Size–Weight Illusion, Anticipation, and Adaptation of Fingertip Forces in Patients With Cerebellar Degeneration

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Submitted 23 September 2008; accepted in final form 24 November 2008

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 a 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. Eighteen 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 with the small object in the control and cerebellar groups. For the load-force rate and lifting acceleration, effects of anticipation were significantly less in the cerebellar compared with 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 that receives no or few efferents from the cerebellum. The findings of preserved anticipation and adaptation of grip forces in cerebellar patients, however, were 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 objects are lifted, grip and load forces are produced according to the physical characteristics of the object, such as the object’s 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. 1991a,b, 1993). Based on the predicted weight of an object initially apply less grip and load forces to the smaller object and higher grip forces to the larger object. Different from the sustained false perception of an object’s weight, grip force is adapted to the true weight of the object within a few lifting trials (Flanagan and Beltzner 2000). These findings support the hypothesis that perceptual and sensorimotor systems process an object’s information in different ways (Flanagan and Beltzner 2000; Goodale et al. 1991, 1994; Milner and Goodale 1995). Which anatomical correlates are involved within the CNS is not completely understood. Perceptual 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 that are continuously updated to anticipate and adapt grip forces to the certain properties of the object (Hermsdörfer et al. 2005; Kawato et al. 1987, 1992, 1999, 2003; Nowak et al. 2007). 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 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 (Nowak et al. 2002; Rost et al. 2005). The ability to anticipate an object’s properties—such as the size–weight relationships and adjusting 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; Müller 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, both to visual perturbations and to changes in force fields, is impaired in cerebellar participants (Deuschl et al. 1996; Maschke et al. 2004; Tseng et al. 2007).

The aim of the present study was to investigate possible contributions of the cerebellum to perceptual SWI and grip-force control based on the expected and the real weight of an object. It was hypothesized that cerebellar participants were impaired in anticipatory grip-
ing the weight of the objects. Cerebellar participants may apply the same (high) grip force to the small and large objects 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 weight of an object 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.

**METHODS**

**Participants**

In all, 18 participants (Table 1) with isolated cerebellar degeneration [11 male, 7 female; mean age 61 (SD 9.6) yr] 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) yr] participated in the study. In the cerebellar group, 12 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 primarily affect the cerebellar cortex (Gomez et al. 1997). The severity of cerebellar symptoms was assessed by an experienced neurologist (D.T.) based on the Scale for the Assessment and Rating of Ataxia (SARA; Schmitz-Hubsch et al. 2006). In the group of cerebellar participants the mean SARA score was 12.1 (SD 6.5; range 0–24; maximum SARA score 40). All participants gave informed consent approved by the ethics committee of the medical faculty of the University of Duisburg-Essen (Essen, Germany). The experiment was conducted in accordance with the Declaration of Helsinki.

**Magnetic resonance (MR) imaging 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 three-dimensional (3D) sagittal MRI of the entire brain was made using a T1-weighted magnetization-prepared rapid-acquisition gradient echo (MPRAGE; repetition time = 2,400 ms, time to echo = 4.38 ms, field of view = 256 mm, 160 slices, voxel size 1.0 × 1.0 × 1.0 mm³) sequence. Images were used to calculate the volumes of the cerebellum, cerebrum, and total intracranial volume (TICV). 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 computed tomography data. Details of analysis have been reported previously (Brandauer et al. 2008; Dimitrova et al. 2006). In brief, the brain stem was semiautomatically segmented and separated from the cerebellar peduncles, which were included in the cerebellar volume. Next the cerebellum was semiautomatically 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 zones (for details see Brandauer et al. 2008). For further analysis the means of the right and left intermediate and 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 a percentage of the mean volume of all controls set as 100% \{degree of atrophy (% controls) = \frac{\text{cerebellar volume (in % TICV)}}{\text{mean cerebellar volume in controls (in % TICV)}} \times 100\}.

**Size–weight illusion**

Participants were instructed to lift three objects of equal weight (380 g; 3.7 N) but different size (large object: 15.9 × 15.9 × 15.9 cm³; medium object: 9.8 × 9.8 × 9.8 cm³; small object: 6.3 × 6.3 × 6.3 cm³). All objects were made of wooden boards with a metal block fixed in the center 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.

**TABLE 1. Characteristics of cerebellar subjects**

<table>
<thead>
<tr>
<th>Subject Number</th>
<th>Diagnosis</th>
<th>Gender</th>
<th>Age</th>
<th>Score Total</th>
<th>Score Right Hand</th>
<th>Cerebellum in % TICV</th>
<th>Degree of Atrophy, % controls</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>SCA6</td>
<td>F</td>
<td>68</td>
<td>15.0/40</td>
<td>5.0/12</td>
<td>5.94</td>
<td>66.44</td>
</tr>
<tr>
<td>2</td>
<td>SCA6</td>
<td>F</td>
<td>69</td>
<td>15.0/40</td>
<td>3.0/12</td>
<td>7.54</td>
<td>84.34</td>
</tr>
<tr>
<td>3</td>
<td>SCA6</td>
<td>F</td>
<td>59</td>
<td>18.5/40</td>
<td>5.0/12</td>
<td>7.99</td>
<td>89.37</td>
</tr>
<tr>
<td>4</td>
<td>SAOA</td>
<td>F</td>
<td>61</td>
<td>9.5/40</td>
<td>2.0/12</td>
<td>7.55</td>
<td>84.45</td>
</tr>
<tr>
<td>5</td>
<td>SCA6</td>
<td>F</td>
<td>69</td>
<td>12.5/40</td>
<td>4.0/12</td>
<td>7.36</td>
<td>82.76</td>
</tr>
<tr>
<td>6</td>
<td>SCA6</td>
<td>F</td>
<td>63</td>
<td>12.0/40</td>
<td>3.0/12</td>
<td>7.73</td>
<td>86.47</td>
</tr>
<tr>
<td>7</td>
<td>ADCA III</td>
<td>F</td>
<td>43</td>
<td>4.0/40</td>
<td>1.0/12</td>
<td>5.71</td>
<td>63.87</td>
</tr>
<tr>
<td>8</td>
<td>SAOA</td>
<td>M</td>
<td>50</td>
<td>11.5/40</td>
<td>3.0/12</td>
<td>7.86</td>
<td>87.92</td>
</tr>
<tr>
<td>9</td>
<td>SAOA</td>
<td>M</td>
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<td>15.5/40</td>
<td>3.0/12</td>
<td>6.81</td>
<td>76.17</td>
</tr>
<tr>
<td>10</td>
<td>SCA6</td>
<td>M</td>
<td>66</td>
<td>14.0/40</td>
<td>3.0/12</td>
<td>6.48</td>
<td>72.48</td>
</tr>
<tr>
<td>11</td>
<td>SCA6</td>
<td>M</td>
<td>72</td>
<td>6.5/40</td>
<td>2.0/12</td>
<td>7.90</td>
<td>88.37</td>
</tr>
<tr>
<td>12</td>
<td>SCA6</td>
<td>M</td>
<td>62</td>
<td>24.0/40</td>
<td>11.0/12</td>
<td>6.30</td>
<td>67.34</td>
</tr>
<tr>
<td>13</td>
<td>SCA6</td>
<td>M</td>
<td>52</td>
<td>1.5/40</td>
<td>0.0/12</td>
<td>8.94</td>
<td>100.00</td>
</tr>
<tr>
<td>14</td>
<td>SAOA</td>
<td>M</td>
<td>62</td>
<td>20.5/40</td>
<td>6.0/12</td>
<td>6.99</td>
<td>78.19</td>
</tr>
<tr>
<td>15</td>
<td>SCA6</td>
<td>M</td>
<td>50</td>
<td>7.0/40</td>
<td>0.0/12</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>16</td>
<td>SCA6</td>
<td>M</td>
<td>74</td>
<td>18.0/40</td>
<td>4.0/12</td>
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<td>75.62</td>
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<tr>
<td>17</td>
<td>SAOA</td>
<td>M</td>
<td>76</td>
<td>13.0/40</td>
<td>4.0/12</td>
<td>6.87</td>
<td>76.85</td>
</tr>
<tr>
<td>18</td>
<td>SAOA</td>
<td>M</td>
<td>61</td>
<td>7.0/40</td>
<td>1.0/12</td>
<td>8.39</td>
<td>93.85</td>
</tr>
</tbody>
</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 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 (in % TICV) was 8.94% in the controls.

The object was placed in front of the participant aligned to his/her center (midsagittal plane) about 30 cm in front of the sternum. The small object was placed onto a base so that the center of the handle was always in the same position without regard to 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 about 60–80° anteverision, the elbow was flexed at about 100–110°, and the hand was slightly supinated. Participants were instructed to move quickly but not abruptly while lifting the objects. Lifting, holding, and replacing the object had to be performed within 6 s. Participants first lifted the medium object for eight trials to become 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 then the small object. Our intention was to maximize the differences in forces used for the first lift of the large and small objects. 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 fifth and the last pair of lifting the small and large objects, participants were asked to choose the object that felt heavier. Before the first lifting trials of the medium object and after the last lifting pair of the small and large objects, participants were requested to mark on a visual analogue scale with a length of 20 cm the presumed weight of the small and large objects. A drawing of a weight at the bottom end of the scale indicated a heavy weight, whereas 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 centimeters) 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 object’s surface) between the thumb and both 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 liftoff, 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 analyzed 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 (cutoff frequency, 12 Hz), which provide a nonparametric estimation of regression functions by moving weighted averages (Marquardt and Mai 1994). Time to liftoff was set as the time difference between grip-force onset and onset of acceleration (i.e., liftoff).

To assess the effects of anticipation, parameters of the first lifting trial of the large object and of the small object were compared. ANOVA with repeated measures was performed with grip-force parameters as dependent measures, trial (first lifting trial of the large and the small objects) and size (large vs. small object) as within-group factors, and group (cerebellar vs. control) as between-group factor. Significant main effects of size indicate the effects of anticipation and significant size × 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 two successive blocks of 8 paired trials. ANOVA with repeated measures was performed with grip-force parameters as dependent measures, size (large vs. small object) and trial (1–8 and 9–16) as within-group factors, and group (cerebellar vs. controls) as between-group factor. Significant size × trial effects indicate effects of adaptation and significant size × trial × group effects differences in adaptation between cerebellar and control participants.

Finally, degree of anticipation and degree of adaptation were correlated with ataxia scores 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 the difference of force parameters between the first lifting trials of the large and small objects. The extent of adaptation was calculated as the quotient between the difference of the first two lifting trials (i.e., 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–Geisser were performed when appropriate.

Results

Perceptive size–weight illusion

When asked to visually examine the heaviness of objects 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 fifth lift and the last lift 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. Figure 2 illustrates the difference of the estimated weight between the small and large objects using the analogue scale before the first lifting and after the last lifting trial. Before the first lift, the mean difference between the small and large objects 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 objects.

Effects of anticipation

Statistical results are summarized in Table 2.

Grip force and grip-force rate. Figure 3, A and B shows grip force and grip-force rate recordings of the first lifting trial of the large and small objects in a characteristic control and two cerebellar participants (12 and 13 in Table 1). 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 the slow force increase and low grip-force rates, but nevertheless showed the normal pattern. Effects of anticipation of parameters were present in both the 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 lower forces to the small object. Group data confirm these findings (Fig. 4, A and 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. 5, A and B). ANOVAs considering the first lifting trial of the large and small objects revealed significant effects of size (all values of P < 0.001; Table 2), but no significant size × group interactions (P ≥ 0.542; Table 2).

Load-force rate and lifting acceleration. The difference in load-force rate and lifting acceleration between the large and small objects was less in the cerebellar participants compared with the control (Fig. 3, C–E). Accordingly, group data showed greater differences between the large and small objects during the first lifting trials in controls compared with the cerebellar group (Fig. 5, C and D). ANOVA revealed significant effects of size (P < 0.001) and significant size × group interactions (P ≤ 0.030).

Time to liftoff. Figure 4E shows that in both the control and the cerebellar participant time to liftoff is longer if the weight of the object is underestimated and shorter if the weight of the object is overestimated. The difference between both objects in time to liftoff was larger in the control group than in the cerebellar group (Fig. 5E). ANOVA considering the first paired lifting trial showed a significant effect of size (P = 0.005), but no size × 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 weight of an object within a few trials, that is, participants used similar forces for both objects (Fig. 4, A and 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 × size effects (P ≤ 0.002), but no trial × size × group interaction effects (P ≥ 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 × 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 × group interaction: P = 0.284). Trial × size and size ×

Table 2. ANOVA considering the first paired lifting trial

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Within-Group Factors (F; P)</th>
<th>Between-Group Factor (F; P)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Size</td>
<td>Size × Group</td>
</tr>
<tr>
<td>Grip force</td>
<td>63.26; &lt;0.001</td>
<td>n.s.</td>
</tr>
<tr>
<td>Grip-force rate</td>
<td>22.70; &lt;0.001</td>
<td>n.s.</td>
</tr>
<tr>
<td>Load-force rate</td>
<td>15.48; &lt;0.001</td>
<td>5.14; 0.030</td>
</tr>
<tr>
<td>Lifting acceleration</td>
<td>66.74; &lt;0.001</td>
<td>13.05; 0.001</td>
</tr>
<tr>
<td>Time to liftoff</td>
<td>8.90; 0.005</td>
<td>5.64; 0.023</td>
</tr>
</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 actions (peaks of grip force and grip-force rate, peak load force rate, lifting acceleration, and time to liftoff).
trial × 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. ANOVA considering the first and last eight lifting pairs revealed a significant group effect \((P = 0.001\) and \(P = 0.005\); Tables 3 and 4).

**Load-force rate and lifting acceleration.** Load-force rate and lifting acceleration adapted in relation to the true weight of the object within a few trials. ANOVA considering the first eight paired lifting trials (Table 3) showed significant trial × size effects \((P < 0.021)\). Trial, trial × group, and trial × size × group interaction effects were not significant for load-force rate \((P \geq 0.207)\), but trial × size and trial × size × 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. 4, C and D). ANOVA of the last eight paired lifting trials (Table 4) showed no significant size effect \((P = 0.575)\) or trial, trial × size, and size × trial × group interaction effects \((P \geq 0.126)\).

Time to liftoff was longer in the cerebellar group compared with the control group. Considering the first and last eight paired lifting trials, there was a significant group effect \((P = 0.021\) and \(P = 0.002\); Tables 3 and 4), reflecting the longer time to liftoff 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 yr; 3 female, 6 male) compared with the controls. Results did not differ significantly from those considering all cerebellar participants except that in addition to grip force and time to liftoff, the load-force rate reached a statistically 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) < 7.0%; n = 8; mean age 62.5 yr; 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 from 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 liftoff, 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 zones; anterior and posterior lobes; 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 and 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 weights of objects and adapted forces in relation to the true weight of objects. 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 weights of objects tended to be less in cerebellar participants compared with 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 objects 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 were still larger for the large object and smaller for the small object in their first lifting trials. Thus despite the fact that 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 independence of conscious belief or knowledge about characteristics of an object 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 in the weight of objects are observed without manual interaction (Nowak and Hermsdorfer 2003).

The perceptual SWI can be explained by sensory mismatch between the expected weight of an object 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, the density of an object appears to be the most salient object feature and participants may base their decision on this attribute rather than on the weight of an object (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 feature of an object that is most relevant for understanding its heaviness, which is the relative density of the object in this particular situation. This does not exclude the fact that cerebellar participants have disorders in correctly perceiving the heaviness of the object.

In addition to its known role in motor control and learning, a role of the cerebellum in nonmotor functions including perception is increasingly discussed. Somatosensory deficits, such as difficulty in weight perception (Holmes 1917) or kinesthesia (Grill et al. 1994; but for a contrary view, see Maschke et al. 2003), have been reported after cerebellar lesions. Studies using cortical somatosensory evoked potentials indicated that participants with cerebellar damage are impaired in the 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 reafferents (Blakemore et al. 2001). In a functional magnetic resonance imaging (fMRI) study, the cerebellum was particularly activated by externally produced

**Fig. 5.** Mean difference of parameters between the first lift of the large and of the small objects (means and SDs). Control subjects show a significantly higher difference of load-force rate and lifting acceleration than cerebellar participants. *, difference; **P < 0.05; **P < 0.01.

### TABLE 3. ANOVA considering the first eight paired lifting trials

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Within-Group Factors (F; P)</th>
<th>Between-Group Factor (F; P)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Size</td>
<td>Size × Group</td>
</tr>
<tr>
<td>Grip force</td>
<td>24.2; &lt;0.001</td>
<td>n.s.</td>
</tr>
<tr>
<td>Grip-force rate</td>
<td>13.8; 0.001</td>
<td>n.s.</td>
</tr>
<tr>
<td>Load-force rate</td>
<td>24.7; &lt;0.001</td>
<td>n.s.</td>
</tr>
<tr>
<td>Lifting acceleration</td>
<td>44.3; &lt;0.001</td>
<td>n.s.</td>
</tr>
<tr>
<td>Time to liftoff</td>
<td>n.s.</td>
<td>n.s.</td>
</tr>
</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 actions (peaks of grip force and grip-force rate, peak load-force rate, lifting acceleration, and time to liftoff).
tickling, that is, in a situation where 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 arises from a sensory discrepancy. However, whereas processes involving an internal model are highly automated, the weight estimation affords an explicit judgment 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. 2009; 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 Sowards 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 to 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 that are involved in the size–weight illusion. A recent fMRI study investigated brain regions that are responsible for computing object size, mass, and density for lifting tasks and that 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 the 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. 2009). 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 characteristics of an object, such as weight, surface friction, and shape (Jenmalm and Johansson 1997; Johansson 1998; Johansson and Westling 1984, 1988). Our findings confirm the results of previous studies, that participants with cerebellar disorders produce excessive grip forces (Babin-Ratte et al. 1999; Fellows et al. 2001; Hermsdorfer et al. 2005; Nowak et al. 2002, 2004) and show a prolongation of the time interval between the onset of grip-force development and the liftoff of the object (Kagerer et al. 1998). The increase of grip force and the extended time to liftoff 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 weight of an object. The expectation is formed from previous experience, in particular, the knowledge that objects of different size and same material (i.e., constant density) have different weights. 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 (Flanagan and Tresilian 1994; Hermsdorfer et al. 2005; Kawato et al. 2003; Nowak and Hermsdorfer 2006; Wolpert and Ghahramani 2000). 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 representations are built and stored. The present findings, however, suggest that internal representation of an object’s characteristics is not exclusively represented in the cerebellum.

Although grip forces were generally larger in cerebellar participants than in controls and the time to liftoff was prolonged, cerebellar participants’ grip forces anticipated the size of an object 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. (2005) 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 overlearned 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 pre-
served 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 (Babin-Ratte et al. 1999; Nowak et al. 2002; Rost et al. 2005). Although 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 is mainly based on the weight of the object and surface friction. It is possible that the cerebellum plays an important role in processing dynamics (Bastian et al. 1996; Topka et al. 1998), although it is of minor importance when selecting grip forces according to visually inferable object characteristics. In a recent fMRI study, Chouinard et al. (2009) reported activation in somatosensory and posterior parietal areas when objects of varying size were lifted as compared with 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 color association after transcranial magnetic stimulation of the ventral premotor cortex, also suggesting a cortical representation of an object’s 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 overlearned 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 in addressing this issue. Negative findings in this study are unlikely explained because cerebellar participants were not severely affected enough. Some 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 altered grip force anticipation in comparison to only mildly affected participants.

Different from 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 with 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 with 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 Fig. 4. C and D and simultaneous recordings during a reach-to-grasp task showed that signs 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; Flanagan et al. 2003; Quaney et al. 2005; Salimi et al. 2000, 2003). 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, although 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 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 an object’s 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, whereas grip forces are predicted by processes outside the cerebellum.

**Grip-force adaptation**

Both controls and cerebellar participants adapted to the true weight of an object, that is, within a few trials grip forces were the same for both the large and the small objects. As also obvious from the lack of 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 handheld 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 (Deuschl et al. 1996; Maschke et al. 2004; Tseng et al. 2007). 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.

**Acknowledgments**

We thank Prof. Volker Aurich and Dr. Andreas Beck for providing the ECCET-software and offering support and B. Brol for help in data analysis.

**Grants**

This study was supported by Deutsche Forschungsgemeinschaft Joint Grants DFG TI 239/8-1 and HE 3592/4-1 to D. Timmann and J. Herrmsdörfer, Bundesministerium für Bildung und Forschung Grant BMBF FKZ 01GW0571 to J. Herrmsdörfer, University of Duisburg-Essen Medical School Grant Interne Forschungsförderung D/D/107–40130/IFORES to K. Rabe, and by a grant from the Deutsche Heredo-Ataxie Gesellschaft to K. Rabe.

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