Exp Brain Res (2008) 189:211–220
DOI 10.1007/s00221-008-1418-5

RESEARCH ARTICLE

Calibrating grasp size and reach distance: interactions reveal integral organization of reaching-to-grasp movements

Rachel Coats · Geoffrey P. Bingham · Mark Mon-Williams

Received: 5 February 2008 / Accepted: 30 April 2008 / Published online: 21 May 2008

Abstract Feedback is a central feature of neural systems and of crucial importance to human behaviour as shown in goal directed actions such as reaching-to-grasp. One important source of feedback in reach-to-grasp behaviour arises from the haptic information obtained after grasping an object. We manipulated the felt distance and/or size of a visually constant object to explore the role of haptic information in the calibration of reaching and grasping. Crucially, our design explored post-adaptation effects rather than the previously documented role of haptic information in movement organisation. A post-adaptation reach-to-grasp task showed: (1) distorted haptic feedback caused recalibration; (2) reach distance and grasp size could be calibrated separately but, if calibrated simultaneously, then (3) recalibration was greater when distance and size changed in a consistent (e.g. reaching for a larger object at a greater distance) rather than an inconsistent (e.g. a smaller object at a greater distance) fashion. These interactions reveal the integral nature of reach-to-grasp organization, that is, that reaching and grasping are integrated components of a single action system.

Keywords Prehension · Motor control · Calibration · Somatosensory · Haptic · Feedback

R. Coats · M. Mon-Williams
School of Psychology, University of Aberdeen,
AB24 2UB Aberdeen, Scotland, UK

G. P. Bingham (✉)
Department of Psychology, Indiana University,
Bloomington, IN 47405, USA
e-mail: gbingham@indiana.edu

Introduction

Modern computational approaches within neuroscience emphasize a nervous system whose outputs are motor commands originating from a controller whose inputs consist of sensory feedback signals that are a function of effector state (Wolpert et al. 2001). Feedback is used at two different time scales. At a time scale of milliseconds, feedback is used online to correct inaccuracies during an ongoing reach (Desmurget and Grafton 2000). At a time scale of seconds (or greater), feedback about end-point accuracy is used for calibration of the feedforward control of subsequent reaches (Bingham and Pagano 1998; Wolpert et al. 2001). The role of visual feedback in calibrating reach direction has been studied extensively (Bingham and Romack 1999; Redding and Wallace 1997) but the role of haptic information in calibrating reach-to-grasp movements is not well documented.

Reaching-to-grasp an object requires the nervous system to determine an object's properties and location (typically through visual information) and then generate an appropriate movement. The nervous system selects a movement that drives the hand to a visually specified object whilst visual and/or somatosensory feedback allows the system to implement any necessary on-line corrections and register error to modify future trajectories. The online use of visual and somatosensory feedback information ensures success in the majority of human adult reaches. Inaccuracies in the motor output cause the system to recalibrate itself.[1] For example, Helmholtz (1894/1924) showed that yoked optical prisms placed in front of the eyes: (1) initially cause large corrections

[1] Bingham and Romack (1999) showed that errors in reach direction resulted in recalibration of subsequent feedforward control even when feedback guidance allowed online correction of errors to yield accurate acquisition of the target at the end of each reach.

towards the end of a reach; (2) have a decreasing effect over trials; (3) produce corrections in the opposite direction when first removed. Thus, it is known that visual error feedback is sufficient for the purpose of adaptation (and a number of human behaviours, including moving a computer mouse, rely on the nervous system using vision to calibrate action). It is also known that the absence of both visual and somatosensory feedback causes the system to lose both precision and accuracy systematically over time (Vindras and Viviani 1998).

The visual calibration of pointing has been much studied but the role of haptic feedback has received less attention within the research literature (though the response of the reach-to-grasp system to haptic perturbations is documented, e.g. Gentilucci et al. 1997). Mon-Williams and Bingham (2007) investigated the haptic calibration of reach distance by gradually distorting the somatosensory feedback obtained when grasping visible target objects. Participants reached-to-grasp virtual cylindrical targets located at three distances (the visual targets were generated using a mirror arrangement). Haptic feedback could then be provided at the different target locations with the 'haptic' targets moving gradually either closer or further to provide distorted haptic feedback (feedback blocks). To investigate the stability of calibration after feedback was removed, Mon-Williams and Bingham added blocks of trials without feedback ('snapback' blocks). Mon-Williams and Bingham found that the modified relationship between visually specified distance and reach distance could be captured by a straight-line mapping function using two parameters: bias and slope. They showed that the calibration of reach distance generalized across reach space with respect to changes in bias and slope and demonstrated that bias and slope can be calibrated independently of one another, each with a different adaptation time course. Moreover, Mon-Williams and Bingham showed that these calibration effects are not cognitively penetrable.

It can be seen that some progress has been made in studying the role of haptic information with regard to reach distance. In contrast, there has been little work regarding haptic information and grasp calibration and the potential interaction between reaching and grasping in the context of calibration. The lack of knowledge regarding the role of haptic feedback in the calibration of grasp is most disappointing. Haptic perception of an object in the hand would be the most natural and effective way to calibrate grasping because portions of the hand in contact with the object are typically occluded from vision. Furthermore, the study of concurrent calibration of distance for reaching and size for grasping offers a window on the organization of reaches-to-grasp. Are visually guided reaching and visually guided grasping relatively independent components of a reach-to-grasp action or is the organization integral?

A couple of previous studies have used distorted haptic feedback to investigate grasping. Gentilucci et al. (1995) used distorted haptic feedback and showed that movement organisation was changed accordingly. However, this study did not unequivocally demonstrate calibration of grasping because generalization of the effect to the control of grasps of other objects was not tested. Gentilucci et al. (1995) asked eight participants to grasp an object of constant visual appearance but manipulated the felt size of the object (making it bigger or smaller) using a mirror system that allowed such dissociations to be created. They found that maximum grip aperture was increased or decreased when the felt target object was either increased or decreased in size. To tackle the issue of generalization, Gentilucci et al. (1995) asked participants to indicate the size of the object that they were grasping in a matching test after the prehension task. Gentilucci et al. used a judgment task and such tasks have been shown in numerous studies to yield different results than found in studies of actual movement (e.g. Mon-Williams and Tresilian 1999). Thus, the data from the matching test could only suggest that the participants might have calibrated their movement as their size matches were biased in a direction predictable from the direction of manipulation of the haptic feedback. In another relevant study, Patchay et al. (2003) investigated whether haptic input from an unseen object held in the non-reaching hand influenced the reaching hand whilst it moved towards a visual target. Patchay et al. found that the amplitude of maximum grip aperture was smaller (and the time to maximum grip aperture earlier) when the unseen handheld object was smaller than the target. Patchay et al. suggested that the neural processing of distracting haptic information produced the observed interference effects.

The data of Gentilucci et al. (1995) and Patchay et al. (2003) are interesting but do not establish that grasping behaviour itself is recalibrated by haptic feedback because generalisation of actual reach-to-grasp behaviour was not measured directly. Additionally, the data leave unresolved issues regarding the relationship between the calibration of grasping and reaching. Thus, we investigated, first, whether haptic feedback regarding object size calibrates the size of the grasp aperture in visually guided reaches. To explore this issue we asked participants to reach-and-grasp an object that they could both see and feel without sight of their own hand. The absence of visual overlap with the hand excluded visual calibration and isolated the use of haptic information. The visual appearance of the object remained constant throughout the experiment but we gradually altered the physical size and/or location of the felt object to provide distorted haptic feedback. Critically, we tested for calibration by comparing reaches to a "virtual" target (that could be seen but not felt) before and after exposure to the distorted haptic feedback. Reaches to such virtual targets have been described previously as 'pantomime' reaches (Goodale et al. 1994). Goodale et al. (1994) have shown that pantomime reaches are often characterised by slower movements (indexed by decreased peak tangential speed and increased duration) and a reduction in maximum grasp aperture. Moreover, Goodale et al. have found that pantomimed reach-to-grasps can be shorter (i.e. participants undershoot the target location). Nevertheless, Bingham et al. (2007) have shown that these differences from normal reaches-to-grasp are eliminated if participants are allowed to calibrate their movements (i.e. are provided with visual or haptic feedback) across an experimental session. The results of Bingham et al. (2007) have demonstrated that reaches to virtual targets can provide a useful measure of whether the system has calibrated its behaviour.

The important question, given the coordinated nature of reach-to-grasp actions, was whether reach distance and grasp size could be calibrated separately (either when each is calibrated alone or when both are calibrated simultaneously) or whether these components would interact when recalibrated. The latter result would reveal that reaches-to-grasp are integral in organization. There is a debate within the literature regarding the control structure of the reach and grasp components of prehension (particularly the extent to which these components are under separate control, see Smeets and Brenner 1999; Jeannerod 1988; Mon-Williams and McIntosh 2000). We investigated whether the components interact at the calibration timescale, meaning that the organization is integral. Another well-known example of such an integral system is the visual system itself in which accommodation and vergence interact because the dynamics are cross-coupled (e.g. Schor and Narayan 1982). Thus, the present study set out to investigate directly the calibration of the grasp component in reach-to-grasp movements—an issue that has not been addressed previously.

Experiment 1

Participants

Twenty undergraduates (aged 20–23 years) participated in the experiment on a voluntary basis. The participants were all right handed. The participants were randomly assigned to sub-groups within the experiment as discussed later. The participants had no history of neurological, ophthalmological or musculoskeletal disorders, and were naïve to the purpose of the study. All participants were able to comprehend the instructions, and carry out the task without difficulty. Ethical approval was given by the Psychology Ethics Committee at the University of Aberdeen and the experiments were conducted in accordance with the Declaration of Helsinki. All participants gave written informed consent.

Measurements

Prehensile movements were recorded using infra-red emitting diodes (IREDs) positioned on the participant's reaching limb, and their position was recorded using Optotrak. IREDs were attached to the tip of the index finger and thumb (distal end second phalanx), and the inside edge of wrist (radial stylus/styloid process). Participants were asked to make natural reaches with their right hand, grasping the real or virtual object with their thumb and index finger. The reaching hand was not allowed to touch the surface of the table (requiring a grasp from above). IRED position was recorded using Optotrak™, and analysed using customised Labview software.

During each reaching movement kinematic data were acquired at 100 Hz for 3 s. Data were filtered using a dual-pass Butterworth second order filter with a cut-off frequency of 16 Hz (equivalent to a fourth order zero phase lag filter of 10 Hz). Custom analysis routines were used to compute the dependent kinematic variables of interest in this study. The tangential speed of the wrist IRED was computed and the onset and offset of the movement (together with the peak tangential speed and the time at which it occurred) was estimated using a standard algorithm (threshold for movement onset and offset was 5 cm/s). Following this, the distance between the thumb and index finger IREDs was computed (the aperture). We used the offset of movement as a temporal marker and computed the resultant reach distance (from the starting point) and the terminal grip aperture at this moment in time. Analysis of the movement before this moment in time provided us with the following dependent variables: duration, peak speed; maximum grip aperture; time to maximum grip aperture.

Experimental procedure

Participants sat at an L-shaped 'mirror table' (Fig. 1) with their hand resting on a visible start location. The table allowed participants to reach comfortably behind the mirror. The mirror allowed us to create the illusion that an object was behind the mirror by using an image of an object physically located in front of the mirror. It is possible to block the view of the front object from the participant's peripheral vision but we have found that this makes no difference to the participants' behaviour. The mirror was manufactured specially so that it was front surface silvered and had a removable back panel. Removing the back panel allowed the image of the object in front of the mirror to be aligned perfectly with a physically identical object behind the mirror. The object was always positioned so that its long axis was parallel to the length of the mirror (Fig. 1). This arrangement meant that the participants grasped the object in a plane orthogonal to the length of the mirror. This

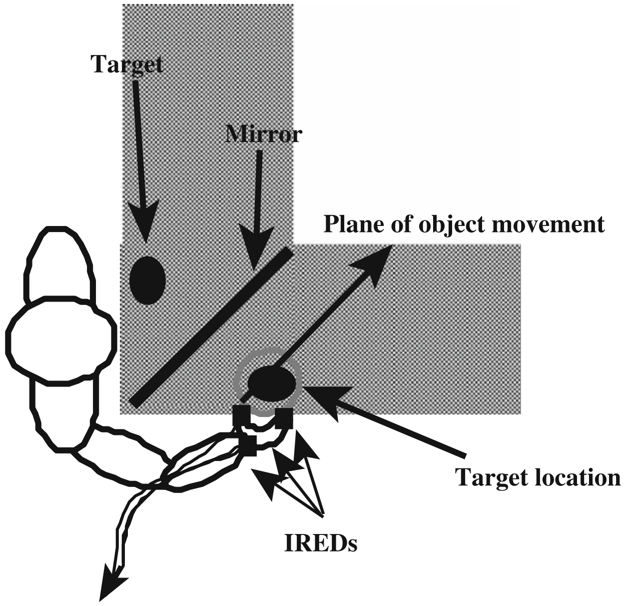

Fig. 1 Schematic of the experimental apparatus. Participants reached behind a mirror to grasp an object they could see in the mirror. The experiment had a measurement phase and an adaptation phase. In the measurement phase, participants reached to a 6 cm visually specified object at 20 cm from the starting point when there was no physical object present ('virtual' reaches). The reach distance and the grasp size were compared before and after adaptation (ten trials in both) to determine whether adaptation occurred. In the adaptation phase, participants began by reaching to a physical object behind the mirror whose physical properties (size and distance) were in perfect correspondence to the visual specifications. The visual specifications remained the same throughout the adaptation phase but the unseen object behind the mirror was altered in distance by 10 cm and/or size by 4 cm over 70 trials

design allowed us to produce a visually perfect 'virtual object' by removing the physical object behind the mirror. It also allowed us to produce an environment in which the visual and physical properties of an object were in perfect agreement or an environment where there was a mismatch. We made the objects by attaching a 1 cm diameter dowel to a supporting block (the block provided stability). Thus, the grasp surface of the object was held constant (1 cm) but its width could vary. All participants first were given reasonably extensive experience of reaching behind the mirror to an object with identical location and dimensions to the image they could see in the mirror (notably within three trials all participants produced accurate reaches and found the task straight-forward).

The sequence of reaches-to-grasp was: (1) ten pre-adaptation baseline virtual reaches; (2) seventy calibration reaches with distorted haptic feedback; (3) ten post-calibration baseline virtual reaches. The total number of trials for all participants in all conditions was 90 (10 virtual reaches then 70 reaches to a felt object then 10 virtual reaches) not including the initial practice trials.

Virtual reaches

All participants were asked to reach-and-grasp ten times to a 6 cm wide virtual object placed 20 cm from the starting position before being exposed to distorted haptic feedback. Participants always viewed the control object (6 cm width at 20 cm) during all virtual reaches. It was explained to the participants that they would not feel an object behind the mirror but they should make a movement as if an object really were there. We asked participants not to hunt for an object. Participants readily understood the situation and none had any problems in following this instruction. In the final stage of both experiments, all participants again reached-and-grasped ten times to the 6-cm wide virtual object placed at 20 cm. The average reach distance and final grasp aperture were calculated from the first ten 'virtual' trials and these values were subtracted from the final ten 'virtual' trials to discover whether the system adapted to the distorted haptic feedback.

Calibration reaches

There were two groups of ten participants in "Experiment 1": a distance group and a size group. Following the baseline 'virtual' reaches-to-grasp, the two groups were exposed to distorted haptic feedback (the adaptation phase of the experiment). In the adaptation phase, participants always viewed the object-distance combination corresponding to the first felt event during the reaches to the physical targets. In both groups, participants were not told about the manipulation and care was taken to occlude vision between trials and remove any possible information that might arise through sound. Participants shut their eyes and were fitted with occluding spectacles whilst an experimenter placed a block loudly on the tabletop on every trial regardless of whether there was any alteration in the target configuration. These distracting procedures on every trial ensured that there was no cue regarding the experimental manipulation and this was confirmed after the experiment through a debriefing questionnaire.

In the adaptation phase, five of the distance group began to reach for a 6 cm object at 15 cm (which is what they saw throughout the calibration trials) whilst the other five began to reach for a 6 cm object at 25 cm (which is also what they saw throughout the calibration trials). The participants performed ten reaches after which the object was either moved outwards by 1 cm from 15 cm or inwards by 1 cm from 25 cm. The object was moved in the same plane as the semi-silvered mirror (Fig. 1). The change in reach distance was repeated every five trials. This procedure continued until the object had moved 10 cm at which point the participants made an additional ten reaches.

Five of the size group began to reach for a 4 cm object at 20 cm whilst the other five began to reach for an 8 cm object at 20 cm and this was respectively what they saw throughout the calibration trials. The participants performed twenty reaches after which the object was either increased by 1 cm in size from 4 cm or decreased by 1 cm in size from 8 cm. The change in grasp size was repeated every ten trials. This procedure continued until the object had changed in size by 4 cm at which point the participants made an additional ten reaches.

Results

We first analysed the kinematic data collected when the participants reached for physical objects (under visual open-loop conditions). The data showed the normal qualitative pattern of prehension behaviour. Thus, the hand accelerated to a peak speed and then decelerated as it approached the target object. The reach exhibited a smooth 'bell-shaped' velocity profile with a somewhat longer deceleration phase. The maximum grip aperture and closing of the aperture occurred during this deceleration phase (see Smeets and Brenner 1999; Mon-Williams and Tresilian 2001). Table 1 shows the data from initial reaches (capital letter column headings) and final reaches (lowercase column headings). To be certain that participants were scaling their prehensile behaviour appropriately, we used student *t* tests to compare reaches to objects placed far with objects placed near (in the distance group) in the adaptation phase. Likewise, we compared reaches to the large object with reaches to the small object (in the size group). We calculated the average value over the first ten reaches and over the last ten reaches for each participant. Thus, we ended up with one value for the initial reach and one value for the final reach for each participant. The initial and final data across the ten participants were then entered into a student *t* test. We predicted that the movement duration and peak speed would be higher when the 'distance' group were reaching to the furthest target (vs the closest) but maximum grip aperture would be the same. In line with these predictions, duration [$t(9) = 4.248$, $P < 0.05$] and peak speed [$t(9) = 6.723$, $P < 0.05$] were higher but MGA was not reliably different [$t(9) = 0.828$, $P > 0.05$]. We predicted that maximum grip aperture would be larger when the 'size' group were reaching to the largest target (vs. the smallest) but movement duration and peak speed would be the same. In line with these predictions, MGA was larger [$t(9) = 6.723$, $P < 0.05$] but movement duration [$t(9) = 0.074$, $P > 0.05$] and peak speed [$t(9) = 1.803$, $P > 0.05$] were not reliably different. Time to MGA was not reliably affected in either group (it typically occurs later for further reaches and reaches to larger objects—this pattern was observed but failed to reach statistical significance). In short, the reaches to the physical objects showed the normal kinematic scaling that occurs when distance and/or size alters.

These data confirm previous reports regarding the response of the system to haptic perturbations (e.g. Gentilucci et al. 1997) but shed no light on the issue of calibration central to our investigation. Thus, we concentrated our efforts on comparing the pre- and post-adaptation prehension data (Table 2). We compared the reach distance and grasp aperture of the 'distance' and 'size' group (Fig. 2a) using a mixed ANOVA that also explored effect of trial number (i.e. whether any effect dissipated over the ten post-adaptation trials). We calculated the average reach distance and grasp size for each participant from their first ten virtual reaches. This value was then subtracted from each of the values for the final ten reaches giving the effect of the manipulation over the ten post-adaptation trials. Trial number (1–10) was then used as a within participant factor whilst condition (distance or size) was the between participant factor. The analysis showed no interactions between condition and trial [$F_{(9,162)} = 1.397$, $P > 0.05$] but confirmed a reliable change in reach distance [$F_{(1,18)} = 11.789$; $P < 0.05$] and grasp [$F_{(1,18)} = 6.923$, $P < 0.05$] with no effect of trial in either situation [$F_{(9,162)} = 1.385$, $P > 0.05$ and $F_{(9,162)} = 0.469$, $P > 0.05$, respectively]. We also tested two directions of change: distances nearer or farther and sizes smaller or larger. A separate ANOVA with factors direction and condition established that the direction of the

Table 1 Kinematic data from "Experiment 1" when participants reached to a real object that either started big or small and was initially positioned either far or near

	FAR	near	NEAR	far	SMALL	big	BIG	small
Peak speed	690	527	559	785	496	580	500	405
Movement duration (ms)	746	667	592	898	877	677	752	796
Maximum grip aperture (cm)	8.96	8.37	9.43	10.04	7.91	9.95	10.42	8.72
Time to MGA (ms)	475	383	384	399	454	496	533	503

Column headings with capital letters show the data from the initial reaches (before adaptation) whilst the column with lower case letters show the data from the final reaches (at the end of the adaptation period). This table shows how the within participant reach kinematics altered as the object size or location altered (e.g. FAR vs. near or SMALL vs. big)

Table 2 Reach distance and grasp size after adaptation in "Experiment 1" (the column indicates the direction of adaptation) with the between participant standard deviations in parentheses

	Far	Near	Big	Small
Reach distance (cm)	22.34 (1.34)	17.31 (0.91)	19.30 (1.35)	19.34 (1.41)
Grasp size (cm)	7.04 (0.36)	6.98 (0.59)	8.07 (0.57)	6.14 (0.62)

adaptation did not produce a reliable difference in effect magnitude [distance $F_{(1,8)} = 0.168$, $P > 0.05$, grasp $F_{(1,8)} = 0.168$, $P > 0.05$].

The changes in final reach distance and final grasp aperture demonstrate unequivocally that calibration had occurred. Nonetheless, the calibration might be restricted to the final adjustments of the movement rather than affecting the whole movement organization. To determine whether the whole movement had calibrated, we studied the reach-to-grasp kinematics (shown in Table 3) from the two baseline virtual reach phases. The data from grasping the physical objects leads to the prediction that duration and peak speed will be higher following adaptation to the further target and vice versa if the whole movement has been re-organised. In fact, this is what we found with a longer duration [$t(4) = 5.181$, $P < 0.05$] and higher peak speed [$t(4) = 5.372$, $P < 0.05$] following near-to-far adaptation and a shorter duration [$t(4) = 2.904$, $P < 0.05$] and lower peak speed [$t(4) = 9.705$, $P < 0.05$] following far-to-near adaptation. Likewise, re-organisation of the movement leads to the prediction that MGA will be larger following adaptation to the larger target and vice versa for the 'size' group. Indeed, a larger MGA was found following small-to-large adaptation [$t(4) = 2.967$, $P < 0.05$] and a smaller MGA measured following large-to-small adaptation [$t(4) = 3.445$, $P < 0.05$].

Discussion

The participants exposed to distorted reach distance information (the 'distance' group) showed a shift in their reaching distance in the predicted direction with no change in grasp size. Likewise, all of the participants exposed to the size manipulation (the 'size' group) showed a predictable shift in their grasp aperture size with no change in reach distance. The kinematic data showed that the differences in reach distance and grasp size reflected calibration of the whole reach-to-grasp movement (rather than just reflecting alterations in final movement adjustments). These data demonstrate that the reach and grasp component can be calibrated independently of one another. We next sought to determine what happens when the two components are calibrated concurrently.

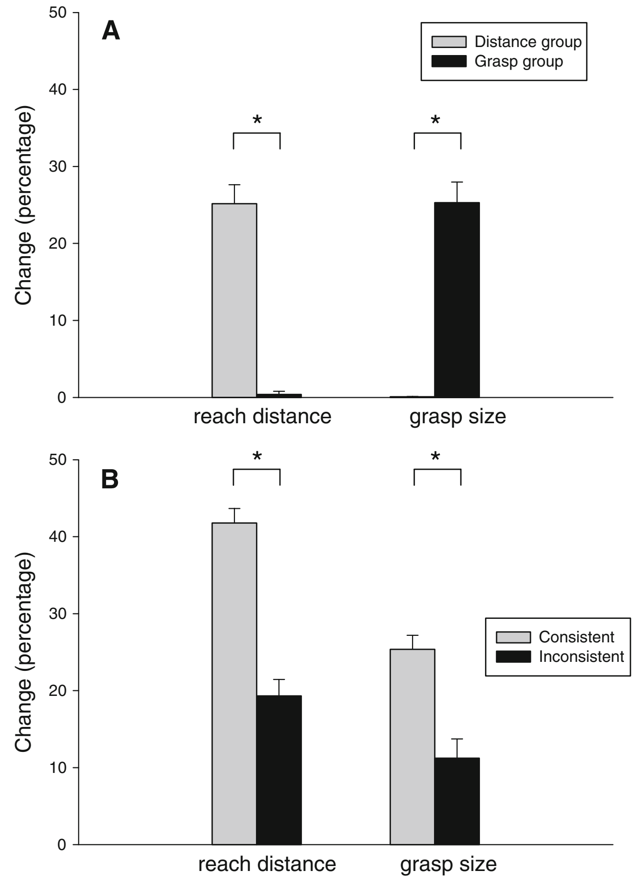

Fig. 2 **a** The results from the first experiment. The change in reach distance and the change in grasp size have been plotted as a percentage of the potential adaptation (thus, a change in reach distance of 10 cm would be 100%, but a change of 5 cm would be 50% and likewise a change in grasp size of 4 cm would be 100% but a change of 2 cm would be 50%). In the experiment, one group were exposed to a change in distance but not size (the 'distance' group) and vice versa (the 'size' group). The *asterisk* indicates a statistically reliable difference between the change in reach distance (*left columns*) or the change in grasp size (*right columns*) for the distance versus size group. It can be seen that the distance group altered their reach distance but not their grasp and vice versa. **b** The results from the second experiment. The change in reach distance and the change in grasp size again have been plotted as a percentage of the potential adaptation. In "Experiment 2", one group were exposed to a consistent change in distance and size (the 'consistent' group) and vice versa (the 'inconsistent' group). The *asterisk* indicates a statistically reliable difference between the change in reach distance (*left columns*) and the change in grasp size (*right columns*) for the consistent versus inconsistent group. It can be seen that the effect magnitude was larger for the consistent than the inconsistent group

Experiment 2

The procedure and measurements used in "Experiment 2" were identical to those employed in "Experiment 1". Once more, the participants were asked to reach-and-grasp ten times to a 6 cm wide virtual object placed 20 cm from the

Table 3 Kinematic data from "Experiment 1" when participants reached to a virtual object that either started big or small and was initially positioned either far or near

	Far to near		Near to far		Small to big		Big to small	
	Pre	Post	Pre	Post	Pre	Post	Pre	Post
Peak speed	653	575	549	692	525	505	531	469
Movement duration (ms)	783	688	699	783	888	820	988	825
Maximum grip aperture (cm)	8.96	9.95	9.77	9.81	8.68	9.56	8.89	7.79
Time to MGA (ms)	349	449	378	441	391	332	452	336

The pre–post differences are within participant

starting position before being exposed to distorted haptic feedback. Participants always viewed the control object (6 cm width at 20 cm) during all virtual reaches. The virtual reaches provided a baseline performance from before and after the calibration phase.

Participants

Forty undergraduates (aged 20–23 years) participated in the experiment on a voluntary basis. The participants were all right handed. The participants were randomly assigned to sub-groups as discussed later. The participants had no history of neurological, ophthalmological or musculoskeletal disorders, and were naïve to the purpose of the study. All participants were able to comprehend the instructions, and carry out the task without difficulty. The Psychology Ethics Committee at the University of Aberdeen gave ethical approval and the experiments were conducted in accordance with the Declaration of Helsinki. All participants gave written informed consent.

Design

There were four groups of ten participants in "Experiment 2": two consistent groups (A and B) and two inconsistent groups (C and D). The consistent group A began to reach for a 4-cm object at 15 cm and this is what they saw throughout the calibration trials. The participants performed ten reaches after which the object was moved outwards by 1 cm every five trials and after the first twenty trials increased in size by 1 cm after every ten trials. This procedure continued until the object had moved outwards by 10 cm and increased in size by 4 cm at which point the participants made an additional ten reaches. The consistent group B began to reach for (and viewed throughout) an 8-cm object at 25 cm. The participants performed ten reaches after which the object was moved inwards by 1 cm every five trials and after the first twenty trials decreased in size by 1 cm every ten trials. This procedure continued until the object had moved inwards by 10 cm and decreased in size by 4 cm at which point the participants made an additional ten reaches.

The inconsistent group C began to reach for (and viewed throughout) a 4 cm object at 25 cm. The participants performed ten reaches after which the object was moved inwards by 1 cm every 5 trials and after the first 20 trials increased in size by 1 cm after 10 trials. This procedure continued until the object had moved inwards by 10 cm and increased in size by 4 cm at which point the participants made an additional ten reaches. The inconsistent group D began to reach for (and viewed throughout) an 8-cm object at 15 cm. The participants performed 10 reaches after which the object was moved outwards by 1 cm every 5 trials and after the first 20 trials decreased in size by 1 cm every 10 trials. This procedure continued until the object had moved outwards by 10 cm and decreased in size by 4 cm at which point the participants made an additional ten reaches.

Results

We first analysed the kinematic data collected when the participants reached for physical objects (under visual open-loop conditions). The data again showed the normal qualitative pattern of prehension behaviour. Table 4 shows the data from initial reaches (capital letter column headings) and final reaches (lowercase column headings) from the adaptation phase. To be certain that participants were scaling their prehensile behaviour appropriately, we used student *t* tests to compare reaches to objects at the beginning of the adaptation period (of one size in a given location) to objects at the end of the period (of a different size and in a different location). We calculated the average value over the first ten reaches and over the last ten reaches for each participant. Thus, we ended up with one value for the initial reach and one value for the final reach for each participant. The initial and final data across the participants were then entered into a student *t* test. As shown in Table 4, the kinematic data altered in a reliable and predictable manner when the target changed location (longer duration and higher peak speed to further targets) and dimensions (larger grip aperture when the object was wider). In summary, the reach-and-grasps to the physical objects showed the normal kinematic scaling that occurs when distance and size alters. These results are consistent with the findings of Gentilucci et al. (1995).

The primary interest within the study was, however, whether the movements were calibrated after the adaptation period. To explore this issue we looked at the reaches to the

Table 4 Kinematic data from "Experiment 2" when participants reached to a real object

	FAR BIG	near small	NEAR BIG	far small	NEAR SMALL	far big	FAR SMALL	near big
Peak speed	688	480[a]	434	544[a]	445	535[a]	490	435[a]
Movement Duration (ms)	767	617[a]	733	912[a]	662	836[a]	966	704[a]
Maximum grip aperture (cm)	9.82	7.38[a]	9.77	7.53[a]	6.76	9.49[a]	6.93	9.71[a]
Time to MGA (ms)	521	398[a]	469	437[a]	379	486[a]	433	488[a]

Column headings with capital letters show the data from the initial reach (before adaptation) whilst the column with lower case letters show the data from the final reach (at the end of the adaptation period). The lower case column is to the right of the column showing the target configuration at the beginning of the adaptation period

[a] In the lower case column indicates that the within participant data are reliably different at the end of the adaptation period (student *t* test $P < 0.05$, $df = 9$)

virtual target before and after the adaptation period (see Table 5). We calculated the average reach distance and grasp size for each participant from their first ten virtual reaches. This value was then subtracted from each of the values for the final ten reaches giving the effect of the manipulation, with condition (four levels) as the between participant factor. We first established that there was a reliable difference amongst groups in both distance reached [$F_{(3,36)} = 38.817$; $P < 0.05$] and grasp aperture [$F_{(3,36)} = 11.651$; $P < 0.05$]. Figure 2b shows that the consistent trials produced a greater effect than the inconsistent trials and this was confirmed statistically for distance [$F_{(1,38)} = 12.426$, $P < 0.05$] and grasp [$F_{(1,38)} = 9.394$, $P < 0.05$]. There was no reliable difference between adaptation direction for either distance [$F_{(1,18)} = 0.008$, $P > 0.05$] or grasp [$F_{(1,18)} = 0.293$, $P > 0.05$].

Table 5 Reach distance and grasp size after adaptation in "Experiment 2" (the column indicates the direction of adaptation) with the between participant standard deviations in parentheses

	Near small	Far small	Far big	Near big
Reach distance (cm)	14.25 (0.81)	22.05 (1.6)	22.87 (1.25)	18.73 (0.86)
Grasp size (cm)	5.09 (0.64)	7.02 (0.77)	7.91 (0.44)	7.39 (0.81)

To determine whether the whole movement had calibrated, we studied the reach-to-grasp kinematics (see Table 6). We calculated the average value over the pre-adaptation ten virtual reaches and over the post-adaptation ten virtual reaches for each participant. Thus, we ended up with one value for the pre-adaptation virtual reaches and one value for the post-adaptation virtual reaches for each participant. The pre-adaptation and post-adaptation data across the participants were then entered into a student *t* test. We simply studied the maximum grip aperture when participants were adapted to a larger object ($n = 20$) and when adapted to a smaller object ($n = 20$). There was a reliable increase in MGA after adaptation to a large object [$t(19) = 4.127$, $P < 0.05$] and a reliable decrease after adaptation to a small object [$t(19) = 3.596$, $P < 0.05$]. We likewise studied movement duration and peak speed when participants were adapted to a further reach distance ($n = 20$) and when adapted to a closer object ($n = 20$). There was a reliable increase in duration after adaptation to a further object [$t(19) = 2.143$, $P < 0.05$] with a correspondingly higher peak speed [$t(19) = 2.115$, $P < 0.05$]. There was also a reliable decrease in duration after adaptation to a closer object [$t(19) = 4.635$, $P < 0.05$] with a correspondingly lower peak speed [$t(19) = 3.703$, $P < 0.05$].

Discussion

These kinematic data are in agreement with those collected in "Experiment 1" showing that the measured changes in

Table 6 Kinematic data from "Experiment 2" when participants reached to a virtual object. The pre-post differences are within participant

	Far big to near small		Near big to far small		Near small to far big		Far small to near big	
	Pre	Post	Pre	Post	Pre	Post	Pre	Post
Peak speed	489	440	464	474	437	509	421	386
Time to peak speed (ms)	314	292	321	353	334	381	381	322
Maximum grip aperture (cm)	9.32	8.43	8.28	7.73	8.5	9.53	9.71	9.9
Time to MGA (ms)	419	370	387	351	376	464	409	418

final reach distance and grasp reflect calibration of the whole reach-to-grasp movement. Participants were asked after the experiment regarding their understanding of the experimental manipulation. The participants were unaware that the physical properties of the object were altering. This is consistent with our previous work (Mon-Williams and Bingham 2007) where we found that calibration processes are not cognitively penetrable.

Two reviewers raised the issue of whether the differences between the 'consistent' and 'inconsistent' conditions were related to visual size constancy where objects that approach an observer do not appear to change visual size despite subtending a larger visual angle on the retinae. There are two reasons to suppose that visual size constancy is not a factor within the results reported. First, haptic feedback regarding an object's size does not alter as a function of distance from the observer. Second, the objects were not moved along the participant's midline. In the experimental setup, the objects were moved at 45° to the line of sight (i.e. in the same plane as the semi-silvered mirror). The changes in size were orthogonal to this plane. In this situation, the objects were not simply approaching or receding from the participant but were concurrently altering egocentric visual direction and distance. It therefore seems reasonable to assume that the effects reported within the present manuscript are not related to mechanisms of visual size constancy.

The question then remains as to why differences occurred between the 'consistent' and 'inconsistent' conditions? As we discuss below, we interpret this result to mean that reaches-to-grasp have an integral dynamic in which the reaching and grasping components are cross-coupled.

General discussion

The data from both experiments provide unequivocal evidence that distorted haptic feedback causes a recalibration of the reach-to-grasp action to a visually specified target. This finding was remarkably robust with every participant showing recalibration in the predicted direction. Moreover, we found no evidence of the effect dissipating over the ten post-adaptation trials consistent with previous studies we have conducted (Mon-Williams and Bingham 2007). The lack of dissipation is perhaps unsurprising when one considers that the post-adaptation trials provided no visual or haptic error signal. Nevertheless, and more to the point, lack of dissipation indicates that there is no preferred state to which the system returns and that calibration is a natural component of reach-to-grasp actions required to resolve intrinsic noise in the system.

In "Experiment 1", we found that reach distance and grasp size could be calibrated separately. The calibration of grasp confirms the earlier work of Gentilucci et al. (1995). Thus, as one would ultimately expect, there is more than one degree of freedom in calibrating the reach-to-grasp action. Nonetheless, in "Experiment 2" we found a difference between the results when distance and size were co-varied in a consistent manner (distance and size both grew larger or smaller) and the results where these changes were inconsistent (distance increased but size grew smaller or vice versa). These findings suggest that the calibration of reach distance and grasp size are not independent of one another. These combined results are consistent with an understanding of the dynamics of reaches-to-grasp as akin to those of accommodation and vergence, which are cross-coupled components of the visual system. The coupling in each direction is subject to a strength parameter. With individual differences in the strength of this coupling, people vary in the ease with which they are able to learn to accommodate and to verge to different distances, an ability that is required to be able to use any virtual environment system whether it is Computer Automatic Virtual Environment or head mounted display based (e.g. Wann et al. 1995; Bingham et al. 2001). Likewise, a moderate coupling strength in the case of reaches-to-grasp would allow some measure of independence in the separate calibration of reach distance and grasp size, but a limited amount that would eventually exhibit clear interaction effects. Furthermore, the recalibrations of reaching and grasping would reinforce one another through the cross-coupling in the consistent case yielding stronger effects and then interfere with one another in the inconsistent case yielding weaker effects. Clearly, reach-to-grasp actions are integral in this way.

Notably, in all conditions the gain of the calibration process was considerably less than one. Mon-Williams and Bingham (2007) studied the dynamics of calibration and found that the gain <1 reflected delay or inertia in the calibration process. While the calibration level may pursue the feedback, it is unable to jump instantaneously to the level indicated by the feedback. The magnitudes of recalibration found in the results are a function of interruption to this process. The system presumably would settle eventually at greater recalibration magnitudes had it been left to continue with the feedback at the terminal values provided. Inertia (or more generally, some resistance to change) confers stability to the system whilst allowing flexibility for change in the perception-action cycle. These findings imply that the differences in recalibration magnitude found as a function of the consistency of the feedback about size and distance reflect rates of change in calibration level. If so, then the fact that reach distance and grasp size can be calibrated separately is important. The implication is that large magnitudes of recalibration could be achieved in opposite directions for reach distance and grasp size if enough time is provided. It would be the recalibration process that is slowed by the inconsistency. Nevertheless, the relative slowness of recalibration should be interpreted as a feature of the process designed to ensure stability in the face of change. A system that responded too rapidly to perturbations might ultimately be uncontrollable.

References

Bingham G, Pagano C (1998) The necessity of a perception/action approach to definite distance perception: monocular distance perception to guide reaching. J Exp Psychol Hum Percept Perform 24:145–168

Bingham GP, Romack JL (1999) The rate of adaptation to displacement prisms remains constant despite acquisition of rapid calibration. J Exp Psychol Hum Percept Perform 25(5):1331–1346

Bingham GP, Bradley A, Bailey M, Vinner R (2001) Accommodation, occlusion and disparity matching are used to guide reaching: a comparison of actual versus virtual environments. J Exp Psychol Hum Percept Perform 27(6):1314–1344

Bingham GP, Coats RO, Mon-Williams M (2007) Natural prehension in the absence of haptic feedback when calibration is allowed. Neuropsychologia 45:288–294

Desmurget M, Grafton S (2000) Forward modeling allows feedback control for fast reaching movement. Trends Cogn Sci 4:423–431

Gentilucci M, Daprati E, Toni I, Chieffi S, Saetti MC (1995) Unconscious updating of grasp motor program. Exp Brain Res 105:291–303

Gentilucci M, Toni I, Daprati E, Gangitano M (1997) Tactile input of the hand and the control of reaching to grasp movements. Exp Brain Res 114:130–137

Goodale MA, Jakobson LS, Keillor JM (1994) Differences in the visual control of pantomimed and natural grasping movements. Neuropsychologia 32:1159–1178

Jeannerod M (1988) The neural and behavioural organization of goal-directed movements. Oxford University Press, Oxford

Mon-Williams M, Bingham GP (2007) Calibrating reach distance to visual targets. J Exp Psychol HPP 33:645–656

Mon-Williams M, McIntosh RD (2000) A test between two hypotheses and a possible third way for the control of prehension. Exp Brain Res 134:268–273

Mon-Williams M, Tresilian JR (1999) The size-distance paradox is a cognitive phenomenon. Exp Brain Res 126:578–582

Mon-Williams M, Tresilian JR (2001) A simple rule of thumb for elegant prehension. Curr Biol 11:1058–1061

Patchay S, Haggard P, Castiello U (2003) A cross-modal interference effect in grasping objects. Psychon Bull Rev 10:924–931

Redding GM, Wallace B (1997) Adaptive spatial alignment. Lawrence Erlbaum, New Jersey

Schor CM, Narayan V (1982) Graphical analysis of prism adaptation, convergence accommodation, and accommodative convergence. Am J Optom Physiol Opt 59:774–784

Smeets JBJ, Brenner E (1999) A new view on grasping. Motor Control 3:237–271

Vindras P, Viviani P (1998) Frames of reference and control parameters in visuomanual pointing. J Exp Psychol Hum Percept Perform 24:569–591

von Helmholtz H (1894/1924) Physiological Optics (New York: Dover 1962); English translation by J.P.C. Southall for the Optical Society of America (1924) from the 3rd German edition of Handbuch der Physiologiscen Optik (Hamburg: Voss 1909)

Wann JP, Rushton SK, Mon-Williams M (1995) Natural problems in the perception of virtual environments. Vision Res 35:2731–2736

Wolpert DM, Ghahramani Z, Flanagan JR (2001) Perspectives and problems in motor learning. Trends Cogn Sci 5:487–494