FORMATION AND LATERALIZATION OF INTERNAL REPRESENTATIONS UNDERLYING MOTOR COMMANDS DURING PRECISION GRIP

ANDREW M. GORDON,* HANS FORSSBERG† and NOBUAKI IWASAKI‡

Nobel Institute for Neurophysiology and Department of Pediatrics, Karolinska Institute, S-10401 Stockholm, Sweden

(Received 1 July 1993; accepted 26 October 1993)

Abstract—The capability to store and retrieve weight-related information from a lift to scale the force output during a subsequent lift was examined in 10 healthy adults and 50 children (age 2–10 years), as well as a 22-year-old patient with corpus callosum agenesis. Subjects lifted a test object between the thumb and index finger while the isometric fingertip forces were measured. The results suggest that both healthy children and adults can transfer weight-related information between the right and left hand, although a lateralization was found. Also, the storage and retrieval of weight-related information appears to be a dynamic process dependent on both previous sensory information and knowledge of future movements. Late maturation of interhemispheric connections and asymmetric loss of some information during the transfer between hemispheres suggest a lateralization of the internal representation. The patient with a corpus callosum agenesis supported this hypothesis.

INTRODUCTION

LITTLE is known about the lateralization and interhemispheric transfer of various motor memories. When GLICKSTEIN and SPERRY [20] studied the intermanual transfer of learned tactile discrimination in Rhesus monkeys, they found that gross aspects of the testing procedure acquired during learning with the trained hand could be transferred to the untrained hand in all cases, while the specific ability to transfer learned tactile discrimination could not be transferred when the corpus callosum was sectioned. Studies on the transfer of mirror-drawing and maze-learning in partially brain-bisected humans indicate that the corpus callosum is not essential for bilateral transfer of learned motor tasks, although the capacity is partly reduced in some tasks [44]. These partially diverging results indicate that different components of learned movements (i.e. different types of motor memories) may vary in the degree to which they are subjected to transfer between the hemispheres. Several motor programs are organized and controlled in a general context, independent of the side of the body in which the motor task is performed (i.e. with common features which are independent of specific muscles employed or parameters varied). For example, during

*Address for correspondence: Andrew M. Gordon, Department of Physiology, 6-255 Millard Hall, University of Minnesota, Minneapolis, MN 55455, U.S.A.
†To whom reprint requests should be addressed.
‡Present address: Institute of Special Education, University of Tsukuba, 1-1-1 Tennodai, Tsukuba-city, Ibaraki 305, Japan.
writing, there are spatio-temporal patterns which are invariant, regardless of the limb (but see Ref. [51]). At the same time, other features, such as the size of the letters, are controlled separately for each limb [39].

During manipulation of small objects, the programming of isometric fingertip forces is initially based on internal representations of the object’s physical properties (i.e. sensorimotor memories). Weight- and friction-related information gained during previous lifts [30–32, 48], as well as visual and haptic size information from the current lift [24–26], form the basis of an anticipatory control strategy in which the forces are scaled in advance. Such feedforward control is highly purposeful since it allows quick and accurate manipulation that is not subject to limitations imposed by strict dependence on moment-to-moment sensory feedback control. Such control of the grip (squeeze) force and load (vertical lifting) force is characterized by generally unimodal and rather symmetric (bell-shaped) force-rate profiles during the phase of isometric force increase [32] (cf. [5]). The maximum force rates are scaled to match the object’s weight, and the rates are appropriately dampened prior to lift-off. This allows smooth vertical acceleration of the object and prevents unnecessarily high grip forces.

Such precise coordination is not innate (for review see Refs [21] and [22]). Instead of unimodal force-rate profiles, young children display multi-peaked force-rate profiles, in which the grip and load forces increase in small increments [12]. This suggests that they do not program the force increase in one pulse. During the later half of the second year, the force-rate profiles start to become more unimodal. At the same time, the amplitude of the force rates begins to be influenced by the object’s weight and friction during the previous lift, i.e. the children begin to scale the force output using anticipatory control [13]. This ability continues to improve for several years. By 3 years of age visual size cues may be used to estimate the weight for the force scaling [23] and by 6–8 years of age, the vertical acceleration of the object can be controlled properly [13].

It is not known where the internal representation of the object’s physical properties, which is used to parameterize the motor output during the precision grip, is localized, whether it is distributed in both hemispheres or lateralized and transferred between the hemispheres depending on the hand used (cf. Refs [30] and [32]). In the present study, we compare the development of control mechanisms underlying the transfer of weight-related information between the left and right hands.

**METHOD**

Ten healthy adults (age 18–40) and 50 children (age 2–10) participated in Experiment 1. The subjects were grouped by age, with each group consisting of 10 subjects. The age groups were 2, 3–4, 5–6, 7–8 and 9–10 years and the adults. An additional 22-year-old patient with complete corpus callosum agenesis (J.F.) participated in Experiment 1. He was admitted to the hospital following a seizure, starting with focal symptoms in the right arm and hand, followed by a general grand mal seizure. The complete agenesis was detected by CT and MRI scans. The patient had no earlier history of neurological impairments and none were found during careful neurological examination. In addition, the 10 healthy adults also participated in Experiments 2 and 3. All subjects were found to be right-handed based on the hand used during common motor tasks and exhibited normal motor and mental behavior. Handedness was also verified in the youngest children by placing a raisin in various positions in front of them and noting that the right hand was used to grasp the raisin. All subjects were unaware of the purpose of the study.

The grip instrument has been described in earlier studies (see Ref. [12] for details). It had two parallel vertical grip surfaces on the top (35 x 35 mm, 20 mm apart) covered with fine sand paper (No. 200) (Fig. 1). Appropriate masses could be inserted in a slot in the base of the object, providing a total weight of 300 or 900 g, without changing its visual appearance. The load force and the grip force at each grip surface were measured with strain gauge transducers (d.c.—160 Hz). The signals from the test object were sampled at 400 Hz and digitized with 12 bit
 resolution into a flexible computer system (sc/zoom, University of Umeå). The grip force rate (dGF/dt) and the load force rate (dLF/dt) were calculated from the mean of the grip forces at each contact surface and the sum of the load force at each contact surface, respectively, using a ± 5 point numerical differentiation (see Ref. [12]). The first distinct peak of the grip and load force rates was measured. This almost always corresponded to the maximum force rates. The duration of the loading phase (period of isometric load force increase) was measured from the point when the load force showed a consistent increase until the object moved from its support (i.e. the load force overcame the gravitational force of the object). The vertical acceleration was measured from the overshoot in the peak load force following lift-off (see Ref. [10] for details). In addition, the grip force at the onset of positive load force and the peak grip force were measured.

The subjects sat on a chair in front of an adjustable table, which was positioned such that the forearm was approximately parallel to the floor when the object was grasped. The subjects grasped the instrument from above with the precision grip (between the thumb and index finger), lifted the instrument 5–10 cm and maintained the lift for ca. 5 sec before replacing and releasing the object. The youngest children used additional fingers for support, and often replaced the object prior to the 5 sec. The task was carefully explained to each subject and demonstrated by the experimenter.

The weight presentation and hand order were either serial (remained the same across trials and were predictable) or random (varied in an unpredictable order). In each experiment, four conditions were used for analysis: left–left, right–right, right–left, left–right. For each condition, five lifts were recorded for each weight (300 and 900 g) (although 10 lifts were recorded for each weight for patient J.F.). Thus, 40 trials were recorded for each subject. The time between subsequent trials was approx. 10 sec.

An age group x weight analysis of variance (ANOVA) was performed on the means of each subject to assess statistical differences (P < 0.05) in the response parameters for each condition and to compare the influence of the object's weight between each experiment for the adults. Patient J.F. was analyzed separately and served as his own control (i.e. 300 and 900 g lifts were compared for each condition using t-tests). Where appropriate, Newman–Keuls post-hoc tests were performed. For descriptive purposes, the relative difference between the peak force rates were calculated as a percent difference between the peak force rates employed for lifts with the 300 g weight and the peak force rates employed for lifts with the 900 g weight.

EXPERIMENT 1

Random presentation of weights. Serial hand order

This experiment tested whether somatosensory weight-related information could be used equally well in the right and left hands as well as transferred between hands to scale the grip and load force rates in advance. All subjects participated in this experiment. Three series of lifts were performed and the order varied across subjects: (i) 21 consecutive lifts with the right hand only, (ii) 21 consecutive lifts with the left hand only, and (iii) 41 lifts alternating every trial between the right and left hands (i.e. left–right–left–right, etc.). The 300 and 900 g
weights were presented in an order which was unpredictable to the subjects (i.e. the same weight was often reinserted). The weight was changed behind a screen between trials, and the object was replaced on a pad covering the table to prevent sound cues which might disclose the actual weight. Thus, subjects could predict which hand would be used during the subsequent lift, but not the weight (i.e. random presentation of weights but serial hand order). Five practice trials with each weight were given before the start of the experiment. Since it has been shown earlier that only one lift is required to update the internal representation [27, 32], only the second lift of two serial lifts with the same weight was analyzed for each condition. Most children under 7 years of age required two sessions to complete the experiment. The youngest children were motivated to lift the instrument by placing a picture card under it. Influences of the object's previous weight during lifts with the contralateral hand would suggest that somatosensory weight-related information can be transferred between hemispheres.

**Results**

*Force scaling during consecutive lifts with each hand.* When subjects knew the hand order in advance, but not the weight, the influence of the object's weight in the preceding lift on the force scaling in both the healthy adults and children was similar to that described in previous studies, although the magnitude of the influence was smaller than previously described [13, 32]. The peak grip and load force rates were higher for lifts with the 900 g weight compared to lifts with the 300 g weight as indicated by a main effect for weight in both the right and left hands at all ages ($P<0.05$) (Fig. 2E,F).

As seen in Fig. 2, the load force rate was influenced by the previous weight already in the 2-year-old children in both the right and left hands, i.e. the peak load force rate was higher for serial lifts with the 900 g weight compared to serial lifts with the 300 g weight. The relative difference between the force rates was slightly larger in the left hand (about 35%) than in the right hand (about 25%) at that age (Figs 2A,B and 3A,B). The influence on the load force rate increased steadily in lifts with the right hand until 7–8 years of age, where it reached the adult level (Fig. 3A), while no trend was seen in lifts with the left hand, due to the large influence already in the youngest children (Fig. 3B).

In contrast, the amplitude of the grip force rate was not greatly influenced by the object's weight in the 2-year-old children, for either the right hand (about 5%) or left hand (about 10%) (Fig. 3A,B). The influence on the scaling of the peak grip force rate increased in the left hand at 3–4 years of age, and in the right hand at 5–6 years of age (Fig. 3A,B). There was a successive increase in the influence of the object's weight with increasing age, until adult-like scaling (i.e. large differences in the force rates) was seen at 5–6 years of age for the left hand and 7–8 years of age for the right hand (Fig. 3A,B).

Similar to the healthy adults, patient J.F. had higher peak grip and load force rates for lifts with the 900 g weight compared to lifts with the 300 g weight in both the right and left hands ($P<0.05$) (Table 1). The influence was similar for the grip and load force rates ($P>0.05$) and similar to the healthy adult subjects (Fig. 3A,B).

*Force scaling during alternating lifts between hands.* When the lifts alternated between the right and left hand, while the weights were randomly presented, the load force rate was still influenced by the weight during the previous (contralateral) lift in healthy adults and children. The peak load force rate was larger for lifts with the 900 g weight compared to lifts with the 300 g weight, as seen by a main effect for weight at all ages ($P<0.05$) (Fig. 2G,H). The transfer was not symmetrical since the relative difference in the load force rate was
Fig. 2. Grip force, grip force rate, load force and load force rate from the index finger in the right hand (A, E), left hand (B, F), the right hand following a lift with the left hand (C, G) and the left hand following a lift with the right hand (D, H) as a function of time for three superimposed lifts with the 300 g weight (dotted) and 900 g weight (solid) for (A–D) a 2-year-old child, and (E–H) an adult. Note—the grip and load force rates are shown using a ± 10 point numerical differentiation. While the 2-year-old child in this figure had longer loading phase durations for the lifts involving alternations between hands, this was not the overall case for the 2-year-old group.
greater during alternations from the right to the left hand (about 30–40%) than vice versa (about 10–30%) at all ages ($P<0.05$) (Fig. 3C,D). Likewise, it was smaller during alternations from the left to the right hand than consecutive lifts with the right hand (about 25–40%) ($P<0.05$) (Fig. 3A,C), while there was little difference between left-handed lifts preceded by a lift with the ipsilateral or contralateral hand (Fig. 3B,D). There was no clear age-related trend in the load force rate for either hand.

![Graphs A-D showing relative change in grip and load force rate between 300 and 900 g as a function of age during lifts with different hand combinations.](image)

Fig. 3. The relative difference (mean and S.E.M. of individual means) in grip force rate (dotted) and load force rate (solid) between the 300 and 900 g weight as a function of age during lifts with (A) only the right hand, (B) only the left hand, (C) the right hand following a lift with the left hand, and (D) the left hand following a lift with the right hand.

The grip force rate was influenced less during alternations between hands (i.e. the force rates for the different weights were more similar than within hand lifts) (Fig. 2C,D). The ANOVA yielded a main effect for weight at all ages during alternations from the right hand to the left hand ($P<0.05$) (Fig. 3D), but not from the left to the right hand ($P>0.05$) (Fig. 3C). During the later alternation the opposite influence was seen until 7–8 years of age (Fig. 3C). Alternations from the right hand to the left hand did not demonstrate a clear age-related trend (Fig. 3D).

For patient J.F., the grip force rate was uninfluenced by the object’s weight during alternations from the left hand to the right hand ($P>0.05$) (Fig. 3C) (Table 1). For
Table 1. Grip and load force rates for patient J.F.

<table>
<thead>
<tr>
<th></th>
<th>Grip force rate (N/sec)</th>
<th>Load force rate (N/sec)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>300 g</td>
<td>900 g</td>
</tr>
<tr>
<td>R–R</td>
<td>46.9 (15.0)</td>
<td>62.8 (15.5)</td>
</tr>
<tr>
<td>L–L</td>
<td>23.7 (12.6)</td>
<td>36.5 (11.6)</td>
</tr>
<tr>
<td>L–R</td>
<td>42.4 (11.6)</td>
<td>43.5 (12.1)</td>
</tr>
<tr>
<td>R–L</td>
<td>25.4 (5.4)</td>
<td>32.3 (8.2)</td>
</tr>
</tbody>
</table>

Note: Numbers represent mean (±S.D.) of 10 lifts in each condition.

alternations in the other direction, the grip force rate was higher for lifts with the 900 g weight, but not significantly ($P > 0.05$) (Table 1). As in the healthy adults and children, the load force rate was influenced more than the grip force rate, but only significantly for lifts alternating from the right to left hand ($P < 0.05$) (Fig. 3C,D). The influences on both the grip and load force rates were less during alternations between hands than during consecutive lifts with the same hand.

Comparison of time characteristics and force coordination in left vs right hands. The previous analyses suggested a tendency for earlier development of force scaling in the left hand than in the right hand. To investigate possible differences between the two hands, the temporal and force parameters, as well as the coordination of grip and load force were compared for lifts with the 300 g weight in both the right and left hands.

The force coordination was determined by (i) the simultaneous onset of grip force and load force (grip force at load force zero), (ii) the parallel grip and load force increase (grip force as a function of load force), and (iii) bell shaped force-rate profiles (grip and load force rates plotted against load force) (see Refs [12], [13] and [32] for details). In both hands, the development proceeded as described in earlier studies [12, 13] (see Introduction). Younger children exhibited more variability between trials, but no systematic difference could be seen between hands in any of the age groups. There was no difference between hands for the grip force at the onset of positive load force, loading phase duration, peak grip force or the peak vertical acceleration in any age group ($P > 0.05$ in all cases), and no overall differences could be seen by observing the grip force as a function of load force, or the force-rate profiles.

EXPERIMENT 2

Serial presentation of weights. Serial hand order

The results of the previous experiment indicated a smaller influence of the object's weight on the grip and load force rates than previously described in adults, even when subsequent lifts were performed with the same hand [32]. The present experiment was designed to test whether the small influence was due to the differences in the presentation of the weights. The 10 healthy adults from Experiment 1 performed three series of lifts: (i) five consecutive lifts of the 300 g weight and then five consecutive lifts of the 900 g weight with the right hand only, (ii) five consecutive lifts of the 300 g weight and then five consecutive lifts of the 900 g weight with the left hand only, and (iii) 10 consecutive lifts of the 300 g weight and then 10 consecutive lifts of the 900 g weight alternating every trial between the right and left hands (i.e. left–right–left–right, etc.). Five practice lifts were performed before lifting each weight for
the first time. The order in which these three series were performed varied across subjects, but subjects always knew the weight of the object and which hand would be used during subsequent lifts (i.e. serial weight presentation and hand order). A finding of higher relative influences of the object weight on the force rates than in the previous experiment would suggest that the force scaling depends not only on information from previous lifts, but also on how relevant this information is for future lifts.

Results

When both the weight and the hand order were known, the relative difference in both the grip and load force rates between the two weights was in all conditions (e.g. right–right, left–left, right–left, left–right) more than double those differences in Experiment 1, when the weight was unknown ($P < 0.05$ in all cases) (Figs 4 and 5). The force rates were nearly twice as high for the 900 g weight compared to the 300 g weight ($P < 0.05$). No differences were seen between lifts following alternations between hands compared to consecutive lifts with the same hand ($P > 0.05$ in all cases) (Figs 4 and 5).

Fig. 4. Grip force, grip force rate, load force and load force rate from the index finger in the right hand, left hand, the right hand following a lift with the left hand and the left hand following a lift with the right hand as a function of time for three superimposed lifts by one subject with the 300 g weight (dotted) and 900 g weight (solid) in each experiment. Note—the grip and load force rates are shown using a ± 10 point numerical differentiation.
EXPERIMENT 3

Random presentation of weights. Random hand order

The predictable weight presentation and hand order (Experiment 2) resulted in larger influences on the force rates compared to when only the hand order was predictable (Experiment 1). The present study examined the lifting behavior when both the weight presentation and hand order were unpredictable (i.e. random presentation of weights and hand order). The 10 healthy adults from Experiments 1 and 2 participated in this experiment. Eighty lifts were performed, in which the weight lifted and hand used were presented in a pseudorandom order. Only the second lift of two consecutive lifts with the same weight was analyzed for each condition. A finding of lower relative influences of the object weight on the force rates than in the previous study would further support the hypothesis that the storage of weight-related information for force scaling is dependent on the knowledge and planning of future lifts.

Results

When adult subjects did not know which weight would be presented and which hand would be used in subsequent lifts, the grip force rates were higher for the 900 g weight compared to the 300 g weight ($P < 0.05$) only during consecutive lifts with the same hand (Fig. 5). The load force rates were higher for the 900 g weight for all conditions ($P < 0.05$), but the relative difference between the force rates used for the 300 and 900 g weights was smaller for lifts involving alternations between hands compared to consecutive lifts with the same hand. The relative difference in the force rates between the 300 and 900 g weight was similar to Experiment 1 ($P > 0.05$ except left–left) and much lower than Experiment 2 ($P < 0.05$ in all cases) (Figs 4 and 5). The lower relative differences for lifts following alternations between hands compared to consecutive lifts with the same hand ($P < 0.05$ in both cases) (Figs 4 and 5) suggest that when subjects did not have any information about subsequent lifts, the influence from the previous lifts was greater when the lifts required use of the same hand than
the opposite hand. The loading phase durations were similar to those in Experiment 1 \( (P > 0.05) \).

**DISCUSSION**

*Inter-hemispheric transfer of somatosensory information*

Adults store weight-related information gained during manipulation with one hand, and use it to scale the load and grip force output during subsequent lifts with the opposite hand. Similarly, tactile information from one hand, related to the friction between the thumb and fingertips, can influence the grip force output of the anesthetized contralateral hand [30]. Independent finger movement during manipulation and precision grip is controlled by the contralateral motor cortex via the corticospinal tract (e.g. Refs [35], [37] and [42]). Somatosensory information during "active touch" [19] and proprioception is also lateralized to the contralateral hemisphere, transmitted via the dorsal-column-medial-lemniscal system [2, 43, 45]. In studies of brain-bisectioned subjects in which the corpus callosum and the anterior commissure are sectioned, this type of somatosensory information is not transferred to the other hemisphere [16]. This implies that during a bimanual task, relevant somatosensory information related to the object's weight and friction is likely transferred from one hemisphere to the other via the forebrain commissures. The influence of weight-related information was often reduced when derived from preceding lifts in the contralateral hand compared to consecutive lifts with the same hand. Therefore, some information may be lost during this transfer.

Recent findings by Georgopoulos and his colleagues suggest that there may be a hemispheric asymmetry in motor cortical activity during contralateral and ipsilateral finger movements [33]. Using magnetic resonance imaging (MRI) at high field strength, they found while the right motor cortex was activated mainly during contralateral finger movements, the left motor cortex was activated during both contralateral and ipsilateral finger movements. Thus, during our task, transitions from the right to the left hand may be easier than vice versa since the left hemisphere may be actively involved in the control of both hands, requiring little or no transfer between hemispheres. Since the right hand would only be controlled by the left motor cortex, transitions in the opposite direction would require inter-hemispheric transfer, possibly resulting in some loss of sensory information.

*Laterlization of manipulospatial functions*

During development of the precision grip, there is an asymmetry in the scaling of the force output. The peak grip force rate is influenced by the object's weight earlier in lifts with the left hand than in lifts with the right hand and earlier during alternations from the right hand to the left hand than vice versa. A similar effect is seen in the load force rate until the age of 9–10 years. These data may suggest better scaling of the isometric force output in lifts using the left (non-preferred) hand during the early stages of development.

Handedness emerges early during ontogeny (cf. Ref. [3]). Despite extensive research (see Ref. [8] for review), the mechanisms underlying handedness and whether qualitative differences exist in motor skills between the preferred and non-preferred hand are largely unknown. It has been suggested that the preferred hand is controlled by neural mechanisms which are better able to make use of sensory information [11]. The present results suggest that other than slight differences in the force scaling early during development, precision grip is not performed differently in the non-preferred hand, at least for right-handed individuals.
This is consistent with the findings that several motor tasks requiring fine movements are performed equally by both hands (see Ref. [38]; for contrast cf. Ref. [6]).

The inability to scale the force output in the right hand following lifts with the left hand in younger children is probably due to a reduced capability to use weight-related information gained from the opposite hand in combination with an overall decreased scaling capability (cf. Ref. [13]). The corpus callosum is one of the last structures of the brain to mature. Myelination does not begin until the end of the first year and continues until at least 10 years of age [29]. Similarly there is a late onset (3.5 years) and slow maturation (over 8.5 years) of the forebrain commissures [41]. A slow development of tactile information transfer between the hemispheres has also been reported for children under 5 years of age [14]. The asymmetry of the transfer between hands could be due to an asymmetric development of the forebrain commissural connections, e.g. neuronal cell death (cf. Ref. [34]) with asymmetric loss of axons of the corpus callosum, which has recently been proposed as a mechanism underlying the development of handedness (cf. Refs [49] and [50]).

The asymmetry could also be a reflection of the lateralization of the brain. WEISENBURG and McBRIDE [47] reported that patients with right-hemisphere lesions, unlike those with left-hemisphere lesions, performed poorly on tests involving manipulation and appreciation of forms and spatial relationships. Several clinical studies have confirmed the disruptive effects of right-hemisphere lesions on “manipulospatial” function (e.g. Refs [1], [46]; cf. [18]). Studies on brain-bisectioned subjects have shown a superior function of the right hemisphere on a variety of manipulative tasks, including the perception of spatial stimuli and exploratory finger movements [4, 17]. GAZZANIGA and LeDOUX [18] suggested that the motor inferiority of the left hemisphere is due to a redistribution of function in the posterior association area. That is, “synaptic space” previously (in a phylogenetic sense) devoted to “manipulospatial” functions in the left hemisphere is sacrificed in the process of acquiring language. Hence, coordinated manipulative skills in the right hand would require information from the right hemisphere via the forebrain commissures, in addition to the “reduced” left association cortex. Indeed, manipulative movements are bilaterally represented in frontal motor areas [40].

MARZI et al. [36] recently used a meta-analysis of unimanual reaction time studies and found an overall advantage of the left visual field over the right and the right hand over the left. They suggest that this is due to an asymmetry of interhemispheric transfer of information, with transfer from the right to the left faster than the reverse. A similar pattern in reaction times was recently found in children [9], suggesting that the asymmetry may emerge early during development. Before the forebrain commissures have matured, neural circuits generating lifts with the right hand (i.e. motor centers in the left hemisphere) may not have access to weight-related information from the right hemisphere. Along with the maturation of the forebrain commissures, the information from the right hemisphere becomes available to the neural circuits in the left hemisphere, allowing a more proper force scaling.

The results of the patient with callosum agenesis (J.F.) in the present study may support a lateralization of the weight-related internal representation. J.F. could scale the peak grip and load force rates in both hands during consecutive lifts with the same hand. In contrast, during alternations between hands, he could only scale the peak load force rate in the left hand following lifts with the right hand, but not in transitions in the other direction. A similar impairment was reported in a patient whose posterior half of the callosum was sectioned [15]. This patient had no difficulties locating a tactile stimulus on the phalanx of a finger as long as the stimulus and response were restricted to the same hand. However, when the task
required finding the corresponding point on the opposite hand, there were deficits with the cross-integration of information only from the left to right hand. The asymmetry of transfer of weight-related information in our task could be a part of a lateralization process, favoring the transfer of somatosensory information to the right hemisphere and to neural structures storing this information.

Formation of the internal representation—different motor strategies

The weight-related information derived from the previous lift in Experiment 1 did not influence the force output as strongly as earlier reported (cf. Refs [13] and [32]). This weaker effect is probably due to the random presentation of weights since the influences doubled during consecutive lifts with the same weight (Experiment 2).

Subjects may have compromised the anticipatory control strategy during Experiment 1 by using a "probing strategy" in which the forces are generated in small increments, carefully waiting for feedback from lift-off to terminate the force increase [25]. This strategy is used when subjects are not confident about the object's physical properties. However, unlike during a "probing strategy," the force rate profiles were always continuous and mainly bell-shaped, and the peaks were still slightly influenced by the previous weight. Also, the loading phase durations were similar. This suggests that subjects may have used a default strategy in which the force output is scaled towards the middle of the gravitational forces of the two objects. This occurs during isometric contractions toward a target force when subjects are not sure which of two targets will be presented (cf. Refs [7] and [28]).

It appears that knowledge of how weight information from previous lifts will be used in subsequent lifts also influences the storage of such information since there was little influence on lifts with the contralateral hand when also the hand order was randomized (Experiment 3). Thus, the storage and retrieval of weight-related information is a dynamic process dependent on both previous sensory-related information and knowledge of future movements.

Acknowledgements—The first author was supported by a grant from the Stiftelsen Wenner-Gren Center. This study was supported by the Swedish Medical Research Council (5925), Stiftelsen Sven Jerrings Fónd, First of Mayflower Annual Campaign for Children's Health, Stiftelsen Solstuckan, Sunnerdahls Handikappfónd. We are grateful to Professor Roland Johansson for providing the equipment and software, as well as providing helpful comments on an earlier version of this manuscript. We also thank Ann-Christin Eliasson for assistance with data collection, and Ingmarie Eriksson and Sue Scrivener for assistance with data entry.

REFERENCES


