were corrupted and could not be analyzed.

Results

Evidence for a size–weight and a weight–size illusion

Participants showed a clear susceptibility for a haptically induced SWI. Despite the fact that all *comparison* boxes had the same weight, boxes which were smaller than the *standard* box were more frequently perceived as *heavier*, and conversely, *comparison* boxes larger than the *standard* box were perceived as *lighter* (Fig. 1). The frequency of the illusion decreased as the size difference between the *comparison* and the *standard* box became smaller. Illusion frequency for each individual participant ranged from 26.8 to 83.9 % (mean 62.2 ± 3.34 % S.E.).

Participants were also susceptible to a WSI. Figure 1 shows the mean percentage of all participants *shorter,* or *longer* responses for each *comparison* box. Despite the fact that all comparison boxes had equal size (6.5 cm), participants perceived the size of individual boxes differently. *Comparison* boxes, which were lighter than the standard box, were more frequently perceived as *shorter* by the participants than the heavier *comparison* boxes. Heavier *comparison* boxes, in contrast, were perceived as *longer*. Illusion frequency decreased as the weight difference between the *comparison* and the *standard* box became smaller. WSI illusion frequency varied between participants ranging from 10.0 to 97.5 % (mean 49.4 ± 4.46 % S.E.).

The data shown in Fig. 2 indicate that participants were differentially sensitive to either the SWI or the WSI. For further analysis, participants, who perceived the SWI more often than the WSI were assigned to a SWI-Group ($N = 15$), while participants with a higher frequency for WSI were categorized as the WSI-Group ($N = 6$). Subsequent regression procedures determined the respective slopes and intercepts (SWI group: FreqSWI = 39.5 + 0.63 FreqWSI ($p_{slope} < 0.001$); WSI group: FreqSWI = 39.7 + 0.22 FreqWSI ($p_{slope} = 0.36$).

Evidence for an illusion effect on hand aperture scaling

Participants scaled their hand opening according to expected size based on perceived weight and not according to the physical size of the box (which was a constant 6.5 cm) (see Fig. 3). The respective mean hand apertures associated with holding the 100 g versus the 600 g *comparison* box were significantly different for both groups (SWI-Group: $p < 0.0001$; WSI-Group: $p < 0.0001$) indicating that hand aperture-to-weight scaling was observed irrespective of differences in cue sensitivity. The data in Fig. 3 also indicate that both the WSI and SWI groups scaled their hand apertures consistently smaller than the physical size of the box across the tested range of weights,

that is, participants tended to underestimate the true object size. Moreover, the amount of bias, that is the extent of underestimating size, was significantly larger in the SWI group when compared to the WSI group (WSI mean: 5.6 cm ± 0.13 S.E.; SWI mean: 4.9 cm ± 0.07 S.E.; $p < 0.0001$). Relating the observed aperture bias to physical object size showed that the hand aperture of the WSI group was 13.3 % (0.9 cm) smaller than the physical size, while the SWI-Group exhibited a bias of 25.5 % (1.6 cm).

To investigate whether participants adapted their hand aperture during repeated testing, the first and last hand aperture values for the 100 and 600 g *comparison* boxes were compared for each participant. No significant difference was found for either weight (100 g: SWI-Group: $p = 0.415$, WSI-Group: $p = 0.186$; 600 g: SWI-Group $p = 0.150$, WSI-Group $p = 0.83$).

Comparison between perception and hand aperture scaling

Using perceived magnitude difference (PMD) and hand aperture difference (HAD) as relative measures allowed for a comparison of weight–size illusion effect on the perceptual versus the motor system. Both variables were highly correlated with each other ($r = 0.88$). This strong association between perceptual judgments and sensorimotor judgments was also observed when considering their respective raw measures (PME and HA, $r = 0.77$) that indicate size in absolute units (cm), that is, the association is not explained by the transformation from absolute to
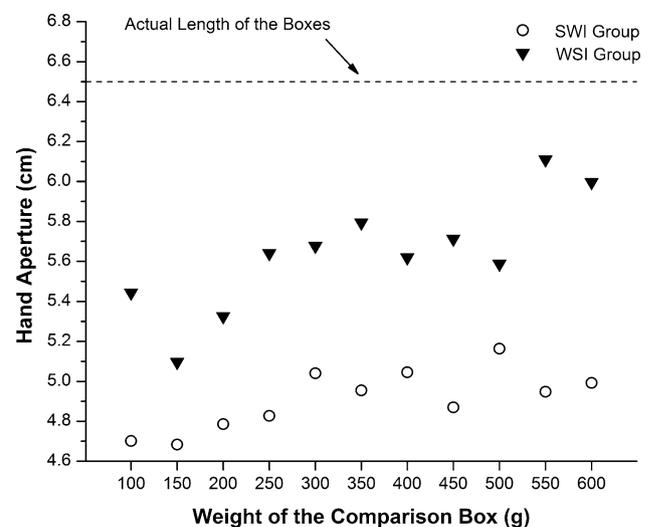

Fig. 3 Hand aperture as a function of physical weight of a box. The *dashed line* indicates the actual size of each box (6.5 cm). Data points represent the mean aperture across each group (SWI or WSI group). Note that aperture values were below the physical size in both groups with the magnitude of the underestimation being consistently smaller in the WSI-Group

relative values. The PME mean values for each of the 10 comparison weights ranged from 4.99 to 6.04, while the corresponding mean hand apertures ranged from 4.79 to 5.26 (cm) indicating that, on average, both perceptual as well as sensorimotor judgments underestimated physical object size (6.5 cm).

For the SWI-Group, the strongest illusion for the lighter *comparison* boxes was perceived for the 100 g box (6.2 cm or 4.7 % shorter). The 400 g box was perceived as the longest *comparison* box compared to the *standard* box (5.5 % longer). For the WSI-Group, the strongest illusions were perceived for the lightest and heaviest *comparison* boxes (100 and 600 g). Converting the relative percentage scores to perceived size, the 100 g box was rated as 5.0 cm (21.9 % shorter) and the 600 g box as 8.3 cm (27.5 % longer) than the standard, that is, there was a mean range of 3.3 cm between the smallest and largest perceived size for a box; both boxes had the same physical size (6.5 cm).

The relative difference data (PMD, HAD) of the weight–size illusion experiment revealed that both the perceptual and motor systems were influenced by the illusion (see Fig. 4). Respective linear regression procedures were computed to discern differences in slopes. For the SWI-Group, the slopes (*s*) were not significantly different from each other (PMD: $s = 0.014$, HAD: $s = 0.015$; $p = 0.83$; see Fig. 4 top), indicating that both systems were comparably biased by the different weights of the *comparison* boxes. In the WSI-Group, the respective regression coefficients for the slopes were different from each other (PMD: $s = 0.093$, HAD: $s = 0.023$; $p < 0.0001$; see Fig. 4 bottom). However, when performing the equivalent analysis on the raw aperture data, this later difference is no longer present. Thus, caution is warranted in concluding a difference in gain between the two systems in the WSI group.

Discussion

This study was designed to achieve two aims: First, to obtain a better understanding of the underlying mechanisms of object perception by investigating how afferent feedback about size and weight and prior experience are combined by the perceptual system to achieve a stable percept. Second, to examine whether size and weight cues are differentially evaluated by the perceptual and sensorimotor system. Studying the saliency of size and weight as cues for perception and action in the context of illusions allowed for the systematic manipulation of either size or weight to examine the effect on perceptual as well as motor performance. The main results of the study were as follows: First, the study demonstrated the existence of a haptically induced *weight–size illusion*. This finding implies that size is not a dominant cue for both weight and
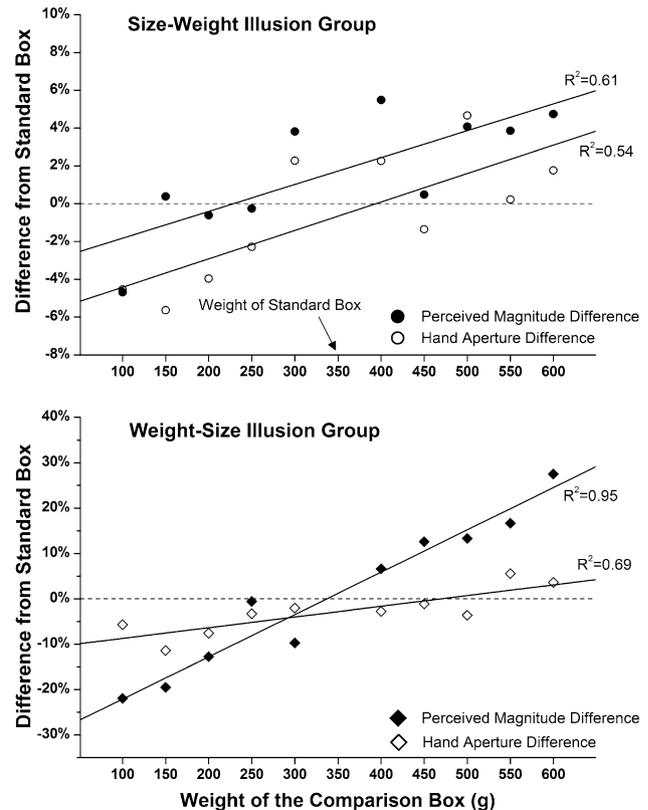

Fig. 4 Comparing perceptual and motor measures of object size as a function of object weight. Shown are the means for each subgroup (SWI vs. WSI-Group) when judging size as a function of weight. The abscissa shows the weight of the comparison boxes (standard = 350 g), the ordinate represents the relative difference between the constant physical size (6.5 cm for all boxes) and the verbal and motor-based size judgments (perceived magnitude difference vs. hand aperture difference). Note that ordinate scales differ between graphs as the WSI group exhibited larger differences in perceived magnitude than the SWI group

size perception. Instead, size and weight cues are both taken into account for both forms of perception. Second, not only weight but also size perception is based on an integration of both former experience and sensory input. Third, individuals had a tendency to be more sensitive to either weight or size cues, revealing individual differences in the way those cues were weighted during cue integration. Finally, perceived weight and not afferent haptic size information determined the aperture of the non-exploring hand, indicating that the motor system was influenced by the WSI.

The size–weight and the weight–size illusion

Ellis and Lederman ([1993](#)) concluded that the size–weight illusion is primarily a haptic phenomenon and that haptic cues alone had the same influence as the combination of haptic and visual cues on weight perception. Nevertheless,

they also showed that SWI can be elicited by vision alone, although its effect is smaller. The current study replicated these earlier findings that haptic size cues alone can induce a size–weight illusion. As shown in Fig. 1, the frequency of the illusion increased as the difference between the *comparison* and *standard* box became larger in either direction, indicating a linear effect of haptic size cues on the perception of heaviness.

The primary focus of this study was to obtain a better understanding about size and weight cue integration and to examine whether and under what circumstances humans perceive a weight–size illusion. The influence from weight on volume perception had been studied before by Usnadze (1931). He reported that a tactile WSI can be elicited when objects of the same size, but different weights are placed on palmar surface of each hand with participants perceiving heavier objects as being smaller and lighter as being larger. We extended this tactile discrimination task to systematically investigate the influence of former experience about weight on the sensorimotor system. The results of the present study indicate the influence of previous experience about object weight on size perception, as participants perceived the lighter *comparison* boxes as shorter and the heavier as longer than the *standard* box (see Fig. 1). While this result seems to stand in contrast to the findings by Usnadze (1931), the differences in experimental procedure likely account for the different results. In the Usnadze experiment, object volume and not length was manipulated, and volume was assessed solely by placing the object on the surface of the palm, while participants actively grasped and lifted the object in our study. That is, in our paradigm, participants received tactile and proprioceptive signals as well as having access to predicted sensory feedback from the goal-directed action.

The WSI occurs through a combination of the experience-based expected size of the box (*prior*), and afferent sensory input about the object's size (*likelihood*). When the weight difference between the *standard* and *comparison* box increased, the WSI was more frequently perceived. This result is analogous to the SWI where the increasing difference between the sizes of the two boxes influenced weight perception.

Yet, our data also indicate that the integration of the *prior* and *likelihood* for weight and size perception may be based on different integration mechanisms. In the size–weight illusion, participants perceived the smaller *comparison* box to be heavier than the *standard* box, but based on former experience, the smaller box should weigh less. This means that for weight perception, participants combined *prior* and afferent feedback in a manner contradictory to their experience (see Fig. 5). Brayanov and Smith (2010) referred to this as an anti-Bayesian form of integration.

Based on the experience, we would also expect a lighter box to be smaller and a heavier box to be larger. In the weight–size illusion, participants indeed perceived the lighter *comparison* boxes to be smaller and the heavier *comparison* boxes to be larger (see Fig. 1). This is consistent with the view that for size perception, participants combined prior and likelihood information in a Bayesian way of integration (see Fig. 5). The results from both illusion experiments therefore suggest that the nervous system uses different cue integration mechanisms for weight and size perception.

Evidence for different sensitivities to size–weight cues

Participants had a tendency to be more susceptible to either the SWI or the WSI. Given that participants were exposed to unimodal haptic size and weight cues in both experiments, the individual differences in the susceptibility to a particular illusion reflect differences in weight cue processing. Recent work demonstrated that humans exhibit different sensitivities to weight cues and that their individual weight cue sensitivity positively correlates with their susceptibility to the SWI (Kawai et al. 2007). Participants less sensitive to weight needed a larger difference between two weights to perceive them as dissimilar. The authors suggested that the illusion frequency for the size–weight experiment is based on the difference between the *standard* and the *comparison* box and, at least partially, on differences in the sensitivity to weight cues. With respect to our findings, this interpretation implies that the difference in the frequency of the two illusions is due to individual differences in the sensitivity to either haptic size or weight cues. This differential cue susceptibility also had an effect on motor function, because those who were more susceptible to the WSI also had significantly larger hand openings to indicate perceived size that those more sensitive to weight cues (see Fig. 3).

Using size cues for perception or sensorimotor action

The assumption of two separate systems evaluating sensory information for perception and action is not new. The idea of two separate streams for processing visual information, the ventral and dorsal stream, was first described by Mishkin and Ungerleider (1982). In the framework of the Ebbinghaus illusion, Aglioti et al. (1995) reported that participants used the same hand aperture to grasp objects, which they had perceived as being different in size. Such dissociation between the motor and the perceptual system has also been observed within the context of the size–weight illusion (Flanagan and Beltzner 2000; Grandy and Westwood 2006). These studies showed that grip force rapidly adapts to the physical weight of the box even
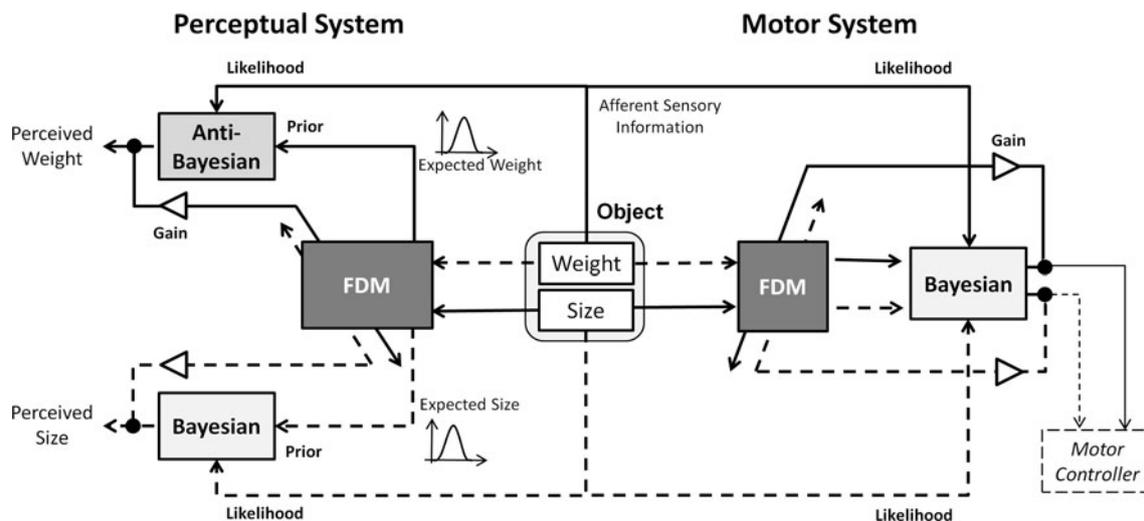
Fig. 5 Processing model of weight and size cues integration for action and perception. The object has two physical properties: weight and size. *Solid arrows* indicate processing flow for weight perception, while *dashed arrows* refer to size perception. For the perceptual and the motor system, the object's size and weight cues are inputs to a Forward Dynamic Model (FDM) representing the stored object experience. The FDM output is the experience-based expected weight or size, which can be described as a Gaussian distribution, and is referred to as the *prior*. The *prior* is then integrated with the *likelihood*, which represents the afferent sensory information about object weight and size. Two separate processing streams with two different integration mechanisms (Anti-Bayesian vs. Bayesian) are assumed for weight and size perception, respectively. A feedback loop with a specified gain provides the FDM with the final estimate of weight or size, which serves as a learning signal (*arrows* crossing the FDM boxes) for adapting object experience (e.g., when weight or size changes). Experimental findings in the context of the size–weight illusion and the weight–size illusion suggest separate cue integration processes for the perceptual and motor system

though the participants still perceived the smaller object as heavier and the larger as lighter. Nevertheless, Flanagan et al. (2008) were able show that weight perception also adapts, but more slowly. Instead of five to ten trials, the perceptual system needs thousands of lifts. These findings may indicate that the perception *prior* differs from the action *prior* as it appears to be more resistant to change. The results of Brayanov and Smith (2010) indicate that although the *prior* and *likelihood* were integrated in an anti-Bayesian way for weight perception, the motor system seems to use a Bayesian integration method. These findings suggest a separation between the perceptual and sensorimotor system (i.e., grip force control was not guided by the lifter's perception of object weight—see Fig. 5). However, with respect to our data obtained in the WSI experiment, the strong correlation between sensorimotor and perceptual judgments of object size (hand aperture and verbal judgment) could also be interpreted as an indication that perceptual and sensorimotor systems at least share some information about object weight and size, that is, they may share neural resources and are not rigidly separated.

This study focused on the influence of the WSI on the motor system and how haptic size and weight cues are integrated. Our results show that the performance of the motor task was clearly influenced by varying the weights of the lifted boxes, as hand aperture increased as a function of increasing object weight (see Figs. 3, 4). The motor effect

of the illusion persisted from the first lift to the last lift of a particular box as the scaling of the hand aperture did not change significantly over trials. Given that no feedback about performance was provided, the lack of an explicit error signal impeded learning.

However, this lack of adaptation during the WSI experiment allowed us to inspect how size cues are evaluated for sensorimotor action. If the sensorimotor system depends solely on afferent sensory information to adjust the opening of the hand to the size of an object, no variation in hand aperture for the different *comparison* boxes would have been observed, that is, hand aperture size would have been the same for all eleven boxes as all had the same physical size. This is not what we observed. In contrast, if the sensorimotor system only considers former experience (the *prior*) that size and weight increase linearly for boxes of the same density, then hand aperture should match the expected size for each weight. For example, if an object weighs a fourth of another object, the size of the lighter object should also be four times smaller than the size of the heavier object and the hand aperture should also be a fourth of the size of heavier box (i.e., 75 % smaller). Yet, the smallest observed hand apertures were only 5 % (SWI-Group) or 22 % (WSI-Group) smaller than the *standard* box (see Fig. 4). These findings refute the assumption that the sensorimotor system relies solely on the *prior* to evaluate weight of a graspable object. Instead,

it is consistent with a view that cue integration by the sensorimotor system combines both *prior* and *likelihood* in a Bayesian manner. Furthermore, our data show that the weighting of the *prior* and *likelihood* are dependent on the individual's sensitivity to either the weight or the size cues.

Finally, we need to consider that participants scaled their hand aperture consistently smaller than the physical size of the box across the tested range of weights (see Fig. 3), that is, while one hand explored the object, the other "matching" hand tended to underestimate true object size. Moreover, the amount of bias, that is the extent of underestimating size, was significantly larger in the SWI group when compared to the WSI group. The latter finding is explained by the individual differences in weight–size cue integration. However, the consistent underestimation cannot be explained as a sensory integration phenomenon. It is likely due to a bias introduced in subsequent sensorimotor transformations, that is, the processes necessary to transform perceived size to the motor commands of the opposite hand.

A model for integrating size and weight cues for action and perception

What does the finding of a weight–size illusion and its influence on the motor system mean for our understanding of cue integration for perception and sensorimotor action? Based on our results and previous work, it now becomes possible to arrive at a processing model that summarizes the differences in integration of sensory and prior information for perception and action (Fig. 5).

Consider first that during the lifting of a box, afferent haptic information about the object's weight and size becomes available centrally. Further assume that former object experience is stored in a Forward Dynamic Model (FDM) that captures the physical properties of the object. The input of the FDM is sensory cue information about size and weight, its output is the expected size or weight of the object. Thus, FDMs link size cues with expected weight and weight cues with expected size. The expected object features (weight/size) can then be described as a Gaussian distribution (given the system is not noise free) and can be referred to as the *prior*, representing the expectation based on former experience. One explanation for the occurrence of the SWI is a mismatch between the predicted sensory feedback generated by a forward dynamic model and the actual sensory feedback from the periphery (Ross 1969), although this sensorimotor mismatch hypothesis has been criticized (Ernst 2009), because it has been shown that the sensorimotor system adapts and corrects for this initial mismatch (Flanagan and Beltzner 2000).

The results from this study indicate that weight and size perception are based on the different combinations of *prior* and *likelihood*. For weight perception, the *prior* and the *likelihood* are integrated in an anti-Bayesian manner, overstating the value of unexpected sensory information. In contrast, for size perception, *prior* and *likelihood* are integrated in a Bayesian way. A feedback loop with a specified gain provides the FDM with a copy from the estimated weight enabling it to adapt to the actual physical weight/size of the lifted box. Based on the assumption that weight as well as size perception are based on the same FDM, the gain of the feedback loop has to be the same for the size as well as for weight perception.

The finding that the frequency of a particular illusion is related to an individual's varying sensitivity to weight or size is also explained by the model. For individuals who are more sensitive to size, the expected size (*prior* for size) has a higher perceptual weighting than the expected weight (*prior* for weight). The inverse would be true for an individual more sensitive to weight. Weighting one prior higher is only possible, if there is a separation at the level of integration (see Fig. 5).

Based on the findings of our and previous SWI experiments (Flanagan and Beltzner 2000; Grandy and Westwood 2006), a separation between processing object cues for perception and action is plausible. Here, the two systems only share the afferent sensory input (size and weight), but operate otherwise independently from each other. However, we need to be cognizant to the fact that this experiment cannot fully dissociate, if differences in scaling are the result of two separate neural processes (cue integration for perceptual or sensorimotor tasks) or are the result of one process with two distinct response continua. Nevertheless, the model can explain the existence of both size–weight illusions and provides a framework for the development of a more complete computational model.

Conclusion

The results of this study indicate that not only weight but also size perception are biased by former experience. In addition, the integration of *prior* and *likelihood* seems to be different for haptic size and weight perception (Bayesian vs. anti-Bayesian). Further, humans may be more susceptible to one specific haptic cue, either weight or size. Finally, the results of this study clearly indicate that both, the perceptual and the sensorimotor system, are biased by the WSI. However, in comparison with the SWI, it is not clear whether both systems work independently or if hand aperture was guided by the same processes that underlie size perception.

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