

Manipulating an Equivocal World

How Force Control and Weight Perception
use Probabilistic Information

Dissertation
zur Erlangung des Doktorgrades
der Philosophischen Fakultät
der Christian-Albrechts-Universität
zu Kiel

vorgelegt von
Leif Trampenau

Kiel 2017

Erstgutachterin:Dr. Gesa Hartwigsen

Zweitgutachter:.....Prof. Dr. Thilo van Eimeren

Tag der mündlichen Prüfung:10. Mai 2017

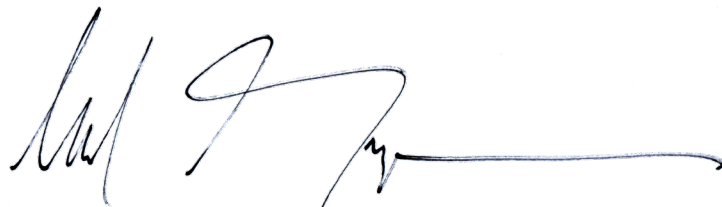
Durch den Prodekan Prof. Dr. Elmar Eggert zum Druck genehmigt am:11. Mai 2017

Hiermit erkläre ich, dass ich die vorliegende Dissertation selbständig angefertigt habe und keine anderen als die angegebenen Quellen und Hilfsmittel von mir eingesetzt worden sind. Des weiteren versichere ich, dass die vorliegende Dissertation weder ganz noch zum Teil bei einer anderen Stelle im Rahmen eines Prüfungsverfahrens vorgelegen hat.

Kiel, den 24. Februar 2017

I hereby declare that this thesis is my own work and information derived from the literature or unpublished work of others has been acknowledged in the text and a list of references provided. This thesis has not been submitted in any form for another degree at any university.

Kiel, February 24th, 2017



Leif Trampenau

Danksagung

An dieser Stelle möchte ich all denen meinen Dank aussprechen, die mich bei der Entstehung dieser Arbeit unterstützt haben. Zuerst gilt mein Dank Prof. Dr. Thilo van Eimeren, der mir die Möglichkeit gegeben hat, in diesem faszinierenden Forschungsbereich zu arbeiten. Er hat mit seinen Ideen und Überlegungen den Grundstein für diese Arbeit gelegt. Ich danke ihm auch für das Vertrauen, dass er als Leiter des Labors für funktionelle Bildgebung an der Klinik für Neurologie (UKSH) mir hinsichtlich meiner Arbeit entgegengebracht hat. Bei Dr. Gesa Hartwigsen möchte ich mich herzlich für die Betreuung und die Begutachtung dieser Arbeit bedanken. Darüber hinaus hat sie mir mit vielen freundlichen Hinweisen und Ratschläge weitergeholfen.

Ein großes Dankeschön geht an Prof. Dr. Johann Kuhtz-Buschbeck, der mich während der gesamten Zeit meiner Arbeit begleitet und tatkräftig unterstützt hat. Ausdrücklich möchte ich ihm für die vielen lehrreichen und inspirierenden Gespräche danken, die maßgeblich diese Arbeit beeinflusst haben, sowie für die fruchtbare und produktive Zusammenarbeit bei dem Verfassen wissenschaftlicher Artikel.

Mein Dank gilt des Weiteren Frau PD Dr. Kirsten Zeuner. Durch ihre finanzielle Unterstützung hat sie zum Abschluss dieser Arbeit beigetragen.

Mein weiterer Dank gilt dem Team und meinen Freundinnen und Freunden aus der Klinik für Neurologie: Alexander Baumann, Arne Knutzen, Katharina Probst und Inken Tödt. Insbesondere danke ich Oliver Granert, der mir beim Programmieren mit Rat und Tat zur Seite stand und sich immer Zeit für meine Fragen genommen hat.

Dr. Christian Schlenstedt danke ich für die englischsprachliche Unterstützung. Stephan Wolf danke ich für die Zusammenarbeit im MRT und die Unterstützung bei technischen Fragen.

Weiterer Dank gilt PD Dr. Franz Faul, der mich von Beginn meines Studium an begleitet hat und bei dem ich als HiWi lernte, wissenschaftlich zu denken und zu arbeiten. Ich danke ihm vor allem für die vielen Gespräche, die ich mit ihm zum Thema meiner Arbeit geführt habe.

An dieser Stelle möchte ich vor allem meinen Eltern Sigrid und Horst Trampenau danken, die mich stets bei meinen Vorhaben unterstützt und gefördert haben. Ohne die Freiheiten, die sie mir in meiner Entfaltung gegeben haben und ohne ihr Vertrauen in meine Entscheidungen wäre diese Arbeit nicht entstanden. Ich danke auch meinem verstorbenen Großvater Ernst-Otto Gericke, dessen Zuversicht in die eigene Schaffensfähigkeit mich stark beeinflusst hat.

Zuletzt danke ich meiner Frau Dr. Nina Lau, die mir die Ruhe und emotionale Ausgeglichenheit gegeben hat, diese Arbeit zu schreiben. Ich danke ihr für die umfangreiche und liebevolle Unterstützung, ihre Toleranz und Akzeptanz. Nun freue ich mich darauf, gemeinsam unseren Sohn Klaas groß zu ziehen.

List of Publications

The present dissertation is based on three research articles referred to in the text as ARTICLES I–III (see appendix).

ARTICLE I Trampenau, L., Kutzt-Buschbeck, J. P., & van Eimeren, T. (2015). Probabilistic information on object weight shapes force dynamics in a grip-lift task. *Experimental Brain Research*, 233(6), 1711–1720.

DOI 10.1007/s00221-015-4244-6

The final publication is available at Springer via
<http://dx.doi.org/10.1007/s00221-015-4244-6>

ARTICLE II Trampenau, L., van Eimeren, T., & Kutzt-Buschbeck, J. P. (2017). Processing of probabilistic information in weight perception and motor prediction. *Attention, Perception & Psychophysics*, 79(2), 404–414.

DOI 10.3758/s13414-016-1266-5

The final publication is available at Springer via
<http://dx.doi.org/10.3758/s13414-016-1266-5>

ARTICLE III Trampenau, L., van Eimeren, T., & Kutzt-Buschbeck, J. P. (in preparation). Parkinsonian patients fail to use probabilistic cues for force scaling in a grip-lift task. In preparation for *Experimental Brain Research*.

Contents

1 Introduction.....	9
 Part I: Theoretical Background	
2 Force Control.....	11
2.1 Mechanisms of Precision Grip-Lift Action.....	11
2.2 Decision-Making for Anticipatory Motor Programming	16
2.3 Motor Programming in Parkinson’s Disease	19
2.4 Summary and Leading Questions	20
3 Scientific Methods and Considerations.....	21
3.1 General Considerations	21
3.2 Experimental Setup.....	23
3.3 Experimental Tasks	25
 Part II: Experiments	
4 Summary of the Empirical Studies	29
4.1 A General Introduction to the Empirical Studies	29
4.2 Probabilistic Information on Object Weight Shapes Force Dynamics in a Grip-Lift Task – ARTICLE I.....	30
4.3 Processing of Probabilistic Information in Weight Perception and Motor Perception – ARTICLE II	32
4.4 Parkinsonian Patients Fail to Use Probabilistic Cues for Force Scaling in a Grip-Lift Task – ARTICLE III	34
 Part III: Perspective	
5 Discussion.....	37

5.1 Using a Probabilistic Paradigm to Study Dexterous Fine Motor Control – ,Proof of Concept‘	37
5.2 Adaption of Probabilistic Information to the Demands of a Task remains Stable over Time	38
5.3 Association between Weight Perception and Force Prediction	40
5.4 Parkinson’s Disease Affects Predictive Scaling of Fingertip Forces.....	41
6 Perspective.....	43
7 Summary	45
8 Summary in German (Deutsche Zusammenfassung).....	50
9 List of Abbreviations.....	61
10 References.....	62
11 Appendix	69

ARTICLE I

Trampenau, L., Kuhtz-Buschbeck, J. P., & van Eimeren, T. (2015). Probabilistic information on object weight shapes force dynamics in a grip-lift task. *Experimental Brain Research*, 233(6), 1711–1720.

ARTICLE II

Trampenau, L., van Eimeren, T., & Kuhtz-Buschbeck, J. P. (2017). Processing of probabilistic information in weight perception and motor prediction. *Attention, Perception & Psychophysics*, 79(2), 404–414.

ARTICLE III

Trampenau, L., van Eimeren, T., & Kuhtz-Buschbeck, J. P. (in preparation). Parkinsonian patients fail to use probabilistic cues for force scaling in a grip-lift task. In preparation for *Experimental Brain Research*.

1 Introduction

An effective strategy for lifting an object is to choose an adequate motor performance prior to manipulation with finger forces scaled anticipatorily toward its properties (Johansson & Westling, 1988). Yet, several object properties, e. g. the weight and the surface condition are first available once the object is grasped and lifted. To guarantee an anticipatory motor strategy one may predict missing object properties. Therefore, visual information related to sensorimotor memories obtained during previous experience with the same object is an important, albeit equivocal source of information. For example, when grasping a juice carton, whose screw cap has obviously been opened previously and whose edges are indented in many places, one may assume that it should be almost empty. However, if the juice carton was full just a few moments ago, one would rather assume that it is almost full. Prior knowledge or experience may help to estimate which of these opportunities seems more likely given the actual sensory information. During this process, choosing an adequate motor performance becomes a case of decision-making based on probabilities. However, it is not resolved if probabilities are used to modify expectations about object properties and how they impact motor control.

The ability to choose an appropriate motor program can be disrupted which leads to abnormalities in the control of forces, e. g. excessively slow movements, staccato movements or problems with the initiation of a movement. These are common motor symptoms of subjects suffering from Parkinson's disease (PD). Conflicting approaches have been presented to explain PD subjects motor deficits. In particular there is disagreement about whether Parkinson's disease affects anticipatory motor control

The present dissertation aims at investigating how different probabilities of equivocal information are used for motor control and weight perception. Part I of this thesis will address the theoretical background. An overview of force control for precision grip-lift action will be given. In this context two main features of force control will be outlined: Adaption and prediction. Furthermore, the role of decision-making for motor control in general will be discussed and changes in motor control of PD subjects will be characterized. Finally, the leading research questions of this thesis will be introduced and the scientific methods explained. In Part II the three research articles of this thesis are presented. In *ARTICLE I* a probabilistic grip-lift paradigm will be established. In a grip-lift task healthy young subjects will use probabilistic advance information about an upcoming object's weight to scale their finger forces predictively. By this precision grip force scaling will be used as objective for the research of force control. In *ARTICLE II* the probabilistic paradigm will be adapted to a perceptual weight adjustment task. This weight adjustment task and the grip-lift task will be used to examine weight perception and force prediction during the interpretation and use of probabi-

listic weight information. ARTICLE III focus on the use of probabilistic cues for force scaling in subjects with Parkinson's disease and healthy control subjects. In Part III of this thesis evidence from the three articles will be discussed and their quintessence will be debated.

This thesis is part of a current research project leaded by Thilo van Eimeren. The purpose of this research project is to examine the role of the dopaminergic frontostriatal circuits in precision grip force scaling. The basal ganglia as part of this pathway have been associated with the control of voluntary motor movements, including precision grip force scaling. However, the role of basal ganglia for voluntary motor movements is still unclear. One prevalent current theory of the role of basal ganglia is the 'reward prediction error' hypothesis. It assumes that the selection of action is based on reward expectations (Schonberg, Daw, Joel, & O'Doherty, 2007). These expectations are updated by so called prediction errors. They code the deviation between the predicted reward expectation prior to execution and the reward actually obtained after finishing an action. Physiological evidence suggests that basal ganglia dopaminergic neurons provide a physiological correlate of the reward prediction error signal (Mirenowicz & Schultz, 1994; Schultz, Apicella, & Ljungberg, 1993; Schultz, Dayan, & Montague, 1997). Based on these considerations the motivation behind this research project is to examine if the selection of precision grip force scaling is influenced by a similar error signal as assumed by the 'reward prediction error' hypothesis. A so called motor load prediction error could code the deviation between the predicted finger forces prior to a lift and the actually needed finger forces obtained after lifting. This will be examined by behavioral methods and functional magnetic resonance imaging (fMRI). The present thesis will provide a detailed behavioral fundament for further neurophysiological examinations to reveal the role of the dopaminergic frontostriatal circuits in precision grip force scaling. The later will not be part of this dissertation.

2 Force Control

The hand is one of the most versatile tools of humanity. From the very beginning of our life we use our hands to interact with the world. One of the most outstanding characteristics of the human hand is the dual functionality of perceiving and acting. Its haptic sense (based on tactile and somatosensory information) is an important component of perception. We use the fingers of our hands to perceive object qualities as surface texture, form, material, temperature and weight. At the same time its manual dexterity enables us to act on the world. With our hands we are able to communicate with other beings using gestures and touch, and we use our hands to reshape our environment through manipulation of objects and the use of tools.

One of the most important manipulatory features of the human hand is the precision grip, when an object is grasped and held between the opposed tactile pads of the tips of the index finger and the thumb. The precision grip serves as a basis for further precision handling which may involve rotation of an object about its own axes or transposition of the object in space (Westling & Johansson, 1984). Two forces are required during the lift of an object with the precision grip. A vertical force called lift force (load force) is recorded parallel to the contact surfaces, and a grip force, perpendicular to the contact surfaces.

In precision grip two control principles of grip and load forces are noteworthy: reactive control (feedback) toward sensory properties of the world and anticipatory (feedforward) control of manipulatory performance toward expected properties of the world (Flanagan & Johansson, 2002). Reactive control of fingertip forces is characterized by an adaptation of grip force toward the load information, whereas both forces are scaled in parallel using an anticipatory control mechanism (Johansson & Westling, 1984). Both control mechanisms are closely linked. Reactive control is essential to correct for discrepancies between actual sensory feedback and the expected sensory feedback, and to update expected properties to reduce future prediction errors (Flanagan & Johansson, 2002).

2.1 Mechanisms of Precision Grip-Lift Action

Precision grip lifting movements have first been described in detail by the pioneer studies of Westling and Johansson (1984), and Johansson and Westling (1984). Six distinct phases of a lifting trial (Fig. 1) can be identified (Johansson & Westling, 1984). The first phase is called the preload phase. It begins from the moment when the index finger and thumb initially touches the object. It is denoted by an increase in grip force while the lift force only reveals small changes (a in Fig. 1). The preload phase ends as

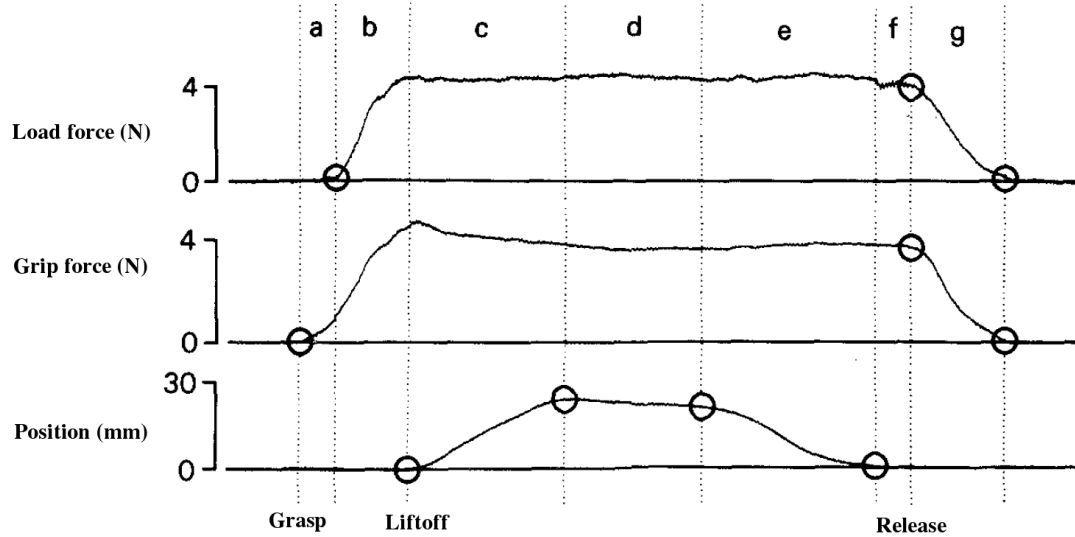


Fig. 1 Load force, grip force, and vertical position as a function of time for a sample trial (weight of object = 400 g, surface structure = sandpaper). The phases indicated are: a - preload phase; b - loading phase; c - transitional phase; d - static phase; e - replacement phase; f - delay; g - unloading phase (adapted from Johansson & Westling, 1984).

soon as the lift force begins to increase in parallel with the grip force, indicating the beginning of the load-phase (b in Fig. 1). As soon as the lift force overcomes the force of gravity the object liftoff and starts to move. This moment denotes the beginning of the transitional phase (c in Fig. 1). Early during the transitional phase the grip force and the lift force reach their peak values. While the grip force decays after its peak at a rate that gradually declined with time, the lift force remains relatively stable on its peak level. The transitional phase is terminated as soon as the object reaches the intended vertical position. From this moment the static phase begins, where grip force and lift force remains on a constant level (d in Fig. 1). During the following replacement phase the object is put down to the table (e in Fig. 1). This movement takes place without marked force changes and is terminated when the object is in contact with the table. This contact gives rise to a small but sudden fall in the lift force whereas grip force remains stable. Following this short delay (f in Fig. 1) the grip force and the lift force declines in parallel, denoted as the unloading phase (g in Fig. 1). This last phase continues until the index finger and thumb releases the object, which then is completely supported by the table. Both grip force and lift force reach zero almost simultaneously.

Beside grip and lift force much attention was given to their rates of change. Force rates are calculated from the difference in force between consecutive samples (Johansson & Westling, 1988). During a lift trial, where grip and lift force are scaled in parallel toward a target force reached in the static phase, the rates of force (i. e. the grip force rate and the lift force rate) are denoted by mainly single-peaked and bell-shaped trajectories, scaled from their onsets to the target force, with low force rates at the point

when the object liftoff (Johansson & Westling, 1988). Trajectories with this shape are considered typical for lifts with adequately produced forces in accordance with an object's properties (Johansson & Westling, 1988).

Force Adaption

To lift an object successfully the nervous system has to scale the finger-tip forces toward properties of the object. Too much grip force may result in damage of the object or the hand and might cause unnecessary muscle fatigue, whereas too weak grip force would cause slipping the object. To prevent slipping of a hand-held object the grasping force is adjusted to the friction between the fingertips and the object surface (Aoki, Niu, Latash, & Zatsiorsky, 2006; Aoki, Latash, & Zatsiorsky, 2007; Birznieks, Burstedt, Edin, & Johansson, 1998; Burstedt, Flanagan, & Johansson, 1999; Cadoret & Smith, 1996; Edin, Westling, & Johansson, 1992; Forssberg, Eliasson, Kinoshita, Westling, & Johansson, 1995; Goodwin, Jenmalm, & Johansson, 1998; Johansson & Westling, 1984; Kinoshita, Bäckström, Flanagan, & Johansson, 1997; Westling & Johansson, 1984). Somatosensory information related to the frictional condition between the fingers and the object are used to adjust the grasping force (Johansson & Westling, 1987). Reducing the friction between the skin of the fingers and the surface of an object requires enhanced grip force to lift the object. Among others, the frictional condition is influenced by the object's weight. If mass is added to an object (increasing the amount of normal force), one needs to grasp even harder to get it lifted. Consequently, lifting a heavy object requires more grip and lift force than lifting a lighter object with equal surface texture (Johansson & Westling, 1988). Additionally, the rates of force (i. e. the grip force rate and the lift force rate) are influenced by the frictional condition. Johansson and Westling (1988) demonstrated that heavy objects are lifted with higher grip and lift force rates than light objects.

The surface texture of an object is another property influencing the frictional condition. A slippery surface decreases the friction between the object and the fingers, whereas a rough texture increases the friction. Lifting an object with a slippery contact-surface involves higher grip force than lifting an equally-weighted object with a rough contact-surface texture (Johansson & Westling, 1984).

Force Prediction

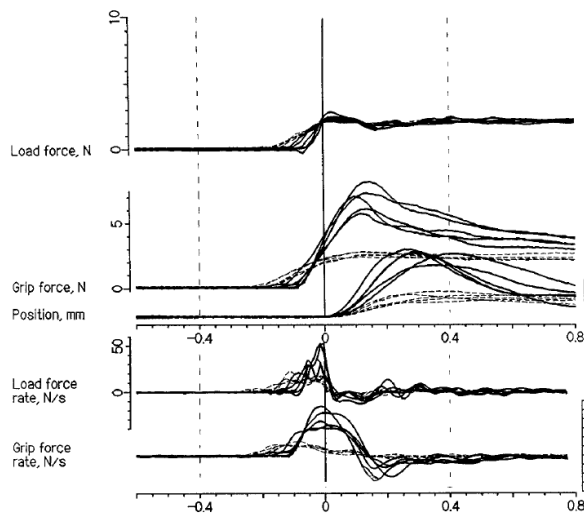
Adaption of fingertip forces toward object properties is important to successfully perform a grip-lift task. However, a purely adaptive strategy of force control is not sufficient to handle an object effectively (Johansson, 1998). Under many circumstances this would result in prolonged load-phase duration with frequent force undershoots.

An essential feature of dexterous fine motor control during object manipulation is the predictive adjustment of forces prior to liftoff according to pertinent task demands. Anticipatory control of grip and lift force ensures a smooth and critically damped lift and obviates initial force overshoots or undershoots, which would entail corrections (Johansson & Westling, 1988). Since explicit sensory information about actual object properties is not available until liftoff, the peak values of the force rates (reached prior to liftoff) are considered to reflect preprogrammed forces, as they vary in parallel with the targeted object weight (Chouinard, Leonard, & Paus, 2005; Jenmalm, Schmitz, Forssberg, & Ehrsson, 2006; Johansson & Westling, 1988; Li et al., 2009; Nowak, Glasauer, & Hermsdörfer, 2013).

Experience gathered during previous lifting tasks has an important influence on predictive scaling of fingertip forces (Jenmalm & Johansson, 1997; Johansson & Westling, 1984; 1988; Westling & Johansson, 1984). Johansson and colleagues referred to this phenomenon as a 'sensorimotor memory'. This memory process influences the scaling of fingertip forces from the very beginning of a lifting task. The influence of sensorimotor memory on predictive force scaling has been experimentally demonstrated with disrupted tactile afferent signals. As a result of finger anesthesia, the motor output is oriented toward the last successful lift, e. g. the last sensorimotor memory. Johansson and Westling (1984) showed this for lifts of an object with a slippery texture preceded by several lifts of an object with a rough texture. The grip force applied to the slippery object was targeted toward the rough texture of the previously lifted object. As a consequence the fingers slid over the slippery surface and the object remained on its position. But, if attending consciously to the firmness of the grip, the grip force increased consecutively during several lifting attempts until the lift finally was accomplished. If once adapted toward the surface texture approximately the same grip force level was targeted in subsequent lifts.

In another experiment demonstrating the influence of sensorimotor memory, Johansson and Westling (1988) used a grip-lift task where an object's weight changed unpredictably after several lifts with a constant weight. When an object was lifted with a lighter weight than the previous lift, the initial force development during the pre-load and loading phase was similar to the previously lifted heavier object (Fig. 2a). In comparison to a lift preceded by the same light object force rate trajectories were obviously steeper and had higher peaks if a lighter object was lifted previously. This higher force rate was accompanied by a shortened load phase resulting in an unexpectedly early liftoff. Peak force rates were reached at the moment the object began to move. By contrast, force rates of lifts preceded by a light weight were approximately scaled to baseline values after liftoff. This higher rate of force development resulted in an elevated lifting position and a pronounced overshoot in grip force compared to a lift of a foregoing equal weight. On the other hand, when an object was lifted with a

(a) Lifts erroneously programmed for a heavier weight



(b) Lifts erroneously programmed for a lighter weight

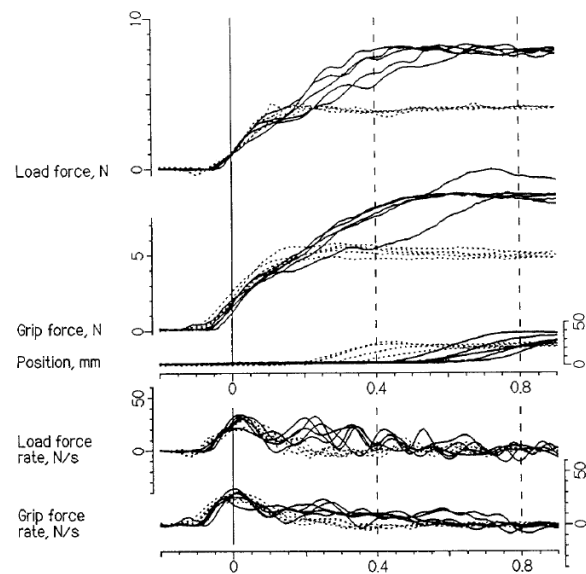


Fig. 2 Initial parts of lifts erroneously programmed for a heavier weight (a): Load force, grip force, vertical position and their time derivatives as a function of time for 5 lifts with 200 g programmed for 800 g (—) and for 5 adequately-programmed 200 g trials (.....). E.m.g. signals refer to the erroneously-programmed 200 g lifts (average data). (b) Initial parts of lifts with 800 g erroneously programmed for a lighter weight (400 g): Load force, grip force, vertical position and their time derivatives as a function of time for 5 sample trials with 800 g (—) preceded by adequately-programmed 400 g lifts (.....). Trials synchronized in time at the moment the load force reached 1 N (time = 0) (adapted from Johansson & Westling, 1984).

heavier weight than the previous lift, the initial force development was similar to that of the previous lighter weight until the lighter object started to move (Fig. 2b). The force rates of the heavy lift showed an approximately simultaneous and equal scaled peak in relation to the previous lighter lift. However, when the movement of the lighter object started, the exerted force was beneath the level required to overcome gravity of the heavy object. Consequently the movement failed to start. During the following part of the loading phase, force increase persisted, but more slowly and with multiple peaks until the force of gravity was overcome and the object liftoff. Consequently, the loading phase was prolonged compared to the previous lighter lift. Still, grip and lift force are processed simultaneously, no matter if the object properties changes unpredictably between two lifts. Simultaneous grip and lift force processing is considered as an essential feature of anticipatory motor control (Johansson & Flanagan, 2009; Johansson & Westling, 1988).

In order to choose an anticipatory motor program the nervous system is not limited to experience from preceding lifts. Visual size cues play an important role in the initial programming of grip force when unfamiliar objects are lifted. Gordon, Forssberg, Johansson, and Westling (1991) and Gordon, Westling, Cole, and Johansson (1993) and Mon-Williams and Murray (2000) showed that visual size cues made a reasonable con-

tribution to the programming of force when lifting a novel object. Both groups showed that peak force rates are scaled to the expected weight, based on visual cues to object size. Mon-Williams and Murray (2000) pointed out, that the influence of the size cue decreases when objects with equal weight but different size were lifted repetitively. Visual cues about object size and material-density (Baugh, Kao, Johansson, & Flanagan, 2012; Buckingham, Cant, & Goodale, 2009), weight distribution (Jenmalm, Dahlstedt, & Johansson, 2000; Johansson, Backlin, & Burstedt, 1999; Wing & Lederman, 1998), and object identity (Gordon et al., 1993) are used to scale the force output adequately prior to object liftoff.

In order to use visual cues to lift an object with adequate exertion of force the nervous system must be able to link visual information to motor programs. Nowak, Koupan, and Hermsdörfer (2007) showed that subjects quickly established memory links between arbitrary sensory cues (object color, auditory signals) and the weight of an object to be grasped and lifted (Nowak et al., 2007). Once this kind of association is learned, the forces are scaled according to the weight that is announced by the advance information (Bensmail, Sarfeld, Ameli, Fink, & Nowak, 2012; Li et al., 2009). Such procedural learning has been demonstrated for explicit sensory cues that unmistakably predicted the object weight (Ameli, Dafotakis, Fink, & Nowak, 2008) or the texture of the gripped surfaces (Cole & Rotella, 2002).

2.2 Decision-Making for Anticipatory Motor Programming

Due to noisy motor commands and imprecise and ambiguous sensory information, the location of our body in relation to objects in the environment is often unclear (Christopoulos & Schrater, 2009). As a consequence, the probability for a correct prediction of particular object properties, e. g. the position, varies. Several studies have shown that the choice of a motor plan takes ambiguity into account. When preparing to grasp a moving object, the aperture of the index finger for a precision grasp has to be adjusted precisely to produce a stable grasp at first contact. The predictability of a moving object's path can influence this motor behavior. In order to minimizing the probability of unstable grasp, the approach angle for a precision grasp tends to align with the maximum uncertainty of the position of the object to be grasped (Christopoulos & Schrater, 2009). Also the predictability of an object's fixed position can impact motor behavior. When reaching for an object, grip aperture widens when the viewing condition is poor, e. g. viewing the object in peripheral vision (Schlicht & Schrater, 2007). When reaching for an object around an obstacle, the minimum distance to the obstacle increases when sensory information is poor (Cohen, Biddle, & Rosenbaum, 2009). Ambiguity may also be related to object properties. The normal mapping bet-

ween material and weight is violated when surface material and core material of an object differ, e. g. when a small brass-filled cube is covered with wood veneer (Ellis & Lederman, 1999). When people repeatedly lift such an unusual object and then predict the weight of a larger object of similar appearance, sensorimotor memory from lifts of the ‘outlier object’ interferes with well-learned prior associations between material and density (Baugh et al., 2012). Hence different internal models regarding the weight of an object can coexist, and predictive scaling of the force depends on the respective probability of each model.

Sensory information can be equivocal. Imagine opening your fridge early in the morning. Still tired you grasp for the opener of the fridge and start pulling it. Without having noticed that the fridge wasn’t closed correctly the door would open rapidly and without control. Out of the corner of your eye, you see how a juice carton starts falling out of the inner retainer of the fridge door. You see that its’ screw cap has obviously been opened previously and that the edges of the carton are indented in many places. Still, you know that you put in an almost full filled juice carton in your fridge yesterday evening. Consequently conflicting weight predictions of the juice carton arise. As a consequence several motor programs can be selected corresponding to the different weight prediction of the juice carton. This leads to the question how the nervous system decides between these different options.

This question is addressed by a contemporary field of research that considers movement planning from the viewpoint of decision-making under risk, when participants have access to different probabilities associated with discrete outcomes, and applies the same mathematical framework that formalizes decision-making in economics and psychology (Nagengast, Braun, & Wolpert, 2010; Wolpert & Landy, 2012; Wu, Delgado, & Maloney, 2009). Following this view, probabilities of predicted outcomes are used to choose a certain motor program among many. The weight predictions of the juice carton from the example may also have different probabilities for their upcoming. For example you could be very sure about that you put in an almost full filled juice carton in your fridge yesterday evening. Consequently, you would use a grasp with finger-forces predictively scaled for a high force level.

Moreover, also costs and benefits of a movement are considered to play a significant role in this decision-making process (Wolpert & Landy, 2012). In the example above costs may arise if one fails to catch the carton due to too weak grip-force exertion or conversely, if the carton is squeezed as a consequence of too high grip-force exertion. On the other side possible benefits of a planned motor program may arise from catching the carton appropriately and saving it from falling on the floor. Wolpert and Landy (2012) suggest, that the decision for a certain motor program could rely on weighing costs and benefits of all possible motor programs.

In preparing a reach for an object, the movement plan can encode where the reach

will land on average (aim-point), which path to take and the expected duration (Wolpert & Landy, 2012). The demands for these movement characteristics differ between tasks and influence the movement behavior. Several studies have demonstrated that the demands for movement characteristics are sensitive to monetary reward or punishment. In a study by Trommershäuser, Maloney and Landy (2003) subjects could earn money by performing an accurate movement. On a display two regions were presented within a blue rectangle, one green target region and a red penalty region. After a go signal subjects had 700 ms to touch the screen or they would incur a 'timeout' penalty of 700 points. If subjects succeeded to touch the green region before timeout they were rewarded with 100 points, whereas they would incur a variable (0, 100, 500 points) pre-defined penalty if touching the red region. To predict subjects' motor behavior reward landscapes were calculated reflecting the expected reward for each aim-point and experimental condition. The reward landscapes took subject's motor variability into account. Results of Trommershäuser et al. (2003) show, that subjects choose target points that maximized the expected reward in accordance with the prediction by the reward landscapes.

Another movement characteristic important for motor behavior is the path of a movement. Zhang, Maddula and Maloney (2010) designed an economic task to investigate navigation in landscapes, during which traveling in different kinds of terrain incurred different costs. Subjects' task was to move their index finger along a surface of a touch screen from a starting point to a target point. There was no time limit for initiation or execution of the movement. The screen consisted of a field region and a desert region. Each unit of distance moved incurred a cost (e. g. moving in the yellow desert region cost three times more per unit distance than moving in the field region, and moving in the red desert region cost five times more per unit distance than moving in the field region). Participants were encouraged to find the route where the costs per distance were lowest. As a main result, subject's routes varied systematically with the cost of the desert region. However, their choice resulted in 30 % less income on average than the optimal path.

The timing of a movement is crucial in many motor tasks. Planning an adequately timed movement requires the nervous system to take its internal duration-dependent temporal variability and the task-dependent timing variability into account (Rakitin et al., 1998). Hudson, Maloney and Landy (2008) rewarded movements performed within a specified time window, and penalizing slower movements in some conditions and faster movements in others. They found that subjects compensated almost optimally for temporal uncertainty, both the internal duration-dependent and experimentally imposed overall uncertainty, in the sense of maximizing expected gain in the task.

2.3 Motor Programming in Parkinson's Disease

Studying motor control in subjects with deficits in this area may help to understand how the motor system works. Impaired motor control is a common deficit associated with Parkinson's disease (Turner & Desmurget, 2010). Several studies showed delayed movement initiation (Brumlik & Bosches, 1966; Sheridan, Flowers & Hurrell, 1987; Stelmach, Teasdale, Phillips, & Worringham, 1989), and slowness in movement execution (Brumlik & Bosches, 1966; Fellows, Noth, & Schwarz, 1998; Gordon, Ingvarsson, & Forssberg, 1997; Müller & Abbs, 1990) during dexterous fine motor control. These changes reflect the prominent symptom of bradykinesia in Parkinson's disease.

Turner and Desmurget (2010) viewed Bradykinesia as an impaired regulation of speed and size of movement (motor gain). In Parkinson's disease gain control is known to be impaired in several motor domains including reaching (hypometria), handwriting (micrographia), and speech (hypophonia). A common observation in these domains is that Parkinson's disease affects a downregulation in motor gain (Desmurget, Grafton, Vindras, Grea, & Turner, 2003; Ramig, Fox, & Sapir, 2008; Viviani, Burkhard, Chiuve, Corradi-Dell'Acqua, & Vindras, 2009).

In line with Turner and Desmurget (2010) it has been reported that PD subjects show severe problems using advance weight information to adapt the rate of grip force prior to liftoff (Fellows et al., 1998; Müller & Abbs, 1990). Problems in anticipatory fine motor control became also apparent in studies reporting on a dis-coordination of grip and load force processing (Alberts, Tresilian, & Stelmach, 1998; Alberts, Elder, Okun, & Vitek, 2004). In line with this Turner and Desmurget (2010) argued that motor abnormalities in PD subjects could be driven by deficient mechanisms of fine motor control.

On the other side, Gordon, et al. (1997) argued that PD subjects are able to use an anticipatory control strategy to scale the force of their fingers prior to liftoff. In their study PD subjects used cues (size of an object) announcing an object's weight to scale their peak force rates. Moreover, Forssberg, Ingvarsson, Iwasaki, Johansson and Gordon (2000) showed that PD subjects initiated the main grip and load force drive simultaneously, and with a overall parallel increase of grip and load forces. Similar results have been presented by Ingvarsson, Gordon and Forssberg (1997).

Mazzoni, Hristova and Krakauer (2007) presented evidence that PD patients are capable of moving as fast as healthy subjects, but that they implicitly prefer to move more slowly, thereby expending less energy. Mazzoni et al. (2007) hypothesized that parkinsonian bradykinesia reflects impairment in the link between motivation (drive) and the control of movement gain.

2.4 Summary and Leading Questions

Recent studies showed that visual cues predicting different object properties are used to scale force adequately prior to object liftoff (Baugh et al., 2012; Buckingham et al., 2009; Goodwin et al., 1998; Gordon et al., 1993; Jenmalm & Johansson, 1998; Jenmalm et al., 2000; Johansson et al., 1999; Wing & Lederman, 1998). However, when lifting an object we often have to deal with equivocal information about its properties. Execution of movement has been shown to be influenced by ambiguity regarding the predictability of particular object properties (Christopoulos & Schrater, 2009; Cohen et al., 2009; Schlicht & Schrater, 2007). Ambiguity can be viewed as information that is compatible with multiple outcomes. Thus, the information given by a visual cue could be compatible with multiple weights. The probability for the upcoming of these different weights may vary e. g. according to prior knowledge. Under these circumstances various conflicting motor programs could exist with different force profiles, each preprogrammed for one of the possible weights. The selection for one of these motor programs could rely on the highest probability, or one could weigh out the odds and choose a motor program with forces scaled to a weight in between both prediction. So far, very little is known about how probability information is used for the selection of a motor program.

An effective strategy for lifting objects is to choose an adequate motor program prior to manipulation with finger forces scaled predictively toward an object's properties (Flanagan & Wing, 1997; Johansson & Westling, 1984; 1988). This was shown by manipulating several object properties including the weight. In situations with equivocal information about object properties conflicting predictions about perceptual object properties and motor programs may exist. However, it remains unclear whether the perceptual weight interpretation reflects the predicted force scaling of a selected motor program.

Revealing insights into how the motor system has been presented by studies examining impaired motor control in PD subjects. In several studies changes of dexterous fine motor control of PD subjects became apparent in delayed movement initiation and slowness of movement execution (Brumlik & Bosches, 1966; Fellows et al., 1998; Gordon et al., 1997; Müller & Abbs, 1990; Sheridan et al., 1987; Stelmach et al., 1989). Conflicting results were reported regarding PD subjects ability to use visual cues for predictive scaling of finger forces. Examining how PD subjects use probabilistic information for predictive motor control could add more insights into the implication of PD on motor control. In particular this would shed light on the role of decision-making strategies for motor symptoms in Parkinson's disease. Moreover, comparing perceptual weight interpretation with predictive force scaling could add evidence to the understanding of the relation between perception and action.

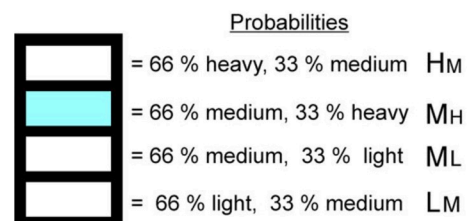
3 Scientific Methods and Considerations

3.1 General Considerations

Contemporary research considered movement planning from the viewpoint of decision-making under risk. So-called decisions under risk are made when participants have access to the probabilities associated with possible actions. For example, evidence was presented that monetary costs of different task demands influenced movement selection in a way that followed the maximum of the expected reward. Surprisingly, the use of explicit probabilistic advance information for predictive motor control has been virtually neglected in this field of research.

In this thesis a novel probabilistic paradigm will be used to study how the motor system deals with explicit probabilistic information about object weight, and to study how the same explicit probabilistic information about object weight is interpreted perceptually. In a grip-lift (GL) task and a weight adjustment (WP) task a visual cue either predicted the upcoming weight with 100 % certainty or by a fixed ratio of probabilities (66.7 % / 33.3 %) for two out of three clearly distinguishable weights (light, medium, and heavy). The latter, the probabilistic cue, was a ‘traffic light’ with four different positions of a blue rectangle in a black frame (Fig. 3). When the rectangle was located in the lowest position (LM cue), the object weight was light in 66.7 % and medium in 33.3 % of the trials. When the rectangle was located in the second position from bottom (ML cue), these frequencies were reversed. When the rectangle was located in the second position from top (MH cue), the weight of the block was medium in 66.7 % and heavy in 33.3 % of cases. In the topmost position (HM cue), these frequencies where reversed. Hence, four different weight predictions were associated with four probabilistic cues (LM, ML, MH, and HM). In the GL task participants were encouraged to use the probabilistic cue to prepare their grip-lift action adequately. A main feature of the GL task was that it allowed examining how the motor system uses

Fig. 3 Four probabilistic visual cues. Each position of the blue rectangle in the black frame (here cue Mh) signified the probabilities of two possible object weights for the upcoming trial. The four probabilistic cues are abbreviated: LM, ML, MH, HM.



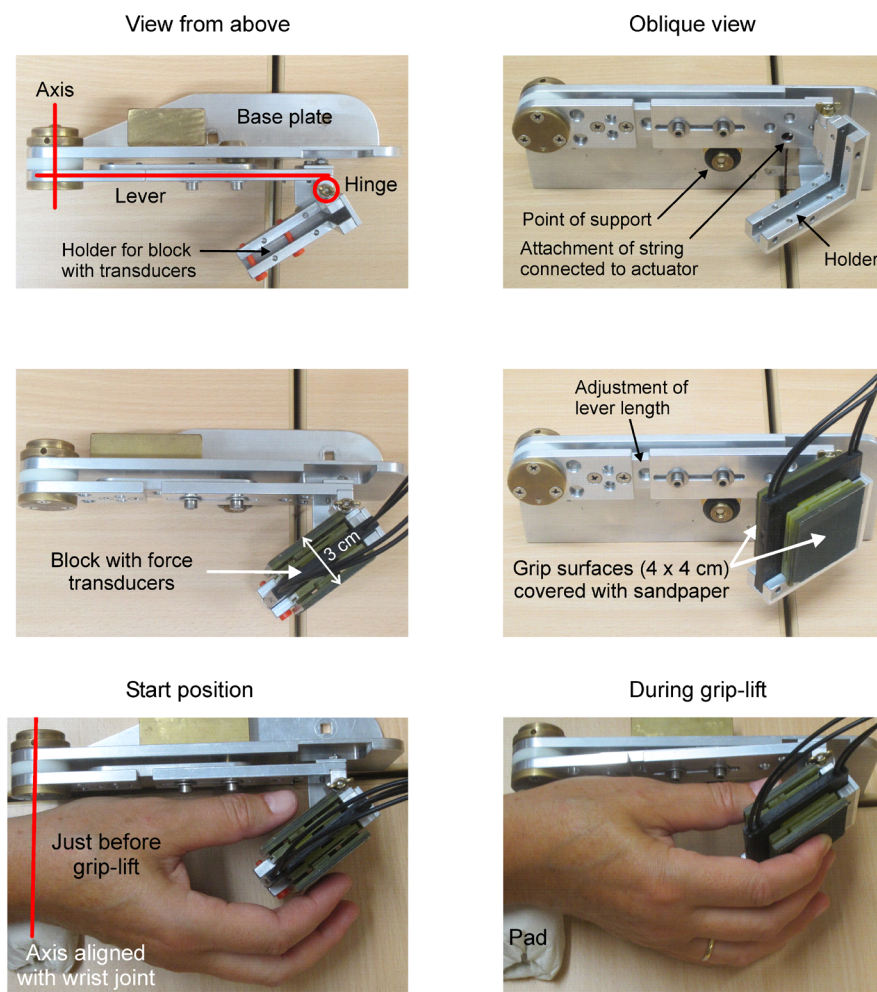


Fig. 4 Experimental Set-up. The object consists of a block equipped with force transducers, which is fastened to a holder (bracket) that is connected to a lever. The angle between holder and lever is adjusted via a hinge that is secured in an appropriate position. The length of the lever is variable as well, so that it can be adapted to the individual size of the hand. The axis of the lever is aligned with the wrist (radiocarpal) joint so that the handle is lifted with a radial duction of the wrist. The wrist is supported by a pad (taken from supplementary figure 1, Trampenau, van Eimeren, & Kuhtz-Buschbeck, 2016).

four different probabilistic weight information when lifting an object with a constant (medium) weight.

In the WP task participants were asked to adjust a weight until it matched the expected weight of the probabilistic cue. This method was used to measure the perceptual interpretation of the four different probabilistic weight predictions. Comparing the results of both tasks will help to understand how explicit probabilistic information is implemented in motor prediction and in perceptual weight prediction. Moreover, results of the WP task can indicate whether the probabilistic cues are interpreted differently. This would be important to know if results of the GL task reveal no cue effects.

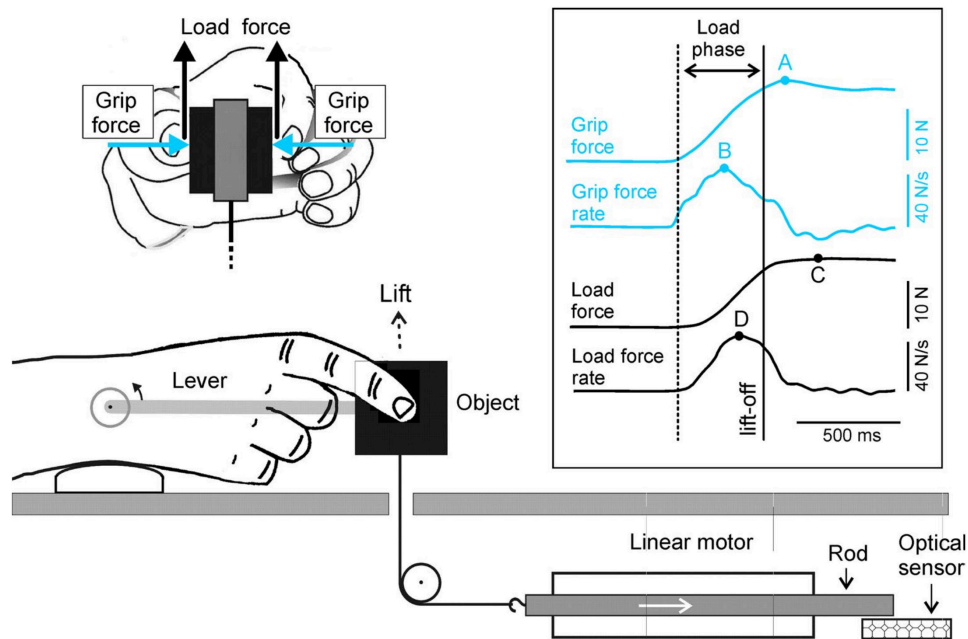


Fig. 5 Experimental setup. The grip object with force sensors was attached to a lever, whose hinge was aligned with the wrist. Its weight was controlled by a linear motor, whose rod exerted programmable pull force (white arrow) via a nonelastic string connected to the object. An optical sensor recorded the sliding movements of the rod. The inset shows typical force and force rate curves of a grip-lift trial with the peak GF (A), peak GF rate (B), peak LF (C) and peak LF rate (D). The onset of LF increase (dotted vertical line) and the moment of liftoff (solid vertical line) delimit the load phase (taken from Trampennau, Kutz-Buschbeck, & van Eimeren, 2015).

3.2 Experimental Setup

The same experimental setup was used in both GL and WP tasks. Participants were sitting on an adjustable chair at a table (70 × 140 cm) with the equipment and faced a monitor (15" lcd display) located a viewing distance of about 40 cm. A visual shield behind the monitor covered the technical equipment used to run the experiment. A grip object (a small block) was located close to the tips of the right thumb and index finger (Fig. 4). The block was attached to a lever, whose rotary axis was aligned with the pivot axis of the radiocarpal joint. The position and angle of the object and connected lever were adapted to fit individual anatomical conditions. The weight of the object was systematically changed from trial to trial during the experiment by a linear actuator (Servotube actuator STA1116, Dunkermotoren, Essex, UK), which was hidden behind the visual shield and capsuled under a sound insulation. The sliding rod of the actuator was connected to the lever and object via a non-expandable string (Fig. 5). It exerted programmable pull forces, which remained constant during each grip-lift trial. Changes in force output between the trials were performed in a series of small steps, which did not result in any noise or any vibrations. Movements of the rod were recorded with a self-build optical sensor to register the position of the grip object.

This position signal was used for a visual feedback of the lifting height given on the monitor. Additionally, a small switch attached to the lever indicated the moment of liftoff. The object had two flat vertical grip surfaces (40 x 40 mm, spaced 30 mm apart) covered with thin sandpaper (grit size 600), and it was equipped with non-metallic force transducers (Dasch, Kiel, Germany). The isometric grip force, applied perpendicular to the grip surfaces, and the lift force (tangential to the surfaces) were measured (range 0–20 N). A buzzer connected with the force transducers sounded whenever the grip force applied to the grip surface exceeded 18 N. This was invented to ensure that subject's grip force stayed within the range of 0–20 N. Together with the signal of the switch (liftoff), grip force and lift force data were sampled with a frequency of 50 Hz. This temporal resolution is below typical data sampling rates of grip and lift forces.

Before this setup was ready to use solutions for technical requirements had to be found. To control the experiment a technical solution for the programming and recording of the various experimental parts had to be developed. I choose one application to fulfill these tasks to guarantee an easy handling of the experiment, even for novice examiner, and to coordinated all parts of the experiment by one device. The last aspect was very important, as it assured a chronologic correct recording of all events in the experiment (presentation of cue and weight, time of liftoff) and force data sampled during a grip-lift action. To realize this demand I choose to use the open-source application PsychoPy (Peirce, 2007). PsychoPy comes with an easy to use timeline surface that makes it easy to schedule experimental processes. More importantly Psychopy is a flexible application that allows to implement own pieces of source code. This was a required feature that enabled to control the linear actuator, analyze the signal from the optical sensor, capture the signal of the switch, and sample data from the force transducers.

The development of this technical solution was followed by the investigation of its operability. Particularly, this was important for the grip-lift task. First and foremost, the visual cues should have a high validity for the grip-lift task. One could describe this validity as a merger between the cues and the respective motor experience; the impression of lifting the cues. This could be achieved by relating the vertical cue position on the monitor to the vertical position of the grip object. To accomplish this, movements of the rod of the linear motor were recorded with a self-build optical sensor to register the position of the grip object (Fig. 5), and assigned in real-time to the cue position on the monitor. Another benefit of a simultaneous cue-lever movement was that the cue position could be used to restrict the lifting height of the lever and, thus, standardize the lifting performance. Therefore, a target zone on the monitor where the cue should be lifted into was needed. A blue rectangle as target zone was chosen. Its height was about 150 % of the cue height, so there was no particular demand for precision. To promote preparation for an adequate motor action it was important that

subjects had enough time to interpret a given visual cue. Therefore, there was no time limit to initiate the grip-lift action. Moreover, subjects should be given the opportunity to perform a smooth grip-lift action. Such an action would avoid jerking movements that adds noise to the measurement of force rates. At the same time, the duration of a trial should be limited to minimize experimental time. To do so subjects had a rather generous time window of 1500 ms after liftoff to reach a lifting height of ~3 cm with a self-selected speed.

Probabilities

The probabilistic prediction related to the four probabilistic cues was set to a fixed ratio of 66.7 % / 33.3 %. The decision for this ratio had three reasons. First, it allowed examining how four different probabilistic weight predictions (LM, ML, MH, and HM) influenced the motor output while lifting a constant (medium) weight. That would not be possible using a 50 % / 50 % ratio. Another reason for the 66.7 % / 33.3 % ratio was its comprehensibility and usability, e. g. it corresponded to a situation where a lift would be heavy in 2 out of 3 lifts and medium in 1 out of 3 lifts. This seemed easier to understand than a ratio of 60 % / 40 %. Furthermore, in comparison to a higher ratio of probabilities (such as 75 % / 25 %) it involved a reduction of experimental trials

Weights

Three object weights were used, namely 300 g (light), 800 g (medium), and 1400 g (heavy). I selected these weights based on insights from pilot experiments where these fulfilled best the requirement of being clearly distinguishable between each other, between the probabilistic predictions, and between each probabilistic prediction and the medium weight. Moreover, similar weights have been used in a well-known study of anticipatory lift force scaling during lifts of common and novel objects (Gordon et al., 1993).

3.3 Experimental Tasks

Prior to execution of the experimental examination, all participants conducted a training session. First they were instructed to lift three real bottles with distinct filling levels using a pinch-grip at the screw cap, as if they would pull them out of a beverage crate. The weights of the bottles exactly matched the three object weights used in the following experiment. We chose this procedure to enforce a naturalistic, intuitive comprehension of the three weights. In the following instruction, the real bottles

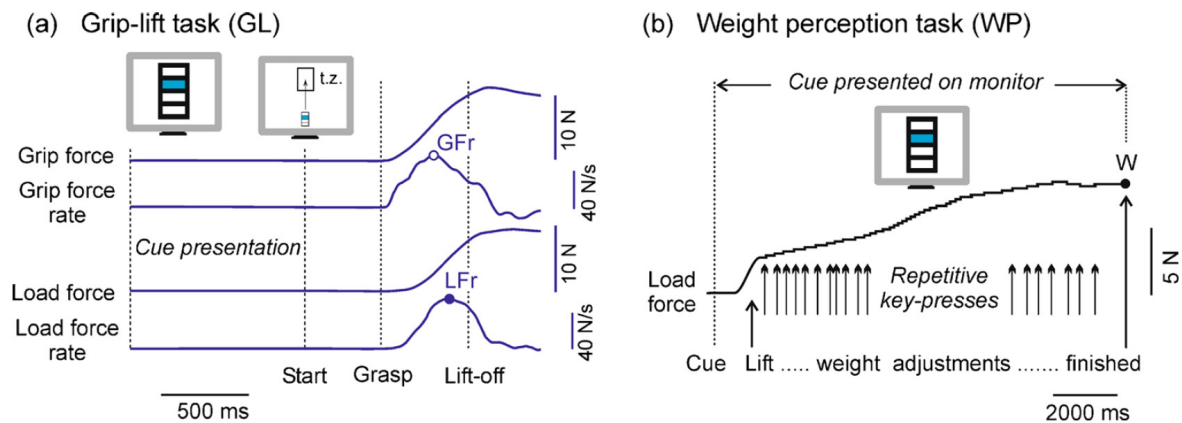


Fig. 6 Tasks. (a) In the grip-lift (GL), one probabilistic cue was shown for 1 second on a monitor, followed by a start cue with a target zone (t.z.). Then the object was grasped and lifted. Peak load force rate (LFr, filled blue circle) and peak grip force rate (GFr, open blue circle) are typically reached before lift-off. (b) In the weight perception task (WP), the object was lifted and its weight was adjusted by repetitive key-presses which operated the linear actuator (see Fig. 5) until the perceived weight W matched the weight announced by the probabilistic cue. The cue (here MH) was visible all the time. Note the different time scales in (a) and (b) (taken from Trampenau et al., 2016).

were replaced by the experimental grip object. The probabilistic cues were explained in-depth and practiced with the grip object. The training session could be repeated if participants were not able to explain the probabilities of the cues.

Subjects with Parkinson's disease were recruited from the Neurological Clinic of the University Medical Center Kiel. Each participant was briefly informed about the procedure and the tasks of the experiment two days before their participation. Afterwards each participant conducted the training session described above. On the day of the experiment the training session was repeated.

In the grip-lift (GL) task participants were encouraged to use the probabilistic cue to prepare their grip-lift action adequately. At the onset of each trial, the announcing visual cue was shown in the middle of the monitor display for one second (Fig. 6a). It then disappeared and emerged in smaller size at the bottom of the screen beneath a rectangular target zone. This second 'action cue' signaled that the object should be grasped with a pinch grip of the right hand and lifted by ~ 3 cm, thereby moving the cue into the target zone. There was no time limit to initiate the grip-lift, and after liftoff the participants had a rather generous time window of 1500 ms to reach the target zone with a self-selected speed. 1500 ms after liftoff the action cue disappeared, and a release cue requested to place the object back down and to release the grip. An inter-trial rest period of 3500 ms was used to reset the force of the linear actuator for the next trial. Overall, the task was rather undemanding regarding speed and accuracy of

the lift.

In the weight perception (WP) task the same three weights and four probabilistic cues as in the GL task were used. During each trial one probabilistic cue was shown on the monitor (Fig. 6b). Participants were asked to associate the cue with a specific object weight, which matched the expected weight of the probabilistic prediction. Then they lifted and held the object with a pinch grip of their right hand, and then gradually changed its weight by pressing the arrow keys ($\downarrow\uparrow$) of a computer keyboard with the left hand, until the perceived weight matched the probabilistic cue. Each key-press altered the pull force of the linear motor by ~ 10 g. The initial (pre-adjustment) weight varied between 250 g and 1550 g. No time constraint was given, and it was allowed to lift and to put down/release the grip object while adjusting its weight. When the trial was completed, the space-bar was pressed, and the next cue was presented on the monitor (next trial).

The method of the two tasks has limitations. One is the recording frequency of grip and load force. My colleagues and I used the same setup to examine brain activations associated with the present motor task in neuroimaging experiments (fMRI). Therefore we had to use a custom-made non-metallic force transducer, whose digital output provides the force data at 50 Hz. This transducer has been used successfully in a previous fMRI study (Kuhtz-Buschbeck et al., 2008).

Second, the apparatus does not precisely model the way freely moveable objects would respond to lift forces. The linear actuator provides a constant force during each GL trial, and the object, i.e. the handle with the force transducers, is lifted along a predetermined movement path. This may influence weight perception. However, the analysis in the GL task mainly focus on the force rate peaks, which are typically reached before lift-off, before the slightly unnatural lifting movement took place. Experiments with multiple real objects may be an issue of future research.

4 Summary of the Empirical Studies

4.1 A General Introduction to the Empirical Studies

The present dissertation aims at investigating how different probabilities of equivocal information are used for motor control and perceptual weight estimation in healthy subjects, and in subjects suffering from Parkinson's disease.

To attain this objective this thesis addresses four questions:

- (Q1) How does probabilistic information shape force dynamics?
- (Q2) How is probabilistic information used for motor prediction and perceptual weight estimation?
- (Q3) Is motor prediction and perceptual weight estimation connected?
- (Q4) Do subjects with Parkinson's disease make use of probabilistic information for motor prediction and do they differ from healthy age matched subjects?

Three different articles will be presented in the following chapter to address these questions. With respect to Q1 a novel paradigm is presented in *ARTICLE I* to investigate the effects of probabilistic cues announcing object weight on force dynamics in a grip-lift task. *ARTICLE II* reports on how the perceptual and the motor system deal with explicit probabilistic cues to an object's weight (Q2) and compares the use of probabilistic cues between both systems (Q3). *ARTICLE III* reports on how Parkinson's disease affects motor control, and more specifically, how it affects anticipatory scaling of finger-tip force based on probabilistic advance information (Q4).

In the following subsections, each article will be presented concisely, including a summary of the experimental design and the main results. Each section will be closed by a brief conclusion of the respective study. A deep presentation of statistical or methodological details, as well as a complete presentation of the results and a more comprehensive discussion is behind the scope of this overview. For more details the reader is kindly referred to the respective original research article provided in the appendix.

4.2 Probabilistic Information on Object Weight Shapes Force Dynamics in a Grip-Lift Task – ARTICLE I

Appropriate predictive scaling of the grip and lift forces is straightforward when familiar objects with constant properties are handled (Gordon et al., 1993). Memory links between sensory cues (visual and auditory) and the weight of an object to be grasped and lifted can be established quickly (Nowak et al., 2007). Once this association is learned, the forces are scaled according to the weight that is announced by the advance information (Bensmail et al., 2012; Li et al., 2009).

Visual cues play also an important role for the initial programming of the grip force when unfamiliar objects are lifted (e. g. Mon-Williams & Murray, 2000, Westwood, Heath, & Roy, 2000a; Westwood, Dubrowsky, Carnahan, & Roy, 2000b). Size cues and an assumed material-density are used to estimate an object's weight and to scale the force output adequately (Baugh et al., 2012; Buckingham et al., 2009). Yet sensory information about the weight of an object may be ambiguous. Consequently, competing internal models regarding the weight of a certain object may exist and the model that is used to program grip-lift forces will depend on the respective probability of each model.

Aim

The present study was designed to examine how the motor system of healthy young subjects deals with prior probabilistic information in the preparation and execution of a precision grip-lift.

Method

In this study a grip-lift (GL) task was accomplished under three experimental conditions. In the full prediction condition, a visual cue was displayed a screen, which fully predicted the object weight (100 % certainty). Visual cues in this condition were bottles with distinct filling levels (nearly empty, medium, full) indicating the forthcoming weight (light, medium, or heavy). In the fixed ratio condition, the cue was a ,traffic light' with four different positions of a blue rectangle in a black frame. The uppermost position (HM cue) indicated that the next object would be heavy in 66.7 % and medium in 33.3 % of the trials. The second position (MH cue) indicated that these percentages were reversed (66.7 % medium/ 33.3 % heavy). The third position (ML cue) indicated that object weight would be medium in 66.7 % and light in 33.3 % of the next trials, and the lowest position (LM cue) signified that these frequencies were reversed. Hence four probabilistic cues were used (LM, ML, MH, HM), each designating

a fixed ratio of probabilities for two possible object weights.

From the force curves and their corresponding force rate curves, five measures were determined for each trial: (1) peak grip force GF, (2) peak grip force rate GFr, (3) peak load force LF, (4) peak load force rate LFr, and (5) the duration of the load phase, which lasted from the onset of the load force ($LFr > 5 \text{ N/s}$) until liftoff. We analyzed these measures in all trials of the full prediction condition, and trials in which the same actual weight (medium = 800 g) was grasped and lifted, yet preceded by the four different probabilistic cues in fixed ratio condition.

We hypothesized that the probabilistic cues would systematically influence grip and lift force rates prior to liftoff. If this was true, the same object of medium weight would be handled differently, depending on the expectation evoked by the advance information.

Results

Analysis of force data in the full prediction condition revealed that GF, GFr (see ARTICLE I Fig. 3a), LF, and LFr (see ARTICLE I Fig. 3b) increased progressively as the object weight increased. Despite the anticipatory increase of the peak lift force rate, the load phase lengthened as the object weight increased.

As hypothesized, the probabilistic cues of the fixed-ratio condition influenced the predictive scaling of the manipulative forces. During lifts of the same object of medium weight (800 g) GF, GFr, (see ARTICLE I Fig. 3a), and LFr (see ARTICLE I Fig. 3b) increased progressively as the predicted object weight increased. Simultaneously the load phase shortened as the predicted object weight increased. However, visual cues that announced a high probability (66.7 %) of a weight differing from medium (800 g) in the upcoming trial had disproportionately larger influence on the scaling of the force rates prior to liftoff than cues predicting a low probability (33.3 %) of a different weight (see ARTICLE I Fig. 4a–d).

Conclusions

A main novel aspect of the present study is how the motor system uses probabilistic advance information to predictively adjust the fingertip forces during a grasp-lift action. The results indicate that the same object of medium weight is handled differently, depending on the probabilistic information provided by the visual cues. The higher the announced likelihood of a heavy object, the higher the peak grip and lift force rate and the shorter were the load phase duration (ref. Q1). These results indicate that participants scaled their fingertip forces anticipatory toward the predicted weight by the cue. Compatible results were reported in a recent study using a more simplistic

probabilistic paradigm than the present one (van Nuenen et al., 2012).

As a second important aspect non-linear effects of the probabilistic cues were noticeable. Cues predicting a low likelihood (33.3 %) of a weight differing from the medium value (800 g) had disproportionately smaller influence on anticipatory force rate scaling than cues indicating a high likelihood (66.7 %) of such a divergence. Distortion of probabilistic information in human judgment and decision is not exceptional, but has been demonstrated with other paradigms, such as frequency estimation, signal detection theory, and use of probability in decision-making under risk and uncertainty (Zhang & Maloney, 2012).

4.3 Processing of Probabilistic Information in Weight Perception and Motor Prediction – ARTICLE II

Contemporary research considers movement planning from the viewpoint of decision-making under risk and applies the same mathematical framework that formalizes decision-making in economics and psychology (Nagengast et al., 2010; Wolpert & Landy, 2012; Wu et al., 2009). So-called decisions under risk are made when participants have access to the probabilities associated with possible actions. In line with this approach, we recently showed that probabilistic cues systematically influenced predictive scaling of fingertip forces in a precision grip-lift task (see ARTICLE I). However, the effect of probabilistic advance information was non-linear. We interpreted this effect as a distortion of probabilistic information on object weight during preparation of the grip-lift.

To understand this pattern further, the present study investigates whether the perceptual system and the motor system utilize probabilistic information to an object's weight in a similar way. For this probabilistic advance information on object weight should be interpreted in the context of an action task (GL: grip-lift) and of a perceptual task (WP: weight perception).

However, interpretation of probabilistic information can depend on the task with its particular focus (Zhang & Maloney, 2012). Similar effects of the probabilistic cues in the GL task and the WP task may indicate a strong connection between perception and action. By contrast, different effects of the probabilistic cues in both tasks may point to a dissociation of action and perception. Such dissociations have been shown previously e. g. in the context of size-weight illusions for grip force scaling and weight perception (Chouinard, Large, Chang, & Goodale, 2009; Flanagan & Beltzner, 2000; Grandy & Westwood, 2006). Comparing the use of probabilistic cues in the GL and WP tasks thus provides new insights into the way the perceptual and the motor systems process and implement probabilistic information about an object's weight.

Aim

The present study was designed to understand distortion of probabilistic information further, and aimed at investigating whether the perceptual system and the motor system utilize probabilistic information to an object's weight similarly.

Method

Participants accomplished the GL and WP tasks successively. In the GL task the participants should utilize four probabilistic cues (LM, ML, MH, HM) to initiate their grip-lift actions with appropriate scaled grip and lift force rates (cues were identical to those introduced in ARTICLE I). From the force rate curves, two measures were determined for each trial: (1) peak grip force rate GFr and (2) peak load force rate LFr. We analyzed these measures in all trials in which the same actual weight (medium = 800 g) was grasped and lifted, yet preceded by the four different probabilistic cues.

The same cues were also used in the WP task, during which participants gradually adjusted the weight of an object, with continuous proprioceptive and tactile feedback, until the heaviness (*W*) matched the expectation for a given probabilistic cue. The WP task thus provided explicit information about the weight that is attributed to each probabilistic cue, whereas the GL task provides explicit information about the force that is attributed to each probabilistic cue.

To compare the results of both tasks (GL and WP), subject-wise standardization (*z*-transformation) of the raw GFr, LFr, and *W* data were conducted (*z*-GFr, *z*-LFr, and *z*-*W*). Overall correlations between the standardized results of the perceptual (WP) and motor (GL) tasks were described with Pearson's correlation coefficients. To account for possible task effects, two groups of participants accomplished the GL and WP task in different order (A: task sequence GL→WP; B: task sequence WP→GL→WP).

Results

In both group GFr, LFr and *W* increased as the predicted probabilistic object weight increased. However, in group A non-linear effects of the probabilistic cues were noticeable for GFr, LFr, and *W* (see ARTICLE II Fig. 3). Moreover, classification of the four cues resulted in three distinct categories of weight adjustment and predictive force scaling of the grip and lift forces (LM < ML ≈ MH < HM). In group B, by contrast, classification of the four cues resulted in four distinct categories (LM < ML < MH < HM) of weight adjustments and predictive scaling of the grip and lift forces (see ARTICLE II Fig. 4).

To analyze the impact of the cues ML and MH on participants' peak force rates across the two groups in more detail, we tested for possible interactions between group and cue on peak force rates with a post-hoc mixed within-between 2 x 2 ANOVA (cues:

ML, MH; groups: A, B). Results indicated interaction between cue and group affiliation, for GFr, LFr and W.

As a third main finding, we obtained high correlation between the standardized results of both tasks (z -LFr and z -W; z -GFr and z -W) in both groups. Furthermore, results of two-sample Kolmogorov-Smirnov tests indicated no differences between the distributions of the standardized results of both tasks within each group.

Conclusion

As a first finding, this study demonstrated that the use of probabilistic cues differed between the groups. Members of group A, who started with the GL task, related three distinct categories of peak force rates to the four probabilistic cues. On the other hand members of group B, who started with the WP task, related four different weights to the four cues (ref. Q2).

As second finding, the use of probabilistic cues for both tasks was very similar within the groups. This became evident from the number of distinct categories of peak force rate and adjusted weight in each group (three in group A vs. four in group B), from the high correlation between the standardized measures of the two tasks in each group, and from the very similar distributions of the standardized measures of both tasks within each group. These results add evidence to a close connection between perception and action in our experiment (ref. Q3).

Taken together these results demonstrate that the distortion of the probabilistic information of the cues was influenced by the initial task with its particular focus. The first experience thus had a significant influence on the categorization of the cue-related information.

4.4 Parkinsonian Patients Fail to Use Probabilistic Cues for Force Scaling in a Grip-Lift Task – ARTICLE III

In precision grip-lift tasks subjects with Parkinson's disease (PD) often exhibit lower rates of force increase (Gordon et al., 1997), slower movement initiation (Brumlik & Bosches, 1966; Sheridan et al., 1987; Stelmach et al., 1989), and slower movement execution than healthy subjects (Brumlik & Bosches, 1966; Fellows et al., 1998; Gordon et al., 1997; Müller & Abbs, 1990).

Conflicting approaches have been presented to explain motor deficits in PD. On the one side it has been argued that motor abnormalities in PD subjects could be caused by impaired fine motor control (Turner & Desmurget, 2010). In line with this approach it has been reported that PD subjects show severe problems to use advance weight infor-

mation to adapt the rate of grip force increase prior to liftoff (Fellows et al., 1998; Müller & Abbs, 1990). Problems in anticipatory fine motor control became also apparent in studies reporting on temporal dis-coordination of forces, with grip forces scaled and lift force production (Alberts et al., 1998; 2004).

On the other side, Gordon et al. (1997) argued that PD subjects are able to use an anticipatory strategy to effectively scale the force output of their fingers prior to liftoff. In their study PD subjects used size cues announcing an object's weight to scale their peak force rates. Moreover, Forssberg et al. (2000) showed that PD subjects initiated main grip and lift force drive simultaneously, and with a generally parallel increase of grip and lift force. Similar data has been presented by Ingvarsson et al. (1997). This study was motivated by these conflicting approaches to explain motor deficits in PD.

Aim

This study aimed at investigating how the motor system of PD subjects interprets and utilizes a priori weight information for preparation and execution of fingertip forces in a grip-lift task.

Method

In this study PD subjects and healthy control (HC) subjects accomplished the GL task under the same conditions as described in ARTICLE I. From the force curves and their corresponding force rate curves, five measures were determined for each trial: (1) peak grip force GF, (2) peak grip force rate GFr, (3) peak load force LF, (4) peak load force rate LFr, and (5) load phase duration LPD, which lasted from the onset of the load force ($LFr > 5 \text{ N/s}$) until lift-off. We analyzed these measures in all trials of the full prediction condition, and trials in which the same actual weight (medium = 800 g) was grasped and lifted, yet preceded by the four different probabilistic cues in fixed ratio condition.

To evaluate the coordination of grip and load force processing subject-wise mean grip and lift force curves were calculated for each weight in the full prediction condition and each cue in the fixed ratio condition. Pearson correlation coefficients were calculated and Fisher z-transformed (Fisher, 1921) to test for differences in the correlation between grip and lift force for each condition and group. Moreover, we analyzed the interval between the onset of GF ($GFr > 5 \text{ N/s}$) and the onset of LF ($LFr > 5 \text{ N/s}$) at the beginning of the grip-lift action in both conditions.

The ability to associate probabilistic weight information with a perceptual weight expectation could be an important prerequisite for the use of probabilistic weight information for anticipatory force control. To check for this ability both groups accom-

plished the WP task introduced in ARTICLE II.

Results

Analysis of force data from PD subjects in the full prediction condition revealed that GF, LF, and LFr increased progressively as the object weight increased. Data from HC subjects in the full prediction condition revealed that GF, LF, GFr, and LFr increased progressively as the object weight increased. Moreover, in both groups and condition initiation of grip and lift force occurred approximately simultaneously and the relation of grip and lift force was almost linear during the load phase and after liftoff (see ARTICLE III Fig. 9).

Beside these similarities we found that PD subjects compared to HC subjects exhibited a longer LPD for all weights in the full prediction condition and all cues in the fixed ratio condition. Moreover, in both conditions PD subjects produced lower GFr and LFr than the HC subjects. Also the effect of probabilistic cues on peak force rates differed between the groups. In HC subject's GFr and LFr increased in progression with the probabilistic cues, although in a non-linear fashion (see ARTICLE III Fig. 8). Predictive scaling of fingertip forces in PD subjects, in contrast, remained almost unaffected by the probabilistic cues (see ARTICLE III Fig. 6) 4 x 2 ANOVA indicated significant interactions between cue and group, for GFr ($F(3,84) = 11.96, p < 0.001$) and LFr ($F(3,84) = 10.57, p < 0.001$).

Weight adjustments of both PD and HC subjects were affected by the probabilistic cues. However, HC subjects did not differentiate between the cues predicting the 800 g weight with high probability (ML and MH), whereas PD subjects adjusted the object weight in progression with the predicted weight. 4 x 2 ANOVA indicated significant interactions between cue and group for W ($F(3,84) = 9.549, p < 0.001$).

Conclusion

Both groups of subjects were able to associate the probabilistic cues with perceptual weight predictions. Nevertheless, PD subjects had impaired ability to use visual cues for the predictive scaling of fingertip forces (ref. Q4). This deficit was most pronounced when probabilistic cues predicted the upcoming weight. However, PD subjects produced a tight coupling of grip and lift force. Simultaneous grip and lift force processing is considered as an essential feature of anticipatory motor control (Johansson & Flanagan, 2009; Johansson & Westling, 1988). Overall we hypothesize that PD subjects may have scaled their fingertip forces predictively toward a certain expected weight, yet, independent of the probabilistic cue.

5 Discussion

When aiming to lift an object we often have to deal with equivocal information about its properties. For example, information given by a visual cue could be compatible with multiple weights. The probability for the upcoming of these different weights may vary, e. g. according to prior knowledge. Under this circumstance various conflicting motor programs could exist, each preprogrammed for one of the possible weights. The selection for one of these motor programs could take the different probabilities for upcoming weights into account.

Empirical studies that constitute this thesis were designed to reveal insights into the use of probabilistic information for dexterous fine motor control in healthy subjects and in subjects with Parkinson's disease. A key to its understanding lies in uncovering underlying mechanisms that steer perceptual representations (e. g. the predicted weight of an object) and motor representations (e. g. predicted fingertip forces) based on probabilistic information. For this I used a novel probabilistic paradigm adapted to measure force control and weight perception.

In the following section I will generally focus on embedding my own findings in the context of the existing scientific literature of motor control. The studies will be discussed in the same order as introduced in chapter 4 (see pp. 29–36) For detailed interpretations of the empirical results I kindly refer the reader to the respective original research articles in the appendix of this thesis.

5.1 Using a Probabilistic Paradigm to Study Dexterous fine Motor Control – ‚Proof of Concept‘

ARTICLE I introduced a novel probabilistic paradigm to study anticipatory scaling of prehensile finger forces in a grip-lift task. Visual cues announcing the likelihoods of specific object weights were presented prior to a grip-lift action and participants were encouraged to utilize the announcing cue to predict the object weight and to prepare their action adequately. In the full prediction, when a cue predicted a certain weight, peak grip and lift force increase progressively as the object weight increase. Coincidentally, anticipatory scaling of grip and lift force is geared toward the announced object weight in a nearly linear fashion.

All in all, these results indicate that participants utilized visual cues that reliably predicted the object weight to pre-program their manipulative forces accordingly. In congruence, earlier studies found that healthy subjects can rapidly establish associations between unambiguous sensory cues (full prediction) and object weight or texture of the grip surfaces (Chouinard et al., 2005; Cole & Rotella, 2002; Li et al., 2009; Nowak

et al., 2007). Such visuomotor mapping takes place irrespective of the sensory modality of the cue (visual, auditory) or the hand used for grasping (Ameli et al., 2008). Veridical and illusory size cues (pictorial illusions of object size) influence both, prehensile movements and manipulative forces (Mon-Williams & Murray, 2000; Westwood et al., 2000a). The peak GF is higher for larger objects than for smaller objects of the same weight (Westwood et al., 2000b).

A main novel aspect demonstrated in ARTICLE I is that the same object of medium weight is handled differently, depending on the probabilistic information provided by the visual cues (fixed-ratio condition). The higher the announced likelihood of a heavy object, the higher the rate of grip and lift force, and the shorter the load phase duration. In a recent study using a grip-lift task (van Nuenen et al., 2012), two subsequent visual cues (indicating either high or low weight) were either congruent (75 % of trials), or incongruent (25 % of trials). Since the actual weight was always correctly predicted by the second pre-cue, the first cue can also be seen as a probabilistic pre-cue. Indeed, the results of this study can also be explained by deviations from a predicted weight based on a probabilistic pre-cue. However, since the above mentioned study lacks baseline values without pre-cue, one cannot assess the full impact of this probabilistic advance information.

Adaptive scaling did not exactly match the predicted object weight. In any case, peak force rate changes remained smaller than the predicted % deviations of the object weight and were possibly influenced by a motor strategy that overestimated the frequency of the medium weight.

Overall, these results show that the grip-lift task introduced in ARTICLE I is a very useful and reliable method to examine processing of finger forces, and facilitates to study the use of probabilistic advance information for anticipatory scaling of prehensile finger forces. The strength of this method lies in its option to separate effects of the probabilistic cues from effects of the actual lifted weight.

5.2 Adaption of Probabilistic Information to the Demands of a Task remains Stable over Time

Successful adaptation to a probabilistic world requires an effective strategy utilizing probabilistic information. A remarkable feature of the utilization of probabilistic information is that its interpretation is not fixed, but adapted to the demands of a task (Hudson et al., 2008; Rakitin et al., 1998; Trommershäuser et al., 2003; Wolpert & Landy, 2012; Zhang et al., 2010).

Results presented in ARTICLE II demonstrate that the first experience utilizing probabilistic information had a significant influence on its interpretation. Participants in

group A started utilizing probabilistic information during the GL task, where they experienced three different weights that were actually lifted, and related three distinct categories of peak force rates to the four probabilistic cues ($LM < ML \approx MH < HM$), indicating three different modes of action initiation. Conversely, the four cues were associated with four different perceptual weights ($LM < ML < MH < HM$) when the WP task was performed initially (group B).

In the discussion of ARTICLE II it is argued that members of both groups may have used different strategies to utilize the probabilistic cues. Out of the many possible policies we outlined three hypothetical strategies, each representing an extreme option. We drafted these policies with respect to the GL task, but in principle, they could be used to interpret the cues during WP task as well. In the following section I will briefly review these strategies.

One theoretical strategy (a) may be to disregard all probabilistic cues, and instead to always scale the forces to the medium weight, which turns up most often (in 70 of 150 trials). This strategy would be associated with frequent large errors of initial force scaling and is incompatible with the demonstrated effects of the cues on grip and lift force dynamics.

Another strategy (b) could always scale the force rates to the current predicted weight P (calculated as a weighted combination of the two possible weights predicted by each cue), resulting in a linear relation between the P values and peak force rates. Across all GL trials the sum of all positive deviations (,actual weight is heavier than P') with ensuing corrections will then equal the sum of all negative mismatches (,actual weight is lighter than P'). As a consequence Strategy b avoids large errors of initial force scaling and repetitive unidirectional corrections of the preprogrammed forces, which may be beneficial.

A third strategy (c) may always aim for the more likely weight, i. e. treat the higher probability (66.7 %) like a certain prediction (100 %). In two thirds of all trials, preprogramming will then be optimal because a given cue is actually followed by the more likely weight, but in one third of all trials, large initial force over- or undershoots will occur, because the participant has aimed for the 'wrong' weight. As an advantage of this strategy, the sum of all mismatches and subsequent corrections, regardless of their direction, will be smaller than with any other policy.

Our results suggest that members of group A, who started with the GL task, did not clearly differentiate between cues ML and MH, as evident from the similar peak force rates. Thereby their predictive force scaling reflects, in essence, strategy c. In line with strategy c non-linear relation between the force rates and the P values were clearly apparent. Distortion of probabilistic information has also been found in other motor paradigms, such as a rapid-pointing task that involved decisions under risk (Wu et al., 2009). Subjects underweighted small probabilities and overweighted large probabili-

ties, as the participants in our experiment did.

For members of group B the initial experiment, which determined the interpretation of the probabilistic information, was the WP task. Their weight adjustments suggest that they match up P values which reflects, in essence, strategy b.

On the other side, we speculated that selection of appropriate weights during the WP task, when performed first (group B), could have been based on abstract knowledge of the probabilities, and thus involved a decision from description according to the terminology of Hertwig, Barron, Weber and Erev (2004). Still, the relation between the adjusted weights and P values did not appear perfectly linear. One might interpret this pattern as a compromise, where the subjects tried to match up P values, but at the same time aim towards the more likely medium weight.

Overall, these results indicate that interpretation of probabilistic information could have been adapted to the demands of the initial task. The first experience thus had a significant influence on the categorization of the cue-related information.

5.3 Association between Weight Perception and Force Prediction

An effective strategy for lifting objects is to choose an adequate motor performance prior to manipulation with finger forces scaled predictively toward an object's properties (Flanagan & Wing, 1997; Johansson & Westling, 1984; 1988). Among others, the weight as an essential object property is not perceivable before an object is grasped and lifted. However, it has been demonstrated, that the nervous system is able to use size cues and an assumed material-density to estimate an object's weight and to scale the force output adequately (Baugh et al., 2012; Buckingham et al., 2009).

Results presented in ARTICLE II demonstrate that probabilistic cues influenced force prediction and weight adjustment in a similar way within each group. This became evident from the number of distinct categories of peak force rate and adjusted weight in each group (three in group A vs. four in group B). Despite the different nature of both tasks their results were highly correlated, suggesting that an overarching concept ruled the implementation of the probabilistic information during weight perception and action (grip-lift). With respect to the conclusion pointed out section in 5.2 it seems plausible that this concept was established during the task that was performed first.

Also previous research found associations between perceptual weight estimates and scaling of the fingertip forces. If more grip force is needed to grasp an object due to a lower friction (smooth surface texture) or because the contact area between fingers and object is small, then the object is perceived to be heavier (Flanagan & Bandomir, 2000; Flanagan, Wing, Allison, & Spenceley, 1995). Van Polanen and Davare (2015) recently demonstrated that if there is a mismatch between expected and actual ob-

ject weight in a grip-lift task, the execution of force corrections will influence weight perception in a proportional manner.

5.4 Parkinson's Disease Affects Predictive Scaling of Fingertip Forces

Several studies have reported deficits of anticipatory control of grasp in PD subjects (Brumlik & Bosch, 1966; Fellows, et al., 1998; Gordon et al., 1997; Müller & Abbs, 1990; Sheridan et al., 1987; Stelmach et al., 1989). However, it is still up for discussion to explain motor deficits in Parkinson's disease.

Results presented in ARTICLE III show that the lifted weight had a significant effect on force scaling in PD and HC subjects (full prediction condition). In both groups subjects scaled their fingertip forces according to the lifted weight, reflecting a common finding (e. g. Fellows et al., 1998; Gordon et al., 1997). Force adaptation toward the lifted weight has been interpreted as evidence for an intact ability of subjects with Parkinson's disease to use peripheral sensory information from the grasping digits to assist the scaling of grip force (Nowak & Hermsdörfer, 2006). However, lifts of PD subjects were significantly slower compared to HC subjects. This slowness became apparent from significantly lower force rates and prolonged load phase duration, which is in line with results reported previously (e. g. Fellows et al., 1998; Fellows & Noth, 2004; Jordan, Sagar, & Cooper, 1992; Sheridan et al., 1987; Stelmach et al., 1989).

Inspection of grip force rates from PD subjects revealed problems in anticipatory force scaling. It was most pronounced when the probabilistic cues predicted the upcoming weight. Under this condition force rates did not vary systematically. However, results of the WP task indicate that both PD and HC subjects were able to use the probabilistic cues to adjust the weight of the lever. Thus, PD subject's disuse of probabilistic cues for anticipatory force control cannot be attributed to a missing understanding of the probabilistic information.

Examination of grip-lift force coordination from PD subjects and HC subjects revealed no significant differences. Initiation of grip and lift force occurred approximately simultaneously and both forces were scaled in parallel during the load phase and after liftoff, indicating a tight temporal coupling of fingertip forces. According to Johansson and Westling (1988) a tight coupling of grip and lift force is an essential feature of anticipatory motor control, with forces scaled predictively according to expected object properties. This can be seen to imply that also PD subjects use a predictive mode of force control.

Based on these insights we hypothesize that PD subjects may have scaled their fingertip forces predictively toward a certain expected weight, yet, independent of the

probabilistic cue. Using the probabilistic cues requires to interpret their information and to decide which motor program one should execute.

PD subjects showed an altered decision-making for anticipatory motor programming compared with the healthy subjects. Many studies have reported on the influence of dopamine on Decision-making (for an overview see Frank, 2006; Glimcher & Fehr, 2013). Thus, our results could point toward a broader influence of dopamine on decision-making, which also features motor control.

In line with this Mazzoni et al. (2007) hypothesized that movement in parkinsonian subjects reflects impairment in the link between motivation and the control of movement gain, resulting in a higher sensitivity to movement energy costs.

Out of the many possible policies to select cue-independent force rates, PD subjects could have used two hypothetical strategies, each representing an extreme option. One theoretical option may be to scale the forces toward the medium weight, which turns up most often (in 70 of 150 trials). In nearly half of the trials this strategy would lead to a sense of achievement, due to adequately scaled fingertip forces. However, this strategy would also be associated with frequent large errors of initial force scaling. The other strategy may be to always scale the force rates toward sensory information acquired during prior lifts. As a consequence of the randomized presentation of weights in our study this strategy may lead to even more large errors of initial force scaling than the first strategy. Whether PD subjects used one of these strategies or a compromise between both is beyond of the scope of this study. More importantly, both strategies do not force subjects to decide which motor program they would perform.

6 Perspective

Findings reported in this thesis revealed distinct differences between healthy subjects and subjects suffering from Parkinson's disease. On the one hand, healthy subjects (young and old) used probabilistic information about an object's weight to derive perceptual estimates about the weight and scale their fingertip forces predictively. PD subjects on the other side, used the same probabilistic information to evaluate the perceptual weight, but their force prediction remained unaffected by the cues. As a consequence PD subjects used the probabilistic cues differently for force scaling and weight perception.

Especially the results of PD subjects could point toward that perception and action operate independent of each other. Also other studies reported on dissociation between perception and action. Experiments with optical illusions have shown that perceived illusory cues to an object's size are not matched by motor parameters such as the aperture of the hand during prehension (Aglioti et al., 1995; Buckingham et al., 2009; Buckingham & Goodale, 2010; Ellis & Lederman, 1999; Flanagan & Beltzner, 2000), which conforms to the dual-stream theory of the visual system proposed by Goodale and Milner (1992). This theory assumes a ventral stream that processes visual information for perception (e. g. object recognition, form representation), and a dorsal stream that processes visual information for action (e. g. processing of spatial awareness, guidance of movements). According to Goodale and Milner (1992) each stream uses visual information about objects and events in the world in different ways. The authors explain this difference with specific requirements of perception and action.

Supporting evidence for a different use of sensory information for perception and action have also been presented in ARTICLE II. In this article we demonstrated that if the probabilistic cues were initially used to generate a grip-lift action (GL task), non-linear effects of probabilistic cues became obvious in the predictive scaling of fingertip forces (group A in ARTICLE II). On the other side, if the initial interpretation of probabilistic cues was made with respect to the perceptual weight (WP task), subjects assigned an almost linear relationship between the cues and the adjusted weight (group B in ARTICLE II). This is in line with Goodale and Milner's (1992) assumption that perception and action uses visual information in different ways.

By contrast, results of the GL and WP tasks were highly correlated when conducted in a row. If the perceptual task was performed first, the four probabilistic cues were related to four distinct categories of heaviness and force prediction (group B in ARTICLE II). If the motor task was performed first, the same four cues were assigned to three different force predictions and categories of heaviness (group A in ARTICLE II). This points to the suggestion that the initial interpretation of the sensory input may be stored for later use, and that perception and action have access to this memory. A

reinterpretation of the sensory information seems not to take place. These results add evidence to strong connection between perception and action, probably in line with the more general theory that perception and action rely on common abstract concepts (Franz, Gegenfurtner, Bühlhoff, & Fahle, 2000; Müsseler, 1999; Prinz, 1990). A fundamental assumption within this theoretical framework is that perception and action are linked. According to Prinz (1984) this linkage can be described as follows: perceiving an object activates the action associated with it, and performing an action with the object activates the associated perceptual concept.

Findings reported in this thesis do not favor one of these theories. Rather they indicate, that specific requirements of a task critically influence the interpretation and use of probabilistic information. Different methods (e. g. the decision-making strategy) where used to interpret probabilistic information for perceptual evaluation (WP task) and action (GL task). As soon as an interpretation of probabilistic information was established it was stored for later use. Therefore, the use of probabilistic information for action and perception was critically influenced by the system which interpreted it depending on the specific requirement of the task.

7 Summary

An effective strategy for lifting objects is to choose an adequate motor performance prior to manipulation with finger forces scaled predictively toward an object's properties (Flanagan & Wing, 1997; Johansson & Westling, 1984; 1988). This anticipatory control strategy ensures a smooth and critically damped lift and obviates initial force overshoots or undershoots, which would entail corrections (Johansson & Westling, 1988). Peak values of the force rates (reached prior to liftoff) are considered to reflect preprogrammed forces, as they vary in parallel with the targeted object weight (Chouinard et al., 2005; Jenmalm et al., 2006; Johansson & Westling, 1988; Li et al., 2009; Nowak et al., 2013).

However, the sensory input that constitutes the basis for perceiving and interacting with the world is often equivocal. As a consequence a certain sensory input may evoke different predictions about the world. In order to use equivocal information we have to decide how to interpret the different predictions. Execution of movements has been shown to be influenced by ambiguity regarding the predictability of particular object properties (Christopoulos & Schrater, 2009; Cohen et al., 2009; Schlicht & Schrater, 2007) and of different task demands (Trommershäuser et al., 2003; Wolpert & Landy, 2012; Zhang et al., 2010).

Contemporary research considers movement planning from the viewpoint of decision-making under risk and applies the same mathematical framework that formalizes decision-making in economics and psychology (Nagengast et al., 2010; Wolpert & Landy, 2012; Wu et al., 2009). So-called decisions under risk are made when participants have access to the probabilities associated with possible actions. According to Wolpert and Landy (2012) motor behavior could be viewed as a problem of maximizing the utility of a movement outcome. Following their view equivocal information about properties of the world and the own body are combined with prior knowledge of probabilities for their various outcomes to produce posterior predictions about properties of the world and the own body.

Revealing insights to understand how the motor system works has been presented by studies examining impaired motor control in PD subjects. In several studies changes of dexterous fine motor control of PD subjects became apparent in slowness in movement initiation and slowness in movement execution (Brumlik & Bosch, 1966; Fellows et al., 1998; Gordon et al., 1997; Müller & Abbs, 1990; Sheridan et al., 1987; Stelmach et al., 1989). Conflicting results were reported regarding PD subjects ability to use visual cues for predictive scaling of finger forces

Conflicting approaches have been presented to explain motor deficits in Parkinson's disease. On the one side it has been argued that motor abnormalities in PD subjects could be caused by impaired fine motor control (Turner & Desmurget, 2010). In

line with this approach it has been reported that PD subjects show severe problems to use advance weight information to adapt the rate of grip force increase prior to liftoff (Fellows et al., 1998; Müller & Abbs, 1990). Problems in anticipatory fine motor control became also apparent in studies reporting on temporal dis-coordination of forces, with grip forces scaled and lift force production (Alberts et al., 1998; Alberts et al., 2004).

On the other side, Gordon et al. (1997) argued that PD subjects are able to use an anticipatory strategy to effectively scale the force output of their fingers prior to liftoff. In their study PD subjects used size cues announcing an object's weight to scale their peak force rates. Moreover, Forssberg et al. (2000) showed that PD subjects initiated main grip and lift force drive simultaneously, and with a generally parallel increase of grip and lift force. Similar data has been presented by Ingvarsson et al. (1997). Examining how PD subjects use probabilistic information for predictive motor control could add more insights into the implication of Parkinson's disease on motor control.

The present dissertation aimed at investigating how probabilistic information about an object's weight is used for motor control, and how this information is represented in perception. For this a novel paradigm was established to study the use of explicit probabilistic information about an object's weight. In a grip-lift (GL) task an object equipped with a force transducer was repeatedly grasped and lifted between thumb and index finger. The weight of the object varied in three steps: 300 g, 800 g, and 1400 g. Prior to each lift, the probabilities for the three object weights were given by a visual cue. It either predicted the upcoming with 100 % certainty or by a fixed ratio of probabilities (66.7 % / 33.3 %) for two out of three clearly distinguishable weights (light, medium, and heavy). This probabilistic cue was a 'traffic light' with four different positions of a blue rectangle in a black frame. When the rectangle was located in the lowest position (LM cue), the object weight was light in 66.7 % and medium in 33.3 % of the trials. When the rectangle was located in the second position from bottom (ML cue), these frequencies were reversed. When the rectangle was located in the second position from top (MH cue), the weight of the block was medium in 66.7 % and heavy in 33.3 % of cases. In the topmost position (HM cue), these frequencies were reversed. Hence, four different weight predictions were associated with four probabilistic cues (LM, ML, MH, and HM). In the GL task participants were encouraged to use the cue to prepare their grip-lift action adequately.

In the first study (reported in ARTICLE I) my colleagues and I examined the effect of probabilistic cues on grip and lift force dynamics. We observed that peak grip and lift force rates, and the peak grip force increased progressively as the object weight increased. During lifts of the same object of medium weight (800 g) predictive scaling of grip and lift force, and the peak grip force increased progressively as the predicted object weight increased. Simultaneously the load phase shortened as the predicted object weight increased. However, visual cues that announced a high probability (66.7 %) of

a weight differing from medium (800 g) in the upcoming trial had disproportionately larger influence on the scaling of the force rates prior to liftoff than cues predicting a low probability (33.3 %) of a different weight. We interpreted this as non-linear effects of the probabilistic cues. Distortion of probabilistic information in human judgment and decision is not exceptional, but has been demonstrated with other paradigms, such as frequency estimation, signal detection theory, and use of probability in decision-making under risk and uncertainty (Zhang & Maloney, 2012).

The second study (reported in ARTICLE II) was designed to understand distortion of probabilistic information further, and to investigate whether the perceptual system and the motor system utilize probabilistic information to an object's weight similarly. We studied effects of the probabilistic cues (same as in ARTICLE I) in the context of two tasks. One was the grip lift (GL) task introduced in the first article, providing the predictive force scaling related to each cue, and the other was a perceptual weight adjustment (WP) task, providing the predicted heaviness related to each cue. To compare the results of both tasks (GL and WP), subject-wise standardization (z-transformation) of the raw peak grip-force rate, peak lift-force rate, and weight adjustment data were conducted. Overall correlations between the standardized results of the perceptual (WP) and motor (GL) tasks were analyzed. To test whether their distributions differed, we conducted two-sample Kolmogorov-Smirnov tests. To account for possible sequence effects subjects were randomly divided into two groups, where the one started with the GL task and the other with the WP task.

Results revealed that the GL and WP tasks were highly correlated in each group. In line with this, distributions of the results of both task were very similar in each group. Moreover, if the perceptual task was performed first (group B), the four probabilistic cues were related to four distinct categories of heaviness and force prediction. If the motor task was performed first (group A), the same four cues were assigned to three different force predictions and categories of heaviness. We argued, that the high correlation of both tasks point toward an overarching concept that ruled the implementation of the probabilistic information during weight perception and action (grip-lift). This could add evidence to connection between perception and action, probably in line with the more general theory that perception and action rely on common abstract concepts (Franz et al., 2000; Müsseler, 1999; Prinz, 1990). We explain the different interpretation of probabilistic cues in the groups with different strategies that may have ruled the interpretation of probabilistic information in both groups. Interpretation of probabilistic information was therefore not fixed, but adapted to the demands of the initial task. The first experience thus might have had a significant influence on the categorization of the cue-related information.

The third study (reported in ARTICLE III) aimed to investigate how the motor system of PD subjects interprets and utilizes a priori weight information for preparation

and execution of fingertip forces in a grip-lift task. PD subjects and healthy control (HC) subjects accomplished the same two tasks that were already used in the second study. We examined the effect of probabilistic cues on grip and lift force dynamics, and analyzed grip-lift force coordination during the lifts. The WP task was used to check for the ability to associate probabilistic weight information with a perceptual weight expectation. We regarded this ability to be an important prerequisite for the use of probabilistic weight information for anticipatory force control.

Results of this study show that both groups of subjects initiated grip and lift force approximately simultaneously. Thereby the relation of grip and lift force was almost linear during the load phase and after liftoff. Moreover, PD and HC subjects scaled grip and lift force according to the lifted weight. Beside these similarities we found that PD subjects compared to HC subjects exhibited a profound slowing of grip and lift force development for all weights in the full prediction condition and all cues in the fixed ratio condition. Differences in predictive scaling of fingertip forces became evident in the fixed ratio condition. In HC subject's probabilistic cues significantly influenced predictive scaling of the manipulative force, although in a non-linear fashion. A similar distortion of probabilistic information was also evident in weight adjustment (WP tasks). Predictive scaling of fingertip forces in PD subjects, by contrast, remained almost unaffected by the probabilistic cues. Nevertheless, PD subjects adjusted the object weight in progression with the predicted weight. The presented results demonstrated that both groups of subjects were able to perceptual weight predictions to the probabilistic cues. Nevertheless, PD subjects had impaired ability to use visual cues for the predictive scaling of fingertip forces. This deficit was most pronounced when probabilistic cues predicted the upcoming weight. However, PD subjects produced a tight coupling of grip and lift force. Simultaneous grip and lift force processing is considered as an essential feature of anticipatory motor control (Johansson & Flanagan, 2009; Johansson & Westling, 1988). Overall we hypothesize that PD subjects may have scaled their fingertip forces predictively toward a certain expected weight, yet, independent of the probabilistic cue. We speculate whether problem in decision-making for motor action might explain the results of the PD subjects.

PD subjects showed an altered decision-making for anticipatory motor programming compared with the healthy subjects. Many studies have reported on the influence of dopamine on Decision-making (for an overview see Frank, 2006; Glimcher & Fehr, 2013). Thus, our results could point toward a broader influence of dopamine on decision-making, which also features motor control.

In line with this Mazzoni et al. (2007) hypothesized that movement in parkinsonian subjects reflects impairment in the link between motivation and the control of movement gain, resulting in a higher sensitivity to movement energy costs.

Several theories have been presented to explain human motor control and how

perception and action are related. In my discussion I end up with comparing my finding with the dual-stream theory of the visual system (Goodale & Milner, 1992) and the common-coding approach (Franz, et al., 2000; Müsseler, 1999; Prinz, 1990). I argue that findings reported in this thesis are in line with aspects of both theories but that they do not favor one of them. Rather they indicate, that specific requirements of a task critically influence the interpretation and use of probabilistic information. Different methods (e. g. the decision-making strategy) are used to interpret probabilistic information for perceptual evaluation (WP task) and action (GL task). As soon as an interpretation of probabilistic information is established it is stored for later use.

8 Summary in German (Deutsche Zusammenfassung)

Theoretischer Hintergrund

Die Hand ist das wohl vielseitigste und wichtigste Werkzeug des Menschen. Von Geburt an spielt das Greifen nach Gegenständen eine große Rolle. Das Greifen ermöglicht uns, unsere Welt zu ertasten, um so wichtige Informationen über ihre Beschaffenheit zu erlangen. Gleichzeitig setzen wir unsere Hände zur Kommunikation ein, indem wir mit ihnen gestikulieren oder Berührungen ausüben. Nicht zuletzt nutzen wir unsere Hände dafür, unsere Welt nach unseren Vorstellungen zu verändern. Damit uns dies gelingt, ist es wichtig, dass wir unsere Hände zielgerichtet einsetzen können. Am genauesten gelingt uns dies mit dem Präzisionsgriff. Dieser beschreibt das Anheben von Objekten zwischen Daumen und Zeigefinger. Zwei Kräfte spielen beim Präzisionsgriff eine wichtige Rolle. Die Griffkraft, welche den ausgeübten Druck auf das Objekt angibt, und die Hubkraft, die beim Anheben des Objektes angewandt wird.

Um ein Objekt anheben zu können, müssen Griff- und Hubkraft an das entsprechende Objekt angepasst werden. Eine zu hohe Griffkraft könnte eher fragile Objekte beschädigen und würde zu einem unnötig hohen Energieaufwand der Muskeln in den Fingern führen. Ein zu geringes Kraftniveau hingegen würde ein Durchrutschen des Objekts zur Folge haben. Um zu hohen oder zu niedrigen Fingerkräften entgegenzuwirken, können prinzipiell zwei Kontrollmechanismen der Griff- und Hubkraft zur Anwendung kommen. Auf der einen Seite ist das Nervensystem in der Lage, während eines Hebevorgangs somatosensorische Informationen über die Reibung zwischen den Fingeroberflächen und der Objektoberfläche zu nutzen, um die Griff- und Hubkraft anzupassen (Aoki et al., 2006; Aoki et al., 2007; Birznieks et al., 1998; Burstedt et al., 1999; Cadoret & Smith, 1996; Edin et al., 1992; Forssberg et al., 1995; Goodwin et al., 1998; Johansson & Westling, 1984; Kinoshita et al., 1997; Westling & Johansson, 1984). Verantwortlich für unterschiedliche Reibung sind unter anderem das Gewicht des Objektes und die Oberflächenbeschaffenheit des Objektes und der Haut.

Eine Anpassung der Motorik an die Gegebenheiten der Außenwelt und sich verändernde Zustände des Körpers ist eine sehr wichtige Eigenschaft der Motorik. Allerdings reicht eine reine Anpassungssteuerung der Fingerkräfte nicht aus, um Objekte effizient anzuheben (Johansson, 1998). Um ein Objekt zielgerichtet mit dem Präzisionsgriff anzuheben, ist es wichtig, vor dem Anheben Informationen über die Beschaffenheit des Objektes zu haben, um so die Motorik der Greifbewegung auf die kommende Aufgabe vorzubereiten (Johansson & Westling, 1988). Gemeint ist die prädiktive Skalierung der Griff- und Hubkraft. Dabei wird vor der Ausführung der Greifmotorik ein Kraftniveau festgelegt, das bei der Ausführung angesteuert wird (Johansson & West-

ling, 1988). Diese so genannte antizipatorische Kontrolle der Griff- und Hubkraft sorgt für ein gleichmäßiges und angepasstes Anheben und beugt Über- und Untersteuern der Fingerkräfte vor (Johansson & Westling, 1988). Ist die prädiktive Skalierung der Griff- und Hubkraft entsprechend der Objekteigenschaften gewählt, so kommt es beim Anheben zu einem parallelen Verlauf der Griff- und Hubkraft (Johansson & Westling, 1988). Die Kraftrate beider Kräfte (angegeben in N/s) verläuft glockenförmig und erreicht ihr Maximum vor dem Abheben des Objekts (Johansson & Westling, 1988). Wie die Griff- und die Hubkraft hängen die Kraftraten vor allem vom Gewicht eines Objektes ab (Chouinard et al., 2005; Jenmalm et al., 2006; Johansson & Westling, 1988; Li et al., 2009; Nowak et al., 2013; Westling & Johansson, 1984). Aufgrund der Tatsache, dass vor dem Abheben eines Objektes nicht alle somatosensorischen Informationen zur Verfügung stehen, werden die Maxima der Kraftraten als Maß für die angesteuerte Kraft angesehen (Westling & Johansson, 1984). Um ein Motorikprogramm antizipatorisch zu wählen, kann das Nervensystem auf verschiedene sensorische Informationen zurückgreifen. Besonders wichtig sind dabei visuelle Informationen über die Größe eines Objektes, da darüber Rückschlüsse über das Gewicht möglich sind (Gordon et al., 1991; 1993; Mon-Williams & Murray, 2000).

Sensorische Informationen sind oft ungenau. Mehrere Studien konnten zeigen, dass bei der Planung von Motorik sensorische Ungenauigkeiten berücksichtigt werden (Christopoulos & Schrater, 2009; Cohen et al., 2010; Ellis & Lederman, 1999; Schlicht & Schrater, 2007). Wenn beispielsweise nach einem Objekt gegriffen wird, dessen Größe nur ungenau zu erkennen ist, griffen Versuchspersonen mit einem größeren Fingerabstand nach diesem Objekt (Schlicht & Schrater, 2007).

Neben der Ungenauigkeit sind sensorische Informationen oft mehrdeutig hinsichtlich der Vorhersage einer Objekteigenschaft. Man stelle sich zum Beispiel vor, dass man früh morgens seinen Kühlschrank öffnet. Durch den Ruck der Kühlschranktür kippt plötzlich ein Saftkarton und fällt Richtung Boden. Beim Betrachten des Saftkartons erkennt man, dass sein Deckel bereits geöffnet wurde, und dass die Ecken des Kartons an vielen Stellen eingedellt sind. Hieraus könnte man schließen, dass der Saftkarton fast leer sein müsste und daher leicht sein sollte. Da man diesen Karton jedoch am Abend zuvor fast voll in den Kühlschrank gestellt hatte, würde man eher erwarten, dass er schwer sein müsste. Zu diesen unterschiedlichen Gewichtsvorhersagen lassen sich nun passende motorische Programme antizipieren. Folglich stellt sich die Frage, auf welcher Grundlage das Nervensystem sich für die Ausführung eines motorischen Programms entschließt.

Mit dieser Frage beschäftigen sich aktuelle wissenschaftliche Ansätze, die motorische Planung als Entscheidungsverfahren betrachten, bei dem eine Entscheidung auf Grundlage von Wahrscheinlichkeiten für das Auftreten unterschiedlicher Ergebnisse getroffen wird (Nagengast et al., 2010; Wolpert & Landy, 2012; Wu et al., 2009). Bezo-

gen auf das obige Beispiel könnten sich die Wahrscheinlichkeiten für die beiden zu erwartenden Gewichte des Saftkartons unterscheiden.

Ein weiterer wichtiger Aspekt bei der Auswahl von Motorik spielen Kosten- und Nutzenabwägungen verschiedener möglicher motorischer Programme (Wolpert & Landy, 2012). So würde bei der Planung der Greifmotorik im oben genannte Beispiel berücksichtigt werden, wie wichtig es ist, den Saftkarton mit einem sicheren Griff festzuhalten. Erscheint dies wichtig, würde man selbst bei einem wahrscheinlich leeren Saftkarton eine Übersteuerung der Motorik in Kauf nehmen.

In vielen Studien der letzten 20 Jahre gelang es, motorische Entscheidungsverfahren durch monetäre Belohnung oder monetären Verlust zu beeinflussen. So ließen sich Aspekte wie die Zielausrichtung, der Bewegungspfad und die zeitliche Planung von Bewegungen gezielt durch Belohnung und Bestrafung modifizieren (Hudson et al., 2008; Rakitin et al., 1998; Trommershäuser et al., 2003; Wolpert & Landy, 2012; Zhang et al., 2010).

Die Fähigkeit, zielgerichtete Motorik auszuführen, kann zum Beispiel als Folge der Parkinsonerkrankung beeinträchtigt sein. Am Beispiel der Greifbewegungen wurde dies ausführlich untersucht. Im Vergleich zu gesunden Menschen ihres Alters weisen Menschen mit Parkinsonerkrankung eine deutliche Verzögerung in der Initiierung einer Greifbewegung auf (Brumlik & Bosches, 1966; Sheridan et al., 1987; Stelmach et al., 1989) und führen diese Bewegung deutlich verlangsamt aus (Brumlik & Bosches, 1966; Fellows et al., 1998; Gordon et al., 1997; Müller & Abbs, 1990).

Turner und Desmurget (2010) sehen in der verzögerten Initiierung und der deutlichen Verlangsamung von Bewegungen Hinweise für eine fehlerhafte Regulation der Kraftstärke und Probleme in der Steuerung von Feinmotorik. Diese Annahme wird von Studien gestützt, die bei Parkinsonpatient*innen Probleme bei der Nutzung von Vorabinformationen für die prädiktive Skalierung der Fingerkräfte zeigen konnten (Fellows et al., 1998; Müller & Abbs, 1990). Weitere Hinweise für Steuerungsprobleme der Feinmotorik wurden von Alberts et al. (1998; 2004) berichtet. In ihren Studien berichten die Autor*innen von einer Diskoordination der Griff- und Hubkraft.

Im Gegensatz zu diesen Ergebnissen berichten Gordon et al. (1997), dass sie in ihrer Studie keinerlei Hinweise für Beeinträchtigungen der prädiktiven Kraftskalierung bei Menschen mit Parkinsonerkrankung finden konnten. Zwar sei die Motorik von Parkinsonpatient*innen verlangsamt gewesen, jedoch sei es ihnen gelungen, Größenhinweise zur prädiktiven Skalierung ihrer Griff- und Hubkraft zu nutzen. Entgegen der Ergebnisse von Alberts et al. (1998; 2004) berichten Forsberg et al. (2000) und Ingvarsson et al. (1997) von einer ausgeprägten Koordination der Griff- und Hubkraft bei Parkinsonpatient*innen.

Es scheint also nicht klar zu sein, welche Veränderungen im motorischen System die Beeinträchtigungen der Feinmotorik bei Menschen mit Parkinsonerkrankung er-

klären können. Eine interessante Sichtweise wird von Mazzoni et al. (2007) vertreten. Sie nehmen an, dass motivationale Aspekte die verzögerte Initiierung und die deutliche Verlangsamung von Feinmotorik bei Menschen mit Parkinsonerkrankung erklären könnten. Ihrer Ansicht nach würden Menschen mit Parkinsonerkrankung es vorziehen, weniger Energie bei der Ausführung von Motorik aufzuwenden.

Wissenschaftliche Fragestellung und Methoden

In Situationen, in denen Zielkonflikte bestehen, können Entscheidungen auf Grundlage von Wahrscheinlichkeiten für das Auftreten unterschiedlicher Ergebnisse getroffen werden (Nagengast et al., 2010; Wolpert & Landy, 2012; Wu et al., 2009). Auch Kosten- und Nutzenabwägungen verschiedener Handlungsmöglichkeiten können berücksichtigt werden (Wolpert & Landy, 2012).

Obwohl schon viele wissenschaftliche Erkenntnisse in diesem Bereich gewonnen werden konnten, ist es bis heute unklar, wie Wahrscheinlichkeiten vom motorischen System interpretiert und genutzt werden, um bestimmte Handlungen auszuwählen und durchzuführen. Insbesondere stellt sich die Frage nach dem Zusammenhang zwischen perzeptueller Interpretation und Kraftprädiktion auf Grundlage probabilistischer Gewichtsinformationen.

Wichtige Erkenntnisse, die unsere Vorstellung über das motorische System geprägt haben, wurden im Rahmen von Studien mit Parkinsonpatient*innen gewonnen. Als Folge der Parkinsonerkrankung kommt es auch zu Problemen der Greifmotorik. Am deutlichsten wird dies durch eine Verzögerung bei der Initialisierung von Greifmotorik und durch eine deutliche Verlangsamung dieser Bewegungen. Turner und Desmurget (2010) sehen als Ursache hierfür eine fehlerhafte Regulation der Kraftstärke und Probleme in der Steuerung von Feinmotorik. Die Datenlage hierfür ist jedoch widersprüchlich. Der Umgang mit probabilistischen Gewichtsinformationen könnte wichtige neue Erkenntnisse darüber liefern, ob Veränderungen in der Entscheidungsfindung bei der Auswahl der Motorik von Menschen mit Parkinsonerkrankung eine Rolle spielen.

Um diese unterschiedlichen Aspekte zu untersuchen, wurde ein experimentelles Paradigma entwickelt, in dem probabilistische Gewichtsinformationen einerseits für das zielgerichtete Anheben eines Objektes und andererseits für die Einstellung des zu erwartenden Gewichtes genutzt werden sollten. Hierfür wurden im Rahmen der der Dissertation zugrunde liegenden Studien zwei Experimentalaufgaben entworfen. Die eine war eine Greif-Hebe-Aufgabe (GH Aufgabe), bei der ein Hebel unter Verwendung des Präzisionsgriffs gezielt auf eine vorgegebenen Höhe angehoben werden sollte. Das Gewicht des Hebels wechselte zufällig zwischen 300 g (leicht), 800 g (mittel) und 1400 g (schwer). Um schnell und unauffällig zwischen den drei Gewichten wechseln zu

können, wurde ein Linearmotor (Servotube actuator STA1116, Dunkermotoren, Essex, UK) über einen Flaschenzug mit dem Hebel verbunden. Die Versuchsteilnehmer*innen saßen an einem Tisch mit dem Hebel rechts und einem Monitor frontal vor ihnen. Vor dem Anheben des Hebels bekamen die Versuchsteilnehmer*innen eine Ankündigung über das folgende Gewicht auf dem Monitor zu sehen. Die Ankündigungen konnten entweder ein Gewicht sicher vorhersagen, keine Vorhersage treffen oder probabilistische Ankündigungen sein, die zwei Gewichte mit unterschiedlicher Wahrscheinlichkeit vorhersagen. Bei der probabilistischen Ankündigung sahen die Versuchsteilnehmer*innen eine „Ampel“ mit vier Feldern auf dem Monitor. Wenn das unterste Feld (LM Stimulus) leuchtete, wussten die Versuchsteilnehmer*innen, dass das folgende Gewicht des Hebels in 66,7 % der Fälle leicht sein würde, während es in 33,3 % der Fälle mittelschwer sein würde. Leuchtete das zweite Feld von unten (ML Stimulus), folgte in 66,7 % der Fälle das mittlere Gewicht und in 33,3 % der Fälle das leichte Gewicht. In der dritten Position von unten (MH Stimulus) gab die Ampel an, dass in 66,7 % der Fälle das mittlere Gewicht folgte und in 33,3 % der Fälle das schwere Gewicht. In der obersten Position (HM Stimulus) folgte in 66,7 % der Fälle das schwere Gewicht und in 33,3 % der Fälle das mittlere Gewicht.

Während der GH Aufgabe wurden Griff- und Hubkraft mit einem Kraftsensor (Dasch, Kiel) aufgezeichnet. Der Kraftsensor war mit dem Hebel befestigt und stellte gleichzeitig die Grifffläche des Hebels dar (40 x 40 x 30 cm). Der Kraftsensor erlaubte eine Aufnahme mit einer zeitlichen Auflösung von 50 Hz und einem Aufnahmebereich von 0–20 N. Mit der GH Aufgabe ließ sich der Einfluss vier unterschiedlicher probabilistischer Ankündigungen (LM, ML, MH, HM) auf das Anheben eines Objektes mit konstantem Gewicht (800 g) untersuchen.

In der zweiten Aufgaben ging es darum, das Gewicht eines Hebels entsprechend einer Gewichtserwartung einzustellen (GE Aufgabe). Es wurden hierfür dieselben probabilistischen Ankündigungen genutzt wie in der GH Aufgabe. Für die Einstellungen hatten die Versuchsteilnehmer*innen beliebig viel Zeit. Um das Gewicht ausführlich zu spüren, konnten die Teilnehmer*innen den Hebel so oft sie wollten anheben und absetzen. Das Gewicht des Hebels konnten sie über Pfeiltasten (\downarrow \uparrow) der vor ihnen liegenden Tastatur in Schritten von 10 g einstellen.

Experimente

Die vorliegende Dissertation verfolgt das übergeordnete Ziel zu untersuchen, wie probabilistische Informationen für die Kraftprädiktion beim zielgerichteten Anheben von Objekten gebildet werden und wie auf ihrer Grundlage Vorhersagen perzeptueller Gewichtserwartungen genutzt werden. Dabei stellt sich auch die Frage nach dem Zusammenhang zwischen perzeptueller Interpretation und Kraftprädiktion auf

Grundlage probabilistischer Gewichtsinformationen. Ferner wird die Nutzung probabilistischer Gewichtsinformationen beim Anheben von Objekten auch bei Parkinsonpatient*innen untersucht. Die Ergebnisse liefern wichtige neue Erkenntnisse darüber, ob Veränderungen in der Entscheidungsfindung bei der Auswahl der Motorik von Menschen mit Parkinsonerkrankung eine Rolle spielen. Hierzu wurden die vier folgenden Fragestellungen beantwortet.

- (Q1) Welchen Einfluss haben probabilistische Gewichtsinformationen auf die Ausführung eines Präzisionsgriffs?
- (Q2) Wie werden probabilistische Gewichtsinformationen in perzeptuelle und motorische Erwartungen umgesetzt?
- (Q3) Besteht ein Zusammenhang zwischen perzeptueller Gewichtserwartung und motorischer Kraftprädiktion?
- (Q4) Nutzen Menschen mit Parkinsonerkrankung probabilistische Gewichtsinformationen für die Ausführung eines Präzisionsgriffs und inwiefern unterscheiden sie sich darin von gleichaltrigen gesunden Menschen?

Zur Beantwortung dieser Fragen wurden drei Studien durchgeführt (siehe ARTIKEL I–III). Die erste Studie (*Probabilistic information on object weight shapes force dynamics in a grip-lift task; ARTICLE I*) wurde zur Analyse, wie das motorische System probabilistische Gewichtsinformationen zur Vorbereitung und Ausführung eines Präzisionsgriffs nutzt, entworfen. Neben dem Gewinn theoretischer Erkenntnisse ging es in der ersten Studie um die Etablierung des probabilistischen Paradigmas in Form der GH Aufgabe.

Es wurde einerseits untersucht, wie sich die unterschiedlichen Ankündigungen (sicher, keine, probabilistisch) auf die Maxima der Griff- und Hubkraft sowie auf ihre jeweiligen Krafraten auswirkten. Ein Hauptaugenmerk wurde auf den Effekt der probabilistischen Gewichtsankündigung gelegt. Dafür wurden für die Auswertung nur die Durchgänge im Experiment berücksichtigt, bei denen das mittlere Gewicht (800 g) angehoben wurde.

Die Ergebnisse der ersten Studie zeigen einen progressiven Anstieg der maximalen Krafraten sowie der maximalen Griffkraft bei sicherer Ankündigung des Gewichts. Auch die probabilistischen Gewichtsankündigungen hatten einen Einfluss auf die prädiktive Skalierung der Fingerkräfte. In Hebedurchgängen, in denen das mittlere Gewicht angehoben wurde, konnte ein progressiver Anstieg der maximalen Krafraten sowie der maximalen Griffkraft gemessen werden. Bei näherer Analyse zeigte sich jedoch, dass die Vorhersagen, bei denen mit hoher Wahrscheinlichkeit (66,7 %) eine Abweichung vom mittleren Gewicht zu erwarten war (Stimuli LM und HM) einen

größeren Effekt auf die Skalierung der Krafraten hatten als Vorhersagen, bei denen diese Abweichung unwahrscheinlicher (33,3 %) war (Stimuli ML und MH).

Als Hauptergebnis dieser Studie kann postuliert werden, dass probabilistische Gewichtsinformationen für die Ausführung eines Präzisionsgriffs genutzt werden können. Umso höher die Wahrscheinlichkeit für ein schweres Gewicht ist, desto höher ist auch die maximale Skalierung der Griff- und Hubkrafraten (Ref. Q1). Dies zeigt, dass probabilistische Informationen die prädiktive Skalierung der Fingerkraft beeinflussen. Ähnliche Ergebnisse wurde von van Nuenen et al. (2012) berichtet. Allerdings nutzen die Autoren ein weitaus simpleres Paradigma, bei dem die Differenzierung der probabilistischen Gewichtsinformation nicht so sehr im Fokus standen wie in der dieser Dissertation zugrunde liegenden Studie.

Die unterschiedlichen Effekte der probabilistischen Gewichtsvorhersagen deuten auf eine Verzerrung von Wahrscheinlichkeitsinformationen hin. Ähnliche Effekte werden auch für die menschliche Urteilsbildung und Entscheidungsfindung berichtet (Zhang & Maloney, 2012).

Die zweite Studie (*Processing of Probabilistic Information in Weight Perception and Motor Prediction; ARTICLE II*) wurde entworfen, um die Verzerrung von Wahrscheinlichkeitsinformationen besser zu verstehen. Ein weiteres Ziel war es zu untersuchen, wie perzeptuelle Gewichtserwartungen im Verhältnis zur prädiktiven Kraftskalierung auf Grundlage von probabilistischen Gewichtsankündigung gebildet werden.

Um dies zu untersuchen, führten Versuchspersonen die GH Aufgabe und die GE Aufgabe aus (s.o.). Um den Effekt der probabilistischen Gewichtsankündigung auf die prädiktive Kraftskalierung zu ermitteln, wurden die Maxima der Griff- und Hubkrafraten bei der Ausführung der GH Aufgabe gemessen. Es wurden nur die Durchgänge im Experiment berücksichtigt, bei denen das mittlere Gewicht (800 g) angehoben wurde. Um den Effekt der probabilistischen Gewichtsankündigung auf die perzeptuelle Gewichtserwartung zu ermitteln, wurden die Gewichtseinstellungen der GE Aufgabe erhoben. Um Effekte der probabilistischen Gewichtsankündigung auf beide Aufgaben besser miteinander vergleichen zu können, wurden ihre Messergebnisse auf Basis einer z-Transformation standardisiert. Die Korrelation zwischen den standardisierten Ergebnissen der GH und der GE Aufgabe wurde errechnet, und ihre Verteilungen wurden miteinander verglichen (Zwei-Gruppen Kolmogorov-Smirnov Tests).

Die Interpretation probabilistischer Informationen kann durch die Aufgabenstellung beeinflusst werden (Zhang & Maloney, 2012). Dies könnte zu Unterschieden zwischen den Ergebnissen der GH und GE Aufgabe führen. Um dies zu berücksichtigen, führten zwei Gruppen von Versuchsteilnehmer*innen beide Aufgaben in einer unterschiedlichen Reihenfolge durch (A: GH→GE; B: GE→GH→GE).

Die Ergebnisse der Studie zeigen in beiden Gruppen einen Anstieg der prädiktiven

Kraftskalierung und der perzeptuellen Gewichtserwartung in Abhängigkeit von der probabilistischen Gewichtsankündigung (Ref. Q2). In Gruppe A zeigte sich eine deutlich verzerrte Umsetzung der probabilistischen Gewichtsankündigung in die maximalen Griff- und Hubkrafttraten sowie in die Gewichtseinstellung. Die Verzerrung war in beiden Aufgaben so stark ausgeprägt, dass die Klassifikation der vier probabilistischen Gewichtsankündigung zu drei unterschiedlichen Gewichtseinstellungen und zu drei unterschiedlichen prädiktiven Griff- und Hubkraftskalierungen führte ($LM < ML \approx MH < HM$). Im Unterschied dazu wurden die vier probabilistischen Gewichtsankündigungen von den Versuchsteilnehmer*innen in Gruppe B zu in jeweils vier Klassen von Gewichtseinstellungen und prädiktiven Griff- und Hubkraftskalierungen eingeteilt ($LM < ML < MH < HM$). In beiden Gruppen deuteten die Korrelationen auf einen starken Zusammenhang zwischen den Gewichtseinstellungen und den prädiktiven Griff- und Hubkraftskalierungen hin. Ferner fanden sich beim Vergleich der Verteilung der standardisierten Ergebnisse der GH und der GE Aufgabe keine Hinweise auf Unterschiede.

Eine wichtige Folgerung dieser Studie ist, dass sich Gewichtseinstellungen und prädiktive Griff- und Hubkraftskalierung innerhalb der beiden Gruppen sehr stark ähneln. Dies deutet auf einen starken Zusammenhang zwischen perzeptueller Gewichtserwartung und der prädiktiver Skalierung der Motorik hin (Ref. Q3). Möglicherweise greifen beide auf ein gemeinsames abstraktes Konzept zurück, wie es von Vertretern so genannter „common-coding“ Ansätze postuliert wird (Franz et al., 2000; Hommel et al., 2001; Müsseler, 1999; Prinz, 1990).

Eine weitere Folgerung aus den Ergebnissen dieser Studie ist, dass die erste Erfahrung, die mit den probabilistischen Gewichtsankündigungen gemacht wird, prägend ist für ihre Interpretation im gesamten Experiment. In der Diskussion des dritten Artikels stellen wir die Vermutung auf, dass die Versuchsteilnehmer*innen beider Gruppen möglicherweise unterschiedliche Strategien zum Umgang mit Wahrscheinlichkeit genutzt haben. Im Folgenden werden drei mögliche Strategien dargestellt.

Eine mögliche Strategie (A) wäre die Nichtbeachtung der Wahrscheinlichkeitsinformationen. Eine weitere Strategie (B) wäre, die Griff- und Hubkräfte sowie die Gewichtserwartung an das durchschnittlich zu erwartende Gewicht auszurichten. Diese Strategie würde im Bereich der Motorik starke Abweichungen in Form von hohen Über- und Untersteuerungen vermeiden. Allerdings wäre eine ständige Nachjustierung der Kräfte nötig, da das durchschnittlich zu erwartenden Gewicht nie angehoben wird. Eine dritte Strategie (C) wäre, die Griff- und Hubkräfte sowie die Gewichtserwartung an die wahrscheinlichere Gewichtsvorhersage auszurichten. Diese Strategie würde im Bereich der Motorik die Anzahl an Nachjustierungen der Kräfte minimieren. Allerdings käme es dabei auch zu zum Teil starken Über- und Untersteuerungen der Motorik. Die Ergebnisse der Gruppe A sind dabei am besten mit Strategie C in

Einklang zu bringen, während die Ergebnisse der Gruppe B am besten zur Strategie B passen.

Insgesamt deuten die Ergebnisse dieser Studie darauf hin, dass die Interpretation probabilistischer Gewichtsankündigung an die Anforderungen der ersten Aufgabe angepasst wurde. Die erste Erfahrung im Umgang mit den probabilistischen Gewichtsankündigungen hatte also einen entscheidenden Einfluss auf die Kategorisierung der Stimuli im gesamten Experiment.

Die dritte Studie (*Parkinsonian Patients Fail to use Probabilistic Cues for Force Scaling in a Grip-Lift Task; ARTICLE III*) wurde entworfen, um zu untersuchen, wie Menschen mit Parkinsonerkrankung probabilistische Gewichtsinformationen zur Vorbereitung und Ausführung eines Präzisionsgriffs nutzen.

In dieser Studie nahmen Parkinsonpatient*innen und gesunde gleichaltrige Kontrollproband*innen teil. Beide Gruppen führten die Aufgaben durch, die bereits in der zweiten Studie genutzt wurden. Dabei wurde zunächst die GH Aufgabe ausgeführt, anschließend die GE Aufgabe. Es wurden die Maxima der Griff- und Hubkraft sowie der dazugehörigen Krafraten bei der Ausführung der GH Aufgabe gemessen und die Dauer der Vorlastphase erhoben. Aus der GE Aufgabe wurden die Gewichtseinstellungen erhoben.

Zur Untersuchung, ob es durch die Parkinsonerkrankung zu Veränderungen in der motorischen Steuerung kommt, wurde die Koordination zwischen Griff- und Hubkraft untersucht. Hierfür wurden alle Versuchsteilnehmer*innen zunächst die durchschnittlichen Griff- und Hubkraftverläufe der sicheren Vorhersage der drei Gewichte und der probabilistischen Gewichtsankündigungen beim Anheben des mittleren Gewichts errechnet. Die Pearson-Korrelation zwischen den durchschnittlichen Griff- und Hubkraftverläufen wurde errechnet und anschließend nach Fisher z-transformiert (Fisher, 1921). Auf dieser Basis konnte untersucht werden, ob sich die Korrelation zwischen den Griff- und Hubkräften unterscheidet. Zusätzlich wurde noch das Intervall zwischen der Griffkraft- und der Hubkraftinitialisierung untersucht.

Anhand der Analyse der Kraftdaten beider Gruppen zeigte sich ein progressiver Zusammenhang zwischen dem gehobenen Gewichten und der maximalen Griff- und Hubkraft sowie der Hubkraftrate. Ferner wiesen die Verläufe der Griff- und Hubkraft in beiden Gruppen bei allen Gewichtsankündigung einen beinahe linearen Zusammenhang auf.

Unterschiede zwischen den Gruppen fanden sich bezüglich der Dauer der Vorlastphase. Hier wiesen die Parkinsonpatient*innen bei den sicheren Vorhersagen und bei den probabilistischen Gewichtsankündigungen deutlich längere Phasen auf. Am deutlichsten zeigten sich die Unterschiede zwischen den Gruppen in der Nutzung der probabilistischen Gewichtsankündigungen. Während die Maxima der Griff- und Hubkraftraten der Kontrollproband*innen deutlich von den probabilistischen Ge-

wichtsankündigungen beeinflusst wurden (wenn auch in verzerrter Weise), blieb dieser Einfluss bei den Parkinsonpatient*innen aus (Ref. Q4).

Auch die Gewichtseinstellungen unterschieden sich zwischen den Gruppen. Während die Parkinsonpatient*innen das Gewicht des Hebels in Relation zu den probabilistischen Gewichtsankündigungen erhöhten, wiesen die Kontrollproband*innen wie auch schon in der GH Aufgabe eine deutliche Verzerrung auf.

Eine Folgerung aus den hier erhobenen Ergebnissen ist, dass die Proband*innen beider Gruppen in der Lage waren, den probabilistischen Gewichtsankündigungen unterschiedliche perzeptuelle Gewichtserwartungen zuzuordnen. Allerdings gelang es den Parkinsonpatient*innen nicht, die probabilistischen Gewichtsankündigungen zur Vorbereitung und Ausführung eines Präzisionsgriffs zu nutzen.

Die Untersuchungen der Griff- und Hubkraftkorrelation sowie des Intervalls zwischen der Griff- und Hubkraftinitialisierung deuten auf eine simultane Verarbeitung beider Kräfte hin. Diese wird als wichtiges Kennzeichen antizipatorischer Kraftkontrolle angesehen (Johansson & Flanagan, 2009; Johansson & Westling, 1988).

Insgesamt deuten die Daten der Parkinsonpatient*innen darauf hin, dass sie ihre Ausführungen von Griff- und Hubkraft prädiktiv auf ein Kraftniveau hin geplant haben, welches allerdings nicht von den probabilistischen Gewichtsankündigungen beeinflusst wurde.

Im Vergleich zur Gruppe der gesunden Proband*innen zeigte sich eine Veränderung der motorischen Entscheidungsfindung bei den Parkinsonpatient*innen. Dies könnte ein Indiz dafür sein, dass der Botenstoff Dopamine sich nicht nur auf den Prozess der Entscheidungsfindung auswirkt (für eine Übersicht siehe Frank, 2006; Glimcher & Fehr, 2013), sondern auch auf die motorische Entscheidungsfindung.

Diese Arbeit schließt mit einer Diskussion der vorgestellten Ergebnisse ab. Dabei wird auf einen möglichen Zusammenhang von Wahrnehmung und Motorik eingegangen. Dieser wird von Vertretern so genannten common-coding Ansätze angenommen (Franz et al., 2000; Müsseler, 1999; Prinz, 1990). Für Gemeinsamkeiten zwischen Wahrnehmung und Motorik spricht, dass sich Gewichtseinstellungen und prädiktive Griff- und Hubkraftskalierung innerhalb der beiden Gruppen sehr stark ähnelten. Jedoch zeigten sich auch Unterschiede zwischen der GH und der GE Aufgabe, wenn ihre jeweils ersten Ausführungen betrachtet wurden. Auch die Ergebnisse der Parkinsonpatient*innen sprechen gegen einen notwendigen Zusammenhang von Wahrnehmung und Motorik. Dies wird auch von der dual-stream Theorie vertreten, die eine Dissoziation zwischen der Verarbeitung visueller Informationen für Wahrnehmung und Motorik annimmt (Goodale & Milner, 1992). Insgesamt lässt sich sagen, dass Aspekte beider Theorien zu den hier vorstellten Ergebnissen passen.

Als Schlussfolgerung lässt sich festhalten, dass unterschiedliche Anforderungen

der beiden Aufgaben die Interpretation der probabilistischen Gewichtsinformationen beeinflusst haben können. Dabei scheint eine andere Methode für die motorische Interpretation genutzt worden zu sein als für die perzeptuelle Interpretation. Wurde eine Interpretation erstmals angelegt, so griffen beide Systeme bei späterer Nutzung auf diese zu. Entscheidend für den Umgang (perzeptuell wie motorisch) mit den probabilistischen Gewichtsinformationen war also, welches System auf Grund der Aufgabenstellung die Interpretation der probabilistischen Gewichtsinformationen übernahm.

9 List of Abbreviations

In alphabetical order

cm	Centimeters
e. g.	Exempli gratia
F	F-test statistic
g	Gram
GF	Peak grip force
GFr	Peak grip force rate
GL	Grip-lift
HC	Healthy age matched control subjects
Hz	Hertz
i. e.	Id est
LF	Peak lift force
LFr	Peak lift force rate
LPD	Load phase duration
mm	Millimeters
ms	Milliseconds
N	Newton
Ns	Newton per second
p	Statistical p-value
P	Weighted combination of the two possible weights predicted by each cue
PD	Parkinson's disease
s	Seconds
WP	Weight perception

Probabilistic cues

HM	Prediction: 66.7 % heavy (1400 g), 33.3 % medium (800 g)
MH	Prediction : 66.7 % medium (800 g), 33.3 % heavy (1400 g)
ML	Prediction: 66.7 % medium (800 g), 33.3 % light (300 g)
LM	Prediction: 66.7 % light (300 g), 33.3 % medium (800 g)

10 References

- Aglioti, S., DeSouza, J. F. X., & Goodale, M. A. (1995). Size-contrast illusions deceive the eye but not the hand. *Current Biology*, 5, 679–685.
- Alberts, J. L., Elder, C. M., Okun, M. S., & Vitek, J. L. (2004). Comparison of pallidal and subthalamic stimulation on force control in patient's with Parkinson's disease. *Motor Control*, 8(4), 484–499.
- Alberts, J. L., Tresilian, J. R., & Stelmach, G. E. (1998). The co-ordination and phasing of a bimanual prehension task: the influence of Parkinsonism. *Brain*, 121(4), 725–742.
- Ameli, M., Dafotakis, M., Fink, G. R., & Nowak, D. A. (2008). Predictive force programming in the grip-lift task: the role of memory links between arbitrary cues and object weight. *Neuropsychologia*, 46(9), 2383–2388.
- Aoki, T., Latash, M. L., & Zatsiorsky, V. M. (2007). Adjustments to local friction in multi-finger prehension. *Journal of motor behavior*, 39(4), 276–290.
- Aoki, T., Niu, X., Latash, M. L., & Zatsiorsky, V. M. (2006). Effects of friction at the digit-object interface on the digit forces in multi-finger prehension. *Experimental Brain Research*, 172(4), 425–438.
- Baugh, L. A., Kao, M., Johansson, R. S., & Flanagan, J. R. (2012). Material evidence: interaction of well-learned priors and sensorimotor memory when lifting objects. *Journal of Neurophysiology*, 108(5), 1262–1269.
- Bensmail, D., Sarfeld, A. S., Ameli, M., Fink, G. R., & Nowak, D. A. (2012). Arbitrary visuomotor mapping in the grip-lift task: dissociation of performance deficits in right and left middle cerebral artery stroke. *Neuroscience*, 210, 128–136.
- Birznieks, I., Burstedt, M. K., Edin, B. B., & Johansson, R. S. (1998). Mechanisms for force adjustments to unpredictable frictional changes at individual digits during two-fingered manipulation. *Journal of Neurophysiology*, 80(4), 1989–2002.
- Brumlik, J., & Bosches, B. (1966). The mechanism of bradykinesia in Parkinsonism. *Neurology*, 16(4), 337–344.
- Buckingham, G., Cant, J. S., & Goodale, M. A. (2009). Living in a material world: How visual cues to material properties affect the way that we lift objects and perceive their weight. *Journal of Neurophysiology*, 102, 3111–3118.
- Buckingham, G., & Goodale, M. A. (2010). Lifting without seeing: The role of vision in perceiving and acting upon the size weight illusion. *PLoS ONE*, 5(3), e9709.
- Burstedt, M. K., Flanagan, J. R., & Johansson, R. S. (1999). Control of grasp stability in humans under different frictional conditions during multidigit manipulation. *Journal of neurophysiology*, 82(5), 2393–2405.
- Cadoret, G., & Smith, A. M. (1996). Friction, not texture, dictates grip forces used du-

- ring object manipulation. *Journal of Neurophysiology*, 75(5), 1963–1969.
- Chouinard, P. A., Large, M. E., Chang, E. C., & Goodale, M. A. (2009). 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. *Neuroimage*, 44, 200–212.
- Chouinard, P. A., Leonard, G., & Paus, T. (2005). Role of the primary motor and dorsal premotor cortices in the anticipation of forces during object lifting. *The Journal of Neuroscience*, 25(9), 2277–2284.
- Christopoulos, V. N., & Schrater, P. R. (2009). Grasping objects with environmentally induced position uncertainty. *PLoS Comput Biol*, 5(10), e1000538.
- Cohen, R. G., Biddle, J. C., & Rosenbaum, D. A. (2010). Manual obstacle avoidance takes into account visual uncertainty, motor noise, and biomechanical costs. *Experimental Brain Research*, 201(3), 587–592.
- Cole, K. J., & Rotella, D. L. (2002). Old age impairs the use of arbitrary visual cues for predictive control of fingertip forces during grasp. *Experimental Brain Research*, 143(1), 35–41.
- Desmurget, M., Grafton, S. T., Vindras, P., Grea, H., & Turner, R. S. (2003). Basal ganglia network mediates the control of movement amplitude. *Experimental Brain Research*, 153(2), 197–209.
- Edin, B. B., Westling, G., & Johansson, R. S. (1992). Independent control of human finger-tip forces at individual digits during precision lifting. *The Journal of physiology*, 450, 547.
- Ellis, R. R., & Lederman, S. J. (1999). The material–weight illusion revisited. *Perception & Psychophysics*, 61, 1564–1576.
- Fellows, S. J., & Noth, J. (2004). Grip force abnormalities in de novo Parkinson's disease. *Movement Disorders*, 19(5), 560–565.
- Fellows, S. J., Noth, J., & Schwarz, M. (1998). Precision grip and Parkinson's disease. *Brain*, 121(9), 1771–1784.
- Fisher, R. A. (1921). On the probable error of a coefficient of correlation deduced from a small sample. *Metron*, 1, 3–32.
- Flanagan, J. R., & Bandomir, C. A. (2000). Coming to grips with weight perception: Effects of grasp configuration on perceived heaviness. *Perception & Psychophysics*, 62, 1204–1219.
- Flanagan, J. R., & Beltzner, M. A. (2000). Independence of perceptual and sensorimotor predictions in the size-weight illusion. *Nature Neuroscience*, 3, 737–741.
- Flanagan, J. R., & Johansson, R. S. (2002). Hand movements. *Encyclopedia of the human brain*, 2, 399–414.
- Flanagan, J. R., & Wing, A. M. (1997). The role of internal models in motion planning and control: evidence from grip force adjustments during movements of hand-

- held loads. *Journal of Neuroscience*, 17(4), 1519–1528.
- Flanagan, J. R., Wing, A. M., Allison, S., & Spenceley, A. (1995). Effects of surface texture on weight perception when lifting objects with a precision grip. *Perception & Psychophysics*, 57, 282–290.
- Forsberg, H., Eliasson, A. C., Kinoshita, H., Westling, G., & Johansson, R. S. (1995). Development of human precision grip. *Experimental Brain Research*, 104(2), 323–330.
- Forsberg, H., Ingvarsson, P. E., Iwasaki, N., Johansson, R. S., & Gordon, A. M. (2000). Action tremor during object manipulation in Parkinson's disease. *Movement Disorders*, 15 (2), 244–254.
- Frank, M. J. (2006). Hold your horses: a dynamic computational role for the subthalamic nucleus in decision making. *Neural Networks*, 19(8), 1120–1136.
- Franz, V. H., Gegenfurtner, K. R., Bühlhoff, H. H., & Fahle, M. (2000). No evidence for a dissociation between perception and action. *Psychological Science*, 11, 20–25.
- Gleichgerricht, E., Ibáñez, A., Roca, M., Torralva, T., & Manes, F. (2010). Decision-making cognition in neurodegenerative diseases. *Nature Reviews Neurology*, 6(11), 611–623.
- Glimcher, P. W., & Fehr, E. (Eds.). (2013). *Neuroeconomics: Decision making and the brain*. Academic Press.
- Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, 15, 20–25.
- Goodwin, A. W., Jenmalm, P., & Johansson, R. S. (1998). Control of grip force when tilting objects: effect of curvature of grasped surfaces and applied tangential torque. *Journal of Neuroscience*, 18(24), 10724–10734.
- Gordon, A. M., Ingvarsson, P. E., & Forsberg, H. (1997). Anticipatory control of manipulative forces in Parkinson's disease. *Experimental Neurology*, 145(2), 477–488.
- Gordon, A. M., Forsberg, H., Johansson, R. S. & Westling, G. (1991). The integration of sensory information during the programming of precision grip: comments on the contribution of size cues. *Experimental Brain Research*, 85(1), 226–229.
- Gordon, A. M., & Reilmann, R. (1999). Getting a grasp on research: does treatment taint testing of parkinsonian patients? *Brain*, 122, 1597–1598.
- Gordon, A. M., Westling, G., Cole, K. J., & Johansson, R. S. (1993). Memory representations underlying motor commands used during manipulation of common and novel objects. *Journal of Neurophysiology*, 69(6), 1789–1796.
- Grandy, M. S., & Westwood, D. A. (2006). Opposite perceptual and sensorimotor responses to a size–weight illusion. *Journal of Neurophysiology*, 95, 3887–3892.
- Hertwig, R., Barron, G., Weber, E. U., & Erev, I. (2004). Decisions from experience and the effect of rare events in risky choice. *Psychological Science*, 15, 534–539.
- Hudson, T. E., Maloney, L. T., & Landy, M. S. (2008). Optimal compensation for temporal uncertainty in movement planning. *PLoS Comput Biol*, 4(7), e1000130.

- Ingvarsson, P. E., Gordon, A. M., & Forssberg, H. (1997). Coordination of manipulative forces in Parkinson's disease. *Experimental Neurology*, 145(2), 489–501.
- Jenmalm, P., Dahlstedt, S., & Johansson, R. S. (2000). Visual and tactile information about object-curvature control fingertip forces and grasp kinematics in human dexterous manipulation. *Journal of Neurophysiology*, 84(6), 2984–2997.
- Jenmalm, P., & Johansson, R. S. (1997). Visual and somatosensory information about object shape control manipulative fingertip forces. *Journal of Neuroscience*, 17(11), 4486–4499.
- Jenmalm, P., Schmitz, C., Forssberg, H., & Ehrsson, H. H. (2006). Lighter or heavier than predicted: neural correlates of corrective mechanisms during erroneously programmed lifts. *The Journal of Neuroscience*, 26(35), 9015–9021.
- Johansson, R. S. (1998). *Sensory input and control of grip. Sensory guidance of movement*, 45–59.
- Johansson, R. S., Backlin, J. L., & Burstedt, M. K. (1999). Control of grasp stability during pronation and supination movements. *Experimental Brain Research*, 128(1–2), 20–30.
- Johansson, R. S., & Flanagan, J. R. (2009). Coding and use of tactile signals from the fingertips in object manipulation tasks. *Nature Reviews Neuroscience*, 10, 345–359.
- Johansson, R. S., & Westling, G. (1984). Roles of glabrous skin receptors and sensorimotor memory in automatic control of precision grip when lifting rougher or more slippery objects. *Experimental Brain Research*, 56(3), 550–564.
- Johansson, R. S., & Westling, G. (1987). Signals in tactile afferents from the fingers eliciting adaptive motor responses during precision grip. *Experimental Brain Research*, 66(1), 141–154.
- Johansson, R. S., & Westling, G. (1988). Coordinated isometric muscle commands adequately and erroneously programmed for the weight during lifting task with precision grip. *Experimental Brain Research*, 71(1), 59–71.
- Jordan, N., Sagar, H. J., & Cooper, J. A. (1992). A component analysis of the generation and release of isometric force in Parkinson's disease. *Journal of Neurology, Neurosurgery & Psychiatry*, 55(7), 572–576.
- Kinoshita, H., Bäckström, L., Flanagan, J. R., & Johansson, R. S. (1997). Tangential torque effects on the control of grip forces when holding objects with a precision grip. *Journal of Neurophysiology*, 78(3), 1619–1630.
- Kuhtz-Buschbeck, J. P., Gilster, R., Wolff, S., Ulmer, S., Siebner, H., & Jansen, O. (2008). Brain activity is similar during precision and power gripping with light force: an fMRI study. *Neuroimage*, 40(4), 1469–1481.
- Li, Y., Randerath, J., Bauer, H., Marquardt, C., Goldenberg, G., & Hermsdörfer, J. (2009). Object properties and cognitive load in the formation of associative memory during precision lifting. *Behavioural brain research*, 196(1), 123–130.

- Mazzoni, P., Hristova, A., & Krakauer, J. W. (2007). Why don't we move faster? Parkinson's disease, movement vigor, and implicit motivation. *The Journal of Neuroscience*, 27(27), 7105–7116.
- Mirenowicz, J. & Schultz, W. (1994). Importance of unpredictability for reward responses in primate dopamine neurons. *Journal of Neurophysiology*, 72, 1024–1027.
- Mon-Williams, M., & Murray, A. H. (2000). The size of the visual size cue used for programming manipulative forces during precision grip. *Experimental Brain Research* 135(3), 405–410.
- Müller, F., & Abbs, J. H. (1990). Precision grip in parkinsonian patients. in (eds.) Streifer, M. B., Korezyn, A. D., Melamed, E., & Youdim, M. B. H. *Advances in neurology*. Raven, New York, 191–195.
- Müsseler, J. (1999). How independent from action control is perception? An event-coding account for more equally-ranked crosstalks. In G. Aschersleben, T. Bachmann, & J. Müsseler (Eds.), *Cognitive contributions to the perception of spatial and temporal events (Advances in Psychology (Vol. 129, pp. 121–147)*. Amsterdam: Elsevier.
- Nagengast, A. J., Braun, D. A., & Wolpert, D. M. (2010). Risk-sensitive optimal feedback control accounts for sensorimotor behavior under uncertainty. *PLoS Computational Biology*, 6(7), e1000857.
- Nowak, D. A., & Hermsdörfer, J. (2006). Predictive and reactive control of grasping forces: on the role of the basal ganglia and sensory feedback. *Experimental Brain Research*, 173(4), 650–660.
- Nowak, D. A., Glasauer, S., & Hermsdörfer, J. (2013). Force control in object manipulation – a model for the study of sensorimotor control strategies. *Neuroscience & Biobehavioral Reviews*, 37(8), 1578–1586.
- Nowak, D. A., Koupan, C., & Hermsdörfer, J. (2007). Formation and decay of sensorimotor and associative memory in object lifting. *European Journal of Applied Physiology*, 100(6), 719–726
- Peirce, J. W. (2007). PsychoPy – psychophysics software in Python. *Journal of Neuroscience Methods*, 162(1–2), 8–13.
- Prinz, W. (1984). Modes of linkage between perception and action. In *Cognition and motor processes* (pp. 185–193). Springer Berlin Heidelberg.
- Prinz, W. (1990). A common coding approach to perception and action. In O. Neumann & W. Prinz (Eds.), *Relationships between perception and action* (pp. 167–201). Berlin: Springer-Verlag.
- Rakitin, B. C., Gibbon, J., Penney, T. B., Malapani, C., Hinton, S. C., & Meck, W. H. (1998). Scalar expectancy theory and peak-interval timing in humans. *Journal of Experimental Psychology: Animal Behavior Processes*, 24(1), 15.
- Ramig, L. O., Fox, C., & Sapiro, S. (2008). Speech treatment for Parkinson's disease. *Ex-*

- pert Rev. Neurotherapeutics*, 8(2), 297–309.
- Schlicht, E. J., & Schrater, P. R. (2007). Effects of visual uncertainty on grasping movements. *Experimental Brain Research*, 182(1), 47–57.
- Schonberg, T., Daw, N. D., Joel, D., & O’Doherty, J. P. (2007). Reinforcement learning signals in the human striatum distinguish learners from nonlearners during reward-based decision making. *The Journal of Neuroscience*, 27(47), 12860–12867.
- Schultz, W., Apicella, P., & Ljungberg, T. (1993). Responses of monkey dopamine neurons to reward and conditioned stimuli during successive steps of learning a delayed response task. *Journal of Neuroscience*, 13, 900–913.
- Schultz, W., Dayan, P., & Montague, P. R. (1997). A neural substrate of prediction and reward. *Science*, 275(5306), 1593–1599.
- Sheridan, M. R., Flowers, K. A., & Hurrell, J. (1987). Programming and execution of movement in Parkinson’s disease. *Brain*, 110(5), 1247–1271.
- Stelmach, G. E., Teasdale, N., Phillips, J., & Worringham, C. J. (1989). Force production characteristics in Parkinson’s disease. *Experimental Brain Research*, 76(1), 165–172.
- Trampenau, L., Kuitz-Buschbeck, J. P., & van Eimeren, T. (2015). Probabilistic information on object weight shapes force dynamics in a grip-lift task. *Experimental Brain Research*, 233(6), 1711–1720.
- Trampenau, L., van Eimeren, T., & Kuitz-Buschbeck, J. (2016). Processing of probabilistic information in weight perception and motor prediction. *Attention, Perception, & Psychophysics*, 1
- Trampenau, L., van Eimeren, T., & Kuitz-Buschbeck, J. (2016). Processing of probabilistic information in weight perception and motor prediction. *Attention, Perception, & Psychophysics*, 1-11.
- Trommershäuser, J., Maloney, L. T., & Landy, M. S. (2003). Statistical decision theory and the selection of rapid, goal-directed movements. *JOSA A*, 20(7), 1419–1433.
- Turner, R. S., & Desmurget, M. (2010). Basal ganglia contributions to motor control: a vigorous tutor. *Current opinion in neurobiology*, 20(6), 704–716.
- van Nuenen, B. F., Kuitz-Buschbeck, J., Schulz, C., Bloem, B. R., & Siebner, H. R. (2012). Weight-specific anticipatory coding of grip force in human dorsal premotor cortex. *The Journal of Neuroscience*, 32(15), 5272–5283.
- van Polanen, V. & Davare, M. (2015). Sensorimotor Memory Biases Weight Perception During Object Lifting. *Frontiers in Human Neuroscience*, 9, Article 700.
- Viviani, P., Burkhard, P. R., Chiuve, S. C., Corradi-Dell’Acqua, C., & Vindras, P. (2009). Velocity control in Parkinson’s disease: a quantitative analysis of isochrony in scribbling movements. *Experimental Brain Research*, 194(2), 259–283.
- Westling, G., & Johansson, R. S. (1984). Factors influencing the force control during precision grip. *Experimental Brain Research* 53(2), 277–284.
- Westwood, D. A., Dubrowsky, A., Carnahan, H., & Roy, E. A. (2000b). The effects of illusory size on force production when grasping objects. *Experimental Brain Rese-*

- arch*, 135(4), 535–543.
- Westwood, D. A., Heath, M., & Roy, E. A. (2000a). The effect of a pictorial illusion on closed-loop and open-loop prehension. *Experimental Brain Research*, 134(4), 456–463.
- Wing, A. M., & Lederman, S. J. (1998). Anticipatory load torques produced by voluntary movements. *Journal of Experimental Psychology: Human Perception and Performance*, 24(6), 1571.
- Wolpert, D. M., & Landy, M. S. (2012). Motor control is decision-making. *Current Opinion in Neurobiology*, 22, 996–1003.
- Wu, S. H., Delgado, M. R., & Maloney, L. T. (2009). Economic decision-making compared with an equivalent motor task. *Proceedings of the National Academy of Sciences*, 106(15), 6088–6093.
- Zhang, H., Maddula, S. V., & Maloney, L. T. (2010). Planning routes across economic terrains: maximizing utility, following heuristics. *Frontiers in psychology*, 1, 214.
- Zhang, H., & Maloney, L. T. (2012). Ubiquitous log odds: a common representation of probability and frequency distortion in perception, action, and cognition. *Frontiers in Neuroscience*, 6(1), 1.

11 Appendix

Trampenau, L., Kuhtz-Buschbeck, J. P., & van Eimeren, T. (2015). Probabilistic information on object weight shapes force dynamics in a grip-lift task. *Experimental Brain Research*, 233(6), 1711–1720.

DOI 10.1007/s00221-015-4244-6

The final publication is available at Springer via
<http://dx.doi.org/10.1007/s00221-015-4244-6>

Probabilistic information on object weight shapes force dynamics in a grip-lift task

Leif Trampenau¹ · Johann P. Kuhtz-Buschbeck² · Thilo van Eimeren¹

Received: 27 October 2014 / Accepted: 28 February 2015 / Published online: 12 March 2015
© Springer-Verlag Berlin Heidelberg 2015

Abstract Advance information, such as object weight, size and texture, modifies predictive scaling of grip forces in a grip-lift task. Here, we examined the influence of probabilistic advance information about object weight. Fifteen healthy volunteers repeatedly grasped and lifted an object equipped with a force transducer between their thumb and index finger. Three clearly distinguishable object weights were used. Prior to each lift, the probabilities for the three object weights were given by a visual cue. We examined the effect of probabilistic pre-cues on grip and lift force dynamics. We expected predictive scaling of grip force parameters to follow predicted values calculated according to probabilistic contingencies of the cues. We observed that probabilistic cues systematically influenced peak grip and load force rates, as an index of predictive motor scaling. However, the effects of probabilistic cues on force rates were nonlinear, and anticipatory adaptations of the motor output generally seemed to overestimate high probabilities and underestimate low probabilities. These findings support the suggestion that anticipatory adaptations and force scaling of the motor system can integrate probabilistic information. However, probabilistic information seems to influence motor programs in a nonlinear fashion.

Keywords Adaptation · Anticipation · Motor system · Motor load · Force rate · Predictive

Introduction

An essential feature of dexterous fine motor control in humans is the predictive scaling of the forces applied by the fingers according to pertinent task demands. When an object is grasped and lifted, the grip force (normal to the grip surfaces) secures the object against slipping while the load force overcomes gravity. Anticipatory control of these forces ensures a smooth and critically damped lift and obviates initial force overshoots or undershoots, which would entail corrections (Johansson and Westling 1988). During skilled performance, when the same object is lifted repetitively, grip and load forces increase in parallel and are scaled according to object properties such as weight, shape and the texture of the contact surfaces (Johansson and Flanagan 2009). The force rate trajectories are approximately bell-shaped and reach their maxima prior to liftoff (Johansson and Westling 1988). Since explicit sensory information about the actual object weight is not available until liftoff, peak grip and load force rates are considered as variables that reflect preprogrammed forces (Gordon et al. 1993; Nowak et al. 2013). The peak force rates are scaled to the expected weight when novel objects are lifted (Buckingham et al. 2009). A mismatch between the predicted and the actual sensory inflow (tactile, proprioceptive) occurs when a lift is programmed erroneously. When the object is, e.g., heavier than expected, the grip and load forces increase too slowly so that the time until liftoff is prolonged (Jenmalm et al. 2006). Moreover, the force rate trajectories then often show multiple peaks due to reactive corrections of the

Electronic supplementary material The online version of this article (doi:10.1007/s00221-015-4244-6) contains supplementary material, which is available to authorized users.

✉ Thilo van Eimeren
tvaneimeren@gmail.com

¹ Department of Neurology, Kiel University, Arnold-Heller-Str. 3, 24105 Kiel, Germany

² Department of Physiology, Kiel University, Kiel, Germany

force output (Johansson and Westling 1988; Jenmalm et al. 2006).

Visual size cues play an important role in the initial programming of the grip force when unfamiliar objects are lifted (Mon-Williams and Murray 2000; Westwood et al. 2000a, b). Size cues and an assumed material density are used to estimate an object's weight and to scale the force output adequately (Baugh et al. 2012; Buckingham et al. 2009). Cues announcing the weight of a target object are also known to influence the kinematics of reach-to-grasp movements (Brouwer et al. 2006; Eastough and Edwards 2007). In the present study of a grip-lift task, object size and object shape remained constant, but weight changed systematically. Thereby we examine the effects of certain and probabilistic visual cues about the current object weight on grip and load force programming.

Appropriate predictive scaling of the grip and load forces is straightforward when familiar objects with constant properties are handled (Gordon et al. 1993). Memory links between arbitrary sensory cues (object color, auditory signals) and the weight of an object to be grasped and lifted can be established quickly (Nowak et al. 2007). Once this association is learned, the forces are scaled according to the weight that is announced by the advance information (Li et al. 2009; Bensmail et al. 2012). Such procedural learning has been demonstrated for explicit sensory cues that unmistakably predicted the object weight (Ameli et al. 2008) or the texture of the gripped surfaces (Cole and Rotella 2002). Yet sensory information about object properties may be ambiguous. For example, when grasping a milk carton, whose screw cap has obviously been opened previously and whose edges are indented in many places, one may assume that it should be almost empty. However, if the milk carton was full just a few hours ago, one would rather predict that it is almost full. Consequently, competing internal models regarding the weight of a certain object can exist, and the model that is used to program grip-lift forces will depend on the respective probability of each model. The present study examines how the motor system deals with uncertain weight information in form of probabilistic cues, i.e., advance information of limited certainty, in the preparation and execution of a grip-lift task. Healthy volunteers repetitively grasped and lifted a block equipped with force transducers, whose weight varied from trial to trial between light, medium and heavy. Just before each trial, visual cues provided probabilistic information about the upcoming weight (e.g., 66 % probability of medium weight, 33 % probability of heavy weight).

We hypothesize that the probabilistic cues would systematically influence grip and load force rates prior to liftoff. If this was true, one and the same object of medium weight would be handled differently, depending on the

expectation evoked by the advance information. We furthermore anticipate that probabilistic advance information might have nonlinear effects on the predictive scaling of the grip and load forces. In other domains, distortion of probability information has been reported to influence perceptual and cognitive paradigms (Zhang and Maloney 2012).

Methods

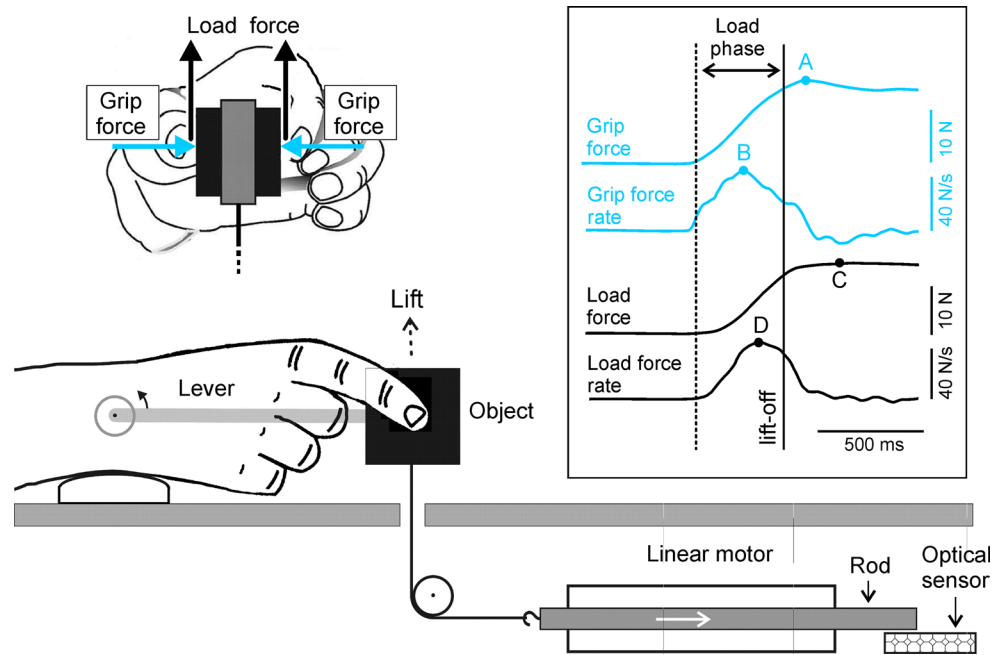
Fifteen healthy volunteers (5 men) with a mean age of 22 ± 3 years (SD, standard deviation) participated in the study. They gave their written informed consent and were naive to the specific purpose of the experiments, which had been approved by the Ethics Committee of the Medical Faculty of the University of Kiel. All participants were right-handed according to a handedness questionnaire (Oldfield 1971).

Experimental setup

Participants sat on an adjustable chair at a table (70×70 cm) with the equipment in a brightly lit room and faced a monitor (15" LCD display) located a viewing distance of about 40 cm. The right upper arm was flexed approximately 30° , so that the forearm rested flatly on the table parallel to the sagittal plane in a relaxed posture. A molded pad supported the wrist (Fig. 1). A grip object (a small block) was located close to the tips of the right thumb and index finger. The participants repeatedly grasped the object with a pinch grip and lifted it ~3 cm high by a radial adduction of the wrist. The block was attached to a lever, whose rotary axis was aligned with the pivot axis of the radiocarpal joint. Position and angle of the object and connected lever were adapted to fit individual anatomical conditions.

The weight of the object was systematically changed from trial to trial during the experiment by a linear actuator (Servotube actuator STA1116, Dunkermotoren, Essex, UK), which was hidden beneath the table. The sliding rod of the actuator was connected to the lever and object via a nonexpandable string (Fig. 1). It exerted programmable pull forces, which remained constant during each grip-lift trial. Changes in force output between the trials were performed in a series of small steps, which did not result in any noise or any vibrations. Movements of the rod were recorded with an optical sensor to register the position of the grip object. Additionally, a small switch attached to the lever indicated the moment of liftoff. The object had two flat vertical grip surfaces (40×40 mm, spaced 30 mm apart) covered with thin sandpaper (grit size 600), and it was equipped with nonmetallic force transducers (Dasch,

Fig. 1 Experimental setup. The grip object with force sensors was attached to a lever, whose hinge was aligned with the wrist. Its weight was controlled by a linear motor, whose rod exerted programmable pull force (white arrow) via a nonelastic string connected to the object. An optical sensor recorded the sliding movements of the rod. The inset shows typical force and force rate curves of a grip-lift trial with the peak GF (A), peak GF rate (B), peak LF (C) and peak LF rate (D). The onset of LF increase (dotted vertical line) and the moment of liftoff (solid vertical line) delimit the load phase. Superimposed original force rate profiles of two subjects are shown in a supplementary figure



Kiel, Germany). The isometric grip force, applied perpendicular to the grip surfaces, and the load force (tangential to the surfaces) were measured (range 0–20 N). Typical force curves are illustrated in Fig. 1 (inset) and in a supplementary figure. Together with the signal of the switch (liftoff), grip force and load force data were sampled with a frequency of 50 Hz. We are aware that this temporal resolution is below typical data sampling rates of grip and load forces. Our equipment has been custom-made for neuroimaging (fMRI) studies (Kuhntz-Buschbeck et al. 2008), which we plan to conduct with this paradigm and experimental setup. Programming of the linear actuator, presentation of the visual stimuli (see below) and data recording were performed with the open-source application PsychoPy (Peirce 2007).

Stimuli and procedure

Three object weights were used, namely 300 g (light), 800 g (medium) and 1400 g (heavy). We selected these weights based on insights from pilot experiments where these fulfilled best the requirement of being clearly distinguishable between each other, between the probabilistic predictions, and between each probabilistic prediction and the medium weight. The weights correspond to those of a well-known study of anticipatory load force scaling during lifts of common and novel objects (Gordon et al. 1993). We calculated the perceived heaviness (see Tables 1, 2) based on S.S. Stevens' power law

$$\Psi(I) = (I - I_0)^a$$

where $\Psi(I)$ is the subjective sensation of heaviness evoked by the weight I , I_0 is the stimulus intensity at sensation threshold ($I_0 = 5$ g), and a is a modality-dependent exponent; for heaviness, $a = 1.45$ (Stevens 1971).

Regarding prior probabilistic information about the object weight in the upcoming grip-lift trial, three experimental conditions were examined. In the *full prediction* condition, a visual cue was displayed on the monitor, which fully predicted the object weight (100 % certainty). Visual cues in this condition were bottles with distinct filling levels (nearly empty, medium and full) indicating the forthcoming weight (light, medium or heavy). In the *no prediction* condition, a neutral cue was shown, which neither predicted any particular weight nor any probability of possible weights. The effective, unknown probabilities in this condition were evenly distributed, i.e., they were 33 % for each of the weights light, medium and heavy. In the *fixed ratio* condition, the cue was a “traffic light” with four different positions of a blue rectangle in a black frame, which provided fixed probabilities (Fig. 2a). When the rectangle was located in the lowest position (LM cue), the object weight was light in 66 % and medium in 33 % of the trials. When the rectangle was located in the second position from bottom (ML cue), these frequencies were reversed. When the rectangle was located in the second position from top (MH cue), the weight of the block was medium in 66 % and heavy in 33 % of cases. In the topmost position (HM cue), these frequencies were reversed. Hence, four probabilistic cues (LM, ML, MH, HM), each designating a *fixed ratio* of probabilities (66/33 %) for two out of three weights, were used.

Table 1 Lifting light, medium and heavy objects in the *full prediction* condition

Cue	Unambiguous visual cues announce upcoming weight			ANOVA		
	Light	Medium	Heavy			
Actual object weight (g)	300	800	1400			
Perceived heaviness ψ	3813	16,052	36,277			
				$F_{2,28}$		
Peak grip force GF (N)	5.00 ± 1.08	**	11.08 ± 1.13	**	16.70 ± 1.14	853.8
Time of peak GF (ms)	270 ± 210		218 ± 132		224 ± 117	n.s.
Peak GF rate (N/s)	45.78 ± 14.35	**	77.94 ± 17.10	**	105.52 ± 18.39	127.2
Time of peak GF rate (ms)	-17 ± 28	**	-88 ± 38	**	-236 ± 70	103.1
Peak load force LF (N)	3.62 ± 0.21	**	8.51 ± 0.38	**	14.35 ± 0.61	5986.1
Time of peak LF (ms)	428 ± 212	**	272 ± 121	**	321 ± 95	10.3
Peak LF rate (N/s)	40.18 ± 10.32	**	72.37 ± 17.70	**	97.69 ± 19.63	165.8
Time of peak LF rate (ms)	-35 ± 54	**	-117 ± 37	*	-252 ± 68	99.2
Load phase duration (ms)	252 ± 83	**	407 ± 91	**	542 ± 106	109.8

Means ± SD of the individual means ($n = 15$ subjects; ten trials per object weight in each subject). Negative time intervals denote events before liftoff (=0 ms). All but one of the ANOVA F values given in right column are significant ($P < 0.01$). n.s. not significant

* Significant difference between values in adjacent columns; * $P < 0.05$; ** $P < 0.01$ (t tests for paired samples; Bonferroni corrected for multiple comparisons)

Table 2 Lifting light, medium and heavy objects in the *no prediction* condition

Cue	Visual cues without information on upcoming weight			ANOVA		
	300	800	1400			
Actual object weight (g)	300	800	1400			
Perceived heaviness ψ	3813	16,052	36,277			
				$F_{2,28}$		
Peak grip force GF (N)	7.95 ± 1.86	**	12.00 ± 1.22	**	17.06 ± 1.07	284.2
Time of peak GF (ms)	169 ± 103		190 ± 121	*	290 ± 126	5.6
Peak GF rate (N/s)	84.94 ± 30.02		87.00 ± 20.56		90.93 ± 19.70	n.s.
Time of peak GF rate (ms)	18 ± 28	**	-46 ± 34	**	-170 ± 86	56.5
Peak load force LF (N)	3.82 ± 0.31	**	8.51 ± 0.42	**	14.31 ± 0.63	6313.5
Time of peak LF (ms)	266 ± 210		315 ± 148		381 ± 143	4.7
Peak LF rate (N/s)	52.37 ± 15.27	*	74.02 ± 21.87		75.43 ± 20.79	39.7
Time of peak LF rate (ms)	-32 ± 37	**	-96 ± 35	**	-244 ± 94	63.4
Load phase duration (ms)	213 ± 70	**	413 ± 122	**	694 ± 152	179.8

Means ± SD of the individual means ($n = 15$ subjects; ten trials per object weight in each subject). Negative time intervals denote events before liftoff (=0 ms). All but one of the ANOVA F values given in the right column are significant ($P < 0.05$). n.s. not significant

* Significant difference between values in flanking columns; * $P < 0.05$; ** $P < 0.01$ (t tests for paired samples; Bonferroni corrected for multiple comparisons)

At the onset of each trial, the announcing visual cue was shown in the middle of the monitor display for one second (Fig. 2b). It then disappeared and emerged in smaller size at the bottom of the screen beneath a rectangular target zone. This second “action cue” indicated that the subjects should now grasp and lift the object, thereby moving the cue into the target zone. We implemented the target zone to restrict the lifting height and to standardize performance. As the height of the target zone was about 150 % of the

cue height, there was no particular demand for precision. All participants were encouraged to utilize the announcing cue to predict the object weight and to prepare their action adequately. There was no time limit to initiate the grip lift, and after liftoff, the participants had a rather generous time window of 1500 ms (see Fig. 2) to reach the target zone with a self-selected speed. The action cue disappeared 1500 ms after liftoff, and a release cue requested to place the object back down and to release the grip. An inter-trial

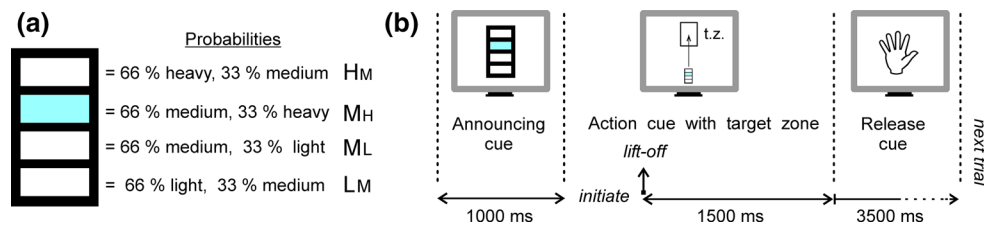


Fig. 2 Visual cues. **a** The *fixed ratio* condition involved four probabilistic visual cues. Each position of the *blue rectangle* in the *black frame* (here cue MH) signified the probabilities of two possible object weights for the upcoming trial. The four probabilistic cues are abbreviated: LM,

ML, MH, HM. **b** The announcing cue was shown for 1000 ms, followed by the action cue with the target zone (t.z.). The release cue appeared 1500 ms after liftoff, followed by the next trial after 3500 ms. Movement initiation time (initiate) was not limited (color figure online)

rest period of 3.5 s was used to reset the force of the linear actuator for the next trial. All in all, the task was rather undemanding regarding speed and accuracy of the lift.

Before recording started, all participants conducted a practice session. First they were instructed to lift three real bottles with distinct filling levels using a pinch grip at the screw cap, as if they would pull them out of a beverage crate. The weights of the bottles exactly matched the three object weights used in the following experiment. We chose this procedure to enforce a naturalistic, intuitive comprehension of the three weights. In the following instruction, the real bottles were replaced by the experimental grip object. All visual cues [i.e., bottles in the *full prediction* condition, rectangles (Fig. 2) in the *fixed ratio* condition] were explained, and all experimental conditions were practiced with the grip object. Each participant then completed 180 successive grip-lift trials, with short pauses interspersed. The *full prediction* condition comprised 30 trials (10 per weight) that were performed in five bouts (of 6 trials), placed regularly throughout the experiment. The *no prediction* condition included 30 trials (10 per weight), and the *fixed ratio* condition 120 trials. The trials of the latter two conditions were intermixed and pseudorandomized to avoid systematic influences of the previous trial on a given condition (Cole and Rotella 2002; Ameli et al. 2008; Nowak et al. 2013). Across all three experimental conditions, the light and the heavy object were lifted 50 times each, and the medium object 80 times.

Data analysis

Analyses of the forces and statistical calculations were performed using the R project for statistical computing (R Development Core Team 2008). From the force curves and their first-time derivatives (i.e., the force rate curves), four measures were determined for each trial: (1) peak grip force GF, (2) peak grip force rate GFr, (3) peak load force LF and (4) peak load force rate LFr (see Fig. 1, inset). We also evaluated the timings of these maxima relative to lift-off and the duration of the load phase, which lasted from the onset of the load force (LFr > 5 N/s) until liftoff.

Subject-wise averages were calculated for each experimental condition; group results (inter-individual means \pm SD) are given in tables. We analyzed effects of probabilistic information on predictive force scaling in the *fixed ratio* condition by comparing the trials where the same actual weight (medium = 800 g) was lifted, yet preceded by four different probabilistic cues (LM, ML, MH, HM). For each probabilistic cue, the predicted object weight (resp. predicted heaviness) was calculated as weighed combination of the two possible object weights (resp. possible perceptions of heaviness), e.g., the cue HM (66 % heavy, 33 % light) corresponds to a predicted object weight of $(0.667 \times 1400 \text{ g}) + (0.333 \times 800 \text{ g}) = 1200 \text{ g}$. To detect significant cue-dependent changes of the forces and force rates, the subject-wise means were entered into analyses of variance (ANOVA) for repeated measurements, with the probabilistic cue as within-subject factor. We expected the peak force rates to increase with the predicted object weight (LM < ML < MH < HM). Paired samples *t* tests were calculated to detect significant cue-dependent differences, with $P < 0.0167$ after Bonferroni correction for multiple comparisons. We also calculated relative (percentage) deviations of peak force rates during lifts of the medium (800 g) object for the different cues (*fixed ratio* condition), by considering the force rates measured in the *full prediction* condition (medium weight) as baseline, i.e., % difference = $[(\text{value in } \textit{fixed ratio cond.}/\text{baseline value}) \times 100] - 100$.

Results

Full prediction and no prediction conditions

When the visual cues predicted the upcoming object weight with 100 % certainty, the participants scaled their grip and load force rates anticipatorily (Table 1). Peak GFr and peak LFr increased progressively as the object weight increased in a nearly linear fashion (L < M < H) (Fig. 3, black squares). Despite the anticipatory increase of the

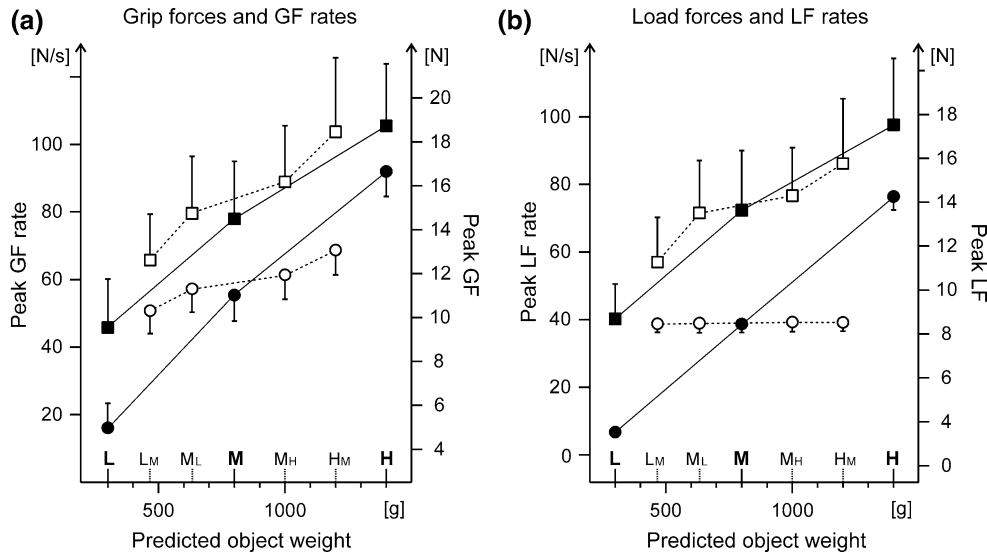


Fig. 3 Peak force rates (*squares*) and peak forces (*circles*). **a** In the *full prediction* condition (*black symbols*), peak GF and GF rate increase almost linearly with object weight. Predicted (=actual) weights are indicated L, M, H in this condition. For the *fixed ratio* condition (*white symbols*), data of trials with the medium object (800 g) are shown. Note the nonlinear increase (*dotted lines*) of GF

and GF rate with the predicted object weight announced by the cues (LM, ML, MH, HM). **b** Peak LF and LF rate. The peak LF (*white circles*) remains nearly constant in the *fixed ratio* condition, since the actual object weight was always 800 g, while the peak LF rate increases. Otherwise, as in **a**, *symbols* indicate inter-individual means and SD (*error bars*)

maximum LFr, the load phase and the intervals between force rate peaks and liftoff lengthened as the object weight increased (Table 1). The force rate maxima were reached about 20–250 ms before liftoff. Also peak GF and LF varied in parallel with object weight (Fig. 3, black circles), but these maxima were reached about 200–400 ms after liftoff. Anticipatory scaling of the force rates according to the upcoming object weight was impossible in the *no prediction* condition (no informative cue available). Consequently, peak GFr was similar for the three object weights (Table 2). On the other hand, the peak LFr decreased when the light object was lifted without prior cue, yet this LFr change was less pronounced than in the *full prediction* condition, as indicated by a significant condition-dependent interaction ($F_{2,28} = 92.0$; $P < 0.01$). Due to inadequately slow buildup of the LF when heavy objects were lifted, the load phase lasted about 150 ms longer in the *no prediction* than in the *full prediction* condition. Peak LF, as the product of mass and vertical acceleration, exceeded object weight by around 0.5 N in all conditions (see Tables 1, 2, 3). All in all, these results indicate that participants utilized visual cues that reliably predicted the object weight to pre-program their manipulative forces accordingly.

Fixed ratio condition

The results of the *fixed ratio* condition are listed in Table 3 and illustrated in Figs. 3 and 4. As hypothesized, the probabilistic cues influenced the predictive scaling of the manipulative

forces before liftoff. ANOVA indicated significant ($P < 0.01$) cue-dependent changes of peak GF ($F_{3,42} = 39.6$), peak GFr ($F_{3,42} = 31.6$), peak LFr ($F_{3,42} = 33.9$) and small albeit significant changes of the peak LF ($F_{3,42} = 5.1$; $P < 0.05$). Hence, the same object of medium weight (800 g) was grasped and handled differently, depending on the expectation evoked by the announcing cue (Fig. 3, white symbols). The peak GFr and LFr (Fig. 3, white squares) and the peak GF (Fig. 3a, white circles) increased progressively as the *predicted* object weight increased (LM < ML < MH < HM). At the individual level, 12 out of our 15 subjects scaled their force rates according to the weight prediction, whereas three participants did not scale in this way. To illustrate inter-individual differences, original force rate profiles of two subjects are shown in a supplementary figure.

Figure 4 shows the relative deviations of the peak force rates during lifts of the medium weight in the *fixed ratio* condition. The percentage deviations of the peak force rates from baseline, i.e., from lifting the medium weight in the *full prediction* condition, were smaller than the predicted % deviations of the object weight (Fig. 4a) and heaviness (Fig. 4b). Hence, the anticipatory adjustment of the peak force rates prior to liftoff was, in relative terms, smaller than the deviation announced by the probabilistic cues. Furthermore, the cue ML, announcing a low probability (33 %) of a light weight, had no significant effects on peak GFr and peak LFr; instead, the peak force rates remained close to baseline values (Fig. 4c). By contrast, a significant (paired *t* test, $P < 0.01$) decrease of peak force rates

Table 3 Lifting objects of medium weight in the *fixed ratio* condition

	Probabilistic visual cues announce upcoming weight						
	66 % L, 33 % M	66 % M, 33 % L	66 % M, 33 % H	66 % H, 33 % M			
Probability ratio	66 % L, 33 % M	66 % M, 33 % L	66 % M, 33 % H	66 % H, 33 % M			
Abbreviation of cue	LM	ML	MH	HM			
Actual object weight (g)	800	800	800	800			
Predicted object weight (g)	467	633	1000	1200			
Predicted heaviness ψ	7893	11,973	22,794	29,536			
Peak grip force GF (N)	10.34 ± 1.05	**	11.33 ± 1.08	**	11.97 ± 1.09	*	13.10 ± 1.17
Time of peak GF (ms)	299 ± 175		235 ± 181		163 ± 67		140 ± 45
Peak GF rate (N/s)	65.72 ± 13.60	**	79.54 ± 16.95	**	88.97 ± 16.58	*	103.75 ± 21.90
Time of peak GF rate (ms)	-52 ± 38		-79 ± 43		-60 ± 41		-63 ± 41
Peak load force LF (N)	8.48 ± 0.39		8.51 ± 0.43	*	8.57 ± 0.42		8.56 ± 0.40
Time of peak LF (ms)	338 ± 140		317 ± 108	*	276 ± 108		247 ± 121
Peak LF rate (N/s)	56.98 ± 13.24	**	71.52 ± 15.59	**	76.66 ± 14.25	**	86.24 ± 19.18
Time of peak LF rate (ms)	-161 ± 52	*	-117 ± 42		-98 ± 30		-83 ± 29
Load phase duration (ms)	564 ± 165	**	429 ± 94	**	384 ± 67	**	344 ± 69

Means ± SD of the individual means ($n = 15$ subjects; with 10–20 trials per probability ratio in each subject). For each ratio, the predicted object weight (resp. heaviness) is calculated as weighed combination of the two possible actual object weights (resp. perceptions). For example, 66 % H, 33 % M (HM) yields a predicted object weight of $(0.666 \cdot 1400 \text{ g}) + (0.333 \cdot 800 \text{ g}) = 1200 \text{ g}$

* Significant difference between values in flanking columns; * $P < 0.05$; ** $P < 0.01$ (t tests for paired samples; Bonferroni corrected for multiple comparisons). ANOVA F values are given in results text

to values ~15 % below baseline was observed after the cue LM, which announced a high likelihood (66 %) of a light weight. The effects of the cue HM, indicating a high probability (66 %) of a heavy weight, on the force rates were more than twice as strong as the effects of the cue MH, which denoted low probability (33 %) of a heavy weight (Fig. 4d). The difference between the effect of the MH cue on the LFr and the *additional* increment (i.e., step from MH to HM) that occurred after HM cues did, however, not reach significance (paired t test, $P = 0.07$; see Fig. 4d). In summary, visual cues that announced a high probability (66 %) of a weight differing from medium (800 g) in the upcoming trial had *disproportionately* larger influence on the scaling of the force rates prior to liftoff than cues predicting a low probability (33 %) of a different weight. A detailed inspection of individual GFr and LFr curves often revealed several smaller local maxima apart from the global maximum (see supplementary figure). A detailed analysis of these local maxima is beyond the scope of the present study, but should be performed in future experiments.

In parallel with the increased *predicted* object weight, the temporal occurrence of most peaks changed ($P < 0.05$), i.e., the timings of peak GF (8.6), peak LF (5.6), peak LFr (15.3) and the duration of the load phase (28.15); the respective ANOVA ($F_{3,42}$) values are given in parentheses. The results of the t tests, summarized in Table 3, verify significant cue-dependent differences of the force rates, and a

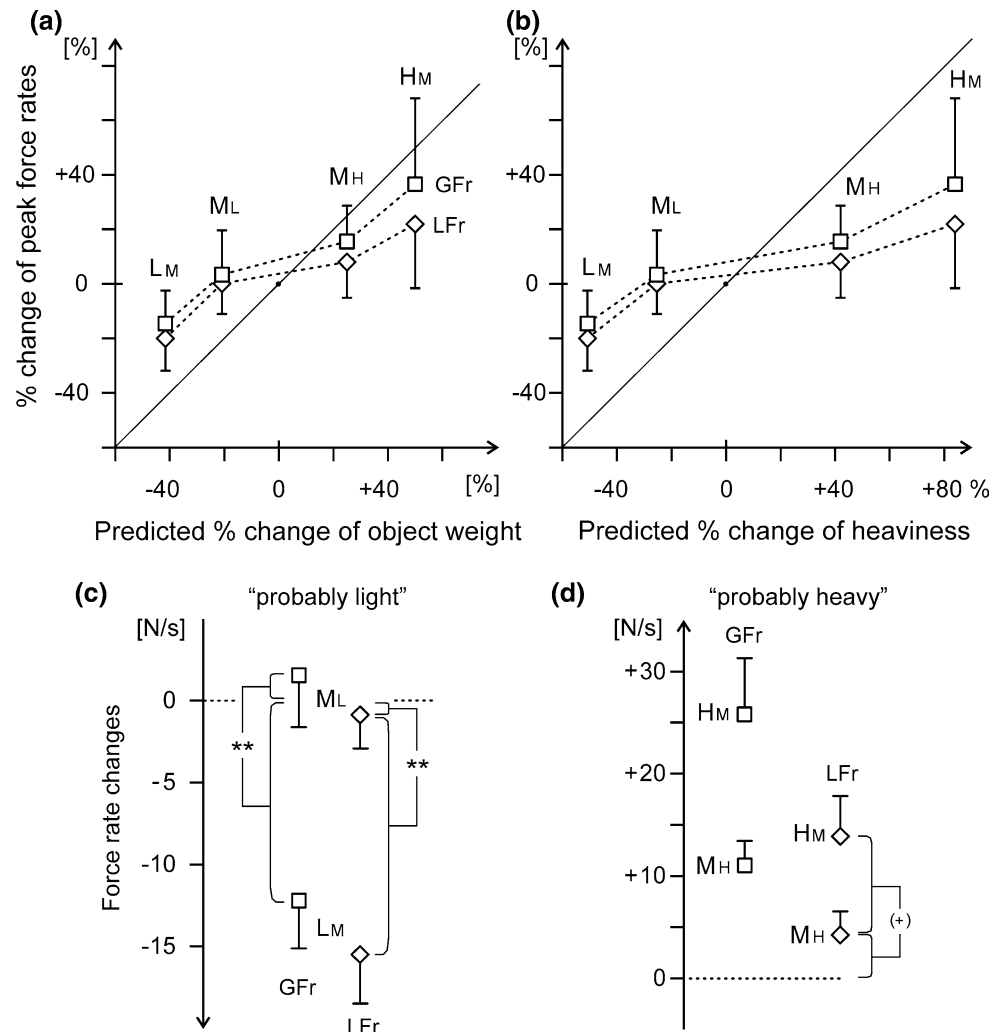
gradual shortening of the load phase as the predicted object weight increased (LM > ML > MH > HM).

Discussion

This study explored how visual cues indicating the likelihoods of specific object weights influence anticipatory scaling of prehensile finger forces in a grip-lift task. Predictive control with force rate profiles targeted for the expected object weight has been known since the pioneer study of Gordon et al. (1993). The maxima of the force rates, which are typically reached before liftoff, are considered to reflect anticipatory force scaling, as they vary in parallel with object weight (Johansson and Westling 1988; Li et al. 2009; Nowak et al. 2013). One very recent study used the first (local) peak of the load force rate as an indicator of the expected object weight (Baugh et al. 2012). We found that also probabilistic information, despite its uncertainty, systematically influences the peak GFr and LFr before liftoff. Moreover, the effects of the probabilistic cues on the force rates were nonlinear, with high probabilities seeming to have an overproportionally greater influence on anticipatory adaptations of the motor output than low probabilities.

In a changing and unfamiliar environment, the visual appearance of an object does not always allow for an exact prediction of its weight. When grasping and lifting, e.g.,

Fig. 4 Cue-dependent changes of the peak GF rate (GFr, squares) and peak LF rate (LFr, diamonds) in the *fixed ratio* condition. Percentage changes of force rates are plotted against % changes of **a** the predicted object weight and **b** the predicted heaviness. Strictly parallel variations involving identical percentages would adhere to the *thin diagonal lines*. **c** Decreases of the GFr and LFr below baseline after ML and LM cues (prediction “probably light”). **d** Increases of the GFr and LFr above baseline after MH and HM cues (“probably heavy”). Asterisks in **c, d** denote significant differences (paired *t* tests, $P < 0.01$) between cue-dependent effects, and (+) indicates a trend ($P = 0.07$). Baseline values (=zero) in **a–d** correspond to lifts of the medium object (predicted = actual weight = 800 g) in the *full prediction* condition. Inter-individual means, with error bars denoting SD in **a, b** and SEM in **c, d**



pieces of new clay crockery, one may rely on size cues and estimated values of object density (Buckingham et al. 2009; Baugh et al. 2012), but this information has limited certainty. A main novel aspect of the present study is how the motor system uses *probabilistic* advance information to predictively adjust the fingertip forces during a grasp-lift action. We found that the same object of medium weight is handled differently, depending on the probabilistic information provided by the visual cues. The higher the announced likelihood of a heavy object, the higher the peak GFr and LFr, and the shorter the load phase duration and the interval between peak LFr and liftoff. In a recent study using a grip-lift task (van Nuenen et al. 2012), two subsequent visual cues (indicating either high or low weight) were either congruent (75 % of trials), or incongruent (25 % of trials). Since the actual weight was always correctly predicted by the second pre-cue, the first cue can also be seen as a probabilistic pre-cue. Indeed, the results of this study can also be explained by deviations from a predicted weight based on a probabilistic pre-cue. However, since the

above mentioned study lacks baseline values without pre-cue, one cannot assess the full impact of this probabilistic advance information.

Although peak GFr and LFr were influenced by the probabilistic cues in the present study, their adaptive scaling did not exactly match the predicted object weight. In any case, peak GFr and LFr changes remained smaller than the predicted % deviations of the object weight (Fig. 4) and were possibly influenced by a motor strategy that overestimated the frequency of the medium weight. One may argue that the sensorimotor system does not plan an action according to a physical object weight, but according to an expected perception of heaviness. However, when the force rate changes were plotted against the predicted heaviness, our results remained essentially the same (compare Fig. 4a, b). The motor strategy could be a consequence of the experimental design, because the frequency of the 800-g weight was twice as high as the frequency of the 300- and 1400-g weights in the *fixed ratio* condition. In this context, we wish to point out that the sequence of the weights

cannot account for the effects of the probabilistic cues, as the order of object weights was pseudorandomized to avoid a systematic influence of the previously lifted weight on trials of the *fixed ratio* condition (e.g., cue LM was not systematically preceded by lifts of a light object).

Nonlinear effects of the probabilistic cues were noticeable. Cues predicting a low likelihood (33 %) of a weight differing from the medium value (800 g) had disproportionately smaller influence on anticipatory force rate scaling than cues indicating a high likelihood (66 %) of such a divergence. The preparatory response of the motor system, hence, resembles the behavior of a person who does not (or hardly) react when the weather forecast predicts 33 % chance of rain, but habitually puts on a raincoat when the predicted rain probability is stated as 66 %. Distortion of probabilistic information in human judgment and decision is not exceptional, but has been demonstrated with other paradigms, such as frequency estimation, signal detection theory, and use of probability in decision-making under risk and uncertainty (Zhang and Maloney 2012).

Davidson and Wolpert (2004) investigated anticipatory scaling of the grip force in a task where well-known objects were combined by stacking them and then lifted with a precision grip. When a combination of two known objects was lifted for the first time, participants systematically underestimated the weight of heavy combinations and overestimated the weight of light combinations, as indicated by the peak GFr values (their Fig. 2). Predictive grip force scaling was, therefore, biased by a default weight estimate for combined objects, and not exclusively based on an addition of the two known weights. The authors inferred that the motor system acts in a Bayesian way to plan forces in the face of uncertainty, taking into account information about the likely weight of combined objects (default) and previous experience from lifts of solitary objects. Applied to our study, anticipatory force output in the *fixed ratio* condition may be programmed by combining the announced probabilities for two weights and an average estimation (default) of all weights.

The present data of the *full prediction* condition show that peak force rates (GFr, LFr) are scaled to the announced object weight in a nearly linear fashion (see Fig. 3). In congruence, earlier studies found that healthy subjects can rapidly establish associations between unambiguous sensory cues (*full prediction*) and object weight or texture of the grip surfaces (Cole and Rotella 2002; Chouinard et al. 2005; Nowak et al. 2007; Li et al. 2009). Such visuomotor mapping takes place irrespective of the sensory modality of the cue (visual, auditory) or the hand used for grasping (Ameli et al. 2008). Visually indicated changes of the weight of a target object influence prior-to-contact grasp kinematics, too (Brouwer et al. 2006; Eastough and Edwards 2007). When heavy cylindrical objects are

grasped and lifted, the peak grip aperture is higher than in trials where lighter objects of the same size and shape are grasped. Grip placement on the object is more exact for heavy cylinders, so that the axis between the index finger and thumb passes more closely through the object center of gravity, which reduces the chance of object rotation during the lift (Eastough and Edwards 2007). Such precaution was not necessary in our experiment, where the object was a cuboidal block attached to a lever. Veridical and illusory size cues (pictorial illusions of object size) influence both prehensile movements and manipulative forces (Mon-Williams and Murray 2000; Westwood et al. 2000a). The peak GF is higher for larger objects than for smaller objects of the same weight (Westwood et al. 2000b). Visual size cues, however, did not play a role in the present paradigm, because object size and cue size remained constant.

The present study analyzed cue-dependent force scaling, i.e., motor behavior, of young healthy volunteers. Future directions should entail a study of functional neuronal correlates of the present paradigm (task-related brain activity) and further tests with different probabilistic contingencies to better describe the nature of probabilistic distortions in this task. Furthermore, it would be interesting to investigate age-related changes as well as the effect of diseases with known impairments in motor force scaling, such as Parkinson's disease, dystonia and cerebellar degeneration.

Acknowledgments We would like to thank Gesa Hartwigsen for her input regarding the experimental setup and Martin Müller for technical advice and for constructing the lever.

References

- Ameli M, Dafotakis M, Fink GR, Nowak DA (2008) Predictive force programming in the grip-lift task: the role of memory links between arbitrary cues and object weight. *Neuropsychologia* 46(9):2383–2388
- Baugh LA, Kao M, Johansson RS, Flanagan JR (2012) Material evidence: interaction of well-learned priors and sensorimotor memory when lifting objects. *J Neurophysiol* 108(5):1262–1269
- Bensmail D, Sarfeld AS, Ameli M, Fink GR, Nowak DA (2012) Arbitrary visuomotor mapping in the grip-lift task: dissociation of performance deficits in right and left middle cerebral artery stroke. *Neuroscience* 210:128–136
- Brouwer AM, Georgiou G, Glover S, Castiello U (2006) Adjusting reach to lift movements to sudden visible changes in target's weight. *Exp Brain Res* 173:629–636
- Buckingham G, Cant JS, Goodale MA (2009) Living in a material world: how visual cues to material properties affect the way that we lift objects and perceive their weight. *J Neurophysiol* 102:3111–3118
- Chouinard PA, Leonard G, Paus T (2005) Role of the primary motor and dorsal premotor cortices in the anticipation of forces during object lifting. *J Neurosci* 25(9):2277–2284
- Cole KJ, Rotella DL (2002) Old age impairs the use of arbitrary visual cues for predictive control of fingertip forces during grasp. *Exp Brain Res* 143(1):35–41

- Davidson PR, Wolpert DM (2004) Internal models underlying grasp can be additively combined. *Exp Brain Res* 155(3):334–340
- Eastough D, Edwards MG (2007) Movement kinematics in prehension are affected by grasping objects of different mass. *Exp Brain Res* 10(6):193–198
- Gordon AM, Westling G, Cole KJ, Johansson RS (1993) Memory representations underlying motor commands used during manipulation of common and novel objects. *J Neurophysiol* 69(6):1789–1796
- Jenmalm P, Schmitz C, Forssberg H, Ehrsson HH (2006) Lighter or heavier than predicted: neural correlates of corrective mechanisms during erroneously programmed lifts. *J Neurosci* 26(35):9015–9021
- Johansson RS, Flanagan R (2009) Sensory control of object manipulation. In: Nowak D, Hermsdörfer J (eds) *Sensorimotor control of grasping*. Cambridge University Press, Cambridge, pp 141–160
- Johansson RS, Westling G (1988) Coordinated isometric muscle commands adequately and erroneously programmed for the weight during lifting task with precision grip. *Exp Brain Res* 71(1):59–71
- Kuhtz-Buschbeck JP, Gilster R, Wolff S, Ulmer S, Siebner H, Jansen O (2008) Brain activity is similar during precision and power gripping with light force: an fMRI study. *Neuroimage* 40:1469–1481
- Li Y, Randerath J, Bauer H, Marquardt C, Goldenberg G, Hermsdörfer J (2009) Object properties and cognitive load in the formation of associative memory during precision lifting. *Behav Brain Res* 196(1):123–130
- Mon-Williams M, Murray AH (2000) The size of the visual size cue used for programming manipulative forces during precision grip. *Exp Brain Res* 135:405–410
- Nowak DA, Koupan C, Hermsdörfer J (2007) Formation and decay of sensorimotor and associative memory in object lifting. *Eur J Appl Physiol* 100(6):719–726
- Nowak DA, Glasauer S, Hermsdörfer J (2013) Force control in object manipulation—a model for the study of sensorimotor control strategies. *Neurosci Biobehav Rev* 37(8):1578–1586
- Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia* 9(1):97–113
- Peirce JW (2007) PsychoPy—psychophysics software in Python. *J Neurosci Methods* 162(1–2):8–13
- R Development Core Team (2008) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>
- Stevens SS (1971) Sensory power functions and neural events. In: Atrium H, Jung R, Loewenstein WR, MacKay DM, Teuber HL (eds) *Handbook of sensory physiology*, vol 1, 1st edn. Springer, Heidelberg, pp 226–242
- Van Nuenen BF, Kuhtz-Buschbeck J, Schulz C, Bloem BR, Siebner HR (2012) Weight-specific anticipatory coding of grip force in human dorsal premotor cortex. *J Neurosci* 32:5272–5283
- Westwood DA, Heath M, Roy EA (2000a) The effect of a pictorial illusion on closed-loop and open-loop prehension. *Exp Brain Res* 134:456–463
- Westwood DA, Dubrowsky A, Carnahan H, Roy EA (2000b) The effects of illusory size on force production when grasping objects. *Exp Brain Res* 135:535–543
- Zhang H, Maloney LT (2012) Ubiquitous log odds: a common representation of probability and frequency distortion in perception, action, and cognition. *Front Neurosci* 6:1

Trampenau, L., van Eimeren, T., & Kutz-Buschbeck, J. P. (2017). Processing of probabilistic information in weight perception and motor prediction. *Attention, Perception & Psychophysics*, 79(2), 404–414.

DOI 10.3758/s13414-016-1266-5

The final publication is available at Springer via
<http://dx.doi.org/10.3758/s13414-016-1266-5>

Processing of probabilistic information in weight perception and motor prediction

Leif Trampenau¹ · Thilo van Eimeren² · Johann Kuitz-Buschbeck³

Published online: 29 December 2016
© The Psychonomic Society, Inc. 2016

Abstract We studied the effects of probabilistic cues, i.e., of information of limited certainty, in the context of an action task (GL: grip-lift) and of a perceptual task (WP: weight perception). Normal subjects ($n = 22$) saw four different probabilistic visual cues, each of which announced the likely weight of an object. In the GL task, the object was grasped and lifted with a pinch grip, and the peak force rates indicated that the grip and load forces were scaled predictively according to the probabilistic information. The WP task provided the expected heaviness related to each probabilistic cue; the participants gradually adjusted the object's weight until its heaviness matched the expected weight for a given cue. Subjects were randomly assigned to two groups: one started with the GL task and the other one with the WP task. The four different probabilistic cues influenced weight adjustments in the WP task and peak force rates in the GL task in a similar manner. The interpretation and utilization of the probabilistic information was critically influenced by the initial task. Participants who started with the WP task classified the four probabilistic cues into four distinct categories and applied these categories to the subsequent GL task. On the other side, participants who

started with the GL task applied three distinct categories to the four cues and retained this classification in the following WP task. The initial strategy, once established, determined the way how the probabilistic information was interpreted and implemented.

Keywords Probabilities · Anticipation · Motor system · Weight perception · Perception-action

Introduction

Dexterous manual performance is characterized by predictive scaling of the forces applied by the fingers according to pertinent task demands. When an object is grasped and lifted with a precision grip, the vertical load force (lift force) overcomes the force of gravity, while the grip force (normal to the grip surfaces) must be large enough to prevent slipping of the object. During skilled performance, both forces increase in concert and are scaled predictively according to relevant object properties such as shape, weight, and texture of the grip surfaces (Johansson & Westling, 1984). Accurate anticipatory scaling of the forces is undemanding when well-known objects with unchanging properties are handled (Gordon, Westling, Cole, & Johansson, 1993). Such force control ensures an efficient and critically damped lift and avoids initial force undershoots or overshoots, which would require corrections (Johansson & Flanagan, 2009; Nowak & Hermsdörfer, 2005). The curves of the grip and load force rates are approximately bell-shaped and typically reach their maxima before lift-off (Johansson & Westling, 1988). Because exact sensory information about the object's weight is not available until lift-off, the peak values of the force rates are considered to indicate preprogrammed forces (Chouinard, Leonard, & Paus, 2005;

Electronic supplementary material The online version of this article (doi:10.3758/s13414-016-1266-5) contains supplementary material, which is available to authorized users.

✉ Leif Trampenau
l_trampenau@hotmail.com

¹ Klinik für Neurologie, Universitätsklinikum Schleswig-Holstein Campus Kiel, Kiel, Germany

² Department of Nuclear, Medicine, Universitätsklinikum Köln, Köln, Germany

³ Physiologisches Institut, Christian-Albrechts-Universität Kiel, Kiel, Germany

Jenmalm, Schmitz, Forssberg, & Ehrsson, 2006; Nowak, Glasauer, & Hermsdörfer, 2013).

When novel objects are grasped and lifted, the peak force rates are scaled to the expected weight, based on visual cues to object size, material, and density (Gordon et al., 1993; Baugh, Kao, Johansson, & Flanagan, 2012; Buckingham, Cant, & Goodale, 2009). Normal volunteers also quickly learn to utilize arbitrary sensory cues (e.g., symbols presented on a monitor, sounds), which unmistakably predict object weight or texture of the gripped surfaces, for an adequate preprogramming of their grip and load forces (Ameli, Dafotakis, Fink & Nowak, 2008; Cole & Rotella, 2002). Such associative learning conceivably involves a close cooperation between perception and action. However, sensory information about object properties can be equivocal. For instance, the normal mapping between material and weight is violated when surface material and core material of an object differ, e.g., when a small brass-filled cube is covered with wood veneer (Ellis & Lederman, 1999). When people repeatedly lift such an unusual object and then predict the weight of a larger object of similar appearance, sensorimotor memory from lifts of the “outlier object” interferes with well-learned prior associations between material and density (Baugh et al., 2012). Hence, different internal models regarding the weight of an object can coexist, and predictive scaling of the force depends on the respective probability of each model.

Contemporary research considers movement planning from the viewpoint of decision-making under risk and applies the same mathematical framework that formalizes decision-making in economics and psychology (Nagengast, Braun, & Wolpert, 2010; Wolpert & Landy, 2012; Wu, Delgado, & Maloney, 2009). So-called decisions under risk are made when participants have access to the probabilities associated with possible actions. In line with this approach, we recently examined the influence of explicit probabilistic advance information about object weight in a grip-lift (GL) task (Trampenau, Kutz-Buschbeck, & van Eimeren, 2015). Three clearly discernible weights (medium, light, and heavy) were grasped and lifted. Before each lift, a visual cue provided probabilistic information about the forthcoming weight (e.g., 33.3% medium, 66.7% heavy) of the object, namely a moveable handle equipped with force transducers, whose weight was varied by a linear actuator.

The probabilistic cues systematically influenced peak grip and load force rates, as an index of predictive motor scaling. The same object of medium weight (800 g) was grasped and lifted differently, depending on the expectation evoked by the probabilistic advance information. Cues that predicted a high likelihood of a weight differing from the medium value (800 g) had disproportionately stronger influence on predictive force scaling than cues that indicated a low likelihood of such a divergence, so that the anticipatory adaptations of the motor output seemed to overestimate high probabilities and to

underestimate low probabilities. We interpreted this nonlinear effect as a distortion of probabilistic information on object weight during preparation of the grip-lift, as it has been demonstrated previously with other paradigms (Zhang & Maloney, 2012).

To understand this pattern further, the present study investigated whether the perceptual system and the motor system utilize probabilistic information to an object’s weight in a similar way. We devised a weight perception (WP) task, where participants adjusted the weight of the above-mentioned object (handle with force transducers) until the perceived heaviness was equal to what the participant believed would be the expected weight, based on the probabilistic cue. The WP task provided explicit information about the weight that is attributed to each probabilistic cue, which is not directly available from the force rate data of a grip-lift task (Trampenau et al., 2015). In a separate experiment, the same probabilistic cues were presented before the object was grasped and lifted (GL task). Following standardization of the results (z-transformation), we compared the effects of the probabilistic information on action initiation (GL task) and weight perception (WP task). Two groups of participants performed both tasks (WP and GL) in a different order to detect possible sequence effects.

The interpretation of probabilistic information can depend on the type of a task with its particular focus (Zhang & Maloney, 2012). Similar effects of the probabilistic cues in both tasks (GL and WP) may indicate that perception and action rely on common abstract concepts in these experiments. By contrast, different effects of the probabilistic cues in both tasks may point to a dissociation of action and perception. Such dissociations have been shown previously, e.g., in the context of size-weight illusions for grip force scaling and weight perception (Flanagan & Beltzner, 2000; Grandy & Westwood, 2006; Chouinard, Large, Chang, & Goodale, 2009). Comparing the use of probabilistic cues in the GL and WP tasks provides new insights into the way the perceptual and the motor systems process and implement probabilistic information about an object’s weight.

Methods

Twenty-two right-handed healthy volunteers (10 men), age 25 ± 5 years (mean, SD), were randomly assigned to two groups A and B (n = 11 participants per group of 5 men). This sample size was based on a power analysis using the maximum effect size ($d_{\text{Cohen}} = 1.781$) of six effects from our previous grip-lift experiments (Trampenau et al., 2015), aiming for a power greater than 0.99167 with alpha = 0.00168 (one-tailed). Group A started with the grip-lift (GL) task and afterwards performed the weight perception task (WP). Group B started with the latter task (WP₁), followed by the GL task, and finally

performed the weight perception task once more (WP₂). All participants gave their informed consent to the experiments, which had been approved by the local ethics committee. They were naive to the purpose of the study.

Grip-lift task

The subjects sat on an adjustable chair at a table facing a monitor. The right forearm and wrist were oriented parallel to the sagittal plane and rested in a relaxed posture on a pad. The elbow joint angle was approximately 130°, and the hand was positioned in a semiprone posture with an ulnar adduction of the wrist joint of ~10° in the starting position. The grip object was essentially a moveable handle, consisting of a cuboid block attached to an adjustable lever (Fig. 1a). The length of the lever was set so that its rotational axis was aligned with the dorsopalmar axis of the radiocarpal joint. The distance between the axis of the lever and the center of the cuboid block varied between 12 and 15 cm, depending on the size of the hand. The block had two flat vertical grip surfaces (4 x 4 cm, spaced 3-cm apart) covered with sandpaper (grit size 600) and was equipped with custom-made nonmetallic force transducers (Dasch, Kiel, Germany). The angle between the block and lever was adjusted so that the grip surfaces were located close to the tips of the thumb and index finger in the starting position; for details see Supplementary Figure 1. Thus, the block could be grasped comfortably with a pinch grip between thumb and index finger, and it was lifted approximately 3-cm high by a radial abduction of the wrist joint of ~20°. The axis of the lever permitted a lifting movement in a vertical plane along a slightly curved movement path. The weight of the object was systematically changed from trial to trial during the experiment by a linear actuator (Servotube actuator

STA1116, Dunkermotoren, Essex, UK), which was hidden beneath the table. Its sliding rod was connected to the block via a nonexpandable string (Fig. 1a). Movements of the block were registered with an optical sensor connected to the rod at a sampling frequency of 50 Hz. Grip and load force data were sampled with the same frequency. Original force curves are illustrated in supplementary Figure 2.

Three object weights were used throughout the GL task, namely 300 g (light), 800 g (medium), and 1400 g (heavy). Initially, the participants became familiar with these three typical weights, which were lifted ten times each in randomized order. Each weight was announced explicitly. Following the initial training, the four probabilistic visual cues were introduced and thoroughly explained. Each cue provided information about the likely object weight in the upcoming grip-lift trial (Fig. 1b). A blue rectangle could take four different positions in a black frame. The uppermost position (HM cue) indicated that the next object would be heavy in 66.7% and medium in 33.3% of the trials. The second position (MH cue) indicated that these percentages were reversed (66.7% medium/33.3% heavy). The third position (ML cue) indicated that object weight would be medium in 66.7% and light in 33.3% of the next trials, and the lowest position (LM cue) signified that these frequencies were reversed. Hence four probabilistic cues were used (LM, ML, MH, HM), each designating a fixed ratio of probabilities for two possible object weights.

All participants were encouraged to use these cues to prepare their grip-lift action. At the onset of each trial, a cue was shown on the monitor for one second (Fig. 2a). It then disappeared and emerged in smaller size beneath a target zone. This signaled that the object should, without long hesitation, be grasped and lifted by ~3 cm, thereby moving the cue into the target zone. A release-cue then requested to place the

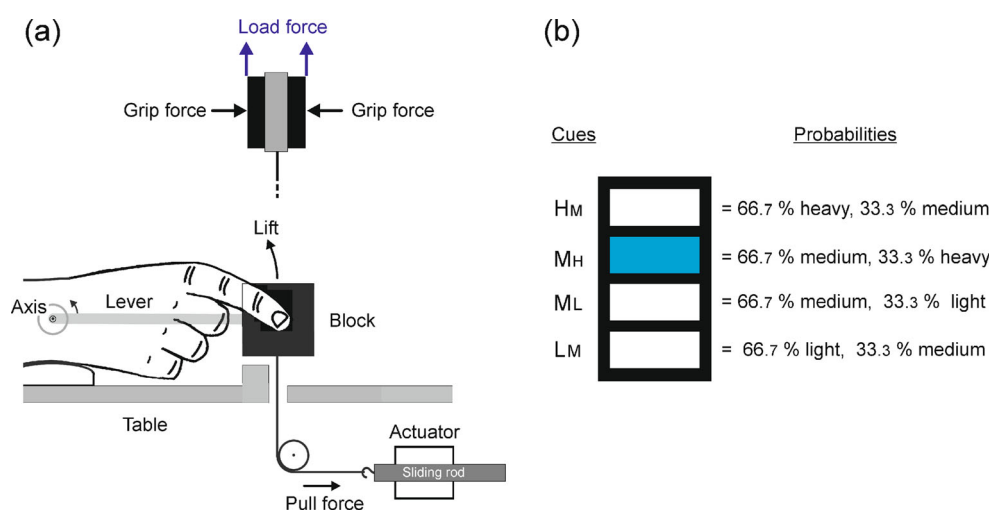


Fig. 1 Experimental set-up. (a) The object consisted of a block with force transducers attached to an adjustable lever, whose axis was aligned with the wrist joint. The block was grasped between thumb, index and middle finger and lifted along a slightly curved movement path. Object weight was set by a linear actuator, whose sliding rod

exerted programmable pull force via a non-elastic string that was attached to the lever. For details see supplementary figure I. (b) Probabilistic visual cues (here cue MH). Each position of the blue rectangle in the black frame signified the probabilities of two possible object weights. Four different cues were used (HM, MH, ML, LM)

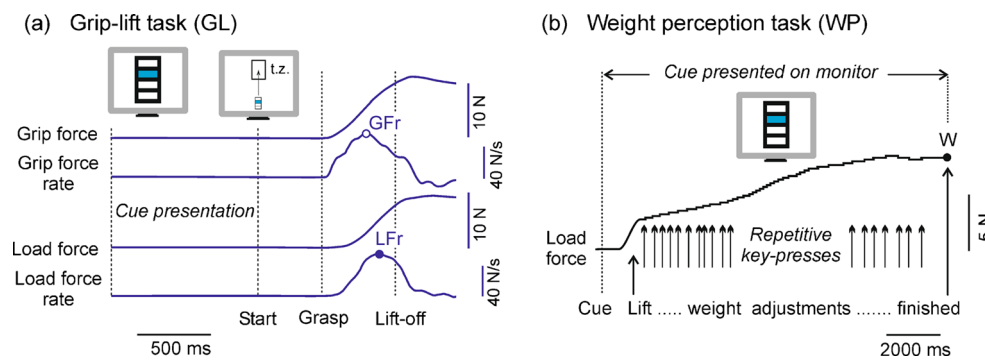


Fig. 2 Tasks. (a) In the grip-lift (GL), one probabilistic cue was shown for 1 second on a monitor, followed by a start cue with a target zone (t.z.). Then the object was grasped and lifted. Peak load force rate (LFr, filled blue circle) and peak grip force rate (GFr, open blue circle) are typically reached before lift-off; see also supplementary figure II for original data.

object back down and to release it. The next trial followed 3.5 seconds later. Each participant completed 150 consecutive grip-lift actions. Probabilistic visual cues announced the object weight in 120 trials. In another 30 trials, placed regularly throughout the experiment, object weight was announced unequivocally. All trials were performed in a pseudo-randomized order that avoided possible systematic effects (Cole & Rotella, 2002; Ameli et al., 2008; Nowak et al., 2013) of the preceding object weight. The light and the heavy object were lifted 40 times each, and the medium object was lifted 70 times. The grip-lift task lasted approximately 40 minutes (including instructions and initial training). Further methodical details have been published elsewhere (Trampenau et al., 2015).

Weight perception task

Participants of group B, who started with the WP task, were initially made acquainted with the three typical weights of the object (light: 300 g, medium: 800 g, heavy: 1,400 g), which were grasped and lifted ten times each in randomized order. Each weight was announced explicitly. Then the same four probabilistic cues as in the GL task were introduced and explained (see above), i.e., subjects were told that each cue signaled the probabilities (66.7%/33.3%) for two possible object weights. Participants of group A, who had already accomplished the GL task, skipped the initial familiarization phase and started directly with the WP task.

During each trial of this task one probabilistic cue was shown on the monitor (Fig. 2b). Participants were asked to associate the cue with a specific object weight, which matched the expected weight of the probabilistic prediction. For this, they lifted and held the object with a pinch grip (as in the GL task) of their right hand and then gradually changed its weight by pressing the arrow keys (↓↑) of a computer keyboard with the left hand until the perceived weight matched the probabilistic cue. Each key-press altered the pull force of the linear

(b) In the weight perception task (WP), the object was lifted and its weight was adjusted by repetitive key-presses which operated the linear actuator (see Fig. 1a) until the perceived weight *W* matched the weight announced by the probabilistic cue. The cue (here MH) was visible all the time. Note the different time scales in (a) and (b)

motor by ~10 g (0.1 N). The initial (preadjustment) weight varied between 250 g and 1550 g. No time constraint was given, and it was allowed to lift and to put down/release the grip object while adjusting its weight. When the trial was completed, the space-bar was pressed, and the next cue was presented on the monitor (next trial). Each probabilistic cue was presented 10 times, resulting in 40 trials. The order of the cues was randomized. Each WP trial lasted 10–20 seconds; the entire task was ~20 minutes. The grasp configuration, which is known to affect perceived heaviness (Flanagan & Bandomir, 2000), was the same in the GL and WP tasks.

Data analysis

Statistical analyses were performed using the R project for statistical computing (R Development Core Team, 2008; www.R-project.org). For each probabilistic cue, the predicted object weight *P* was calculated as a weighted combination of the two possible weights, so cue HM (66.7% heavy, 33.3% medium) predicted a *P* of 1,200 g [(0.667 x 1,400 g) + (0.333 x 800 g) = 1,200 g]. The other *p* values were 1,000 g for cue MH, 633 g for cue ML, and 467 g for cue LM. The *p* values do not represent the subjects' individual expectations but indicate the statistically expected values for each cue, in line with research that applies statistical decision theory to motor behavior (Nagengast et al., 2010; Wolpert & Landy, 2012).

GL task We analyzed trials in which the *same* actual weight (medium = 800 g) was grasped and lifted, yet preceded by the four *different* probabilistic cues (LM, ML, MH, HM). No pre-processing of the data was performed. The first time derivatives of the grip and load forces, i.e., the grip force rate and load force rate (unit of measure: N/s), were calculated. Their maxima, the peak grip force rate (GFr) and peak load force rate (LFr), are reached before the object is lifted from its support (Fig. 2a; see Supplementary Figure 2 for raw data). These

peak rates indicate anticipatory scaling of force output according to the weight that the subject expects to lift (Gordon et al., 1993; Nowak et al., 2013).

WP task The adjusted object weight W (unit of measure: gram), whose heaviness was perceived to match the prediction of a given probabilistic cue, was determined for each trial (Fig. 2b).

For each of the four probabilistic cues, subject-wise mean GFr and LFr and W values were calculated. To test for cue-dependent changes of GFr, LFr, and W , analyses of variance (ANOVA) for repeated measurements with cue as within-subject factor (4 levels) were performed on these subject-wise means. ANOVAs were calculated separately for groups A and B. We expected GFr, LFr, and W to increase with the predicted object weight P . One-sided paired samples t tests were calculated to test for a cue-dependent increase, with $p < 0.0167$ after Bonferroni correction for multiple comparisons. For each contrast, the effect size was calculated, with $d_{\text{cohen}} = (m1-m2)/\sqrt{(s1^2+s2^2)}/2$.

We plotted peak force rates (GFr, LFr) and W values against the weight P that was (statistically) predicted by the probabilistic cues (Figs. 3a and 4a). To compare the results of both tasks (GL and WP), subject-wise standardization (z -transformation) of the raw GFr, LFr, and W data were conducted. The mean values of the standardized weight adjustments (z - W) and peak force rates (z -GFr, z -LFr) were plotted against each other (Figs. 3b and 4b, and Supplementary Figure 3). Overall correlations between the standardized results of the perceptual (WP) and motor (GL) tasks were described with Pearson's correlation coefficients (r), and t tests for significance of correlation were calculated. To examine the relation between the effects of the cues on weight adjustments and peak force rates paired 95% confidence regions were

calculated for each of the four probabilistic cues, based on cue-wise correlation matrices, and illustrated (ellipsoids in Figs. 3 and 4). Finally, to test whether the distributions of z - W and z -GFr (respectively z -LFr) differed, we conducted two-sample Kolmogorov-Smirnov tests.

Results

Group A. The results of this group (task sequence GL→WP) are listed in Table 1 and illustrated in Fig. 3. The probabilistic cues influenced predictive force scaling during lifts of the medium weight (800 g) in the GL task. ANOVA indicated significant cue-dependent changes of the load force rate LFr [$F(3,30) = 34.81, p < 0.0001$] and of the grip force rate GFr [$F(3,30) = 18.82, p < 0.0001$]. Significant cue-dependent changes [$F(3,30) = 142.11, p < 0.0001$] also were found for the weights (W) that were adjusted in the WP task. The two force rates (LFr, GFr) and the adjusted weight (W) generally increased as the (statistically) predicted weight P increased. However, these changes were significant only between cues LM and ML and between cues MH and HM, but not between cues ML and MH, as paired samples t tests indicated (Table 1). Figure 3a illustrates the resultant non-linear relations between the predicted weight P and the three variables (GFr, LFr, W), which increased less between cues ML and MH than between the other cues (LM and ML; MH and HM).

Figure 3b shows the relationship between normalized (z -transformed) data of the perceptual (WP) and the motor task (GL) with the weight adjustments (z - W) and load force rates (z -LFr). Corresponding data (intrasubject averages) are depicted for each cue as points in a uniform color together with their attendant ellipsoid 95% confidence region. The confidence

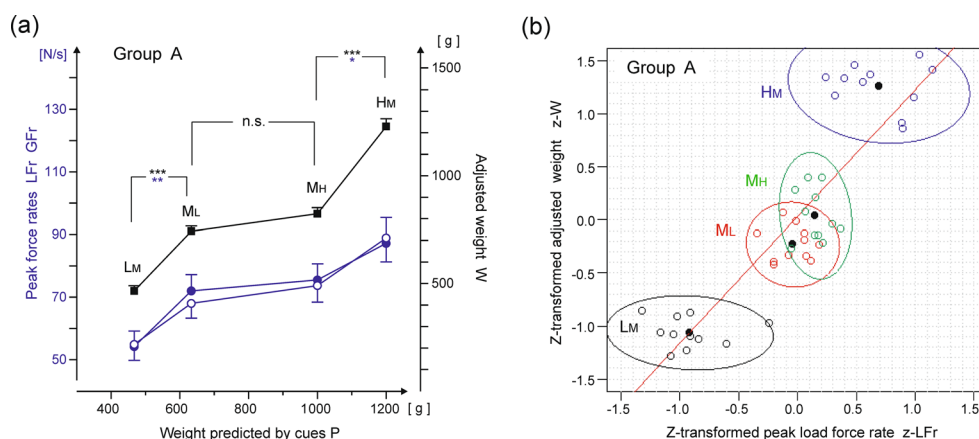


Fig. 3 Results of Group A (task sequence GL→WP). **(a)** Peak load force rates (LFr, filled blue circles), grip force rates (GFr, open blue circles) and adjusted weights W (black squares) increase with the weight P that the cues predicted (statistically). Means and SEM. Asterisks indicate significant cue-dependent differences (paired t -tests, * $p < .05$, ** $p < .01$, *** $p < .001$ after correction for multiple comparisons) for the tasks (GL, blue; WP, black). **(b)** Relation between z -transformed weight

adjustments (z - W) and peak load force rates (z -LFr). Ellipsoids encircle the 95%-confidence region of each cue; open symbols denote the subject-wise mean values, black dots the centers of the ellipsoids. Note that in (a) and (b) those trials are included where the *same* actual weight (800 g) was lifted, yet preceded by four *different* probabilistic cues (LM, ML, MH, HM). For a corresponding plot of z - W versus z -GFr see supplementary figure III

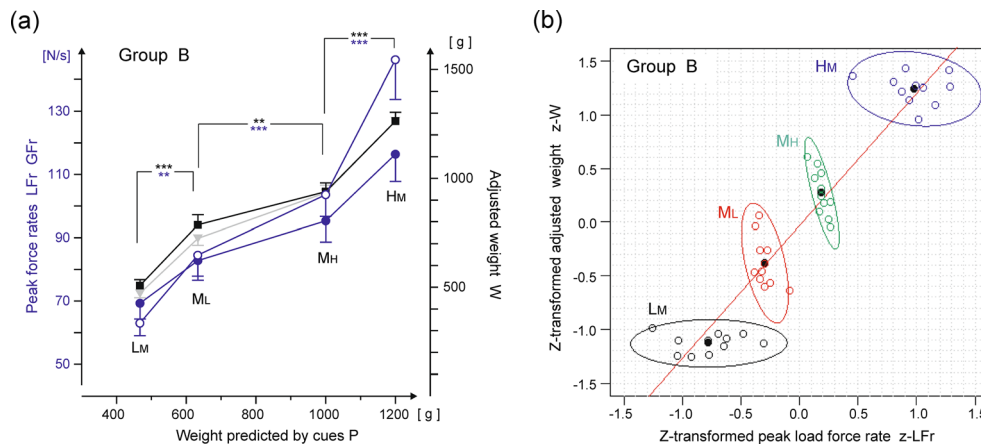


Fig. 4 Results of Group B (task sequence WP₁→GL→WP₂). **(a)** Peak load force rates (LFr, filled blue circles), and grip force rates (GFr, open blue circles), and adjusted weights for the first (WP₁: black squares) and the repeated weight perception task (WP₂: grey lines with triangles). Error bars denote SEM. Asterisks indicate significant cue-dependent

differences (paired *t*-tests, ***p* < .01, ****p* < .001 after correction for multiple comparisons) **(b)** Relation between z-transformed weight adjustments (z-W) and peak load force rates (z-LFr). Otherwise as in Fig. 3. An analogous plot of z-W and z-GFr is shown in supplementary figure III

regions of cues ML and MH overlap considerably, with their center points (black dots) lying in the overlapping region. Thus, cue-dependent differences of the load force rate were significant only between LM and ML and between MH and HM, but not between cues ML and MH. Equivalent results were obtained for the normalized grip force rate z-GFr (Supplementary Figure 3). Consequently, classification of the *four* cues resulted in *three* distinct relational categories between weight adjustment and predictive force scaling (LM < ML ≈ MH < HM) in group A. Pearson's product-moment correlation revealed a high correlation between z-GFr and z-W, with *r* = 0.847, *t*(42) = 10.31, *p* < 0.0001) and between z-LFr and z-W, with *r* = 0.870, *t*(42) = 11.41, *p* < 0.0001. No significant differences between the distributions of z-GFr and z-W (*p* = 0.316), as well as z-LFr and z-W

(*p* = 0.206) were found with Kolmogorov-Smirnov tests. Overall, a close correlation between the subject-wise mean values of the standardized weight adjustments and peak force rates was apparent.

Group B Data of this group (task sequence WP₁→GL→WP₂) are depicted in Fig. 4 and listed in Table 2. Exemplary original force curves are given in supplementary Figure 2. As in group A, ANOVA indicated significant cue-dependent changes of the force rates LFr [*F*(3,30) = 65.90, *p* < 0.001] and GFr [*F*(3,30) = 8.84, *p* = 0.0017] and also of the adjusted weights W₁ [*F*(3,30) = 112.1, *p* < 0.0001] and W₂ [*F*(3,30) = 152.2, *p* < 0.0001] that had been set in the two WP tasks. All values increased significantly (*p* < 0.01; Table 2) in parallel

Table 1 Group A (order of tasks GL → WP): Effects of the probabilistic cues on predictive force scaling in the grip-lift task (GL) and on weight adjustments in the perceptual task (WP)

		Visual cues announcing upcoming weight							
Abbreviation of cue		LM	ML		MH		HM		
Probability ratio		67% L, 33% M	67% M, 33% L		67% M, 33% H		67% H, 33% M		
Predicted weight P [g]		467		633		1000		1200	
GL	max. grip force rate GFr [N/s]	54.9 ± 14.3	<i>t</i> = 4.229 <i>p</i> = .0027 <i>d</i> = 1.23	68.0 ± 15.6	<i>t</i> = 2.290 <i>p</i> = .0675 <i>d</i> = 0.49	73.7 ± 17.6	<i>t</i> = 2.777 <i>p</i> = .0294 <i>d</i> = 1.09	88.9 ± 21.6	
GL	max. load force rate LFr [N/s]	54.2 ± 14.6	<i>t</i> = 5.471 <i>p</i> = .0005 <i>d</i> = 1.57	72.0 ± 17.2	<i>t</i> = 2.246 <i>p</i> = .0729 <i>d</i> = 0.29	75.5 ± 17.0	<i>t</i> = 3.81 <i>p</i> = .0051 <i>d</i> = 0.91	87.2 ± 19.6	
WP	adjusted weight W [g]	465.7 ± 79.6	<i>t</i> = 9.236 <i>p</i> < .0001 <i>d</i> = 3.48	742.6 ± 79.8	<i>t</i> = 2.408 <i>p</i> = .0552 <i>d</i> = 0.93	823.3 ± 92.6	<i>t</i> = 7.921 <i>p</i> < .0001 <i>d</i> = 3.80	1229.3 ± 119.3	

Means ± standard deviations of the individual means of group A (n = 11 subjects; with 10–20 trials per probabilistic cue in each subject). *t* values and *p* values (Bonferroni corrected for multiple comparisons) of one-sided paired samples *t* tests (post ANOVA; 10 degrees of freedom) comparing the values of adjacent columns. *d* = effect size *d*_{cohen}

Table 2 Group B (order of tasks WP₁ → GL → WP₂): Effects of the probabilistic cues on predictive force scaling in the grip-lift action (GL) and on weight adjustments in the perceptual task (WP_{1,2})

		Visual cues announcing upcoming weight							
Abbreviation of cue		LM		ML		MH		HM	
Probability ratio		67% L, 33% M		67% M, 33% L		67% M, 33% H		67% H, 33% M	
Predicted weight P [g]		467		633		1000		1200	
WP ₁	adjusted weight W ₁ [g]	507.6 ± 89.0	<i>t</i> = 7.856 <i>p</i> < .0001 <i>d</i> = 2.22	786.0 ± 153.7	<i>t</i> = 3.655 <i>p</i> = .0066 <i>d</i> = 1.08	939.4 ± 130.7	<i>t</i> = 8.137 <i>p</i> < .0001 <i>d</i> = 2.44	1263.9 ± 134.3	
GL	max. grip force rate GFr [N/s]	63.03 ± 13.3	<i>t</i> = 4.343 <i>p</i> = .0022 <i>d</i> = 1.67	84.5 ± 21.9	<i>t</i> = 7.805 <i>p</i> < .0001 <i>d</i> = 1.21	103.6 ± 22.8	<i>t</i> = 5.928 <i>p</i> = .0002 <i>d</i> = 1.81	146.2 ± 41.3	
GL	max. load force rate LFr [N/s]	69.3 ± 16.5	<i>t</i> = 4.341 <i>p</i> = .0022 <i>d</i> = 1.03	82.8 ± 20.4	<i>t</i> = 10.46 <i>p</i> < .0001 <i>d</i> = 0.83	95.3 ± 22.2	<i>t</i> = 8.637 <i>p</i> < .0001 <i>d</i> = 1.16	116.4 ± 28.5	
WP ₂	adjusted weight W ₂ [g]	471.5 ± 66.1	<i>t</i> = 7.332 <i>p</i> < .0001 <i>d</i> = 2.84	724.5 ± 107.4	<i>t</i> = 5.743 <i>p</i> = .0003 <i>d</i> = 1.90	934.5 ± 113.5	<i>t</i> = 8.916 <i>p</i> < .0001 <i>d</i> = 2.78	1264.6 ± 123.9	

Means ± standard deviations of the individual means of group B (n = 11 subjects; with 10–20 trials per probabilistic cue in each subject). The perceptual task was performed twice (WP₁, WP₂). *t* values and *p* values (Bonferroni corrected for multiple comparisons) of one-sided paired samples *t* tests (post ANOVA; 10 degrees of freedom) comparing the values of adjacent columns. *d* = effect size *d*_{cohen}

with the predicted object weight P (LM < ML < MH < HM). In contrast to group A, the differences between cues ML and MH were now significant, i.e., LFr, GFr, and W values were now clearly higher after presentation of cue MH than after cue ML (Fig. 4a; Table 2 for *p* and *t* values). We found no significant differences between the first (W₁) and the second (W₂) weight adjustment experiments [*F*(1,10) = 0.14, *p* = 0.71].

Figure 4b depicts the relation between weight adjustments (z-W) and predictive load force scaling (z-LFr) in group B with normalized data and 95% confidence regions (ellipsoids) for each cue. The results of the normalized grip force rate (z-GFr) and z-W are very similar (Supplementary Figure 3). The confidence regions of the cues show no overlap in group B, for both, the normalized load force rate (z-LFr, Fig. 4b) and grip force rate (z-GFr) in relation to the weight adjustments (z-W). Unlike in group A, the differences were now significant between all cues. Consequently, classification of the four cues resulted in four distinct categories of weight adjustments and predictive scaling of the load and grip forces. Again there was a high correlation between z-LFr and z-W, with *r* = 0.936, *t*(42) = 17.229, *p* < 0.0001; and also between z-GFr and z-W, with *r* = 0.934, *t*(42) = 16.976, *p* < 0.0001. Kolmogorov-Smirnov tests did not disclose any significant differences between the distributions of z-GFr and z-W (*p* = 0.6336), and z-LF and z-W (*p* = 0.3161), respectively. The mean differences between groups A and B are listed in a supplementary table.

To analyze the impact of the cues ML and MH on participants' peak force rates (GFr and LFr) across the two groups in more detail, we tested for possible interactions between group

and cue on peak force rates with a post-hoc mixed within-between 2 x 2 ANOVA (cues: ML, MH; groups: A, B). There were significant interactions between cue and group affiliation, for both, LFr [*F*(1,20) = 21.53, *p* < 0.001] and GFr [*F*(1,20) = 14.39, *p* = 0.0012]. A further post-hoc 2 x 2 ANOVA indicated such an interaction also for the adjusted weights [*F*(1,20) = 6.79, *p* = 0.0017].

All in all, the results indicated 1) effects of the probabilistic cues on predictive force scaling (LFr and GFr) in the grip-lift task and on weight adjustment (W) in the perceptual task, 2) a high correlation between the standardized results of both tasks (z-LFr and z-W; z-GFr and z-W) without significant differences between their distributions, and 3) an influence of the task sequence (group A vs. group B) that resulted in a different implementation of the probabilistic information in predictive force scaling and weight adjustment, depending on the task that was performed first.

Discussion

We have devised a novel paradigm to study how the perceptual and the motor system deal with explicit probabilistic cues to an object's weight. Two groups of participants accomplished a grip-lift (GL) and a weight perception (WP) task in different order. In the GL task, the participants should utilize four probabilistic cues (LM, ML, MH, HM) to initiate their grip-lift actions with appropriately scaled grip and lift force rates. In line with a previous study (Trampenau et al., 2015) we analyzed

trials where the same actual weight (medium = 800 g) was grasped and lifted, yet preceded by the four different probabilistic cues. These cues also were presented in the WP task, where participants gradually adjusted the weight of an object, with continuous proprioceptive and tactile feedback, until the heaviness matched the expectation for a given probabilistic cue. Three aspects are noteworthy, namely an effect of the task sequence, high correlations and similar distributions of the standardized results of both tasks, and distortion of the probabilistic information of the cues.

As a sequence effect, the initial task determined handling of the probabilistic information in the whole experiment. Members of group A started with the GL task, where they *experienced* three different weights that were actually lifted. Moreover, as a consequence of our paradigm, the frequency of the medium weight was 1.75 times higher than the frequencies of the other two weights across all trials of the GL task. Consequently, the four probabilistic cues were related to three distinct categories of peak force rates ($LM < ML \approx MH < HM$), indicating three different modes of action initiation. In the subsequent WP task, the same four cues were again assigned to three categories of heaviness, so that the initially established implementation of the probabilistic information was maintained. Conversely, the four cues were associated with four different weights ($LM < ML < MH < HM$) when the WP task was performed before the GL task (group B), in accordance with stepwise increases of the statistically predicted weight P . Anticipatory scaling of the force rates in the subsequent GL task then replicated the same pattern of four distinct predictions ($LM < ML < MH < HM$), which again became evident during a final repetition of the WP task.

During the WP task, the subjects had ample time to adjust the object's weight and heaviness while considering the probabilistic information of the cue; up to 20 seconds were needed for each trial. Selection of appropriate weights during the WP task, when performed first, was based on abstract knowledge of the probabilities, and thus involved a decision from description according to the terminology of Hertwig, Barron, Weber, and Erev (2004). In the GL task, a cue was presented for just a second and then the grip-lift was initiated, so that the probabilistic information was implemented without long hesitation. Because the subjects encountered the three different weights more or less often during the series of 150 trials, the choice of an appropriate force rate was at least in part a decision from experience (Hau, Pleskac, & Hertwig, 2010; Hertwig et al., 2004). Despite the different nature of both tasks, their results were highly correlated, following the pattern that had been established during the task performed first (see above). This correlation adds evidence to a close connection between perception and action in our experiment, perhaps in line with the more general theory that perception and action rely on common abstract concepts (Franz, Gegenfurtner, Bühlhoff, & Fahle, 2000; Müsseler, 1999; Prinz, 1990). Similar

assumptions were also formulated for social behavior in the theory of intentional schemas (Barresi & Moore, 1996), and in the motor theory of speech perception (Lieberman & Mattingly, 1985).

Also, previous research found associations between perceptual weight estimates and scaling of the fingertip forces. If more grip force is needed to grasp an object due to a lower friction (smooth surface texture) or because the contact area between fingers and object is small, then the object is perceived to be heavier (Flanagan, Wing, Allison, & Spenceley, 1995; Flanagan & Bandomir, 2000). Van Polanen and Davare (2015) recently demonstrated that if there is a mismatch between expected and actual object weight in a grip-lift task, the execution of force corrections will influence weight perception in a proportional manner. Still, action and perception can dissociate under certain conditions. Experiments with optical illusions have shown that perceived illusory cues to an object's size are not matched by motor parameters such as the aperture of the hand during prehension (Agloti, DeSouza, & Goodale, 1995), which conforms to the dual-stream theory of the visual system proposed by Goodale & Milner (1992). A material-weight illusion occurs when subjects lift objects of identical mass and size that are coated with lighter- or heavier-looking material (e.g., wood and metal), so that their actual mass differs from the expectation for the particular material (Ellis & Lederman, 1999). Objects made from light-looking material feel heavier than objects made from heavy-looking material, although the grip and load forces are scaled to the actual identical weight after several grip-lift trials (Buckingham, Cant, & Goodale, 2009). The classical size-weight illusion takes place when two objects of equal mass but different sizes are lifted (Charpentier, 1891). The smaller object is perceived to be heavier, although again the fingertip forces are scaled to its actual weight after several grip-lift trials (Buckingham & Goodale, 2010; Flanagan & Beltzner, 2000). Judgements of perceived heaviness in experiments with these illusions typically involve numerical rating scales or a forced choice to decide which object feels heavier. It might be interesting to examine whether such judgements can be replicated with a WP task, where the weight of a neutral object (or handle, etc.) is adjusted so that its heaviness matches the effect of the illusion. If this was the case, then results of the WP task (load force reflecting the effect of the illusion) and of the GL task (force is scaled to the actual object weight) would indeed dissociate. The paradigm of the present study, however, did not evoke a mismatch between perception and action; the probabilistic information was implemented in a similar way during both tasks (WP and GL).

In accordance with our previous report (Trampenau et al., 2015), we found a nonlinear relationship between the peak force rates and the statistically predicted object weight P , in particular in group A who started with the GL task. For each cue, we calculated the predicted object weight P as a weighted combination of the two possible weights. This corresponds

with research that views motor control as decision-making and applies equations that formalize decisions in economics, which are typically modeled as a choice among lotteries (Nagengast et al., 2010; Wolpert & Landy, 2012; Wu et al., 2009). The expected value of a lottery is the sum of the values weighted by the corresponding probabilities, so that a 50:50 gamble of winning either \$100 or \$10 results in an expected gain of \$55. The predicted weight P was calculated in the same way. Still, how are these p values related to the subjects' performance? Members of group A started with the GL task, i.e., the initial task that determined the interpretation of the probabilistic information comprised repetitive grip-lift actions. Of the many possible policies to utilize p values for a selection of appropriate force rates, three hypothetical strategies are outlined, each representing an extreme option.

One theoretical option (a) may be to disregard all probabilistic cues and associated p values and instead to always scale the forces to the medium weight, which turns up most often (70/150 trials). This strategy would be associated with frequent large errors of initial force scaling and is incompatible with the demonstrated effects of the cues on grip and load force dynamics. Another strategy (b) could always scale the force rates to the current predicted weight P , resulting in a linear relation between the p values and peak force rates. Across all GL trials, the sum of all positive deviations ("actual weight is heavier than P ") with ensuing corrections will then equal the sum of all negative mismatches ("actual weight is lighter than P "). Consider ΔW as the difference between the two possible weights that follow a cue, e.g., $\Delta W = 1400 \text{ g} - 800 \text{ g} = 600 \text{ g}$ for cue MH. The actual weight will be $(0.67 \Delta W)$ heavier than P in one third of all MH trials and $(0.33 \Delta W)$ lighter than P in the other two thirds of such trials. Analogous calculations pertain to the other cues; the sum of all signed deviations from the targeted weight P will always be zero. Strategy (b) avoids large errors of initial force scaling and repetitive unidirectional corrections of the preprogrammed forces, which may be beneficial.

A third strategy (c) may always aim for the more likely weight, i.e. treat the higher probability (66.7%) like a certain prediction (100%). In two thirds of all trials, preprogramming will then be optimal because a given cue is actually followed by the more likely weight, but in one third of all trials, large initial force over- or undershoots will occur, because the participant has aimed for the "wrong" weight (deviation = ΔW). As an advantage of this strategy, the sum of the absolute values of all deviations across a series of n trials will be minimal, amounting to $[0.33 n (\Delta W)]$. In other words, the sum of all mismatches and subsequent corrections, regardless of their direction, will be smaller than with any other policy. Strategy (c) will bring forth a clearly nonlinear relation between the force rates and the P values, because cues MH and ML are equivalent; both indicate 66.7% probability of the medium weight.

Our results suggest that members of group A, who started with the GL task, did not clearly differentiate between cues

ML and MH, as evident from the similar peak force rates and, correspondingly, similar weight adjustments during the subsequent WP task (Fig. 3a; Table 1). This is in line with strategy (c), perhaps attenuated by a tendency to avoid very large initial errors, as the force rate maxima were not exactly identical for cues ML and MH. In other words, cues indicating a low probability (33.3%) of a weight differing from the medium value had much smaller influence on force scaling than cues predicting a high likelihood (66.7%) of such a difference, confirming our previous results (Trampenau et al., 2015). Distortion of probabilistic information also has been found in other motor paradigms, such as a rapid-pointing task that involved decisions under risk (Wu et al., 2009). Subjects underweighted small probabilities and overweighted large probabilities, as the participants in our experiment did.

For members of group B the initial experiment, which determined the interpretation of the probabilistic information, was the WP task. In principle, members of group B could use the aforementioned strategies to interpret the cues during their weight adjustments. Certainly with the difference that they could fine-tune the weight until the proprioceptive and tactile feedback matched their expectation for a given cue. Weight adjustments that match up P values would adhere to the explicitly known probabilities (33.3%, 66.6%) and thus represent the average weight across a series of grip-lift trials following a given cue. In line with this, subjects of group B associated cues ML and MH with two different weights during the initial WP task and, correspondingly, then applied dissimilar force rates during the GL task (Fig. 4a; Table 2). Still, the relationship between the force rates and the P values did not appear perfectly linear. One might interpret this pattern as a compromise, where the subjects avoid large errors of initial force scaling by considering the different predictions of cues MH and ML [strategy (b)], but at the same time aim towards the more likely medium weight, which is in line with an influence of strategy (c).

Concerning the balance between different internal models of object properties, another explanation can be deduced from the report of Davidson and Wolpert (2004), who studied a GL task where two familiar objects were combined by stacking them and then lifted. Predictive force scaling during the initial trials was not entirely based on an addition of the two well-known weights in their study but biased by a default weight estimate for all possible combined weights. In our experiment, the participants therefore may have combined different internal models of object dynamics, which were based on probabilistic information given by the current cue, on an average estimation (default) of all weights, and on a general strategy of utilizing probabilistic information, which had been established during the initial task (GL or WP).

The present study has limitations. A detailed analysis of the relationship (exact shape of the function) between predicted weights P and the force rates would require a finer gradation, i.e., further probabilistic conditions. It might be interesting to

know whether a different mode of cue presentation (shape, arrangement) can influence the results. Our apparatus did not precisely model the way freely moveable objects would respond to lift forces. The linear actuator provided a constant force during each GL trial, and the object, i.e. the handle with the force transducers, was lifted along a predetermined movement path. Yet the original force curves (Supplementary Figure 2) resemble data that were recorded with real objects. Moreover, our analysis was based on the force rate peaks, which were typically reached before lift-off, before the slightly unnatural lifting movement took place. Experiments with multiple real objects may be an issue of future research.

In summary, normal volunteers performed a perceptual task and a motor task that both involved the interpretation and utilization of four probabilistic cues to an object's weight. The results of both tasks were highly correlated, suggesting that an overarching concept ruled the implementation of the probabilistic information during weight perception and action (grip-lift). This concept was established during the task that was performed first, as evident from the effect of the sequence of the tasks. If the perceptual task was performed first, the four probabilistic cues were related to four distinct categories of heaviness. If the motor task was performed first, the same four cues were assigned to three different categories, corresponding to the experience that three different weights were actually offered after the four cues. Interpretation of probabilistic information therefore was not fixed but adapted to the demands of the initial task. The first experience thus had a significant influence on the categorization of the cue-related information. In a more general sense, the initial strategy, once established, determines the way probabilistic information is interpreted and used.

Acknowledgements The authors thank Martin Müller for construction of the mechanical experimental set-up, Franz Faul for his outstanding methodical and theoretical contribution, Nina Lau for her helpful comments, and Kirsten Zeuner for her support.

References

- Aglioti, S., DeSouza, J. F. X., & Goodale, M. A. (1995). Size-contrast illusions deceive the eye but not the hand. *Current Biology*, *5*, 679–685.
- Ameli, M., Dafotakis, M., Fink, G. R., & Nowak, D. A. (2008). Predictive force programming in the grip-lift task: The role of memory links between arbitrary cues and object weight. *Neuropsychologia*, *46*(9), 2383–2388.
- Barresi, J., & Moore, C. (1996). Intentional relations and social understanding. *Behavioral and Brain Sciences*, *19*, 107–129.
- Baugh, L. A., Kao, M., Johansson, R. S., & Flanagan, J. R. (2012). Material evidence: Interaction of well-learned priors and sensorimotor memory when lifting objects. *Journal of Neurophysiology*, *108*, 1262–1269.
- Buckingham, G., Cant, J. S., & Goodale, M. A. (2009). Living in a material world: How visual cues to material properties affect the way that we lift objects and perceive their weight. *Journal of Neurophysiology*, *102*, 3111–3118.
- Buckingham, G., & Goodale, M. A. (2010). Lifting without seeing: The role of vision in perceiving and acting upon the size weight illusion. *PLoS ONE*, *5*(3), e9709.
- Charpentier, A. (1891). Analyse expérimentale: De quelques éléments de la sensation de poids. *Archives de Physiologie Normale et Pathologique*, *3*, 122–135.
- Chouinard, P. A., Large, M. E., Chang, E. C., & Goodale, M. A. (2009). 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. *NeuroImage*, *44*, 200–212.
- Chouinard, P. A., Leonard, G., & Paus, T. (2005). Role of the primary motor and dorsal premotor cortices in the anticipation of forces during object lifting. *Journal of Neuroscience*, *25*(9), 2277–2284.
- Cole, K. J., & Rotella, D. L. (2002). Old age impairs the use of arbitrary visual cues for predictive control of fingertip forces during grasp. *Experimental Brain Research*, *143*, 35–41.
- Davidson, W. R., & Wolpert, D. M. (2004). Internal models underlying grasp can be additively combined. *Experimental Brain Research*, *155*(3), 334–340.
- Development Core Team, R. (2008). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. <https://www.r-project.org>
- Ellis, R. R., & Lederman, S. J. (1999). The material-weight illusion revisited. *Perception & Psychophysics*, *61*, 1564–1576.
- Flanagan, J. R., & Bandomir, C. A. (2000). Coming to grips with weight perception: Effects of grasp configuration on perceived heaviness. *Perception & Psychophysics*, *62*, 1204–1219.
- Flanagan, J. R., & Beltzner, M. A. (2000). Independence of perceptual and sensorimotor predictions in the size-weight illusion. *Nature Neuroscience*, *3*, 737–741.
- Flanagan, J. R., Wing, A. M., Allison, S., & Spenceley, A. (1995). Effects of surface texture on weight perception when lifting objects with a precision grip. *Perception & Psychophysics*, *57*, 282–290.
- Franz, V. H., Gegenfurtner, K. R., Bühlhoff, H. H., & Fahle, M. (2000). No evidence for a dissociation between perception and action. *Psychological Science*, *11*, 20–25.
- Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, *15*, 20–25.
- Gordon, A. M., Westling, G., Cole, K. J., & Johansson, R. S. (1993). Memory representations underlying motor commands used during manipulation of common and novel objects. *Journal of Neurophysiology*, *69*, 1789–1796.
- Grandy, M. S., & Westwood, D. A. (2006). Opposite perceptual and sensorimotor responses to a size-weight illusion. *Journal of Neurophysiology*, *95*, 3887–3892.
- Hau, R., Pleskac, T. J., & Hertwig, R. (2010). Decisions from experience and statistical probabilities: Why they trigger different choices than a priori probabilities. *Journal of Behavioral Decision Making*, *23*, 48–68.
- Hertwig, R., Barron, G., Weber, E. U., & Erev, I. (2004). Decisions from experience and the effect of rare events in risky choice. *Psychological Science*, *15*, 534–539.
- Jenmalm, P., Schmitz, C., Forssberg, H., & Ehrsson, H. H. (2006). Lighter or heavier than predicted: Neural correlates of corrective mechanisms during erroneously programmed lifts. *Journal of Neuroscience*, *26*(35), 9015–9021.
- Johansson, R. S., & Flanagan, J. R. (2009). Coding and use of tactile signals from the fingertips in object manipulation tasks. *Nature Reviews Neuroscience*, *10*, 345–359.
- Johansson, R. S., & Westling, G. (1984). Roles of glabrous skin receptors and sensorimotor memory in automatic-control of precision grip when lifting rougher or more slippery objects. *Experimental Brain Research*, *56*, 550–564.

- Johansson, R. S., & Westling, G. (1988). Coordinated isometric muscle commands adequately and erroneously programmed for the weight during lifting task with precision grip. *Experimental Brain Research*, *71*(1), 59–71.
- Lieberman, A. M., & Mattingly, I. G. (1985). The motor theory of speech perception revised. *Cognition*, *21*, 1–36.
- Müsseler, J. (1999). How independent from action control is perception? An event-coding account for more equally-ranked crosstalks. In G. Aschersleben, T. Bachmann, & J. Müsseler (Eds.), *Cognitive contributions to the perception of spatial and temporal events (Advances in Psychology (Vol. 129, pp. 121–147))*. Amsterdam: Elsevier.
- Nagengast, A. J., Braun, D. A., & Wolpert, D. M. (2010). Risk-sensitive optimal feedback control accounts for sensorimotor behavior under uncertainty. *PLoS Computational Biology*, *6*(7), e1000857.
- Nowak, D. A., Glasauer, S., & Hermsdörfer, J. (2013). Force control in object manipulation—a model for the study of sensorimotor control strategies. *Neuroscience & Biobehavioral Reviews*, *37*, 1578–1586.
- Nowak, D. A., & Hermsdörfer, J. (2005). Grip force behavior during object manipulation in neurological disorders: Toward an objective evaluation of manual performance deficits. *Movement Disorders*, *20*, 11–25.
- Prinz, W. (1990). A common coding approach to perception and action. In O. Neumann & W. Prinz (Eds.), *Relationships between perception and action* (pp. 167–201). Berlin: Springer-Verlag.
- Trampenau, L., Kuitz-Buschbeck, J. P., & van Eimeren, T. (2015). Probabilistic information on object weight shapes force dynamics in a grip-lift task. *Experimental Brain Research*, *233*, 1711–1720.
- Van Polanen, V., & Davare, M. (2015). Sensorimotor Memory Biases Weight Perception During Object Lifting. *Frontiers in Human Neuroscience 2015*, *9*, Article 700.
- Wolpert, D. M., & Landy, M. S. (2012). Motor control is decision-making. *Current Opinion in Neurobiology*, *22*, 996–1003.
- Wu, S. H., Delgado, M. R., & Maloney, L. T. (2009). Economic decision-making compared with an equivalent motor task. *Proceedings of the National Academy of Sciences*, *106*(15), 6088–6093.
- Zhang, H., & Maloney, L. T. (2012). Ubiquitous log odds: A common representation of probability and frequency distortion in perception, action, and cognition. *Frontiers in Neuroscience*, *6*, 1–14.

Trampenau, L., van Eimeren, T., & Kutz-Buschbeck, J. P. (in preparation). Parkinsonian patients fail to use probabilistic cues for force scaling in a grip-lift task. In preparation for *Experimental Brain Research*.

Parkinsonian patients fail to use probabilistic cues for force scaling in a grip-lift task

Leif Trampenau¹ · Thilo van Eimeren² ·
Johann P. Kuitz-Buschbeck³

In preparation for Experimental Brain Research

Abstract We studied force control and weight perception based on probabilistic cues in Parkinson's disease subjects (n=15) and healthy age-matched control subjects (n=15). Participants were encouraged to conduct a grip-lift task and a weight adjustment task. In both tasks four different probabilistic visual cues were presented, each of which announced the likely weight of an object. In the grip lift-task the object was grasped and lifted with a pinch grip, in the weight adjustment task the object's weight was gradually adjusted until the perceived heaviness matched the expected weight for a given probabilistic cue. Healthy age-matched control subjects used the probabilistic cues for predictive force scaling in the grip lift-task. In contrast, subjects with Parkinson's disease generally used a predictive mode of force control, but neglected the probabilistic cues in the grip-lift task. Still, in the adjustment task they were able to assign a unique weight to each cue which matched the weight prediction nearly one-by-one. This indicates that the parkinsonian patients understood the meaning of the probabilistic information well, but failed to utilize it in the context of a grip-lift action.

Keywords Parkinson's disease · Predictive force scaling · Motor system · Decision-making · Force rate · Probability

Introduction

An essential feature of dexterous fine motor control in healthy subjects is the predictive scaling of the forces applied by the fingers according to pertinent task demands. The nervous system selects a motor program prior to execution with efficient grip force and load force output according to the object's properties with which it interacts (Johansson and Westling 1984, 1988; Flanagan and Wing 1997; Nowak and Hermsdörfer 2005). For this, sensorimotor memories have to be formed, retrieved and associated with perceptual memories of the corresponding object (Lukos et al. 2010). Typically, force rate trajectories are approximately bell-shaped and reach their maxima prior to lift-off (Johansson and Westling 1988). Since explicit sensory information about critical object properties (e.g. object weight) is not available until liftoff, peak grip and load force rates are considered as variables that reflect preprogrammed forces (Gordon et al. 1993; Nowak et al. 2013).

In precision grip-lift tasks subjects with Parkinson's disease (PD) often exhibit lower rates of force increase (Gordon et al. 1997), slower movement initiation (Brumlik and Bosches 1966; Sheridan et al. 1987; Stelmach et al. 1989), and slower movement execution (Brumlik and Bosches 1966; Fellows et al. 1998; Gordon et al. 1997; Müller and Abbs 1990) than healthy subjects. Conflicting approaches have been presented to explain PD subjects motor deficits. On one side it has been argued that motor abnormalities in PD subjects could be driven by deficient mechanisms of fine motor control (Turner and Desmur-

✉ Leif Trampenau
l_trampenau@hotmail.com

¹ Institute for Sexual Medicine and Forensic Psychiatry, Centre for Integrative Psychiatry (ZIP gG mbH) Kiel, Germany

² Department of Nuclear Medicine, University Hospital Cologne, Germany

³ Department of Physiology, Kiel University, Germany

Table 1 Description of control subjects and Parkinson's disease subjects

PD Subjects				HC subjects		
Number	Age	Sex	UPDRS	Number	Age	Sex
1	66	F	22	16	56	M
2	46	M	39	17	60	M
3	67	M	33	18	56	W
4	70	F	43	19	64	M
5	64	F	44	20	50	W
6	51	F	36	21	72	M
7	63	M	33	22	47	M
8	69	W	62	23	61	M
9	64	M	27	24	66	W
10	50	M	56	25	68	W
11	67	M	54	26	53	M
12	57	M	35	27	47	M
13	52	M	45	28	71	W
14	45	M	37	29	73	W
15	71	W	53	30	34	M

get 2010). In line with this approach it has been reported that PD subjects show severe problems using advance weight information to adapt the rate of grip force increase prior to lift-off (Fellows et al. 1998; Müller and Abbs 1990). Problems in anticipatory fine motor control became also apparent in studies reporting on a dis-coordination of grip and load force processing (Alberts et al. 1998; Alberts et al. 2004).

On the other side, Gordon, Ingvarsson, & Forsberg (1997) argued that PD subjects are able to use an anticipatory control strategy to scale the force output of their fingers prior to liftoff. In their study PD subjects used size cues announcing an object's weight to scale their peak force rates. Moreover, Forsberg et al. (2000) showed that PD subjects initiated the main grip and load force drive simultaneously, and with a generally parallel increase of grip and load force. Similar data have been presented by Ingvarsson et al. (1997).

Motivated by these conflicting results the present study aims to examine predictive force scaling in PD subjects. In particular, we analyzed how the motor system of PD subjects and healthy control (HC) subjects interprets and utilizes a priori weight information for preparation and execution of forces. For this we used an experimental paradigm recently published in two studies (Trampenau et al. 2015; Trampenau et al. 2017). In a grip-lift (GL) task an object that could have three clearly discernible weights (medium, light, and heavy) was grasped and lifted, namely a moveable handle equipped with force transducers, whose weight was varied by a linear actuator. Before each lift, a visual cue provided probabilistic information about the forthcoming weight of the object (e.g., 33.3 % medium, 66.7 % heavy). The GL task allows comparing PD and HC subjects' grip and lifting force scaling and temporal

processing during lifts of an object with constant actual weight but different a priori probabilities for its upcoming weight. In addition, we examined PD and HC subjects' ability to associate the probabilistic cues with different weights. Both groups conducted a weight perception (WP) task, recently published by our group (Trampenau et al. 2017). In this task participants adjusted the weight of the above-mentioned object (handle with force transducers) until the perceived heaviness was equal to what the participant believed would be the expected weight, based on the probabilistic cue.

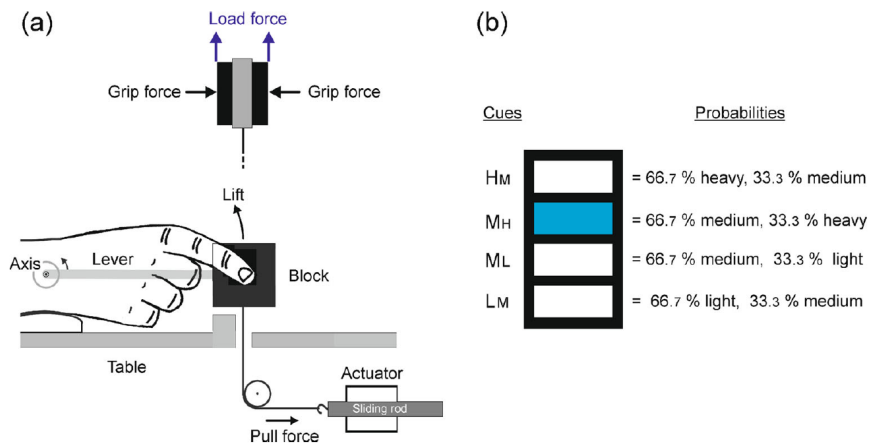
Methods

Participants

Fifteen subjects with diagnosed idiopathic parkinson's disease (6 women), as defined by the UK Brain Bank criteria (Gelb et al. 1999), and with a mean age of 60 ± 9 years (mean \pm SD) participated in this study (see Table 1). Patients were recruited from the neurological clinic of the Kiel university medical center and had normal or corrected-to-normal vision. All were studied exclusively without antiparkinsonian medication (in case of regular treatment with antiparkinsonian drugs after an overnight withdrawal, at least 12 hours). PD patients were excluded, if they showed symptoms of dementia, according to a broad neuropsychological assessment. The group of PD patients was compared to a group of fifteen HC subjects of similar age and sex. HC subjects were volunteers from the community and none of them reported any neurological or psychiatric conditions.

Both groups accomplished the GL task followed by the WP task. A small break of 5 minutes was interspersed between the two tasks. All participants were right-handed

Fig. 1 Experimental set-up. (a) The grip object with force transducers was attached to a lever, whose hinge was aligned with the wrist. Object weight was controlled by a linear actuator, whose sliding rod exerted programmable pull force via a non-elastic string to the grip object. (b) Probabilistic visual cues (here cue MH). Each position of the blue rectangle in the black frame signified the probabilities of two possible object weights. Four different cues were used (HM, MH, ML, LM).



according to a handedness questionnaire (Oldfield 1971) and naive to the specific purpose of the experiments. All studies were approved by the Ethics Committee of the Medical Faculty of the University of Kiel. All subjects gave their written informed consent according to the declaration of Helsinki, prior to entering the study.

Experimental setup

Grip-lift task. The participants were sitting at a table facing a monitor. The right forearm rested on the table with a pad supporting the right wrist. The object, a cuboid block (4x4x3 cm) covered with sandpaper, was located close to the tips of the right thumb and index finger (Fig. 1a). It was attached to a lever and connected via a string to a hidden computer-controlled linear actuator (STA1116, Dunkermotoren, UK). Object weight was determined by the programmable pull force of the actuator. Three object weights were used throughout the GL task, namely 300 g (light), 800 g (medium) and 1400 g (heavy). The vertical grip surfaces of the object were equipped with force transducers that measured the grip and lift force exerted by the grasping fingers with a sampling frequency of 50 Hz. The object position was registered with an optical sensor.

Initially, the participants became familiar with these three typical weights, which were lifted 10 times each in randomized order. They learned to associate each of the three weights to a visual cue displayed on the monitor, which fully predicted the object weight (100 % certainty). These visual cues were bottles with distinct filling levels (nearly empty, medium and full), each indicating the forthcoming

of a certain weight (light, medium or heavy) with *full prediction*. Following the initial training, the four probabilistic visual cues were introduced and thoroughly explained. Each cue provided information about the likely object weight in the upcoming grip-lift trial (Fig. 1b). A blue rectangle could take four different positions in a black frame. The uppermost position (HM cue) indicated that the next object would be heavy in 66.67 % and medium in 33.33 % of the trials. The second position (MH cue) indicated that these percentages were reversed (66.67 % medium / 33.33 % heavy). The third position (ML cue) indicated that object weight would be medium in 66.67 % and light in 33.33 % of the next trials, and the lowest position (LM cue) signified that these frequencies were reversed. Hence four probabilistic cues were used (LM, ML, MH, HM), each designating a *fixed ratio* of probabilities for two possible object weights.

All participants were encouraged to use the *full prediction* cues as well as the *fixed ratio* cues to prepare their grip-lift action. At the onset of each trial, a cue was shown on the monitor for one second (Fig. 2a). It then disappeared and emerged in smaller size beneath a target zone. This signaled that the object should be grasped with a pinch grip of the right hand and lifted by ~ 3 cm, thereby moving the cue into the target zone, which should be reached within 1.5 seconds after lift-off. A release-cue then requested to place the object back down and to release it. The next trial followed 3.5 seconds later. Each participant completed 150 consecutive grip-lift actions. In the *fixed ratio* condition probabilistic visual cues announced object weight in 120 trials, whereas visual cues in the *full prediction* condi-

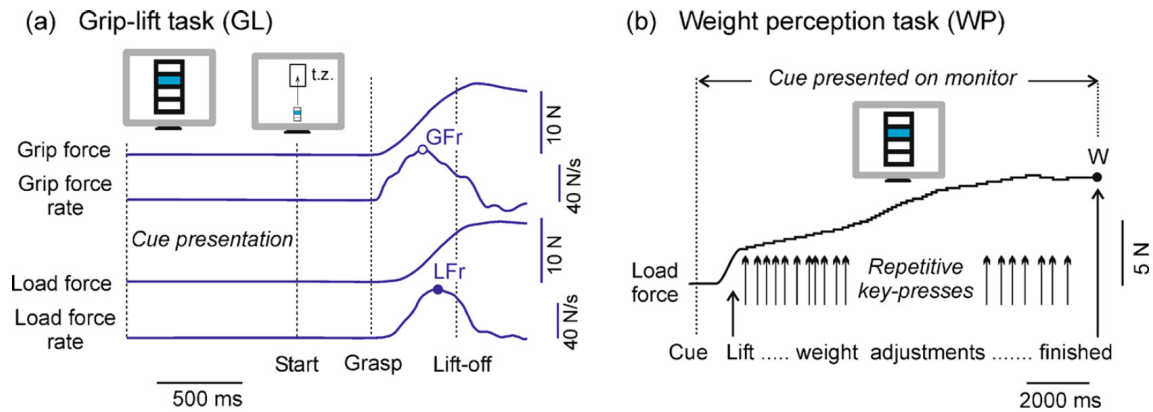


Fig. 2 Tasks.

(a) In the grip-lift (GL), one probabilistic cue was shown for 1 second on a monitor, followed by the start cue with a target zone (t.z.). The object was grasped and the peak grip force rate (GFr) and peak lift force rate (LFr) was reached in the load phase, i.e. before lift-off.

(b) In the weight perception task (WP), the object was lifted and its weight was adjusted by repetitive key-presses (which operated the linear actuator, see Fig. 1a), until the perceived weight W matched the probabilistic cue. The cue (here MH) was visible all the time. Note the different time scales in (a) and (b).

on announced object weight in another 30 trials. All trials were performed in a pseudo-randomized order that avoided possible systematic effects (Cole and Rotella 2002) of the preceding object weight. The light and the heavy object were lifted 40 times each, and the medium object was lifted 70 times. The GL task lasted approximately 40 minutes (including instructions and initial training). Methodical details and force curves have been published elsewhere (Trampenau et al. 2015).

Weight perception task. The same four probabilistic cues as in the GL task were used. Participants were asked to associate each cue with a specific object weight, which matched the expected weight of the probabilistic prediction. For this they lifted and held the object with a pinch grip of their right hand, and then gradually changed its weight by pressing the arrow keys (\downarrow) of a computer keyboard with the left hand, until the perceived weight matched the probabilistic cue. Each key-press altered the pull force of the linear motor by ~ 10 g. The initial (pre-adjustment) weight varied between 250 g and 1550 g. No time constraint was given, and it was allowed to lift and to put down/release the grip object while adjusting its weight. When the trial was completed, the space-bar was pressed, and the next cue was presented on the monitor (next trial). Each probabilistic cue was presented ten times, resulting in 40 trials. The order of the cues was randomized. Each WP trial lasted 10-20 seconds, the entire task ~ 20 minutes. The grasp configuration, which is known to affect perceived heaviness (Flanagan and Ban-

domir 2000), was the same in the GL and WP tasks.

Data analysis

Statistical analyses were performed using the R project for statistical computing (R Development Core Team 2008; www.R-project.org.). The predicted weight P (expected value) was calculated for each probabilistic cue as a weighted combination of the two possible weights, that is a P value for cue HM (66.67 % heavy, 33.33 % medium) of 1200 g [$(0.667 \times 1400 \text{ g}) + (0.333 \times 800 \text{ g}) = 1200 \text{ g}$]. The other P values were 1000 g for cue MH, 633 g for cue ML, and 467 g for cue LM. The P values do not represent the subjects' individual expectations but indicate the statistically expected values for each cue, in line with research that applies statistical decision theory to motor behavior (Nagengast et al. 2010; Wolpert and Landy 2012).

GL task. We analyzed all trials of the *full prediction* condition. For the *fixed ratio* condition, we analyzed trials in which the same actual weight (medium = 800 g) was grasped and lifted, yet preceded by the four different probabilistic cues (LM, ML, MH, HM). No preprocessing of the data was performed. To assess the influence of the weights and the probabilistic cues on force scaling, we determined five measures from the force curves and their first-time derivatives (i.e., the force rate curves) for each trial: (1) peak grip force GF, (2) peak grip force rate GFr, (3) peak load force LF, (4) peak load force rate LFr, and (5) load phase duration LPD, which lasted from the onset of the load force ($LFr > 5 \text{ N/s}$) until lift-off (see Fig. 1,

inset). Peak GFr and LFr are reached before the object is lifted from its support (Fig. 2a), and reflect the anticipatory scaling of force according to the expected weight (Gordon et al. 1993; Nowak et al. 2013). To evaluate the coordination of grip and load force processing subject-wise mean GF and LF were calculated for each weight in the *full prediction* condition and each cue in the *fixed ratio* condition. Pearson correlation coefficients were calculated and Fisher z-transformed (Fisher 1921) to obtain a mean correlation (r') between GF and LF for each condition and group. Moreover, we analyzed the interval between the onset of GF (GFr > 5 N/s) and the onset of LF (LFr > 5 N/s) at the beginning of the grip-lift action.

WP task. The adjusted object weight W (unit of measure: gram), whose heaviness was perceived to match the prediction of a given probabilistic cue, was determined for each trial (Fig. 2b).

For each of the three weights in the *full prediction* condition subject-wise means were calculated for each of the five variables from the GL task. For the four probabilistic cues of the *fixed ratio* condition subject-wise mean of the same five variables from the GL task and the adjusted object weight W from the WP task were calculated. To test for weight-dependent changes of variables in the *full prediction* condition of the GL task, analyses of variance (ANOVA) for repeated measurements with weight as within-subject factor (3 levels) were performed on these subject-wise means. ANOVAs were calculated separately for PD and HC groups. To test for cue-dependent changes of variables in the *fixed ratio* condition of the GL and in the WP task, analyses of variance (ANOVA) for repeated measurements with cue as within-subject factor (4 levels) were performed on these subject-wise means. ANOVAs were calculated separately for PD and HC groups. One-sided paired samples t tests were calculated to test for a cue-dependent increase, with $p < 0.0167$ after Bonferroni correction for multiple comparisons. For each contrast, the effect size was calculated, with $d\text{-cohen} = (m1 - m2) / \sqrt{(s1^2 + s2^2) / 2}$.

To test for group differences of Pearson correlation coefficients in both condition, we calculated the test statistic, with $z = (r'1 - r'2) / \sqrt{(1 / (n1 - 3)) + (1 / (n2 - 3))}$, and obtained p for the computed z (Cohen and Cohen 1983, p. 54).

Results

Full prediction condition: PD group. When the visual cues predicted the upcoming object weight with 100% certainty, influences of the weights on force scaling were recognizable (Table 2). Typical grip and load force profiles of PD subjects are illustrated in Fig. 3. The upper three panels in Fig. 3 show mean GF (blue lines) and mean LF (red lines) curves of each subject lifting the three weights. Obviously the scaling of force curves increases in parallel with the weight. ANOVA indicated significant weight-dependent changes of peak GF ($F_{2,14} = 265.85$, $p < 0.001$) and peak LF ($F_{2,14} = 3697.63$, $p < 0.001$). Peak GF and LF increased significantly ($p < 0.01$) as the object weight increased (L < M < H).

The influence of the weights on GFr and LFr curves is less evident (lower panels Fig. 3, mean GFr: blue solid lines, mean LFr: black dashed lines). Still, ANOVA indicated significant weight-dependent changes of peak GFr ($F_{2,14} = 6.31$, $p < 0.01$) and peak LFr ($F_{2,14} = 33.99$, $p < 0.001$). However, only peak LFr increased significantly ($p < 0.01$) as the object weight increased (L < M < H). Although peak LFr increased with object weight, ANOVA revealed lengthened LPD ($F_{2,14} = 72.15$, $p < 0.001$) as the object weight increased.

Full prediction condition: HC group. Influences of weights on force scaling of HC subjects in the *full prediction* condition were similar to those presented for the PD subjects (Table 3). Scaling of mean GF and LF profiles of HC subjects varied distinctly with the weight (upper panels of Fig. 4). ANOVA indicated significant weight-dependent changes of peak GF ($F_{2,14} = 379.64.02$, $p < 0.001$) and peak LF ($F_{2,14} = 15904.20$, $p < 0.001$). Both increased significantly ($p < 0.01$) as the object weight increased (L < M < H), see Table 3. Moreover, also mean GFr and LFr profiles were influenced by the weight (lower panels of Fig. 4). ANOVA indicated significant weight-dependent changes of peak GFr ($F_{2,14} = 29.42$, $p < 0.001$) and peak LFr ($F_{2,14} = 106.62$, $p < 0.001$). Also these peak values increased significantly ($p < 0.01$) as the object weight increased (L < M < H), see Table 3. The same was true for the LPD ($F_{2,14} = 62.20$, $p < 0.001$) which lengthened significantly as the object weight increased.

In general, force rates in the *full prediction* condition were lower in the PD group than in the HC group for peak GFr ($F_{1,28} = 14.68$, $p < 0.001$) and peak LFr ($F_{1,28} = 9.76$, $p < 0.001$). Maximum forces, however, did not differ significantly between both groups, as ANOVA indi-

Table 2 Lifting light, medium and heavy objects in the full prediction condition of the PD group^a

Unambiguous visual cues announcing upcoming weight in the PD group					
	Light		Medium		Heavy
Actual object weight [g]	300		800		1400
Peak GF [N]	7.00 ± 2.48	d=2.59 **	10.70 ± 1.42	d=4.89 **	15.16 ± 1.46
Peak LF [N]	4.00 ± 0.83	d=9.73 **	8.68 ± 0.48	d=14.42 **	14.66 ± 0.67
Peak GFr [N/s]	54.87 ± 22.81	d=0.29 -	59.05 ± 18.02	d=0.64 -	67.78 ± 20.51
Peak LFr [N/s]	45.68 ± 19.51	d=0.97 **	61.36 ± 25.80	d=0.55 **	71.87 ± 28.15
Load phase duration [ms]	583 ± 182	d=1.56 **	776 ± 167	d=1.93 **	994 ± 151
Interval GF/LF onset [ms]	-73.37 ± 131.96		-43.56 ± 90.28		-42.55 ± 55.73

^a Means ± standard deviations of the individual means (n=15 subjects; ten trials per object weight in each subject). Negative time intervals denote events before lift-off (= 0 ms). Significant difference between values in adjacent columns; * $P < 0.05$; ** $P < 0.01$ (t -tests for paired samples; Bonferroni corrected for multiple comparisons).

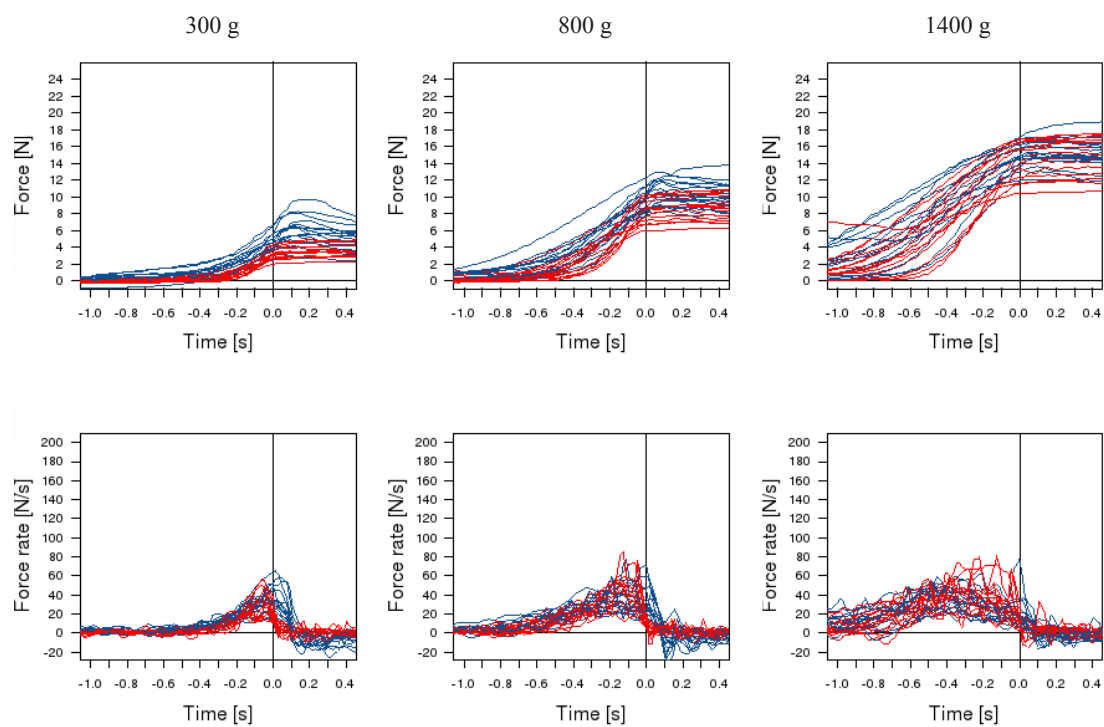


Fig. 3 Typical grip and load force profiles of PD subjects for lifts of the three weights (L, M, H) lifted in the full prediction condition. The upper three panels show mean grip force (GF, blue) and mean lift force (LF, red) curves, the lower three panels show mean grip force rates (Gfr, blue) and mean lift force rates (Lfr, red) curves of each subject lifting the three weights.

Table 3 Lifting light, medium and heavy objects in the full prediction condition of the HC group^a

Unambiguous visual cues announcing upcoming weight in the HC group					
	Light		Medium		Heavy
Actual object weight [g]	300		800		1400
Peak GF [N]	5.60 ± 2.45	d=2.97 **	10.18 ± 1.72	d=5.53 **	15.34 ± 1.32
Peak LF [N]	3.86 ± 0.37	d=21.87 **	8.60 ± 0.25	d=28.34* *	14.51 ± 0.35
Peak GFr [N/s]	56.48 ± 38.46	d=0.61 **	74.98 ± 26.75	d=1.35 **	100.18 ± 28.97
Peak LFr [N/s]	48.31 ± 22.33	d=1.60 **	74.81 ± 22.65	d=1.34 **	100.00 ± 24.19
Load phase duration [ms]	342 ± 127	d=1.46 **	467 ± 126	d=1.18 **	606 ± 161
Interval GF/LF onset [ms]	-28.00 ± 47.96		-47.96 ± 58.17		-42.09 ± 48.69

^a Means ± standard deviations of the individual means (n=15 subjects; ten trials per object weight in each subject). Negative time intervals denote events before lift-off (= 0 ms). Significant difference between values in adjacent columns; * $P < 0.05$; ** $P < 0.01$ (t -tests for paired samples; Bonferroni corrected for multiple comparisons).

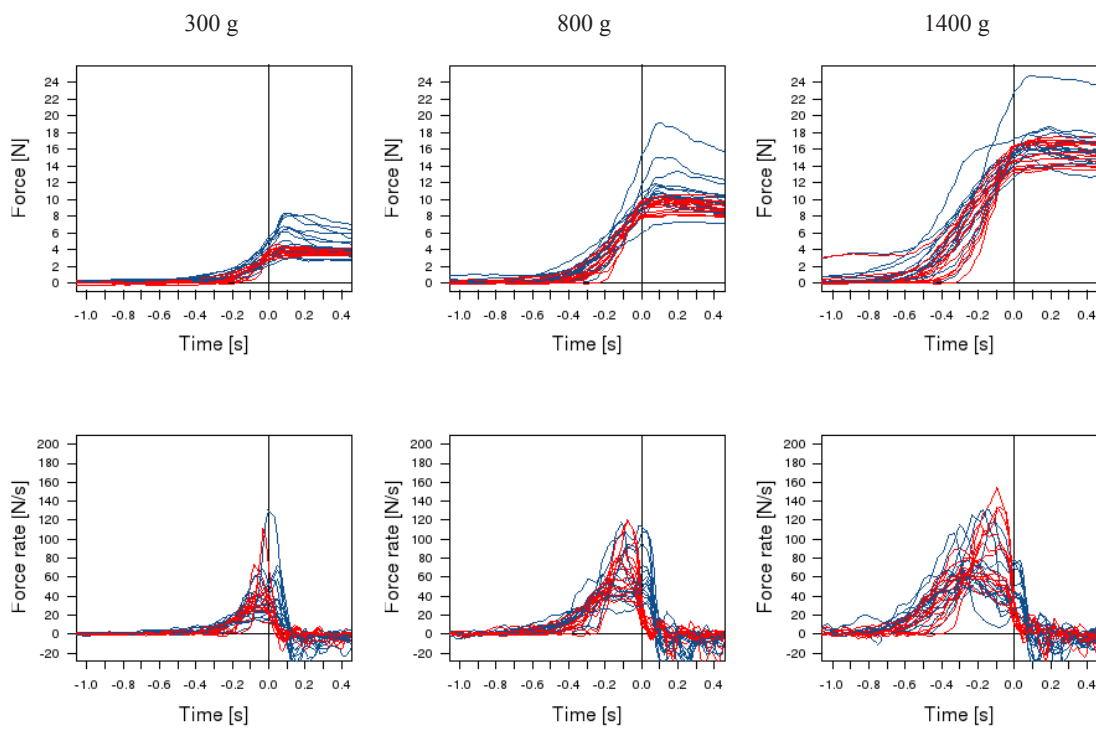


Fig. 4 Typical grip and load force profiles of HC subjects for lifts of the three weights (L, M, H) lifted in the full prediction condition. The upper three panels show mean grip force (GF, blue) and mean lift force (LF, red) curves, the lower three panels show mean grip force rates (Gfr, blue) and mean lift force rates (Lfr, red) curves of each subject lifting the three weights.

Table 4 Lifting objects of medium weight (PD-Group)^a

Probabilistic visual cues announce upcoming weight in the PD group								
Probability ratio	66% L, 33% M		66% M, 33% L		66% M, 33% H		66% H, 33% M	
Abbreviation of cue	LM		ML		MH		HM	
Actual object weight [g]	800		800		800		800	
Predicted obj. weight [g]	467		633		1000		1200	
Peak grip force GF [N]	9.78 ± 1.08	d=0.83 **	10.39 ± 1.01	d=0.50 -	10.75 ± 1.04	d=0.37 -	11.03 ± 1.04	
Peak load force LF [N]	8.52 ± 0.46	d=0.16 -	8.57 ± 0.41	d=0.11 -	8.54 ± 0.45	d=0.22 -	8.60 ± 0.44	
Peak GF rate [N/s]	53.23 ± 16.32	d=0.27 *	56.37 ± 17.05	d=0.23 -	59.23 ± 17.97	d=0.25 -	62.47 ± 18.36	
Peak LF rate [N/s]	61.14 ± 24.16	d=0.03 -	60.66 ± 24.95	d=0.13 -	62.91 ± 23.10	d=0.16 -	65.76 ± 26.69	
Load phase duration [ms]	758.87 ± 212.54	d=0.15 -	778.77 ± 153.90	d=0.20 -	756.70 ± 165.11	d=0.10 -	745.97 ± 145.03	
Interval GF/LF onset [ms]	-41.75 ± 93.71		-37.57 ± 79.89		-48.38 ± 79.27		-53.38 ± 57.93	
Adjusted weight W [g]	452.11 ± 97.23	d=2.81 **	642.20 ± 94.08	d=4.95 **	961.34 ± 88.04	d=3.33 **	1209.27 ± 124.26	

^a Means ± standard deviations of the individual means (n=15 subjects; with 10 – 20 trials per probability ratio in each subject). For each ratio, the predicted object weight is calculated as weighed combination of the two possible actual object weights. E.g. 66.67% H, 33.33% M (HM) yields a predicted object weight of $(0.667 \cdot 1400 \text{ g}) + (0.333 \cdot 800 \text{ g}) = 1200 \text{ g}$. Significant difference between values in flanking columns; * $P < 0.05$; ** $P < 0.01$ (t -tests for paired samples; Bonferroni corrected for multiple comparisons). ANOVA F-values are given in results text.

cated for peak GF ($F_{1,28} = 0.36$, $p < 0.55$) and for peak LF ($F_{1,28} = 0.012$, $p < 0.91$). Furthermore, LDP was significantly ($p < 0.001$) longer in the PD group ($F_{1,28} = 45$, $p < 0.001$). To analyze the impact of the weight on participants force production across the two groups in more detail, we tested for possible interactions between group and weight on peak force and peak force rate with a post-hoc mixed within-between 3 x 2 ANOVA. There were significant interactions between weight and group, for GF ($F_{2,56} = 5.021$, $p < 0.0099$), GFr ($F_{2,56} = 34.95$, $p < 0.001$), and LFr ($F_{2,56} = 14.4$, $p < 0.001$), but not for LF ($F_{2,56} = 0.132$, $p = 0.876$).

Fixed ratio condition: PD group. The effects of probabilistic cues are listed in Table 4 and illustrated in Fig. 5. Effects of probabilistic cues were predominantly observable for weight adjustments in the WP task, whereas effects of force scaling recorded in the GL task were clearly diminished (Fig. 5). The disturbed adjustment of forces

and force rates toward the probabilistic cues becomes evident in Fig. 6, too. ANOVA indicated significant cue-dependent changes of W ($F_{3,14,42} = 240.70$, $p < 0.001$), GF ($F_{3,14,42} = 15.16$, $p < 0.001$) and GFr ($F_{3,14,42} = 7.82$, $p < 0.01$) but not of LF ($F_{3,14,42} = 2.12$, $p < 0.11$) and LFr ($F_{3,14,42} = 2.48$, $p < 0.74$). Cue-wise W values increased significantly ($p < 0.01$) in progression with the predicted weight (Fig. 6), whereas the only significant ($p < 0.01$) gradual increase of GF and GFr was observed between cues LM and ML. ANOVA revealed no significant cue-dependent changes of LDP ($F_{3,14,42} = 0.80$, $p < 0.50$).

Fixed ratio condition: HC group. For the healthy control subjects, effects of probabilistic cues in are listed in Table 5 and illustrated in Fig. 7 and 8. A marked influence of probabilistic cues on both weight adjustment and force scaling was observable. When the 800g weight was lifted mean GF and LF curves revealed a different scaling depending on the presented probabilistic cue (up-

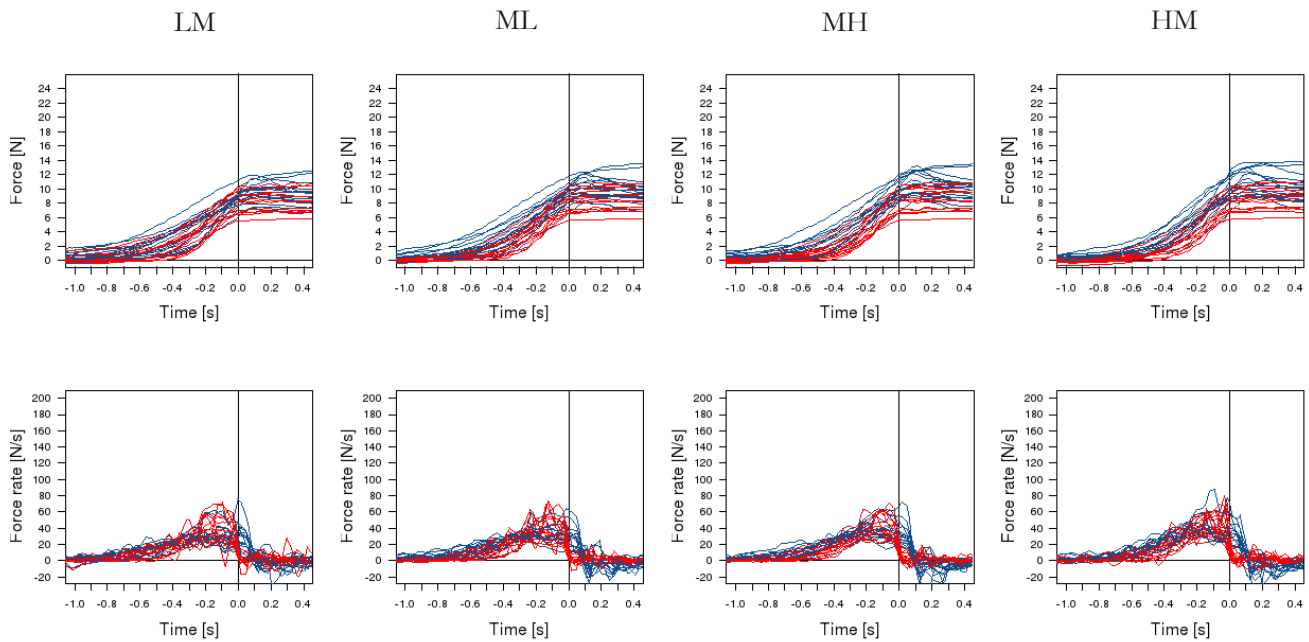
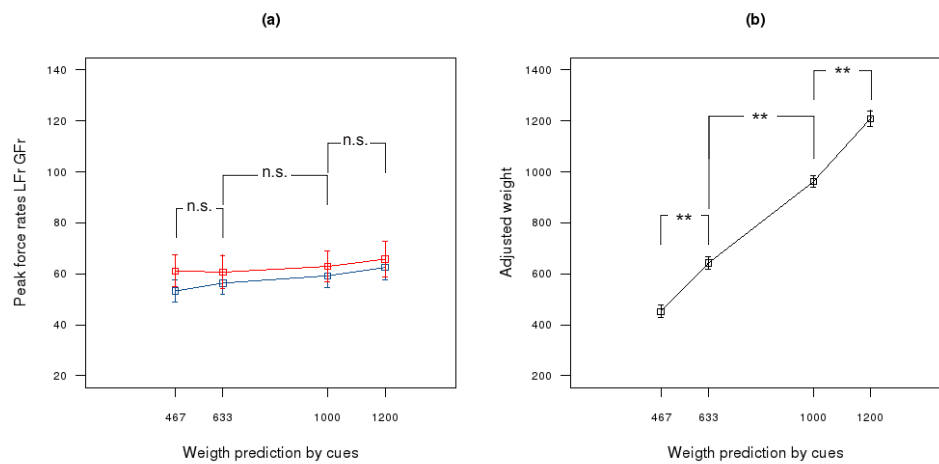


Fig. 5 Typical grip and load force profiles of PD subjects for lifts of the medium weight (800 g) lifted for each cue (LM, ML, MH, HM) in the fixed ratio condition. The upper three panels show mean grip force (GF, blue) and mean lift force (LF, red) curves, the lower three panels show mean grip force rates (Gfr, blue) and mean lift force rates (Lfr, red) curves of each subject lifting the three weights.

Fig. 6 Results of PD subjects. (a) Peak load force rates (LFr, red squared), grip force rates (GFr, blue squares). Means and SEM. (b) Adjusted weights W (black squares) increase with the weight P that the cues predicted (statistically). Means and SEM. Asterisks indicate significant cue-dependent differences (paired t-tests, * $p < .05$, ** $p < .01$, *** $p < .001$ after correction for multiple comparisons)



per panels of Fig. 7). A similar relation could be observed between the probabilistic cues and both force rate curves (lower panels of Fig. 7). ANOVA indicated significant cue-dependent changes of W ($F_{3,14} = 189.03$, $p < 0.001$), GF ($F_{3,14} = 30.15$, $p < 0.001$), GFr ($F_{3,14} = 26.26$, $p < 0.001$) and LFr ($F_{3,14} = 22.57$, $p < 0.001$) but not for LF ($F_{3,14} = 2.61$, $p < 0.064$). W increased significantly ($p < 0.01$) between LM and ML as well as between MH and HM (Fig. 8), whereas GF , GFr and LFr increased significantly ($p < 0.01$) in progression with the predicted weight (LM < ML < MH < HM). Concurrently LPD decreased significantly ($p < 0.01$) in progression with the predic-

ted weight (LM > ML > MH > HM).

Comparison of PD and HC subjects' data in the *fixed ratio* condition showed that peak force rates and maximum load force were lower in the parkinsonian patients than in controls. ANOVA indicated significant group-dependent changes of GFr ($F_{1,28} = 65.25$, $p < 0.001$), LF ($F_{1,28} = 7.04$, $p < 0.01$) and LFr ($F_{1,28} = 56.28$, $p < 0.001$), but no significant group differences for peak GF ($F_{1,28} = 0.09$, $p < 0.77$). Moreover, LPD in the PD group was significantly ($p < 0.001$) longer than in the HC group ($F_{1,28} = 265.01$). 4 x 2 ANOVA indicated significant interactions between cue and group, for GF $F_{3,84} = 8.62$, $p < 0.001$),

Table 5 Lifting objects of medium weight (HC-Group)^a

Probabilistic visual cues announce upcoming weight in the HC group								
Probability ratio	66% L, 33% M		66% M, 33% L		66% M, 33% H		66% H, 33% M	
Abbreviation of cue	LM		ML		MH		HM	
Actual object weight [g]	800		800		800		800	
Predicted obj. weight [g]	467		633		1000		1200	
Peak GF [N]	9.06 ± 1.41	d=1.00 **	9.95 ± 1.06	d=0.76 **	10.57 ± 1.25	d=1.24 **	12.12 ± 2.14	
Peak LF [N]	8.58 ± 0.27	d=0.04 -	8.58 ± 0.28	d=0.12 -	8.61 ± 0.27	d=0.06 -	8.62 ± 0.25	
Peak GFr [N/s]	62.25 ± 26.08	d=0.67 *	73.79 ± 22.64	d=0.37 **	79.90 ± 23.86	d=0.86 **	98.70 ± 36.40	
Peak LFr [N/s]	63.20 ± 26.74	d=0.70 **	75.42 ± 22.98	d=0.26 **	79.77 ± 24.33	d=0.47 **	87.74 ± 23.92	
Load phase duration [ms]	617.17 ± 173.75	d=1.02 **	497.97 ± 154.90	d=0.40 **	455.53 ± 141.40	d=0.40 **	414.17 ± 151.63	
Interval GF/LF onset [ms]	-20.13 ± 39.48		-26.95 ± 38.35		-40.99 ± 47.07		-45.31 ± 50.73	
Adjusted weight W [g]	429.60 ± 88.88	d=3.90 **	713.80 ± 115.52	d=1.35 -	805.29 ± 71.57	d=6.72 **	1255.64 ± 113.27	

^a Means ± standard deviations of the individual means (n=15 subjects; with 10 – 20 trials per probability ratio in each subject). For each ratio, the predicted object weight is calculated as weighed combination of the two possible actual object weights. E.g. 66.67% H, 33.33% M (HM) yields a predicted object weight of $(0.667 \cdot 1400 \text{ g}) + (0.333 \cdot 800 \text{ g}) = 1200 \text{ g}$.

* Significant difference between values in flanking columns; * $P < 0.05$; ** $P < 0.01$ (t -tests for paired samples; Bonferroni corrected for multiple comparisons). ANOVA F -values are given in results text.

GFr ($F_{3,84} = 11.96$, $p < 0.001$), LFr ($F_{3,84} = 10.57$, $p < 0.001$), and W ($F_{3,84} = 9.549$, $p < 0.001$) but not for LF ($F_{3,84} = 1.048$, $p = .346$).

Force Coordination (PD vs. HC). To assess whether PD subjects' force co-ordination differed from HC subjects in the *full prediction* condition, we calculated group-wise mean Pearson correlation coefficients for the relation between subject-wise mean GF and LF. In both groups the mean correlation between GF and LF was very high (PD: $r = 0.988$, HC: $r = 0.993$). No significant group-dependent differences of the mean correlations were found ($n_1 = 45$, $n_2 = 45$, $z = 1.258$, p two-sided = 0.208). Typical grip and load force relations of PD and HC subjects are illustrated in Fig. 9. The upper panels in Fig. 9 illustrate PD subjects' force co-ordination, HC subjects are illustrated in the lower panels. In both groups the relation between GF and LF appears fairly linear, except for irregularities at the end of the recording. In both

groups, GF and LF were initiated almost simultaneously. In PD subjects, on average, GF started to increase 53.16 ms prior to LF. A slightly shorter mean interval (39.35 ms) was measured in the HC group. This time interval between GF and LF onsets did not differ significantly between groups ($F_{1,28} = 0.99$, $p < 0.33$). Also in the fixed-ratio condition, the co-ordination of GF and LF was very similar in PD and HC subjects. In both groups the mean correlation between GF and LF was very high (PD: $r = 0.989$, HC: $r = 0.992$). The mean correlations did not differ significantly between both groups ($n_1 = 60$, $n_2 = 60$, $z = 1.028$, p two-sided = 0.303). Again we plotted typical grip and load force relations of PD and HC subjects (Fig. 9). This shows that cues-wise force co-ordinations of both groups were very similar on trial-level (PD: upper panels, HC: lower panels). Inspection of the GF→LF onset interval revealed that GF started to increase 45.27 ms prior to LF in the PD group, and 33.35 ms prior to LF in the HC group. This difference did

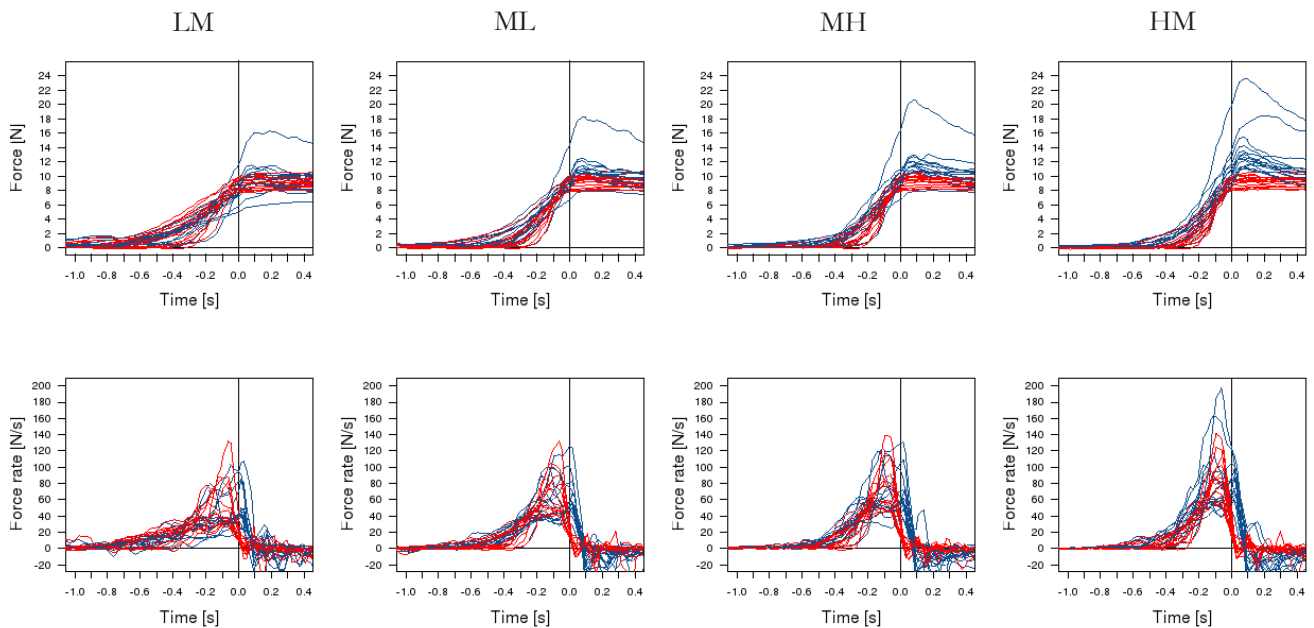
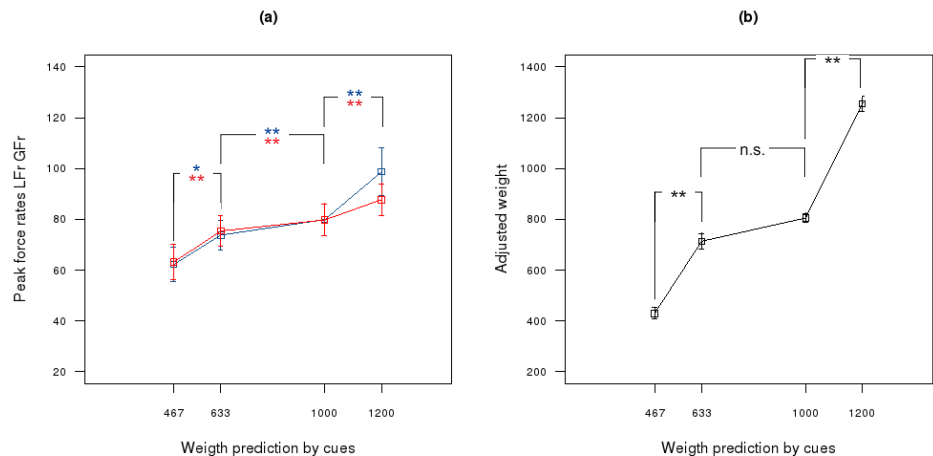


Fig. 7 Typical grip and load force profiles of HC subjects for lifts of the medium weight (800 g) lifted for each cue (LM, ML, MH, HM) in the fixed ratio condition . The upper three panels show mean grip force (GF, blue) and mean lift force (LF, red) curves, the lower three panels show mean grip force rates (Gfr, blue) and mean lift force rates (Lfr, red) curves of each subject lifting the three weights.

Fig. 8 Results of HC subjects.

(a) Peak load force rates (LFr, red squared), grip force rates (GFr, blue squares). Means and SEM. Asterisks indicate significant cue-dependent differences (paired t-tests, * $p < .05$, ** $p < .01$, *** $p < .001$ after correction for multiple comparisons) (b) Adjusted weights W (black squares) increase with the weight P that the cues predicted (statistically). Means and SEM. Asterisks indicate significant cue-dependent differences (paired t-tests, * $p < .05$, ** $p < .01$, *** $p < .001$ after correction for multiple comparisons)



not reach significance ($F_{1,28} = 2.00, p < 0.16$).

Discussion

The purpose of this study was to examine Parkinson’s disease subjects’ ability to interpret and utilize a priori weight information for preparation and execution of

forces. Healthy age-matched subjects were included as reference group. Both groups of participants accomplished a grip-lift task followed by a weight perception task. In the grip-lift task participants were asked to utilize cues indicating the likelihoods of specific object weights to initiate their grip-lift actions with appropriately scaled grip and lift force rates. In line with our previous studies (Trampe-

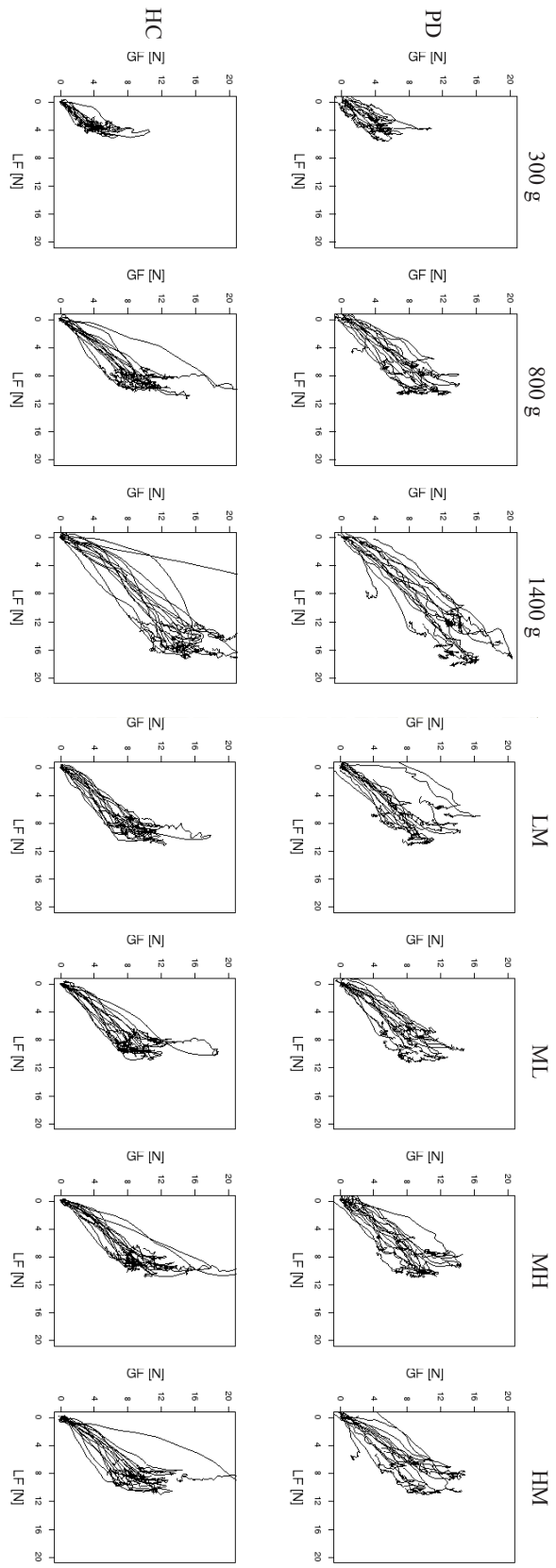


Fig. 9 Force co-ordination between grip force (ordinate) and lift force (abscissa). The upper panels illustrate PD subjects' force co-ordination, HC subjects are illustrated in the lower panels.

nau et al. 2015; 2017) we analyzed effects of probabilistic cues in trials where the same actual weight (medium = 800 g) was grasped and lifted, yet preceded by four different probabilistic cues. These cues were also presented in the weight perception task, where participants gradually adjusted the weight of an object, with continuous proprioceptive and tactile feedback, until the heaviness matched the expectation for a given probabilistic cue. We found evidence for a simultaneous processing of grip and load force in parkinsonian and healthy subjects, indicating a predictive mechanism of force control. However, the use of explicit probabilistic cues to an object's weight for the predictive scaling of forces differed between groups. While healthy subjects used probabilistic advance information, despite its uncertainty, to scale their fingertip forces predictively prior to lift-off, subjects with Parkinson's disease neglected these cues.

The lifted weight had a significant effect on force scaling in parkinsonian and healthy subjects in the *full prediction* condition. Subjects of both groups scaled their grip and load force according to the lifted weight, reflecting a common finding in parkinsonian subjects (e.g. Gordon et al. 1997; Fellows et al. 1998). Force adaptation toward the lifted weight has been interpreted as evidence for an intact ability of subjects with Parkinson's disease to use peripheral sensory information from the grasping digits to assist the scaling of grip force (Nowak and Hermsdörfer 2006). Peak grip and lift force levels for the respective weights did not differ between groups. Also other studies pointed out that scaling of peak fingertip forces is not affected by Parkinson's disease (Gordon et al. 1997; Ingvarsson et al. 1997; Forssberg et al. 2000). Yet other studies reported on excessive grip force scaling as a consequence of Parkinson's disease (Fellows et al. 1998; Fellows and Noth 2004; Nowak and Hermsdörfer 2005). Elevated grip force levels, however, have been ascribed to levodopa treatment (Ingvarsson et al. 1997; Gordon et al. 1997; Gordon and Reilmann 1999) and levodopa induced dyskinesia (Wenzelburger et al. 2002). Parkinsonian subject in our study, however, were in the "OFF state," defined as 12 h without medication.

Besides these similarities we found that subjects with Parkinson's disease, compared to healthy controls, exhibited a profound slowing of grip and load force development for all weights in the *full prediction* condition and all cues in the *fixed ratio* condition. This slowness became apparent from significantly lower force rates and from a prolonged load phase duration. This is a common finding in Parkinson's subjects (e.g. Sheridan et al. 1987; Stelmach et

al. 1989; Jordan et al. 1992; Fellows et al. 1998; Fellows and Noth 2004). In contrast, Ingvarsson et al. (1997) reported on similar load phase durations in subjects with Parkinson's disease and healthy subjects. As opposed to our study, however, Ingvarsson et al. (1997) used only one weight (300 g) that corresponded to our light weight. Probably a prolongation of the load phase in parkinsonian subjects becomes more apparent with heavier weights. Data presented in our study underpin this assumption.

In a constant and familiar environment, parkinsonian subjects are capable of scaling their isometric force increase in advance according to weight-related sensory information acquired during previous lifts (Gordon et al. 1997). The ability to use sensorimotor memories for anticipatory scaling of forces has been demonstrated for healthy subjects (Cole and Rotella 2002; Ameli et al. 2008; Nowak et al. 2013), and for subjects with Parkinson's disease (Müller and Abbs 1990; Fellows et al. 1998). In a changing and unfamiliar environment, when novel objects are grasped and lifted, healthy subjects scaled the peak force rates to the expected weight, based on visual cues to object size, material, and density (Gordon et al. 1993; Baugh et al. 2012; Buckingham et al. 2009). Results presented by Gordon et al. (1997) imply that subjects with Parkinson's disease (ON/OFF medication) are able to associate two different size cues with two different weights and utilize this association for anticipatory force control. Inspection of grip force rates from parkinsonian subjects in the present study revealed problems using in a situation where three cues were associated with three different weights. Related to the results of Gordon et al. (1997) our result indicate that parkinsonian subjects' use of visual cues for anticipatory force control deteriorates in more complex situations. Moreover, cue-led predictive scaling of fingertip forces was in fact disrupted when the probabilistic cues predicted the upcoming weight with a *fixed ratio* of probabilities (66 % / 33 %). Under this condition grip and load force rates did not vary systematically. Healthy subjects, on the other side, handled the same object of medium weight differently, depending on the probabilistic information provided by the visual cues. In two recent studies we presented similar results of healthy young subjects (Trampenau et al. 2015; 2017). Results of the weight adjustment task indicate that parkinsonian subject's disuse of probabilistic cues cannot be attributed to a missing understanding of the probabilistic information.

Examination of grip-load force coordination from parkinsonian subjects and healthy subject revealed no significant differences. Grip and load forces were initiated

approximately simultaneously in both groups. When grip force was plotted as a function of resultant load force, both groups displayed an almost linear relationship between the two forces during the load phase and after lift-off. In line with this, Ingvarsson et al. (1997) reported that PD subjects (ON and OFF medication) had a simultaneous onset of grip and load force and that they showed a generally parallel increase of grip and load force. A tight coupling of grip and load force is considered as an essential feature of anticipatory motor control, with forces scaled predictively according to expected object properties (Johansson and Westling 1988; Johansson and Flanagan 2009).

It seems that parkinsonian subjects disregarded all probabilistic cues, and instead scaled the forces toward a certain weight, yet, independent of the probabilistic cue. Using the probabilistic cues requires to interpret their information and to decide which motor program one should execute. Many studies have reported on the influence of dopamine on decision-making (for an overview see Frank 2006; Glimcher and Fehr 2013). Also decision-making in parkinsonian subjects is altered (Gleichgerricht et al. 2010). In line with this Mazzoni et al. (2007) hypothesized that movement in parkinsonian subjects reflects impairment in the link between motivation and the control of movement gain, resulting in a higher sensitivity to movement energy costs. Out of the many possible policies to select cue-independent force rates, parkinsonian subjects could have used two hypothetical strategies, each representing an extreme option. One theoretical option may be to scale the forces toward the medium weight, which turns up most often (in 70 of 150 trials). In nearly half of the trials this strategy would lead to a sense of achievement, due to adequately scaled fingertip forces. However, this strategy would also be associated with frequent large errors of initial force scaling. The other strategy may be to always scale the force rates toward sensory information acquired during prior lifts. As a consequence of the randomized presentation of weights in our study this strategy may lead to even more large errors of initial force scaling than the first strategy. Whether parkinsonian subjects used one of these strategies or a compromise between both is beyond of the scope of this study. More importantly, in both strategies subjects are not forced to decide which motor program they would perform.

References

- Alberts JL, Elder CM, Okun MS, Vitek JL (2004) Comparison of pallidal and subthalamic stimulation on force control in patient's with Parkinson's disease. *Motor Control* 8(4):484–499
- Alberts JL, Tresilian JR, Stelmach GE (1998) The coordination and phasing of a bimanual prehension task: the influence of Parkinsonism. *Brain* 121:725–742
- Ameli M, Dafotakis M, Fink GR, Nowak DA (2008) Predictive force programming in the grip-lift task: the role of memory links between arbitrary cues and object weight. *Neuropsychologia* 46(9):2383–2388
- Baugh LA, Kao M, Johansson RS, Flanagan JR (2012) Material evidence: interaction of well-learned priors and sensorimotor memory when lifting objects. *J Neurophysiol* 108(5):1262–1269
- Brumlik J, Bosches B. (1966) The mechanism of bradykinesia in Parkinsonism. *Neurology* 16(4):337–344
- Buckingham G, Cant JS, Goodale MA (2009) Living in a material world: How visual cues to material properties affect the way that we lift objects and perceive their weight. *J Neurophysiol* 102:3111–3118
- Chevalier G, Deniau J-M (1990) Disinhibition as a basic process in the expression of striatal functions. *Trends Neurosci* 13:277–280
- Cohen J, Cohen P (1983) *Applied multiple regression/correlation analysis for the behavioral sciences*. Hillsdale, NJ: Erlbaum.
- Cole KJ, Rotella DL (2002) Old age impairs the use of arbitrary visual cues for predictive control of fingertip forces during grasp. *Exp Brain Res* 143:35–41
- Fellows SJ, Noth J (2004) Grip force abnormalities in de novo Parkinson's disease. *Mov Disord* 19:560–565
- Fellows SJ, Noth J, Schwarz M (1998) Precision grip and Parkinson's disease. *Brain* 121:1771–1784
- Fisher RA (1921) On the probable error of a coefficient of correlation deduced from a small sample. *Metron* 1:3–32
- Flanagan JR, Bandomir CA (2000) Coming to grips with weight perception: Effects of grasp configuration on perceived heaviness. *Perception & Psychophysics* 62:1204–1219
- Flanagan JR, Wing AM (1997) The role of internal models in motion planning and control: evidence from grip force adjustments during movements of hand-held loads. *J Neurosci* 17:1519–1528
- Forsberg H, Ingvarsson PE, Iwasaki N, Johansson RS, Gordon AM (2000) Action tremor during object manipulation in Parkinson's disease. *Mov Disord*

- 15:244–254
- Frank MJ (2006) Hold your horses: a dynamic computational role for the subthalamic nucleus in decision making. *Neural Networks* 19(8):1120–1136
- Gelb DJ, Oliver E, Gilman S (1999) Diagnostic criteria for Parkinson disease. *Arch Neurol* 56:33–39
- Gleichgerricht E, Ibáñez A, Roca M, Torralva T, Manes F (2010) Decision-making cognition in neurodegenerative diseases. *Nature Reviews Neurology* 6(11):611–623
- Glimcher PW, Fehr E (Eds.) (2013) *Neuroeconomics: Decision making and the brain*. Academic Press
- Gordon AM, Ingvarsson PE, Forssberg H (1997) Anticipatory control of manipulative forces in Parkinson's disease. *Exp Neurol* 145:477–488
- Gordon AM, Reilmann R (1999) Getting a grasp on research: does treatment taint testing of parkinsonian patients? *Brain* 122:1597–1598
- Gordon AM, Westling G, Cole KJ, Johansson RS (1993) Memory representations underlying motor commands used during manipulation of common and novel objects. *J Neurophysiol* 69:1789–1796
- Ingvarsson PE, Gordon AM, Forssberg H (1997) Coordination of manipulative forces in Parkinson's disease. *Exp Neurol* 145:489–501
- Johansson RS (1998) Sensory input and control of grip. *Novartis Found Symp* 218:45–59
- Johansson RS, Flanagan JR (2009) Coding and use of tactile signals from the fingertips in object manipulation tasks. *Nature Rev Neurosci* 10:345–359
- Johansson RS, Westling G (1984) Roles of glabrous skin receptors and sensorimotor memory in automatic-control of precision grip when lifting rougher or more slippery objects. *Exp Brain Res* 56:550–564
- Johansson RS, Westling G (1988) Coordinated isometric muscle commands adequately and erroneously programmed for the weight during lifting task with precision grip. *Exp Brain Res* 71(1):59–71
- Jordan N, Sagar HJ, Cooper JA (1992) A component analysis of the generation and release of isometric force in Parkinson's disease. *Journal of Neurology, Neurosurgery & Psychiatry* 55(7):572–576
- Lukos J, Ansuini C, Santello M (2007) Choice of contact points during multidigit grasping: effect of predictability of object center of mass location. *J Neurosci* 27:3894–3903
- Mazzoni P, Hristova A, Krakauer JW (2007) Why don't we move faster? Parkinson's disease, movement vigor, and implicit motivation. *J Neurosci* 27:7105–7116
- Mink JW, Thach WT (1991) Basal ganglia motor control. II. Late pallidal timing relative to movement onset and inconsistent pallidal coding of movement parameters. *J Neurophysiol* 65:301–329
- Müller F, Abbs JH (1990) Precision grip in parkinsonian patients. In Streifer MB, Korezyn AD, Melamed E, Youdim MBH (eds.) *Advances in neurology*, Raven, New York, 191–19
- Nagengast AJ, Braun DA, Wolpert DM (2010) Risk-sensitive optimal feedback control accounts for sensorimotor behavior under uncertainty. *PLoS Computational Biology* 6(7):e1000857
- Nowak DA, Glasauer S, Hermsdörfer J (2013) Force control in object manipulation – a model for the study of sensorimotor control strategies. *Neuroscience & Biobehavioral Rev* 37:1578–1586
- Nowak DA, Hermsdörfer J (2005) Grip force behavior during object manipulation in neurological disorders: toward an objective evaluation of manual performance deficits. *Mov Disord* 20:11–25
- Nowak DA, Hermsdörfer J (2006) Predictive and reactive control of grasping forces: on the role of the basal ganglia and sensory feedback. *Exp Brain Res* 173(4):650–660
- Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia* 9(1):97–113
- R Development Core Team (2008) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.r-project.org>
- Schneider JS (1987) Basal ganglia-motor influences: Role of sensory gating. In Schneider JS, Lidsky TI (Eds.), *Basal ganglia and behavior: Sensory aspects of motor functioning*, Toronto: Hans Huber, 103–121
- Sheridan MR, Flowers KA, Hurrell J (1987) Programming and execution of movement in Parkinson's disease. *Brain* 110:1247–1271
- Stelmach GE, Teasdale N, Phillips J, Worringham CJ (1989) Force production characteristics in Parkinson's disease. *Exp Brain Res* 76:165–172
- Trampenau L, Kuhtz-Buschbeck JP, van Eimeren T (2015) Probabilistic information on object weight shapes force dynamics in a grip-lift task. *Exp Brain Res* 233:1711–1720
- Trampenau L, van Eimeren T, Kuhtz-Buschbeck JP (2017) Processing of probabilistic information in weight perception and motor prediction. *Attention, Perception & Psychophysics* 79(2):404–417.
- Turner RS, Desmurget M (2010) Basal ganglia contributions to motor control: a vigorous tutor. *Current opinion in neurobiology* 20(6):704–716

- Wenzelburger R, Zhang BR, Poepping M, Schrader B, Müller D, Kopper F, Fietzek U, Mehdorn HM, Deuschl G, Krack P (2002) Dyskinesias and grip control in Parkinson's disease are normalized by chronic stimulation of the subthalamic nucleus. *Ann Neurol* 52:240–243
- Wolpert DM, Landy MS (2012) Motor control is decision-making. *Current Opinion in Neurobiology* 22:996–1003

Curriculum Vitae

Persönliche Angaben

Name: Leif Trampenau
 Geburtstag: 15. Dezember 1981
 Geburtsort: Tönning
 Staatsangehörigkeit: deutsch
 Familienstand: verheiratet

Akademische Qualifikation

2006–2012 Studium der Psychologie an der Christian-Albrechts-Universität zu Kiel
 2012 Diplom in Psychologie an der Christian-Albrechts-Universität zu Kiel; Thema der Diplomarbeit: „Zum Zusammenhang der Größen- und Distanzwahrnehmung im Kontext der Mondillusion“;
 Betreuer Prof. Dr. Vejbjørn Ekroll
 2015–2017 Promotion an der Christian-Albrechts-Universität zu Kiel im Fach Psychologie
 seit 2015 Postgraduale Ausbildung zum Psychologischen Psychotherapeuten am IFT-Nord, Kiel
 2017 Erlangung des Doktorgrades der Philosophie an der Christian-Albrechts-Universität zu Kiel im Fach Psychologie
 Thema der Dissertation: „Manipulating an Equivocal World – How Force Control and Weight Perception use Probabilistic Information“
 Betreuer Prof. Dr. Thilo van Eimeren, Dr. Gesa Hartwigsen

Akademische Berufserfahrung

2007–2012 Studentische Hilfskraft im Labor für visuelle Psychophysik unter der Leitung von Prof. Dr. Rainer Mausfeld, Christian-Albrechts-Universität zu Kiel
 2013–2015 Wissenschaftlicher Mitarbeiter in der Arbeitsgruppe Funktionelle Bildgebung an der Klinik für Neurologie, UKSH, Campus Kiel
 seit 2016 Anstellung als Diplom Psychologe am Institut für Sexualmedizin und Forensische Psychiatrie, Zentrum für Integrative Psychiatrie (ZIP gGmbH) Kiel