Wilmut, K and Barnett, A

Tailoring reach-to-grasp to intended action: the role of motor practice.

Wilmut, K and Barnett, A (2014) Tailoring reach-to-grasp to intended action: the role of motor practice. *Experimental Brain Research*, 232 (1). pp. 159-168.

doi: 10.1007/s00221-013-3728-5

Tailoring reach-to-grasp to intended action: the role of motor practice

Kate Wilmut and Anna L. Barnett

Affiliation for both authors

Perception and Motion Analysis Research Group, Faculty of Health and Life Sciences, Oxford Brookes University, Oxford, OX2 9EA

Corresponding address:

Dr. Kate Wilmut

Faculty of Health and Life Sciences

Oxford Brookes University

Oxford

OX3 0BP

k.wilmut@brookes.ac.uk

Tel: 01865 483 781

Acknowledgements:

We would like to thank all of the participants who took part in this study, Ian Wilmut who made the equipment and Prof. John Wann who kindly lent the VICON system.

Abstract

Motor learning results from repeated exposure to the same movement and allows a mover to increase movement optimality. Typically this has only been considered in single step movements. In sequential movements an initial reach movement is tailored to the demands of the onward movement. However, the exact role of motor practice in the tailoring to onward task demands is unknown. Eighteen adults performed blocks of 15 movements; each movement consisted of a *reach phase* and an *onward phase* (the object was placed in a tight fitting hole, placed in a loose fitting hole or thrown). Simple practice effects were seen; for the *reach phase* the amount of time spent decelerating decreased over trials and; for the *onward phase* the accuracy of the place / throw movements increased over trials. Furthermore, approximately 30% of variance in the practice effect of the *onward phase* could be explained by the practice effect in the *reach phase*. Therefore, we suggest that the changes in the *reach* phase are directly linked to the changes in the *efficiency* of action and that this is necessary but not sufficient in explaining the calibration of the onward action.

Keywords:

Motor learning, Motor practice, reach-to-grasp, task demands, movement intentions

Introduction

Experience plays a role in nearly all human behaviour and motor responses are no exception. Motor learning involves changes to movement which arise as a consequence of our experience with the environment and which result in a change in performance such as an improvement in accuracy. During movement execution appropriate changes can be made to a movement to reduce potential end-point error. This can be done through a feed-forward process if done early in the movement or through a feedback process if made later in the movement (see (Elliott et al. 2010) for a review of this process). These adjustments to ongoing movements can improve end-point accuracy and, together with information regarding the final outcome of the movement, inform how the next movement is planned. In this way the error generated from trial-to-trial is reduced (Elliott et al. 2010).

An example of this type of change to a motor plan is seen when humans make adaptations following an error caused by an external perturbation. For example, when asked to wear glasses which create a prismatic displacement to vision participants will start by making large errors in pointing behaviour. However, over a number of trials this mismatch between the desired sensory outcome (an accurate movement) and the actual sensory outcome (an error due to distorted visual information) is corrected and error decreases. If the glasses are then removed participants will show an after-effect adaptation where their movements are executed as though they were still wearing the glasses (MacGonigle and Flook 1978; Welch et al. 1993; Hansen et al. 2007). Similarly, non-visual perturbations can be used to demonstrate learning in manual aiming movements; participants are asked to generate a point-to-point movement using a handle, unbeknownst to the participants an additional force is added to this handle causing participants to undershoot the targets, however, their movements soon adapt and when it is removed they are seen to overshoot the target (Shadmehr and Mussa-Ivaldi 1994; Levy et al. 2010). These studies demonstrate that the human movement system is very responsive to error created by the environment and can adapt and refine a movement when the actual outcome deviates from the expected outcome. In fact, other studies which have used perturbations such as these have suggested that we correct between 20% and 38% of error when planning our next movement (Scheidt et al. 2001; Cheng and Sabes 2007). Similar results have been found when considering prehensile movements, for example Rand et al. (2004) found that if force perturbations are made to the moving limb during a reach to grasp movement participants adapt to this over time and given enough trials their reach movements in perturbation trials are indistinguishable from control trials. Similarly, creating a mismatch between visual and haptic information initially results in reaching error, however over time a re-calibration of movement is seen thus demonstrating a learning effect (Coats et al. 2008). All of these perturbation studies impose error on movement through external manipulation; these force participants to adjust their movement in line with the perturbation. As such the studies are not a naturalistic description of motor learning. Given that a certain degree of error is inherent in all movement a more naturalistic way to consider motor learning is to consider how motor plans are updated to minimise this error.

van Beers (2009) considered how motor behaviour is shaped by recent actions in the absence of target perturbation. Participants made 30 pointing movements to the same target. Error was taken as the distance between the endpoint of the movement and the target. Learning curves indicated the error rapidly decreased over the first few trials and then remained small for the remaining trials, with 46% of error on one trial corrected for in the next. Similarly Verstynen and Sabes (2011) asked participants to make over 100 pointing movements each time pointing to a single target which could appear in a range of positions. The possible target positions were either within a very small range of positions (standard deviation of target position 1^o) or within a larger range (standard deviation of target position 15^o). The initial movement angle and corresponding variance were taken as an indication of error. Verstynen and Sabes (2011) found that repetition of very similar movements (small target range) improved performance and reduced initial movement angle error. Such an effect was not found for the large target range. These studies have demonstrated refinement of motor control in the absence of an external manipulation, which suggests that when we generate a movement the error (inherent in all movement) is identified and the subsequent movement corrected in a way to reduce that error. Thus sensory error experienced on one trial can feed into the planning of the next by updating the motor plan accordingly. In terms of reach-to-grasp movements the authors are not aware of any studies which have considered motor learning in adults in the absence of perturbation. However, there is no reason to think the mechanisms would be different. A mover would respond to sensory error, this error could either be identified during the movement (the hand is not heading in the direction of the object) and subsequently corrected using online control. Or alternatively, error could be identified at the end of the movement and corrected in the motor plan that is used for the subsequent movement. Typically in pointing paradigms error is measured in terms of how close the finger was to the center of the target, an equivalent in a reach paradigm would be that the hand failed to grasp the object or the hand knocked the object over. It is unclear whether the system can respond to more subtle error in reach paradigms, i.e. the reach was sub-optimal but did not result in an overt error. Up to this point changes to motor performance over time have been referred to as motor learning. However, this term implies a lasting change which is typically not considered in the aiming/reach-to-grasp literature discussed in this paper. Therefore, in this manuscript changes to motor performance over time will henceforth referred to as motor calibration.

The research discussed so far is concerned with the motor learning of an individual movement such as a pointing movement, however, more often than not we make multiple sequenced movements such as a reach-to-grasp followed by an onward action. Interestingly, the nature of a single movement changes when it is coupled with a second movement. For example the reaction time and the movement time to a target is shorter when that movement is performed in isolation compared to when it precedes a second movement (see articles on the one-target advantage for example Adam et al. 2000). This one target advantage remains even after a substantial number of training trials (Lavrysen et al. 2003). This demonstrates that a two movement sequence is not simply the sum of its parts. In fact, if we consider two-movement sequences more closely we see that an initial movement is influence by the nature of the subsequent movement. Marteniuk et al. (1987) and later Armbruster and Spijkers (2006) asked participants to reach and 'fit' a disc into a hole or reach and 'throw' the same disc into a container. Despite the fact that the initial reach demands were identical an elongated deceleration phase was seen in the reach movement preceding the 'fit' compared to the 'throw'. One explanation for this finding is that the second movement, the 'fit' or 'throw' is planned during the online control phase of the reach movement and given that more complex movements take longer to plan (Thompson et al. 2007) this elongates the deceleration period for the reach preceding the 'fit' more than that preceding the 'throw'. This is supported by the finding that the deceleration period during the reach preceding a fit (or as referred to in some studies ‘a place’) with high precision requirements is longer than that preceding a place with low precision requirements (Wilmut et al. 2013b). Further differences are seen in the way in which the fingers are positioned on an object when comparing reach movements preceding a lift, a high accuracy fitting movement and a low action fitting movement (Ansuini et al. 2006), when comparing reach movement preceding a place, a pour, a throw and a pass (Ansuini et al. 2008) and when comparing a pour and a lift (Craje et al. 2011). Furthermore, a handful of studies have also demonstrated differences to the reaching movement in *both* the ballistic stage (prior to peak velocity) and the online control phase of the reach movement (Gentilucci et al. 1997; Naish et al. 2013; Wilmut et al. 2013a). The combination of these findings suggests that the second movement, the throw or the place is planned prior to any movement execution, hence why changes to the ‘pre-planned’ phase of the reach movement are seen but that some planning also occurs during the online control phase of the reach movement. Recently we considered the functionality of this tailoring to onward action, we found that the degree to which movements were tailored in the reach phase predicted the efficiency of the onward place phase (Wilmut et al; 2013a;2013b). The novel finding of these studies was that the magnitude of tailoring of deceleration period (during the reach phase) between a tight place and loose place action was directly related to the efficiency of that place action (i.e. the time spent adjusting the movement prior to placement of the object). This effect demonstrates a possible purpose of tailoring one movement to the next whereby anticipating the appropriate action for both the first and the second movement results in a more efficient second movement.

If actions are planned and linked together in this way there must be a possibility of motor calibration whereby error in the onward movement can be corrected on subsequent trials by a change to the reach-to-grasp movement. Here error may refer to any aspect of the movement that is not optimal, such as prolonged online adjustments. If this is the case we would expect to see a change in the initial reach movement which relates to a change in the error made in the onward place movement. The aim of the current study was to consider whether motor calibration occurs in two-step movements in adults. It used the same paradigm adopted by Wilmut et al. (2013a; 2013b) whereby participants performed a reach movement followed by one of three onward actions: a tight place, a loose place or a throw. The tailoring between the *reach phase* and the *onward phase* over time and the impact of that tailoring on the efficiency of the onward action was considered.

Method

Participants

18 adults were recruited from Oxford Brookes University, the group had an average age of 28 years ranging from and an age range of 18 years 8 months to 51 years and 9 months[1]. Six participants were male and 12 female. All participants had normal or corrected to normal eyesight. Ethical approval was sought and granted by the host institution.

Materials

Participants sat at a table in front of a wooden cylinder 7cm in height and 2cm in diameter which was placed 0.3 times arm length in front of a start node which was to be grasped between the

[1] This upper age is higher than would normally be seen in similar studies and was primarily driven by two participants over 40 years (upper age without these participants was 38 years and nine months). However, the data were analysed both with and without these two participants and the outcome did not differ. Therefore, these participants are included throughout the analysis section.

thumb and index finger of the dominant hand at the start of each trial. One of three 'target' objects was placed 0.2 total arm length behind and to the right of the cylinder for left handed participants and behind and to the left for right handed participants (see Figure 1 for exact locations). 'Target' objects all consisted of a 8cm by 8cm wooden square with: a hole with a diameter of 2cm (the same diameter as the cylinder, for the tight place action), a hole with a diameter of 4cm (for the loose place action); and a 4cm deep tray measuring 8cm by 8cm (for the throw action). A Vicon 3D motion capture system (Oxford Metrics, United Kingdom), consisting of six infra-red cameras and running at 120Hz, was used to track the movement of five reflective markers (6mm in diameter) placed on the thumb, index finger, knuckle and wrist of the preferred hand. A fifth marker was placed centrally on top of the cylinder.

Procedure and design

Each action type (*throw, tight place, loose place*) was performed in a block of 15 consecutive trials. All trials consisted of the participant grasping the start node and then when instructed to do so reaching out and grasping the cylinder and: placing the cylinder in a hole the same size as the cylinder *(tight place)*; placing the cylinder in a hole twice the size of the cylinder *(loose place)*; or throwing the cylinder into the tray *(throw)*. Each action was explained to the participant prior to the start of each block. The order of the action type trial block was pseudo-randomized for each participant. Participants were simply told to reach out and perform the named action as quickly and accurately as possible.

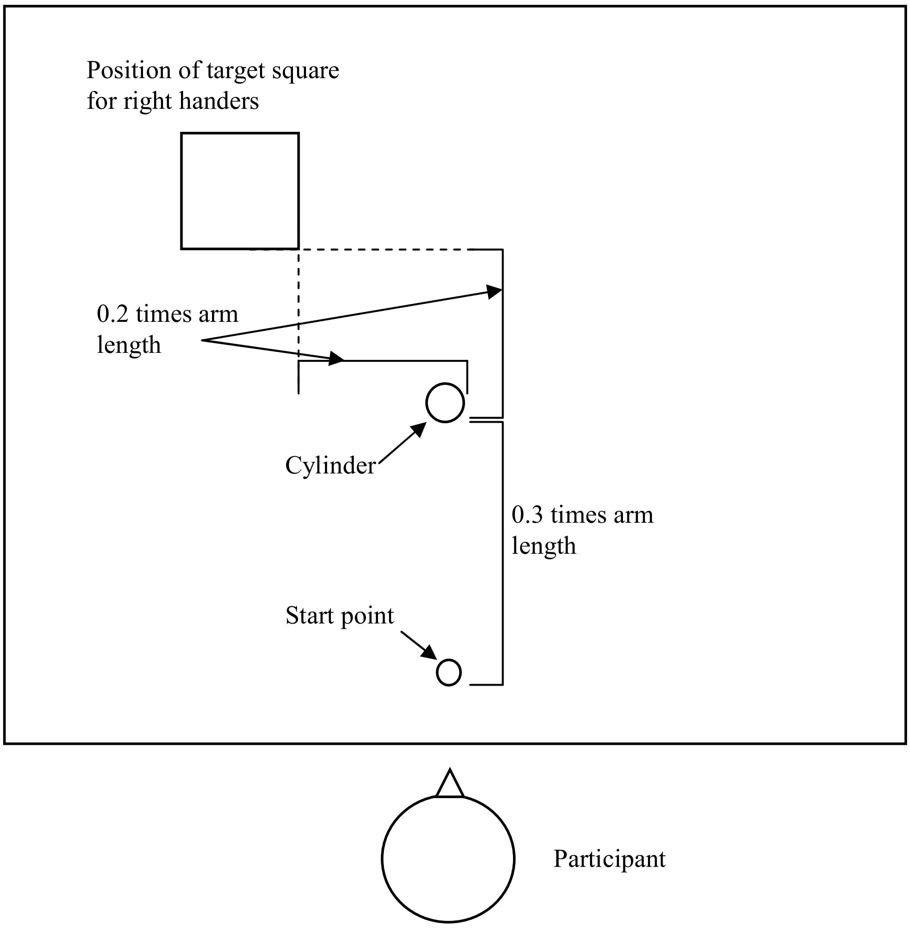


Figure 1. A schematic illustration of the experimental set-up. The set-up shown is for a right handed participant,. The target for each action was a wooden 8cm x 8cm square, this had a small hole for the tight place action, a larger hole for the loose place action and was a tray for the throw action.

Data analysis

Trials were excluded if the data lost due to occlusion of markers exceeded 10 consecutive frames. In total this resulted in a loss of 12%, this loss of trials was roughly equal across all participants and action type. VICON hand movement data were filtered with an optimized Woltring filter (low pass 12Hz) and tailored MatLab routines were used for analysis. Hand movement onset was defined as the time point at which velocity departed from zero (>3% max velocity) and hand movement offset as the point velocity returned to zero (<3% max velocity). From these time points duration of movement (ms), proportion of time spent decelerating (start of deceleration period determined by peak velocity) were calculated. In addition the maximum distance between the finger and thumb was taken as maximum grip aperture and the greatest velocity between hand movement onset and offset taken as peak velocity. For the *reach phase* the kinematic variables extracted were: movement duration, proportion of time spent decelerating, maximum grip aperture and peak velocity. For the *onward phase* movement duration, proportion of time spent decelerating and peak velocity were extracted. Discontinuities in the velocity profile towards the end of a movement indicate that an individual has corrected an impending error (Khan et al. 2006), therefore the movement time following a discontinuity (or adjustment) can be used as an inverse measure of planning efficiency. The timing / presence of these adjustments to movement can be determined by inspection of the velocity and acceleration profiles (Khan et al. 2006). Typically zero-order crossings of velocity indicate an over-shoot to a target and zero-order crossings or significant deviations of acceleration an under-shoot to a target (Khan et al. 2006). Over-shooting during a reaching movement infers collision with the object and so is a less appropriate consideration than in manual aiming. Therefore, we only considered adjustments following an under-shoot and did this by inspecting zero-order crossings of acceleration (as this is less subjective than determining a 'significant' deviation of acceleration). This method of measuring adjustments has been adopted in previous reach-to-grasp studies (Rand et al. 2000; Seidler and Stelmach 2000). The time between the first secondary peak and the end of the movement was defined as time spent adjusting. In all cases these zero-order crossings always occurred after peak deceleration. This was only possible for the 'place movements.

For the place movements, the nature of the reach movement could be compared across the two onward actions, this allowed the quantification of how much a participant tailored a movement to the specific onward action. To do this the change in proportion spent decelerating was calculated across action types. This measured the degree to which a reach for one onward action (say loose place) differed from a reach to a different onward action (say tight place). If a participant showed a deceleration period for a tight place action of 50% and for a loose place action of 40% then the change would be 10%. This could then be compared to another participant who may have shown more (30%) or less (5%) discrimination between the reach movements for the different onward actions. For each action type the 15 trials were broken into 3 blocks of 5 trials, block 1 included trials 1-5, block 2 trials 6-10 and block 3 11-15.

Results

Differences between action types for the *reach phase*

No differences were found for movement duration, maximum grip aperture or peak velocity these are not discussed further in this section, data for these variables can be found in Table 1.

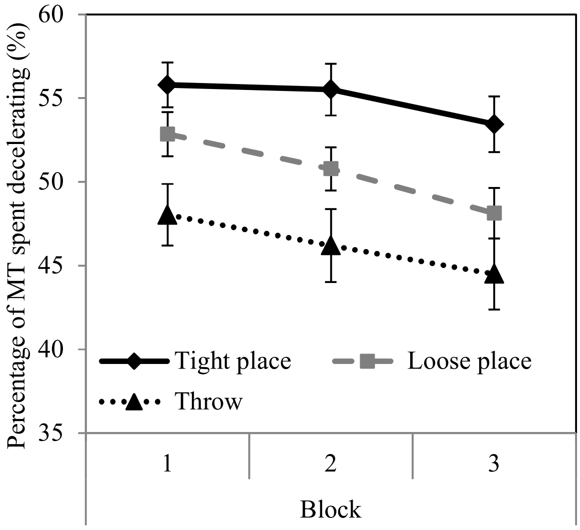
Table 1. Kinematic variables for the reach phase each of the three action types, detailed across all trials and for each block. Standard deviation is given in brackets.

	Block 1 Trials 1-5	Block 2 Trials 6-10	Block 3 Trials 11-15
		Movement Duration (ms)	
Tight Place	532 (82)	530 (62)	515 (55)
Loose Place	559 (106)	531 (74)	513 (86)
Throw	503 (67)	496 (62)	482 (84)
		Peak Velocity (ms^{-1})	
Tight Place	6.3 (1.3)	6.6 (1.4)	6.5 (1.3)
Loose Place	6.3 (1.5)	6.4 (1.6)	6.3 (1.3)
Throw	6.5 (1.6)	6.6 (1.8)	6.8 (1.8)
		Maximum grip aperture (mm)	
Tight Place	63.6 (6.6)	64.6 (8.1)	65.8 (12.8)
Loose Place	66.1 (5.2)	67.2 (6.9)	64.3 (7.0)
Throw	62.0 (7.3)	61.1 (7.1)	62.8 (7.3)

Percentage of movement time spent decelerating

The percentage of movement time spent decelerating across blocks can be seen in Figure 2 for each action type. A two-way ANOVA (action type x block) found a main effect of action type [$F(2,34)=19.97$ $p<.001$ $\eta^2=.54$]. Post-hoc tests indicated that this was due to the percentage of movement time spent decelerating being longer for the tight place action compared to the loose place action and longer for the loose place action compared to the throw action (throw < loose place < tight place, $p<.05$ using Bonferroni correction). In addition, a main effect of block was found [$F(2,34)=12.86$ $p=.001$ $\eta^2=.43$], this was due to a decrease in the deceleration period from block 1 to block 2 and 3. No interaction between action type and block was found suggesting that the decrease in deceleration period across block was the same for all action types.

Figure 2: An illustration of the percentage of movement time spent decelerating during the reach phase for each action type across the three blocks. Error bars represent standard error.



Changes over time to the *onward action phase*

Changes over time to the onward action, place or throw, were also examined using the same variables and with the addition of the time spent adjusting for the place movements. Data concerning the duration of movement, peak velocity and time spent decelerating can be seen in Table 2. Since movement duration and time spent decelerating only showed an effect of action type this is not reported, as differences in kinematics across different actions are expected.

Table 2. Kinematic variables for the onward phase (place or throw) each of the three action types, detailed across all trials and for each block. Standard deviation is given in brackets.

	Block 1 Trials 1-5	Block 2 Trials 6-10	Block 3 Trials 11-15
		Movement Duration (ms)	
Tight Place	788 (84)	779 (70)	762 (90)
Loose Place	754 (141)	739 (97)	729 (88)
Throw	385 (94)	403 (153)	405 (145)
		Peak Velocity (ms^{-1})	
Tight Place	8.1 (1.2)	7.6 (1.6)	8.2 (1.5)
Loose Place	8.1 (1.3)	8.1 (1.2)	8.1 (1.2)
Throw	9.6 (1.8)	10.4 (1.8)	11.0 (1.9)
		Deceleration period (%)	
Tight Place	68.5 (3.1)	68.8 (3.0)	66.7 (3.4)
Loose Place	66.6 (3.4)	66.1 (2.6)	66.5 (4.0)
Throw	40.5 (14.0)	39.9 (17.2)	40.1 (17.3)

Peak velocity

A two-way ANOVA (action type x block) found a main effect of action type [$F(2,34)=29.43$ $p=.001$ $\eta^2=.63$], whereby peak velocity was higher for throw movements compared to place movements ($p<.05$ using Bonferroni correction). In addition, a main effect of block [$F(2,34)=6.14$ $p=.005$ $\eta^2=.27$] and an interaction between block and action type [$F(4,68)=8.75$ $p<.001$ $\eta^2=.34$] was found. To explore the interaction simple main effects, Pillai's Trace, were used to look at the effect of block for each action type separately. A main effect of block was found for the throw action [$F(2,16)=12.98$ $p<.001$ $\eta^2=.62$] which was due to a higher peak velocity in block 3 compared to block 1 or 2 and a higher peak velocity in block 2 compared to block 1 (all $p<0.05$ using Bonferroni correction). No effect of block was found for tight or loose place.

Efficiency of onward action

The time spent adjusting to the loose place and tight place action was also considered across blocks using a two-way ANOVA (action type x block). A main effect of action type [$F(1,17)=23.61$ $p=.001$ $\eta^2=.58$] and block was found [$F(2,34)=17.91$ $p<.001$ $\eta^2=.53$]. Indicating that adjustment time was longer for tight place compared to loose place movements and that the time spent adjusting decreased from block 1 to block 2 and 3 (post hoc tests using Bonferroni correction). No significant interaction between block and action was found ($p=.184$). Data can be found in Figure 3.

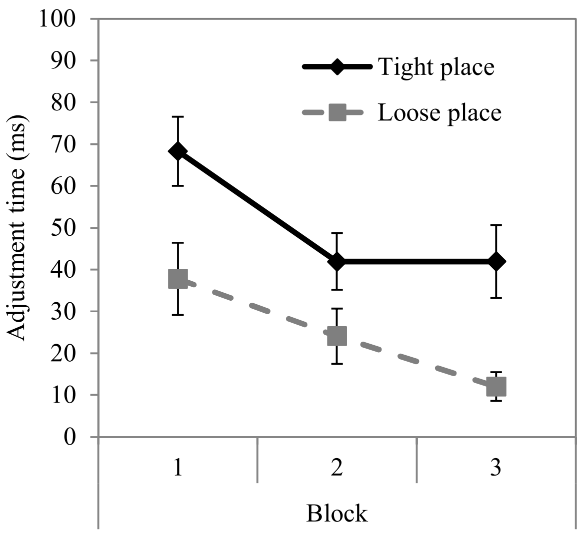
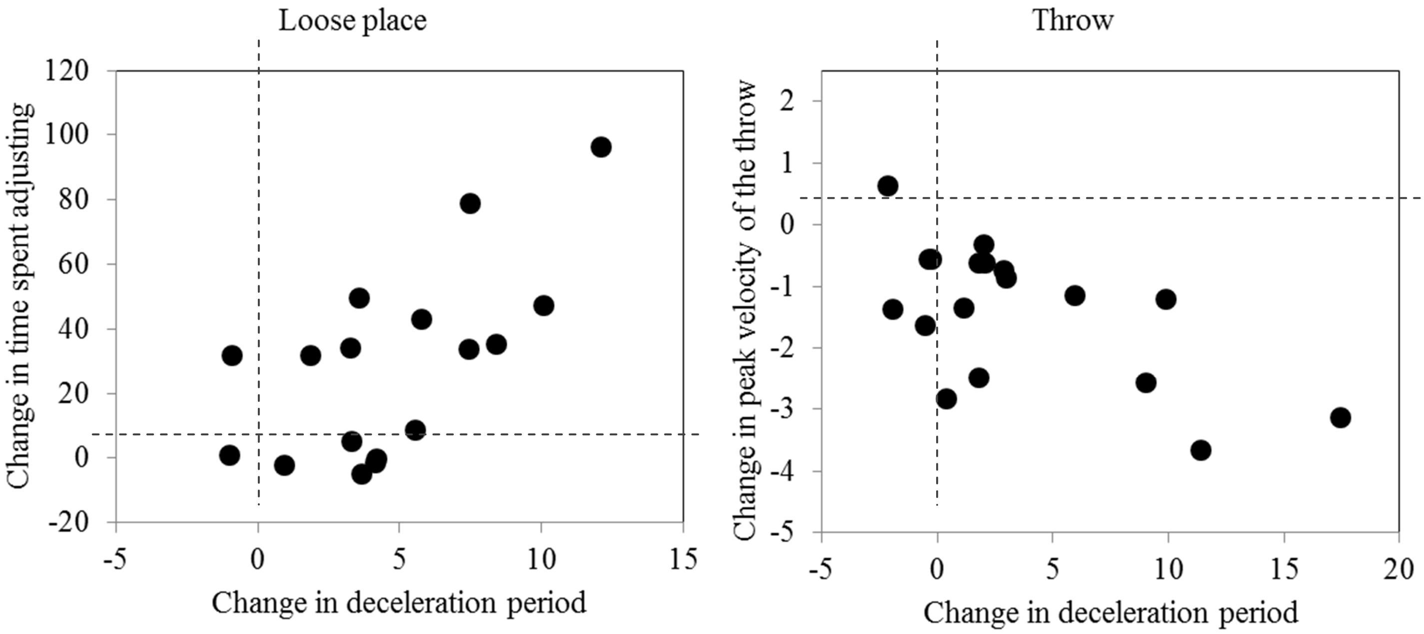


Figure 3. Time spent adjusting during the onward phase for the loose place and tight place movements. Time refers to the final adjustments of movement prior to placement of the cylinder. Error bars show standard error of the mean.

Differences within action types

The analyses above have concentrated on movement difference across the three action types (loose place, tight place and throw). However, the changes within each action type across block are also important. We have seen that the time spent decelerating in the reach phase decreases over time for all three actions. Furthermore, in the onward action phase the time spent adjusting just prior to placement decreases over time for the place actions and the peak velocity increases over time for the throw action. Therefore, the next question to address is whether a relationship exists between these changes. To answer this, the relationship between the change in deceleration period for the reach phase from block 1 to block 3 was calculated for all action types. A positive value indicates a decrease in time spent decelerating from block 1 to block 3, a negative value an increase. This was then compared against the change in time spent adjusting in the onward phase from blocks 1 to 3 for the place actions and against the change in peak velocity in the onward phase for the throw action. A significant regression model was found for the loose place action [R^2=.33, F(1,17)=7.96 p=.012 β=5.137] whereby the change in deceleration period from block 1 to block 3 can predict the change in time spent adjusting over the same period, a decrease in time spent decelerating during the reach phase results in a decrease in time spent adjusting when placing the object. In addition, a significant regression model was found for the throw action [R^2=.39, F(1,17)=10.08 p=.006 β=-.13] whereby the change in deceleration period from block 1 to block 3 can predict the change in peak velocity of the throw, a decrease in time spent decelerating during the reach phase results in an increase in peak velocity. Scatter plots of the significant relationships can be found in Figure 4. No significant relationship was seen for the tight place action.

Figure 4. Scatter plots of the relationship between the change in deceleration period of the reach phase from block 1 to block 3 for the loose place and the throw action. For the loose place action change in deceleration period is compared to change in time spent adjusting. For the throw action change in deceleration period is compared against the peak velocity of the throw movement. For both, values above the horizontal dotted line indicate a decrease in the amount of time spent adjusting from block 1 to block 3; values below indicate an increase. Similarly, values to the right of the vertical line indicate a decrease in time spent decelerating from block 1 to block 3 or peak velocity from block 1 to block 3 and values to the left an increase.



Discussion

Previous research has demonstrated that an initial movement is planned on the demands of both that movement but also the movement that will follow (Marteniuk et al. 1987; Gentilucci et al. 1997; Wilmut et al. 2013a; Wilmut et al. 2013b). This study has replicated these findings, with the deceleration period of the reach phase being shorter when the onward intention was to throw compared to place and being shorter for a place action with low precision requirements compared to high precision requirements. This effect may be due to the planning of the final place action during the online control period of the reach movement. Given that more complex movements take longer to plan (Thompson et al. 2007), one would expect that a place with high precision requirements would take longer to plan than one with low precision requirements. To allow for this extra planning the deceleration phase of the reach is lengthened to a greater extent when preceding a tight place compared to a loose place. Neither this study nor related studies (Weir et al. 1998; Wilmut et al. 2013a; Wilmut et al. 2013b) found a difference in the movement time of the reach preceding place movements with differing precision requirements. This contrasts with the finding that in two-step pointing movements movement time of step one was influenced by the size of the target of step two (Ricker et al. 1999). However, given that a reaching movement takes longer than the equivalent pointing movement; it may be that the elongated movement time in reaching allows for the planning of both a high precision and low precision onward action but that this is achieved by adjusting symmetry of the velocity profile.

This study also demonstrated how tailoring to onward action changes with practice, with a decrease in the amount of time spent decelerating during the reach phase for all action types. This finding suggests that within the reach phase motor calibration occurred allowing the adults to spend less time decelerating. This change occurred despite the ‘successful’ nature of the movement, i.e. the cylinder was picked up and placed without falling. This demonstrates a refinement in motor control occurs in the absence of a large ‘error’ in movement. A similar motor calibration effect is seen in other studies whereby practice results in a decrease in the spread of movement endpoints (variability of movement decreases with practice), it is thought that this is achieved as the mover becomes more precise at specifying the duration and magnitude of the muscular forces needed to move the limb (for example see Khan et al. 1998; Cheng et al. 2008; Elliott et al. 2010). The period of deceleration time decreased across the three blocks in this study. This raises the question of whether this would continue during subsequent trials. The deceleration period of movement is typically seen as the 'control' phase of movement allowing feedback information to refine an ongoing movement (see Elliott et al. 2010). A reduction in deceleration period is seen for manual aiming movements over repeated exposure whereby deceleration period starts at ~40% of movement time, decreases to ~30% of movement time and then plateaus for the remaining trials (Khan et al. 1998). Due to differences between manual aiming movement and reach-to-grasp movement it is difficult to draw a parallel between Khan et al.'s work and the current study, however, it suggests that in the current paradigm we would expect further reduction in deceleration period over subsequent trials.

The second part of this study considered calibration during the onward phase of the action, once again we see that the kinematics for all three onward actions changed over time: Time spent adjusting at the end point of the movement decreased over blocks for the place actions and peak velocity increased over blocks for the throw action. In terms of the place action these movement adjustments are made online in response to sensory feedback and are indicative of a correction to the initial ballistic movement (Woodworth 1899; Elliott et al. 2010). These adjustments can be thought of as a measure of efficiency, with movement calibration these corrective movements become faster and more efficient due to a more accurate internal representation of the movement (Abrams and Pratt 1993). Therefore, the reduction in these adjustments over time indicates a calibration effect with the movement plan becoming more efficient. Whether the increase in peak velocity seen in the throw action over time is an indicator of movement 'improvement' is less clear. Previous research looking at manual aiming has found a decrease in endpoint variability occurs in conjunction with an increase in the peak velocity of the limb (Elliott et al. 1995) and so the change we see here may be indicative of a decrease in throwing variability, i.e. a more accurate movement.

The discovery of motor calibration effects such as those described here are not new. However, the way in which these calibration effects are linked is novel. For the loose place action and the throw action the magnitude of calibration in the reach phase could directly predict the magnitude of calibration in the onward phase. For the loose place action this meant that a large change in the deceleration period of the reach phase resulted in a large reduction of time spent adjusting during the onward phase. For the throw action a large change in deceleration period during the reach phase resulted in a large increase in peak velocity during the onward phase. The nature of this calibration effect is unclear and depends somewhat on how sequential movements are planned. If both actions are planned as one over-arching action prior to any movement execution then the calibration effects in the reach and onward phase must be directly linked as the movements are planned simultaneously. Alternatively, if the onward action is planned after initial movement execution, i.e. during the deceleration of the reach, then the relationship between the calibration effects is more difficult to unpick.

No relationship between change in deceleration period and adjustment time was seen for the tight place action. This could be due to a floor effect in the change in deceleration period of the reach phase from block 1 to block 3, a reduction of only 2.4% of time spent decelerating was seen for tight place, compared to a reduction of 4.7% for loose place. This ‘lack’ of a calibration effect for the tight place action could simply be due to insufficient trials. It is generally accepted that longer periods of exposure lead to better learning (Newell 1991), with healthy adults needing to practice simple single-joint movements over 200 times before effects of muscle activation were seen (Corcos et al. 1993), however, studies considering overt movement have shown that improvements can be seen following between 5 and 20 practice trials (Berardelli et al. 1984; Karst and Hasan 1987; Cirstea et al. 2003). These differences seem primarily driven by the cohort under examination and the difficulty of the motor task at hand. Therefore, it is possible that a movement with a high precision requirement may require more practice than one with a lower precision requirement. However, the number of practice trials provided may have been insufficient to see a large change in deceleration period but they were sufficient to see a change in the onward adjustment time prior to the place. This suggests that the calibration effect in the onward phase is not dependent on the calibration during the reach phase. In fact we see from the relationship in the loose place action that only 29-33% of variance in the onward calibration effect being explained by the reach calibration effect.

These findings suggest that not all calibration effects during the onward phase are due to changes in the reach phase. This tells us something about the calibration of multiple movements. The literature suggests that during a single movement information about how a movement unfolds can be used to inform the next movement, hence resulting in calibration of movement. Putting this in the context of a two step movement, end-point error at both the end of the first movement (the reach movement) and at the end of the second movement (the place or throw) could be used to refine each individual movement *and/or* the overarching movement plan. As such, changes to the second movement (the place or the throw) could be due to changes in the way the two movements are linked, i.e. changes to the reach phase, but they may also be due to changes in the kinematics of the second movement itself. An example of this it that the reduction in adjustments during the loose place movement are in part due to the change during the reach phase, but also due to changes in the earlier kinematics of the place movement, for example a slightly different heading direction may have been used. The difficulty here is determining whether the effects of practice influence an over-arching plan (i.e. changes in the reach and onward phase are dependent on each other) or simply influence each individual movement (i.e. change in the reach and onward phase are independent of each other).

The only indication that the calibration of the reach phase and the calibration of the onward phase are linked is the relationship between these changes. However, it is possible that this relationship may simply be a representation of 'learning speed'. If an individual is a 'fast' learner then we would expect a large calibration effect in both the reach and the onward phase, if an individual is a 'slow' learner we would expect a small calibration effect in both the reach and onward phase. Hence a relationship is created which is mediated by 'learning speed'. One possible way to control for this third variable is to consider the learning profiles of individual participants; however, there is insufficient data in the current data set to do this. Even if this relationship is, in part, mediated by learning speed we would argue that there is still a link between the calibration effects of the two movement phases. There is good evidence in the literature that an initial movement in influenced by the intended action (as shown in the current manuscript; Marteniuk et al. 1987; Armbruster and Spijkers 2006; Ansuini et al. 2009; Craje et al. 2011) and that the greater this influence the more efficient the onward action becomes (as shown in the current manuscript; Wilmut et al. 2013a; 2013b). Furthermore, research suggests that internal models play a role in the planning of sequential movements (Wolpert et al. 2001; Wolpert et al. 2011), allowing one movement to be linked and tailored to the next movement. If this is the case then it would seem that over time the way in which those movements are tailored would become more efficient as the noise inherent in movement becomes more predictable. Therefore, we suggest that the changes in the *reach* phase are directly linked to the changes in the *efficiency* of action and that this is necessary but not sufficient in explaining the calibration of the onward action.

This study is the first to demonstrate that movement experience strengthens the tailoring of an initial movement to the subsequent movement and that there is a clear link between this tailoring and changes seen in the onward action. This strengthens the assertion that movements are planned in conjunction, tailoring each one to the next. Furthermore, we have demonstrated that changes seen in the first movement (the reach) are directly linked to the second movement (the place or the throw). Whether the findings in this study relate to a simple calibration of movement or whether they are due to motor learning is unclear, to distinguish between these future studies would need to consider whether these changes persist without further practice.

References

Abrams RA, Pratt J (1993) Rapid aimed limb movements: Differential effects of practice on component submovements. Journal of Motor Behavior 25: 288-298

Adam JJ, Nieuwenstein JH, Huys R, Pass FGWC, Kingma H, Willems P, Werry M (2000) Control of rapid aiming hand movements: The one-target advantage. Journal of Experimental Psychology: Human Perception and Performance 26: 295-312

Ansuini C, Giosa L, Turella L, Altoe G, Castiello U (2008) An object for an action, the same object for other actions: effects on hand shaping. Experimental Brain Research 185: 111-119

Ansuini C, Santello M, Massaccesi S, Castiello U (2006) Effects of end-goal on hand shaping. Journal of Neurophysiology 95: 2456-2465

Armbruster C, Spijkers W (2006) Movement planning in prehension: do intended actions influence the initial reach and grasp movement? Motor Control 10: 311-329

Berardelli A, Rothwell JC, Day BL, Kachi T, Marsden CD (1984) Duration of the first agonist burst in ballistic arm movements. Brain Research 304: 183-187

Cheng DT, Luis M, Tremblay L (2008) Randomizing visual feedback in manual aiming: Reminiscence of the previous trial condition and prior knowledge of feedback availability. Experimental Brain Research 189: 403-410
Cheng S, Sabes PN (2007) Calibration of visually guided reaching is driven by error-corrective learning and internal dynamics. Journal of Neuroscience 97: 3057-3069
Cirstea MC, Ptito A, Levin MF (2003) Arm reaching improvements with short-term practice depend on the severity of the motor deficit in stroke. Experimental Brain Research 152: 476-488
Corcos DM, Jaric S, Agarwal GC, Gottlieb GL (1993) Principles for learning single-joint movements. Experimental Brain Research 94: 499-513
Craje C, Lukos JR, Ansuini C, Gordon AM, Santello M (2011) The effects of task and content on digit placement on a bottle. Experimental Brain Research 212: 119-124
Elliott D, Chua R, Pollock BJ, Lyons J (1995) Optimizing the use of vision in manual aiming: the role of practice. Quarterly Journal of Experimental Psychology 48: 72-83
Elliott D, Hansen S, Grierson LE, Lyons J, Bennett SJ, Hayes SJ (2010) Goal-directed aiming: two components but multiple processes. Psychological Bulletin 136: 1023-1044
Gentilucci M, Negrotti A, Gangitano M (1997) Planning an action. Experimental Brain Research 115: 116-128
Hansen S, Elliott D, Tremblay L (2007) Online control of discrete action following visual perturbation. Perception 36: 268-287
Karst GM, Hasan Z (1987) Antagonist muscle activity during human forearm movements under varying kinematic and loading conditions. Experimental Brain Research 67: 391-401
Khan MA, Franks IM, Elliott D, Lawrence GP, Chua R, Bernier PM, Hansen S, Weeks DJ (2006) Inferring online and offline processing of visual feedback in target-directed movements from kinematic data. Neuroscience and Biobehavioral Reviews 30: 1106-1121
Khan MA, Franks IM, Goodman D (1998) The effect of practice on the control of rapid aiming movements: Evidence for an interdependency between programming and feedback processing. Quarterly Journal of Experimental Psychology: Human Experimental Psychology 51A: 425-444
Lavrysen A, Helson WF, Tremlaby L, Elliott D, Adam JJ, Feys P, Buekers MJ (2003) The control of sequential aiming movements: The influence of practice and manual asymmetries on the one-target advantage. Cortex 39: 307-325
Levy N, Pressman A, Mussa-Ivaldi FA, Karniel A (2010) Adaptation to Delayed Force Perturbations in Reaching Movements. PLoS ONE 5: 12128
MacGonigle BO, Flook JP (1978) Long-term retention of single and multistate prismatic adaptation by humans. Nature 272
Marteniuk RG, MacKenzie CL, Jeannerod M, Athenes S, Dugas C (1987) Constraints on human arm movement trajectories. Canadian Journal of Psychology 41: 365-678
Naish K, Reader AT, Houston-Price C, Bremner AJ, Holmes NP (2013) To eat or not to eat? Kinematics and muscle activity of reach-to-grasp movement are influenced by the action goal, but observers do not detect these differences. Experimental Brain Research 225: 261-275
Newell K (1991) Motor skill acquisition. Annual Review Psychology 42: 213-237
Rand MK, Shimansky Y, Stelmach GE, Bloedel JR (2004) Adaptation of reach-to-grasp movement in response to force perturbations. Experimental Brain Research 154: 50-65
Rand MK, Stelmach GE, Bloedel JR (2000) Movement accuracy constraints in Parkinson's disease patients. Neuropsychologia 38: 203-212
Ricker KL, Elliott D, Lyons J, Gauldie D, Chua R, Byblow WD (1999) The utilization of visual information in the control of rapid sequential aiming movements. Acta Psychologica 103: 103-123
Scheidt RA, Dingwell JB, Mussa-Ivaldi FA (2001) Learning to move amid uncertainty. Journal of Neurophysiology 86: 971-985
Seidler RD, Stelmach GE (2000) Trunk-assisted prehension: specification of body segments with imposed temporal constraints. Journal of Motor Behavior 32: 379-389
Shadmehr R, Mussa-Ivaldi FA (1994) Adaptive representation of dynamics during learning of a motor task. Journal of Neuroscience 14: 3208-3224
Thompson SG, McConnel DS, Slocum JS, Bohan M (2007) Kinematic analysis of multiple contraints on a pointing task. Human Movement Science 26: 16
van Beers RJ (2009) Motor learning is optimally tuned to the properties of motor noise. Neuron 63: 406-417
Verstynen T, Sabes PN (2011) How each movement changes the next: An experimental and theoretical study of fast adaptive priors in reaching. The Journal of Neuroscience 31: 10050-10059

Weir P, MacDonald JR, Mallat BJ, Leavitt JL, Roy EA (1998) Age-related differences in prehension: The influence of task goals. Journal of Motor Behavior 30: 79-80
Welch RB, Bridgeman B, Anand S, Browman K (1993) Alternating prism exposure causes dual adaptation and generalization to a novel displacment. Perception and Psychophysics 54: 195-204
Wilmut K, Byrne M, Barnett A (2013a) Reaching to throw compared to reaching to place: A comparison across individuals with and without Developmental Coordination Disorder. Research in Developmental Disabilities 34: 174-182
Wilmut K, Byrne M, Barnett A (2013b) To throw or to place an object: Does onward intention affect the way a child reaches for an object. Experimental Brain Research 226: 421-429
Wolpert DM, Diedrichsen J, Flanagan JR (2011) Principles of sensorimotor learning. Nature Reviews Neuroscience 12: 739-751
Wolpert DM, Ghahramani Z, Flanagan JR (2001) Perspectives and probelms in motor learning. Trends in Cognitive Sciences 5: 487-495
Woodworth RS (1899) The accuracy of voluntary movement. Psychological Review 3: 1-119