Title:
Size-weight illusion, anticipation and adaptation of fingertip forces in patients with cerebellar degeneration

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Abstract

The smaller of two equally weighted objects is judged to be heavier when lifted (size-weight illusion, SWI). In contrast, fingertip forces show an initial size effect but adapt to the true object weights within few trials. The aim of this study was to investigate possible contributions of the cerebellum to SWI, force anticipation and adaptation based on object size and weight. 18 participants with isolated cerebellar degeneration and 18 age- and gender-matched controls alternately lifted objects of equal weight but different size in 40 trials. All participants perceived the small object to be heavier after lifting (perceptive SWI). Fingertip forces were significantly higher during the first lift of the large object compared to the small object in the control and cerebellar group. For the load force rate and lifting acceleration, effects of anticipation were significantly less in the cerebellar compared to the control group. Grip and load forces were adapted to object weight during repeated lifts in both groups. Preserved perceptive SWI in cerebellar patients supports the hypothesis that perceptive SWI depends on the function of the ventral visual path which receives no or little efferents from the cerebellum. The findings of preserved anticipation and adaptation of grip forces in cerebellar patients, however, was unexpected. Reduced anticipation of load forces suggests that the neural presentation of predictive grip and load force control may be different. Findings show that representation and adaptation of internal models of object characteristics are not exclusively located in the cerebellum.
Introduction

The smaller of two objects with identical weight but different size is judged to be heavier when lifted (Charpentier 1891). This size-weight illusion (SWI) is likely to be caused by perceptual and high-level cognitive factors (Flanagan and Beltzner 2000), because people acquire early in life expectations about object characteristics like a constant size/weight relationship of objects made of the same material. When lifting objects, grip and load forces are produced according to the physical characteristics of the object, for example the object weight (Johansson and Cole 1994; Johansson and Westling 1984). If size-cues are available, the known relationship between size and weight is processed and grip forces are scaled accordingly (Cole 2008; Gordon et al. 1993, 1991a,b). Based on the predicted object weight people initially apply less grip and load forces to the smaller object and higher grip forces to the larger object. Different to the sustained false perception of the object weight, grip force is adapted to the true object weight within a few lifting trials (Flanagan and Beltzner 2000). These findings support the hypothesis that perceptual and sensorimotor systems process object’s information in different ways (Flanagan and Beltzner 2000; Milner and Goodale 1995; Goodale et al. 1994, 1991). Which anatomical correlates are involved within the central nervous system is not completely understood. Perceptive SWI is thought to depend on the integrity of the ventral visual path, which plays a major role in object recognition. The dorsal visual path is thought to be involved in anticipatory scaling of the hand and fingers to object size during grasping movements (Goodale and Milner 1992). The cerebellum may contribute to the latter, because of its known close connections to the dorsal, but not the ventral visual path (Glickstein 2000).

It has been proposed that internal models of object dynamics exist within the cerebellum which are continuously updated to anticipate and adapt grip forces to the certain object properties (Nowak et al. 2007; Hermsdorfer et al. 2005; Kawato 2003, 1999, 1992, 1987). There is increasing evidence from human cerebellar lesion and brain imaging studies
that the cerebellum is of major importance in the anticipatory control of movements and their adaptation to changes in the environment (Bastian et al. 2006). Previous studies investigating participants with cerebellar lesions found deficits of anticipatory grip force control. For example, cerebellar participants were impaired in the coupling of grip and load forces, which change in parallel in healthy participants when performing a lifting task with self-generated loading (Rost et al. 2005; Nowak et al. 2002). The ability to anticipate object properties such as the size-weight relationships and adjust grip forces accordingly has not been assessed in cerebellar participants. It has been shown that cerebellar participants are in principle able to adapt grip forces to the weight of objects (Fellows et al. 2001; Muller and Dichgans 1994). In these experiments, the roles of anticipatory and adaptive mechanisms as well as reactive processes could not be differentiated. There is good evidence that adaptation of arm movements to visual perturbations and changes in force fields are impaired in cerebellar participants (Tseng et al. 2007; Maschke et al. 2004; Deuschl et al. 1996).

The aim of the present study was to investigate possible contributions of the cerebellum to perceptive SWI and grip force control based on the expected and real object weight. It was hypothesized that cerebellar participants were impaired in anticipating the weight of the objects. Cerebellar participants may apply the same (high) grip force to the small and large object, because they might be impaired in correctly predicting the sensory consequences of lifting objects of different weights. In participants with preserved effects of weight anticipation, adaptation of grip forces to the true object weight may be impaired. These findings would strengthen the idea that the cerebellum plays a major role in retrieval and updating of internal models of object characteristics during hand-object interactive manipulations. Finally, perceptive SWI was thought to be unaffected.
Materials and Methods

Participants

18 participants (Table 1) with isolated cerebellar degeneration [11 male, 7 female; mean age 61 (SD 9.6) years] and 18 age- and gender-matched controls without any known neurological diseases or neurological deficits in examination [11 male, 7 female; mean age 61 (SD 9.7) years] participated in the study. In the cerebellar group, twelve participants presented with spinocerebellar ataxia type 6 (SCA 6), five participants with sporadic adult onset ataxia (SAOA) and one participant with autosomal dominant cerebellar ataxia type III (ADCA III; pure cerebellar ataxia with inconclusive genetic testing). These disorders are known to affect primarily the cerebellar cortex (Gomez 1997). The severity of cerebellar symptoms was assessed by an experienced neurologist (DT) based on the Scale of the Assessment and Rating of Ataxia (SARA; Schmitz-Hubsch et al. 2006). In the group of the cerebellar participants the mean SARA score was 12.1 (SD 6.5; range 0 to 24; maximum SARA score = 40). All participants gave informed consent approved by the ethics committee of the medical faculty of the University of Essen-Duisburg. The experiment was conducted in accordance with the Declaration of Helsinki.

MRI volumetry

MR images of cerebellar participants and controls were acquired with a 1.5 T Siemens Sonata Scanner (Siemens, Erlangen, Germany) using a standard quadratic headcoil. A 3D sagittal volume of the entire brain was made using a T1-weighted magnetization prepared rapid acquisition gradient echo (MPRAGE; TR=2400ms, TE=4.38 ms, FOV=256 mm, 160 slices, voxel size 1.0 x 1.0 x 1.0 mm³) sequence. Images were used to calculate the volumes of the cerebellum, cerebrum and total intracranial volume (TICV). The cerebellum was further divided in the anterior and posterior lobe, and medial (vermal), intermediate and lateral zone. Volumetric analysis of MPRAGE images was performed with the help of
ECCET-software (http://www.eccet.de) developed for visualization and segmentation of MRI and CT data. Details of analysis have been reported previously (Dimitrova et al. 2006; Brandauer et al. 2008). In brief, the brainstem was semi-automatically segmented and separated from the cerebellar peduncles, which were included in the cerebellar volume. Next the cerebellum was semi-automatically marked and then segmented with a 3D filling algorithm that is able to differentiate between brain tissue and surrounding cerebrospinal fluid. Segmentation of cerebellar cortex and white matter was performed automatically using intensity contours (Makris et al. 2005). The cerebellar cortex was further subdivided into the anterior and posterior lobes, and into the medial (vermis), intermediate and lateral zone (for details see Brandauer et al. 2008). For further analysis the means of the right and left intermediate, the right and left lateral zones were calculated. Cerebellar and cerebral volumes were expressed as percentage of TICV. To determine the degree of cerebellar atrophy in individual participants cerebellar volumes (in % TICV) were expressed as percentage of the mean volume of all controls set as 100% [degree of atrophy (% controls) = (cerebellar volume (% TICV) / mean cerebellar volume in controls (% TICV)) x 100)].

**Size-Weight Illusion**

Participants were instructed to lift three objects of equal weight (380g; 3.7 N) but different size (large object 15.9 × 15.9 × 15.9 cm³; medium object 9.8 × 9.8 × 9.8 cm³ and small object 6.3 × 6.3 × 6.3 cm³). All objects were made of wooden boards with a metal block fixed in the centre of each object. A grip force sensor (0 – 80 N) served as a removable handle that was mounted on the top of each object by a magnetic adaptor and could quickly be exchanged between objects (Fig. 1). Participants grasped the handle with a precision grip with their thumb and their index and middle fingers. Pieces of sandpaper were attached on the two vertical contact surfaces to secure good contacts.
The object was placed in front of the participant aligned to his centre (mid-sagittal plane) approximately 30 cm in front of the sternalum. The small object was placed onto a base so that the centre of the handle was always in the same position irrespectively of object size. The handle was slightly rotated so that it could be comfortably grasped. Participants grasped the handle in the middle of the vertical contact surfaces. Before each trial they placed their right hand on the right side of the object. After a verbal instruction (Go!) from the investigator, participants grasped the handle of the object, lifted it about 4 cm and held it on a constant level until the investigator instructed them to replace the object (~ 2 - 4 s). While holding the object on a constant level, the upper arm was positioned in ~ 60° to 80° anteversion, the elbow was flexed at ~ 100° to 110° and the hand slightly supinated. Participants were instructed to move quickly but not abrupt while lifting the objects. Lifting, holding and replacing the object had to be performed within 6 seconds. Participants first lifted the medium object for eight trials to get familiar with the task. These lifts were not included in data analysis. Thereafter, participants lifted the large and small objects alternately for 16 trials each, starting with the large object. All participants first lifted the large object and than the small object. Our intention was to maximize the differences in forces used for the first lift of the large and small object. However, apart from a smaller difference no change of the results would have been expected for the reversed order.

**Perceptive size-weight illusion**

Participants were asked to sort the three objects according to their presumed weight before the first lifting trials. After the 5th and the last pair of lifting the small and large object, participants were asked to choose the object which felt heavier. Before the first lifting trials of the medium object and after the last lifting pair of the small and large object, participants were requested to mark on a visual analogue scale with a length of 20 cm the presumed object weight of the small and large object. A drawing of a weight at the bottom end of the scale
indicated a heavy weight while a feather at the top end of the scale stood for light weight. The difference in centimeters between the marks for both objects in the scale was measured to compare the estimation before and after the lifting trials. These measures of perceptive SWI (in cm) were compared between cerebellar participants and controls using an independent *t*-test.

**Analysis of forces**

Signals from the force sensor were sampled at 100 Hz. Grip force (normalized to the objects surface) between thumb versus index and middle fingers, load force (tangential to the surface) and lifting acceleration were directly extracted from the sensor. Load force is a product of mass and acceleration. Therefore load force and lifting acceleration change in parallel. After lift-off, the load force is largely determined by the weight of the object. During the lifting movement an acceleration-dependent inertial load component adds to the gravitational load. Since the acceleration is analysed as a separate parameter and the weight was constant for both objects, the load signal was not analyzed statistically. Raw data were smoothed and time derivatives were calculated by means of kernel estimates (cut-off frequency 12 Hz) which provide a non-parametric estimation of regression functions by moving weighted averages (Marquardt and Mai 1994). Time to lift-off was set as the time difference between grip force onset and onset of acceleration, i.e. lift-off.

To assess the effects of anticipation, parameters of the first lifting trial of the large and of the small object were compared. Analysis of variance with repeated measures was performed with grip force parameters as dependent measures, trial (first lifting trial of the large and the small object) and size (large vs. small object) as within-group factors and group (cerebellar vs. control) as between-group factor. Significant size main effects indicate the effects of anticipation and significant size by group interactions represent the differences in anticipation between cerebellar and control participants.
To assess effects of adaptation across trials, the 16 paired lifting trials were divided into 2 successive blocks of 8 paired trials. Analysis of variance with repeated measures was performed with grip force parameters as dependent measures, size (large vs. small box) and trial (1-8 and 9-16) as within-group factors and group (cerebellar vs. controls) as between-group factor. Significant size by trial effects indicate effects of adaptation and significant size by trial by group effects differences in adaptation between cerebellar and control participants.

Finally, degree of anticipation and adaptation was correlated with ataxia score and severity of cerebellar atrophy in the cerebellar group. Pearson correlation coefficient was used to assess bivariate correlations. The extent of anticipation was calculated as difference of force parameters between the first lifting trials of the large and small object. The extent of adaptation was calculated as the quotient between the difference of the first two lifting trials (that is anticipation) and the mean difference in the last four lifting trials.

Statistical analysis of the data was performed using SPSS 15.0 for windows. $P$ values were set as $< 0.05$. Adjustments according to Greenhouse-Geysen were performed when appropriate.
Results

Perceptive size-weight illusion

When asked to visually examine the objects’ heaviness before the first lifting trial, the majority of participants estimated the largest object to be the heaviest (15/18 healthy controls; 13/18 participants with cerebellar degeneration). Using the analogue scale, 15/18 controls and 12/18 cerebellar participants judged the larger object as the heavier. After the 5th and the last lifting of the small and the large objects all participants perceived the small object as the heavier of the two, that is, they experienced the perceptive SWI. Fig. 2 illustrates the difference of the estimated weight between the small and large object using the analogue scale before the first and after the last lifting trial. Before the first lift, the mean difference between the small and large object was 5.3 cm (SD 10.3 cm) in cerebellar participants and 8.4 cm (SD 10.2 cm) in controls. After the last trial the mean difference was – 11.1 cm (SD 4.8 cm) in the group of cerebellar participants and – 9.3 (SD 5.6 cm) in the control group. Cerebellar participants and controls showed a comparable difference of estimated weight before the first lift and after the last lift ($P = 0.6$; unpaired t-test).

Grip parameters

Participants who considered the small object as the heavier one before the first lifting trial showed no difference in force development during the first lifting pair of the large and small object.

Effects of anticipation

Statistical results are summarized in Table 2.

Grip force and grip force rate

Figure 3A and B show grip force and grip force rate recordings of the first lifting trial of the large and small object in a characteristic control and two cerebellar participants (12 and
Participant 13 was the clinically least affected and participant 12 the clinically most affected cerebellar participant. Participant 13 applied increased grip forces and grip force rates, which is characteristic for the cerebellar group. The most affected participant (12) was very slow as obvious from slow force increase and low grip force rates but nevertheless shows the normal pattern. Effects of anticipation of parameters were present in both cerebellar and in the control participants. All participants applied forces according to the expected weight of objects, that is, they applied higher forces to the large object and fewer forces to the small object. Group data confirm these findings (Fig. 4A,B, first paired lifting trial). In both groups mean forces applied to the large object were higher than forces applied to the small object. The mean differences (i.e. the effects of anticipation) were of comparable magnitude in both groups (Fig. 5A,B). Analyses of variance considering the first lifting trial of the large and small object revealed significant size effects ($P'$s < 0.001; Table 2), but no significant size by group interactions ($P \geq 0.542$; Table 2).

**Load force rate and lifting acceleration**

The difference in load force rate and lifting acceleration between the large and small object was less in the cerebellar participants compared to the control (Fig. 3C-E). Accordingly, group data showed larger differences between the large and small object during the first lifting trials in controls compared to the cerebellar group (Fig. 5C,D). ANOVA revealed significant size effects ($P < 0.001$), and significant size by group interactions ($P \leq 0.030$).

**Time to lift-off**

Fig. 4E shows that in both the control and the cerebellar participant time to lift-off is longer if the weight of the object is under-estimated and shorter if the weight of the object is over-estimated. The difference between both objects in time to lift-off was larger in the
control group than in the cerebellar group (Fig. 5E). ANOVA considering the first paired lifting trial showed a significant size effect ($P = 0.005$), but no size by group interaction ($P = 0.370$).

Effects of adaptation

Statistical results are summarized in Tables 3 and 4.

**Grip force and grip force rate**

In both groups, grip forces and grip force rates adapted in relation to the true object weight within a few trials, that is, participants used similar forces for both objects (Fig. 4A,B). Forces decreased for the large object and increased for the small object during repeated lifting. ANOVA considering the first eight paired lifting trials (Table 3), revealed significant trial by size effects ($P \leq 0.002$), but no trial by size by group interaction effects ($P \geq 0.369$). In cerebellar participants, grip forces regained slightly larger values for the large object in the second half of the experiment (trial pairs 7-16). Likewise, ANOVA considering lifting pairs 9-16 (Table 4) revealed a significant size effect ($P = 0.025$), trial effect ($P = 0.050$) and a size by group interaction ($P = 0.044$). This effect could not be observed for grip force rate (size effect: $P = 0.056$; trial effect: $P = 0.954$; size by group interaction: $P = 0.284$). Trial by size and size by trial by group interaction effects were not significant ($P \geq 0.367$) for grip force and grip force rate.

Cerebellar participants generally applied higher grip forces than control participants. Analysis of variance considering the first and last eight lifting pairs revealed a significant group effect ($P = 0.001$ and $P = 0.005$; Table 3 and 4).

**Load force rate, lifting acceleration**

Load forces rate and lifting acceleration adapted in relation to the true object weight within a few trials. ANOVA considering the first eight paired lifting trials (Table 3) showed
significant trial by size effects ($P < 0.021$). Trial, trial by group and trial by size by group interaction effects were not significant for load force rate ($P \geq 0.207$), but trial by size and trial by size by group interactions were significant ($P \leq 0.037$) for lifting acceleration due to a higher anticipation in the control group. Adaptation of parameters seemed to be incomplete in both groups with higher values used for the large object in the latter trials (Fig. 4C,D). ANOVA of the last eight paired lifting trials (Table 4) showed a significant size effect in both groups ($P < 0.003$) but no significant size by group interactions ($P < 0.569$). Trial, trial by size and size by trial by group interaction effects were not significant ($P \geq 0.073$).

Load force rates tended to be lower in the cerebellar than in the control group. This difference did not reach significance considering the first ($P = 0.260$) and last eight lifting pairs ($P = 0.051$; Table 4).

*Time to lift-off*

In both groups, time to lift-off adapted in relation to the true object weight after the first lift (Fig. 4E). Considering the first eight paired lifting trials (Table 3), trial effect was significant ($P = 0.039$). Trial by size effect did not reach significance ($P = 0.096$) due to the fast adaptation within two trials. Trial by group and trial by size by group interaction effects were not significant ($P \geq 0.394$). ANOVA considering lifting pairs 9-16 (Table 4) showed no significant size effect ($P = 0.575$), trial, trial by size and size by trial by group interaction effects ($P \geq 0.126$).

Time to lift-off was longer in the cerebellar group compared to the control group. Considering the first and last eight paired lifting trials, there was a significant group effect ($P = 0.021$ and $P = 0.002$; Table 3 and 4) reflecting the longer time to lift-off in cerebellar participants.
**Correlation analysis: severity of ataxia and cerebellar atrophy**

First, analysis was repeated considering only participants with the most severe clinical signs of cerebellar ataxia (total SARA score > 12; \( N = 9; \) mean age 65.0 years; 3 female, 6 male) compared to the controls. Results did not differ significantly from those considering all cerebellar participants except that in addition to grip force and time to lift-off, the load force rate reached a statistical significant difference between groups, with cerebellar participants applying significantly lower force rates (group effect, ANOVA considering the first and last eight lifting trials: \( P = 0.007 \) and \( P = 0.001 \)).

Next, analysis was repeated considering only participants with the most severe signs of cerebellar atrophy [that is cerebellar volume (% TICV) below 7.0 %; \( N = 8; \) mean age 62.5 years; 6 male, 2 female] and the controls. The mean cerebellar volume (% TICV) was 7.23% (SD 0.87%) for all cerebellar participants and 8.94% (SD 0.64%) for all controls. Again, results did not differ to previous findings considering effects of anticipation and adaptation. As it was seen in participants with more severe ataxia, additionally to the group effect of grip force and time to lift-off, cerebellar participants tended to apply a lower load force rate (ANOVA, group effect: \( P < 0.07 \)).

Finally correlation analysis was performed. No significant correlations comparing any of the measures of anticipation or adaptation to the clinical ataxia scores (total SARA, subscore kinetic function right hand) and to cerebellar volumes (total cerebellar volume, volumes of the intermediate, lateral and medial cerebellar zone; anterior and posterior lobe; normalized to total intracranial volume) were observed in the cerebellar group (\( R > 0.11; P > 0.05 \)).
Discussion

Perceptive size-weight illusion (SWI) was preserved in all participants with cerebellar degeneration. It appears to be independent of cerebellar function. In contrast to our expectations, participants with cerebellar degeneration scaled grip forces and grip force rates according to the expected object weights and adapted forces in relation to the true object weight. Predictive grip force control to certain object characteristics, such as weight, may not depend on the integrity of the cerebellum. However, anticipation of load force rate and lifting acceleration to expected object weights, tended to be less in cerebellar participants compared to controls. These findings suggest that the neural representations of predictive grip force and load force control may be different.

Perceptive size-weight illusion (SWI)

Although the small and the large object had the same weight, all cerebellar participants and all controls judged the small object to be the heavier one during and after the experiment, which means that all experienced the perceptive SWI. The intensity of the illusion did not significantly differ between cerebellar participants and controls.

A similar number of controls (3) and cerebellar participants (5) guessed already before the experiment that the smaller object might be the heavier one. This had no influence on their initial scaling of grip and load forces. Forces still were larger for the large object and smaller for the small object in their first lifting trials. Thus, despite these participants claimed opposite expectations, the grip and load forces were initially adjusted according to previous experience that objects of the same material but different size are different in weight. Participants may actually have had a normal processing of the size-weight relationship, but because they assumed to be tricked, they expected the smaller object to be the heavier one. This observation can be taken as further evidence for the independency of conscious belief or knowledge about object characteristics and discrepant sensorimotor control such as the
adaptation of grip forces in the SWI paradigm (Flanagan and Beltzner 2000) or the initial lack of grip force adaptation when changes of object weight are observed without manual interaction (Nowak and Hermsdorfer 2003).

The perceptual SWI can be explained by sensory mismatch between the expected object weight and the actual sensory experience after lifting (Murray et al. 1999). Following the observation that sensory information is processed correctly for the adaptation of grip force and sensory mismatch is at least not obvious on the level of sensorimotor control, an alternative explanation has been raised according to which participants actually judge density instead of physical weight. After the first lift, it becomes obvious that the densities of the two objects are very different. In the SWI paradigm, object density appears to be the most salient object feature and participants may base their decision on this attribute rather than on objects’ weight (Grandy and Westwood 2006). The present findings show that brain regions independent of cerebellar control process the mismatch between expectation and sensory experience. They respond to the object feature that is most relevant for understanding its heaviness. This is the relative density of the object in this particular situation. This does not exclude, that cerebellar participants have disorders in perceiving the heaviness of the object correctly.

In addition to its known role in motor control and learning, a role of the cerebellum in non-motor functions including perception is increasingly discussed. Somatosensory deficits, such as difficulty in weight perception (Holmes 1917) or kinaesthesia (Grill et al. 1994; but see Maschke et al. 2003 for a contrary view), have been reported after cerebellar lesions. Studies using cortical somatosensory evoked potentials indicated that participants with cerebellar damage are impaired in lower level, preattentive cortical processing of incoming somatosensory inputs (Restuccia et al. 2001, 2007). It has been suggested that the cerebellum is involved in the processing of sensory discrepancies between the output of an internal model and actual sensory reaффerents (Blakemore et al. 2001). In an fMRI study, the cerebellum was
particularly activated by externally produced tickling, that is, in a situation were the sensory consequences of a movement cannot be accurately predicted (Blakemore et al. 1998). This seems to contrast with the present findings of a preserved illusion in cerebellar patients if one accepts that the illusion is due to a sensory discrepancy. However, while processes involving an internal model are highly automated, the weight estimation affords an explicit judgement that may be mediated by different brain structures. The size-weight illusion is assumed to be driven by higher cognitive processes but not by lower level sensorimotor processes (Chouinard et al. in press; Flanagan and Beltzner 2000). More generally speaking, object recognition awareness appears to be distinct from purely sensory awareness. Object recognition awareness has been proposed to be mediated by neuronal activities in areas that are separate and distinct from cortical sensory areas (Sewards and Sewards 2002). The cerebellum may contribute to the latter but not to the first.

Maybe the best evidence comes from the work in the visual system. The cerebellum is known to have strong anatomical connection to the dorsal visual stream but not the ventral visual stream (Glickstein 2000). The ventral pathway allows the construction of long-term perceptual representations, from object features and their relations, whereas the dorsal stream and associated pathways are responsible for the programming and for the visual control of skilled movements (Milner and Goodale 1995).

Few studies investigated the neural correlates which are involved in the size-weight illusion. A recent fMRI study investigated brain regions which are responsible for computing object size, mass and density for lifting tasks and which are involved in false perception of the object mass. The authors found that activation in sensory areas changed when grip force adapted to object size variations, in the primary motor area when object weight varied and in left ventral premotor cortex (PMv) when object density varied. The left PMv appeared to be involved in mediating false perceptions about mass (Chouinard et al. in press). There were no
changes related to object density and false perception of mass in the cerebellum, which is consistent with the present findings of preserved perceptive SWI in cerebellar participants.

**Performance deficits of grip and load forces**

In healthy participants, grip force normally is only slightly higher than the minimum force necessary to prevent the object from slipping, and is precisely scaled according to the physical object characteristics, such as weight, surface friction, and shape (Johansson 1998; Jenmalm and Johansson 1997; Johansson and Westling 1988, 1984). Our findings confirm the results of previous studies, that participants with cerebellar disorders produce excessive grip forces (Hermsdorfer et al. 2005; Nowak et al. 2004, 2002; Fellows et al. 2001; Babin-Ratte et al. 1999) and show a prolongation of the time interval between the onset of grip force development and the lift-off of the object (Kagerer et al. 1998). The increase of grip force and the extended time to lift-off might directly reflect impaired motor functions or might be a strategic response to ataxia or tremor (Hermsdorfer et al. 2005).

**Anticipation of grip and load forces to object weight**

For the first lift, grip forces are adjusted according to the expected object weight. The expectation is formed from previous experience, in particular, the knowledge that objects of different size and same material (that is constant density) have different weight. It has been proposed that finger grip and load forces are adjusted on the basis of internal models that predict the consequences of our movements (Nowak and Hermsdorfer 2006; Hermsdorfer et al. 2005; Kawato et al. 2003; Wolpert and Ghahramani 2000; Flanagan and Tresilian 1994). Based on theoretical and anatomical considerations, as well as data in participants with cerebellar disorders and fMRI data in healthy participants, the cerebellum is one likely candidate where internal models are built and stored. The present findings, however, suggest
that internal representation of object characteristics is not exclusively represented in the cerebellum.

Although grip forces were generally larger in cerebellar participants than in controls and the time to lift-off was prolonged, cerebellar participants’ grip forces anticipated object size in a way very similar to controls. That is, cerebellar participants and controls applied relatively high grip forces and grip force rates to the large object and low grip forces and grip force rates to the small object in the first lift. Anticipatory scaling of grip forces and grip force rates to object size appears to be independent from cerebellar function. In accordance with this finding, other studies have also reported some aspects of anticipatory motor control being preserved in cerebellar participants. Diedrichsen et al. (2004) found that the well-learned anticipatory postural adjustment during a bimanual unloading task was mostly intact in participants with unilateral and bilateral cerebellar damage. This suggests that the cerebellum is not mandatory for over-learned anticipatory adjustments. Likewise, Timmann and Horak (1997) found that the predictive scaling of early postural responses to platform perturbation amplitudes was preserved in cerebellar participants. Discrepancies between findings of preserved functions and impaired grip force-load force coupling during movements of a grasped object may result from the different nature of the underlying internal model (Rost et al. 2005; Nowak et al. 2002; Babin-Ratte et al. 1999). While the complex dynamics of the arm movements are an inherent part of models related to the prediction of movement generated-loads, the prediction of grip force during lifting mainly bases on the weight of the object and surface friction. It is possible that the cerebellum plays an important role in processing dynamics (Topka et al. 1998; Bastian et al. 1996) while it is of minor importance when selecting grip forces according to visually inferable object characteristics. In a recent fMRI study, Chouinard et al. (in press) reported activation in somatosensory and posterior parietal areas when objects of varying size were lifted as compared to identical size. No activation was found in the cerebellum for this contrast. Dafotakis et al. (2008) reported impaired
prediction of grip force according to a learned colour association after transcranial magnetic stimulation of the ventral premotor cortex, also suggesting a cortical representation of object properties for grip force scaling.

One may argue that the cerebellum is involved in the acquisition of the proposed internal models during early development and that over-learned internal models are partly stored outside the cerebellum. Cerebellar participants may have used their cerebellum to acquire the internal models early in childhood given that the disease was acquired in adulthood. Studies in participants with cerebellar disease acquired during early childhood are of interest to address this issue.

Negative findings in this study are unlikely explained because cerebellar participants were not severely affected enough. Part of the cerebellar participants presented with marked cerebellar atrophy and moderate to severe signs of cerebellar ataxia. Anticipation of grip force and grip force rate did not depend on the severity of ataxia. More severely affected participants with considerable ataxia of the upper extremities and marked cerebellar atrophy in MRI did not show worse performance than those only mildly affected participants.

Different to grip force control, however, anticipation of load force rate and lifting acceleration according to the different object sizes tended to be less in cerebellar participants compared to controls. The interaction between weight and subject group was significant for load force rate and lifting acceleration, indicating that cerebellar participants differentiated less clearly between the different sizes in their prediction of these lifting related parameters compared to control participants. This surprising finding suggests that different internal models may be responsible for the adjustment of grip forces and load forces during lifting.

Different parts of the motor apparatus are involved in generation of load and grip forces. Shoulder and upper arm are involved in generating load forces, whereas grip forces are generated more distally. One explanation would therefore be that primary motor disorders such as ataxia and tremor affect more the proximal lifting synergies than distal grip force
control causing increased variability or voluntary interventions by a cerebellar participant. However, no increase of variability for the load force parameters is obvious in figure 4C,D and simultaneous recordings during a reach-to-grasp task showed that sign of ataxia and incoordination were even stronger for grip forces than for simultaneously registered proximal movement components (Brandauer et al. 2008).

Importantly, evidence in support of the idea of separate, independently adapted memory representations for the grip and load force control has already been reported (Cole 2006; Quaney et al. 2005; Flanagan et al. 2003; Salimi et al. 2003, 2000). Flanagan et al. (2003) found that grip force adapted faster than arm trajectory to novel loading of a grasped object. Cole, Quaney and colleagues showed that while the generation of an unrelated grip force impulse influenced the next grip force during lifting of a constant object (Quaney et al. 2003), the generation of an unrelated vertical load forces before lifting did not influence load force development during the subsequent lift (Cole et al. 2008). Because the grip force depends on additional factors, like friction or the safety margin, whereas the load force depends only on the physical characteristics of the object, the internal model for grip force control might include memories that are influenced by unrelated actions. These data suggest that different sensorimotor memories or internal models govern the adjustment of grip force and load force according to object properties. Our findings provide new support for this differentiation and further suggest that the load force components are processed at least partly within the cerebellum while grip forces are predicted by processes outside the cerebellum.

**Grip force adaptation**

Both controls and cerebellar participants adapted to the true object weight, that is, within a few trials grip forces were the same for the large and the small object. As also obvious from the lacking interactions with the factor of group, adaptation was largely normal in the cerebellar participants. These results corresponds to reports about successful adaptation
of the grip forces to weight during repeated lifting of objects (Fellows et al. 2001; Muller and Dichgans 1994) and adaptation to different loads when varying the frequency of continuous vertical movements of hand-held objects in cerebellar participants (Rost et al. 2005). It is, however, at odds with reports of perturbed adaptation during visual perturbations and changes in force fields in cerebellar participants (Tseng et al. 2007; Maschke et al. 2004; Deuschl et al. 1996). Whether this discrepancy also results from differences between adaptation of grip force and adaptation of arm movement control cannot be resolved from the present data.
References


Chouinard PA, Large ME, Chang EC, Goodale MA. Dissociable neural mechanisms for determining the perceived heaviness of objects and the predicted weight of objects during lifting: An fMRI investigation of the size-weight illusion. *In press*.


Acknowledgements

The authors wish to thank Prof. Volker Aurich and Dr. Andreas Beck for providing the ECCET-software and offering their support. We also thank Mrs. Beate Brol for her help in data analysis.
Grants

This study was supported by a joint grant from the Deutsche Forschungsgemeinschaft (DFG TI 239/8-1 and HE 3592/4-1) to D. Timmann and J. Hermsdörfer, by grants from the Bundesministerium für Bildung und Forschung (BMBF FKZ 01GW0571) to J. Hermsdörfer, by a grant from the medical school of the University of Duisburg-Essen to K. Rabe (Interne Forschungsförderung D/D/107-40130/IFORES) and by a grant from the Deutsche Heredo-Ataxie Gesellschaft to K. Rabe.
Figure legends

FIG 1. Two objects of different size but equal weight (A) were alternately lifted about 4 cm (indicated by white paper strip; A, B). The grip force sensor, which was used as a handle, could quickly be changed between both objects (B). To ensure comfortable grasping, the objects were positioned in front of the participant and were located on a board, which was moved by the examiner. The handle of both objects was positioned in the same grasping height (A, B).

FIG 2. Participants were instructed to indicate the estimated object weight on an analogue scale before (A) and after the trial (C). Figure B illustrates the difference (in cm) between the marks for the small and for the large object. After lifting the objects, all participants estimated the small object to be the heavier one.

FIG 3.
Recordings of grip force, load force, acceleration and calculated grip and load force rates are shown for a representative control and two cerebellar participants (12 and 13 in Table 1) during the first lift of the large and small object. The cerebellar participant 13 presents with the least and participant 12 with the most severe ataxia. Grip force and the initial rate of grip force increase are higher for the large object than for the small object. In particular, the time to lift-off is prolonged for the small object as obvious from the acceleration signal. While participant 13 applied high grip forces and increasing rates, the highly affected participant (12) produced relatively low grip forces and low increase rates which is different to the group data.

FIG 4. Average values and standard errors of maximum grip force, maximum grip and load force rate, maximum acceleration, and time to lift-off in the group of cerebellar and control
participants separated by object size. After initial anticipation of parameters according to object size, parameters adapt in relation to the true object weight in the control and cerebellar group.

**FIG 5.** Mean difference of parameters between the first lift of the large and of the small object (means and standard deviations). Control subjects show a significant higher difference of load force rate and lifting acceleration than cerebellar participants. Δ, difference; *, $P < 0.05$; **, $P < 0.01$. 
A. Max. grip force
B. Max. grip force rate
C. Max. lifting acceleration
D. Max. load force rate
E. Time to lift off

- Controls - small object
- Controls - large object
- Patients - small object
- Patients - large object
<table>
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<tr>
<th>Subject Number</th>
<th>Diagnosis</th>
<th>Gender</th>
<th>Age</th>
<th>SARA-Score total</th>
<th>SARA-Score right hand</th>
<th>Cerebellum in % TICV</th>
<th>Degree of atrophy (% controls)</th>
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</thead>
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<td>F</td>
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<td>0.0/12</td>
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<td>93.85</td>
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</table>

M, male; F, female; ADCA, autosomal dominant cerebellar ataxia; SAOA, sporadic adult onset ataxia; SCA, spinocerebellar ataxia; SARA, Scale of the Assessment and Rating of

Table 1: Characteristics of cerebellar subjects
Ataxia; TICV, total intracranial volume; Degree of atrophy (% controls), cerebellar volume of individual participant (in % TICV) expressed as percentage of the mean volume of all controls (in % TICV) set as 100%. The mean cerebellar volume (% TICV) was 8.94 % in the controls.
Table 2: ANOVA considering the first paired lifting trial

<table>
<thead>
<tr>
<th></th>
<th>Within-group factors (F; P)</th>
<th>Between-group factor (F; P)</th>
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<tr>
<td></td>
<td>Size</td>
<td>Size by group</td>
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<tr>
<td>Grip force</td>
<td>63.26; &lt; 0.001</td>
<td>n.s.</td>
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<tr>
<td>Grip force rate</td>
<td>22.70; &lt; 0.001</td>
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<td>5.14; 0.030</td>
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<td>66.74; &lt; 0.001</td>
<td>13.05; 0.001</td>
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<tr>
<td>Time to lift-off</td>
<td>8.90; 0.005</td>
<td>n.s.</td>
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</tbody>
</table>

Table summarizes the effects of size (large vs. small object) and group (cerebellar vs. control participants) on parameters characterizing the grasping and lifting action (peaks of grip force and grip force rate, peak load force rate, lifting acceleration, and time to lift-off).
Table 3: ANOVA considering the first eight paired lifting trials

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Within-group factors (F; P)</th>
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</tbody>
</table>

Table summarizes the effects of size (large vs. small object), lifting trial (1 - 8), and group (cerebellar vs. control participants) on parameters characterizing the grasping and lifting action (peaks of grip force and grip force rate, peak load force rate, lifting acceleration, and time to lift-off).
Table 4: ANOVA considering the last eight paired lifting trials

<table>
<thead>
<tr>
<th>Within-group factors (F; P)</th>
<th>Between-group factor (F; P)</th>
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<tr>
<td>Size</td>
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<tr>
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<tr>
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</tr>
<tr>
<td>Time to lift-off</td>
<td>n.s.</td>
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</tbody>
</table>

Table summarizes the effects of size (large vs. small object), lifting trial (9 - 16), and group (cerebellar vs. control participants) on parameters characterizing the grasping and lifting action (peaks of grip force and grip force rate, peak load force rate, lifting acceleration, and time to lift-off).