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RESEARCH ARTICLES

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Internal models underlying grasp can be additively combined

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Abstract Our ability to additively combine two learned internal models was investigated by studying the forces people generate when lifting objects with a precision grip. Subjects were required to alternately lift two objects of identical physical appearance but differing weight. Grip force scaling prior to lift-off was used to estimate the output of the internal model associated with each object. Appropriate internal models were formed when alternately lifting two objects of different weight. The objects were then combined by stacking them one upon the other, and the combined object was lifted. Results show that subjects can additively combine internal models of object dynamics but the sum is biased by a default estimate of the object's weight.

Keywords Precision grip · Motor control · Motor programming · Internal models · Prediction

Introduction

When we manipulate a novel object, sensory feedback provides us with information about its physical properties such as its weight and the roughness of its surface. This information is thought to be used to tune an internal model which is used to predict the behavior of the object and its effects on the body. Our ability to swap between different objects and contexts quickly and effortlessly has led to the suggestion that the central nervous system (CNS) maintains many internal models in memory simultaneously (Neilson et al. 1985; Ghahramani and Wolpert 1997). The brain is thought to select the most appropriate models for the current task and use them in computing appropriate motor commands (Wolpert and Kawato 1998; Haruno et al. 2001).

The forces people employ when lifting an object from a table are precisely coordinated and provide an opportunity to study the formation of internal models. When using a precision grip, subjects scale both the horizontal grip force at the fingertips and the vertical load force opposing the object's weight based on previous experience of the object to be lifted (Johansson and Westling 1984). Accurate scaling of grip force is important because too little causes the object to slip from the fingers while too much may impair sensitivity, damage the object or lead to fatigue. During a lift, grip and load forces are increased in parallel to prevent the object slipping from the fingers.

Since weight-related sensory information is unavailable until after object lift-off, grip and load forces must be programmed in anticipation of the movement. Examination of grip and load forces prior to object lift-off confirms that grip and load forces are pre-programmed. When a subject lifts an object of unknown weight, the peak force rates are initially incorrect, but fully adapt to the new weight after a single trial. The rates used after adaptation are strongly related to object weight and occur prior to object lift-off (Johansson and Westling 1988).

This anticipatory scaling of grip and load force can been seen to represent the output of an internal model. When a new object is encountered, this model seems to be based on visual (Gordon et al. 1991b) and tactile (Gordon et al. 1991a; Edin et al. 1992) information. The model is then updated based on mechanical information obtained in subsequent lifts (Johansson and Westling 1988; Gordon et al. 1993; Burstedt et al. 1997; Jenmalm et al. 1998).

An internal model must capture both the *dynamic* and *kinematic* characteristics of a task. The dynamic characteristics of a task concern the changing relationship between motor commands and body position, while the kinematic characteristics concern the relationship between body position and sensory feedback. Krakauer et al. found that learning and consolidation of kinematic and dynamic transformations occur independently (1999). Flanagan et al. (1999) showed that if subjects learn a visuomotor

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rotation (a kinematic transformation) and then learn a viscous curl field (a dynamic transformation), their performance on the combined transformation is better than if they had no experience of the constituent transformations. This shows that it is possible, under some circumstances, to combine two previously learned internal models. It is unknown whether two dynamic internal models can be learned and appropriately combined in a similar manner. In fact, several studies have shown that it is often very difficult to learn two dynamic internal models at the same time (Karniel and Mussa-Ivaldi 2002). Brashers-Krug et al. (1996) showed that if two opposing force fields generated by a robot manipulandum were learned in rapid succession, then no memory of the first field was retained at the end of training. It appeared that the process of forming the internal model of the second field destructively interfered with the internal model of the first field. If, however, a 5-h period of consolidation was allowed between learning the fields, then both internal models were retained. Gandolfo et al. (1996) showed that two opposing force fields could be learned if subjects used a different arm configuration when moving in each field. This suggests that interference was not observed because the two fields were, in fact, learned as a single dynamic transformation between torque and limb configuration. In contrast, the fields could not be learned if the same arm position was maintained in each field but subjects were given a visual cue, or if the position of the thumb, but not the overall arm, was changed between fields.

Here we investigate the ability of the CNS to combine two previously formed dynamic internal models. Specifically, we examine if the CNS is able to generate a new model appropriate for controlling stacked objects by appropriately combining their internal models. Subjects were required to alternately lift two objects of identical physical appearance but differing weight. This allowed us to examine if they could form an internal model of each object. The two objects were then stacked, one upon the other, and the subjects were required to lift this new combined object. Grip force scaling during the loading phase was used as a window on the output of the internal model employed for the first lift with the combined object. The employment of an appropriate peak grip force rate (PGR) on the first lift with the combined object was used to assess subjects' ability to additively combine internal models.

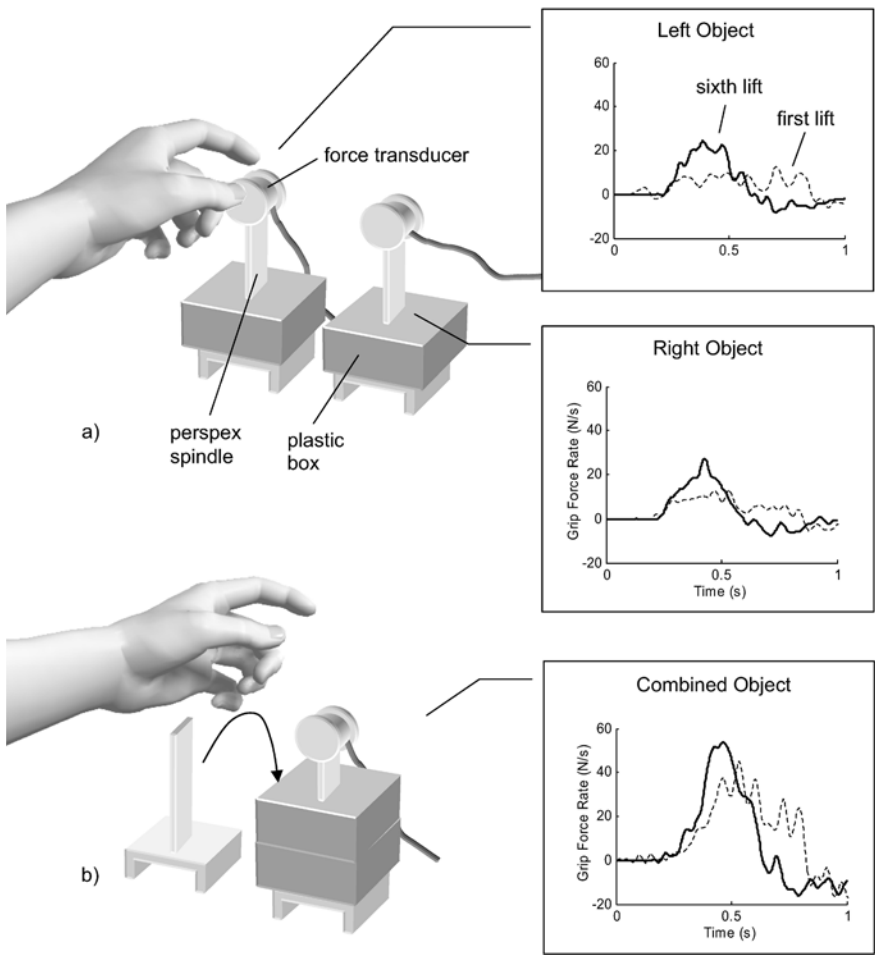

Fig. 1A, B Visually identical plastic boxes were threaded onto plastic spindles. Force transducers were attached to the top of the spindles with a strong clip. **A** The first 12 lifts alternated between the left and right objects. Subjects learned appropriate grip force scaling for each object by the sixth lift. **B** Experimenter placed the left object on top of the right object; subjects then completed six additional lifts. Pattern was repeated twice for all nine combinations of the individual weights. Typical force rate profiles for first (*dotted line*) and last (*solid line*) lifts with two 250-g boxes are shown at right. In this example the object's weight is underestimated on the first combined lift, resulting in pulsatile corrections later in the movement

Materials and methods

Subjects

Eight healthy, right-handed subjects (aged 19–28 years) participated in the experiment after providing written informed consent. None of the subjects reported sensory or motor deficits. A local ethics committee approved the experimental protocol.

Apparatus

The experimental apparatus is shown in Fig. 1. Two six-axis force transducers (Nano, ATI) were used to measure fingertip grip forces. The transducers were mounted on small clips so they could easily be attached or detached from objects. Two faces of each transducer were covered with sandpaper (Grade No. 210) to provide a suitable surface for subjects to grip. Six identical black plastic boxes (39×56×85 mm) were filled with lead shot so that two were of 62.5-g mass, two had a mass of 125 g and two were of 250-g mass. The boxes were then packed with foam to prevent rattling during lifting. Two lightweight (11 g) perspex spindles were constructed. Holes were cut in the top and bottom of the boxes so that they could be threaded onto the spindles. The transducers were attached to the spindles using the clips. The use of spindles ensured that the centre of gravity of the objects remained well below the fingers so that the apparent stability of the object did not bias the pre-programmed grip of forces. Force transducer output was sampled at 500 Hz. The total mass of each object comprised the mass of the plastic boxes plus the spindle and force transducer combination (which increased the mass of each object by 50 g).

The objects were of identical shape to avoid introducing biases caused by size cues and were the same colour to prevent subjects associating colour and weight, which might influence the next lift with same object.

Procedure

Subjects were seated in front of a table and required to use their right arm to lift one of two objects located in front of them. They were asked to keep their forearm approximately parallel to the table and grasp the object between the tips of the thumb and forefinger of their right hand. Subjects were asked to lift the object 3 cm off the surface and to maintain a constant lifting rate. Subjects were first familiarized with the mass of the spindle and force transducer by lifting the combination a few times.

Subjects were required to wear visual occlusion spectacles (PLATO, Translucent Technologies), which were opaque while the objects were being set up and clear during the subjects' lifts, to prevent any visual cues as to the weight of the objects. Subjects also wore headphones which generated white noise to prevent any auditory cues. At the beginning of each set, the experimenter threaded a box onto each of the two spindles. A force transducer was then attached to the end of each spindle.

One set of lifts consisted of six lifts with each of the two separate objects (alternating between objects after each lift, see Fig. 1a) and then six lifts with the two objects stacked vertically (Fig. 1b). The experiment consisted of 18 sets of 18 lifts each. The weights of the objects were changed after each set. The 18 sets comprised two repetitions with all nine possible combinations of two weights (all the objects weighed either 62.5, 125 or 250 g). The first repetition was presented in pseudo-random order and the second repetition was presented in the reverse order.

The headphones generated a tone to indicate that the subject should lift the object and, after a 1-s delay, another tone to replace the object. After 12 lifts alternating between individual objects (starting with the left object), the left object was lifted off its spindle by the experimenter and, in full view of the subject, threaded onto the same spindle as the right object. The weight of the new, combined object was approximately the sum of the weights of the two individual objects (minus the 50 g of the spindle and force transducer). The subject was then required to lift the combined object six times. The time between trials was approximately 1 s.

A control experiment was performed immediately after the main experiment. Instead of swapping between two objects, subjects lifted the same object six times in succession without swapping. This six-trial block was repeated with each individual weight and combination of weights experienced in the main experiment. Hence, the control experiment comprised nine blocks: three lifting each individual object and six lifting each possible combined object. The weights were presented in random order.

Analysis

For each trial the grip force was numerically differentiated with a 50th order FIR least squares differentiator (25-Hz bandwidth) and the peak grip force rate (PGR) was calculated. PGR has been widely used to assess programmed grip force and is particularly robust when the subject expects a heavier weight, since the object lifts off the surface before corrections can be made. PGR is, however, prone to bias when a subject expects a lighter weight due to corrective pulses. Consequently, we also looked at the first peak in grip force rate after the vertical lift force first begins to increase without changing direction (FGR). This measure should more accurately reflect the programmed peak in grip force, but is considerably more variable.

All weights used in analysis, and quoted in the results, include the spindle and force transducer and therefore represent the actual weight lifted by the subject. Where a linear regression with a single predictor variable is quoted in the analysis, the inter-subject component of the variance is not included in the result.

Results

Ability to learn two internal models concurrently

The experiment relies on the hypothesis that appropriate grip forces for two visually identical objects of differing weights can be learned concurrently. This was tested by performing a linear regression between the PGR and the weight of the individual objects. No relationship should exist on the first lift since the subjects have no prior knowledge of the mass of the object. A weak relationship was, in fact, detected (r^2=0.03, p<0.01). This relationship is probably caused by the corrective increases in grip force required to prevent slippage when the object was heavier than expected. By the second lift a much stronger relationship between PGR and weight was evident (r^2=0.31, p<0.0001). This is consistent with previous work showing adaptation is essentially complete after a single lift (Gordon et al. 1993). The relationship strengthened slightly during the following four lifts (sixth lift; r^2=0.37, p<0.0001). In the control data, where the same object was lifted six times, the corresponding relationship was stronger (sixth lift; r^2=0.67, p<0.0001), confirming the well-known result that PGR scales linearly with weight. No differences were found between the PGR, or FGR, employed in the main and control experiments (paired t test, sixth lift; p>0.05). Force rate profiles for typical first and last lifts for a 250-g mass are shown in Fig. 1a.

To examine the influence of the previous lift on the current lift during the alternating lifts in the main experiment, a linear model was fit to the second lift of each object.

$$PGR = \alpha\, w_n + \beta\, w_{n-1} + \delta \qquad (1)$$

where *PGR* (N/s) is the peak grip force rate on the second lifts, w_n is the total weight of the current object (g), w_{n-1} is the total weight of the previous object and δ is a constant. Fitting the model to the data (pooled across all subjects) we found that w_n=0.046, w_{n-1}=0.006 and δ=6 (r^2=0.25, p<0.0001). The only individually significant parameter was w_n (step-wise regression; r^2=0.25, p<0.0001). The same model was also fitted separately to the data from each individual subject. The individual w_n values were greater than zero (*t* test; p<0.0001) while the individual w_{n-1} values were not (*t* test; p>0.05). This shows that the weight of previous object has no influence on the PGR of the current lift.

We repeated the same analysis looking at the magnitude of the first peak in grip force rate (FGR). When we pooled the data across all subjects we found that w_n=0.043, w_{n-1}=0.003 and δ=4.49 (r^2=0.21, p<0.0001). Again, the only individually significant parameter was w_n (step-wise regression; r^2=0.21, p<0.0001). As for the PGR measure, the individual w_n values were greater than zero (*t* test; p<0.0001) while the individual w_{n-1} values were not (*t* test; p>0.05). This suggests that the PGR analysis was not strongly biased by corrective movements.

In summary, these results indicate that subjects were able to learn appropriate grip force scaling for two separate weights, even when alternating between them, and that most of the learning happened within the first few lifts with each object.

Ability to combine two internal models

Since adaptation is essentially complete after the first few lifts, the mean PGR over the final three lifts provides a good estimate of the subjects' preferred PGR for an object of a given weight. If the PGR of the first lift with the combined object is close to the subjects' preferred PGR for the combined weight then subjects are accurately estimating the weight of the combined object. The mean preferred PGR for each combined object is shown in Fig. 2 (*dashed line*). As expected, there is a strong relationship between preferred PGR and the total weight of the object (linear regression; r^2=0.67, p<0.0001).

The PGR of the first lift with the combined object is also related to the total weight of the object (linear regression; r^2=0.35, p<0.0001). The regression line is illustrated in Fig. 2 (*solid line*). A similar, though slightly weaker, relationship exists between the FGR of the first lift with the combined object and its weight (linear regression; r^2=0.19, p<0.0001). The relationship was investigated further by fitting a multiple regression model to the pooled data from all subjects,

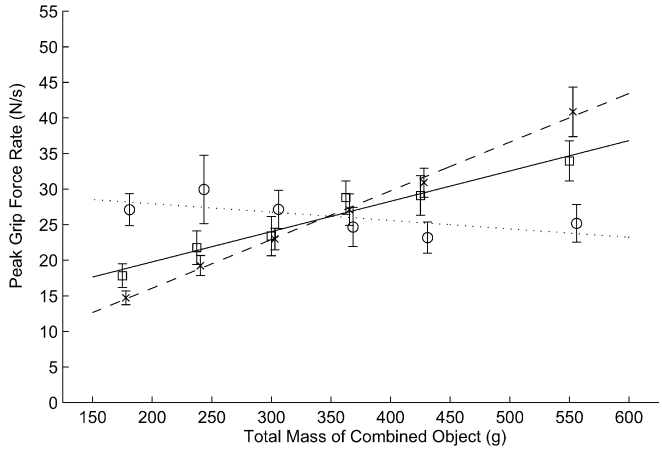

Fig. 2 Variation in peak grip force rate with weight. The ideal peak grip force rates (PGR) for lifts with combined objects are indicated with crosses (mean PGR over last three lifts, regression shown with *dashed line*). The mean peak grip force rate used for first lifts with the combined objects is indicated with squares (regression shown with *solid line*). Ideal performance would result in the *solid line* lying on top of the *dashed line.* Mean PGR for the first lift with the combined objects from the control experiment, where the subjects have no knowledge of the constituent weights, is also shown (*circles, dotted regression lin*e). *Vertical bars* indicate SE

$$PGR = \alpha w_1 + \beta w_2 + \delta \qquad (2)$$

where *PGR* is the peak grip force rate on the second lifts, w_1 is the total weight of the first constituent object, w_2 is the total weight of the second constituent object and δ is a constant. PGR was found to depend approximately equally on the weights of the first and second constituent objects (α=0.0414, β=0.0418, r^2=0.21, p<0.0001). The multiple regression model was also fitted separately to the data from each individual subject. Based on the resulting parameters, PGR was found to depend on the total weight of the first constituent object (*t* test; p<0.001) and of the second object (*t* test; p<0.01) but did not depend more on one weight more than the other (paired *t* test; p>0.05). This also rules out the possibility that subjects simply double the PGR appropriate for the second object and other similar possibilities.

The PGR of the first lift with each combined object during the control experiment was also investigated. Since, in this case, the subjects had no knowledge of weights of the constituent objects, no relationship should exist between weight and PGR. As expected, the results indicate that the PGR is unrelated to the total weight (linear regression; r^2=0.06, p>0.05). FGR is also unrelated to total weight (linear regression; r^2=0.08, p>0.05). The regression line for PGR is shown in Fig. 2 (*dotted line*).

The overall regression line for the first lift in the main experiment, as shown in Fig. 2, differs significantly in slope from both the control data (ANCOVA interaction; F=15.5, p<0.001) and the preferred value (ANCOVA interaction; F=8.6, p<0.005). Repeating the same analysis using FGR reveals similar relationships, with the first lift differing from the control (ANCOVA interaction; F=10.25, p<0.001) and preferred values (ANCOVA interaction; F=11.1, p<0.005).

The PGR used on the first lift appears to be intermediate between the control and the preferred values. This suggests that subjects partially adjust their initial estimate, as gauged by the control data, to take into account the information obtained when lifting the individual objects. Hence, subjects estimate the combined object to be heavier than it is when the individual objects are lighter than average, and lighter than it is when the individual objects are heavier than average.

The nature of this adjustment was investigated by fitting a linear model to the data. The weight subjects expected on the first combined lift was estimated with a linear regression of preferred PGR, as defined above, for the combined object against the total weight of the object (i.e., including the force transducer and spindle). Inter-subject variance was eliminated by performing this initial linear regression separately for each subject. The following model was then fitted to the data for the first lift:

$$w_E = \alpha\, w_1 + \beta\, w_2 + \delta, \qquad (3)$$

where w_E is the weight expected on the first lift, w_1 is the total weight of the first object, w_2 is the total weight of the second object and δ is a constant. If subjects use a simple summation, the model should give $\alpha = \beta = 1$ and $\delta = 0$. The least-squares fit to the model was α=0.67, β=0.66, δ=90. α and β were both significant with p<0.0001. Hence, the weightings given to the first and second objects are both approximately 2/3. A possible interpretation of this result is that an estimate of the total weight is being combined, in a ratio of 2:1, with a default estimate of the weight w_D so that

$$w_E = 2/3.(w_1 + w_2) + 1/3.\ w_D, \qquad (4)$$

and, using the parameters obtained above, $w_D = 3.\delta = 270$ g.

Fitting the model to the FGR data gives a similar result: α=0.52, β=0.56, δ=104, and α and β were both significant with p<0.0001. By this measure, however, the estimate of the total weight is being combined with a default estimate by a ratio closer to 1:1.

Discussion

It has been hypothesized that multiple internal models are stored by the CNS for use in motor control (Neilson et al. 1985; Wolpert and Kawato 1998). There is evidence that, under certain conditions, it is possible to learn these internal models concurrently and combine them. Flanagan et al. (1999) have shown that internal models of novel kinematic and dynamic transformations can be used to improve performance when the two transformations are combined. Our work suggests that, in addition to selecting appropriate models and combining kinematic and dynamic transformations, the CNS may be able to additively combine two dynamic internal models. The results also show that the CNS is able to rapidly form, and maintain, appropriate internal models for lifting two different weights when repeatedly swapping between them. This is in contrast with force-field learning experiments showing that two dynamic internal models cannot be learned concurrently unless the posture of the arm is changed between conditions (Gandolfo et al. 1996; Karniel and Mussa-Ivaldi 2002).

The Modular Selection and Identification for Control (MOSAIC) model was proposed as an architecture the CNS might use to learn, and swap between, multiple modular controllers (Wolpert and Kawato 1998; Haruno et al. 2001). In MOSAIC a set of forward models (predictors) simultaneously predict the behaviour of the motor system when performing previously learned tasks. Each forward model is paired with an inverse model (controller) and the quality of the prediction is used to determine how appropriate a controller is for the current task. The MOSAIC is able to make smooth weighted transitions from one controller to another as contexts change but, in its current form, MOSIAC includes no provision for more complex combinations of controllers. Hence, the MOSAIC model is able to average, but unable to add the outputs of two controllers. Our results suggest that MOSAIC requires revision to include the ability to generate additive combinations of its controllers.

We observed that people tend to underestimate the weight of heavy combinations and overestimate the weight of light objects. Assuming an additive combination were available, these results are consistent with MOSAIC basing the estimated weight on a combination of 2/3 based on the evidence of the two weights from previous lifts and 1/3 based on the a priori default weight of two objects. From a statistical viewpoint, the default weight for two blocks is likely to be twice the average weight experienced for each block. The average experienced weight of each block was 148.8 g (the average of the possible block weights of 250, 125 or 62.5 g). Therefore, the default for two boxes would be 291.7 g, which is similar to the fit value of 270 g. Thus, subjects appear to act in a Bayesian way in the face of uncertainty, combining a priori information about the likely weight of the blocks with evidence about the weights from previous lifts.

It is also possible that rapid memory decay could contribute to the systematic errors we saw on the combined lifts. The memory representations for the individual objects might rapidly decay towards a default weight. The delay between the final lifts with individual objects and the first lift with the combination was kept short to minimize the effects of any memory decay.

Cognitively estimating the weight of the combined object is not the same as forming of an internal model of the object's dynamics per se. This would require the additional step of using the estimated weight to parameterize a transformation to the appropriate motor commands. This experiment cannot distinguish whether the weight parameter is estimated cognitively, but previous work suggests that it is not. When people are asked to lift objects of identical weight but different size the smaller object is consistently perceived to be heavier, an effect known as the “size-weight illusion” (Murray et al. 1999). When subjects repeatedly lift the two objects they quickly learn to scale the grip force appropriately for the actual weight of each object, but the size-weight illusion does not diminish (Flanagan and Beltzner 2000). This suggests that grip force control and conscious perception of object weight are dissociated processes. When making rapid, cyclic arm movements while grasping an object, grip force is precisely modulated in phase with variations in the load force. This modulation persists when subjects are asked to grip the object very tightly, so that modulation is no longer necessary to prevent slips (Flanagan and Wing 1995). This suggests that grip force modulation is an automatic process which subjects are unable to suppress consciously.

When learning the weights of the constituent objects, it could be that subjects employed a simple cognitive association between position and weight. We were able to eliminate this possibility by swapping the positions of two objects after their individual weights had been learned by alternate lifting. Subjects continued to employ the same grip force scaling on each object despite their change in position.

The weight of the spindle and force transducer are a potential confound as they contribute 50 g to the total weight of all objects lifted in the experiment. The spindle was necessary as we needed to attach the masses securely so that subjects would treat the combined object as if it were as mechanically robust as the individual objects. There was no indication of consistent underestimation of the mass of the object, as would be expected if the contribution of spindle were simply ignored. Similarly there was no evidence of consistent overestimation as would be expected if the internal models for the two weights were simply added so that the spindle was included in the combined model twice.

There are other ways addition might occur within the MOSAIC architecture. For example, the responsibility predictor, which generates an a priori estimate of the likelihood a controller might be useful, could be capable of selecting broadly appropriate modules for lifting combined objects. This would require a relatively complex cognitive addition operation using the remembered weights as contextual cues. We feel this complex mapping is not consistent with the existing MOSAIC structure, and maintain that the addition is more likely to occur at the controller outputs.

We found no evidence that the forces used to lift one object were affected by the weight of the previous object on the alternating trials. Previous work looking at lifts with a single object of changing density has shown a strong effect of the previous lift on the current lift (Gordon et al. 1993). A strong effect of the previous trial was also found when subjects manipulated a virtual object in a bimanual task in which the object either present or absent (Witney et al. 2001). An isolated pinch can also strongly influence the force used on subsequent lifts (Quaney et al. 2003). Our results suggest that subjects are able to establish separate memory representations for each object when they are clearly distinct in the environment.

These results are the first demonstration that subjects can additively combine dynamic internal models. Subjects can generate appropriate grip force when two previously experienced objects are lifted for the first time in combination. The grip force used follows a simple combination rule, which has a Bayesian interpretation, based on the experienced weight and a default weight. The internal models, being parameterized by a scalar value, the weight, are perhaps one of the simpler internal models. Whether similar addition can be seen for more complex internal models parameterized by vector values is still an open question.

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References

Brashers-Krug T, Shadmehr R, Bizzo E (1996) Consolidation in human motor memory. Nature 382:252–255

Burstedt MK, Edin BB, Johansson RS (1997) Coordination of fingertip forces during human manipulation can emerge from independent neural networks controlling each engaged digit. Exp Brain Res 117:67–79

Edin BB, Westling G, Johansson RS (1992) Independent control of human finger-tip forces at individual digits during precision lifting. J Physiol 450:547–564

Flanagan JR, Beltzner MA (2000) Independence of perceptual and sensorimotor predictions in the size-weight illusion. Nat Neurosci 3:737–741

Flanagan JR, Wing AM (1995) The stability of precision grip forces during cyclic arm movements with a hand-held load. Exp Brain Res 105:455–464

Flanagan JR, Nakano E, Imamizu H, Osu R, Yoshioka T, Kawato M (1999) Composition and decomposition of internal models in motor learning under altered kinematic and dynamic environments. J Neurosci 19: RC34

Gandolfo F, Mussa-Ivaldi FA, Bizzi E (1996) Motor learning by field approximation. Proc Natl Acad Sci U S A 93:3843–3846

Ghahramani Z, Wolpert DM (1997) Modular decomposition in visuomotor learning. Nature 386:392–395

Gordon AM, Forssberg H, Johansson RS, Westling G (1991a) The integration of haptically acquired size information in the programming of precision grip. Exp Brain Res 83:483–488

Gordon AM, Forssberg H, Johansson RS, Westling G (1991b) Visual size cues in the programming of manipulative forces during precision grip. Exp Brain Res 83:477–482

Gordon AM, Westling G, Cole KJ, Johansson RS (1993) Memory representations underlying motor commands used during manipulation of common and novel objects. J Neurophysiol 69:1789–1796

Haruno M, Wolpert DM, Kawato M (2001) Mosaic model for sensorimotor learning and control. Neural Comput 13:2201–2220

Jenmalm P, Goodwin AW, Johansson RS (1998) Control of grasp stability when humans lift objects with different surface curvatures. J Neurophysiol 79:1643–1652

Johansson RS, Westling G (1984) Roles of glabrous skin receptors and sensorimotor memory in automatic control of precision grip when lifting rougher or more slippery objects. Exp Brain Res 56:550–564

Johansson RS, Westling G (1988) Coordinated isometric muscle commands adequately and erroneously programmed for the weight during lifting task with precision grip. Exp Brain Res 71:59–71

Karniel A, Mussa-Ivaldi FA (2002) Does the motor control system use multiple models and context switching to cope with a variable environment? Exp Brain Res 143:520–524

Krakauer JW, Ghilardi MF, Ghez C (1999) Independent learning of internal models for kinematic and dynamic control of reaching. Nature Neuroscience 2:1026–1031

Murray DJ, Ellis RR, Bandomir CA, Ross HE (1999) Charpentier (1891) on the size-weight illusion. Percept Psychophys 61:1681–1685

Neilson PD, Neilson MD, O'Dwyer NJ (1985) Acquisition of motor skills in tracking tasks: Learning internal models. In: Russell DG, Abernethy B (eds) Motor memory and control. Human Performance Associates, Dunedin, pp 25–36

Quaney BM, Rotella DL, Peterson C, Cole KJ (2003) Sensorimotor memory for fingertip forces: evidence for a task-independent motor memory. J Neurosci 23:1981–1986

Witney AG, Vetter P, Wolpert DM (2001) The influence of previous experience on predictive motor control. Neuroreport 12:649–653

Wolpert DM, Kawato M (1998) Multiple paired forward and inverse models for motor control. Neural Networks 11:1317–1329