Contributions of vision and haptics to grasping

by

Adam Dubrowski

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ABSTRACT

Four experiments are reported which examine the process of integration of vision and haptics during prehension movements. Prehension is defined as the act of reaching, grasping and lifting an object. While vision can be used to guide the hand towards the object, as well as shape finger aperture such that the object can be grasped, haptic information about the object mass is necessary to know how much force should be used for a successful lift. Reach and grasp formation and the force generation operate during different time phases. However, in order to initiate generation of grip force without haptic information, we must anticipate the mass of the object in advance. Several models of sensorimotor integration have been proposed that describe the control of grasp. The main feature of these models is that the system must anticipate the mass of the object based on other modalities, such as vision. The anticipatory programming of grip forces is based on memorial associations between pre and post contact characteristics of sensory information. However, these models fail to describe how such multimodal integration develops. The main purpose of this thesis is to characterize the formation and nature of the integration of visual and haptic information as it pertains to the generation and control of grip forces.

Experiment 1 aimed to describe prehension movements in the absence of haptics in a virtual environment. It has been shown that in such environments vision is important in hand transport and grasp formation in a similar way as when grasping real objects. Experiment 2 was concerned with the development of visual and haptic integration when both sources of information are present. The results suggest that the process of integration of vision and haptics when generating grasping movements is dependent on

what cues were available during practice. Experiment 3 examined the integration of vision and haptics in the on-line control of grasp in a dynamic setting, where the participants were asked to intercept moving objects. The results showed that with practice, the visual, pre-contact information as well as the haptic, post-contact information can be combined to produce an anticipatory model of the apparent mass of the object as it is stopped and grasped by the fingers. At the same time, haptic information about object torque can be used in an on-line fashion. Thus both sources of information can be used concurrently to form a higher order representation of object behavior, and at the same time each sensory modality can contribute independently to the on-line control of grasp. Finally, in Experiment 4 the ability to use vision and haptics was assessed when there was a disruption to the motor system. More specifically, an individual with a unilateral basal ganglia damage due to a stroke was studied. It was shown that with damage to this part of the brain, the integration of these two sources of information is suppressed.

Collectively these studies show that the integration of vision and haptics is a flexible process. Although it has been previously suggested that visual information dominates over haptics when both are present, with training this dominance can be changed. Also, it seems that both sources of sensory information can be combined to form a higher order representation, as well as being used independently. Finally, the basal ganglia have been identified as an important neural structure in the process of sensory integration. These findings, provide insight into the formation of internal models of object behavior. It is proposed that the integration of vision and haptics is guided by a weighting function that is dependent on error detection and correction during the movement.

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CHAPTER 1: GENERAL INTRODUCTION

Reaching toward, grasping and lifting an object (prehension) is a routine activity of everyday life, yet the nature of the underlying control mechanisms is still a matter of debate. According to one view, prehension consists of two components, each reflecting a separate neural processing channel; the transport component brings the hand into the vicinity of the object, while the grasp component ensures that the fingers form a shape which matches that of the object (Jeannerod 1984). However, this act can also be divided into two phases based on its time course; before contact with the object is made (pre-contact phase), and after the object is contacted (post-contact phase). The pre-contact phase is mainly concerned with bringing the hand close to the target object, as well as shaping the finger aperture such that the object can be grasped. During the post-contact phase, haptic information about object mass and surface characteristics from the interacting digits is used to generate the appropriate grip and load forces to successfully lift the object (Johansson 1991; Smith 1994).

The production of forces at the fingers is not initiated in the post-contact phase, but instead is initiated in the pre-contact phase (see Johansson and Cole 1994 for a review). The forces necessary to lift an object must be anticipated suggesting the existence of anticipatory mechanisms that allow for the prediction of these forces based on memorial representations acquired in previous interactions with similar objects. Wolpert and Kawato (1997) and Wolpert and Ghahramani (2000) proposed a general computational model that explains the formation of memorial representations of movement. A schematic of this model is presented in Figure 1.

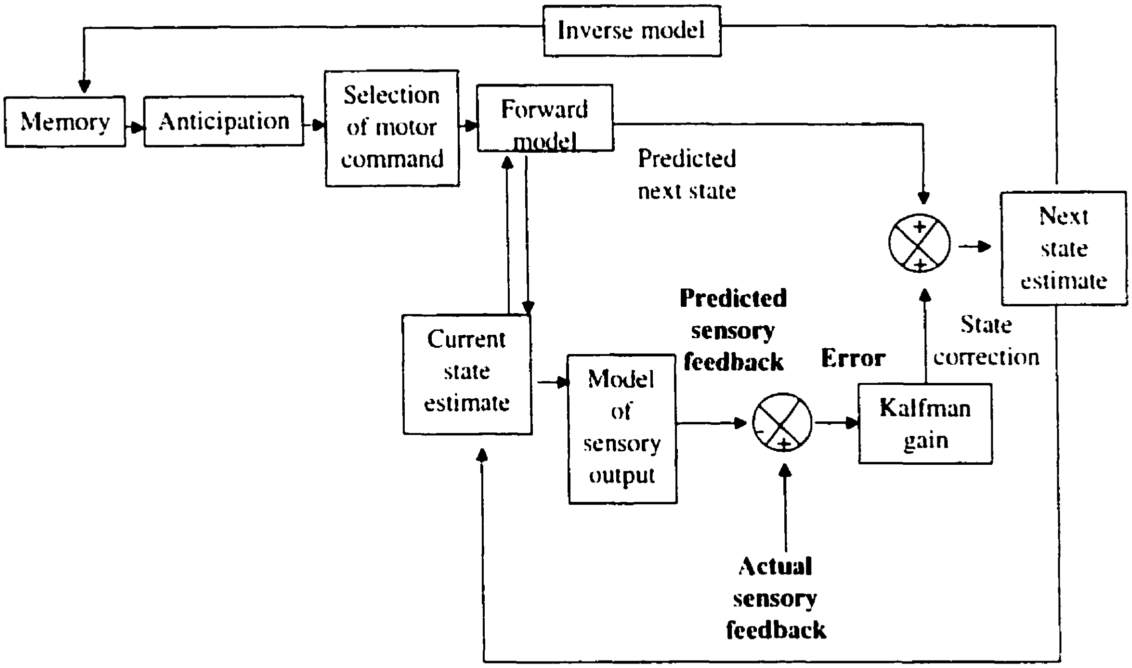


Figure 1. This schematic is adapted from Wolpert and Kowato (1997) and shows a general feedforward model.

With respect to lifting tasks, the basic concept of this model is that as the movement unfolds, multiple forward models are run that mimic the motor output of previous lifts. Each forward model generates the predicted sensory feedback that should be received from the digits. Furthermore, each of the forward models is coupled with an inverse model, which, if the sensory feedback matches the predicted feedback, will be selected, stored and used to determine appropriate motor commands for the subsequent interactions with similar objects.

The concept of feedforward mechanism has been known for decades. Rooted in the visual system, von Holsten (1954) proposed that when a command is issued to an effector (eye) to perform a movement (saccade), a similar copy of that command (termed corollary discharge or efferent copy) is sent to another part of the brain that is sensory in nature (Evarts 1973). In principle, this efferent copy can be evaluated in much the same way as sensory feedback, thus if an error occurs in the motor commend a correction can be made even before the arrival of sensory feedback (Schmidt and Lee 1999). In the domain of precision grip control, Johansson (1996) proposed that this efferent copy also contains information about expected sensory signals from the periphery (i.e., haptic information) along with corrections to the motor program if there is a mismatch between the expected and the true sensory information. Thus the feedforward component of the grip control is highly dependent on the processing of tactile information coming from the interacting digits.

Human fingers are equipped with four types of somatosensory receptors; fast adapting type I (FA I), fast adapting type II (FA II), slow adapting type I (SA I), and slow adapting type II (SA II). These receptors are responsible for signaling certain stages of grip production (Johansson and Westling 1984; 1987). For example, FA II show responses to transient mechanical events at the fingertips, such as object lift off, touch down, and micro slips between the finger pad and the object surface. Furthermore, grip to load force ratio, a crucial variable controlled for in order to prevent the object from slipping, is also believed to be adjusted based on signals from the cutaneous receptors (Johansson and Cole 1994). Slips associated with too low grip to load force ratio are first signaled via brief, discontinuous bursts of activity in FA I, FA II, and SA I afferent, which triggers upgrading of the ratio as early as 70 ms after the slip (Johansson and Westling 1987). The periodic nature of firing by the cutaneous receptors allows for discontinuous control of grasp development, in contrast to continuous feedback in other modalities such as vision. The advantage of discontinuous sensory feedback is that it allows for pre-parameterization of corrective responses when the expected signal does not arrive at appropriate time (Johansson 1996).

Thus, the sensory motor system responsible for grip control is well equipped and able to control grasp stability based on the anticipatory, discrete event, sensory driven, feedforward mechanisms. In summary, it was proposed that preparing a motor program for stable grasp is based mainly on memorial representations of motor programs used when interacting with similar objects in the past. A copy of such program (efferent copy) is sent for comparison of the correctness of movement. Also, this efferent copy contains information about expected sensory signals from the periphery along with corrections to the motor program if there is a mismatch between the expected and the true sensory information.

It is evident that both Johansson's (1996) and Wolpert and Kawato's (1998) models rely heavily on the initial pre-programming of grip forces before the contact with the object occurs. However, it is not well understood what sources of information are used for the initial pre-programming of these forces. It has been proposed that this initial generation of the appropriate motor command is largely based on other modalities e.g. vision. Recently researchers have made attempts to address the issue of integration of vision and haptics in the development of the anticipatory model of object behavior used for the initial generation of grasp forces. Goodwin et al. (1998) and Jenmalm et al. (1998)

have shown that participants use anticipatory information regarding object curvature to generate appropriate forces when grasping. Other examples range from grip force matching based on vision and haptics versus haptics alone (Jones 2000), size-mass perturbation studies (Gordon et al. 1991a), and visually and haptically based size-mass illusions (Flanagan and Beltzner 2000; Gordon et al. 1991b; Gordon et al. 1991c). While we have an appreciation that vision can be used to help build anticipatory models that can be used for force control, it is not well understood how this process of integrating visual and haptic signals develops. That is, does one source of sensory input dominate? Also, can both sources be used on-line or only in a preprogrammed fashion?

It has been speculated that people learn how to visually perceive the world by combining their visual perceptions with precepts obtained through other modalities and through motor interactions with the environment. This idea was initially proposed by Berkeley (1709/1910) based on the observation that the visual perception of depth results from associations between visual cues and the sensations of touch and movement. More recently, Ernst et al. (2000) found that participants were more precise in their estimates of visual slant when the visual cue was congruent with haptic cue, than when the two cues were incongruent. On the contrary, Festinger (1967) postulated that in the perception of object curvature visual information dominates haptics when both sources of information are available and conflicting. In the domain of grip control this was supported by findings of Charpentier (1891) and more recently Gordon et al. (1991a). Gordon et al. (1991a) demonstrated that when lifting small objects of different volumes or sizes but similar masses the visual information about object size dominates the haptic information about its mass. That is, the bigger objets were lifted with greater grip forces than the smaller ones. Recently, the robustness of the size-mass illusion has been questioned by Flanagan and Beltzner (2000), who showed that with practice haptic information about object mass can dominate the visual information about its size, and consequently the grip forces applied on the object were scaled to the true object mass. Although there is plenty of evidence that both visual (Arbib 1981; Goodale and Milner 1992; Jeannerod 1984) and haptic (Johansson 1991; 1996) information is used for prehension, it is not clear how these two sources of sensory input are integrated and which of the two sources is prevailing.

Not only is this of theoretical importance, there are also practical applications for these findings. How is working in a virtual environment affected by the lack of haptic inputs? Dionisio et al. (1997) demonstrated that in some application areas, such as medicine, when training and performing in a virtual reality environment, information sources such as vision and acoustics alone are not sufficient. Therefore, additional information channels, like haptics, need to be simulated. They have found that the addition of haptic feedback in virtual reality environments improves both the impression of reality and the ability to orient in a virtual world. Atkins et al. (2001) studied the hypothesis that in a virtual reality environment observers can use haptic perceptions as a standard to develop visual perceptions. They have demonstrated that their participants involuntarily compared visual and haptic perceptions in order to evaluate the relative reliabilities of the visual cues that were present in the virtual reality environment.

Other, practical applications of this work involve industrial and ergonomic settings. How does the use of gloves that eliminate or reduce haptic inputs influence grasping? How can we use visual cues to facilitate the generation of appropriate forces in the workplace? For example it has been shown that wearing surgical gloves is related to increased grip forces when lifting and manipulating small objects. Increases in glove thickness, by the addition of multiple layers of gloves, causes further increases in grip force (Shih et al. in press). One of the proposed mechanisms for the increase in the grip force produced was related to poor haptic information due to the thickness of the gloves. Prolonged use of such gloves could be linked to overuse injuries due to the increased grip forces produced. One possibility of reducing the impact of glove usage on grip force production could be the addition of other modalities such as vision to inform the worker about the grip force levels exerted.

The focus of this thesis is theoretical and addresses four primary issues. The first issue is to understand how grasping is controlled under visual guidance only, in the absence of haptic inputs. Second, the flexibility of the coordination between visual and haptic inputs is examined using a learning paradigm. Third, the dynamic characteristic of using both visual and haptic inputs while grasping moving targets is of interest. Finally, the elimination of the flexible use of visual and haptic inputs in an individual with brain injury is addressed. Each experiment is presented here in the same form as it has been submitted for publication. Thus, there may be some repetition in the introductions and methods of each paper. A summary of these experiments follows.

Experiment 1: Grasping without feeling.

In collaboration with Dr. O. Bock's laboratory in the Physilogisches Institut Deutsche Sporthochschule Koln, Germany, we investigated the response of the manual motor system to unexpected environmental changes when reaching for virtual objects.

These prehension movements (reach and grasp formation) towards virtual objects involve visual, but no tactile stimulation.

Prehension movements directed towards objects in space are achieved by two components executed in parallel, namely the transport and grasp components. The transport component brings the hand towards the object while the fingers preshape and enclose around the object. The formation of an appropriate hand aperture, which includes the hand orientation and the distance between the grasping fingers to accommodate the object's shape and size, is termed the grasp component (Jeannerod 1992). The transport component is influenced by the object's location, and its size and orientation influence the grasp component. It has been suggested that the two components of prehension are functionally linked (Jeannerod 1992; Marteniuk et al. 1990). Studies investigating the possible control mechanisms and coordination of the reach and grasp components of prehension have primarily used perturbation paradigms. Most have employed double step methods, where participants were asked to grasp a target that either changed location or size. This project, in contrast to the earlier studies, investigated the combined effect of both size and location perturbations during the same movement.

The main results showed that when changes in the target position and its size occur simultaneously, the two components of prehension (i.e., wrist transport and aperture formation) are affected with different delay times suggesting independent control between the reach and grasp channels. Furthermore, evidence of information sharing between the two channels was found. In summary, this study provided support for the two-channel model proposed by Jeannerod (1992).

Experiment 2: How do we learn to integrate vision and haptics; is the coordination plastic?

As previously mentioned, the most prevalent model of grasp control proposed by Johansson and Cole (1992; Johansson and Cole 1994) stresses the importance of anticipatory control of the fingertip forces exerted on the object. This pre-contact anticipation of the required forces is developed through previous interactions with similar objects, where pre-contact visual information about the object is integrated with the post-contact haptic signals. Festinger et al. (1967) and Gibson (1933) have suggested that when vision is present it will be the dominant source of information used to perform the task. This was challenged by Flanagan and Beltzner (2000) who showed that, in the control of fingertip forces, the visually based size-mass illusion can be diminished through practice, suggesting that erroneous visual information can be dominated by the haptic signals. This finding can be taken as indirect support for the learning specificity hypothesis suggested by Proteau at al. (1992). The purpose of this study was to investigate whether visual cues and haptic information can be integrated during visually guided grasping in the fashion predicted by the learning specificity theory, and whether both sources of sensory information can be used to control load and grip forces.

To test these questions, five groups of participants practiced lifting visually identical objects with different masses (200, 300, 400g). After practice there was a transfer phase in which participants performed additional lifts of the 300g object. On some lifts, the object mass was unexpectedly changed to either 200g or 400g. The No Coding Blocked group practiced with blocked color-mass coding (red-200g, black-300g, green-400g), and no color-mass coding during transfer. The No Coding Random group practiced under the same coding conditions, however the order of practice presentations was randomized. The Practice Coding Blocked group practiced lifting the masses in blocks and performed the practice and transfer trials with no coding. The Practice Coding Random practiced under the same no coding condition, however the order of presentation was randomized. The All Coding group practiced with blocked color-mass coding, but the coding remained during the transfer.

Results showed that participants who practiced with visual cues tended to rely on visual cues during transfer, and ignored haptic input. Conversely, participants who practiced without visual cues were able to detect perturbations of object mass using haptic input only. With random practice the fingertip forces were not scaled to object mass, were higher than with blocked practice, and were achieved through multiple muscular impulses. Also, with the random presentation of masses the integration of vision and haptics required more practice compared to the blocked presentations.

Two main conclusions can be drawn from this study. First, in accordance with learning specificity theory, the visual information that cued the color-mass relationship acquired during practice became important for the preprogramming of the lifting forces, and when this information was withdrawn, performance suffered. When only haptic information was available, participants learned to utilize this information in the absence of visual cues. Second, with random practice the fingertip forces, that were not scaled to object mass, were higher than with blocked practice, and were achieved through multiple muscular impulses. Also, during random presentation the integration of vision and haptics required more practice than during blocked presentations. This shows that blocking augments the formation of the anticipatory model of object properties.

Experiment 3: Grasping in dynamic situations: Vision or haptics?

As discussed in the previous section, Jeannerod (1992) proposed the existence of two information processing channels responsible for the control of prehension. Information regarding extrinsic object properties (such as object size) is processed by one channel and is used to control the transport component of prehension. Information about object intrinsic properties (such as object mass) is processed in the second channel and is used to control the grasping phase of the movement. However, in a dynamic situation object velocity has not been categorized as either an intrinsic or extrinsic property. Velocity specifies the change in the location of the object, thus influencing the transport component. Also, moving objects appear to be heavier upon contact with the hand due to the associated linear momentum. Thus velocity could also be considered an intrinsic object property that will influence the grasp component.

The influence of mass on the grip force necessary to lift an object has been studied exclusively in stationary situations, where participants are required to reach and lift, or hold an object. However, dynamic situation, where the object approaches the participant and is then intercepted and lifted, creates an opportunity to investigate the roles of vision and haptics in both the on-line processing of information as well as the anticipatory mechanisms that relay information obtained from previous trials to update an internal model. Turrell and colleagues (Turrell et al. 1999) have suggested that a combination of target mass and velocity (linear momentum) is the controlled variable in planning the grip force. However, this hypothesis was not directly tested in their paper.

In addition, Kinoshita and colleagues (Kinoshita et al. 1997) have shown recently that torques created when objects are held off the center of mass can influence grip force in a similar manner to the load force (i.e., the greater the torque, the greater the grip force in order to hold the object). They have also demonstrated that torque influences grip force independently of the load force. It was hypothesized that since the torque created due to inconsistent finger placement cannot be predicted prior to the contact itself, grip force adjustments due to torque could only be dealt with by the system on-line.

The purpose of this study was to investigate the contributions of several characteristics of a moving target object on the grip and load forces produced at the fingers during capturing and lifting. Specifically, the contributions of target object mass, velocity, momentum, and the transient torque values generated when the fingers contacted the target object were evaluated. Participants grasped heavy, medium and light target objects that were instrumented with force/torque transducers that moved at slow, medium and fast velocities along a moving track. The masses and velocities were chosen such that several of the mass/velocity combinations shared the same momentum values.

The results showed that when transient torques were present, they influenced peak grip force. Furthermore, it was also shown that information about the object's linear momentum and torque were both used by the motor system in programming the grip forces. However, velocity and mass also contribute equally to the generation of interception forces. Together, these results suggest that visual information about object's velocity and haptic information about its mass can be integrated and used to form an anticipatory model of the object's behavior at the moment of its interception. Furthermore, since transient torque had a very strong influence on grip force production, it is evident that the system could deal with these perturbations in an on-line fashion.

Our findings from this study suggest that based on prior interaction with moving objects, linear momentum values due to the mass and speed interaction can be anticipated prior to object contact. Furthermore, the influence of torque on grip force production is also accounted for by Johansson's model. Whether the influence of torque on grip control is neglected by the motor system in the initial motor programming, or whether some average value is anticipated, certain sensory consequences from the finger pads are expected. Due to the unpredictable nature of torque in this study, it is hypothesized that the corrections to the initial muscle commands are pre-programmed, and that torque was dealt with on-line in a feedforward fashion.

Experiment 4. What are the neural structures responsible for feedforward planning of grip forces?

Also, of interest was investigating the underlying neural structures responsible for the preparation of grip forces. Thus, as part of my Ph.D. thesis work, I have conducted three studies with an individual with unilateral basal ganglia damage.

Lifting objects is based on the anticipatory programming of grip forces, where large objects are expected to be heavier than small ones, thus requiring higher grip forces. Also, it has been shown that when the size of the object does not match its anticipated mass, grip and load forces are adjusted based on haptic input to match the object's true mass (Gordon et al. 1991b; Flanagan and Beltzner 2000). The mechanism responsible for these adjustments and the on-line feedforward processes of grip control due to unexpected perturbations have been briefly outlined in the preceding section. The basal ganglia have been shown to be involved in higher order aspects of motor control such as planning a movement, the initiation of internally generated movements, and the execution of complex motor synergies (Stelmach and Philips 1991). Furthermore, the basal ganglia are thought to be involved in the comparison of the efferent copy of the motor program that originates in the frontal fields, with peripheral feedback, which might be useful for regulating the unfolding movement, or for monitoring its consequences (Hikosaka and Wurtz 1983). Jueptner and Weiller (1998) who in a series of studies investigated the roles of the basal ganglia and the cerebellum in the processing of afferent information have recently challenged this view. These authors concluded that the cerebellum, and not the basal ganglia, is involved in the on-line control of evolving movement. In addition Weiller and colleagues (Weiler et al. 1996) have demonstrated that the basal ganglia did not show any increases in activation during passive elbow flexion (afferent sensory information only) in contrast to active flexion (afferent sensory and efferent motor information), and instead only the cerebellum was activated. This was taken as evidence that the basal ganglia were not the site for feedback information processing. Together these studies indicate that the basal ganglia are not used to control movement based on sensory feedback, but rather they are concerned with the selection of appropriate movements (Jueptner and Weiller 1998). In line with this argument, Muller and Abbs (1990) have demonstrated that Parkinsonian patients can adjust their grip force according to the true mass of the object handled suggesting no deficits in sensory feedback processing. What was more important, was that these patients showed slower onset latencies, which suggests an inability to use sensory afferance to trigger the next stage of the lift in accordance with the feedforward model.

Based on the rCBF studies (Jueptner and Weiller 1998), as well as the observations that patients with Parkinson's disease are able to scale their grip force to object mass (Muller and Abbs 1990), it could be hypothesized that the cerebellum is the major site of feedback information processing. However, since the basal ganglia are mainly concerned with the selection of movement and complex muscle synergies (Kandel et al. 1991), it is possible that they play a key role in the releasing of corrective responses in the anticipatory, discrete event, sensory driven, feedforward control of grasp (Johansson and Cole 1994). To examine this issue, an individual with basal ganglia damage was subjected to two tests outlined below.

Test 1

When grasping to lift an object, the grip force is usually scaled to the mass of the object. However, it has been shown that lifting objects of different sizes but equal masses results in the generation of higher forces for larger compared to smaller objects. This is known as the size-mass illusion (Gordon et al., 1991). The objective of this study was to investigate whether a similar size-mass illusion will be present in an individual (OF) with a unilateral lesion to the basal ganglia. It was hypothesized that if the basal ganglia have an influence on the use of haptic feedback in the updating of the internal model used to anticipate the forces required for grasping, damage to these structures should result in the inability of OF's contralesional hand to respond to the size-mass illusion. To test this hypothesis three objects of equal mass but different sizes were grasped and lifted by OF and three control individuals. The controls showed the expected size-mass illusion for peak grip force. OF showed no effect of the illusion for either hand. Controls used on-line control to compensate for torques created when lifting the object. OF only showed evidence of on-line control of torques for his ipsilesional hand, compared to his contralesional hand, which showed no compensation in response to torques. In conclusion, OF's basal ganglia damage affected the on-line control of grip forces and the ability to integrate visual and haptic feedback in the programming of finger forces.

Test 2

Thus far, it has been shown that healthy participants scale their grip force to object size. This was not observed for the individual (OF) with a unilateral basal ganglia damage. It was thus hypothesized that these structures are important in the integration of visual and haptic information, as well as in the on-line correction to grasp. To directly investigate the influence of basal ganglia damage on the on-line control, a perturbation task was used in Test 2.

Johansson and Westling (1988) and Gordon et al. (1993) have demonstrated that grip force produced when lifting big objects that were heavy, and small objects that were light, was scaled to the size and mass of the object. Gordon et al. (1991a) have showed that when the anticipated and the actual mass of the object did not covary, the grip forces were adjusted quickly in an on-line fashion to suit the object mass requirements. In Test 2, two hypotheses were test. First, it was of interest if OF will demonstrate grip force scaling when the objects mass and size were congruent. Second, when this relationship between object mass and size was unexpectedly changed, does basal ganglia damage affect the on-line correction of grip force.

To test these hypotheses two healthy control participants and OF were asked to lift objects with both hands, under two mass-size conditions; congruent (control trials) and incongruent (perturbed trials) size-mass relationship. The perturbed trials were presented unexpectedly with low probability of occurrence. The results showed that on the control trials, OF scaled grip forces to the object mass in a similar manner to the control participants. However, based on the grip forces generated on the perturbed trials, there was no evidence of on-line corrections to the grip force for both hands of OF. Also, when lifting perturbed objects, the grip force was scaled to object size rather than its mass.

The results suggest that when object mass and size covaried, the damage to basal ganglia did not affect the scaling of grip force to object mass. On the contrary, the lesion affected on-line control of grasp bilaterally. That is, both hands of OF were affected in a similar fashion. This suggests that the basal ganglia are involved in the processing and integration of vision and haptics. Also, these results suggest that the basal ganglia are key structures in the feedforward models of grasp control proposed by Johansson (1996) and Wolpert and Kawato (1997).

CHAPTER 2: EXPERIMENT 1

The reaching toward and grasping of an object (prehension) is a routine activity of our everyday life, yet the nature of the underlying control mechanisms is still a matter of debate. According to one view, prehension consist of two components, each reflecting a separate neural processing channel: The *transport component* brings the hand into the vicinity of the object, while the *grasp component* ensures that the fingers form a shape which matches that of the object (Jeannerod, 1984). The two-channel hypothesis is supported by anatomical evidence (see Jeannerod, 1992 for a review), as well as by studies in which either object size or position were altered at the time of movement onset, thus requiring a reprogramming of the original motor response. It was found in the latter studies that perturbations of object *size* modified selectively the grasp but not the transport component of prehension (Paulignan et al. 1991b), while perturbations of object *position* affected both components (Paulignan et al. 1991a). These results were interpreted as support for independent control of transport and grasp processes. Another, particularly persuasive argument was also presented in the above studies: The latency between the perturbation and the onset of a corrective response appeared to be distinctly different for the two components: Following a size perturbation, corrections started after about 300 ms, but following a position perturbation, after only about 100 ms. Such a discrepancy of correction times appears to strongly support the two-channel hypothesis. However, the observed discrepancy could also represent a methodological artifact, since unfortunately, the correction times of grasp and transport were *not* defined by the same algorithm (see below).

In a related study, object size and position were perturbed *concurrently* upon movement onset (Castiello et al. 1998). In this double-perturbation paradigm, correction times were generally longer than in the above two studies, and most importantly, they were very similar for the grasp and the transport component. Along with other kinematic findings, these results were taken as evidence in favour of a close coupling between the two channels.

However, the findings by Castiello et al. (1998) could also be interpreted as support for a dramatically different view of prehension control. Smeets and Brenner (1999) have suggested that the distinction between reach and grasp components is artefactual; rather, prehension should be conceptualised as a holistic act, bringing index finger and thumb from their initial positions into the desired positions on the surface of the object. Indeed, this hypothesis predicts that correction times of the transport and grasp "components" will be the same, as found by Castiello et al. (1998).

In summary, available literature on the correction onset in prehension movements is inconsistent, with single-perturbation experiments claiming that the correction times of grasp and transport are different, and double-perturbation experiments suggesting that they are equal. It would be highly desirable to resolve this discrepancy, and thus help to distinguish between the two principal hypotheses on prehension control.

Unfortunately, all cited studies suffer from a methodological shortcoming which makes any meaningful comparison of reaction times extremely difficult: *Different criteria were used to define correction onset for the transport versus for the grasp component.* Thus in the single-perturbation studies, correction onset was defined by maximum acceleration for the transport, but by minimum velocity for the grasp component; in the double-perturbation study, the criteria were minimum acceleration versus maximum position. The main purpose of the present study was to rectify this shortcoming by *applying the same criterion to both components*: Only with a common metric are direct comparisons possible. Furthermore, our study used a mix of single- and double-perturbation trials in one session, to determine if differences between these perturbation types may have contributed to the inconsistency in literature. If the grasp and transport are controlled with two independent channels then different correction times would be expected on the perturbation trials, and if there is clear dependence between the two channels, then the same correction times should be observed for both the reach and grasp phases of prehension when perturbed. However, if there are interactions for the correction times between the grasp and transport in the double perturbation condition, then there is support that there are independent channels with some cross-talk.

Methods

Participants

Twelve participants executed prehension movements with their right, preferred hand, using the experimental set up outlined in Figure 2A. There were three female and nine male participants (age range 20-46). Eight participants were inexperienced with the present task, and four had participated in a similar study about a year earlier; we found no overt performance differences between these two groups. All participants signed an informed consent statement for this study, which has been approved by the Ethics Committee of the German Sport University.

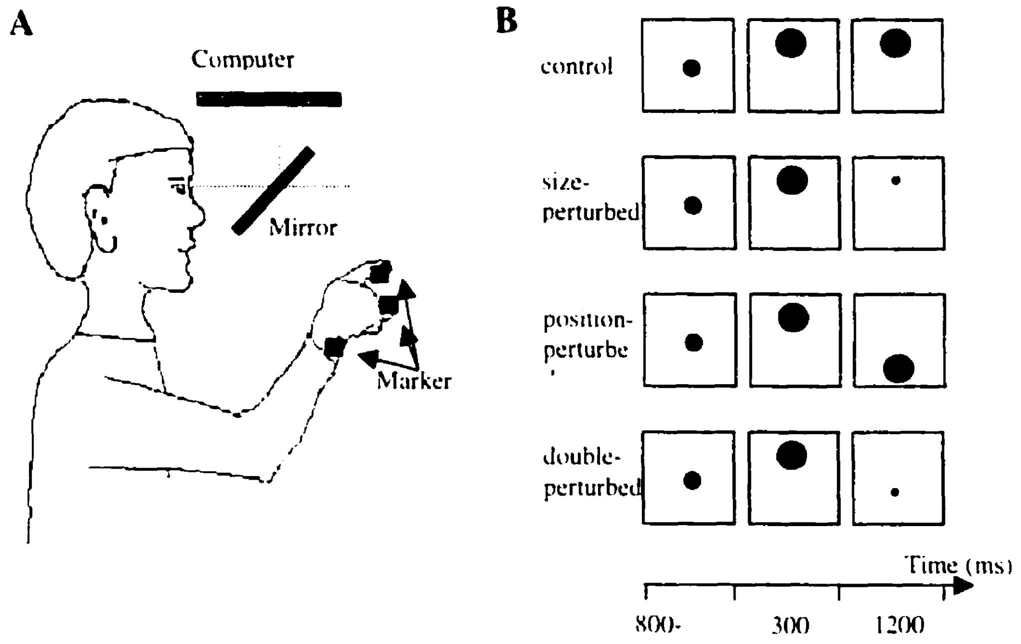


Figure 2. **A:** Schematic outline of our experimental setup, showing the hardware for visual stimulation and for hand position recording. **B:** Events displayed during four different trial types; each row of three frames corresponds to one trial, with black circles representing luminous disks. Each trial began with a central starting disk, presented for 800-1200 ms. A target disk then appeared with one of two sizes in one of two locations (here: a large disk at the top). This disk could remain unchanged for 1500 ms, or change its size, location, or both, depending on the experimental condition. Only one of the four possible trial types per condition is shown.

Procedure

The participant's task was to grasp luminous discs between index finger and thumb as quickly and accurately as possible. The discs were displayed on a computer screen, and projected onto a tilted, semitransparent mirror, such that their virtual image appeared in a frontal plane at eye level, 40 cm ahead. Mirror transparency was sufficient for the participants to be able to view their hand.

Apparatus

We have used mirror-viewed discs successfully in previous prehension studies, including a perturbation study (Bock 1996; Bock and Jüngling 1999), and found response characteristics comparable to those with real objects. The main advantage of our approach is the ease by which size and position can be manipulated, individually and concurrently. This would be much more difficult to achieve when using real objects.

To improve the realism of the virtual grasping task, each session was preceded by 40 warm-up trials, where participants grasped real cylinders of the same size and distance as the subsequently presented virtual discs. These real cylinders were removed before the actual experiment, such that during the virtual grasping trials, participants' fingers never made contact with a real object. Each trial began with the presentation of a starting disc of 5 cm in diameter, located in the centre of the display. 800 to 1200 ms later, the starting disc was replaced by a target disc of 1 or 9 cm diameter, located 11 cm above or below the starting disc. Thus, in order to grasp the virtual targets, participants had to increase or decrease the distance between fingers, and to increase or decrease the vertical position of their wrist.

Table 1. Experimental conditions and trial types. Each trial type is defined by the initial position and size of the target (0 – 300 ms after appearance), as well as by its final position and size (300 – 1500 ms after appearance); the arrows symbolize the transition from initial to final target characteristics.

Condition	Trial type
Control	top large -> top large
	top small -> top small
	bottom large -> bottom large
	bottom small -> bottom small
Size-perturbed	top large -> top small
	top small -> top large
	bottom large -> bottom small
	bottom small -> bottom large
Position-perturbed	top large -> bottom large
	top small -> bottom small
	bottom large -> top large
	bottom small -> top small
Double-perturbed	top large -> bottom small
	top small -> bottom large
	bottom large -> top small
	bottom small -> top large

Four different perturbation conditions were employed, each consisting of four trial types. Conditions and trial types are listed in Table 1, and one trial type from each condition is illustrated in Figure 2B. In the control condition, the target appeared in one of the four possible position x size combinations, and remained unchanged for 1500 ms. In the *size-perturbed* condition, target size changed 300 ms after appearance, while in the *position-perturbed* condition, it was target location that changed. Finally in the *double-perturbed* condition, both position and size changed 300 ms after target appearance. Each trial type of the control condition was presented 36 times, and each trial type from perturbed conditions four times per experimental session, in a randomized sequence. Thus, the probability of perturbation was 25%, and the total number of trials was 192.

The 3-D positions of thumb, index finger and wrist were recorded at a sampling rate of 200 Hz by the SELSPOT® motion analysis system, which employs infrared light emitting diodes (IREDs) and infrared light sensitive cameras. Two IREDs were positioned on the ulnar side of the tips of thumb and index finger, and their 3-D distance was taken as a measure of grip aperture. A third IRED was placed on the ulnar eminence, and its vertical position was used to specify the transport component. The grasp and transport data were smoothed by a 21-sample sliding average before further analysis. For a quantitative analysis of the recorded responses, an interactive computer program calculated a number of parameters for the each response, as defined in Table 2. Importantly, the *same* criteria were used to define a given parameter in the transport, as well as in the grasp component. To determine the correction time for each phase, all single-step responses to a given target were time-adjusted with respect to the peak velocity, and were then averaged. Then, the correction onset of each double-step response was determined as the point in time when the difference between the response and the associated single-step mean first exceeded 5 mm. The program yielded satisfactory results in about 90% of the transport, and 85% of the grasp trajectories. Errors in the automated processing were caused by factors such as noise in the signal. For the remaining data, a human operator had to select the parameter values by visual inspection closely adhering to the same algorithms.

Table 2. Definition of kinematic response parameters used to describe prehension responses. Since the definitions for the grasp and the transport components were identical, they are not separately entered in the table. For example, *grasp* reaction time was reached when *aperture* velocity first exceeded 5 mm/s, and *transport* reaction time when vertical *wrist* velocity first exceeded 5 mm/s.

	control condition	perturbed condition
Reaction time	Interval between target onset, and time when velocity first exceeded 5 mm/s.	Same as control.
Peak velocity	Absolute value of the 1st maximum in the velocity profile.	Absolute value of the 2nd maximum in the velocity profile.
Movement time	Interval between movement onset, and the time when velocity dropped below 5 mm/s.	Interval between zero crossing of velocity, and the time when velocity again dropped below 5 mm/s.
Amplitude	Absolute difference between initial and final grip aperture or wrist position.	Same as control.
Correction time	-	Interval between perturbation, and the correction. The correction was defined as the time when the perturbation trial deviated 5 mm from the mean of the control trials. (As defined in Bock and Jüngling 1999)

Results

Kinematic profiles

Figure 3 illustrates the kinematic characteristics of four individual prehension movements, one from each experimental condition. Each column represents one response, with the top part showing the position and velocity of the grasp, and the bottom part those of the transport component. From this figure, the kinematic profiles of both components appear reasonably similar. This similarity, as well as the use of identical decision criteria for kinematic landmarks, is the prerequisite for a meaningful comparison of the two components.

Further from Figure 3, it appears that a perturbation of object size had an effect on the kinematics of the grasp, but not of the transport component, while a perturbation of object position led to distinct inflections in both components.

Correction time

The correction time of perturbed trials was analysed by a repeated-measures analysis of variance (ANOVA) with four factors: Component (grasp, transport), Perturbation (single, double), Position (top, bottom), and Size (large, small). In this design, the levels of Position and Size pertained to the *final* characteristics of the target (e.g., a 'top small -> top large' perturbation would be coded as Position = top, Size = large). The dependent variable for Perturbation = single was the correction time of size-perturbed trials for the grasp component, and of position-perturbed trials for the transport component; in this way, we compared the responses of each component to the pertinent single perturbation. All significant interactions were subjected to Tukey's HSD test for significant differences between means. Several significant effects ($p<0.01$) were yielded, which can be best appreciated by the three-way plot in Figure 4; note, however, that the three-way interaction was *not* significant. We found a significant effect of Component ($F(1,11) = 19.6$), since correction time was shorter by 31 ms for the grasp than for the transport component. We further found significant Component x Perturbation ($F(1,11)=10.9$) and Component x Size ($F(1,11)=31.1$) interactions: For the grasp component, correction time was on the average shorter for single versus double

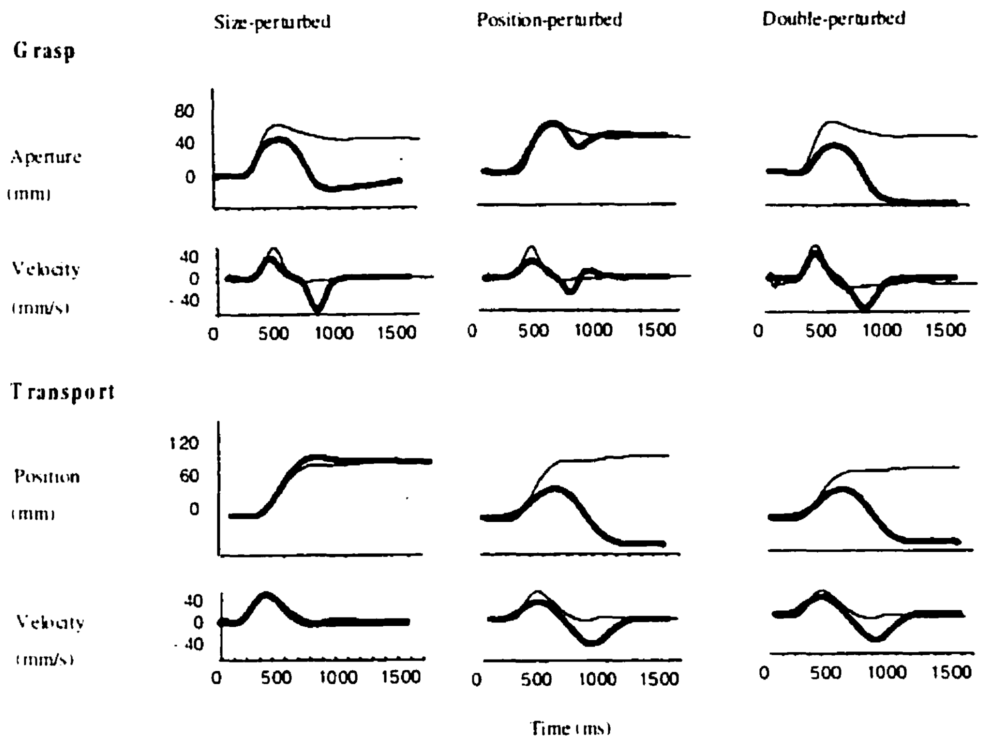


Figure 3. Typical trajectories of prehension movements in the four experimental conditions also shown in Figure 2B. Each column represents one trial; the top two traces pertain to the grasp, and the bottom two to the transport component. Thin lines show control trials and thick lines show perturbed trials. The data reported describes vertical motion because the primary motion was in this direction (targets were located above and below the starting position). Across trials there was some variation in exactly where the fingers were placed because they were not actually making physical contact with anything. To accommodate for this, in the analyses, the starting position of the fingers was considered "zero" and the difference from this starting position to the new fingers positions was quantified.

perturbations, and for large-to-small versus small-to-large perturbations, while there was no significant dependence on perturbation type and target size for the transport component. We also found a significant Perturbation x Size interaction (F(1,11)=24.7): Correction time was 32 ms longer for double-perturbations with the large target, when compared to the other three conditions. The most interesting aspect of this pattern of findings is that several significant effects included the factor Component; we therefore conclude that the dependence of correction time on target characteristics *is distinctly different for the grasp and the transport component.* There is some concern that the perturbations for the grasp and transport phases of the movements are not of equal size, and this could potentially influence the correction times for the grasp and transport differentially. That is, the transport perturbation was larger in magnitude than the size perturbation which could lead to a shorter delay for the transport compared to the grasp. However, contrary to this, there was a main effect where correction time was actually shorter for the grasp in comparison to the transport component. Also note that the larger perturbation for the transport component should produce only a constant bias between component correction times, and would not explain the observed interactions.

Other kinematic parameters

Figure 5 shows for the data patterns for movement time, peak velocity and amplitude. As seen in Figure 5, grasp movement time was longer when only the position changed, in comparison to the other conditions. Furthermore, transport movement time increased with any type of perturbation, in comparison to the control condition.

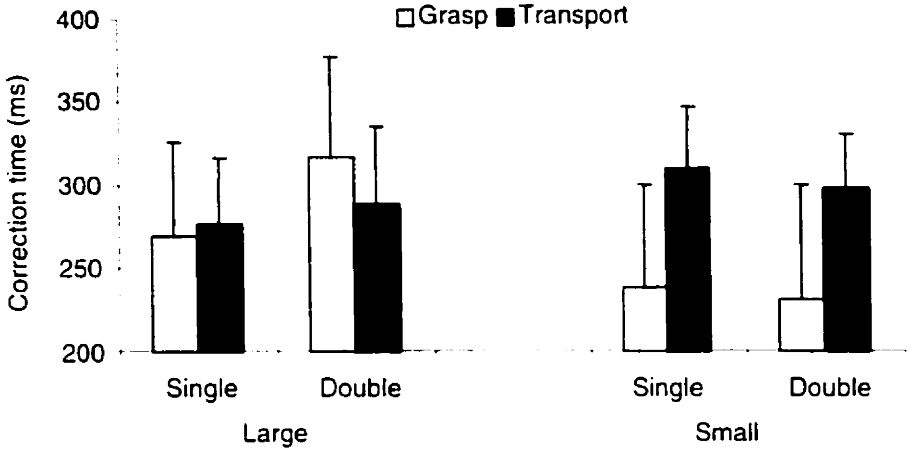


Figure 4. Means and standard deviations for correction times, plotted as a function of perturbation condition (single versus double) and target size (large versus small). Data for the grasp component are shown by white, and those for the transport component by black bars.

Peak grasp velocity was lower when reaching toward the small versus the large target in the control and position-perturbed, but not in the other two conditions. Note that peak grasp velocity for the control and position-perturbed condition involved finger opening, but in the size-perturbed and double perturbation conditions aperture velocity was a measure of closing velocity.

The plot of peak transport velocity shows that peak velocity depended on the initial rather than final target position. As expected, grasp amplitude was larger for the large versus the small disc. Also, grasp amplitude progressively decreased from control to size- to position- to double-perturbed conditions. Transport amplitude was greater for top targets, and for targets of large size (not shown in Figure 5; the difference averaged 4.5 mm).

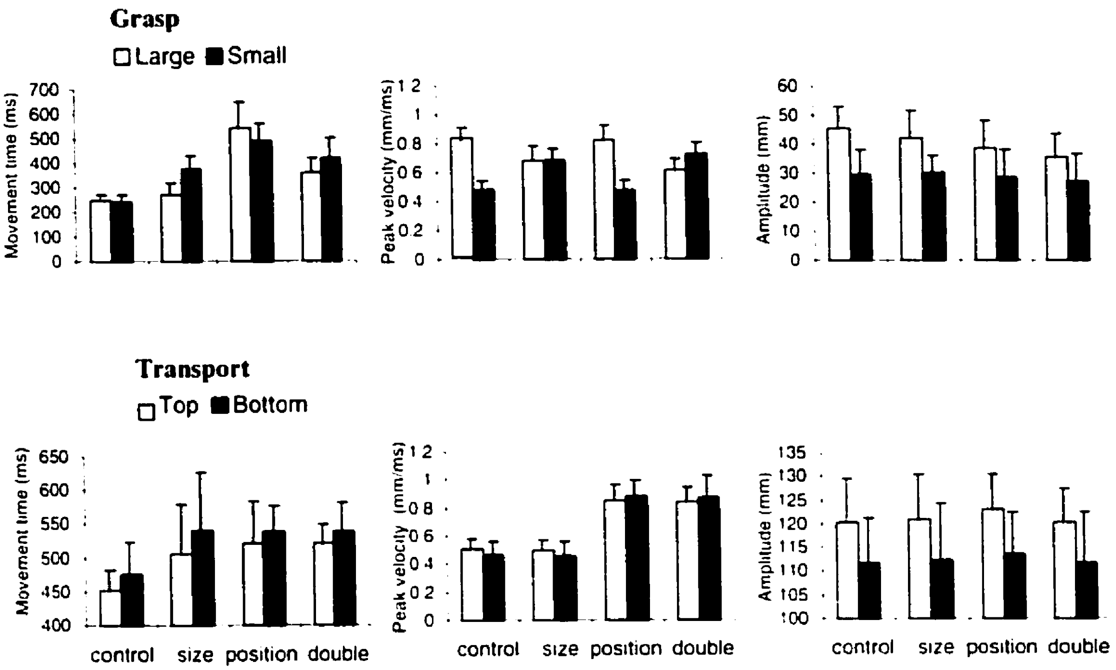


Figure 5. Means and standard deviations of three kinematic variables of grasp (top row) and transport (bottom row) profiles. The top row illustrates Perturbation x Size, and the bottom row Perturbation x Position interactions.

Discussion

The present study addresses two alternative views about the coordination of prehension movements. Prehension could be controlled by two processing channels, one involved in transporting the hand towards the target, and the other in opening and closing the grip (Jeannerod 1984). Alternatively, prehension could be a holistic act which brings the fingers from their initial to the desired final positions, without the involvement of separate channels (Smeets and Brenner 1999). Previous authors have used perturbation paradigms to resolve this issue (Castiello et al. 1998; Paulignan et al. 1991a, b): If perturbations elicit distinctly different corrective responses in the grasp and the transport component of prehension, this would be strong evidence in favour of the two-channel view. If the corrections are similar, this could indicate that the two channels are functionally coupled (Paulignan et al. 1991a), or alternatively, that the control is holistic.

Unfortunately, however, the existing literature yielded a quite inconsistent pattern of findings. We have proposed two possible reasons for this discrepancy: The existence of different control principles for single- and double-perturbed trials, and the use of discrepant criteria to define the onset of grasp versus transport corrections in previous studies. In light of these considerations, the main purpose of the present work was to *combine* single- and double-perturbation trials in a given session, and to apply the *same* criteria when analysing the grasp and the transport component.

In accordance with previous work (Paulignan et al. 1991a), we observed that a perturbation of target position not only modified the transport trajectory, but also produced a distinct inflection in the grasp trajectory, while no similar cross-effects were readily visible following a perturbation of object size. However, our subsequent quantitative kinematic analyses revealed the existence of cross-effects in both directions. For example, grasp movement time was affected by position perturbations, and transport movement time by size perturbations. Our kinematic data further indicate that double-perturbation responses can not be thought of as simple linear combinations of two single-perturbation responses. For example, grasp movement time increases when target position is perturbed alone, but not when position and size are perturbed in combination.

This pattern of our findings is not compatible with the view that grasp and transport are controlled by two independent channels. Instead, it supports the existence of two mutually coupled channels or, alternatively, of a holistic command structure. A distinction between these two remaining hypotheses is not possible based on kinematic parameters - such as reaction time, peak velocity, movement time, and amplitude – since either hypothesis could be equipped with detailed features to accommodate various kinematic patterns.

Unlike the above mentioned parameters, correction time data could yield decisive experimental evidence to distinguish between the two remaining views. A holistic system should start responding to a change of target size and position with the *same* delay, since both perturbations affect the same control mechanism. This is particularly evident in the case of double perturbations, where the holistic system is responding to a single event. In contrast, a control system consisting of two cross-coupled channels could start corrections with the *same or different* delays in the two components. Thus, significant differences between grasp and transport correction times would clearly support the two-channel view, while the absence of such differences would be ambiguous with respect to the two hypotheses.

Our experimental data clearly indicate that correction times of the two components were different, both under single- and under double-perturbation conditions. Only for single perturbations with a large final target did we find comparable correction times. We therefore conclude, as the main outcome of the present work, that the prehension movements investigated in our study were probably not controlled in a holistic fashion, but rather by a two-channel system.

One potential confound that must be considered is that as the target size changes, the position of the edges of the target change, in effect changing the position of the target. Servos et al. (1998) have shown that participants reach toward the far edge of a target instead of to the center during grasping. Thus, it could be considered that the size perturbation is in effect a double perturbation (size and location of a far edge) while the transport perturbation is only a single perturbation (position) However, in spite of this, it should be noted that the perturbation of size resulted in only a 4 cm change in position, while the actual position change resulted in a 11 cm change.

Our finding, that grasp and transport correction times are different under double perturbation conditions, is in apparent conflict with a previous study (Castiello et al. 1998), which found no such difference. This discrepancy is likely related to the method by which correction times were quantified in the two studies: Unlike the present experiment, the previous study used different criteria to define the correction onset in the two components. It is important to note that since the starting and target discs were virtual objects, participants' fingers never made physical contact with them and, therefore, tactile feedback about task performance was absent. This fact distinguishes the present work from the previous studies which have examined perturbations of target size or distance, because in these studies, participants grasped reach physical objects (see however, Bock 1996). It is also possible that since natural objects cannot change size as easily as position, changes to position are dealt with by corrections to ongoing movement, while changes in size require the definition of a new goal, which would require more time. An additional point to consider that is unique to the present study is that the perturbations occurred 300 ms after the target appearance. However, the probability of perturbation was 25%, so it is assumed that participants were not anticipating the onset of the perturbation.

The issue still remains however, as to why our findings differ from those previously reported. In terms of the correction onset of the transport component, Paulignan et al. (1991a) find that wrist acceleration starts to change after about 100 ms, and wrist direction after about 255 to 295 ms. Castiello et al. (1998) find a dip in wrist velocity after 424 ms, and we find a divergence of wrist position from single-step traces after 280-330 ms. Our algorithm for correction time is similar to Paulignan et al.'s, and indeed yields similar values. Corrections could well be visible first in the acceleration profile, then in the path shape, and then produce a drop in wrist velocity. Considering this, the latency times across the studies follow a sensible pattern. As to the aperture component, Paulignan et al. (1991b) reports a trough in the aperture velocity after 330 ms. Castiello et al. (1998) show a similar trough in aperture position after 463 ms (naturally, this time is longer), and we find a divergence point in aperture position after 230-330 ms. The question remains what conclusions do these studies allow concerning differences in CT between reach and grasp? Paulignan et al. (1991a, b) and Castiello et al. (1998) use different criteria to determine grasp and aperture correction times; indeed, none of them offers a statistical analysis comparing correction onset in the two components.

Evidence in favor of a two-channel view has also been presented in other experimental approaches. Thus, it was observed that the kinematic coupling between grasp and transport component could be dissociated by presenting visual distractors (Gangitano et al. 1998), placing an obstruction in front of the object (Tresilian 1998), or manipulating the velocity of a moved object (Mason and Carnahan 1999). However, these findings don't necessarily imply the existence of two channels: It is equally conceivable that modifications to a holistic motor command are just more easily seen in one of the two components. Therefore, those approaches are ambiguous with respect to the single- versus two-channel dispute, as is the analysis of parameters like movement time in the present work. In contrast, our analysis of *correction onset times* - using the same metric on profiles of comparable shape, including those from double-perturbation trials – led us to an unambiguous conclusion, in favor of the existence of two cross-coupled channels.

CHAPTER 3: EXPERIMENT 2

The act of grasping and lifting small objects is comprised of two components: an on-line component based on somatosensory information, and an anticipatory component (Gordon et al. 1991a; Gordon et al. 1991c; Gordon et al. 1993; Johansson and Westling 1988a; 1988b). This anticipatory component can be also somatosensory in nature (Johansson and Westling 1988a; 1988b), but other modalities, such as vision (Gordon et al. 1993; Gordon et al. 1991a,) and tactile inputs about object size (Gordon et al. 1991b) can be used by the central nervous system to anticipate the fingertip forces necessary for a successful grasp. Despite the fact that the nature of the anticipatory mechanisms has been investigated, and a number of models have been proposed (Johansson and Cole 1992; Wolpert and Kawato 1997), it is still unclear how the relative contributions and importance of these sources of information evolves with practice.

Johansson and Cole's (1992) anticipatory, sensory event driven, feedforward model illustrates the importance of the integration of vision and haptics in grip force control. This model suggests that with enough practice the pre-contact information is sufficient to recruit an appropriate motor program to lift the object. More recently Wolpert and Kawato (1997) have proposed a similar model that also stresses the importance of anticipation through feedforward processes that are reinforced by inverse models if the movement produced is appropriate. For example, when lifting two objects of different sizes but similar mass, people judge the smaller object to be heavier than the bigger one. However, the bigger objects are lifted with higher grip forces (i.e., the size-weight illusion; Murray et al. 1999; Gordon et al. 1991a, b). One explanation for this increase in the grip force used to lift the bigger object is that participants assume that there are equal densities for the two objects. This pre-contact information about the object size led participants to anticipate that the bigger object was heavier (Gordon et al. 1993). However, Flanagan and Beltzner (2000) have demonstrated that this illusory effect is not as robust as originally thought. They showed that when participants lifted two objects of equal mass but different sizes, they learned to scale their forces to the true object mass, exhibiting accurate sensorimotor anticipation based on prior haptic experience and ignoring the visual cues that were present. Thus, the initially dominating (Festinger et al. 1967; Gibson 1933) and erroneous visual source of information was soon ignored and the correct haptic information about object mass became the dominant source of information used in the formation of the internal model of the object's mass. This suggests that the dominance of vision over other sensory information can be altered through learning. This in turn leads to the following questions: What is the nature of the representation or the internal model formed during lifting practice? That is, is this memorial representation primarily visual or haptic? Does the formation of the internal model depend on the sensory inputs available during practice? With practice, does the role of one source of sensory input become more dominant?

The development of the dominance of one source of sensory input over another has been previously addressed by learning specificity theory (Proteau et al. 1992; Proteau et al. 1994). The theory states that early in the practice of a motor task one is able to determine the source(s) of afferent information most likely to ensure optimal performance and that this source of information is processed to the detriment of all other sources of information. Thus, if that dominant source of information is suddenly withdrawn after its dominance has been established, one is left without an appropriate reference for movement control and performance sharply decreases.

In summary, the most prevalent model of grasp control proposed by Johansson and Cole (1992; Johansson and Cole 1994) stresses the importance of anticipatory control of the fingertip forces exerted on the object. This pre-contact anticipation of the required forces is developed through previous interactions with similar objects, where pre-contact visual information about the object is integrated with the post-contact haptic signals. Festinger et al. (1967) and Gibson (1933) have suggested that when vision is present it will be the dominant source of information used to perform the task. This view has been challenged by Flanagan and Beltzner (2000) who showed that, in the control of fingertip forces, the visually based size-weight illusion can be diminished through practice, suggesting that erroneous visual information can be dominated by the haptic signals. This finding can be taken as indirect support for the learning specificity hypothesis suggested by Proteau et al. (1992).

The first objective of the present study was to investigate whether practice under different visual conditions can influence the sources of information used to form an internal representation of an object (i.e., whether the pre-contact visual information is always necessary and dominant in the anticipatory control of grip forces). To achieve this goal we investigated the response of the sensorimotor system to perturbations of object mass when the perturbations are delivered with the same or different sources of sensory input than the ones available during practice. The second goal was to investigate whether the coupling between visual and haptic information that is developed during practice is dependent on the order of mass presentation. It was suggested by Johansson

(1996) that if objects are visually indistinguishable and presented in an unpredictable order, the grip forces necessary to pick up the objects are scaled on-line as the movement unfolds based on the sensory signals from the fingertips. However, when the objects are presented in a predictable fashion, object mass can be anticipated after the first few trials (Gordon et al. 1993), meaning that the schedule of object presentation during practice can influence the formation of the anticipatory model. The third goal of this study was to investigate the effect of practice on the coordination of load and grip force. Flanagan and Wing (1997) have shown that in a task where participants were required to move a hand held object up and down, the grip force is scaled in parallel to the load force. However, Johansson (1996) showed that the uncoupling of these forces is also possible in response to changing frictional characteristics between the digits and the object's surface. It is not clear how the practice conditions in the present study will influence this coordination.

In the present study participants lifted small objects with different masses under three visual conditions. One group practiced lifting with no visual cues providing pre-contact information regarding object mass. A second group practiced lifting the same objects, however visual cues about the object mass were introduced for this group; each object mass was coded by a different color (pre-contact visual cues available). Following the practice phase both groups performed a transfer test where an object of one mass was lifted for a number of trials (control object) and on some trials a perturbation object was introduced (pre-contact visual cues not available). There was also a control group of participants that practiced with the visual cues, and the perturbations in the transfer phase were also color-coded. Finally, to assess the influence of practice schedule (blocked versus random) on the formation of the internal object model there were two additional groups. These groups of participants performed the same practice and transfer conditions as the previous groups, however the masses in the practice phase were lifted in a random order.

It was hypothesized that if with practice one source of sensory information can dominate over another (haptics or vision), performance on the practice and transfer tasks will be dependent on the type of visual cues available. Specifically, the presence of color cues in the practice and transfer phases will enhance participants' grip force to mass scaling during practice, and the scaling during transfer. With the removal of color cues in the transfer phase, the retention will suffer, evidenced by the lack of grip force to mass scaling. Based on the findings of Johansson (1996) it is expected that blocking trials by mass in the practice phase will result in more scaling of forces to the object mass, compared to the random presentation during practice because the sensory cues can be predicted. Also, during transfer, the trial following the perturbation will be influenced by the previously perturbed trial for those participants that practiced with blocked schedules.

Method

Participants

Participants were 40 right handed undergraduate students (26 women, 14 men; mean age 20.6 years) with self-reported normal or corrected to normal vision. Participants provided informed consent in accordance with the guidelines established by the University of Waterloo Office of Research Ethics, and received credit towards their grade in an introductory psychomotor behavior course in exchange for their service.

Apparatus

A small, empty container unit was attached to a cylindrical force transducer (Nano F/T transducer; ATI Industrial Automation, Gerner, N.C., USA). The contact surface between the transducer and the digits was made of polyethylene plastic endings attached to the sides of the transducer. The overall width of the transducer and plastic endings was 6.5 cm, with a circular grasping surface with a 2.5 cm diameter. The attached container unit, plastic cups and the transducer were black and had no overt distinguishing features. By changing the mass inserted into the container unit, three target objects were created with total masses of 200, 300, and 400 g (transducer, container unit and additional mass). Refer to Figure 6 for a schematic of the apparatus.

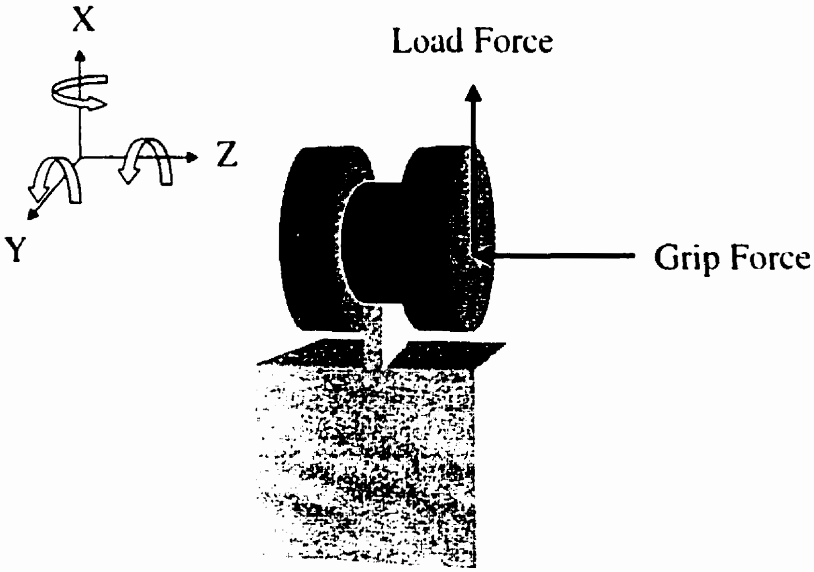


Figure 6. This figure shows the transducer and cylindrical grasping surfaces. The total mass of the object was altered by adding various masses to the containment unit below the transducer.

Procedure

Participants were asked to lift the target object with their index finger and thumb. The movement started with participants' fingers in a pinch position resting 10 cm away from the target object. Participants were asked to reach and lift the target object in a smooth natural motion. The object was lifted 10 cm above the table surface, held steady for 2 seconds and placed back on the table, after which the participants were asked to return their hand to the starting position. After every trial, the target object was removed from the participants' field of view and a different mass was inserted into the container unit and the object was placed in front of the participants for a subsequent trial.

The experimental protocol consisted of two phases separated from each other by a five minute break. In the practice phase the participants lifted each of the three masses for 30 trials (6 blocks of 15 trials) under various coding and exposure schedule conditions. First, participants were randomly assigned to one of the five experimental groups (8 participants per group) that differed from each other in the mass-color coding and practice schedule. The No Coding Blocked group practiced lifting all trials of each object mass in a consecutive block whereas the No Coding Random group practiced lifting the objects presented in a pseudo-random order. The Practice Coding Blocked group practiced lifting all trials of each mass in a single block. However, the various masses differed in their appearance. The 200 g objects were color-coded by placing a 1 cm by 1 cm square of red masking tape on the transducer, the 300 g objects were black (with no colour square), and the 400 g object was color-coded by placing a 1 cm by 1 cm green tape on the transducer. The Practice Coding Random group practiced lifting the mass-coded objects presented in the same pseudo-random order as the No Coding groups.

Lastly, the All Coding group practiced in a condition similar in all points to that of the Practice Coding Blocked group.

Following acquisition, all participants took part in a transfer test in which they were asked to lift the same objects as in acquisition for an additional 20 trials. On 80% of the transfer trials the object used was the mid-mass object (300 g). However, on 20 % of the trials (trials 8 and 16) a perturbation was introduced, where the object mass was either 200 g or 400 g respectively. The perturbations were assumed to be unexpected by the participants. For the No Coding Blocked, Practice Coding Blocked, No Coding Random, and the Practice Coding Random groups, the different masses did not differ in their appearance (all were black colored), whereas for the All Coding group, the color codes used in acquisition were still present. Refer to Figure 7 for a schematic of the various experimental conditions.

Data Collection

When the object was lifted, the grip force was measured along the grip axis defined by the line joining the centers of the object's two grasping surfaces. The forces were collected at 200 Hz with a resolution of 0.025 N. The load force was defined as the vector sum of the two perpendicular forces acting in the orthogonal plane to the grip force axis. Torques (resolution of 0.05 N.mm) applied in all three orthogonal axes to the transducer were also measured and a resultant of these three torques was calculated and used as a summary representative torque value. Refer to Figure 6.

Raw force and torque data were filtered using a second order dual pass Butterworth filter with low pass cutoff frequency of 10 Hz. Thus, the dependent variables of interest were peak load and grip force, and peak resultant torque. In addition, the rates of load and grip force production were examined.

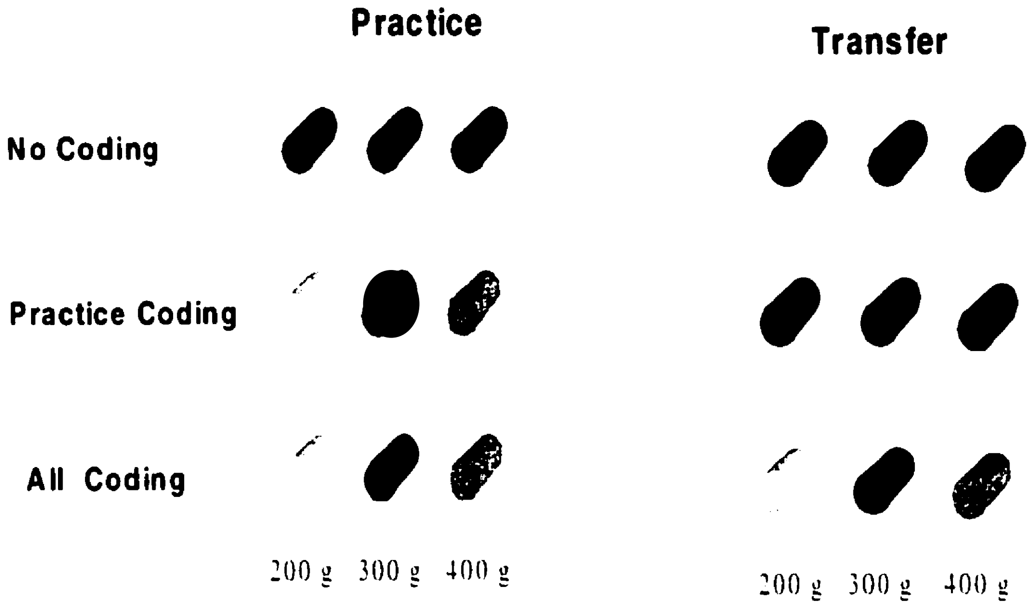


Figure 7. Schematic representation of the trial presentation in the practice and transfer phases. In the practice phase each schematic of the object represents a particular mass and color cue combination. Note that for the random groups the objects were color coded in the same way as for the corresponding blocked groups, however the order of presentation of the objects was randomized. In the transfer phase, there were lifts of two perturbed (200 and 400 g) objects, as well as the control (300 g) objects. Note that the control object in the transfer phase was coded in the same way (black) for all groups, such that it indicated the 300 g color cue (for the groups that practiced with color cues).

Statistical Analysis

The main objective of this study was to determine how the scaling of finger forces to object mass was influenced by the type of sensory cues available during practice. Of interest was the amount of scaling of load and grip forces to the true object mass. To address this, slopes of the line of best fit between dependent measures of interest (peak load and grip force and peak torque) and object mass (200, 300, 400 g) were calculated and entered into separate two way mixed analyses of variance (ANOVAs) (5 Group: No Coding Blocked, No Coding Random, Practice Coding Blocked, Practice Coding Random, All Coding x 2 Phases: practice, transfer). Effects significant at $p< .05$ were further analyzed using the Newman Keuls post hoc method for comparison of means. The peak force rates were not statistically analyzed because a single peak could not be identified, but these curves are presented and described. It was assumed that higher slopes values would indicate a higher degree of scaling of the dependent measure of interest with object mass.

Results

Peak Load Force

When the slopes of the regression lines between the peak load force and object mass were analyzed, there was a significant interaction between group and phase ($F(4,35)=2.79$, $p<0.05$). Means for all significant effects are plotted in Figure 9 and a summary of all mean values used to calculate these slopes is seen in Figure 8.

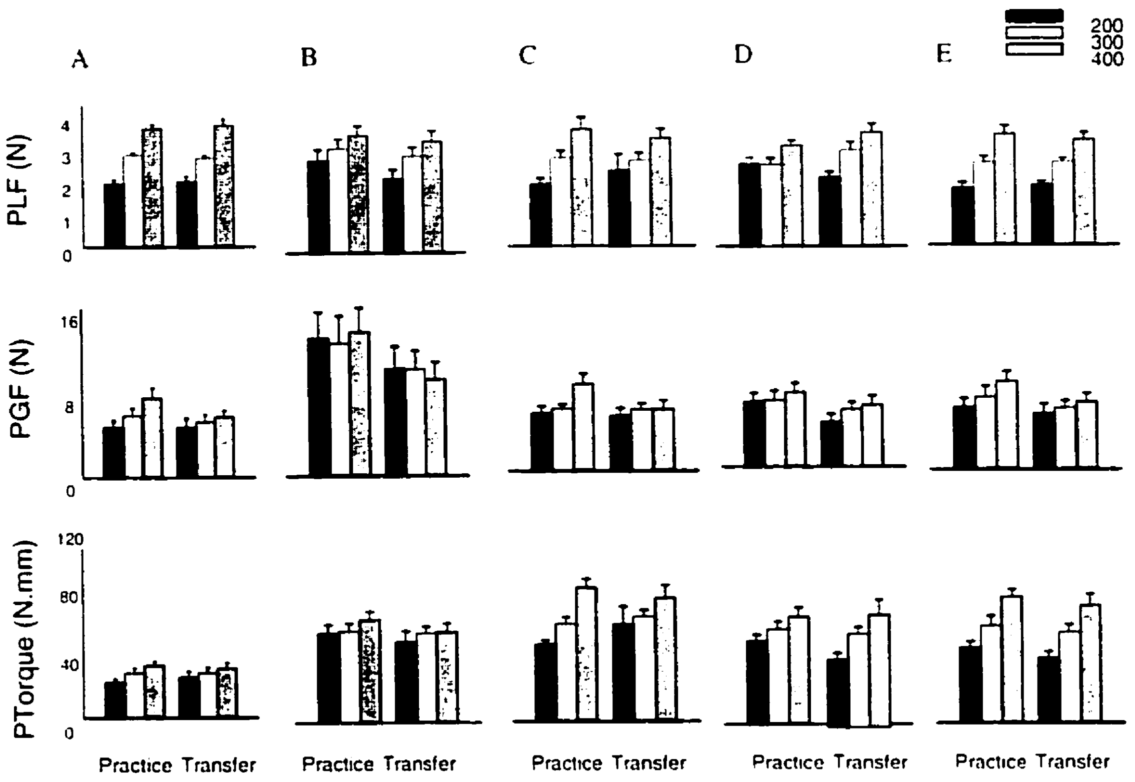


Figure 8. This figure presents mean data for the five groups in Experiment 2. Data for the two phases (practice and transfer) and three object masses (200 g, 300 g, 400 g) are presented. (A = No Coding Blocked, B = No Coding Random, C = Practice Coding Blocked, D = Practice Coding Random, E = All Coding).

Practice. The post hoc analysis revealed that in the practice phase the groups that practiced lifting in a blocked order (No Coding Blocked, Practice Coding Blocked, All Coding) did not differ from each other and had significantly higher slopes than the groups that practiced with random presentations (No Coding Random, Practice Coding Random)

(Figure 9A). The higher slopes for the blocked groups indicates more scaling of load force to the object masses.

Comparisons across Figures 10, 12 and 14 reveal that for the No Coding Blocked, Practice Coding Blocked, and All Coding groups, the load forces increased as object mass increased. Furthermore, as represented in the rates of load force production, there was a single muscular impulse that was also scaled to the object mass. On the contrary, as apparent from Figures 11 and 13, the No Coding Random and Practice Coding Random groups showed less load force to object mass scaling. The multiple peaks of the load force rate curves suggest that the peak load forces were achieved through multiple muscular impulses.

Transfer. In the transfer phase the No Coding Blocked, Practice Coding Random and the All Coding groups had significantly higher slopes than the Practice Coding Blocked and No Coding Random groups, which did not differ from each other (Figure 9A). The higher slopes indicate that participants modified their load force production in response to the perturbed trials (200 g and 400 g). The lower slopes indicate that the load force was modified to a much lesser degree in response to the perturbed trials.

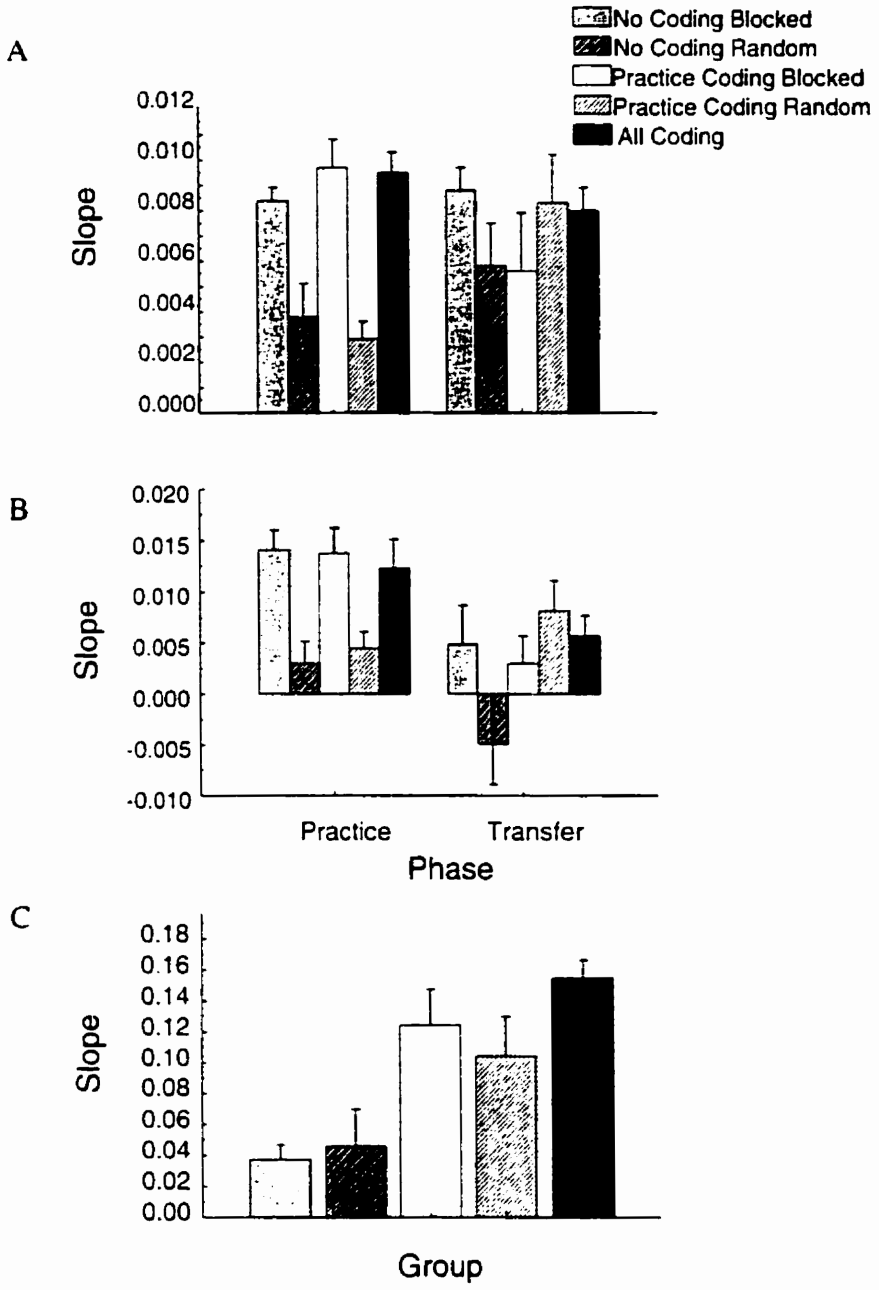
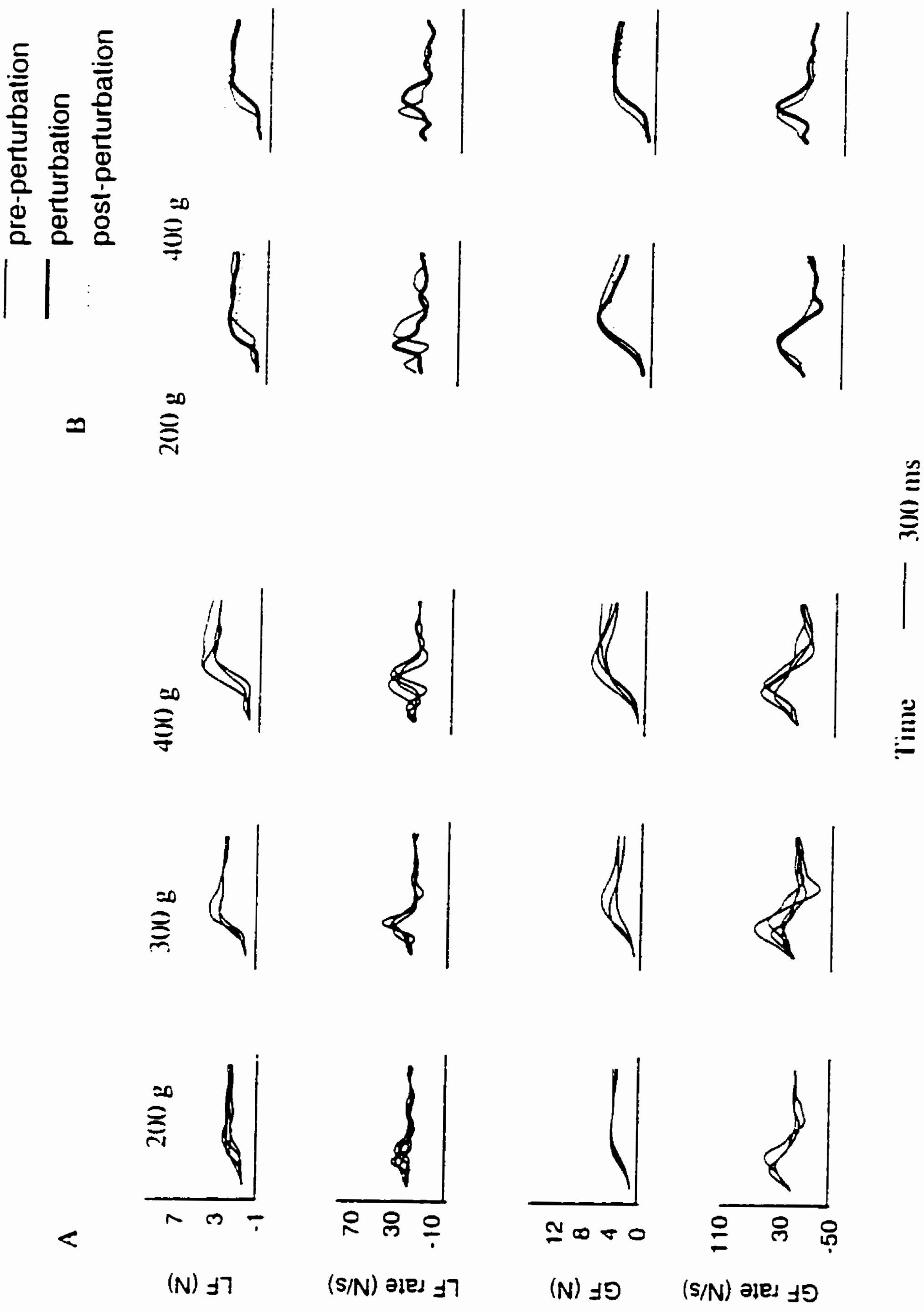


Figure 8. Results of the analysis of the slopes of the regression lines for the scaling of A) load force, B) grip force, and C) torque to object mass for the 5 experimental groups. Panels A and B show significant interactions of group and phase, while panel C shows the significant main effect of group.

Figure 10. Load force (LF), load force rate (LF rate), grip force (GF) and grip force rate (GF rate) profiles for a single participant in the No Coding Blocked group during practice (A) and transfer (B) phases. *Practice.* The participant was able to scale the load and grip forces to object mass. As evidenced by a single peak in the rate of force generation, these peak forces were achieved with a single muscular impulse that was also scaled to the objects mass. *Transfer.* When the 200 g and 400 g perturbation objects were encountered, the load force generation was appropriately scaled to the true object mass, and the grip force generation profiles did not differ substantially from the control trials. These forces were also achieved with single peaked force rate profiles. On the trial following the perturbation (post-perturbed trials), the load and grip force profiles as well as their associated rates showed the influence of the previous perturbation trial. That is, when a 300 g object followed the 200 g perturbation, load and grip forces were lower and their rates were delayed compared to lifts of the control objects. Conversely, when the 300 g object followed a lift of the 400 g perturbation, the peak load and grip forces were higher and their rates were achieved sooner compared to lifts of the control objects.


A
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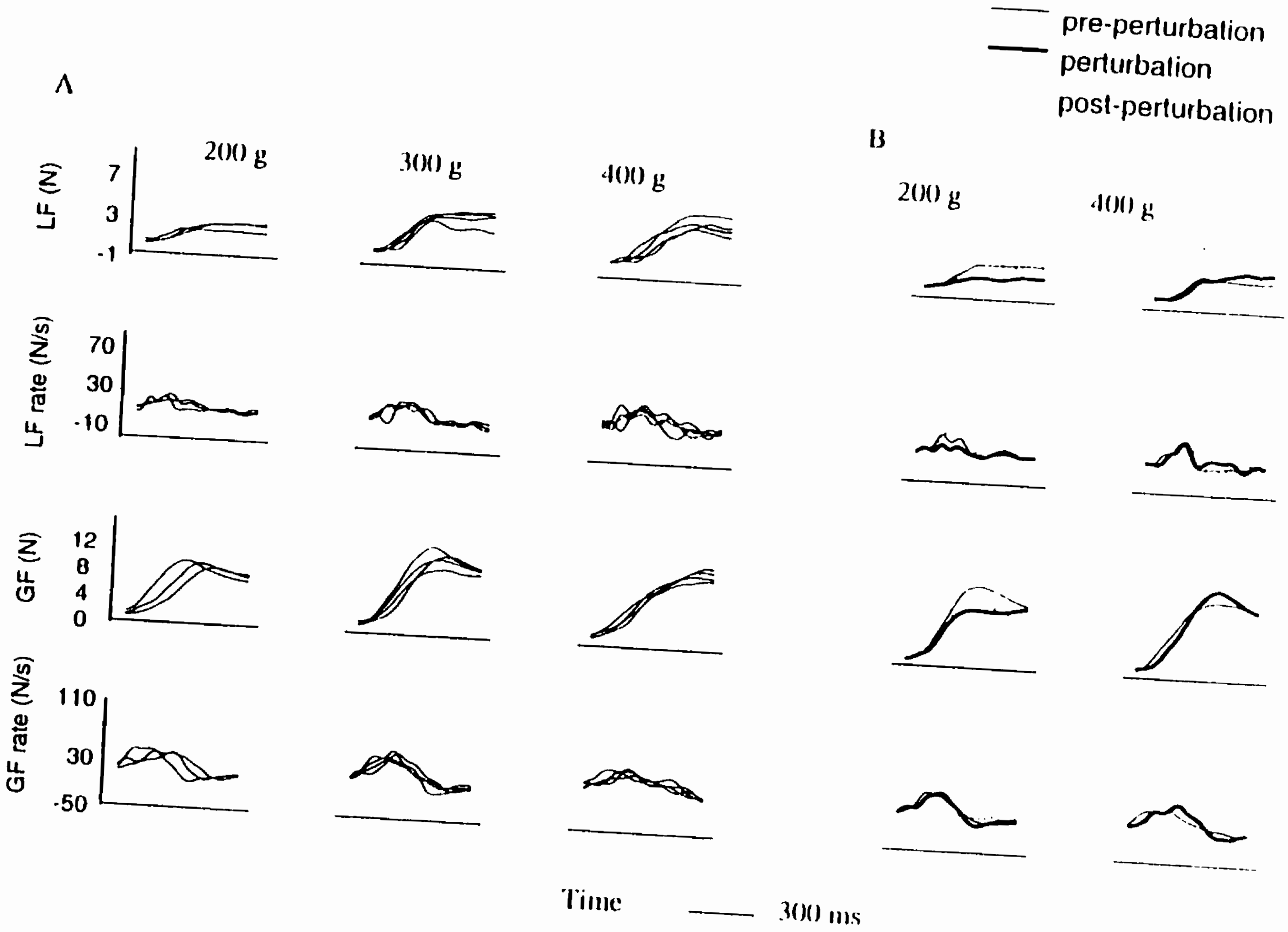
200 g
300 g
400 g
200 g
400 g
pre-perturbation
perturbation
post-perturbation
Time
300 ms

Figure 11. *Practice.* For the No Coding Random group, only the load and not the grip forces were scaled to object mass. As evidenced by the multiple peak curves for load and grip force rate, these peak forces were achieved by multiple muscular impulses. *Transfer.* When the 200 g and 400 g perturbations were encountered, load force generation was appropriately scaled to object mass. On the contrary, the initial grip force generation profiles did not differ from that observed for the control trials. For the post-perturbation trials, the load force was scaled to the object mass. On the contrary, the grip force generation profiles on these trials did not show the effect of the previous trial. Instead, the grip forces were similar to the perturbed trials and they were not scaled to the object mass.


pre-perturbation
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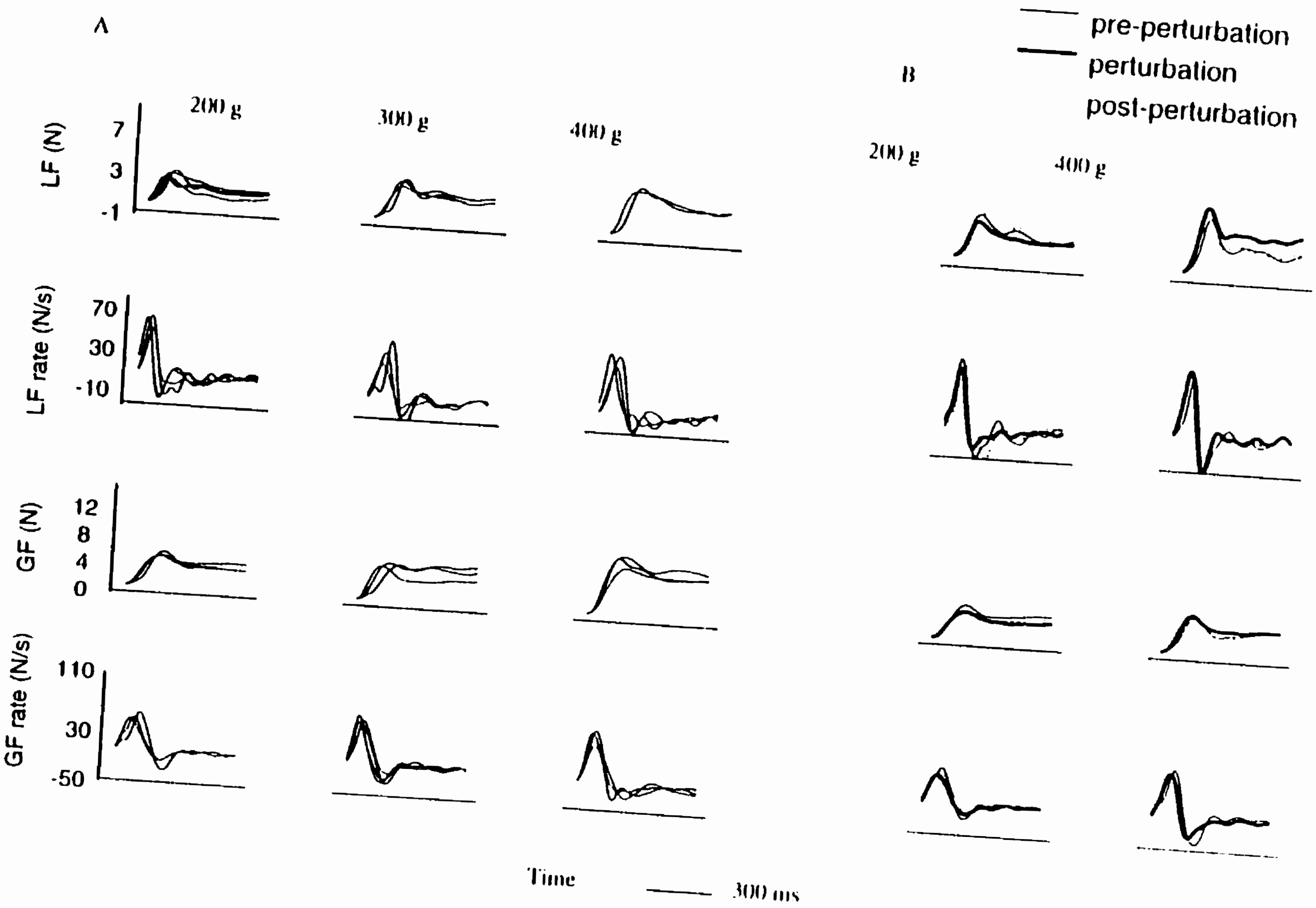
GF rate (N/s)
110
30
-50
B
200 g
400 g
Time
300 ms

Figure 12. *Practice*. The participant trained in the Practice Coding Blocked group was able to scale the load and grip forces produced when lifting the object. As evidenced in the single peaked curves showing the rates of load and grip force, they were achieved through a single muscular impulse also scaled to the objects mass. *Transfer.* When the 200 g and 400 g perturbations were encountered, load force and its rate, but not the grip force and its associated rate were scaled to the object mass. On the post-perturbation trials, the load and grip forces and their rates of production did not differ from the control trials.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GF rate (N/s)
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Time
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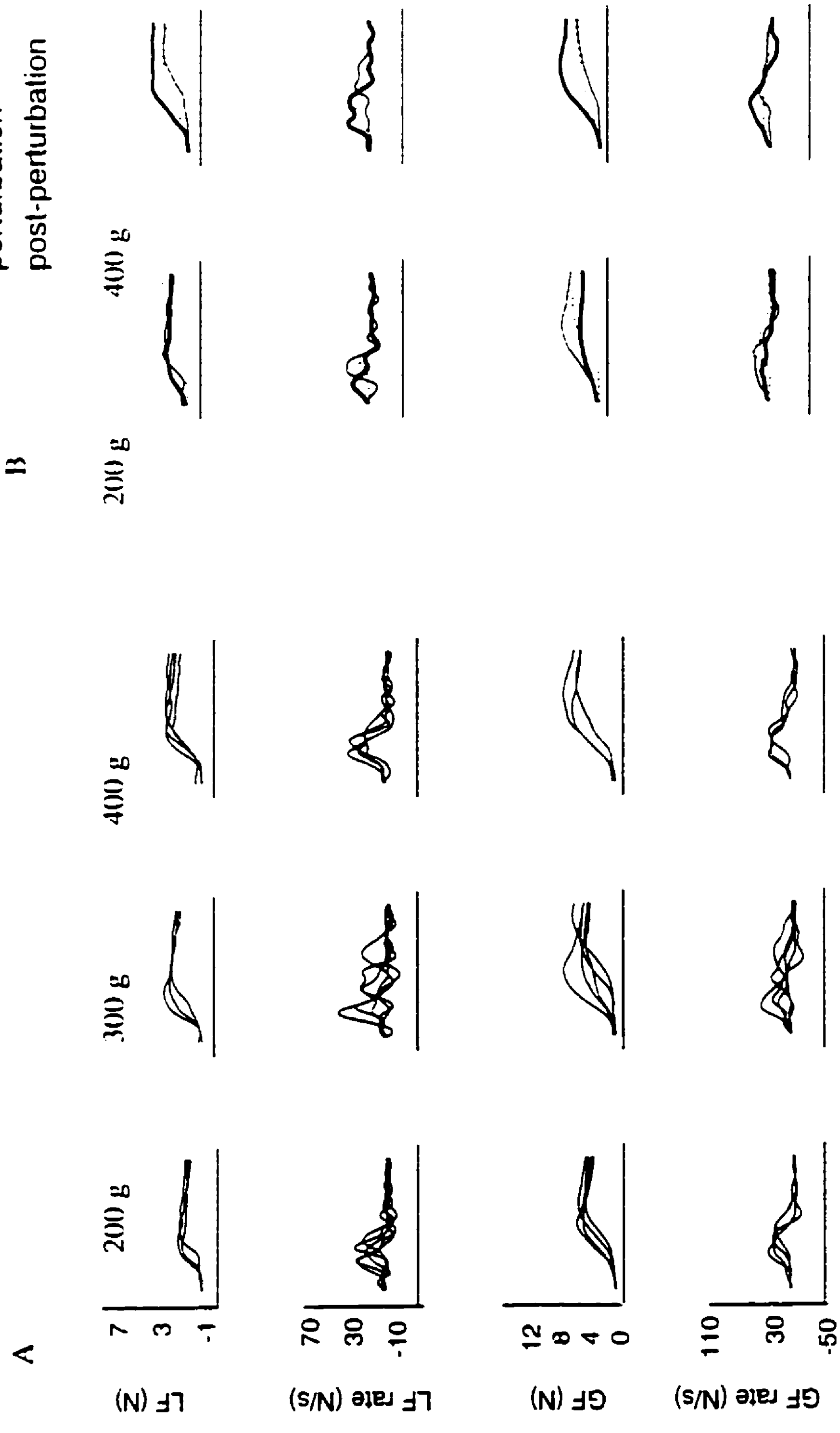
Figure 13. *Practice*. The participant in the Practice Coding Random group showed that the load and not the grip forces were scaled to object mass. As evidenced by the multiple peaked curves for load and grip rate, these peak forces were achieved through multiple muscular impulses. *Transfer*. When the 200 g and 400 g perturbations were encountered, the load and grip force profiles differed from the control trials and were achieved through multiple peaked rates. On the post-perturbation trials, load and grip force were not influenced by the perturbation.

A
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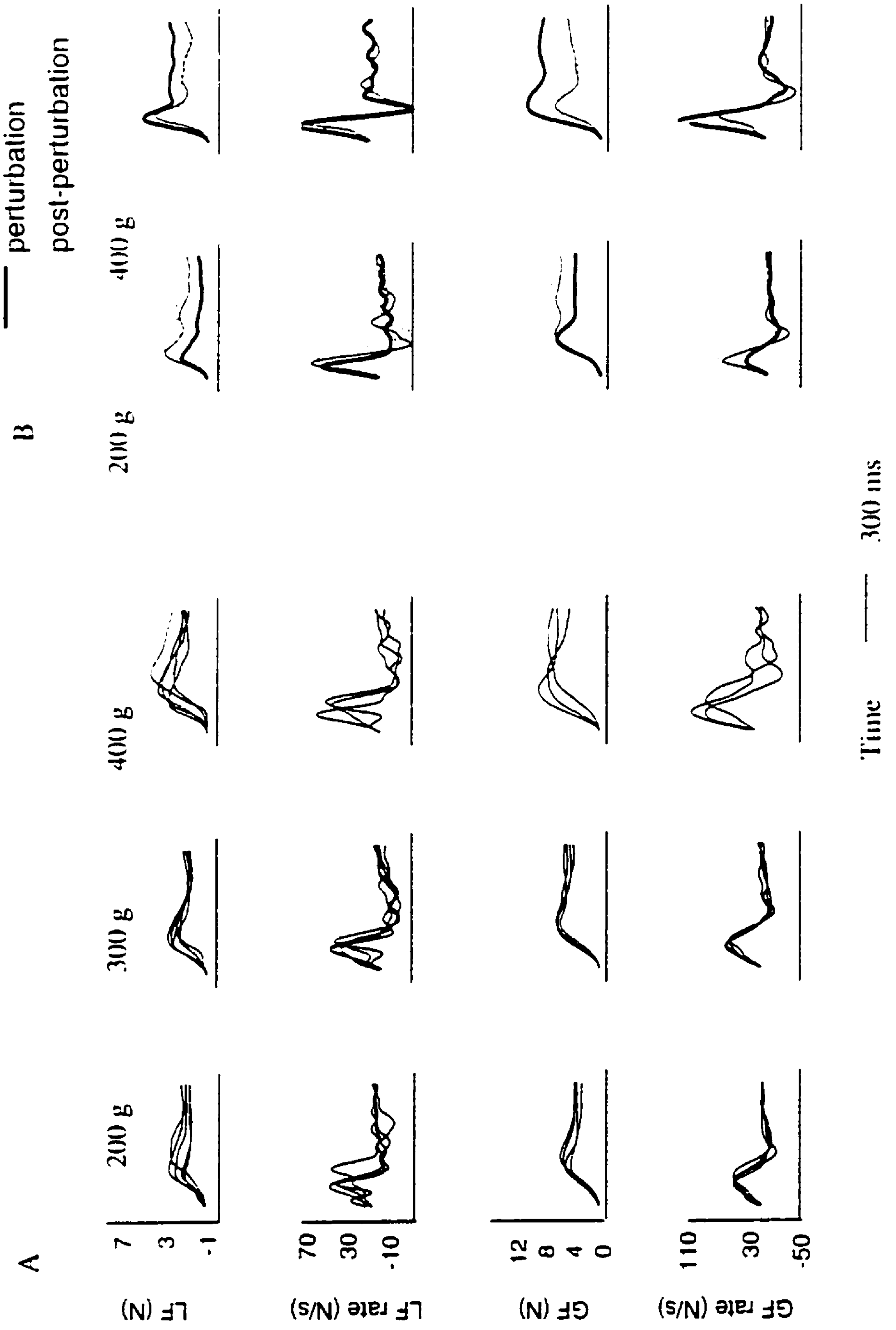
pre-perturbation
perturbation
post-perturbation

Figure 14. *Practice.* Load and grip forces and the associated rates for the participant from the All Coding group were scaled to object mass. As evidenced by the single peaked curves for load and grip rate, these peak forces were achieved through single muscular impulses. Transfer. When the 200 g and 400 g perturbations were encountered, the load and grip force profiles as well as their rates were scaled to object mass. On the post-perturbation trials, the load and grip force profiles showed the effect of color coding, where the load and grip peak forces were not the same as for the control trials, but were similar to the forces produced when lifting the 200 g and 400 g objects during practice.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200 g
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400 g
200 g
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Time
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pre-perturbation
perturbation
post-perturbation

From the comparison of Figures 10, 13, and 14, it is apparent that in the transfer phase, although the scaling of load force to object mass was similar for the No Coding Blocked, Practice Coding Random and the All Coding groups, the load forces were achieved in a different fashion. For the No Coding Blocked (Figure 10), and the All Coding (Figure 14) groups, when the practice was blocked, the peak load force was achieved with a single peaked rate (indicating a singular muscular impulse). On the contrary the Practice Coding Random group (Figure 13) showed similar load force to object mass scaling, however this was achieved with multiple muscular impulses. This was also true for the No Coding Random group (Figure 11), however the participants in this group showed significantly less scaling. Lastly, the Practice Coding Blocked group (Figure 12) showed single peaked rates of load force production, that were less scaled to the object mass in comparison to the other groups.

Peak Grip Force

There was a significant interaction between experimental group and phase (F(4, 35)=2.85, $p<0.05$) in the analysis of the slopes of the regression lines between the peak grip force and object mass.

Practice. The post hoc analysis revealed that the groups that practiced in a blocked order did not differ from each other and had significantly higher slopes than the groups that practiced randomly, again indicating that there was greater scaling for object mass for the blocked trained groups. Refer to Figure 9B.

Similar to the patterns observed for the analysis of the load force profiles, the comparison across Figures 10, 12 and 14 reveals that for the No Coding Blocked, Practice Coding Blocked, and All Coding groups, grip forces increased as object mass increased. It can also be seen from the grip rate curves that these peak forces were achieved with a single muscular impulse. On the contrary, as seen in Figures 11 and 13, the No Coding Random and Practice Coding Random groups showed little grip force to object mass scaling. As evidenced by the multiple peaked grip force rate curves, the peak forces were achieved by multiple muscular impulses. The grip force employed by the No Coding Random group was much higher then the grip forces used by the other groups, suggesting this group used a much higher safety margin.

Transfer. In the transfer phase the No Coding Blocked, Practice Coding Random and All Coding groups had significantly higher slopes than the Practice Coding Blocked group, indicating greater scaling to the perturbed object masses. The No Coding Random group was significantly different than all other groups as participants in this group produced a negative slope between the grip force and the object mass indicating an inappropriate scaling of grip force in response to the perturbations (Figure 9B).

Inspection of Figures 10, 13, and 14 reveals similarities between the grip force scaling for several groups. That is, the No Coding Blocked, Practice Coding Random and All Coding groups demonstrated similar grip force to object mass scaling, but this was achieved by different strategies. Groups that practiced with a blocked trial order showed single peaks in the rate of grip production, however the Practice Coding Random group showed multiple peaks consistent with a probing strategy as suggested by Goldberg et al. (1991). The Practice Coding Blocked group showed single peaked rates of grip force generation, that were less scaled to the object mass, than the previous groups. The observation of multiple peaks in the grip force rate curves was also true for the No Coding Random group, however this group showed a reverse pattern indicated by the negative slopes between grip force and object mass.

Peak Torque

As suggested by Kinoshita et al. (1997) a significant rotational torque present when lifting an object can influence the grip force production in a fashion similar to that seen with increases in object mass. Thus, in order to investigate the effect of torque created when lifting the objects on the load and grip force production, we subjected this measure to the same type of ANOVA as the load and grip forces data. The results showed a significant main effect of group (F(4, 35)= 7.27, p<0.001), indicating that the Practice Coding Blocked and All Coding groups did not differ significantly from each other, and had higher slopes than the No Coding Blocked and No Coding Random groups, which did not differ. The Practice Coding Random group did not differ from any of the other groups (Figure 9C). There was no statistically significant main effect or interaction of phase, p > .05.

Discussion

To investigate the relative contributions of visual and haptic information in the development of an anticipatory model of object properties, and whether learning specificity theory (Proteau et al.1992) applies to this process, five groups of participants practiced lifting small objects under different visual conditions. There were two major manipulations in this study; color-mass coding and the scheduling of practice trials. To assess the effects of these manipulations on learning, a transfer phase was introduced where the participants lifted a mid-mass object for 20 trials, during which there were two unexpected mass perturbations. Results of this study will be discussed in three parts. The effects of color-mass coding and practice schedule on the initial grip force production will first be discussed. Then the effects of practice on load and grip force coupling will be evaluated. Finally, there will be a discussion of the effects of torque on grip force.

Effects of visual cues and practice schedules on force production.

The findings of the present study support the learning specificity hypothesis and show that the use of the sensory inputs necessary for the anticipatory preparation of grip forces depends on their availability during practice. When color cues regarding object mass are present, this information is used to develop an anticipatory model of object mass. That is, the All Coding group (the control group) showed scaling of grip force to object mass in both the practice and transfer phases. The grip forces were achieved with single peaked rates, indicating a precise, pre-programmed burst of muscle activity that was scaled to the anticipated object mass. The Practice Coding Blocked group showed a similar scaling of grip force to mass in the practice phase, but this scaling was absent during the transfer phase. They also produced pre-programmed force impulses (evidenced by single-peaked force rate curves). The performance of this group was altered when the visual cues they learned to rely on during practice were removed during transfer.

As seen in the grip force generation profiles for the No Coding Blocked group (Figure 10), although there was no visual coding during practice, there was still scaling. These data are consistent with Westling and Johansson's (1984) findings regarding the anticipation of object mass based on the initial lifts in a block of trials, when the color cues were not present and the trials were blocked (No Coding Blocked) the participants were able to develop an internal model based on the initial trials in the block. During transfer there was little scaling in response to the perturbed trials. The trials following the 200 g and 400 g perturbations were undershot and overshot respectively. Since the participants practiced lifting the masses in blocks, they anticipated a block of 200 g or 400 g objects following the perturbation. On the contrary, when the masses were randomized during the practice phase and no coding was available (No Coding Random), the participants did not demonstrate the same grip force-mass scaling in either the practice or transfer phases. Also, the forces employed were significantly greater then the ones employed by the participants when the practice phase was blocked (Figure 9). This increase in the grip force magnitude was probably caused by increased safety margins due to the inherent uncertainty in this task and in order to accommodate all the masses presented. As seen in Figure 11, the peak grip force was achieved with multiple peaks in the force generation rate curves. Based on Johansson and Westling's (1988) work this could be interpreted as an indication of a probing strategy, where the participants gradually increase their grip force in a step-like fashion probing for the next largest grip force in order to prevent the slippage of the object. Since the increased safety margins and probing are redundant safety mechanisms, it is not clear why both strategies were used simultaneously. When the visual cues were present in the practice phase, and the various masses were presented randomly (Practice Coding Random) the participants showed no scaling of object mass to grip force, indicating an inability to develop an appropriate internal model of the object characteristics based on the visual cues. This was further supported by the multiple peaked grip force rate profiles indicating a probing strategy (Figure 14). Surprisingly the participants in Practice Coding Random group were able to scale the grip force to the object mass in the transfer phase. It is possible that the superiority of random over blocked practice as revealed on a transfer test, termed contextual interference, is playing a role in these findings (Shea and Morgan 1979). In several tasks, involving the timing of actions (Lee and Magill 1983; Proteau et al. 1994), perceptual anticipation (Del Rey 1989) and the regulation of force (Shea and Kohl 1991) it has been shown that during practice, the participants performance on the specific task is better in a blocked schedule and worse in a random schedule. However, long term retention of a skill as evidenced by performance on a transfer test is superior for a random trained group. In the present study, the random practice experienced by the Practice Coding Random group probably required a more challenging process of integrating visual and haptic cues (see Lee and Magill 1985; Shea and Zimny 1983). This resulted in this group learning how to use haptic information such that when visual cues were removed they could still scale their forces to object mass. An alternative explanation is that the superiority of vision was not yet established for the Practice Coding Random group, thus participants in this group processed and relied heavily on both vision and haptics during practice. In the transfer, withdrawing visual cues was not detrimental to the performance because haptic information was still present, and they had practiced using it (Proteau and Carnahan, in press). It would be interesting to see if this effect could be replicated after extensive practice.

It is proposed that both the development and the subsequent access to the internal model of object characteristics based on pre-contact sensory information is governed by a weighting function. That is, during practice with multiple sources of sensory information, the most reliable and accessible source will be assigned the highest weighting value. After initial practice, when the relationship between the array of available pre-contact and the post-contact sensory information is formed, the same function will be used to retrieve the internal representation of the object for the preparation of grip forces. If, after the initial practice phase, an additional source of sensory information is introduced it will be ignored, or will be detrimental to motor performance.

Coordination of load and grip forces.

Another issue that can be addressed by the findings of this study is the coordination of load and grip forces. It has been shown previously that in order to minimize the degrees of freedom in the control of stable grasp the grip force is scaled in parallel to the load force, which in turn is scaled to the object's characteristics such as its weight (Flanagan and Wing 1997). However, the uncoupling of these forces is also possible. In the present study it was shown that the practice condition affects the scaling of load force generation to a greater extent than grip force generation (based on the analysis of the slopes). The model of force coordination proposed by Flanagan and Wing (1997) was based on studies where the participants were required to move a hand held object up and down. The changes in the object's weight due to the hand movement resulted in a tighter coupling of the load and grip forces. The perturbation in the object weight was created by the participants themselves as the object was moved up and down. Such a modulation is clearly based on an anticipatory mechanism. However, in the present study the mass perturbation was externally generated and not easily predicted for the groups that did not have access to visual cues. Thus, for some participants there was less reliance on purely anticipatory mechanisms, and more reliance on on-line control. This factor may have been related to the lack of grip and load force coordination observed.

Contributions of Torque.

Kinoshita et al. (1997) recently proposed that grip force is affected by both the load created by the mass of the object, and also by the rotational forces created when the object is grasped away from its axis of rotation (torque). This effect was significant in the range between 10 to 100 N.mm of torque, which was also the range experienced by the participants in the present study. Thus, it is possible that the grip force patterns observed were influenced by the peak torque. However, the patterns of results for the load and grip forces is clearly different than the pattern of results for peak torque based on the observation that the group by phase interaction was significant for the load and grip forces, but only a main effect for group was present in the analysis of torques. This suggests that the torque created when lifting the object did not affect the forces significantly in a consistent pattern. As evidenced in the increased torque values in the three groups that were allowed to practice with visual cues (Figure 9C), when the representation of the object mass is formed based on the visual inputs and is accessed through these same cues, the placement of the fingers on the object is not as precise as in the conditions where object properties must be established based on the haptic inputs only.

Summary.

It was demonstrated that learning specificity theory (Proteau 1992) can be applied to grasp control. Flanagan and Beltzner's (2000) notion about the influence of practice on the shift of the dominance of vision over haptics was also supported. The findings of the present study are consistent with Johansson and Cole's (1992) anticipatory grip control model as well as the newly proposed model by Wolpert and Kawato (1997; Wolpert and Ghahramani 2000), where preprogramming of grip forces is based on previous interactions with similar objects. This model could be expanded however, such that the access to the memorial representation of object characteristics is modality specific and does not rely solely on visual cues.

CHAPTER 4: EXPERIMENT 3

People are very good at catching and intercepting moving targets, but the mechanisms behind this process are not clearly understood. One well supported model of motor control proposes that the control of prehension is comprised of two phases, the reach or transport phase, and the grasp phase (Jeannerod 1981; 1984). It has been hypothesized that there exists a visuomotor channel that is specialized for programming the grasp component of prehension and that the channeling of visual input for the control of grasping is related to intrinsic object characteristics such as the size or shape of the object (Arbib 1981; Jeannerod 1984; Wing and Fraser 1982). Extrinsic object characteristics such as target distance or orientation are proposed to not influence grasping, but instead influence the reach or transport phase of prehension. Mason and Carnahan (1999) have outlined that it is difficult to categorize target motion as either an intrinsic or extrinsic object characteristic. That is, the velocity of a target dictates its position at any point in time along its trajectory (an extrinsic property). But, the velocity of a target also dictates its apparent mass upon impact with the hand (an intrinsic property). Based on the increased apparent mass associated with target velocity Mason and Carnahan predicted that when intercepting a moving target, greater finger forces would be required to grasp faster moving targets (see Johansson and Westling 1984).

It has been shown that the characteristics of target motion have a strong influence on the kinematics of the interception movement. For example, as the velocity of the target increases, so does the velocity of the transport of the manual interception movement (Smeets and Brenner 1995; van Donkelaar et al. 1992). It has also been shown that target velocity influences the size of maximum finger aperture and the velocity of aperture formation (Carnahan and McFadyen 1996; Salvesbergh et al. 1992; Wing et al. 1986). The suggestion has been proposed that hand aperture size could influence grip force such that the hand opens wider when greater grip forces are necessary (Smith et al. 1983). Thus it follows that the increased aperture velocities and sizes seen when intercepting moving targets may translate into increased grip forces. This conclusion is consistent with the hypothesis made by Mason and Carnahan (1999) that finger force should increase as target velocity increases.

There are however various patterns of finger forces that could be expected when capturing moving target objects. One could assume that there is only one solution to the challenge of capturing a moving object. That is, simply based on the laws of physics, when an individual grasps a moving object and decelerates it, grip force would be expected to be larger, the faster the object is moving. However, there are other strategies that could be adopted. For example, an individual could keep the amount of force generated constant as a function of increased target velocity, and instead vary the rate at which this force is applied. The closest examination of force control during target interception involved participants holding a force transducer that was struck from the side by a pendulum that was released from various angles (Turrell et al. 1999). Turrell and colleagues found that grip force increased as the impact force increased in anticipation of the contact with the moving pendulum. These authors suggest that an important factor in regulating the grip forces on the transducer is the momentum associated with the transducer and the pendulum at impact. However, the actual values of momentum, or its role, were never directly examined. One purpose of the present study was to investigate the role of momentum during impact, between the fingers and a moving target object, on the production of grip and load force.

When intercepting a moving target object torques are created if the object is not grasped precisely in line with the center of mass. Depending on where the fingers contact the target object, the transient torque values can change, on a trial to trial basis. It has been demonstrated that to prevent the torques from rotating a stationary object that is held between the index finger and thumb, grip forces are increased (Kinoshita et al. 1997). It is hypothesized that in a dynamic situation, when grasping moving target objects the control of torque that is created when the object is grasped outside the center of mass, may be even more important than in the static situation. Torque and momentum are mathematically related such that torque is a product of linear momentum, the moment arm, and acceleration, all divided by velocity. While one purpose of this study was to examine the contributions of torque to predicting grip force, torque was never directly manipulated. Thus far, we have identified transient torques, target velocity and momentum as potential contributors to grip force production when contacting moving target objects. However, momentum and velocity are also not independent; momentum is the product of target velocity and mass. We know that when grasping stationary target objects, mass has been shown to influence grip and load force such that as target mass increases so does force production (Johansson and Westling 1984). Thus, the effects of momentum on grip force could be due to the contributions of target mass (independent of target velocity). Finally, it has been demonstrated that grip and load force are also not independent. During self-generated shaking movements of an object held between the index finger and thumb, it has been shown that grip and load forces are correlated and vary together (Flanagan and Tresilian 1994). Using multiple regression modeling, one goal of this experiment was to partition out the variance in grip control contributed by the variables: torque, load force, target mass, velocity, and momentum.

Methods

Participants

Eight healthy, self-reported right-handed human volunteers (3 females, 5 males; mean age 23.2 years, range 22 to 27 years) participated in the study. The participants had normal or corrected to normal vision. All gave informed consent before participating in this study. Approval from the University of Waterloo Office of Research Ethics was obtained before testing began.

Participants were seated in front of a 2.5m long track that was positioned to the right of their midline. Each participant's hand was positioned in line with the forearm, prone and with the index finger and thumb in a pinch position. The forearm position on the rest pad was determined such that for each participant the thumb and the index finger rested in the middle of the target interception zone, and the elbow joint was at 90^{0}.

Apparatus

The object to be grasped was a six-axis force-torque sensor (Nano F/T transducer; ATI Industrial Automation, Garner, NC) with two exchangeable polyethylene plastic cylindrical mass containers with flat grasping surfaces, mounted on each side of the sensor. The resulting cylinder was 5.5 cm wide and 3 cm in diameter. Changing the mass containers on each side of the sensor varied the total mass of the unit. The unit=s total weight was either 50, 100 or 200 g.

A step motor assembly (Applied Motion Products, motor model # 5023-124; driver model # PD5580) fitted with a chain socket system was used to move an aluminum platform, carrying the force transducer unit, down the track. The travel velocity of the platform could be set with a 0.012 m/s precision, and the travel distance with 0.1 mm precision. The target object moved at either 0.114, 0.227 or 0.457 m/s. The total travel distance of the platform was constant throughout all experimental sessions (360 mm), and was set such that the force transducer unit did not stop in the interception zone, but continued 30 mm past the center of the interception zone. This ensured that the target object was in motion when the participants grasped it. Figure 15 shows a schematic of the experimental setup.

When the target object was lifted, the grip force was measured along the grip axis defined by the line joining the centers of the two grasp surfaces. The forces were collected at 400 Hz with a resolution of 0.025 N. The load force was defined as the vector sum of the two perpendicular forces acting in the orthogonal plane to the grip force axis. The rates of both grip and load force were also calculated. Torque values were measured about the grip force axis (Z as seen in Figure 15) at a resolution of 0.125 Newton millimeters (Nmm). All data were filtered with a 14 Hz dual pass Butterworth filter.

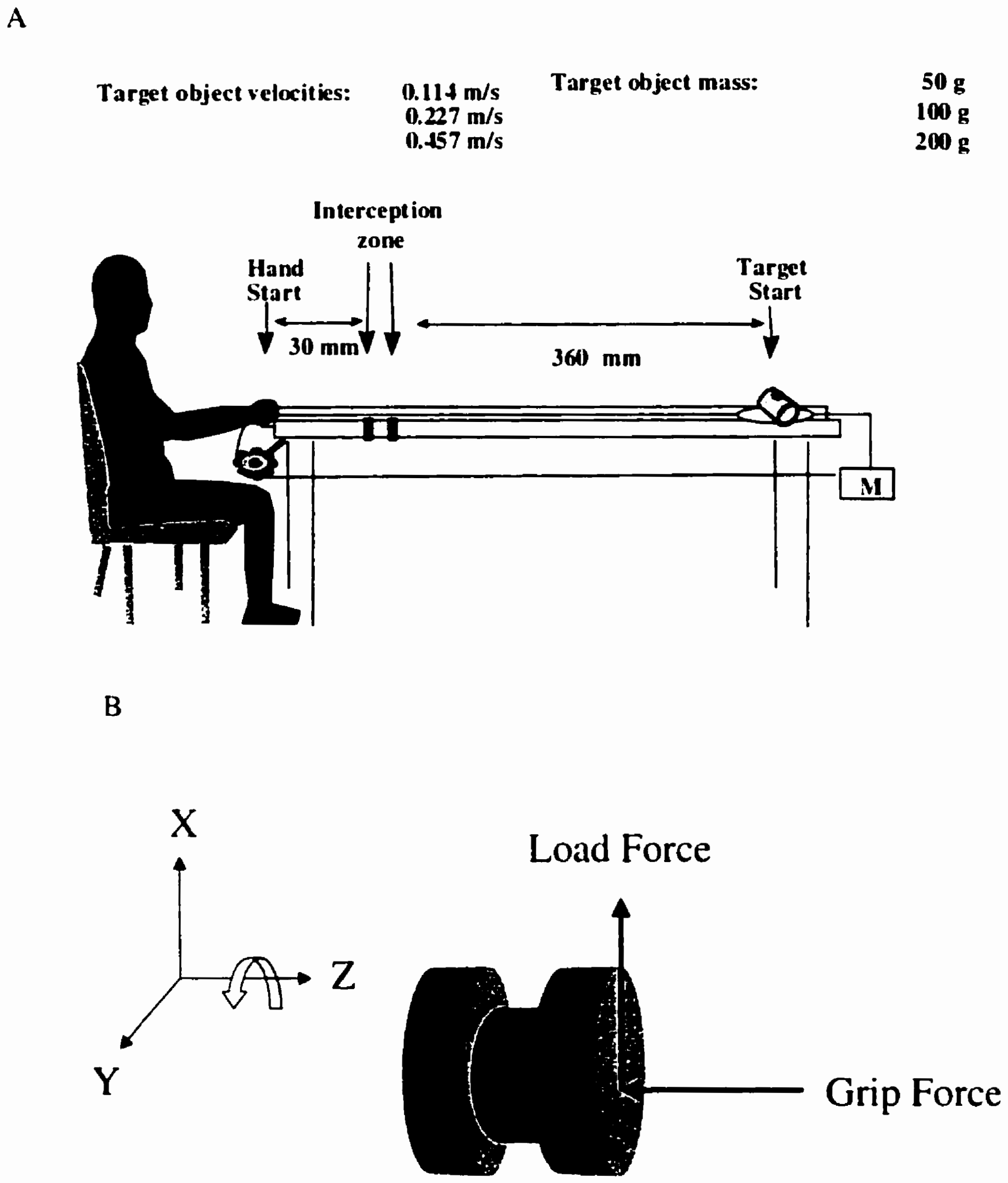

Figure 15. Panel A shows a schematic of the experimental setup. Panel B shows a close-up of the object that was intercepted.

Procedure

Participants were asked to grasp, lift and hold the moving cylindrical target object as it passed through the interception zone. The target object was lifted 5 cm and maintained at this height for 2 seconds using a precision grip between the index finger and the thumb, and repositioned back in the middle of the force transducer's traveling platform. The lifting motion occurred at the wrist joint, with the forearm resting on a pad.

Instantaneous linear momentum of a moving object is defined as a product of its mass and velocity. Thus, there were five possible linear momentum values (based on the three target object velocities and masses) for the target object as it passed through the interception zone and was grasped by the participant. That is, the momentum value of 11.4 gm/s was shared by the 50 g, 0.227 m/s; and the 100 g, 0.114 m/s conditions. A momentum value of 22.8 gm/s was shared by the 50 g, 0.457 m/s; 100 g, 0.227 m/s; and the 200 g, 0.114 m/s conditions. Finally, the momentum value of 45.7 gm/s was shared by the 100 g, 0.457 m/s; and the 200 g, 0.227 m/s conditions. For the 50 g, 0.114 m/s condition the momentum value was 5.7 gm/s, and for the 200 g, 0.457 m/s condition the momentum value was 91.4 gm/s. This manipulation allowed a distinction between the relative contributions of target object mass, velocity and corresponding linear momentum to the generation of grip force.

Ten trials of each of the three target object velocities were performed consecutively for each of the blocks of target object mass. The presentation of these trial blocks was counterbalanced across participants. Prior to testing each participant received a random presentation of two practice trials for each of the mass-velocity combinations.

Statistical Analyses

Analysis I: Effects of Target Velocity and Target Mass

To first assess the contributions of target velocity and mass on the peak torque, peak grip and load forces, and their associated rates, separate 3 (target object mass; 50 g, 100 g, 200 g) x 3 (target object velocity; .114 m/s, .227 m/s, .457 m/s) repeated measures analyses of variance (ANOVA) were run for each of these dependent measures.[1] Effects significant at $p < .05$ were further analyzed using the Tukey HSD methods for post hoc comparison of means.

Analysis II: Multiple Regression

A multiple regression analysis was run that determined which of the predictor variables (torque, load force, target object velocity, target object mass, momentum) accounted for the most variance in grip force. The predictor variables used in the model were: participant (S), torque (T), load force (LF), target velocity (V), target mass (M) and linear momentum (LM) (see Kinoshita et al., 1997). The general model used was; $Y = \mu + \Sigma_i\beta_iX_i + \xi$, where $\Sigma_i\beta_iX_i$ were predictor variables included in the linear regression procedure (X = S, T, LF, V, M, LM), elements from X were dropped during the analysis, ξ was the random error not accounted for by the model, and Y is the dependent variable. Two models were tested. Model 1 was the most parsimonious model selected based on step-wise selection ($p=0.5$ for entry and stay criteria) and CP procedure, which is a statistic used to determine how many variables should be used in the regression model (Daniel and Wood 1980). Model 2 was the same model as model 1, however the linear momentum (LM) term was removed and both target velocity (V) and mass (M) were

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[1] Trials was originally included as a factor but no significant main effects or interactions for this variable were found so it was removed from the analyses.

added in its place. A comparison of model 1 with model 2 allowed for an assessment of whether the amount of explained variance due to the replacement of LM with V and M was statistically significant.

Results

I: Effects of Target Velocity and Target Mass

Peak Grip Force. The peak grip force showed a main effect for target mass (F(2,14)=15.62, p<.01). Grip force increased as the mass of the target object increased. Statistically, less peak grip force was produced for the 50 g condition in comparison to the 100 g and 200 g conditions. The 100 g and 200 g conditions were not statistically different. However, the rate of grip force production showed main effects for both target mass (F(2,14) = 11.27, p< .01) and target velocity (F(2,14)=6.9, p < .01). Grip force was produced more slowly when grasping the 50 g mass in comparison to the 100 g and 200 g masses. There was no statistically significant difference between the 100 g and 200 g masses. Also, the rate of grip force production was greater for the fast condition in comparison to the medium and slow velocities, which did not differ statistically from each other. Means and standard errors for all dependent measures are seen in Figure 16.

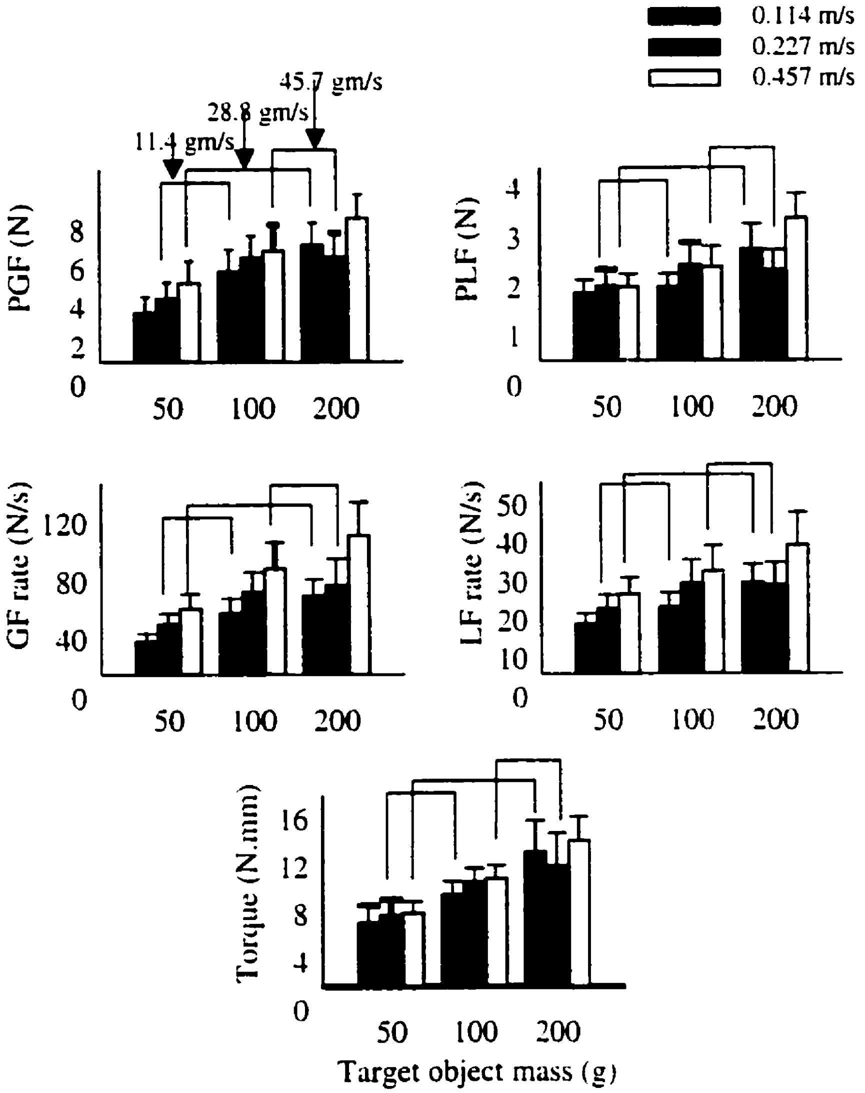

Figure 16. Means and standard errors for torque, peak grip and load force and the associated rates of force production, for the three mass and velocity conditions. Conditions with similar momentum values are indicated by solid lines. Note that there is a trend for conditions that share similar momentum values to also have similar patterns of force production.

Peak Load Force. The analysis of peak load force also showed a main effect for target mass (F(2,14)=6.38, p =.01). Peak load force was greater when lifting the 200 g target object in comparison to the 50 g target object. The peak load force generated when lifting the 100 g object did not differ statistically from either the 50 g or 200 g conditions. The analysis of the rate of peak load force production showed main effects for both target mass (F(2,14)=6.34, p =.01), and target velocity (F(2,14)=5.73, p = .01). Load force rate was greater for the 200 g condition in comparison to the 50 g condition, with the 100 g condition not differing statistically from the other two conditions. Load force rate was also greater for the fast target object condition in comparison to the slow condition, with the medium velocity condition not differing statistically from the other two target velocities.

Peak Torque. A main effect for mass was seen in the analysis of torque (F(2,14)=7.21, p < .01). Peak torque was greater when lifting the 200 g target object in comparison to the 50 g target object. The peak torque generated when lifting the 100 g object did not differ statistically from either the 50 g or 200 g conditions. Figure 17 shows the strong influence of torque on grip force production.

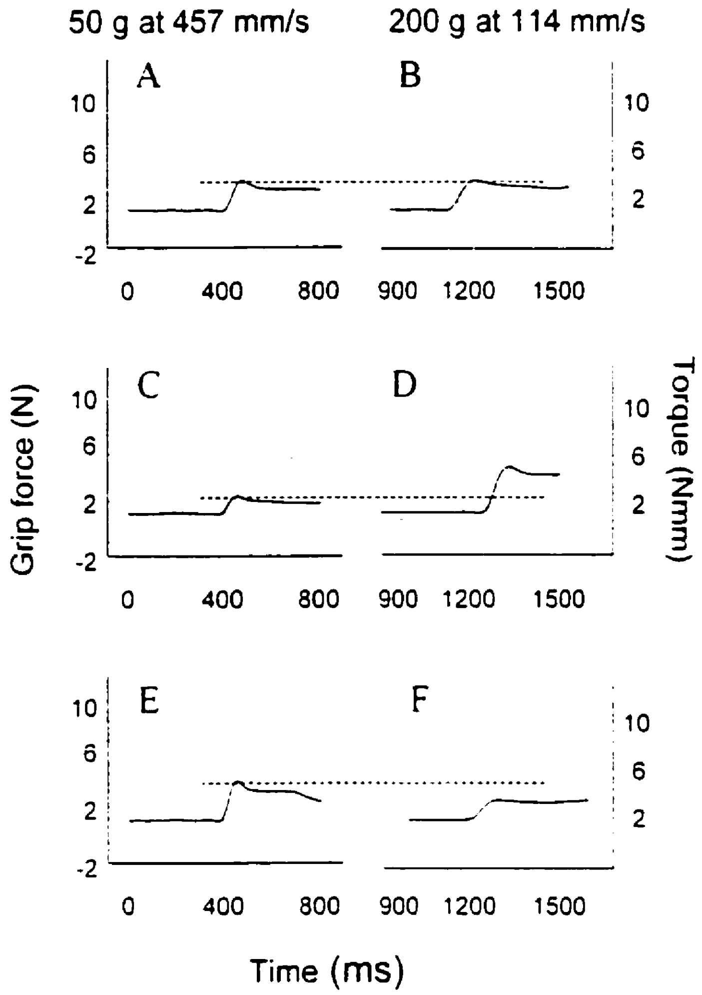

Figure 17. Grip force and the transient torque values are plotted as a function of time for three representative trials for the 50 g, 0.457 m/s condition, and the 200 g, 0.114 m/s condition. The momentum value for both of these conditions was 22.8 gm/s. Grip force is shown by the solid black curve, the torque curves are dotted, and the dashed horizontal line is placed at the peak grip force of the plots for the 50 g, 0.457 m/s condition to serve as a reference. Panel A and panel B provide examples of trials where the torques for the two conditions were similar resulting in similar grip forces. In panel D, the trial (200 g, 0.114 m/s) with the high torque value has a corresponding higher grip force compared to panel C. In panel E, the opposite pattern was seen. In the 50 g, 0.457 m/s condition, a high transient torque value was observed and subsequently there was a higher grip force in comparison to panel F.

II: Multiple Regression

The first set of analyses showed that target mass was an important contributor to both the magnitude and rate of grip force production. Target velocity influenced only the rate of force production. The patterns for the production of load force were very closely related to the patterns observed for grip force. Inspection of Figure 16 reveals that momentum also appears to have an influence on the force production patterns. However, momentum, target object velocity, and target object mass, are all correlated so it is difficult to understand the relative individual contributions of each of these variables to grip and load force production. Torque also showed a pattern similar to that seen for grip force and could thus be influencing the force patterns observed.

Table 3. Results of the multiple regression analyses, where the predictor variables used were participants (S) torque (T) load force (LF), linear momentum (LM), target mass (M), target object velocity (V).

Model		R^2	F (df)
M1	GF = LF + T + S + LM	.99	(4, 66) =7542.1
M2	GF = LF + T + S + M + V	.99	(5, 66) =6007.3

As demonstrated in Table 3, the step-wise procedure selected model 1 (M1) as the most parsimonious model that accounted for the most variance in grip force. This model included load force, transient torque values, inter-participant differences and linear momentum, as the fewest number of variables that accounted for most of the variance in grip force generation. This was confirmed by the CP procedure (C(p)=2.61). Model 2 (M2), in which the momentum term was replaced by velocity and mass terms, did not differ from model 1 (F(1,66) = 0.72), indicating that momentum per se was equally important as the individual terms (target mass and velocity) comprising momentum.

Discussion

The purpose of this study was to examine the influence of the contributions of a moving target objects velocity, mass, momentum, and torque, on the grip forces necessary for successful prehension. It was found that in a blocked presentation, as the target object mass increased, the grip and load forces involved in lifting it also increased (Johansson and Westling 1984). While there was a trend for grasping forces to increase as target velocity increased, this observation was not shown to be statistically significant. This was in contrast to the predictions of Mason and Carnahan (1999), and based on the work of Jeannerod (1984) it could be concluded that target motion is an extrinsic rather than an intrinsic variable. However, as the target object velocity increased so did the rate of force production when contacting and lifting the target object. The observation that the actual generation of forces is influenced differentially by target motion in comparison to the timing of force production, is similar to the observation by Mason and Carnahan that finger aperture size and timing are affected differentially when grasping moving targets. There may be independent mechanisms for grasp control that are responsible for the timing versus the magnitude of associated muscular impulses.

Aside from load force, the multiple regression analysis showed that torque was the most important variable in predicting grip force. This supports work by Kinoshita et al. (1997) who first demonstrated this important factor. Torque varied only as a function of target mass, not velocity. It had been hypothesized that torque would vary more dramatically or be larger when grasping faster as opposed to slower moving targets. However, in the present study this was not the case. The ANOVA showed no significant velocity effect for peak torque. In spite of the lack of influence of target velocity on torque, target velocity did influence grip and load rates, suggesting that these effects were related to increased momentum (target mass or velocity) rather than to changes in torque.

The results of the ANOVA showed that as target mass increased, grip force also increased. While there was a trend for target velocity to show influence on grip force, there was no statistically significant effect. However, the multiple regression analysis chose the model that included the momentum of the target object a more parsimonious predictor of grip force than a model that included mass instead of momentum. Thus, while the effects of velocity were not significant in the ANOVA, velocity did contribute in some form to grip force, as evidenced by the significant contributions of momentum (which is a product of target velocity and mass). These data support the proposal made by Turrell et al. (1999) that momentum is an important variable that is represented in anticipatory models of force control (Johansson and Cole 1994; Wolpert 1977). However, the second model from the multiple regression analysis showed that mass and velocity combined accounted for a similar amount of variance. This makes sense since momentum is a product of these other two variables. What is not clear is how this information about the moving targets is represented. Does the central nervous system recognize the higher order variable (momentum) to simplify the amount of information that needs to be represented? Alternatively, the strategy could be for the simplest forms of information regarding target motion (mass or velocity, or for that matter a change in target displacement rather than velocity (Smeets and Brenner 1995)) to be represented. It seems logical that a successful strategy would involve simplifying the information that must be encoded. The results of the present study cannot distinguish between these two options, but do suggest that this issue is worthy of further investigation.

It has been demonstrated that individuals use internal models when programming grip and load forces in response to variables such as object mass (Johansson and Westling 1984). But, are momentum and torque represented in a similar internal model? In our study both the target object mass and velocity were presented in a blocked order. There were no visual cues regarding the mass, so anticipation based on the haptic experience of the previous trial within the block was the only way for participants to accurately predict the required forces. While it is possible that information about target object velocity was processed on-line (see Savelsbergh et al. 1992; Tresilian 1995), it is more probable that visual information was used in an anticipatory fashion to avoid time lags between the processing of vision, the generation of movement corrections, and the motion of the target (Carnahan and McFadyen 1996; Dubrowski and Carnahan 2001). Regardless of whether the visual information regarding the trajectory is used on-line or is used based on prior experience in an internal model, in both cases, the information is available to the motor system prior to the contact of the target object with the fingers. Since information about target object mass and velocity clearly can be used to develop an anticipatory model of force control, momentum is probably also represented in this type of internal model. However, in the present study, participants were not able to use information about torques in an anticipatory fashion due to their transient nature. That is, the torques differed from trial to trial, depending on precisely where the fingers contacted the target object. They could not be predicted by the participants, but instead could only be reacted to. If the strategy was to deal with torque in an anticipatory manner, then it would be expected that participants would consistently generate more force than required to deal with the range of torques expected. That is, they would chose a large safety margin by generating enough grip force to deal with all potential torques to which they could reasonably be exposed. Clearly this is not the case in the present study. Participants generated a wide range of grip forces to deal with the torques they experienced in a trial by trial basis. Thus, it is concluded that while momentum in a dynamic situation is likely represented in an internal model, grip control in response to transient torques is controlled in an on-line fashion.

CHAPTER 5: EXPERIMENT 4

The effects of damage to the basal ganglia on the control of precision grip are not well understood. To date, the leading model of grip control, proposed by Johansson and colleagues (Johansson 1996; Johansson and Cole 1994) consists of three stages: the precontact anticipation of object properties, the feedforward prediction of expected sensory consequences of the movement, and the analysis of the actual somatosensory information from the periphery.

The anticipatory control of grip is based on acquiring intrinsic and/or extrinsic object properties prior to the actual grasp. Based on haptic or visual recognition of the object, appropriate memorial representations of interactions with similar objects or situations are retrieved and the movement is preprogrammed based on these representations. For example, Johansson and Westling (1988) investigated the anticipatory control mechanism involved when dropping a ball into a small, hand held container. On some trials the participants dropped the ball into a container with one hand, and on other trials the experimenter dropped a similar ball, without the participant's knowledge. The results showed that when the participants dropped the balls by themselves, the grip force increased prior to the ball hitting the container in order to offset the expected impact. On the contrary, when the experimenter dropped the balls without the participant's knowledge, the increases in grip force occurred after the ball contacted the container in a reactive manner (Johansson and Westling 1988).

Johansson and Cole (1994; Johansson 1996) suggest that the forward model for grasp control contains a set of correction commands in addition to the principal motor command that could be accessed quickly if the predicted and actual sensory feedback do not match. For example, if the initial motor command is correct, specific sensory consequences (bursts of activity) arriving from the finger receptors that indicate object lift off, are expected at a certain point in time. However, if the initial motor command is incorrect, there are two possibilities where the expected and actual feedback do not match; first, either the expected sensory signal comes too early, indicating that too much force was produced, or second, the signal does not come at the expected time, indicating that too little force was produced. The addition of the two correction motor commands helps to avoid long feedback loops; if the expected sensory feedback arrives too early it adds less force, or alternatively if the expected sensory feedback does not come more force is added.

To date, it is not very clear which neural structures play a major role at the various stages of grip control. There are two main sub-cortical motor control loops consisting of the cerebellum and the basal ganglia that are involved in the programming and execution of movement. Despite obvious differences between the anatomical connectivity (see Kandel et al. 1991 for review), there are a number of studies showing evidence of the similarities in the functioning between these two structures. Krams et al. (1998) suggested that both the cerebellum and basal ganglia are responsible for movement preparation and execution. Based on rCBF during a sequential finger lifting task, these researchers have demonstrated that the cerebellum, as well as the basal ganglia, are active during movement preparation. Furthermore, when a subsequent movement accompanies the movement preparation, both structures show equally more intensified activation. Also, when examining individuals with lesions to the cerebellum or basal ganglia some striking similarities in the effects on grip control have been demonstrated (Muller and Dichgans 1994). For example, these researchers found that individuals with cerebellar lesions had longer pre-load phases than control participants. In another study, employing a similar paradigm with parkinsonian patients, Muller and Abbs (1990) showed a similar pattern of results.

However, there is compelling evidence that both neural structures differ from each other based on their connectivity to the other parts of the central nervous system, as well as their function. It has been proposed that the cerebellum is mainly involved in the control of multi-joint, complex movements that require visuomotor coordination (Stein and Glickstein 1992). Recently Wolpert et al. (1998) proposed that the internal, anticipatory model required for the control of arm trajectory resides in the cerebellum. Furthermore, it has been suggested that the internal model of grip and load force control in a dynamic manual lifting task is also a cerebellar function (Babin-Ratte et al. 1999; Muller and Dichgans 1994). However, based on observations of cerebellar patients, Babin-Ratte et al. (1999) proposed that in static situations, where the control of grip forces does not depend on limb dynamics, but instead on object characteristics such as mass and friction, that these movements are implemented outside of the cerebellum. Lastly, based on rCBF studies of the human brain, Jueptner and Weiller (1998) concluded that the cerebellum should be considered the main site of movement control based on its role in the processing of sensory feedback.

Alternatively, the basal ganglia have been shown to be involved in higher order aspects of motor control such as movement planning, the initiation of internally generated movements, and the execution of complex motor synergies (Stelmach 1991).

Furthermore, the basal ganglia are thought to be involved in the comparison of the efferent motor program copy from the frontal fields with peripheral feedback, which may be useful for regulating the unfolding movement or for monitoring its consequences (Hikosaka and Wurtz 1983). Jueptner and Weiller (1998), who in a series of studies investigated the roles of the basal ganglia and cerebellum in the processing of afferent information, have recently challenged this view. Jueptner et al. (1996) have demonstrated that the neocerebellum, and not the basal ganglia, was more active when continuous movements were performed. The task required the participants to draw a line using a mouse on a computer screen. In the next session the same lines were presented to the participants who were then asked to re-trace them as precisely as they could. There were no differences in the activation of the basal ganglia or cerebellum in the line drawing task, however, in the re-tracing task only the neocerebellum showed increased activation. This lead the authors to the conclusion that neocerebellum and not basal ganglia are involved in the on-line control of evolving movements. In addition, Weiller et al. (1996) have successfully demonstrated that the basal ganglia did not show any increases in activation during passive elbow flexion (afferent sensory information only) in contrast to active flexion (afferent sensory and efferent motor information) and instead only the cerebellum was activated. This was taken as evidence that the basal ganglia were not the site for feedback information processing. Together these studies suggest that the basal ganglia are not used to control movement based on sensory feedback, but rather they are concerned with the selection of appropriate movements (Jueptner and Weiller 1998). In line with this argument, Muller and Abbs (1994) have demonstrated that parkinsonian patients can adjust their grip force according to the true mass of the object handled, suggesting that there are no deficits in sensory feedback processing. More importantly, these patients showed slower onset latencies, which suggests the inability to use sensory afferent information to trigger the next stage of the lift in accordance with the feedforward model.

Based on the rCBF studies (Jueptner and Weiller 1998), as well as that observations made by Muller and Abbs (1994) that patients with Parkinson's disease were able to scale, it could be hypothesized that the cerebellum is the major site of feedback information processing. However, since the basal ganglia are mainly concerned with the selection of movement and complex muscle synergies (Kandel et al. 1991), it is possible that they play a key role in pre-selecting corrective responses in the anticipatory, discrete event, sensory driven, feedforward control of grasp. If this is true, it is hypothesized that performance on a grasping task by an individual with damage to the basal ganglia would not be mediated by the feedforward mechanism, but instead would depend on feedback processing by the intact cerebellum.

Test 1

Wolpert and Kawato (1998) and Wolpert and Ghahramani (2000) proposed a general computational model that explains the formation of memorial representations of movement. With respect to lifting tasks, the basic concept of this model is that as the movement unfolds, multiple forward models are run that mimic the motor outputs used to pick up the object. Each forward model generates the predicted sensory feedback that should be received from the digits. Furthermore, each of the forward models is coupled with an inverse model, which, if the sensory feedback matches the predicted feedback, will be selected, stored and used to determine appropriate motor commands for subsequent interactions with similar objects. Johansson and Cole (1994) have proposed a comparable feedforward model for grasp control. In their view, the forward model contains a set of correction commands in addition to the principal motor command that could be accessed quickly if the predicted and actual sensory feedback do not match.

Gordon et al. (1993) have shown that when lifting objects of varying dimensions, the size of the object influences the peak grip force exerted on it, such that large objects are lifted with higher peak grip forces than small ones. This finding suggests that the programming of grip forces is dependent on the integration of visual and haptic information. In the present study, both healthy control individuals and an individual with unilateral basal ganglia damage (OF), lifted objects of various sizes that had the same mass. Based on the findings of Gordon et al. (1993) and on the suggested roles of the basal ganglia and cerebellum in the control of grip forces, it was hypothesized that if basal ganglia damage affects the integration of visual and haptic information, OF's contralesional hand should show no scaling of peak grip force to object size, and there might be over-gripping that would be related to increased safety margins. It is also possible however that there may be bilateral effects related to the unilateral lesion and thus it was important to compare the performance of both hands.

Methods

Participants

OF (28 years of age) was a right-handed male with a localised unilateral lesion to the left basal ganglia, resulting from a subcortial infarct in the left middle cerebral artery.

that affected the head of the caudate, anterior internal capsule, putamen and globus pallidus. This was confirmed with a gadolinium-enhanced T^2-weighted MRI. Neurological examination six weeks postinfarct showed mild anomia and otherwise normal neurological function. Six months postinfarct there was evidence of writing dystonia with micrographia, but neuroligic function was otherwise normal. OF could produce equal maximum force on a dynamometer with each hand (Troyer et al. 1999). In addition two healthy, right-handed male control participants with normal or corrected to normal vision were tested; Control 1 (C1) was 24 years old and Control 2 (C2) was 23 years old. Approval from the University of Waterloo Office of Research and Ethics was obtained before testing began.

Apparatus

The object to be grasped was a six-axis force-torque sensor (Nano F/T transducer; ATI Industrial Automation, Garner, NC) with two exchangeable polyethylene plastic cylindrical mass containers with flat grasping surfaces (3.5 cm diameter), mounted on each side of the sensor. Changing these cylinders resulted in a small, medium and large test object that differed in length (4.5, 5.5, 6.5 cm in total length) but not mass (150 g). Refer to Figure 18 for a schematic of the objects lifted.

When the target object was lifted, the peak grip force was measured along the grip axis defined by the line joining the centers of the two grasp surfaces. The forces were collected at 200 Hz with a resolution of 0.025 N. The peak load force was defined as the vector sum of the two perpendicular forces acting in the orthogonal plane to the grip force axis. The rates of both grip and load force were also calculated. It has been

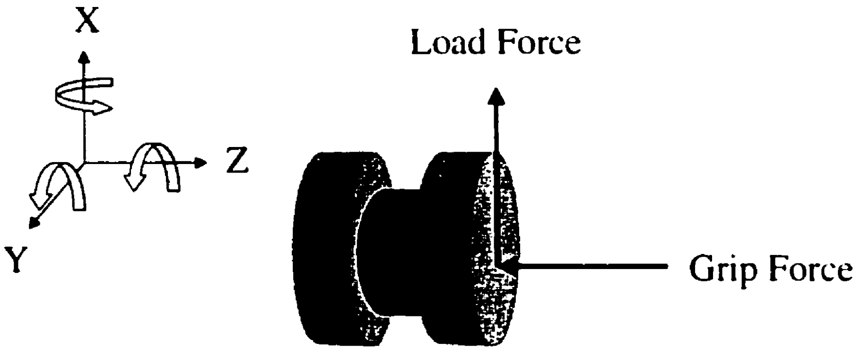

Figure 18. This schematic shows the object that was lifted by participants in this study. Grip and load forces are depicted in this figure, as is the torque, which was the resultant of all three torques.

previously shown that grip force is strongly influenced by load force and torque (Kinoshita et al. 1997). Since the position of the fingers on the grasping surface of the object was not restricted, the torques created on the object by inconsistent finger placement varied from trial to trial. To determine how these transient torque values were handled by OF and the control participants, the resultant peak torque created on the object when lifted was calculated. It was quantified as a vector sum of the torques measured about the three axes at a resolution of 0.125 Newton millimeters (Nmm). All data were filtered with a 10 Hz dual pass Butterworth filter.

Procedures

The participants were asked to lift the test object 10 cm from the table surface, hold it for 2 seconds and replace it back on the table. The grasps were made between the index finger and thumb. The lifts were performed first with each participant's right hand, followed by the left hand. Each object size was presented 8 times for each hand, for a total of 48 trials for each hand. For each hand the objects were presented in a random order. The same random order was used for each of the hands.

Statistical analysis

To assess how the performance of the contralesional and ipsilesional hands of OF differed from that of the control participants, the amount of variance in peak grip force explained by the transient torques, the load force, and the object size was determined by a separate linear regression analysis that was run for each participant. The general model used was; $Y = \mu+\beta x+\xi$, where βx consisted of the predictor variables and ξ was the random error not accounted for by the model. The predictor variables used in the model were: hand used (right and left), trial (1 to 8), object size (4.5, 5.5, 6.5 cm), torque, and load force. Based on the step-wise selection (p=0.5 for entry and stay criteria) and CP procedure, which is a statistic used to determine how many variables should be used in the regression model (Daniel and Wood 1980), the most parsimonious model was selected (M1) for each participant. Finally, the amount of grip force change (parameter) caused by a unitary change in the predictor variable, when the other variables in the model are controlled for, was also calculated. More specifically, this test determined how much peak grip force increased, with a change of 1 cm in object size? A t-test was used to evaluate the hypothesis that the parameter change was different from zero.

Results and Discussion

Table 4. Results of the linear regression modelling performed on the grip force for each participant (OF, and 2 the control participants).

Participant	Model for grip force prediction	R^2	Significance F(df), p	M1 vs. M2 F(df), p
OF	Hand	.28	14.49 (1, 39), .0005	1.94 (1, 39), p>.05
	Hand + Torque	.31	8.23 (2, 39), .001	
C1	Size + Torque + LF	.75	38.10 (3, 41), .0001	1.32 (1, 47), p>.05
	Hand + Size + Torque + LF	.75	29.05 (4, 41), .0001	
C2	Size + Torque + LF	.72	36.10 (3, 45), .0001	.18 (1, 45), p>.05
	Hand + Size + Torque + LF	.72	26.57 (4, 45), .0001	

The results of the linear regression model are presented in Tables 4 and 5. Table 4 shows the most parsimonious models selected by the step-wise and CP procedures for each participant (M1). For OF, the analysis showed that the hand used was the best predictor of the peak grip force produced when lifting the three objects. The peak grip force employed by the left-ipsilesional hand (M= 3.38 N, SD=1.8 N) was smaller than that of the right-contralesional hand (M=5.20 N, SD=2.5 N) (see Figure 19). Other predictor variables, such as object size, trial order, and load force did not contribute significantly to the amount of variance explained by the model. Thus, OF was not scaling his grip force to object size as predicted by Gordon et al. (1993). In order to assess the amount of on-line control of peak grip force due to the unpredictable torque values produced when grasping the object away from its axis of rotation, the torque produced by the fingers on the object for each trial was included in model 2 (M2) in addition to the predictor variables included in M1. The comparison of M1 and M2 for OF showed that the addition of torque into the regression model did not significantly improve the amount of variance explained.

As depicted in Figure 20, the contra and ipsilesional hands were affected differentially by the presence of torque. The correlation between the peak grip force and the torque was lower (R^2=0.10) for the contralesional hand than for the ipsilesional hand (R^2=0.42). It has been shown that for a healthy population of participants, as the torque values increases so does the peak grip force (Kinoshita et al. 1997) and that this is an on-line process. The inability to modulate grip force to the object torque with OF's contralesional hand indicates problems with on-line control.

Table 5. Relative contributions of each of the predictor variables to the most parsimonious model for each participant (OF, C1, and C2). T (p) represents the test for significance of the contributions that the predictor variable makes to the grip force (GF) when the other variables in the model are controlled for.

OF			*C1*			*C2*		
$GF = \mu + Hand + \xi$			$GF = \mu + Size + Torque + LF + \xi$			$GF = \mu + Size + Torque + LF + \xi$		
Predictor	Parameter	T (p)	Predictor	Parameter	T (p)	Predictor	Parameter	T (p)
Hand	1.52	3.8 .0005	Size	.713	5.53 .0001	*Size*	.288	3.13 .0032
			Torque	.015	1.88 .0671	Torque	.019	2.52 .0154
			LF	1.782	9.56 .0001	LF	1.35	8.59 .0001

As evidenced in Tables 4 and 5, both control participants showed different patterns of behavior than those demonstrated by OF. The regression analysis shows that for both control participants, the size of the object, torque and load forces were the best predictors of peak grip force (Table 4). When all predictor variables that were used in this model were controlled for, peak load force was influencing the peak grip force to the greatest extent, followed by object size and then torque (Table 5). In agreement with the size-mass illusion, as object size increased so did the peak grip force. This was apparent for both hands of the control participants as illustrated in Figure 19. However, since the object mass remained constant regardless of its size, the load force necessary to overcome the force of gravity acting on the object should remain constant, resulting in no change in peak grip force due to this variable. However, the correlation of peak grip force to load force yielded a positive value (C1: R^2=0.70, C2: R^2=0.74) indicating that, similar to peak grip force, the changes in load force were caused by the size-mass illusion. That is, the bigger object was expected to be heavier than the two smaller ones, thus the initial hand acceleration upward was greater causing greater load forces. On the contrary, the small object was expected to be lighter, and thus the initial impulse to lift it was smaller than necessary, resulting in a lift with less acceleration, and thus less load force. This is apparent in the load force generation profiles in Figure 19. In order to assess the amount of variance explained by the hand differences for the control participants, another model (M2) that contained hand as a variable was tested. As seen in Table 4 this model was not significantly different than the most parsimonious model, thus the control of participants' grip force production was influenced by the same variables for both hands.

In summary, OF showed higher peak grip force and less scaling of these forces to the unpredictable torque with the contralesional hand than with the ipsilesional hand. The control participants showed the expected influence of object size on peak grip force, as well as a reliance on the on-line control of grip force to compensate for torque created on the object. None of the participants showed any influence of practice on peak grip force. The persistence of the size-mass illusion throughout all the trials for the control participants suggests that not enough practice was present for vision-haptic decoupling. The high peak grip force employed by OF's contralesional hand indicates over-gripping of the test object that was not scaled to object size. Also, the lack of grip force corrections to the unexpected torque suggests that OF's basal ganglia damage affected the on-line control of grip forces.

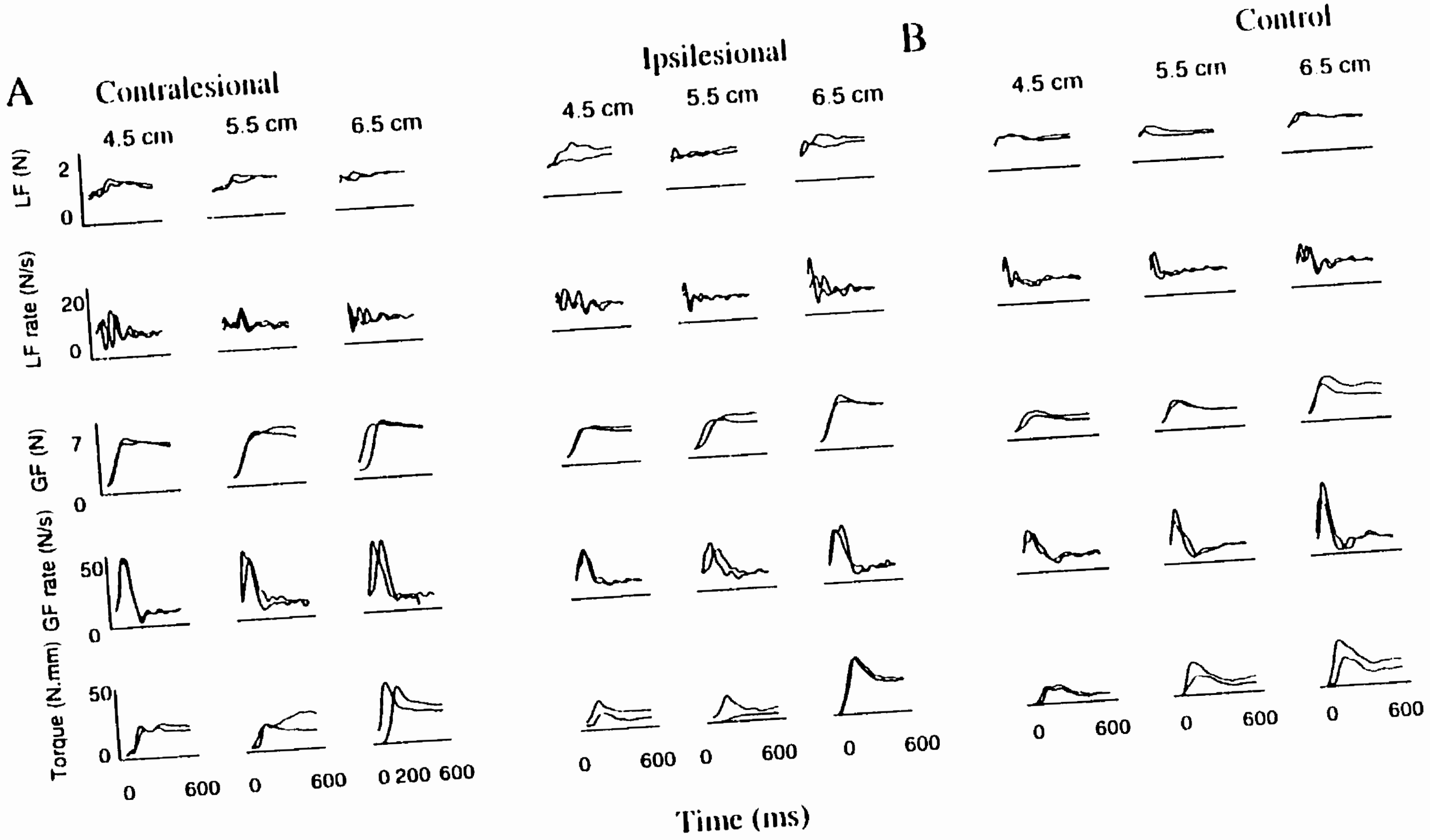

Figure 15. Load force (LF), load force rate (LF rate), grip force (GF), grip force rate (GF rate) and torque profiles for OF's contra and ipsilesional hands (A) and the right hand of the control participant (B).

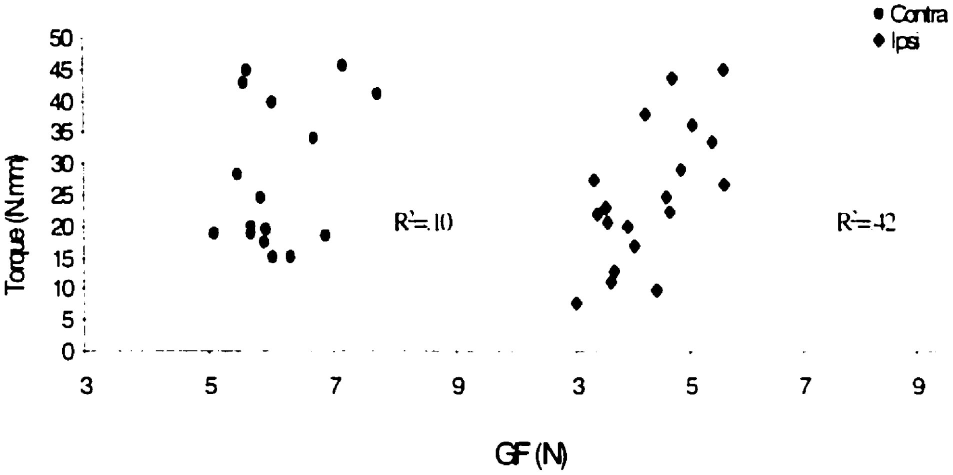

Figure 20. Grip force (GF) plotted as a function of torque for OF's contra and ipsilesional hands.

Test 2

It has been demonstrated that when lifting an object, the initial forces applied to the object reflect the requirements of the previous lift (Johansson and Westling 1988). That is, before the object lifts off, the explicit information about the object mass is not known, thus the initial programming of forces must be based on information acquired from previous lifts of similar objects (Gordon et al. 1993; Johansson and Westling 1988). It is only after object lift off that the afferent information from the fingertips can reflect the true mass of the object. If the initial memorial representation of the object mass was inaccurate, then the grip and load forces are corrected on line. This is based on the afferent activity of the tactile receptors at the finger-object interface, through the feedforward mechanism outlined in the general introduction (Johansson 1996).

Thus, the initial programming of the lifting forces is largely based on the memorial representations of the lifting forces produced on previous experiences of interacting with similar objects. In line with this notion, Charpentier (1891) and Gordon et al. (1991; 1993) demonstrated that the initial programming of the grip force required to lift an object is based on the size of that object. In their study, Gordon et al. (1993) asked participants to lift objects of the same mass, but of different sizes and showed that the grip force produced to lift the objects were scaled to the size rather than to the mass of the objects. It has been proposed that this illusion is due to the assumption that similar objects have similar densities, and thus a bigger object must be heavier than a small one. In a similar study, Johansson and Westling (1984; 1987) demonstrated that when picking up objects where the size and mass relationship was disrupted, the erroneous initial force generation was quickly adjusted based on tactile afferent information, with a duration of approximately 79 ms. It was hypothesized that these adjustments were related to the coordination of grip and load forces. Grasp stability is mainly achieved by parallel changes in the grip and load forces applied to an object. Linking these two forces allows for flexibility when lifting objects with different masses. The load force is proportional to the mass of the object; with heavy objects the load force reaches high values before the mass is overcome and the object lifts off. Conversely, with lighter objects less load force is required before the mass is overcome. The parallel increase in the grip force ensures that there is enough grip force to prevent object slips during this process (Johansson 1996). This parallel coordination of load and grip forces has been demonstrated in dynamic (Flanagan and Wing 1997), as well as static perturbation tasks (Johansson and Westling 1987).

In the following study, the effect of basal ganglia damage on the corrections to the lifting forces was investigated when the relationship between object size and mass was unexpectedly changed. Muller and Abbs (1994) showed that parkinsonian patients were able to adjust their grip force to object mass, suggesting no problems with feedback processing related to basal ganglia dysfunction. It was hypothesized that OF, the individual with unilateral basal ganglia damage, will be able to scale grip force to the true object mass when the visual information about object size will provide accurate information about the mass. However, it was further hypothesized that if the basal ganglia are a part of the discrete event, sensory driven, feedforward correction mechanism, then the damage to this structure will result in the inability to correct the erroneously programmed forces on-line, when the relationship between object size and its mass is unexpectedly changed.

Method

Participants

Three participants were tested, OF (male, 28 years of age) and two male, age matched, healthy controls, C1 (24 years) and C2 (29 years). The participants had normal or corrected to normal vision. All participants provided informed consent before participating in this study. Approval from the University of Waterloo Office of Research Ethics was obtained before testing began.

Apparatus

The object to be grasped was a six-axis force-torque sensor (Nano F/T transducer; ATI Industrial Automation, Garner, NC) with two exchangeable polyethylene plastic cylindrical mass containers with flat grasping surfaces, mounted on each side of the sensor. Changing the cylindrical mass containers resulted in two control test objects that were consistent with a constant density expectation; Big Heavy (6.5 cm and 250 g) and Small Light (4.5 and 150 g). In addition two perturbed objects were also used that were inconsistent with a constant density expectation; Big Light (6.5 cm and 150 g) and Small Heavy (4.5 cm and 250 g).

When the target object was lifted, the grip force was measured along the grip axis defined by the line joining the centers of the two grasp surfaces. The forces were collected at 200 Hz with a resolution of 0.025 N. The load force was defined as the vector sum of the two perpendicular forces acting in the orthogonal plane to the grip force axis. The rates of both the grip and load forces were also calculated. All data were filtered with a 10 Hz dual pass Butterworth filter.

Procedures

The participants were asked to lift the test objects 10 cm from the table surface, hold it for 2 seconds and replace them back on the table. The lifts were performed with the participants' right hand first, followed by the left hand. For each hand, the control objects were presented in the same pseudo random order, each 10 times for a total of 40 trials. Also, for each hand the perturbed objects were presented once for a total of 4 perturbed trials. The order of perturbed object presentations was such that the size of the object coincided with the size of the previous, control presentation. That is, the perturbed Big Light object was presented after the control Big Heavy object and the perturbed Small Heavy object was presented after the control Small Light object.

Statistical Analysis

Control trials.

For the control trials for each participant, separate two way analyses of variance with object (Big Heavy and Small Light) and hand (left and right) as factors were performed on the peak load and grip forces, their timing, and peak rates of generations.

Perturbed trials.

For each participant, hand and control object, 95% confidence intervals around the averages were calculated. The same dependent measures for the perturbed trials as for the control trials were compared against the confidence intervals. To assess the effect of the object perturbation, the responses to objects of the same mass and different sizes were compared. When the value for the perturbed trial fell outside the confidence interval, corrections due to an on-line mechanism were assumed.

Results

All significant effects and their means for the control trials are presented in Table 6. The effects of object perturbation are illustrated in Figure 21 for the right hand of a control participant (C2) and for both hands of OF.

Table 6. Results of the two way ANOVA with factors object (BH – Big Heavy and SL – Small Light) and hand (Right and Left). All effects significant at p<.01 and their associated means and standard deviations for OF and the two control participants are presented. Note that there were no interactions between object and hand for any of the dependent measures.

			OF		C1		C2	
			F(1,36)	Mean (SD)	F(1,36)	Mean (SD)	F(1,36)	Mean (SD)
PGF (N)	Object	BH	45.7	4.53 (.33)	91.8	5.04 (.31)	42.6	3.37 (.31)
		SL		2.22 (.34)		1.6 (.15)		1.37 (.10)
	Hand	Right	36.2	2.34 (.25)				
		Left		4.41 (.43)				
GF rate (N/s)	Object	BH	23.4	36.4 (3.8)	97.6	46.6 (2.2)	29.8	35.6 (3.4)
		SL		19.1 (3.0)		18.8 (1.6)		16.5 (1.2)
	Hand	Right	31.3	17.6 (1.8)				
		Left		37.8 (4.2)				
TTPGF (ms)	Object	BH	9.9	244 (15)	14.2	233 (15)	33.5	189 (5)
		SL		161 (20)		196 (13)		145 (5)
	Hand	Right						
		Left						
PLF (N)	Object	BH	4.2	.586 (.063)	33.6	.95 (.094)	11.6	.50 (.07)
		SL		.398 (.038)		.37 (.056)		.23 (.03)
	Hand	Right			6.4	.78 (.11)		
		Left				.53 (.07)		
LF rate (N/s)	Object	BH			46.7	14.6 (1.4)	7.6	8.05 (1.22)
		SL				6.2 (.59)		4.55 (.59)
	Hand	Right			15.6	12.8 (1.78)		
		Left				8.03 (.73)		
TTPLF (s)	Object	BH	4.5	204 (11)				
		SL		153 (21)				
	Hand	Right						
		Left						

Control trials

Control Participants. For the two control participants the peak grip force and the associated rates of production were higher, and time to peak grip force was longer, for the Big Heavy than for the Small Light object. The peak load forces and associated rates for each of the control participants were influenced by the mass of the object. Peak load force and its rate were higher for the Big Heavy object than for the Small Light object.

There were no hand differences for either of the control participants when grip force, grip rate or time to peak grip force were analyzed. However, one control participant showed an effect for hand, where the right hand generated more peak load force at higher rates when picking up the control objects.

OF. For OF the peak grip force and the associated rates of production were higher, and the time to peak grip force was longer, for the Big Heavy than for the Small Light object. Peak load force and time to peak load force also showed effects of object such that they were greater for the Big Heavy object compared to the Small Light object.

OF showed higher grip forces and rates of generation for the ipsilesional (left) hand. There were no other hand effects.

The grip and load force findings suggest that the control participants were able to scale their peak grip and load forces in anticipation of the object mass, before object contact was made. On the contrary, since the initial rates of load force generation did not differ between the two objects, OF did not show similar expectancy of the object mass prior to the contact. Instead, the increased peak load force for the large object was achieved through a longer force generation time. However, there was evidence of scaling for object mass when OF's grip force was examined. Also, OF showed evidence of altered motor performance in his contralesional hand.

Perturbed trials

Control Participants. Figure 21 shows a comparison of performance when lifting the control objects, compared to the perturbed trials, for a single hand for one control participant and both hands for OF. Only one hand is presented for the control participant.

and only data for one individual is shown because both control participants showed the same pattern for both hands. Note that for the control participant the performance on the perturbed trials for peak grip and load force and the associated rates was always different from that of the control trials. As reflected by the performance on the perturbed trials being outside the confidence intervals, peak grip and load force and their rates were scaled to the size of the object rather than to its mass. However, in accordance with a probing strategy, when the object was lighter than expected (refer to the Small Light column in Table 6), the generation of peak grip and load force stopped as soon as the necessary force was generated. Alternatively, when the object was heavier than anticipated, time to peak force was longer than generated in the control trials.

OF. For most dependent measures, both the contralesional and ipsilesional hands of OF showed that the performance on the perturbed trials did not differ (was within the confidence interval) compared to the control trials. Performance was slightly outside the confidence interval for peak grip force for both hands, and for the ipsilesional hand peak grip rate, and time to peak grip and load force, were also outside the confidence intervals. However, close examination of these effects shows that they are marginally outside of the confidence interval. Also, the timing effects are not in a systematic direction (for example it is expected that shorter probing times would be produced when perturbed objects are lighter than expected). Peak grip force for both hands, while only slightly larger than the confidence interval, are in the predicted directions. This suggests that for both hands, there was limited on-line control such that forces were anticipated prior to the initiation of the trial, on the basis of the size of the object.

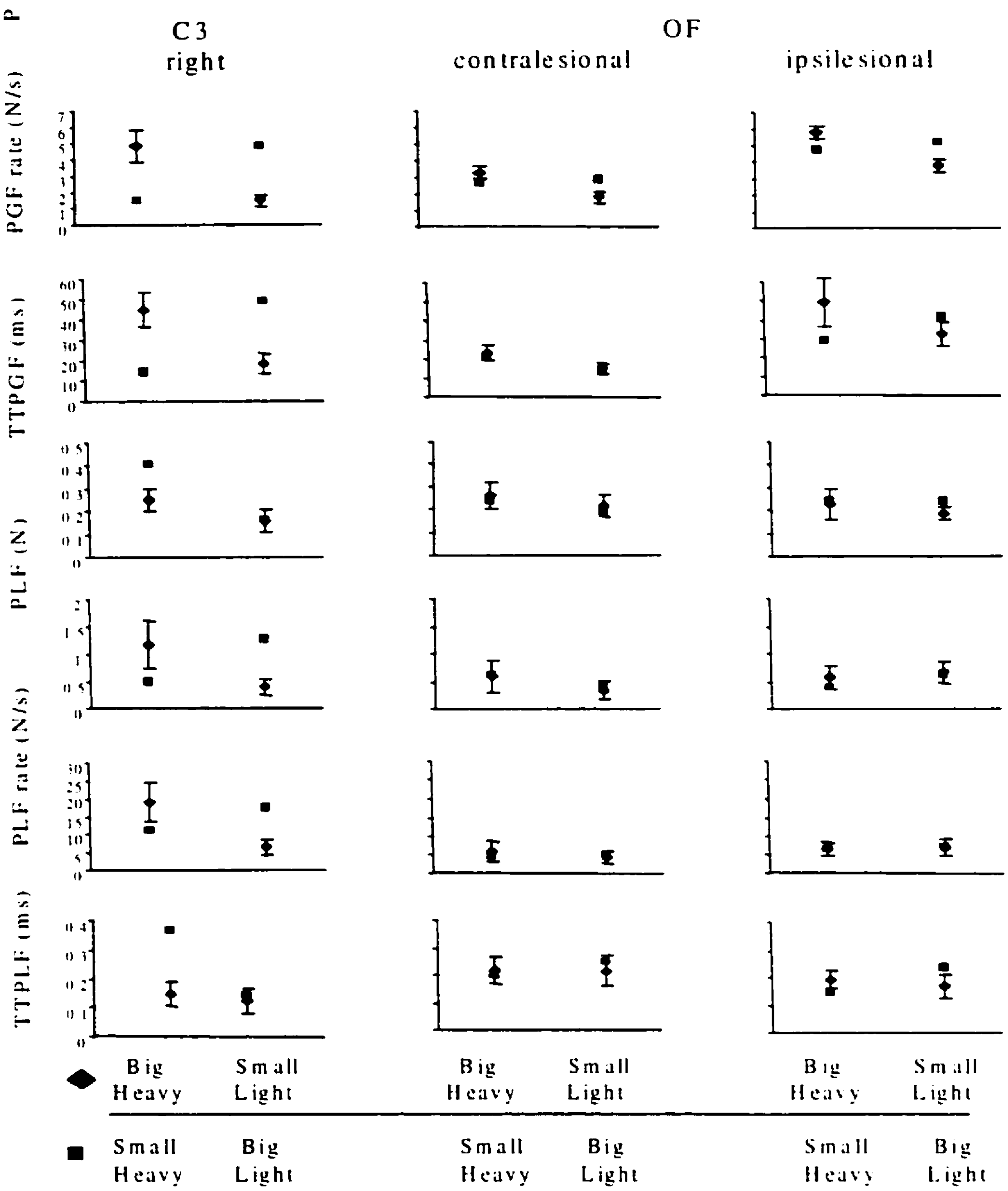

Figure 21. This figure shows where the perturbed trials lie relative to the confidence interval for the object size perturbation. The following dependent measures are plotted: peak grip force, its rate and timing (PGF, PGF rate, TTPGF) and peak load force, its rate and timing.

Discussion

The main objective of this test was to assess the ability of an individual with unilateral basal ganglia damage to correct grip and load forces on-line to unexpected perturbations of the size-mass relationship. It has been shown previously that healthy participants program their finger forces prior to object contact based on the size-mass relationship established on previous lifts (Gordon et al. 1993). When this relationship is unexpectedly perturbed, and the size of the object does not coincide with its expected mass, the grip and load forces are corrected on-line based on tactile information from the fingers once the contact with the object is made (Johansson and Westling 1987; 1988).

In the present study the control participants showed the expected results, where the finger forces were scaled based on the object size prior to contact, and when this relationship was disturbed the forces were corrected to scale to the true object mass. This is evidenced in Figure 22, where the grip force was plotted as a function of the load force. When a Big Light object was presented the initial generation of the grip force was the same as for the Big Heavy object, however, since the load force required to lift Big Light was smaller than that for the Heavy object, the grip force was adjusted on-line to meet this requirement. Conversely, when the Small Heavy object was lifted, the initial grip force generation was similar to that of the Small Light object, however, the load force required for the lift off was greater than anticipated, and more grip force was subsequently generated. This was not the case for the individual with unilateral basal ganglia damage. The results showed that OF was able to scale grip and load forces to the object mass, when the size-mass relationship varied in a predictable manner. That is, the forces were greater for Big Heavy than for the Small Light objects. Furthermore, the grip forces produced by the ipsilesional hand were greater than the ones produced by the contralesional hand. However, the unilateral basal ganglia damage was related to the lack of on-line corrections bilaterally. This is evidenced in Figure 22, where the grip forces employed to lift the Big Light and Big Heavy objects were independent of the load force required. This is in disagreement with the proposed coordination of grip and load forces in healthy participants proposed by Flanagan and Wing (1997), and Johansson and Westling (1988), since OF was not correcting grip forces on-line. Instead, he adopted a strategy of increased overall grip force, and thus safety margins such that all objects in the present test could be lifted, regardless of their masses.

In summary, this study showed that the unilateral basal ganglia damage affected the ability to correct for the unexpected perturbation to the object size-mass relationship, bilaterally. The production of grip and load forces was stereotypical and was scaled to the object size. The ability to scale the fingertip forces to the two different control object size-mass combinations, indicates that OF was able to integrate the visual and haptic feedback to develop a memorial representation of object mass that could be accessed on the next trial. However, for the basal ganglia to be involved in the on-line adjustments of the erroneously programmed initial grip forces and with damage to this structure the process is disrupted.

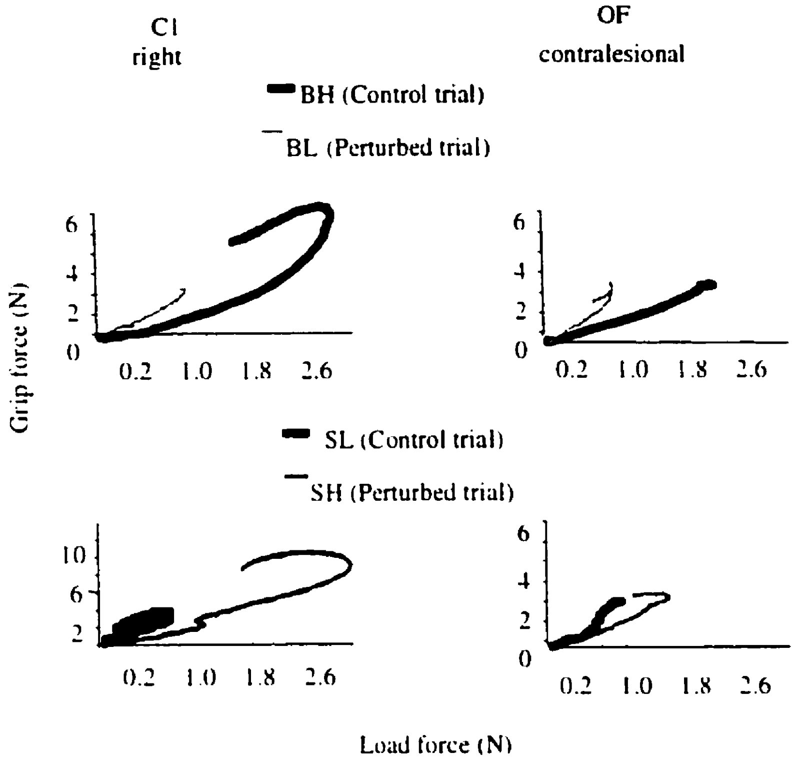

Figure 22. These phase plots represent the coordination of grip and load forces for two perturbed and two typical control trials for the right hand of control participant and OF's contralesional hand. For the control participant, as the required load force increases, so does the grip force. For OF, grip force always reached the same level, despite the changes in load force requirements due to object mass. BH = Big Heavy, BL = Big Light, SL= Small Light, SH = Small Heavy.

Experiment 4 General Discussion

The discrete event, sensory driven, feedforward model proposed by Johansson and colleagues (Johansson 1996; Johansson and Cole 1994) is one of the most prevalent models of grasp control. The main premises of this sensorimotor integration model is that grasp generation proceeds in well defined phases. As the grasp unfolds, certain sensory events from the fingertips are expected by the central nervous system, and when they arrive, the next phase of the grasp is triggered. However, if these events arrive with an inappropriate timing, sets of corrective commands are programmed ahead of time, and are used to correct the grasp generation without a reliance on time consuming, feedback triggered correction loops (Johansson 1996).

It has been proposed that the basal ganglia may be involved in using sensory information to guide the motor commands to control grasping tasks. Based on work with parkinsonian patients, Muller and Abbs (1990) were able to show that although their patients were able to scale the finger forces to object mass, the forces were achieved with greater onset latencies, suggesting an inability to use the arriving feedback to initiate the next phase of the grasp. Also, they showed that the forces employed had higher values, indicating increased safety margins.

The present results of Test 1 and Test 2 support the notion of the involvement of the basal ganglia in the integration of sensory information to form an appropriate grasp. In Test 1, the participants lifted objects of different sizes, but with a constant mass, thus the size and mass of the object were incongruent at all times. In Test 2, in 90% of the trials the size and mass of the object were congruent, and only on 10% of the trials this congruency was disrupted. Based on Test 1, healthy participants showed the expected scaling of grip force to object size, where higher grip forces were produced to lift larger object (Gordon et al. 1991; 1993). OF did not show the same scaling, instead, the grip forces produced were higher than necessary indicating higher safety margins. In Test 2, OF was able scale the grip and load forces, in accordance with the size-mass relationship. However, when this relationship was unexpectedly interrupted, OF was unable to correct for this perturbation on-line. Together these findings indicate that depending on the experimental procedure, OF picked the most reliable source of sensory information to guide his movements. In Test 1, visual information was not relevant to the task, as the object size did not carry any information about its mass. Thus, OF did not combine these two sources of afferent information to program grip forces, but relied primarily on the haptic information from previous lifts. On the contrary, in Test 2, during the control trials, object size and its mass covaried, and thus both sources were equally informative. In the perturbed trials, OF showed high reliance on the visual cues to program his grasp forces. Furthermore, there was no support for the haptic based on-line control of grasp when the initial programming was erroneous.

Surprisingly, in both tests, the unilateral basal ganglia damage had a bilateral effect on the grip force production. The influence of the basal ganglia on motor control is not achieved through the connection of these structures with motor neurons in the spinal cord or in the brainstem, but rather by influencing the outputs of the motor cortex. A widespread area of the cerebral cortex projects to specific regions of the basal ganglia, which are then projected back to the cerebral cortex (typically to frontal or limbic regions) via the thalamus (Nolte 1999). Furthermore, the two hemispheres are widely connected to each other though comissural fibers, the largest of them being corpus callosum. Thus the bilateral influence of unilateral basal ganglia damage could be due to the exchange of information at the cortical, rather then at the subcortical level. Johansson and Westling's (1984; 1988) observation that the information about object mass and frictional characteristics can be transferred from one hand to another in the subsequent manipulation of the same object, gives further support to the notion that the integration of vision and haptics takes place at a higher (i.e. cortical) level. Furthermore, Gordon et al. (1994) studied developmental progress of transfer of information about object mass from one hand to another. An individual with a complete corpus callosum agenesis was studied in addition to a number of age groups. The results showed that for healthy participants the information about object mass can be transferred from one hand to another. This was not the case for the a-callosall patient, who was able to scale grip forces to object mass with both hands, however there was no evidence of transfer of haptic information from one hemisphere to another. This further supports the notion that the representation of the object mass is a cortical function, that in healthy individuals is distributed amongst the hemispheres. Thus, unilateral disruption in haptic information processing could potentially lead to bilateral deficits in the control of forces.

CHAPTER 6: GENERAL DISCUSSION

When we move, the correctness of the movement can be monitored by the motor system in three ways. It can make use of the motor outflow (the correctness of the efferent copy of the motor command used to program the movement), it can use the sensory inflow (the feedback based control), or it can combine the two sources of information to form a forward model of motor behavior. The main problem with motor outflow control is the lack of a reference of correctness of the initial motor command. This would lead to the inability to correct any errors in the command based on the actual outcome of the movement (Evarts 1973). There are three fundamental problems with the feedback based computational approaches to motor control that are relevant to the present work. First, one of the major problems identified in feedback based motor control are delays created by the feedback loops. For example, visual feedback loops are believed to be in the order of 100 to 150 ms (Paulignan et al. 1991a), haptic loops are faster, at about 74+/- 9 ms (Johansson and Westling 1988), which is equivalent to the long latency reflex loops (Marsden et al. 1972). With feedback loops of this duration an accurate initial control of arm trajectory or grip force production seems almost impossible. The second problem, related to the feedback delays, is the initial control of movement. Contrary to the visual system, where the sensory information is present prior to the initiation of the movement, grip force production is even more prone to errors due to the feedback delays. For the control of grasping, if the control was based on feedback alone, the initial 40-80 ms of the grasp would have to be performed with a complete absence of sensory information. The anticipatory-forward model overcomes these problems and enables the control of grasp to be based on other modalities, such as vision, during the initial phase.

The existence of an anticipatory-forward model can also help to understand motor learning. The model can be used to transform errors between the desired and the actual sensory consequences of the movement into corresponding errors in the motor command, therefore providing appropriate learning signals.

The notion of an anticipatory-forward model, which mimics the behavior of a natural process, has been considered to be an important concept in the motor control domain (Wolpert et al. 1995). Although such anticipatory-forward models have been shown to be of theoretical value, the actual existence of these models is still a topic of debate. The major findings presented in this thesis will be discussed in terms of the two most recent models of motor control as they pertain to the control of grip forces (Johansson and Cole 1994; Wolpert and Kawato 1997). Also, these models will be discussed in conjunction with the leaning specificity theory proposed by Proteau et al. (1992).

Wolpert and Kawato (1997) and Wolpert and Ghahramani (2000) proposed a general computational model that explains the formation of memorial representations of movement. With respect to lifting tasks, the basic concept of this model is that as the movement unfolds, multiple forward models are run that mimic the motor output of previous lifts. Each forward model generates predicted sensory feedback that should be received from the digits. Furthermore, each of the forward models is coupled with an inverse model, which, if the sensory feedback matches the predicted feedback, will be selected, stored and used to determine appropriate motor commands for the subsequent interactions with similar objects. Johansson and Westling (1988) and Johansson and Cole (1994) have proposed a comparable feedforward model for grasp control. In their view, a "sensorimotor set" or a task relevant synergy develops through previous experiences and depends on the goal of the movement, the context, and the specific phase of movement.

The main premise of both models is that with practice, memorial representations of appropriate motor commands are created and stored for use in future interactions with similar objects. Also, for both models, errors between the anticipated and the actual feedback are the main determinants of the estimate of the correctness of the motor command. Although both models speculate on the nature of sensorimotor integration for movement planning and execution, they do not directly address the issue of multimodal sensory inputs relevant to that integration. These models need to address whether the use of feedback is context dependent, and how one feedback source is determined to be more reliable than the others.

The development of the reliance on one source of sensory input over another has been previously addressed by the learning specificity theory proposed by Proteau (1992). The theory states that motor learning is specific to the sources of information available during practice. For example, when practicing a specific motor task without visual information, based on other sensory information, such as proprioception, the addition of vision in a later transfer task can be detrimental to performance, despite the increase in the overall amount of information available. The underlying mechanism for the specificity of learning hypothesis comes from the recognition of the fact that increases in performance through practice are not only related to the refinement of motor planning, but also to the refinement of the error detection and correction mechanisms. In other words, the error detection and correction mechanism developed through practice is specific to the most reliable sources of information used during the practice (Proteau 1992; Proteau et al. 1998).

In summary, the two models of sensorimotor integration depend highly on the elimination of error in the initial motor command. The command with the least amount of error between the anticipated and the actual error is stored in memory and used for interactions with similar objects in the future. However, both models ignore the fact that the haptic information regarding the error between the anticipated and actual feedback can not always be used in the programming of the initial command. In the case of grip control, the initial programming of the grip forces are based on vision, however, in the later stages the haptic feedback is used to determine the correctness of the initial motor command. Thus, multimodal sensory integration should be added to these models.

Multisensory (Joined) model

The major premise of the new, multisensory model is that, with practice, the most reliable source of feedback information for a particular task is selected and used. This selection depends on the elimination of the difference between the predicted and actual feedback from the movement. This is achieved by a weighting function, which assigns specific rating factors to each of the feedback information sources available during the preparation and execution of the movement. If multiple sources of information are available, the forward model runs multiple source-related predictions of the expected sensory consequences. As the movement unfolds each of the available sources of feedback information results in movement specific feedback. The predicted feedback consequences are then compared to their actual counterpart and the source that yields the least amount of error is assigned the highest value in the weighting function. The inverse model selects and stores the most appropriate motor command responsible for the change in the state, together with the ratings of the feedback sources. On subsequent interactions with similar objects in a similar context, the stored motor command will be retrieved from memory and used to generate the appropriate movement. However, during this movement the highest rated source of feedback information from the previous movement will be selected as the most accurate feedback source.

To illustrate the operation of this model as it pertains to prehension, a task with three available sources of feedback information that include visual and haptic information will be used. In this hypothetical experiment, the participants would be asked to lift objects of the same mass but different sizes, and different frictional characteristics. Cadoret and Smith (1996) have shown that more grip force is required to lift objects with low a coefficient of friction. Also, it is difficult to visually perceive frictional characteristics of an object before the contact is made with the fingers. Furthermore, the objects with the same frictional characteristics would be presented in a blocked fashion, however the size of these objects would be randomized. The sensorimotor system runs predictions of the sensory consequences based on each of these two sources of sensory input. When the actual feedback arrives, the predicted and the actual consequences are compared and the modality with the least amount of deviance between the predicted and actual feedback is assigned the highest rating. A similar rating system has been suggested previously by Young et al. (1993) in haptically based depth perception. In this example, object size (detected through vision) provides very little information about the frictional characteristics and thus it will be assigned a low rating value in the weighting function. The best predictor of the grip force necessary to lift the object without dropping it in this example is haptics, which delivers information about the frictional characteristics between the object and the interacting digits. Due to the blocking from trial to trial, haptics becomes the major predictor of the expected sensory feedback, and thus the weighting assigned to this source increases.

Fit of the model and the present experimental results.

Visual sensory input is very important for the act of prehension. Vision is primarily used to bring the hand towards the object and at the same time to form an appropriate grasp (Jeannerod 1981). It is also used in the anticipatory preparation of the motor command for grip forces necessary to grasp and lift an object. In Experiment 1 it has been shown that the responses to perturbation when reaching and grasping objects in a virtual reality environment (where haptic info is unavailable) are controlled in a similar way to those in a normal environment. Since this task is primarily dependent on visual inputs, this source of information should receive the highest rating. The haptic information is not highly relevant to the task of transporting the hand and shaping the finger opening so the assigned rating to this source of feedback would be naturally small. The results of this study support the notion that the lack of haptics should not affect hand transport and aperture formation correction times towards visually perturbed objects, since both phases did not depend on haptic stimulation.

However, when visual and haptic sources of information are both available, the sensorimotor system uses them both to anticipate the fingertip forces necessary for lifting. Based on our second study it can be concluded that the system chooses the most reliable source of information in the programming of grip forces in accordance with the model's prediction. The most striking example is from Experiment 2 when the color cues were introduced in the practice phase, and removed in the transfer phase. The haptic information was ignored by the participants, and the grip forces that were produced were scaled to the color cue rather than to the object mass. On the contrary, when no color cues were present in either the practice or transfer phases, and the practice phase was blocked by object mass, the participants relied solely on the haptic information acquired in previous lifts. This suggests that the formation of the anticipatory model is a flexible process that depends on the availability and reliability of this information during the formation of the model.

The flexibility of the process of integrating vision and haptics was further supported by the findings of grasp control in a dynamic situation from Experiment 3. The results have shown that when an object is moving, both vision and haptics can contribute to the on-line control of grasp. The sensorimotor system can also form and use higher order information like linear momentum of an object based on both modalities. In such a task, visual information about object velocity is relevant to the interception task (Carnahan and McFyaden 1996). Also, the haptic information is highly relevant to the task in providing information about the mass of the object (Johansson 1991) as well as the torque values created on the fingers (Kinoshita et al. 1997). According to the multisensory model, both vision and haptics should have equivalently high rating values, which is supported by the results of this study.

In Experiment 4 however, it was also demonstrated that this flexible process of variable integration of vision and haptics is very fragile. Healthy participants have the ability to shuffle between various types of sensory information, depending on their relative importance and reliability to the task, but in an individual with a lesion to basal ganglia this ability was not present. The inability to use vision and haptics congruently was demonstrated by the observation that OF was not fooled by the size-mass illusion in the same way as the control participants. Also, when an unexpected perturbation was introduced, where the object size and mass relationship did not match what was anticipated, the lesion to the basal ganglia resulted in an inability to modulate grip forces on-line. Miall et al. (1993) proposed that the cerebellum is the site for the forward model. Present results suggest that the basal ganglia also play an important role in the sensorimotor integration circuitry. Lesion to these structures resulted in the inability of the participant to assign appropriate ratings to the visual and haptic information based on their relevance to the task.

In conclusion, the major contribution of the multisensory model to the understanding of the integration of vision and haptics is that in addition to the sensorimotor integration proposed by the previous models, this model incorporates the importance of multimodal sensory integration. By combining the most pertinent models of grasp control with learning specificity theory, the multisensory model can explain task dependent integration of vision and haptics. This model can also explain the conflicting results of visual and haptic dominance presented by Festinger (1967), Atkins et al. (2001), as well as the adaptation to the size-mass illusion shown by Flanagan and Beltzner (2000).

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