The influence of previous experience on predictive motor control

Alice G. Witney, Philipp Vetter and Daniel M. Wolpert[CA]

Sobell Department of Neurophysiology, Institute of Neurology, University College London, Queen Square, London WC1N 3BG, UK

[CA]Corresponding Author

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Anticipating the consequences of our motor commands is a fundamental component of sensorimotor control. For example, when one hand pulls on an object held in the other, the restraining hand generates an anticipatory increase in grip force thereby preventing the object from slipping. To investigate how such anticipation is learned subjects held an object, whose properties were under computer control, between their hands. This allowed instant changes in the behaviour of the manipulated object on a trial by trial basis. The extent of grip force modulation seen in one hand, when the other pulled on the object was found to depend in a systematic way on the object's properties experienced over at least the previous three trials. *NeuroReport* 12:649–653 © 2001 Lippincott Williams & Wilkins.

Key words: Grip force; Internal models; Motor learning; Motor prediction

INTRODUCTION

Forward internal models are an essential feature of the motor system, enabling the prediction of the consequences of the motor command [1–4]. Such a prediction can be used to generate anticipatory compensation for the disturbances which an outgoing motor command might cause. For example, when one hand pulls on an object held in the other, the restraining hand generates an anticipatory increase in grip force (perpendicular to the surface) thereby preventing the object from slipping due to the increase in load force (tangential to the surface) that the object exerts on the fingers [5,6]. Due to feedback delays from cutaneous afferents, this modulation cannot be a reactive response to peripheral feedback [7,8]. When the increase in grip force is reactive, it occurs 60–100 ms after the increase in load force. However, anticipatory grip force responses are generated by using a prediction of the consequences of the motor command from a forward internal model of both the motor system and the object [9]. Grip force predictions are tuned to the specific properties of the object, with the appropriate grip force level preset based either on predictions of object properties arising from visual information, or, if this is unavailable, re-afferent information is used to adjust the grip responses [10]. However, within these studies, the influence of previous experiences is difficult to assess, as reactive and predictive grip force responses cannot be separated.

In the current study, a paradigm is used in which anticipatory and reactive grip force can be dissociated, allowing a clear analysis of the influence of the manipulative history of an object on the current predictive grip force response. We used a bimanual task in which each hand held a separate object each mounted on its own 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.

MATERIALS AND METHODS

Eight right-handed subjects (five male, three female) aged 19–30 who were naive to the research aims gave informed consent and participated in the study. None of the subjects reported any sensory or motor deficits.

A schematic diagram of the apparatus is shown in Fig. 1. Subjects held a cylindrical object (50 g) in each hand, with a six axis cylindrical force transducer (Nano, ATI Inc.) embedded in the right hand cylindrical object. The mass of the transducer was centred midway between the object's two parallel grip surfaces that were covered with suede (diameter 30 mm, spaced 40 mm). The force transducer allowed three translational forces to be measured with an accuracy of 0.05 N including cross-talk. Each object was attached by an aluminium rod (length 50 mm) to its own torque motor under robotic control (Phantom Haptic Interfaces, Sensable Devices). The position of both motors was sampled on-line by an optical encoder (10160 counts/rev) with a 35 Hz cut-off low-pass filter. The torques generated by the motors were computer controlled at 1000 Hz.

Subjects performed 250 trials in each condition. Before each trial, subjects positioned the objects in a starting position shown in Fig. 1. Subjects were instructed to pull up on the object held in the left hand and to keep their right hand still, preventing the gripped object from slipping from their grasp. The subject's right forearm was anchored with velcro straps, and for further stability, they

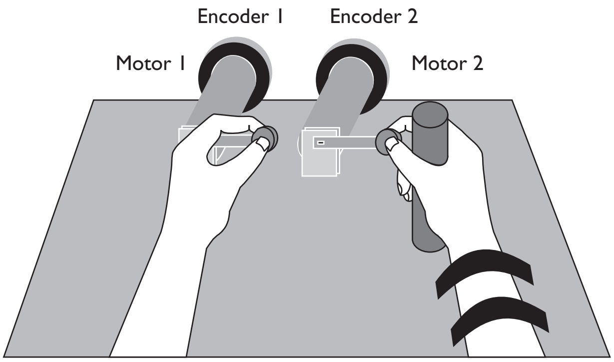

Fig. 1. Schematic diagram of the apparatus used to create a virtual object. Each hand held an object which was attached to its own torque motor. The subject was required to pull up on the object held in the left hand and to maintain the position of the object held in the right hand. The torque motors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

grasped a vertically oriented aluminium rod with their three ulnar fingers. A horizontal wooden rod was then positioned over the gripped right hand index finger and thumb. These measures ensured that the subject's thumb and index finger were used to maintain object stability rather than a more general postural response. The start of a trial was signalled by a tone approximately every 3 s. On hearing this tone, subjects made a short upward pulse with their left hand. The position of the object held in the subject's left hand was displayed as a scrolling trace on a computer monitor. The required amplitude of 6 mm was displayed as a constant horizontal line on the scrolling trace.

In all trials the motion of this left hand acted against a simulated stiff spring of 1 N/mm attached to the object's initial position. On each trial, the movement generated by the subjects on the left-hand object had two possible consequences. In linked trials the system behaved as though there were a real physical object held between the hands; a situation where predictive grip force modulation would normally occur in the right hand [6]. To achieve this, 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. In unlinked trials, motion of the left hand was decoupled from the right hand object, and therefore there was no movement of the right hand object. This mimics the situation where each hand holds separate independent objects, and therefore predictive grip force modulation would not normally be seen in the right hand.

Each subject perfomed three conditions (in a balanced order) in which either 30%, 50% or 70% of trials were linked. The linked and unlinked trials occurred in a pseudorandom order. Linked trials are expected to result in predictive grip force modulation, and unlinked trials may suppress predictive modulation. 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 hand was zero until the tone in all trials. To prevent fatigue, short rest periods were given every 40 trials in all conditions.

For each trial the position of both hands, the grip force, and load force on the object in the right hand were recorded at 200 Hz. To quantify the magnitude and timing 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 (maximum grip force within a 400 ms window on either side of the maximum left hand discursion) and the baseline grip (average value of the grip force in the first 100 ms of each trial). This measure of modulation of grip force, rather than actual grip force was determined as it is increased modulation that is the characteristic feature of predictive grip responses [11]. The grip force modulation lag was calculated as the difference between the time of the peak grip force and the time of peak left hand discursion (with negative values indicating that grip force precedes discursion). 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 the effects of linkage and condition, the grip force modulation and lag for each of the three conditions (30%, 50%, 70%) was averaged over trials for each subject, and a MANOVA performed on this data (dependent variables of grip modulation and lag) as a function of condition (3 levels) and linkage (2 levels).

To assess the effect of previous experience on the predictive grip force response, the magnitude and timing of grip force modulation during the unlinked trials can be examined as a function of the preceding history of linkage. The grip force response seen in the right hand during unlinked trials, where the object behaved as two separate objects reflects a purely predictive response, as in these trials no load force is generated on the fingertips of the right hand. Therefore, the grip force response on unlinked trials can be used to assess the influence of the previous manipulative experience on the current predictive response, separate from any reactive component. To display the influence of the history of linkage for the predictive response in unlinked trials, the grip force modulation was displayed as a binary tree structure. In such a tree, the first layer is the grip force averaged over all unlinked trials. The second layer is represented by two nodes, one for the modulation on unlinked trials which followed a linked trial and the other for unlinked trials which followed an unlinked trial. The third layer divides each of these nodes into two representing the nature of the trial two time steps ago, and so on. To quantify the influence of previous trials, the measures for the unlinked trials (X_j, the measure of interest on unlinked trial j) were regressed against the history of linkage. This was achieved by regressing these measures against indicator variables, I_j, over the last five trials, where $I_j = 1$ if trial j was a linked trial and $I_j = 0$ if trial j was unlinked. The regression therefore fitted $X_j = a_0 + a_1 I_{j-1} + a_2 I_{j-2} + a_3 I_{j-3} + a_4 I_{j-4} + a_5 I_{j-5}$. Separate regressions were performed for each of the eight subjects and three conditions and a *t*-test was used to examine the significance of the regression parameters for each condition (five levels a_1–a_5).

We modeled subjects predictive grip force modulation p by assuming that subjects alter their future response according to their prediction error on the current response. The change in the response is assumed to be proportional to the prediction error. Prediction ranges continuously from no prediction ($p = 0$) to full prediction of linkage ($p = 1$). If the trial experienced was linked, then the corresponding prediction error $e = 1 - p$, (if the trial was unlinked, then $e = p$). The prediction on the following trial will be updated to reduce e, by an amount proportional to e: $p \rightarrow p + ge$, where g is the proportionality gain. To reflect that prediction may be slower (or faster) to decay than to build up, the gain after experiencing a linked trial g_L may differ from that after experiencing an unlinked trial g_U.

To construct a linkage tree from this model, the average prediction for an unlinked trial is given by $\overline{p} = [(P_L g_L)/(P_L(g_L\text{-}g_U)+g_U)]$ where P_L is the overall probability of a linked trial (0.3, 0.5 or 0.7 in the conditions). The average prediction, given that the previous trial was linked is derived as $\overline{p}_L = \overline{p} + (1 - \overline{p})g_L$. Analogously, the average prediction given that the previous trial was unlinked is $\overline{p}_U = \overline{p}(1 - g_U)$. Further tree linkages can be calculated recursively. To fit the peak grip force data with this model, we took grip force as $G_{min} + p(G_{max} - G_{min})$, where G_{min} and G_{max} are the minimum and maximum predictive grip force recorded during each condition. The two free parameters g_U and g_L were fit to the data using a least squares minimization.

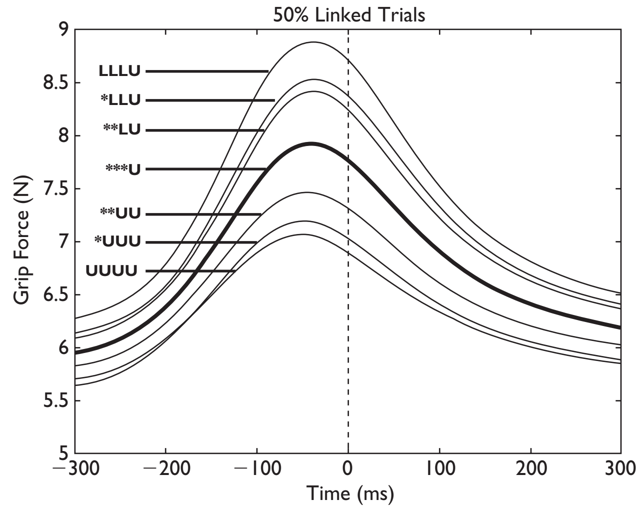

Fig. 2. Grip force response for the unlinked trials when 50% linked. Average of the subject's average grip force profiles, aligned to the maximum left hand position (vertical line). The grip profile is the average of each subject's average grip force response on linked trials where the previous three trials are unlinked, below the thick line, to averages of grip force responses when the previous three trials are linked, above the thick line.

RESULTS

The MANOVA showed that the condition had no effect on grip force modulation or lag. However, there was a significant main effect of linkage on both lag and modulation. For the linked trial the peak modulation was 1.3 N greater ($p < 0.001$) and 30 ms delayed ($p < 0.001$) compared to the unlinked trial. This is consistent with our previous findings that the reactive component of grip force modulation both amplifies and delays the grip force response [12].

Fig. 2 illustrates the dependence of the grip force response profile on the previous history. This shows grip force profiles averaged over the subjects in the unlinked trials of the 50% condition. These show a systematic relationship between the grip force response on unlinked trials and the previous linkage history. The thick black line shows the grip profile when all unlinked trials are considered (***U, where the asterisks represent all possibilities over the previous three trials). The other lines represent subsets of this data depending on the history. Lines above the thick black are for conditions in which either the last (**LU), previous two (*LLU) or previous three trials (LLLU) were linked (representing successively smaller subsets of the data). The predictive grip force modulation is thereby systematically increased by the experience of linked trial. Similarly the profiles below the thick black line are for trials in which either the last (**UU), previous two (*UUU) or previous three trials (UUUU) were unlinked showing that the modulation decreases with experience of unlinked trials.

These differences in the magnitude of the grip force response show a dependence of the current grip force response on the preceding trials that were experienced. To examine the specific influence of previous manipulative experience on the magnitude of the predictive grip force response, the magnitude of grip force modulation on each possible combination of preceding linkage was compared for the unlinked trials over the previous three trials (Fig. 3a). These data were captured by the model in which prediction builds up at a higher rate than it decays (Fig. 3b; see Materials and Methods for details).

In the unlinked trials of the 30% condition, previous experience of a linked or unlinked trial affects the magnitude of the grip force response in the current trial (Fig. 3). The MANOVA showed that the last trial, unlinked or linked has the largest effect on the magnitude of grip force modulation in the following unlinked trial ($p < 0.001$). However, the influence of linkage history is not restricted to the last unlinked trial, with a significant influence ($p < 0.01$) of the penultimate trial, and a significant influence ($p < 0.05$) on grip force magnitude dependent on the linkage of the trial three prior to the current trial. In the 50% condition, the effect of previous linkage on the grip force response was significant over the last three trials. During the 70% condition, there was a significant effect of previous linkage on the grip response during unlinked trials over the last two trials. There was no effect of lag as function of linkage history.

The regression analysis was then performed: *t*-tests over the regression parameters showed a significant influence of the history of linkage in the 30% condition, with a significant influence of the last trial ($p < 0.001$); penultimate trial ($p < 0.001$); third last trial ($p < 0.01$) and fifth trial ($p < 0.05$) (Fig. 4). In the 50% condition, the last ($p < 0.01$) and third from last trial ($p < 0.05$) significantly influenced the magnitude of the grip force response. In the 70% condition, the last trial was significant ($p < 0.001$). None of the regression parameters were significant for the lags.

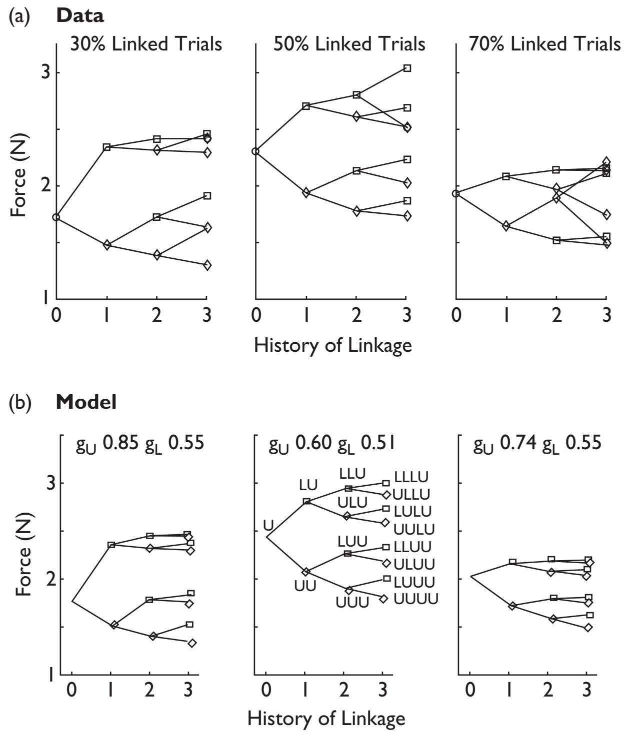

Fig. 3. (**a**) Average of each subject's maximum grip force modulation in unlinked trials plotted as a function of the history of linkage of those unlinked trials. Grip force modulation with trials with previous unlinked trials (diamonds) can be compared with those trials with previous linked trials (squares) for (i) 30% linked trials (ii) 50% linked trials and (iii) 70% linked trials. (**b**) Simulation of the data in the same format as (a). g_L and g_U are the two free parameters fit to the data. The identity of each node of the binary tree structure is shown on bottom, middle graph. The sequence of L (linked) and U (unlinked) reflect the series of trials which precede the unlinked trial (U), which the node represents.

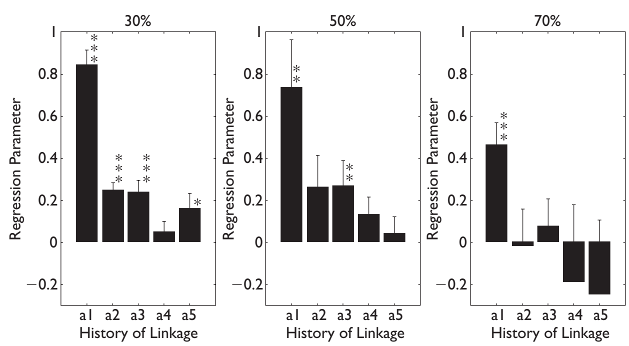

Fig. 4. Average of the regression parameters a_1-a_5 with standard error bars. $^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$.

DISCUSSION

We have studied how the history of experience affects grip force modulation during the bimanual manipulation of a virtual object. This paradigm, with the object's properties under computer control, allowed instant changes in the object's behaviour on a trial-by-trial basis, without providing any cues to the subject. Subject's were 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 acted as though a single object was being manipulated between the hands, or unlinked, so that they acted as two independent objects. Linked and unlinked trials occurred in random series of 30, 50 or 70% linkage dependent on the condition. The unlinked trials in the 30%, 50% and 70% conditions showed an effect of previous experience of object linkage on the magnitude of the grip force response. It was found that the linkage experienced three trials prior to the current trial influenced the magnitude of the grip force, with the influence of these preceding trials diminishing with manipulative history.

Previous studies have shown that previous manipulative experience influences the grip force level used on the current lift [7]. However, this affect was thought to be only transient; with adult subjects adapting quickly to changing physical properties of objects, including weight, frictional surfaces and surface orientation within one to three trials [7,13,14]. However, within these studies, the influence of previous experience on prediction is difficult to assess as reactive and predictive grip force responses are impossible to separate. In this study, as there is no load force present on the object during unlinked trial, any grip response must be predictive, and therefore, it is possible to examine the effect of the history of linkage on prediction. The magnitude of grip force response in such unlinked trials was found not be solely dependent on the previous trial that the subject experienced, but instead on the history of linkage over the last three trials. Grip force profiles indicated that the magnitude of the grip response was increased when a linked trial occurred one, two or three trials beforehand. Conversely, the occurrence of an unlinked trial during the previous three trials led to a decreased magnitude of grip force modulation on the current trial. Examination of the magnitude of the grip force response in each of the possible combinations of history of linkage showed that the magnitude of the grip responses could be separated by where in the history of linkage the linked and unlinked trials occurred. The magnitude of the grip response was most dependent on the linkage of the preceding trial, but the linkage of the trials two and three beforehand also affected the magnitude of the grip response, with the affect becoming less as the trial occurred further away from the current trial.

Our anticipatory behaviour has been attributed to the ability to predict the consequences of our own actions [4,15], 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 signalled by efference copy, and outcome. Forward models are thought to enable the anticipatory modulation of grip force [16]. Our study has shown that anticipatory modulation of grip force is dependent on the history of manipulation over the last three trials.

We modeled this anticipatory modulation by assuming that subjects alter their predictive response on future trials in a fashion that is proportional to the current prediction error. Using only two free parameters for the build-up and the decay, the essential features of the data are captured.

First, it reproduces the shape of the linkage tree (Fig. 3a). Second, the model matches the incremental decay of prediction after a series of unlinked trials.

Previously, discrete two-state Markov models have been proposed to account for sequential responses in anticipatory eye movements [17], and reaction time tasks [18]. Although these models can produce identical average modulation trees to our model, they make the strong assumption that on individual trials, subjects either fully predict linked or unlinked trials. However, as shown in a previous study [12], subjects systematically make intermediate predictions at the single trial level.

CONCLUSION

The anticipation by a forward model of the properties of a manipulated object was found to be dependent on the history of manipulative experience. When subjects experienced a random series of trials which were either linked or unlinked, the current grip force response was found to depend on the history of trials experienced. Analysis of unlinked trials, which represent a purely predictive grip response, show that the level of grip force can be determined by the previously experienced trials. Unlike previous studies, this study showed that the influence of previous experience is not limited to the last trial experienced, but rather the linkage of the last three trials determines the magnitude of the grip force response in the current trial.

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