Learning and Decay of Prediction in Object Manipulation

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Witney, Alice G., Susan J. Goodbody, and Daniel M. Wolpert. Learning and decay of prediction in object manipulation. *J Neurophysiol* 84: 334–343, 2000. Anticipating the consequences of our own actions is a fundamental component of normal sensorimotor control and is seen, for example, during the manipulation of objects. When one hand pulls on an object held in the other hand, there is an anticipatory increase in grip force in the restraining hand that prevents the object from slipping. This anticipation is thought to rely on a forward internal model of the manipulated object and motor system, enabling the prediction of the consequences of our motor commands. Here we investigate the development of such a predictive response. Each hand held an object that was attached to its own torque motor. On each trial the subject was required to pull on the object held in the left hand and to maintain the position of the object held in the right hand. The torque motors were computer controlled so that the objects could be either "linked" so that the forces on the objects were equal and opposite, acting as though they were a single object, or "unlinked," so that they acted as two independent objects. A predictive response in the restraining hand is only necessary when the objects are linked and is unnecessary in the unlinked condition where there is no risk of the object slipping. To examine the learning and decay of predictive responses, we measured the grip force responses during unlinked trials that followed a linked trial. After a single linked trial, anticipatory grip force was quick to develop, but decayed slowly over the following unlinked trials. Varying the time between trials showed that the rate of decay depended on the number of trials since the last linked trial rather than time. Increasing the frequency of linked trials showed an increased level of subsequent grip force modulation, but did not alter the decay rate. When the torque motors simulated a linked object that did not have normal physical properties, prediction was reduced. These results show that the use of predictive responses has a different time course for learning and decay, and the response depends on experience and the physical properties of the objects.

INTRODUCTION

Prediction is a fundamental component of normal sensorimotor control. To predict the consequence of the descending motor command, an internal forward model is required (Jordan 1995; Miall and Wolpert 1996; Wolpert 1997). This model captures the behavior of the motor system and is therefore able to predict the sensory consequences of a motor command (Miall and Wolpert 1996; Wolpert 1997). Recent studies have shown that this estimate is precise in predicting both the nature and timing of the sensory consequences of an action (Blakemore et al. 1999). However, since the consequences of a motor command change with growth and depend on the objects we interact with, this precision cannot be innate (Forssberg et al. 1991). Therefore a mechanism is required to adapt the predictive processes, and it is this adaptation of the forward model that forms the focus of this paper.

Here we use a grip-force modulation paradigm to study forward model learning. When we hold an object in a precision grip between the thumb and forefinger, sufficient grip force (perpendicular to the surfaces) must be generated to prevent the object from slipping (Johansson 1996; Johansson and Cole 1992, 1994; Johansson and Westling 1984; Johansson et al. 1992b). The level of grip force required depends on the load force (tangential to the surfaces) the object exerts on the fingers, that is its weight when at rest, and the frictional properties of the surface of the object. In general, subjects avoid excessive grip forces; applying enough to prevent the object slipping with grip force, rarely exceeding the minimum grip force by more than a 30% safety margin (Johansson and Cole 1992). Therefore as the load force increases, the grip force must also increase to prevent slippage and to maintain this safety margin. When the load force is unexpectedly increased, for example by someone else tapping on the object, a reactive grip force response is triggered by the cutaneous receptors in the fingertips with a latency of around 60–80 ms (Cole and Abbs 1988; Johansson and Westling 1988; Johansson et al. 1992a). However, when the subject's own movements cause the load force to increase, for example by accelerating the object with the gripping hand (Flanagan and Wing 1993, 1995), or pushing on the object with the other hand (Blakemore et al. 1998; Johansson and Westling 1984; Johansson et al. 1992b; Witney et al. 1999), an anticipatory grip force response is seen, with around zero lag compared with the load force changes. Due to the inevitable delays from cutaneous afferents, this predictive modulation of grip force cannot be a reaction to peripheral feedback (Flanagan and Wing 1995; Forssberg et al. 1992; Johansson and Westling 1984). Therefore these anticipatory grip force increases must be generated by using a prediction of the consequences of the action (Blakemore et al. 1998; Flanagan and Tresilian 1994; Flanagan and Wing 1993, 1997).

The predictive coupling between grip force and load force develops throughout childhood reaching adult performance around age 8 yr (Eliasson et al. 1995; Forssberg et al. 1991, 1992, 1995). Several studies have examined how subjects perform when the normal physical properties of an object, such as its weight, frictional surfaces, and surface orientation, are

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changed on each trial (Burstedt et al. 1998; Edin et al. 1992; Gordon et al. 1993; Jenmalm and Johansson 1997; Johansson and Westling 1984). These show a rapid updating within one trial to the new situation. Similarly, studies of unusual dynamic properties of objects show quick learning of the new dynamics (Flanagan and Wing 1997; Wing and Flanagan 1998). However, when a delay is introduced between the action of one hand and the consequence on the load, learning takes over 50 trials (Witney et al. 1999).

Here we have developed a paradigm that allows us to separate the anticipatory grip force from the grip force due to reactive processes, thereby allowing an estimate of the predictive response. To achieve this we used a bimanual task in which each hand held a separate object mounted on a torque motor. By computer controlling the forces generated by the motors, we could create a "virtual" object held between the two hands, which could behave differently on each trial. On each trial, the subject had to generate a movement of the object held in the left hand. The motion of this left hand acted against a simulated stiff spring attached to the objects's initial position. There were two possible consequences of this action of the left hand. In "linked" trials the motion of the left hand caused an equal and opposite force to be generated on the object in the right hand independent of the right hand object's position. Therefore during "linked trials" the system behaved as though there were a real physical object held between the hands with each hand experiencing an equal and opposite force. We have previously shown that when this situation is experienced, predictive grip force modulation is seen in the right hand (Witney et al. 1999). In "unlinked" trials, no force was generated on the right hand object. Therefore in unlinked trials the two objects behave independently, and so predictive grip force modulation in the right hand is not appropriate. In both linked and unlinked trials the forces generated on the left hand object are the same. We examined the grip force in the right hand with the expectation that linked trials will result in predictive grip force modulation, and unlinked trials may suppress predictive modulation. The unlinked trials can be used to assess the development of the forward model. In these trials, any change in grip force seen in the right hand reflects purely predictive components as there is no load force generated on the fingers of this hand. Therefore any grip force response that occurs in unlinked trials must have occurred as a consequence of an internal model.

Three different situations were compared using this paradigm (one-link, three-link, and interval conditions). In the "one-link" condition, a single linked trial occurred on average every eight movements, whereas in the "three-link" condition, three linked trials were presented sequentially on average every eight movements. By examining the grip force in the subsequent unlinked trials in the different conditions, we could assess the time course of internal model generation during the linked movements, and its extinction in the subsequent unlinked movements. To examine whether the rate of extinction in these unlinked movements is determined by time or trials, we examined a one-link condition in which the inter-trial interval was doubled ("interval").

In a fourth condition the linked trials were modified so that we could examine whether such motor learning relies purely on causality, or on normally experienced physics. To do this we examined a one-link condition in which the torque motor on the left-hand object was turned off ("nonphysical"). On the linked trials of this condition, the left hand movement induced a load force on the right hand object, as in the previous conditions proportional to the distance moved by the left hand, but the combined forces experienced by the two hands is not consistent with a passive physical object.

METHODS

Subjects

Eight right-handed subjects (6 male, 2 female), 23–30 yr of age, who were naive to the research aims, participated in the study. None of the subjects reported any sensory or motor deficits. Subjects gave informed consent before participating in the study.

Apparatus

A schematic diagram of the apparatus is shown in Fig. 1. Subjects held separate cylindrical objects, each of which had two parallel grip surfaces of 30 mm diam covered with sandpaper (Grade No. 210, spaced 40 mm apart). The mass of each object was 50 g with the center of mass midway between the two grip surfaces. The object held in the right (restraining) hand had a six-axis cylindrical force transducer (Nano, ATI) embedded in it. The force transducer allowed three translational forces at the thumb to be measured with an accuracy of 0.05 N including cross-talk. This allowed a measurement of the grip force and load force in the right hand. Each object was attached by an aluminum rod of length 50 mm to a torque motor (Phantom Haptic Interfaces, Sensable Devices). The position of the motor was sampled on-line by an optical encoder (10,160 counts per revolution) and filtered with a 35-Hz cutoff low-pass filter. The mechanical bandwidth of the system was 65 Hz (where the gain dropped to $1/\sqrt{2}$). The torques generated by the motor were computer controlled at 1,000 Hz. The subject's right forearm was anchored with velcro straps, and for further stability they grasped a vertically oriented aluminum rod with their three ulnar fingers. A horizontal wooden rod was then positioned over the right thumb and forefinger to minimize upward motion. These measures ensured that the subject's thumb and index finger were used to maintain object stability by changing grip levels rather than producing a more general postural response.

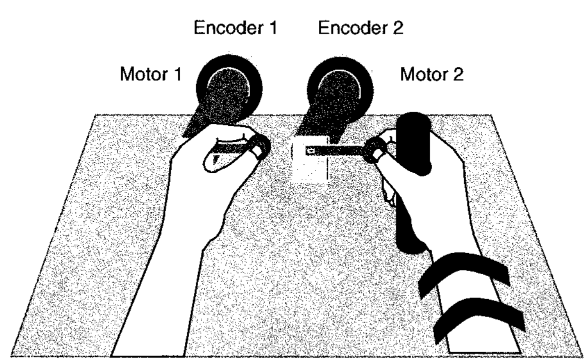

FIG. 1. Schematic diagram of the apparatus used to create a virtual object. Each hand held an object that was attached to its own torque motor. The subject was required to pull up on the object held in the left hand and to maintain the position of the object held in the right hand. The torque motors were computer controlled so that the objects could be either "linked," so that they acted as a single object, or "unlinked," so that they acted as 2 independent objects. The subject's right forearm was anchored with Velcro straps and for further stability, they grasped a vertically oriented aluminum rod with their 3 ulnar fingers. A horizontal wooden rod (not shown) was positioned over the right thumb and forefinger to minimize upward motion.

Procedure

Each subject participated in all four conditions in a balanced order. In every condition subjects were instructed to keep their right hand still and to prevent the gripped object from slipping from their grasp. Subjects were given up to 40 practice trials, comprising linked and unlinked trials from the one-link and the non-physical condition, before the start of the experiment, so that they were able to produce the desired movement profile.

Before each trial, subjects positioned the objects in a starting position shown in Fig. 1. Subjects could look at the apparatus, although they were required to focus on a monitor during the trials. The position of the object held in the subject's left hand was displayed as a scrolling trace on a computer monitor. Each trial lasted 3 s, and a brief tone was played at a randomly selected time between 100 and 300 ms into the trial. Subjects were instructed that, on hearing the tone, they should use their left hand to produce a brief 6-mm upward movement of the object held in the left hand returning quickly to the initial position. The required amplitude of 6 mm was displayed as a constant horizontal line on the scrolling trace. All four conditions consisted of 25 batches of 8 trials. To prevent fatigue, short rest periods were given every 40 trials.

One-link condition

In this condition either linked or unlinked trials were experienced. In a linked trial the objects behaved as a single stiff object held between the hands with the motion of the left hand producing equal and opposite load forces on the two hands. In unlinked trials, the two objects behaved independently. To ensure the load forces to the left hand were the same during linked and unlinked trials, the motion of the left hand acted against a simulated stiff spring of 1 N/mm attached to the left hand object's initial position. On linked trials, a load force equal and opposite to the load force on the left hand object, was applied to the right hand object. On unlinked trials, no load force was generated on the right hand object. To prevent any prior knowledge of whether the trial was linked or unlinked, based on cues from accidental small movements of the left hand, the force on the right object was zero until the tone in all trials. There was one linked trial and seven unlinked trials in each batch of eight trials. For each batch, the linked trial randomly occurred as one of the first three trials. Each linked trial was, therefore followed by at least five, and at most nine unlinked trials (when the 1st trial is linked in one batch and the 3rd in the consecutive batch). There was, therefore a total of 25 linked trials and 175 unlinked trials within the condition.

Three-link condition

The linked and unlinked trials were the same as in the one-link condition. However, in this condition, three successive linked trials occurred in each batch of eight trials. The start of the run of three linked trials was randomized to start on one of the first three trials in the batch of eight. The last linked trial was therefore followed by at least three unlinked trials, and at most seven unlinked trials. There was a total of 75 linked trials and 125 unlinked trials in the condition.

Interval condition

This condition was identical to the one-link condition except that the inter-trial interval was increased to 3 s, so that together with the trial time of 3 s, each movement occurred on average every 6 s. During the intertrial interval the objects were unlinked. As subjects do not move during this period and remain close to the zero position, they are unlikely to be able to tell whether the objects are linked or unlinked.

Non-physical condition

Unlike the other conditions, in the non-physical condition, the motor attached to the left hand object produced no forces. Therefore for linked trials the force on the right hand object was generated as 1N/mm moved by the left hand. For unlinked trials both motors were turned off. The force required to move the left hand object when the motors were turned off was <0.4 N.

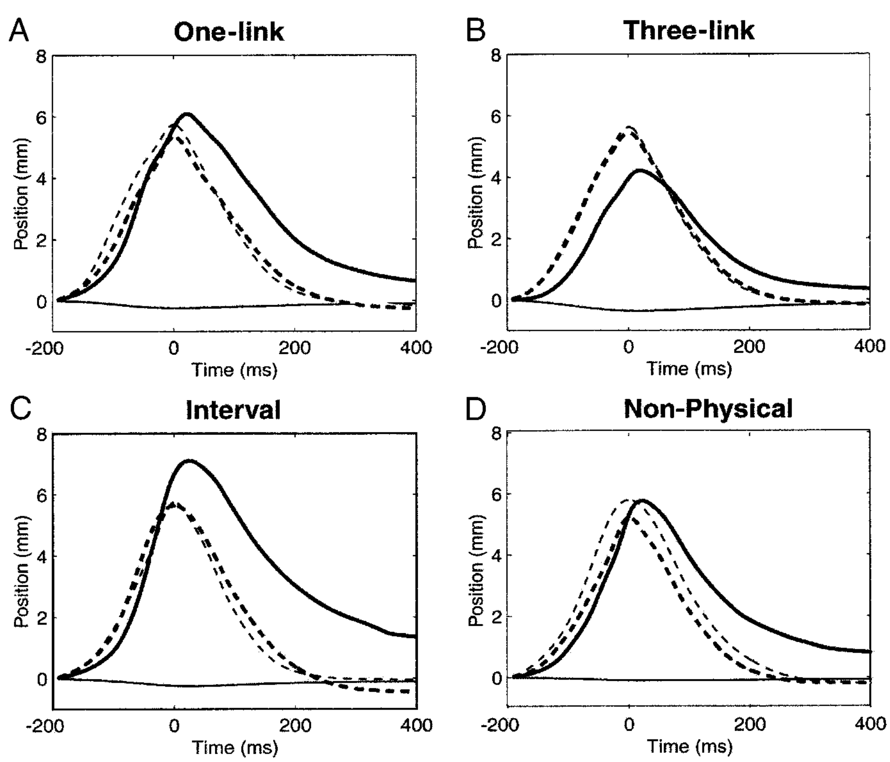

FIG. 2. Hand positions for the One-Link (*A*), Three-Link (*B*), Interval (*C*), and Non-Physical (*D*) conditions. The left hand position (dashed) and right hand position (solid) are the average of each subject's average. Thick lines are for linked trials and thin lines for unlinked trials. Zero time is taken as the time of the maximum left hand discursion.

Analysis

For each trial the position of each object and the three translational forces on the object held in the right hand were recorded at 200 Hz. The translational forces perpendicular to the surface represent the total grip force generate between thumb and finger. The tangential force represents the load on the thumb. As the object was symmetric about the load generation axis, we assumed that the load was evenly distributed between the thumb and finger so that the total load was twice the load measured at the thumb. From these measurements we extracted the grip force and total load force on the right hand object. To quantify the development and decay of anticipatory grip force, the amplitude and timing of the peak grip force modulation was found for each trial. Grip force modulation was taken as the difference between the peak grip force and the baseline grip (the average grip in the 1st 100 ms of each trial). For the analysis of peak grip force timing, trials were excluded if the peak in grip force was outside a 400-ms window either side of the peak left hand discursion where lag estimates would be unreliable. Due to this criterion 6% of the lag values were excluded from the statistical analysis. This measure of grip force modulation, rather than actual grip force, was used as increased modulation is the characteristic feature of the predictive grip response (Johansson and Cole 1992). The grip force modulation lag was calculated as the difference between the time of the peak grip force and the time of the peak discursion of the left hand. The time of peak discursion of the left hand is the time of the peak load force in the linked trials and therefore is the time that the load force would have been expected in the unlinked trials.

To examine any differences between the four conditions in the linked trials, in both magnitude and lag of the grip force response, a repeated measures MANOVA was performed with factor of condition (4 levels). The change in the magnitude and timing of the grip force modulation during each successive linked trial in the three-link condition was assessed with a repeated measures MANOVA with a factor of link (3 levels).

As there is no load force on the object in right hand during the unlinked trials, grip force modulation occurring within these trials must result from a predictive process. Therefore these grip responses are the main focus of the analysis. To assess the differences in grip force in unlinked trials across conditions, the grip force modulation and grip force lag were compared by performing a repeated measures MANOVA with a factor of condition (4 levels). Contrasts were used to compare the magnitude and timing of grip force modulation in the one-link condition with the three-link, interval, and non-physical conditions. The change in grip force modulation over successive unlinked trials was examined by performing a repeated measures MANOVA with factors of condition and trials since the last linked trial (2 levels: 1st unlinked trial and 6th unlinked).

To assess any changes in behavior over the course of the session, the data were divided into five temporal segments (5 batches each) and a MANOVA performed, with factors of condition (4 levels), trials since last linked trial (2 levels: 1st unlinked trial and 6th unlinked) and temporal segments (2 levels: 1st and last).

RESULTS

After practice trials, subjects were able to produce the desired movement amplitude with their left hand in response to the tone for all of the four conditions (Fig. 2). The left hand position (dashed lines) show a smooth profile that reaches the desired amplitude of 6 mm. The right hand position profiles are very similar for both linked and unlinked trials (thick dashed vs. thin dashed lines). In the linked trials, the right hand object (thick solid line) moved a similar distance to the left hand

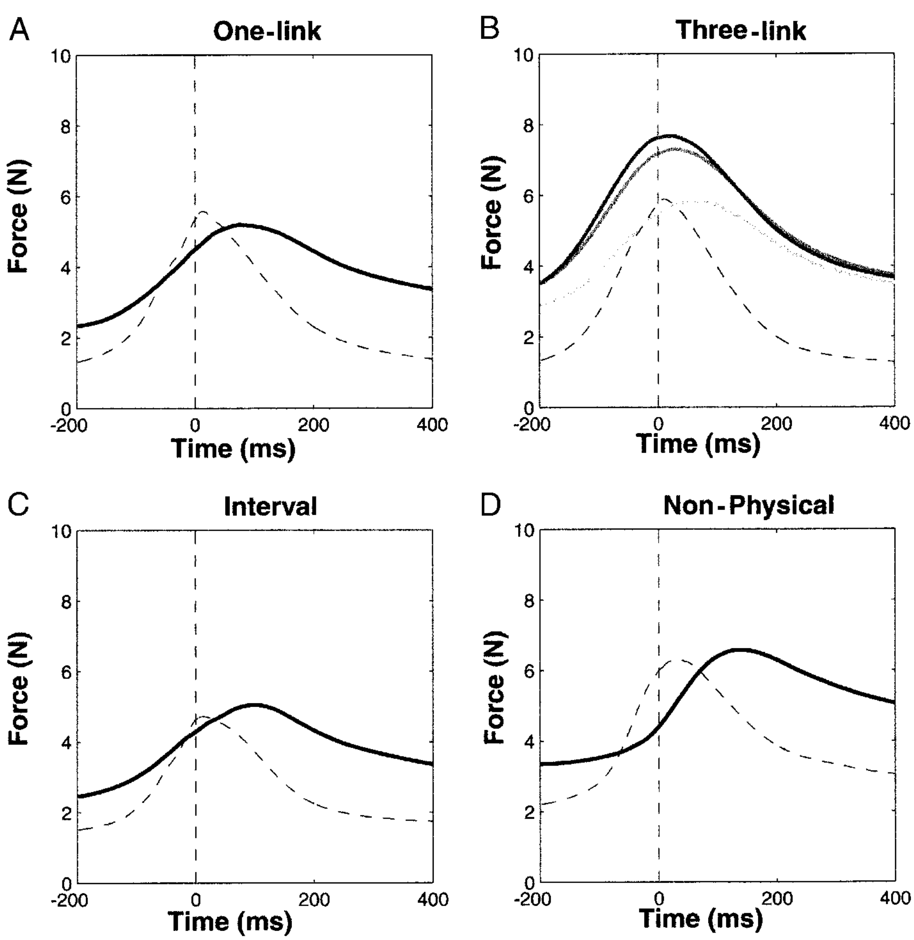

FIG. 3. Grip force responses for the linked trials of the One-Link (*A*), Three-Link (*B*), Interval (*C*), and Non-Physical (*D*) conditions. Average of the subjects' average grip force profiles (solid) and average load force profiles (dashed), aligned to the maximum left hand position (vertical line). In the 3 linked trials, the 1st, 2nd, and 3rd link trial in each sequence are shown from light to dark gray.

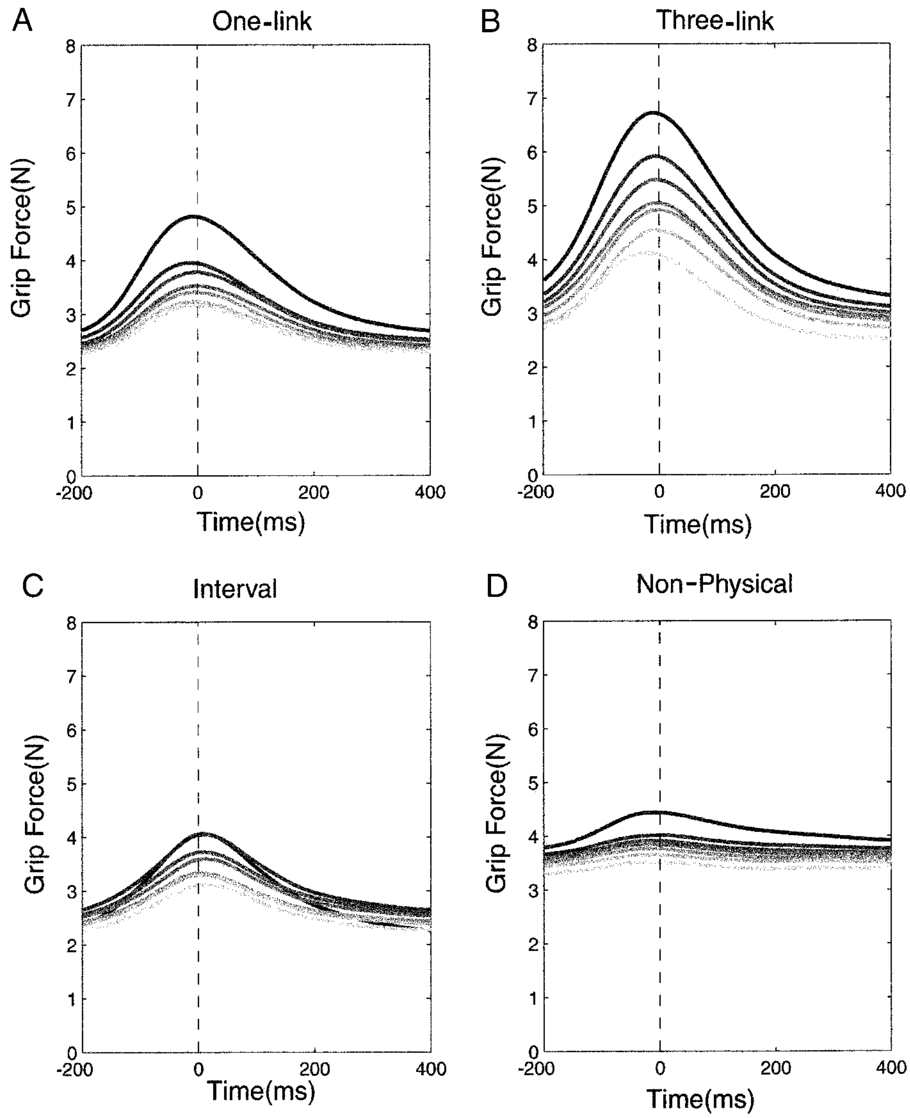

FIG. 4. Grip force responses for the unlinked trials in the One-Link (*A*), Three-Link (*B*), Interval (*C*), and Non-Physical (*D*) conditions. Average of the subject's average grip force profiles, aligned to the maximum left hand position (vertical line). The different shaded lines are for the 1st (dark gray) to the 7th (light gray) successive unlinked trial since the last linked trial.

object, as would be expected for a solid object. For the unlinked trials, there was very little movement of the right hand objects (thin solid line). The small downward deflection of the left hand object in the unlinked trials may reflect an anticipatory adjustment to the expected upward movement from previous linked trials.

To examine whether there were any learning effects over the course of each session, we examined the grip force as a function of batch number (the linked and unlinked trials were presented in batches of 8 trials so that in each condition there were 25 batches in total). MANOVAs found no significant changes in grip force levels as a function of the trial's batch number for any condition.

An examination of the relationship between left hand position and load force in the right hand showed that the peak load force occurred on average 12 ms after peak left hand position. So as to be able to examine the lag in catch trial in which no load force is generated, we report all lags relative to the peak left hand discursion.

One-linked condition

Figure 3*A* shows the average grip force profiles for the linked trial of the one-linked condition. During the linked trials, when the objects behaved as a single object held between the hands, the average peak grip force modulation was 3.5 N, which occurred 44 ms after the maximum left hand discursion, that is 32 m after peak load force.

Figure 4*A* shows the average grip force profiles for the unlinked trials as a function of the number of trials since the last linked trial. On average, compared with linked trials, the unlinked trials had a lower peak grip force modulation of 2.5 N, which occurred 14 ms in advance of the left hand discursion. This reflects a predictive component in the unlinked trial as the object does not move.

The grip force modulation during the unlinked trials was accurately timed for all trials that followed a linked trial. The lag of each grip force profile to the peak of the left hand discursion was close to zero. This response must be purely predictive as there is no load force generated on these trials. The magnitude of grip force modulation decayed over each successive unlinked trial (Fig. 4*A*). The peak grip on the first unlinked trial was 4.8 N, and this decayed to 3.2 N by the sixth unlinked trial. This pattern can also be seen in individual subject's profiles (Fig. 5, *S1–S8*).

To further examine the development of anticipatory grip

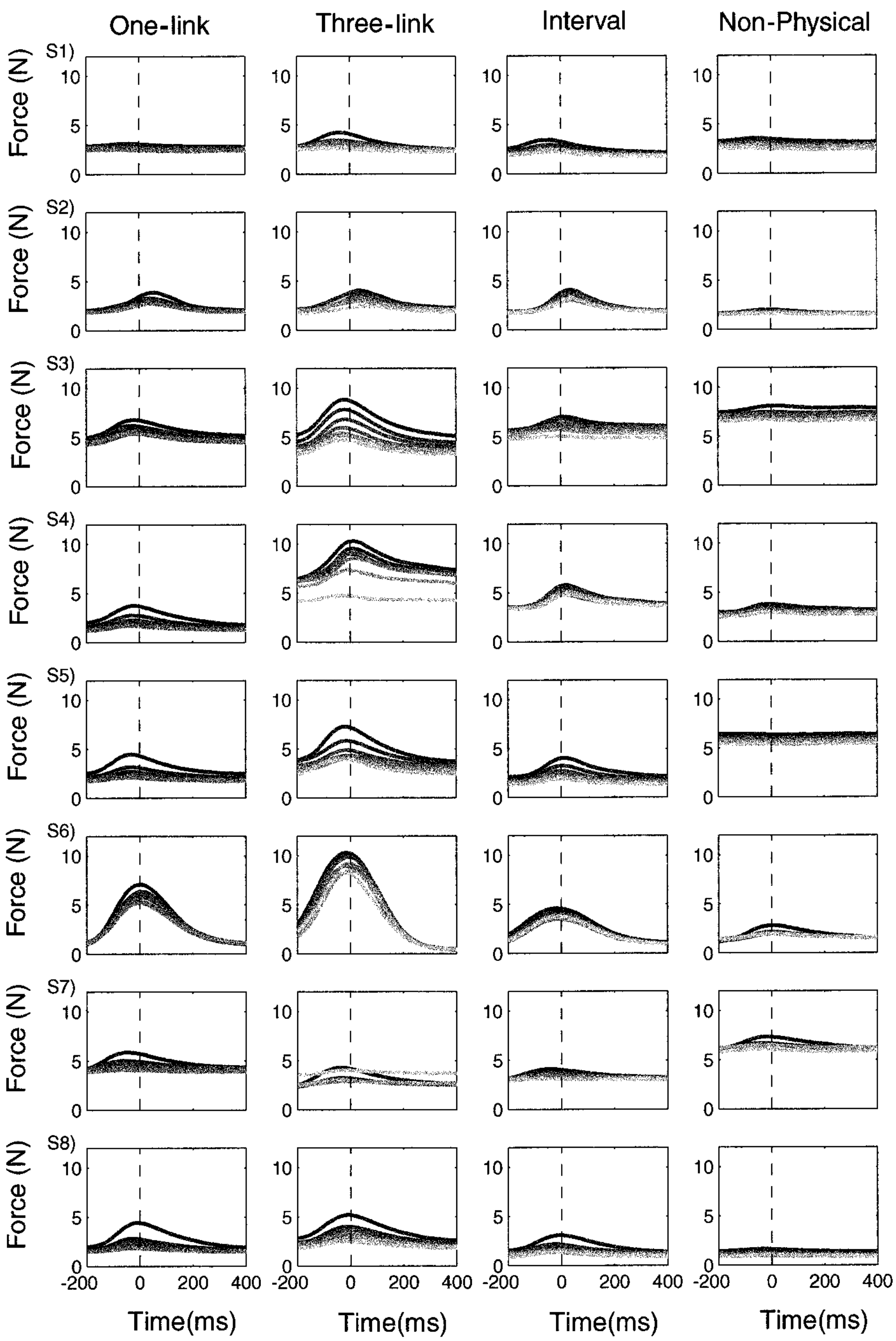

FIG. 5. Average of each individual subject's grip force profiles, aligned to the maximum left hand position (vertical line) for the unlinked trials in the same format as Fig. 4.

force, the grip force modulation and lag were compared for the linked and unlinked trials as a function of trials since the last linked trial (Fig. 6).

In the first unlinked trial the grip force modulation is on average 2.5 N, and this decayed significantly ($P < 0.001$) to a modulation of 1.1 N in the sixth unlinked trial (Fig. 6*A*). Therefore predictive modulation of grip force is still present even after the subject has experienced five previous trials that are all unlinked. The timing of the peak in grip force response (Fig. 6*E*) showed no significant change over the unlinked trials.

These results show that on experiencing a single linked trial the predictive component of the grip force response increases by 1.4 N (from the 1st unlinked trial before a linked trial to the 1st unlinked trial after a linked trial). This suggests that an anticipatory grip force response is quick to build up, but slow to decay, decaying by 0.28 N per trial on average. Therefore a predictive response is still present even though the linked situation is only occasionally experienced. With 1 linked trial in 8, the behavior was stable throughout 200 trials.

Three-linked condition

The behavior in the three-linked condition was qualitatively similar to the one-link condition. Several differences can be seen quantitatively. Over the three sequential linked trials the grip force modulation increased significantly ($P < 0.01$) from 3.8 N on the first trial to 5.0 N on the third (Figs. 3*B* and 6). This increase in magnitude was coupled with a decreasing lag

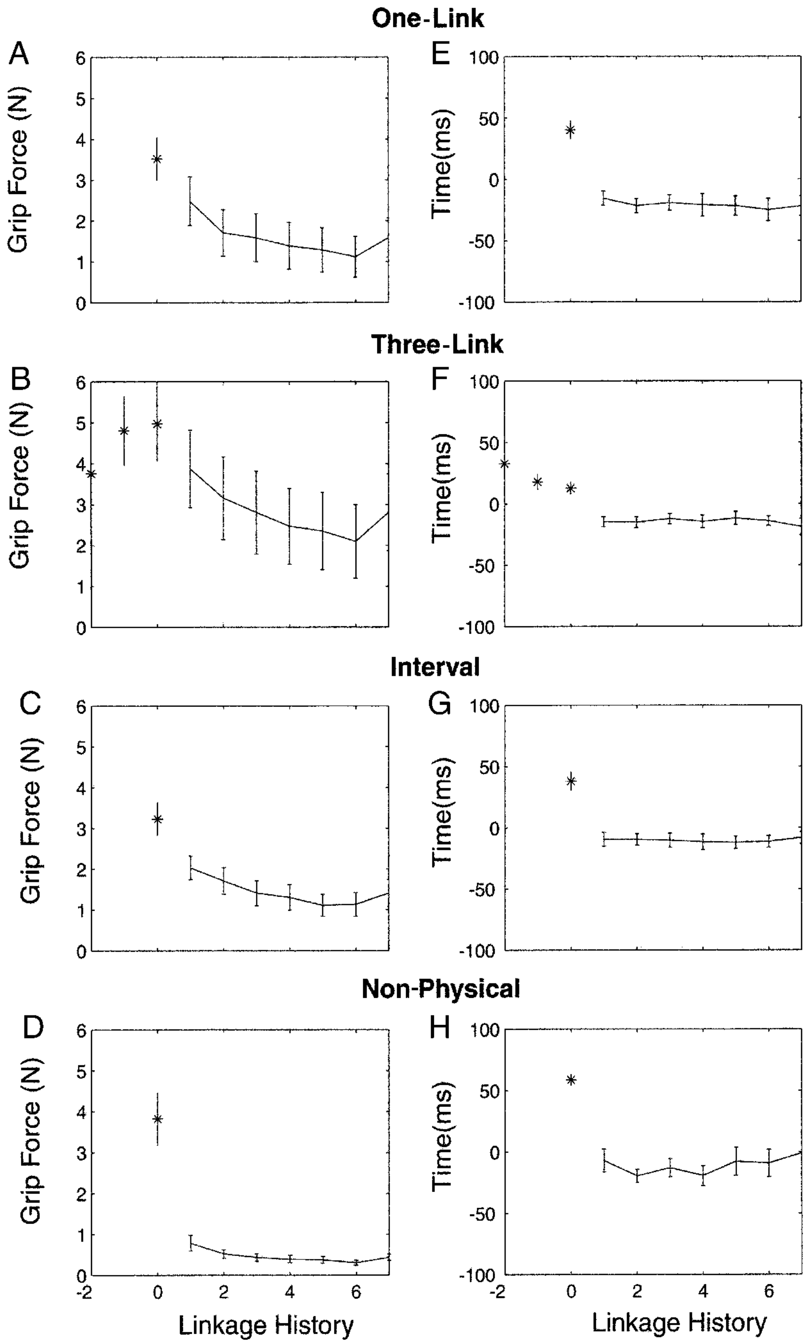

FIG. 6. Average of the subject's mean grip force modulation (*A–D*) and the lag of the grip force peak (*E–H*) for the 4 conditions (rows). Linked trials (*) and unlinked trials (solid) as a function of the number of trials since the last linked trial. Error bars show SE.

on successive trials, from 33 ms on the first, to 18 ms on the second, and 13 ms on the third linked trial ($P < 0.05$). This decreasing lag may indicate an increasing level of anticipatory grip force modulation (Fig. 6, *B* and *F*). Grip force profiles of the unlinked trials show that the grip force modulation is on average increased ($P < 0.05$) compared with the one-link condition (Fig. 4*B*). As with the one-link condition, this modulation is largest in the first unlinked trial at 3.9 N and gradually decays to a lower level of grip force modulation in each successive unlinked trial. By the sixth unlinked trial, grip force modulation is on average 2.1 N (Fig. 6*B*). The decay in grip force modulation, as measured in absolute terms (N), was not significantly different from the one-link condition. This pattern of behavior was stable over the batches within a session. Therefore the effect of three-, rather than one-linked trial preceding the unlinked trials is for the predictive modulation to be increased, coupled with a similar decrease in grip force with each successive unlinked trial. This pattern of response can also be seen in individual subject's profiles (Fig. 5, *S1–S8*).

Interval condition

To examine whether the decay seen in the one-link condition is related to time or events, that is trials, the inter-trial time was increased so as to double the time between movements. Figures 3*C* and 4*C* show the group averages for the linked and unlinked trials in this condition. Individual subject's data are shown in Fig. 5, *S1–S8*. This condition produced grip force responses that were not significantly different from the one-link condition (Fig. 6). In particular, the decay rate was not different from the one-link condition. A temporal decay would predict a decay rate in the interval condition double that of the one-link condition. The peak of the grip force modulation decayed from 2.0 N, on the first unlinked trial to 1.2 N on the sixth unlinked trials compared with decay in the one-link condition from 2.5 N on the first unlinked trial, to 1.1 N on the sixth unlinked trial.

Non-physical condition

During the non-physical condition the relation between the motion of the left hand and the subsequent motion of the right hand object was identical to the one-link condition. However, the only difference was that the motor attached to the left hand object was passive. Under this situation the grip force modulation seen in the unlinked trial has very small amplitude (Fig. 4*D*). Even though only a small predictive modulation builds up, it still tends to decay over the unlinked trials.

For the linked trials the magnitude of the grip force modulation was 3.8 N, with an average lag of 58 ms (Fig. 3*D*). This grip force lag is approximately 20 ms greater than the lag of linked trials within the one-link and interval conditions, and is consistent with an increased reliance on a reactive grip force (Fig. 6, *D* and *H*). For the unlinked trials, the magnitude of the grip force modulation is significantly lower ($P < 0.01$) in this non-physical condition compared with the one-link and interval conditions. The magnitude of the predictive grip force response on the first unlinked trial is 0.8 N. This modulation then decays to 0.3 N in the sixth unlinked trial. Although the lag of the grip force response in the unlinked trials is close to zero in the first three unlinked trials, the grip response on the later unlinked trials is more variable, with the grip peak varying from being 30 ms in advance of the peak left hand movement, to a lag of 50 ms. This increasing variability further indicates that there is little consistent anticipatory grip response after the first unlinked trial (Fig. 6, *D* and *H*).

DISCUSSION

We have studied grip force modulation during bimanual manipulation of a "virtual object" whose properties were under computer control, allowing instant changes in the object's behavior on a trial-to-trial basis, without providing any cues to the subject. In this paradigm the subject was required to pull up on the object held in the left hand and to maintain the position of the object held in the right hand. The forces on each object were controlled so that the two objects could be either linked by a virtual stiff spring, so that they acted as a single object, or unlinked, so that they acted as two independent objects. By examining the grip force in the restraining right hand in unlinked trials where the object held in the right hand did not move in response to the movement of the left hand, the predictive element of grip force response could be isolated.

Subject's performance on unlinked trials, after an experience of a linked trial, showed clear evidence of predictive grip force modulation. Such predictive modulation was quick to develop after a linked trial, but slow to decay with unlinked trials. This decay was found to be independent of inter-trial interval, depending rather on the number of trials since a linked trial. With increased experience of linked trials, the predictive modulation increased, but the rate of decay was unchanged. When the linked object did not have normal physical properties, predictive modulation was greatly reduced.

Previous studies have examined the adaptation of anticipatory grip force response to changing object properties, including the object's shape, weight, and frictional surfaces (Burstedt et al. 1998; Gordon et al. 1993; Jenmalm and Johansson 1997; Johansson and Westling 1984). Adaptation of grip force has been found to occur quickly, with an initial adjustment in 100–200 ms, and total adaptation within one or two trials after the object's properties are changed (Johansson and Cole 1994). Even in the absence of any visual cues, adaptation of grip force prediction to new object properties occurs within one or two trials (Jenmalm and Johansson 1997). Gordon et al. (1993) have shown that when lifting objects that differ in density, parameterization of grip force to load force occurs accurately from the first lift, based on visual cues of object weight, with very little adjustment in subsequent lifts. Likewise, adaptation of grip force levels to alterations in object shape occurred within the first few manipulations (Jenmalm and Johansson 1997). Therefore parameterization of grip force to load force can occur in advance of object movement, by a process described as anticipatory parameter control (Johansson and Cole 1992, 1994), where predictions developed from previous experience are used to adjust grip force. Alternatively, when visual information is not available or is uninformative, grip force is scaled by a process of discrete-event, sensor-driven control, where grip force is quickly adjusted on the basis of feedback from cutaneous afferents (Johansson and Cole 1992, 1994).

Reactive and anticipatory grip force responses were examined by Johansson and Westling (1988) in an experiment where a small ball was dropped into a cup that was gripped by the subject. When the ball was dropped by the experimenter, a reactive grip force response occurred 70–80 ms after impact. Conversely, when the load was self-generated, that is subjects dropped the ball, there was an anticipatory grip force response. This experiment allowed the reactive and predictive components of the grip response to be separated, but the time course of the learning and decay of an anticipatory grip force response was not examined.

In the current study the development of grip force prediction can be accurately determined by measuring the anticipatory grip force modulation that occurs during unlinked trials. In these unlinked trials no load force was generated on the restrained object, and therefore the grip force modulation that occurs must be predictive in origin.

Our anticipatory behavior has been attributed to the ability to predict the consequences of our own actions (Johansson and Cole 1994; Lacquaniti et al. 1992; Massion 1992), a process that requires an internal model of both one's own body and the external world. Such models are known as forward models as they capture the forward or causal relationship between actions, as signaled by efference copy (Jeannerod et al. 1979; Sperry 1950; von Helmholtz 1867; von Holst 1954) and outcome. Forward models have been proposed to play a fundamental role in motor planning, execution, and learning (Jordan 1995; Jordan and Rumelhart 1992; Kawato et al. 1987; Miall and Wolpert 1996; Wolpert 1997; Wolpert and Kawato 1998; Wolpert et al. 1995). Our study shows that anticipatory grip force modulation, appropriate for a single object being manipulated between the subject's two hands, is quick to develop, with predictive modulation of grip force occurring in the unlinked trials after the presentation of a single linked trial. This rapid development is consistent with findings of previous studies that the forward model is quick to adapt to new environments. In contrast to the fast development of prediction, decay occurred slowly. During unlinked trials, when the subject experiences the two objects as being separate, anticipatory grip force modulation was still significant after six unlinked trials. This illustrates that the forward model appropriate for a single object being manipulated is very robust. This maintenance of grip force anticipation was not obvious in previous studies as it is difficult to dissociate predictive and reactive grip force responses to an altered object property.

Additionally, the effect of repeated experience of linked trials on the subsequent level of prediction was assessed by examining the magnitude of anticipatory grip force in unlinked trials. Within the three-link condition, where three consecutive linked trials were presented, there was a higher level of grip force prediction in unlinked trials than after a single linked trial. Therefore, although one linked trial is sufficient to result in anticipatory grip force modulation, prediction is increased with increased experience of the relation between action of one hand and the consequence of movement of the other object. However, the rate of the decay of the predictive response was similar after one or three experiences of linkage.

This decay of anticipatory grip force after exposure to a linkage between the two objects was found to be unrelated to time since the last linked trial. For example, in the interval condition, doubling of the inter-trial interval did not affect the strength of anticipatory grip force in the following series of unlinked trials. Therefore rather than being time dependent, decay of grip force predictions must be event related. This is comparable with previous studies in adaptation to new object properties where an inaccurate grip force prediction occurs by a process of discrete-event sensory-driven control (Johansson and Cole 1992, 1994); feedback from cutaneous afferents results in an updating of grip force predictions.

Our paradigm can be related to studies of classical conditioning such as eye-blink response. Initially, the presentation of a conditioned stimulus (CS) such as a tone has no effect on eye-blink, whereas an unconditioned stimulus (US) such as an air-puff to the eye evokes a reactive, unconditioned response (UR). However, with repeated experiences of CS followed by an US, an association is learned so that the CS alone can initiate an anticipatory and hence beneficial conditioned response (CR) of an eye-blink (Gormezano et al. 1962; Kim and Thompson 1997; Steinmetz 1997). Relating this work to our study, we conclude that the US is the tactile sensation of slip of the object held in the precision grip, and the UR is the reactive grip force response. The CS can be considered to be the action of one hand on an object, which subjects have learned throughout life to have predictable consequences for the other hand, and therefore the CR of anticipatory grip has developed for this situation of a single object being manipulated bimanually. From classical conditioning it is known that once the CS-CR has been learned and the US is removed, the CR, like the predictive grip force in our study, slowly extinguishes. Similarly the re-introduction of the CS-US pairing leads to rapid regain of the CR response, as was seen after a single link trial our study. The acquisition and retention of the classical conditioned response has been shown by lesioning and imaging to be dependent on the cerebellum (Glickstein 1992; Kim and Thompson 1997; Perrett et al. 1993; Yeo and Hardiman 1992). The cerebellum is thought to be the area that enables the prediction of the consequences of our motor commands (Miall and Wolpert 1996; Miall et al. 1993; Wolpert et al. 1998). In support of this cerebellar role in prediction, cerebellar damage can lead to specific deficits in predictive grip force modulation (Babin-Ratte et al. 1999; Muller and Dichgans 1994). Conditioning and anticipatory grip force may therefore share common neurophysiological mechanism.

The reduced predictive response in the non-physical condition is consistent with the study of Blakemore et al. (1998). Their study showed that when subjects self-generate a force pulse on a gripped object, the amount of predictive grip force modulation decreases when the feedback experienced between the two hands deviates away from a situation of equal and opposite forces being applied to each hand. This decline in predictive grip force modulation was explained by the presence of an internal model for objects with normal physical properties, and as sensory feedback becomes increasingly inconsistent with this model's predictions, anticipation decreases.

In conclusion, we have developed a paradigm to isolate the predictive response. These results show that the use of predictive responses has a different time course for learning and decay, that decay is dependent on events rather than time, and that the response depends on experience and the physical properties of the objects.

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