DEVELOPING A TASK TO INVESTIGATE SKILL LEARNING AND MOTOR ADAPTATION IN FMRI

By

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Abstract

Skill learning and motor adaptation are key components within the area of motor control. Skill learning can be described as the process whereby movements become more accurate and are executed more quickly with practice. On the other hand, motor adaptation involves external perturbations which require a response to these altered conditions in order to improve performance. For example prism adaptation where participants are required to point at a target after looking through prism glasses which shift vision horizontally. It is thought that the motor adaptation process updates current internal models to produce the required response to these new demands or perturbations, this can often be shown by the presence of aftereffects when the perturbation is removed. To our knowledge there are no imaging studies within current motor control literature that attempt to specifically identify the different neural substrates that are involved in skill learning and motor adaptation in a single experiment.

The present study attempts to develop a novel rotary behavioural task, involving force field motor adaptation, using an MRI compatible force field robot. Protocol development outlined the most effective behavioural task to differentiate between skill learning and motor adaptation. Time on target and average deviation were selected as the most appropriate outcome measures to distinguish between the components of skill learning and adaptation respectively. Behavioural results demonstrated skill learning by a significant increase of time on target within the

early stages of a learning curve before plateauing. Adaptation and deadaptation curves, along with a significant difference in average deviation between session 1 and 2 identified an initial large adaptation which then also plateaued. Overall, skill learning and motor adaptation were outlined as separate entities within the same behavioural task. fMRI pilot sessions for the behavioural task were promising, confirming the feasibility of running this task in an fMRI scanner. Further development of the fMRI protocol and analysis is to take place within future research in order to obtain results to provide a more thorough understanding of the neural mechanisms which govern skill learning and adaptation.

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Introduction

Within the area of motor control, the concepts of skill learning and motor adaptation have sometimes been used interchangeably to describe transformations or improvements in performance when completing a motor task (Nezafat, Shadmehr and Holcomb, 2001; Graydon *et al., 2005*). However, more recent literature has differentiated between the two concepts, suggesting that they can be classed as separate entities underpinned by unique neural networks (Dierdrichsen *et al.,* 2005; Seidler, Noll and Chinralapati, 2006; Krakauer and Mazzoni, 2011; Diedrichsen and Kornysheva, 2015; Chen, Holland and Galea, 2018). These findings pose the hypothesis whether skill learning and motor adaptation work independently of one another but can also coincide to produce optimal motor performance.

Skill Learning

Skill learning in terms of motor control, refers to an improvement in a pre-determined movement above baseline levels. As the skill is learnt, movements become more accurate and are executed quicker through repetition and practise. An improvement in skill learning results in a positive shift in the speed-accuracy trade-off function (SAF). The SAF represents how effective skill learning is as a trade-off between speed and accuracy when one increases and the other decreases (Reis *et al.,* 2009; Krakauer and Mazzoni, 2011; Diedrichsen and Kornysheva, 2015; Chen, Holland and Galea, 2018). These improvements do not represent a single process and are dependent on several mechanisms, such as action selection, the identification of the environment and context, response selection and action execution (Shmuelof *et al.,* 2014; Chen, Holland and Galea, 2018). Skill learning can take place on multiple time scales. Often in the initial stages of learning, large improvement in performance is observed over a short period of time, followed then by a slower improvement. However, this speed of skill learning is dependent on task complexity and can take place online during practise but also offline during memory consolidation (Dayan and Cohen, 2011). These aspects of skill learning further link to the SAF, and how speed and accuracy must have a trade-off in order to reach the optimal performance when learning a new skill. This theory is used by Reis *et al.* (2009) as a measure of skill, where a change in the trade-off between speed and accuracy would reflect a change in skill. Although if both components, speed and accuracy, opposingly increased or decreased at the same rate, this would not reflect a change in skill and performance would not improve. Therefore a balance of both components is necessary for successful skill learning. Skill learning can also be measured by the level of automaticity; the response to task requirements becomes more automatic without the need for conscious attention (Floyer-Lea and Matthews, 2004). The neural networks involved in this form of skill learning include the cortico-striatal and cortico-cerebellar circuits. In addition to this, fast learning specifically involves use of the dorsolateral prefrontal cortex (DLPFC), the motor cortex (M1) and the presupplementary motor area (preSMA). These areas can differ during the slow stage of motor skill learning which involves neural activation in M1, the primary somatosensory cortex, the supplementary motor area (SMA) and decreased activation in the cerebellum (Doyon and Benali, 2005; Floyer-Lea and Matthews, 2005; Dayan and Cohen, 2011).

Motor Adaptation

Motor adaptation can be defined as a “form of learning characterised by a gradual improvement in performance in response to altered conditions”. In laboratory adaptation tasks, subjects initially complete a baseline performance with no external perturbations, following this an external perturbation is applied to which the subjects must adapt. Initially, subject performance declines from baseline and, at most, subject performance returns to this baseline, but no improvement takes place above this level (Krakauer and Mazzoni, 2011). It is known that our nervous system has the ability to adapt to altered conditions via prediction and correction to prevent errors and manufacture the most efficient movements possible (Shadmehr, Smith and Krakauer, 2010). In addition, motor adaptation is the result of environmental changes or perturbations causing a miscalibration of subject dynamics or kinematics, in a mechanical or visual environment (Shadmehr and Mussa-Ivaldi, 1994; Diedrichsen *et* al., 2005; Krakauer and Mazzoni, 2011).

Specific laboratory tasks used to test motor adaptation, generally require subjects to adapt to the kinematic or dynamic aspects of the movement in question.

Kinematics refers to the “geometrical and time-based properties of motion; the variables of interest are the positions and their corresponding velocities, accelerations, and higher derivatives” (Wolpert, Ghahramani and Jordan, 1995). An example of kinematic adaptation includes visuomotor rotation within a reaching adaptation task, using a hand-held joystick or robotic manipulandum. Visuomotor rotation is an adaptation task which can display aftereffects and consolidation (Diedrichsen *et* al., 2005; Krakauer, Ghez and Ghilardi, 2005). Another example of kinematic adaptation is prism adaptation in which a prism is used to shift the visual environment. Such adaptation tasks clearly identify aftereffects, a key component of adaptation, when the goggles are removed. Aftereffects can be defined as the failure to inhibit a previously formed internal model (Shadmehr and Holcomb, 1999). These aftereffects can be experiences for a long duration, lasting for a number of days (Shadmehr and Mussa-Ivaldi, 1994; Hatada, Miall and Rossetti, 2005). In contrast to kinematics, dynamics refers to “the forces required to produce motion and the properties of arm such as its mass, inertia, and stiffness; the variables of interest include joint torques, forces acting on the hand, and muscle commands” (Wolpert, Ghahramani and Jordan, 1995). Changes in subject dynamics are often formed by a hand held robotic manipulandum producing a force field within a reaching adaptation task. Subjects adapt to move in a way that counteracts the force field, which once removed, reveals aftereffects demonstrated by trajectories with an inverse curve to the original force field trajectory. Aftereffects exist because the participant’s brain still expects a force field when it is no longer present (Shadmehr and Mussa-Ivaldi, 1994; Shadmehr and Brashers-Krug, 1997; Li, Padoa-Schioppa and Bizzi, 2001; Nezafat, Shadmehr and Holcomb, 2001; Diedrichsen *et* al., 2005).

Motor adaptation and internal models

Motor adaptation is an error driven process that allows movements to retain accuracy when faced with changes in the environment. It is widely acknowledged that when movements become inaccurate in the face of environmental changes, error signals alter the internal models of the body schema to make them accurate again (Shadmehr and Mussa-Ivaldi, 1994; Diedrichsen *et* al., 2005; Krakauer and Mazzoni, 2011; Bedard and Sanes, 2014). The concept of the internal model was first presented in literature several decades ago, where when the dynamics of a task change, such as increasing force, the subject must remain in control in order to maintain a successful performance. The subject adapts to the dynamics presented through updating the internal model, which in turn is controlled and updated by the central nervous system (CNS) (Shadmehr and Mussa-Ivaldi, 1994). Internal models can also be seen as motor memories, which were formed mainly by classification of the visual and mechanical properties of the task or object in question. These motor memories are learned and updated through experience. This process of internal model formation is dependent on the ability of the individual to inhibit former dynamic or kinematic responses, or experiences, to similar motor learning tasks. When individuals who form an internal model of a specific motor task are presented with a new motor task, interference takes place. Aftereffects are present when the individual fails to inhibit a previously formed internal model, which cannot be simply cancelled but must be unlearnt or de-adapted. A successful performance therefore relies on inhibition of the previous task and the sufficient acquisition of the new internal model (Shadmehr and Holcomb, 1999).

Later work by Shadmehr and Krakauer (2008) identified neural regions responsible for forming the neural processes mentioned previously. The cerebellum was identified as largely important in the formation of internal models, and therefore had a critical role within motor adaptation. Internal models are updated when a new environmental perturbation requires a specific motor response. During the planning of this motor response, updating of the forward model takes place in the cerebellum. This is in order to provide a motor prediction, along with a prediction of sensory feedback, of the next movement to occur (Blakemore, Frith and Wolpert, 2001; Krakauer and Mazzoni, 2011; Izawa, Criscimagna-Hemminger and Shadmehr, 2012; Marko *et al.,* 2012). The inverse model is then responsible for producing the motor plan, following information being received from the forward model (Izawa, Criscimagna-Hemminger and Shadmehr, 2012; Takemura, Inui and Fukui, 2018). Together, the forward and inverse models (internal models), work in conjunction with one another, as a loop, to form a control mechanism called “model predictive control” (Takemura, Inui and Fukui, 2018), which vastly uses error signals and predictions. Due to these models, it is suggested that adaptation is the result of error signals, formed due to the difference between sensory predictions and sensory feedback in order to produce optimal motor performance (Marko *et al.,* 2012).

Neural correlates of motor adaptation

The cerebellum is highly responsible for controlling processes involved in adaptation (Nezafat, Shadmehr and Holcomb, 2001; Graydon *et al.,* 2005; Shadmehr and Krakauer, 2008; Krakauer and Mazzoni, 2011). Imaging studies suggest the cerebellum is involved in the primary stages of adaptation in force field and visuomotor tasks, where errors take place and the adaptation process ultimately results in error reduction (Floyer-Lea and Matthews, 2004; Diedrichsen *et al.,* 2005; Seidler, Noll and Chinralapati, 2006; Bedard and Sanes, 2014). The error signals in adaptation which occur at the end of arm movements are due to complex spikes produced by purkinje cells in the cerebellum. These complex spikes are also largely involved in the initiation of reaching movements (Kitazawa, Kimura and Yins, 1998), which are widely used in motor adaptation tasks. Tseng *et al.* (2007) provided evidence to prove the cerebellum's vital role in adaptation. The study involved a reaching task, where subjects with cerebellar ataxia, in comparison to healthy controls, experienced performance and adaptation impairment in the trials with regards to error and adaptation rate, both of which the cerebellum is largely responsible for. Moreover, saccadic adaptation studies have proved that the effect of small cerebellar lesions in monkeys results in the permanent loss of the ability to adapt to saccades (Barash *et al.,* 1999). Subjects suffering from different cerebellar diseases also showed similar saccadic deficits relating to adaptation (Golla *et al.,* 2008). Furthermore, there is research which shows cerebellar damage or degeneration has negative effects on reach adaptation tasks involving force field perturbations (Masche *et al.,* 2004; Smith and Shadmehr, 2005; Rabe *et al.,* 2009). Criscimagna-Hemminger, Bastian and Shadmehr (2010) advanced this research by proving that abrupt large force field perturbations had a greater negative effect on adaptation in subjects with cerebellar ataxia, compared with smaller, progressive perturbations. Additionally, it is thought the cerebellum is involved in implicit adaptation processes which can update body movements through prediction of the movement to come, this takes place trial by trial (Statton *et al.,* 2018). Research suggests that both implicit and explicit processes are useful during motor adaptation, within visuomotor rotation and force field motor tasks, but implicit processes are dominant and can override explicit strategy (Mazzoni and Krakauer, 2006; Hwang, Smith and Shadmehr, 2006; Taylor, Krakauer and Ivry, 2014).

In imaging studies, specific areas of the cerebellum have been identified as neural regions which are activated during motor adaptation tasks. Lobule V of the cerebellum is known to be very important in force-field adaptation especially relating to hand movement. This is along with activation in the intermediate and lateral zones of the anterior cortex of the cerebellum, specifically in the early stages of force field adaptation (Rabe *et al.,* 2009; Burciu *et al.,* 2014). Other neural regions are widely supported by literature to be involved in the processes of motor adaptation, specifically in the initial stages of adaptation. These include cortical regions such as prefrontal, bilateral sensorimotor and parietal cortices, as well as the caudate nucleus (Floyer-Lea and Matthews, 2004; Graydon *et al., 2005*). As previously mentioned, neural networks involved in sensorimotor tasks include a high amount of activation from the bilateral cerebellum, but also from the left basal ganglia, shown from the result of a meta-analysis of 70 motor learning experiments (Hardwick *et al.,* 2012). The putamen, a structural part of the basal ganglia, is involved in the processes of motor adaptation beyond the initial stages, as is the thalamus, which is closely interconnected with the basal ganglia (Floyer-Lea and Matthews, 2004; Graydon *et al., 2005*). Neural networks of motor adaptation also include the areas of the motor cortex, which are sensitive to motor and visual aspects of reaching (Dierdrichsen *et al.,* 2005; Eisenberg *et al.,* 2011). Moreover, during reaching movements, visual feedback to the motor system travels from the posterior parietal cortex to the premotor areas, and proprioceptive feedback travels from the somatosensory cortex and the thalamus to the primary motor cortex (Shadmehr and Krakauer, 2008).

The current study

The current study involves a novel rotary motor adaptation task which has similarities to the pursuit rotor task. The pursuit rotor task was developed in the early part of the last century and was extensively used for several decades (Eysenck and Frith, 1977). The pursuit rotor began as a motor task to test the ability of subjects to learn how to track a target using circular movements with their hand and arm. Koerth (1922) describes the first setup of the pursuit rotor, which used a phonograph, a rotating wooden disc, a hinged pointer and a brass target. The pursuit rotor task and apparatus was built upon from Koerth's paradigm (1922) and advanced throughout the 20th century, where it now can be replicated electronically on a computer. In our study we implement the same tracking paradigm with a tracking target, controlled with a magnetic resonance imaging (MRI) compatible manipulandum that can be moved in the horizontal plane.

There are a limited number of imaging studies using positron emission topography (PET) which have attempted to study force field motor adaptation tasks using the arm (Shadmehr and Holcomb, 1999; Nezafat, Shadmehr and Holcomb, 2001). Diedrichsen *et al.,* (2005) completed the only functional magnetic resonance imaging (fmri) study, which investigated neural correlates of learning and adaptation within a dynamic and kinematic reaching task, involving force fields and visuomotor rotation, using similar equipment to that used in our study. The behavioural data obtained from this study identified target errors in response to a visual target jump, and execution errors in response to a force field or visuomotor rotation. Using the state-space model of adaptation, the behavioural data identified a higher rate of motor adaptation within the force field and visuomotor trials. The functional data presented by Diedrichsen *et al.* (2005) is consistent with their behavioural data. Although there was some overlapping with neural correlates of target and execution errors, potentially due to on-line error correction, it was concluded that the neural correlates of target errors included the posterior superior parietal lobe and the striatum. In contrast, the neural correlates of motor adaptation due to execution errors included the anterior parietal cortex, areas of the post central sulcus bilaterally, parietal area five and the dorsal premotor cortex.

To our knowledge there are no imaging studies within current motor control literature that attempt to specifically identify and support the difference between skill learning and motor adaptation in a single experiment. As a result, the present study aims to define both skill learning and motor adaptation whilst using fmri to identify neural correlates for each, and therefore differentiate between the two during the completion of a single motor task by an individual. This study fills a gap in the literature, investigating whole head fmri during a novel rotational motor task. It is hypothesised that skill learning and motor adaptation are separate entities, but they can take place simultaneously within the same motor task. Taking all available evidence into account, we hypothesised that skill learning, described above as an increase in speed and accuracy of response, will take place throughout the duration of the task within all different trial types. Adaptation, by contrast, will only take place during force field perturbation trials, and aftereffects will be evident following adaptation. Additionally, we will be able to observe separate neural correlates for both skill learning and motor adaptation.

Materials and Methods

Participants

A total of 31 neurologically healthy volunteers took part in the current study, consisting of 10 males and 21 females. All participants were between the age of 18-35, with an average age of 23±5 years, 29 participants were right handed and 2 participants were left handed. All participants took part in the current study voluntarily, to earn educational credits in the School of Sport and Rehabilitation Sciences or for a monetary reimbursement. Data sets were collected for 24 participants who took part in one of the three behavioural experiments (8 per experiment). Two participants took part in the imaging experiment. The data sets for the remaining 5 participants were excluded due to task errors. The University of Birmingham Ethics committee approved the current study procedures.

Apparatus

The current study obtained behavioural and functional data using a mock magnetic resonance imaging (MRI) scanner (figure 1.0.) and a functional MRI (fMRI) scanner, at The Birmingham University Imaging Centre. The study used an MRI compatible velocity dependent force field robot (MRIbot) (figure 1.1. **B**), which is a planar robotic manipulandum. The MRIbot allowed two dimensional horizontal movements and produced velocity dependant forces at 200Hz on the

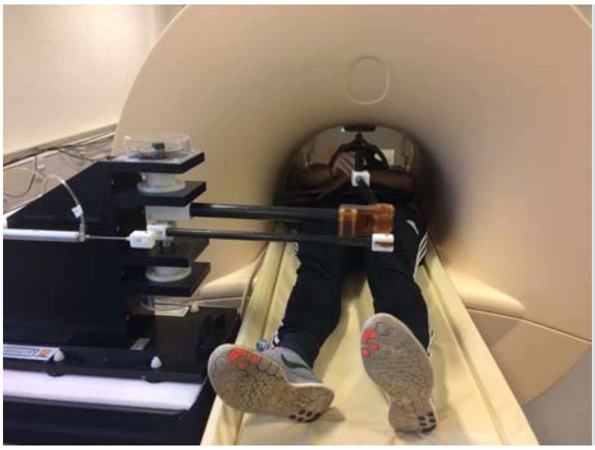

Figure 1.0. Participant located within the mock fMRI scanner during the behavioural study with MRIbot located just outside the scanner within reaching distance of the participant's right hand.

right hand and arm of the participant. The MRIbot arm length extending from the shoulder, to the elbow, to the hand was approximately 114cm. Participants held a handle grip located at the hand of approximately 9cm in height and 3.2cm in diameter. The MRIbot (figure 1.1 B) was connected to an air compressor, at a pressure of 100 PSI, providing air to the manipulandum pistons. The position of the manipulandum was provided by the position of the pistons, determined via linear optical encoders on the elbow and shoulder joints with an endpoint accuracy of 0.01mm. These encoders in turn connected to a PC which controlled the behavioural task, shown on a projected image to the participant via a mirror located directly above eyesight (figure. 1.1 **A**).

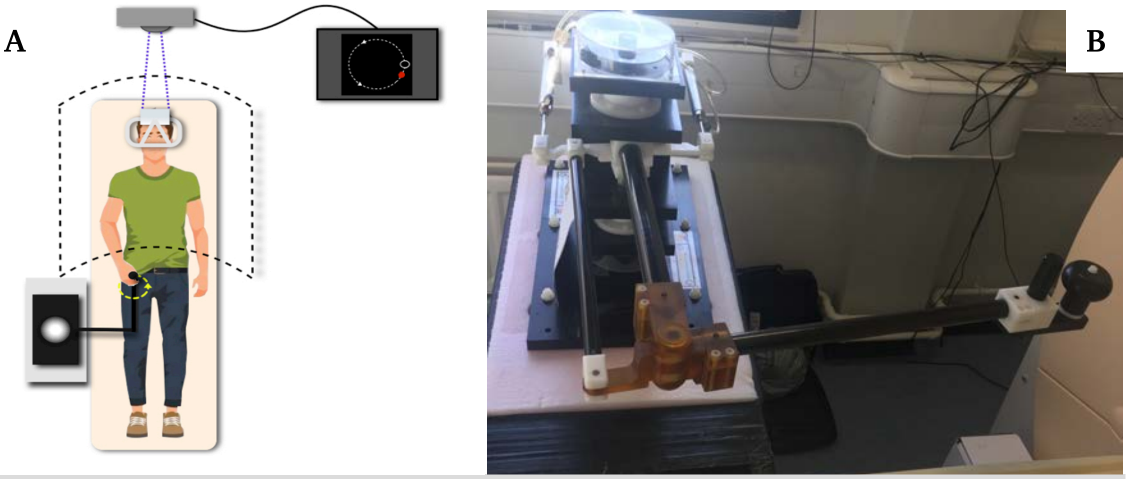

Figure 1.1. A Image of participant within mock fMRI scanner, showing how the projected visual behavioural task is observed by the participant via a projector and mirror directly above eyesight. **B** MRIbot located next to the mock fMRI scanner, attached to a table at the same height as the fMRI bed. This image shows the robot arm controlled by air pistons.

The current study involved the development of a novel motor rotary behavioural task. The overall goal of the study was to develop a task that could be used in the fMRI scanner. Prior to this, it was important to identify the most effective behavioural task which allowed a differentiation to be observed between skill learning and motor adaptation, and to certify that the behavioural task was as compatible as possible with the requirements of fMRI scanning. This process of protocol development took place first using a velocity dependent force field robot (vBOT) which is a robot manipulandum. The vBOT was controlled by the hand and arm in a seated position, where movements took place in a horizontal plane. The following stages of protocol development involved the use of the MRIbot within the mock fMRI scanner.

Desired qualities of protocol:

- Movement qualities
  - Smooth movements for reduced movement artefacts.
  - Continuous movement rather than discrete individual movement for block design.
- Block design
  - To fit contrast design (rest vs movement; force vs no-force).
  - Behavioural task to fit time to repeat (TR time) of fmri scanner.
- Behavioural outcomes
  - Clearly separate measures of skill learning and motor adaptation within task.

Taking the desired qualities of protocol into account, the current study involved four-stages of protocol development, to produce an effective behavioural task. All data from the behavioural sessions were collected on the MRIbot and transferred to a pc for offline analysis. This data was then analysed to extract behavioural parameters related to skill learning and motor adaptation. All behavioural data was analysed using MATLAB and SPSS. Statistics were produced, using dependent t-tests and repeated measures analysis of variance (ANOVAs) where post hoc tests were Bonferroni corrected, to investigate any significance using SPSS. The current novel motor rotary behavioural task is outlined in figure 1.2. The white ring target (diameter, 1.5 cm) had a linear acceleration for 4s at the beginning of each block where this acceleration was a value of 45 degrees per second per second.

Following these 4 seconds, the white ring target then travelled at an angular velocity of 180 degrees per second where each rotation was completed in 2s until the end of the block. The length of each block varied, which is stated within the protocol development section below.

The objective of the task was for the participant to control the red circular cursor (diameter, 1.0 cm), using their right hand holding the robotic manipulandum, and aimed the cursor to remain within the target ring for as long as possible (figure 1.2). The behavioural task included null trials which contained no external perturbation, representing skill learning. Additionally, the behavioural task also included force field trials which contained external force field perturbations of 18Ns-1 in an outward direction away from the target ring, representing both skill learning and motor adaptation.

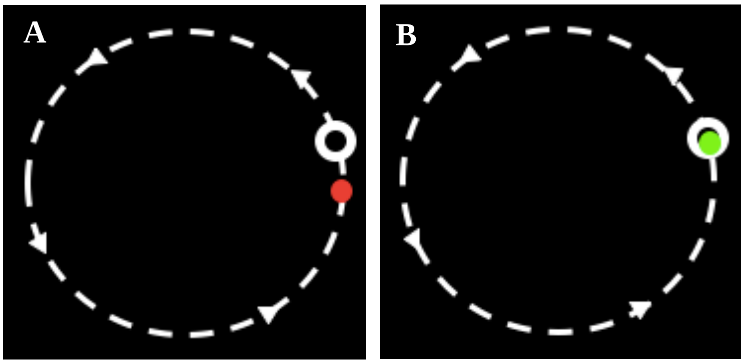

Figure 1.2. Visual image of the rotary task which was projected onto a mirror (14x10cm) directly above the eyesight of the participant. White dashed circle represents the movement of the target but is not visible to the participant throughout the task. **A** Red circle (cursor) chases the white ring (target) in an anticlockwise direction. **B** Red circle turns green when the centre of the circle is inside the white ring. The length of time when the cursor is green defines the time on target measure.

Behavioural task outcome measures

Time on Target (%)

Introduced by Renshaw and Weiss (1926) and used early on in pursuit rotor behavioural studies and has since been widely acknowledged in research (Eysenck and Frith, 1977). Measured as the percentage (%) time during one full rotation in which the centre of the cursor has reached any point of the white target ring. This provided positive feedback to the participant, with the cursor to turning from red to green, showing they successfully reached the target. Outlier removal of a single trial was implemented which included any values outside the mean value ±2xSD (standard deviation).

Average Deviation (cm)

Measured as the average distance and direction from the circumference of the target ring to where the cursor was located in centimetres in one full rotation. Outlier removal of a single trial was implemented which included any values outside the mean value ±2xSD (standard deviation).

Protocol development of the behavioural task: Stage 1

Stage one of protocol development involved testing the new novel rotary task for the first time on five participants. This behavioural task (figure 1.3.0) used the vBOT and included seven baseline null blocks (N) which took place on two consecutive days to test for consolidation of skill learning. Then four force field blocks (F) and two washout blocks (WO) to test for motor adaptation and aftereffects. Each movement block contained ten trials of 20s, interspersed with 20s rest. During the force field blocks, the force field was applied to the cursor in relation to the hand movement of the participant through space.

Figure 1.3.0. Timeline for stage one of protocol development of the behavioural task. N = Null field block, F= Force field block, WO= Washout block.

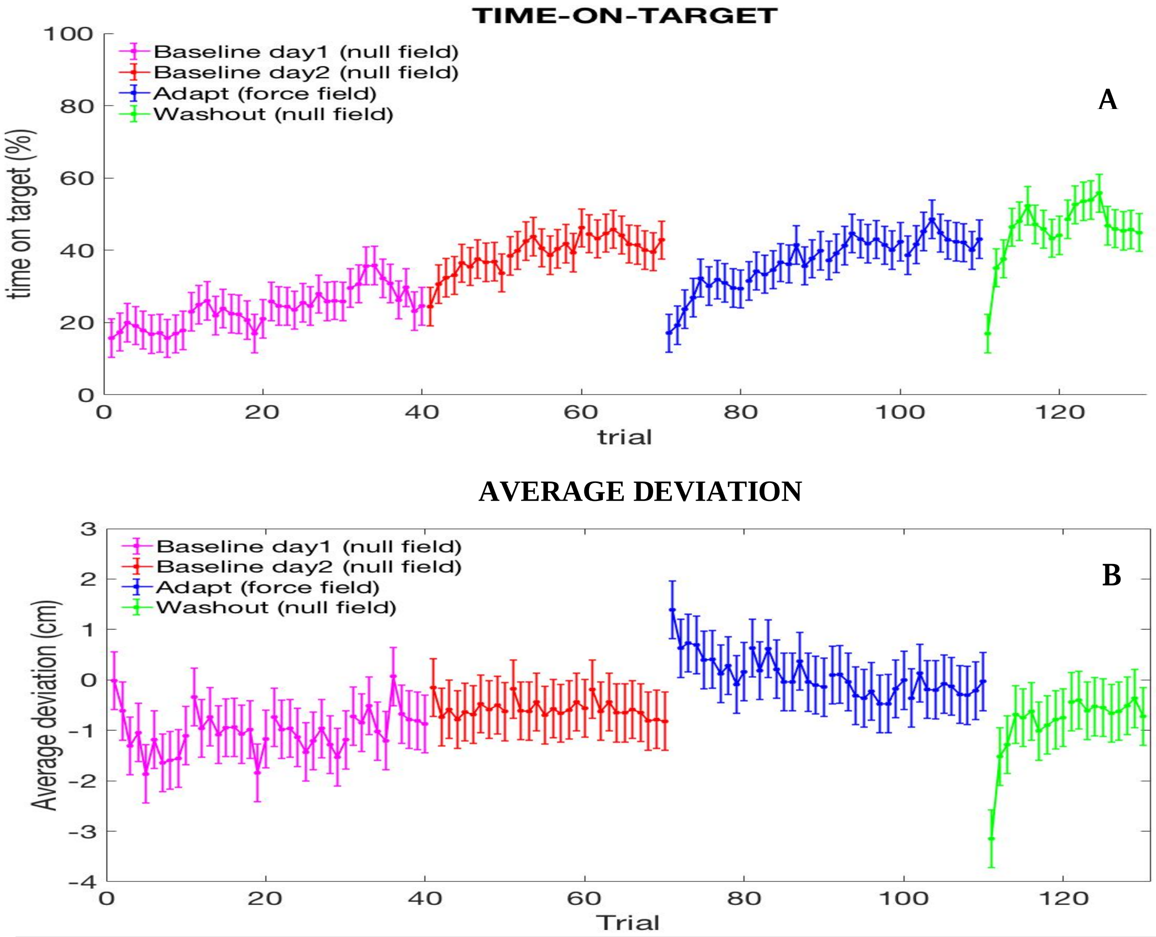

Figure 1.3.1
Results for **A** time on target, and **B** average deviation for stage one of protocol development of the behavioural task. Each point on the graph is an average of five participants' results for one trial. Error bars represent standard error (SE).

Figure 1.3.1. A and 1.3.2 showed a significant increase from start to finish in time on target of 30.858±10.990% (t(4)=6.279, p=.003) as skill learning took place and performance improved for the participants. Additionally, there were significant increases in time on target from start to end of the second baseline block (14.813±11.393%, t(4)=2.907, p=.044), the force field block (24.986±8.800%, t(4)=6.349, p=.003) and the washout block (18.999±13.897%, t(4)=3.057, p=.038). This significance implied skill learning took place efficiently within all types of trial. However, performance never improved above 50% for time on target, which suggested the task needed to be altered to allow for higher level performance.

Figure 1.3.1 B and 1.3.3 outlined two adaptation curves which were produced after the force field was implemented where the ability of the participants to track the target ring closer to the central point of the ring improved over time. During the force field block average deviation decreased by 1.508±.655cm from start to end (t(4)=5.147, p=.007). This significant decrease was followed by a similar but mirrored image for the washout block where average deviation increased by 1.764±.810cm from start to end (t(4)=4.867, p= .008), this displayed aftereffects from the previous force field lock after the perturbation was removed. During this protocol of the behavioural task, skill learning and motor adaptation were observed. However, the overall duration of the task was very long, therefore it was aimed to produce a shorter behavioural task which included skill learning and motor adaptation observed at greater levels.

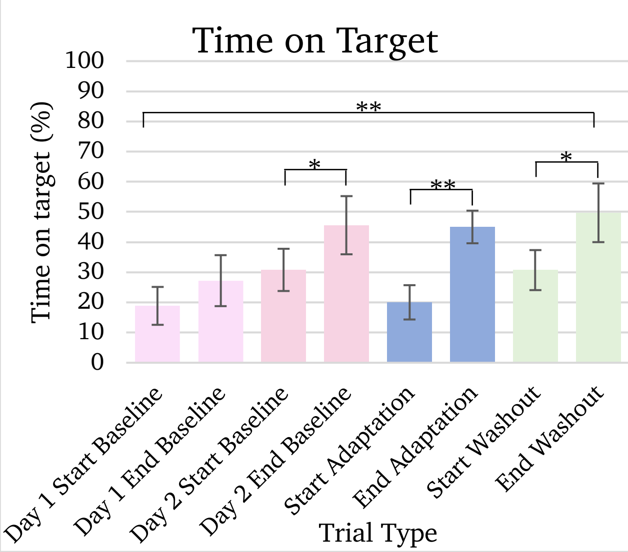

Figure 1.3.2.
Results for time on target, representing skill learning. Each trial type contained the average of two trials from eight participants. Error bars represent SE. Significant differences indicated by *(p<.05) or **(p<.01).

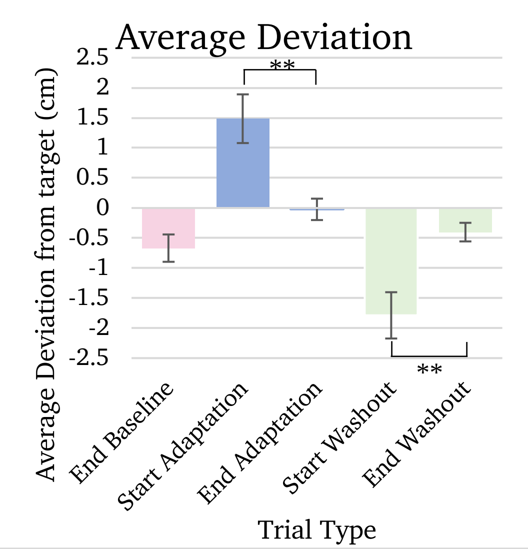

Figure 1.3.3.
Results for average deviation from the target. Each trial type contained the average of two trials from eight participants. Error bars represent SE. Significant differences indicated by **(p<.01).

Protocol development of the behavioural task: Stage 2

Stage one of protocol development demonstrated that the task produced measurable levels of skill learning and motor adaptation. In stage two of protocol development (figure 1.4.0.) the task was transferred to the MRIbot. During piloting it was noticed that the forces applied to the hand became very unstable when the force was dependent on the movement of the cursor controlled by the participant, due to the lags in the pneumatic system on the MRIbot. Therefore, the outward force applied to the hand was dependent on the target cursor to produce a smoother and more predictable force profile. This stage also identified an order of null blocks (N) and force blocks (F) to ensure the study protocol recognised both skill learning and motor adaptation, but was shorter than the previous protocol. Four blocks of null trials were carried out to allow initial skill learning. Following this were four blocks of force trials, to allow for further skill learning, but also motor adaptation due to the external force perturbations where participants had to compensate for the forces applied. Following this were two washout (WO) blocks, made up of null trials, to show aftereffects of the motor adaptation and provide evidence that adaptation took place. Each movement block contained ten trials of ten rotations of the white ring target. Every rotation took approximately two seconds, resulted in each trial lasting approximately 20s. Individual trials were separated by a rest of 15s and each block by a one-minute break to take allow rest time for each participant.

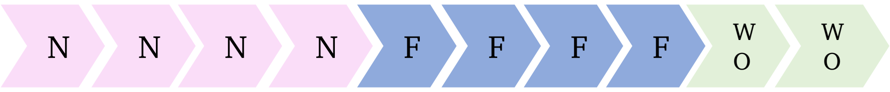

Figure 1.4.0. Timeline for stage one of protocol development of the behavioural task. N = Null field block, F= Force field block, WO= Washout block.

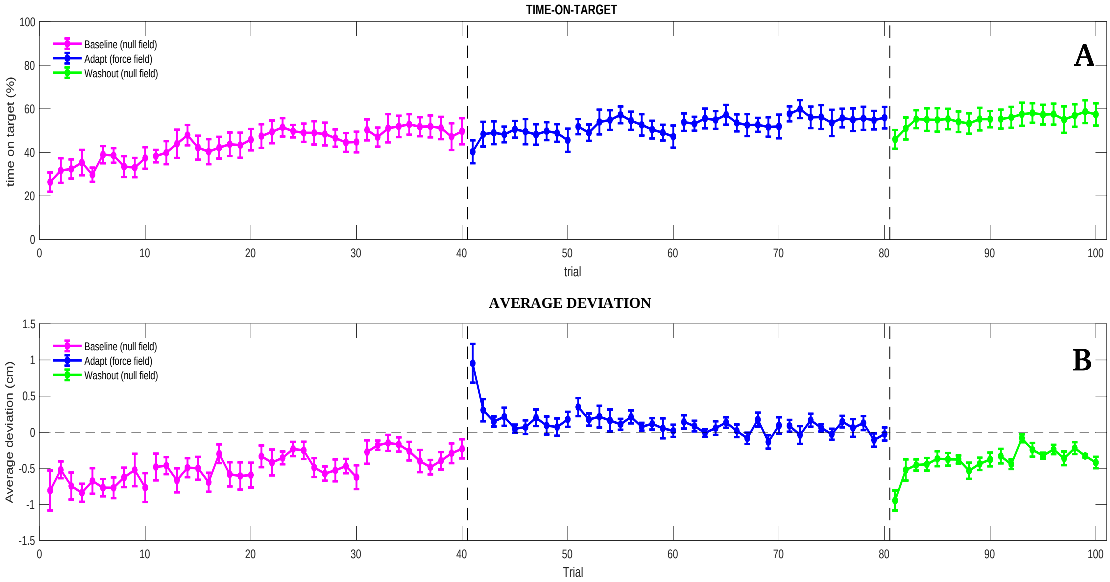

Figure 1.4.1
Results for **A** time on target, and **B** Average deviation for stage one of protocol development of the behavioural task. Each point on the graph is an average of eight participants' results for one trial. Error bars represent SE.

In figures 1.4.1 A and 1.4.2, a dependent samples t-test identified a gentle significant increase of 29.048±7.642% in time-on-target from the beginning of baseline until the end of washout (t(7)=10.751, p<.001), although this was an improvement, the task could have been modified to show a greater rate of skill learning. Although significant increases within blocks were present (figure 1.4.2), a greater improvement would be expected between each trial type to represent constant skill learning (start to end of baseline, 19.457±8.125%, t(7)=6.773, p<.001; start to end of force, 11.043±11.657%, t(7)=2.679, p=.032; start to end washout, 9.583±6.132%, t(7)=4.420, p=.003).

In figure 1.4.3. the difference between “End Baseline’ and ‘Start adaptation’, outlines motor adaptation took place following the force perturbation, where average deviation increased significantly by .891±.514cm (t(7)=4.898,p=.002). Figures 1.4.1. B and 1.4.3. identified motor adaptation within the ‘Adapt (force field)’ section with a motor adaptation curve, in which the significant decrease of average deviation of .0696±.395cm (t(7)=4.983, p=.002) from start to finish of the adaptation block ended near to baseline. This motor adaptation took place at a very fast pace, observed on the graph (figure 1.4.1. B), in the initial force field block after only one trial where performance then plateaued at minimal average deviation. Following ‘End Adaptation’, an opposite de-adaptation curve took place in the ‘Washout (null field)’ (figures 1.4.1. B and 1.4.3.) where the average deviation significantly decreased by .668±.380cm (t(7)=4.965, p=.002). This de-adaptation was evident following the removal of the external force perturbation, also representing aftereffects from the previous force field blocks. Furthermore, the similar deviation of ‘Start Adaptation’ and ‘Start Washout’, but in opposite direction, further confirms motor adaptation (p=.632, when negative values were converted to positive values to directly compare deviation). Although adaptation was present, this could only be seen for two trials before returning to baseline, therefore the task was modified to encourage motor adaptation to be more prominent within the results.

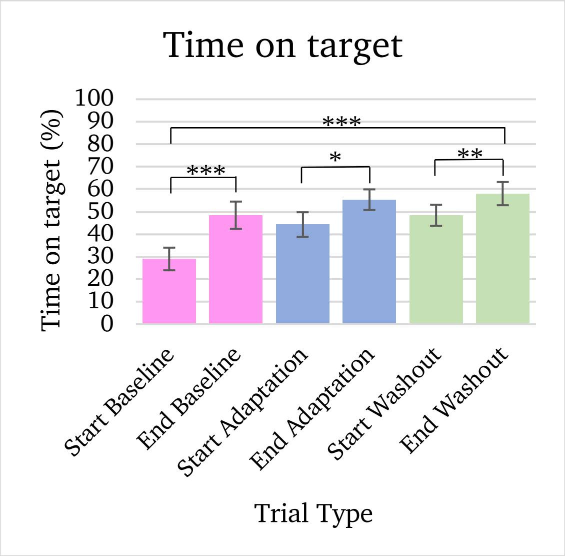

Figure 1.4.2.
Results for time on target, representing skill learning. Each trial type contained the average of two trials from eight participants. Error bars represent SE. Significant differences indicated by *(p<.05), **(p<.01) or ***(p<.001).

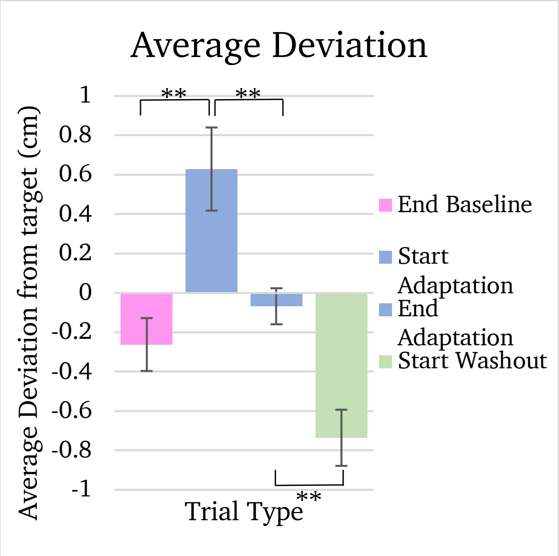

Figure 1.4.3.
Results for average deviation from the target. Each trial type contained the average of two trials from eight participants. Error bars represent SE. Significant differences indicated by **(p<.01).

Protocol development of the behavioural task: stage three

At the end of the second stage of protocol development, it was identified that the rate of skill learning and motor adaptation needed to be increased and made more prominent. The current protocol was adjusted due to learning and adaptation plateauing relatively quickly in stage two of protocol development. The null (N) and force (F) blocks were alternated to increase difficulty to observe if skill learning could continuously take place throughout, but also to see if motor adaptation could occur in every force block (figure 1.5.0.). Both null blocks and force blocks contained five trials in a counter clockwise direction. Additionally, the behavioural task was adjusted to be compatible with timing requirements for BOLD fMRI scanning, therefore the timing of each movement trial was altered to 21s, separated by a rest of 21s. A two-minute break took place at half way through the testing blocks to allow recovery time for the participants.

Figure 1.5.0. Timeline for stage two of protocol development of the behavioural task. N = Null field block, F= Force field block.

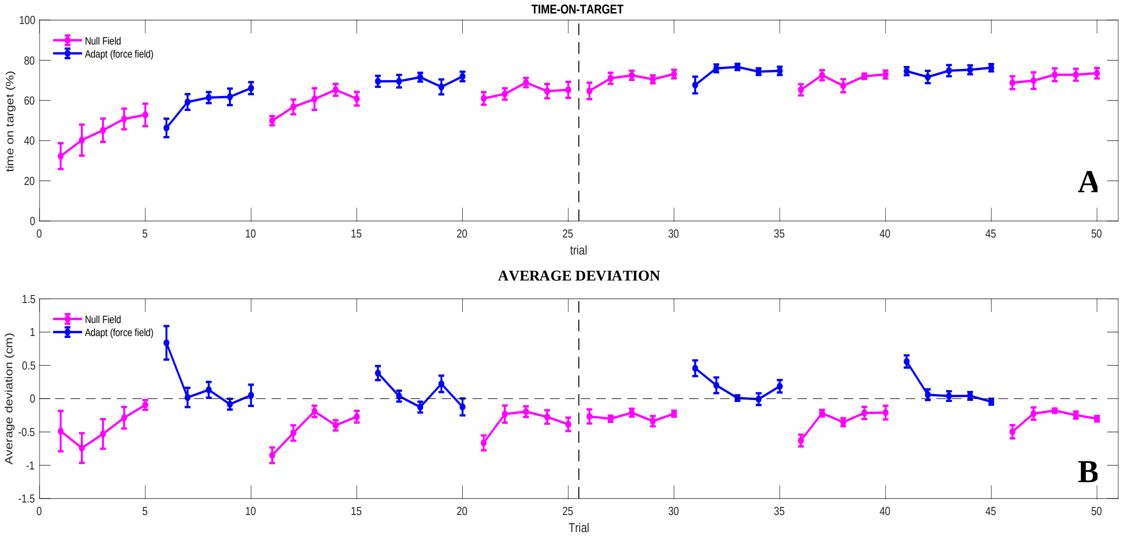

Figure 1.5.1.
Results for **A** time on target and **B** average deviation for stage two of protocol development for the behavioural task. Each point on the graph was an average of 8 participants for one trial. Error bars represent SE.

In figures 1.5.1 A and 1.5.2, an increase in time on target took place from start to finish (‘Null field 1’ to ‘Null field 6’), representing skill learning, with a significant increase of 36.540±14.624% (t(7)=7.067, p<.001). This increase in time on target mainly occurred within the first four blocks where the significant increase from ‘Null field 1’ to ‘Force field 2’ was 37.229±19.159% (t(7)=5.496, p<.001), suggesting a fast rate of initial skill learning. This initial fast rate of skill learning was followed by a much slower rate of skill learning between ‘Force field 2’ and ‘Null field 6’ with a minor overall increase of .690± 8.843% (p=.832). The highest time on target was also observed within the force field trials (‘Force field 2’ = 69.518±7.126%, ‘Force field 4’ = 74.571±5.278%), implying skill learning took place more efficiently within the force field trials and perhaps the subjects found these trials easier.

The average deviation measure in figure 1.5.1 B displayed motor adaptation taking place, observed by the adaptation curves within the force-field blocks decreasing to near zero at the end of each block. Additionally, the null field blocks showed elements of de-adaptation as these results mirrored curves observed in the adaptation blocks. Initial level of high average deviation, following ‘Null field 1’, at ‘Force field 1’ (.744±.579cm, t(7)=3.632, p=.008) and ‘Null field 2’ (.686±.296, t(7)=6.544, p<.001) displayed the first significant stages of the participants adapting to the force field and also being able to de-adapt during the null fields. In the second half of the experimental session, beginning at ‘Null field 4’ overall average deviation had decreased and plateaued, implying adaptation had improved and subjects were able to adapt to the alternating force fields and null blocks. There were no significant differences consecutively between these last 5 blocks or between 'Null field 4' to Null field 6' (.191±.284cm, p=0.099).

Both measures of time on target and average deviation were promising throughout this stage of protocol development, following significant statistical analysis. However, the two null fields which occurred consecutively (Null field 3 and 4) allowed greater repetition of the null field and reduced the repetition of the force field trials, therefore disrupted the rate of adaptation which decreased with the following force field trial. Consequently, in the final stage of protocol development, the current protocol was separated into 2 deliberate sessions with a dividing baseline or washout block to act as a break between the sessions.

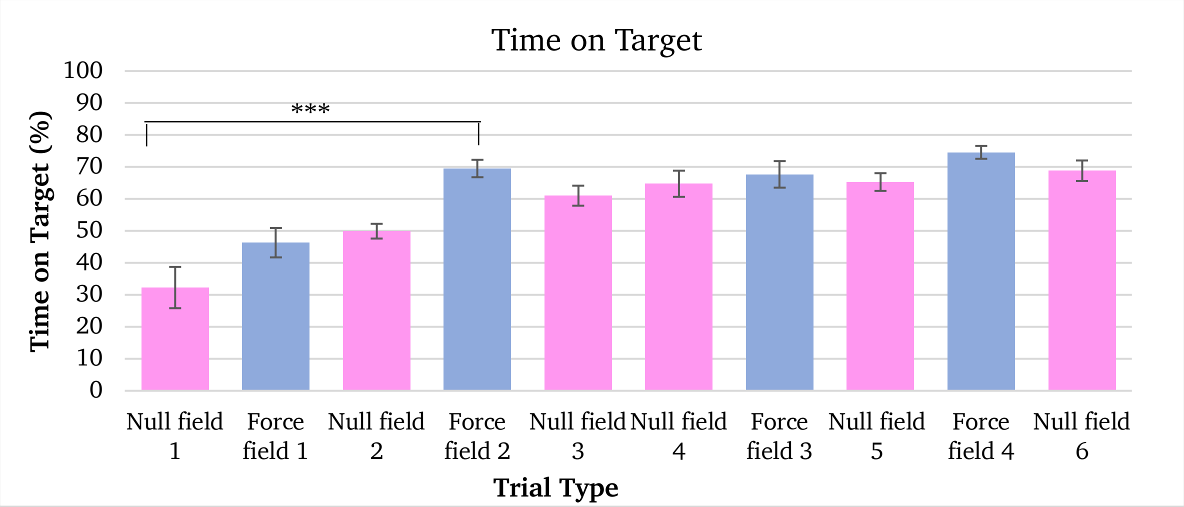

Figure 1.5.2.
Each trial type contained the average of one trial from 8 participants at the beginning of each block. Error bars represent SE. Significant differences indicated by ***(p<.001).

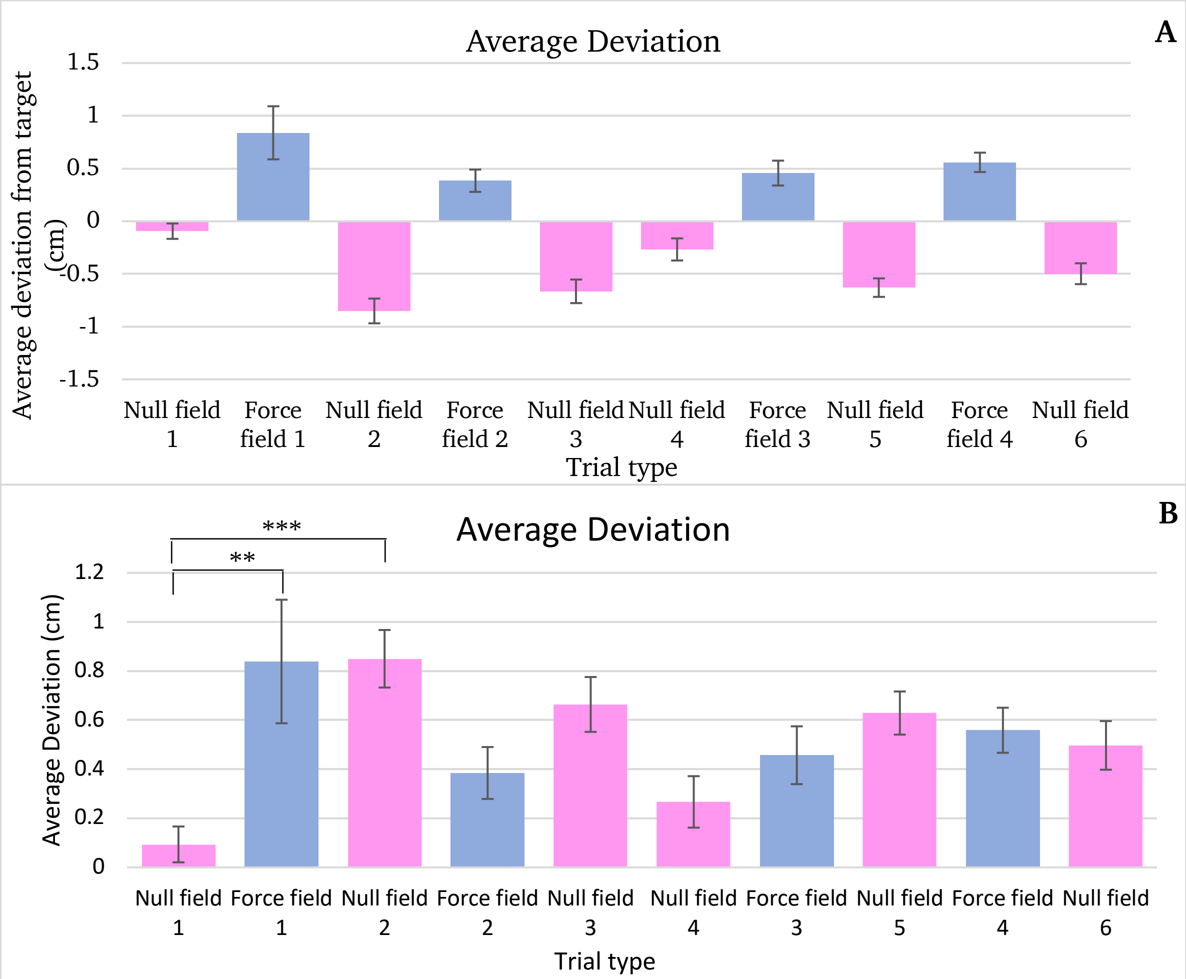

Figure 1.5.3.
A Each trial type contained the average of one trial from 8 participants. Null field 1 was the end trial of this baseline block which presented the mean optimal performance of each participant. Every other plot was the first trial of each block. **B** All results from **A** converted to positive values. Both graphs contain only null and force field blocks. Error bars represent SE. Significant differences indicated by **(p<.01) or ***(p<.001).

Protocol development of the behavioural task: stage four

At the end of the third stage of protocol development of the behavioural task, it was identified that skill learning and motor adaptation became more prominent within the results. Next it was important to make sure the behavioural task complied with fMRI requirements. The individual movement trials were changed to a total time of 21s, with each being separated by a rest period of 21s. This was because the TR time of the fMRI scanner was three seconds, therefore the behavioural task had to have a total time for movement and rest of a multiple of three. Next, reverse blocks were implemented into the protocol (R) which contained only two trials of rotations in the clockwise direction. These blocks were implemented to provide a baseline which could be compared to parts of skill learning and motor adaptation during the behavioural task and specific parts of the BOLD signal during fMRI scanning. These blocks only included two trials to ensure the participant did not repeat the task enough for adaptation to take place and improvement to occur. Null (N) and force (F) blocks contained five trials in the counter clockwise direction. A two-minute break took place approximately half way through the testing blocks in order to allow recovery time for the participants (figure 1.6.0.).

Figure 1.6.0 Timeline for protocol development stage three of the behavioural task. R= Reverse field block, N = Null field block, F= Force field block.

Please see Appendix for methods section relating to fMRI.

Results

Behavioural results from the finalised protocol performed in the mock fMRI scanner are presented here. Additional preliminary imaging data from two subjects who performed the task during fMRI are also presented.

Behavioural results

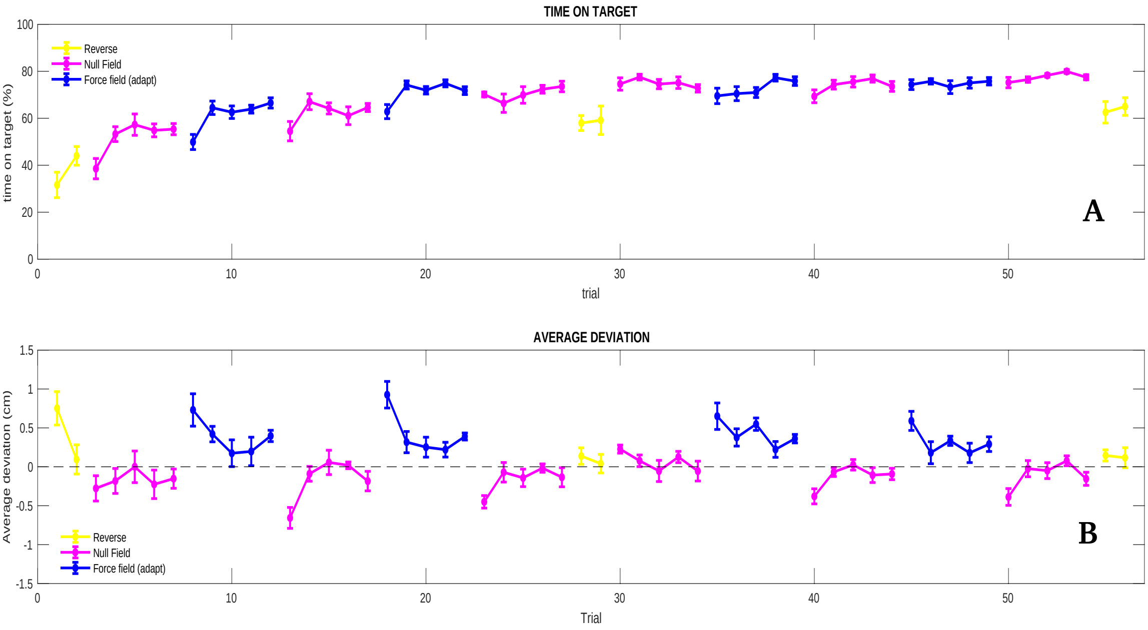

Figure 2.0.
Results for (**A**) 'Time on target' and (**B**) 'Average deviation' for the behavioural task. Each point on the graph represented an average of eight participants for one trial. Error bars represent SE.

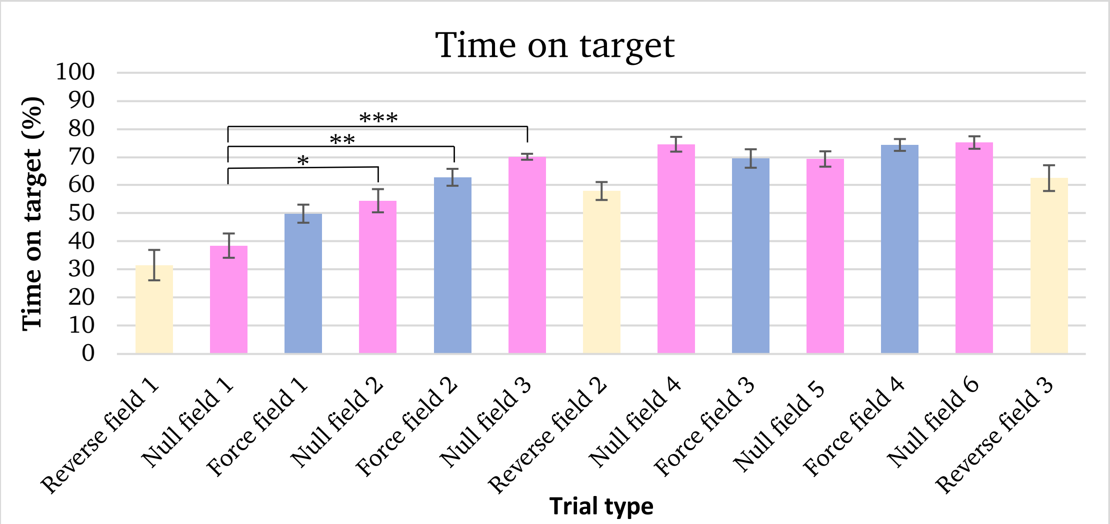

Figure 2.1.
Each trial type contained the average time on target of one trial from eight participants at the end of each block. Error bars represent SE. Significant differences indicated by *(p<.05), **(p<.01) or ***(p<.001).

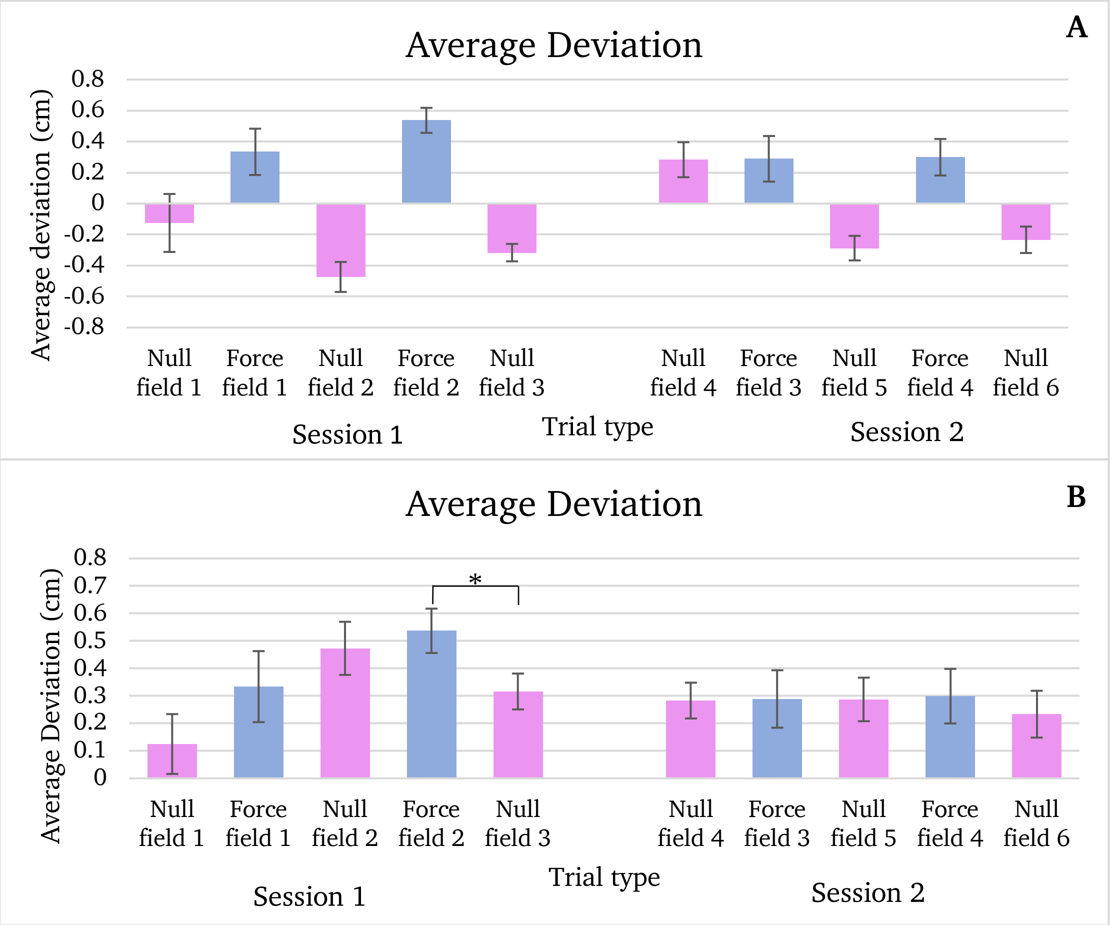

Figure 2.2.
A Each trial type contained the amount of motor adaptation or de-adaptation within each block. These results were determined by difference in average deviation between the beginning and end of each block as an average of eight participants. **B** All results from **A** converted to positive values. Both graphs contain only null and force field blocks. Error bars represent SE. Significant differences indicated by *(p<.05).

Time on target (%)

The measure of time on target in the results represents the level of skill learning of the participants. During statistical analysis of time on target results (figure 2.0. **A** and 2.1.), behavioural data were split into groups. Reverse field blocks were analysed separately from the other behavioural data, as previously mentioned they were used as time point baselines to compare fMRI data to. The participants significantly increased their ability to track the target within the reverse field blocks which only contained two trials in each block. This increase was shown by a repeated measures ANOVA, which revealed a significant time effect between the three reverse field blocks (F(2, 14) = 42.431, p<.001). Post hoc tests, which were Bonferroni corrected, revealed a significant increase between RF1 and RF2 of 18.829±3.556% (p=0.003), RF2 and RF3 of 7.136±2.216% (p=.044), RF1 and RF3 of 25.965±2.809% (p<.001).

The remaining behavioural blocks, which included null and force field blocks, were split into session 1 (null field 1, force field 1, null field 2, force field 2 and null field 3) and session 2 (null field 4, force field 3, null field 5, force field 4 and null field 6), shown in figure 2.1. Participants learnt the behavioural task initially at a fast pace in session 1, this was followed by slower learning in session 2, which overall produced a learning curve in the results. A repeated measures ANOVA displayed this learning curve with analysis of the last trial of each block for every participant, this revealed a significant time effect between session 1 and session 2 (F(1, 7) = 349.796, p<.001). Post hoc tests, which were Bonferroni corrected, revealed significant differences within session 1, where participants very quickly learned how to track the target throughout both null and force field blocks. This fast learning was revealed in the post hoc analysis, which showed significant increases in time on target from the baseline null field 1 to null field 2 of 14.892±2.455% (p=.005), from null field 1 to force field 2 of 21.329±4.692% (p=.027), from null field 1 to null field 3 of 21.360±3.926% (p<.001). Additionally, post hoc analysis revealed no significant differences in any blocks within session 2, the difference in session 2 from null field 4 to null field 6 was 0.454±1.406% ($p=1.000$). These results outlined how performance plateaued and the skill of tracking the target was learnt by the participants and could no longer improve.

Average deviation

Adaptation and the aftereffect (de-adaptation) show decrease in error in the opposite directions. In order to analyse the total amount of adaptation and de-adaptation in each session without direction, positive and negative values were flipped in the de-adaptation trials to match the data of the adaptation trials, and produce a positive average value (figure 2.2B). The measure of mean block adaptation (the difference between the start and end of each block) in the results represented the level of motor adaptation or de-adaptation of the participants.

During statistical analysis of mean block adaptation (figure 2.0. **B**), behavioural data was split into groups. Reverse field blocks were analysed separately from other behavioural data, as previously mentioned they were used as time point baselines to compare fMRI data to. The participants showed no change in behaviour within the reverse field blocks as no force was applied for motor adaptation to take place. It should also be noted that there is no aftereffect in the reverse blocks which suggests there is no transfer from adaptation in one circular direction to the other. These results were obtained by a repeated measures ANOVA which revealed no significant time effect between the three reverse field blocks (F(2, 14) = 1.899, p=.186).

The remaining behavioural blocks, which included null and force field blocks, were split into session 1 (null field 1, force field 1, null field 2, force field 2 and null field 3) and session 2 (null field 4, force field 3, null field 5, force field 4 and null field 6), shown in figure 2.2. Observed by adaptation curves (figure 2.0 **B**), following null field 1, there is within block motor adaptation throughout all force field blocks and de-adaptation observed by a mirrored curve, within all null blocks. Once the force had been implemented in force field 1, the amount of motor adaptation increased in subsequent blocks up until force field 2 (figure 2.2 **B**). This increase outlined the first stages of the participants adapting to the force field and also being able to de-adapt during the null fields. This initial increase however was non-significant, we believe, due to the high variability within the first 3 blocks. This high variability suggested that the number of trials within each block needed to be increased in future testing to allow more practise for each participant. It was not until null field 3 where the rate of adaptation began to plateau as the ability of the participants to de-adapt to the previous force field block became more efficient by effectively by forming a motor memory of the block to come. This de-adaptation was represented in post hock tests, which were Bonferroni corrected, by a significant decrease of .389±.078cm (p=.016) between force field 2 and null field 3.

A repeated measures ANOVA revealed a significant time effect between session 1 and session 2 (F(1, 7)=6.459, p=.039), suggesting a larger amount of motor adaptation taking place within session 1 compared with session 2. Subjects still adapted to force fields in session 2, observed by motor adaptation curves in figure 2.0. **B**, however this motor adaptation plateaued to a similar rate which is why motor adaptation stabilised in blocks in session 2. This stabilisation was outlined by no significant difference (p=1.000) in motor adaptation between all blocks in session 2.

Discussion

The current study was designed to develop a task that would provide a clear differentiation between skill learning and motor adaptation within a single behavioural task, with an ultimate aim to identify the neural networks which underpin both; whilst also providing evidence that skill learning and motor adaptation can take place simultaneously. A protocol development process took place throughout the study, involving a number of protocols which were improved at each stage of development. The novel motor behavioural task, inspired by the pursuit rotor (Koerth, 1922; Eysenck and Frith, 1977), was developed in order to gain the most effective behavioural results relating to skill learning and motor adaptation, which aimed to be replicated within the fMRI scanner.

The findings of the current study show promise for the proposed identification of skill learning and motor adaptation as separate entities. The measures of time on target and average deviation were used to quantify skill learning and motor adaptation, respectively. Skill learning is difficult to define as it does not have a single definable feature. However, as previously mentioned, skill learning represents an improvement in motor movements within a behavioural task following repetition and practise. Skill learning can be captured by measuring improvement in speed and accuracy and therefore represents a positive shift in the speed-accuracy trade-off function (SAF) (Krakauer and Mazzoni, 2011; Diedrichsen and Kornysheva, 2015; Chen, Holland and Galea, 2018).

Previous skill learning studies used the aspects of speed and accuracy present in the SAF to produce measures of skill learning. Floyer-Lea and Matthews (2005) conducted a skill learning imaging study where participants held a magnetic resonance-compatible pressure sensor between their right thumb and fingers. The participants observed two vertical bars on a monitor and were instructed to control the pressure sensor by squeezing it at a required force so that the second vertical bar matched the height of the first vertical bar. Floyer-Lea and Matthews (2005) observed performance improvement in terms of accuracy and timing. Performance error was tracked and measured as the percentage of maximum force. Additionally, Reis *et al.* (2009) conducted another skill learning study, including anodal transcranial direct current stimulation (tDCS) on the motor cortex, which involved a sequential visual isometric pinch task. Participants were required to squeeze a force transducer with their thumb and index finger to control a cursor to produce a specific sequence with speed and accuracy. They produced a measure of skill learning relating to the SAF called the error rate which was measured as 1-accuracy, where accuracy was the trials per block with target hits in the correct sequence. Although the current study cannot directly measure the SAF because there is no measure of response time to a stimulus as the speed of the target is set, aspects of speed and accuracy were still incorporated into the results, via the measure of time on target. The percentage time on target was chosen as a measure of skill learning, as time is a ratio of distance and speed, this measure focused on the ability of the participants to generate the correct speed to track the target and how accurately the cursor could follow the target with minimal distance away from the centre of the target. Time on target was also introduced by Renshaw and Weiss (1926) for the original pursuit rotor task to measure performance.

Following the formation of an efficient measure of skill learning, time on target, trends in results could be observed. It is clear that skill learning is transferable between all movement blocks (whereas motor adaptation is not – see below). This transferable skill learning was evident in the current study, due to the improvement in time on target results throughout alternating of null, force and reverse field blocks. Specific evidence of transfer of skill learning in the current study was outlined in the reverse field blocks. These blocks were initially used to provide a baseline during functional scanning. As only two reverse trials were present in each block, it was expected that no skill learning would be able to take place here. However, the significant increase between reverse blocks shown in the results of time on target suggested motor skill learning took place during these two blocks even in a small amount of time and repetition.

It is important to outline the stages of fast and then slow skill learning which took place consecutively throughout the behavioural blocks. Participants were initially able to increase the speed and accuracy of their responses to tracking the target ring at a quick pace, this can be seen in the first session of results. Following this, results suggest the motor skill learning capacity was reached at the start of session two where skill learning plateaued and no significant increase in time on target was seen. Overall, this behavioural data represents a learning curve, which involves the fast initial motor skill learning, common in behavioural tasks, followed by slow skill learning, where the response to the task becomes more automatic and resistant to interference (Floyer-Lea and Matthews, 2004; Doyon and Benali, 2005; Dayan and Cohen, 2011). In comparison to current literature, previously identified as skill learning imaging studies, Reis *et al.* (2009) observed very similar results where a learning curve was present as skill measure increased and plateaued over time with practise. Floyer-Lea and Matthews (2005) also observed a learning curve as percentage tracking error initially decreased at a fast rate and then plateaued.

Motor adaptation, in comparison to skill learning, is easier to define where an external perturbation requires a response to remain accurate under these altered conditions (Krakauer and Mazzoni, 2011). Previously, force field tasks have typically been used in reaching movements in a straight line where the required straight-line trajectory is deviated by a force (Shadmehr and Mussa-Ivaldi, 1994; Brashers-Krug, Shadmehr and Bizzi, 1996; Nezafat, Shadmehr and Holcomb, 2001; Dierdrichsen *et al.*, 2005). Therefore motor adaptation for these tasks is often measured as deviation, following a perturbation, often from a central line or a specific target. Specifically, lateral deviation or perpendicular displacement are accepted measures of error from a straight line, produced following force field implementation (Shadmehr and Holcomb, 1999; Nezafat, Shadmehr and

Holcomb, 2001; Dierdrichsen *et al.,* 2005). In the current study, due to the circular movement of the behavioural task, average deviation was used rather than lateral deviation. Average deviation gave us a measure of error distance away from the target with direction. Most recent theories of motor adaptation used in force field reaching studies incorporate a multi-rate model. This model suggests that two processes underpin motor adaptation, a fast and slow process. These processes can be captured using clamp or catch trials (Shadmehr, Smith and Krakauer, 2010). During these trials the amount of learning is measured by the lateral forces produced by the participants against the walls of a thin linear channel (Malfait and Ostry, 2004; Shadmehr, Smith and Krakauer, 2010). This specific measure of motor adaptation was not possible in the current study due to the circular trajectory however it is planned in future research to see if an equivalent clamp trial for a rotary task in a circular motion is plausible.

Motor adaptation within the current study, represented by the average deviation measure can be seen as adaptation curves and de-adaptation curves (aftereffects). Unlike skill learning, motor adaptation appears not to transfer from forward to backward rotation, as adaptation curves are only present in force field blocks and opposite de-adaptation curves take place in the following null field blocks. Initially, following the implementation of a force field, participants began producing adaptation curves with large error. In subsequent trials, participants continued to adapt to the perturbations as performance improvement took place, outlined by a curvilinear decrease in average deviation within each block with aftereffects in the opposite direction. This improvement also demonstrates savings where faster re-adaptation and a lower error at start took place every time the subject was exposed to the adaptation condition again (Dayan and Cohen, 2011). Motor adaptation, and therefore performance, then plateaued in session 2 where the adaptation curves observed in each block became much shallower. Internal model formation is key within these processes of motor adaptation where an internal model of the experienced force field is developed. Such developments take place mostly in the early stages of the task, which is why a steep adaptation curve is often observed initially, followed by a more shallow curve where motor error decreases to low levels (Shadmehr and Mussa-Ivaldi, 1994; Nezafat, Shadmehr and Holcomb, 2001).

These theories suggest that motor adaptation involves the adaptation of a forward model in response to the force dynamics which were experienced. This forward model is then able to predict the required response whenever the force field is experienced. This forward model along with the inverse model, which is also adapted to produce the required rotational trajectory of the cursor, together, construct the most effective response to the force field trials (Flanagan *et al.,* 2003).

During the task, participants reported that it was easier to respond to the forces, rather than the null field trials. The constant outward force gives the subjects a reference to continually push against, which naturally would create a circular movement. Therefore, along with the ability to adapt, it may be that a factor leading to improvement in performance in the adaptation trials could be due to the stiffness or stabilisation of the arm, wrist and hand during the task, which reduces the sensitivity to the forces perturbed upon the subject (Shadmehr and Mussa-Ivaldi, 1994; Flanagan *et al.,* 2003).

Further research

The intention of this study was to confirm the feasibility of this behavioural task within an fMRI scanner, including the large amount of equipment associated with the behavioural task such as an air compressor and numerous wired connections. Positively, the behavioural task successfully took place within the fMRI scanner and pilot imaging data was recorded (see Appendix). Initial fMRI imaging data managed to highlight some areas of activation which were comparable to other motor adaptation behavioural tasks, however overall the data was inadequate and needed improving. In future research, the relevant procedures will be implemented to reduce movement artefacts to confirm these results. These procedures will include fMRI scans to gain the neural activations related to vision which will then be discarded from results to acquire the most accurate neural data relate to the production of motor behaviour for the rotary task (Dierdrichsen *et* al., 2005; McGregor and Gribble, 2015). Furthermore, sample size will be increased and an effective general linear model will be produced for higher level fMRI statistical analysis; ultimately producing optimal fMRI results relating to the neural regions which underpin skill learning and motor adaptation.

Conclusion

Overall, this study endeavoured to isolate measures of skill learning and motor adaptation separately within a novel rotary behavioural task. After completing this, it is evident from behavioural results of time on target and average deviation that motor skill learning did take place throughout the entire behavioural task alongside adaptation. Adaptation was only produced and observed within the force field blocks and with after effects observed in following null field blocks. This study aimed to further provide evidence of skill learning and motor adaptation within fMRI results. Nevertheless, the two case studies produced from fMRI scanning identified many areas to improve in order to gain the most effective results. The current behavioural task, in comparison to reaching force field tasks, was ideal for an fMRI study due to its continuous design which lends itself to fMRI scanning. Further research of this behavioural task within fMRI scanning is promising and the protocol and analysis will be improved with greater fMRI experience and practise.

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Appendix

FMRI scan acquisition

All data was acquired on a Philips 3T Achieva system with a 32-sense head coil. For functional scans, four dummy scans initially took place, which were followed by functional scans of 400 dynamics, time to repeat (TR) 3 seconds, flip angle 85°, time to echo (TE) 40ms, resolution 2.5x2.5x3mm, slice thickness 3mm. T1-weighted structural images were acquired with a resolution of 1x1x1mm. A B0 field map was acquired with 3x3x2mm resolution, TR shortest, TE 9.22ms, and 46 slices.

Artifacts

The potential occurrence of artifacts was reduced by asking the participant to keep as still as possible during scanning and any metal was removed from the participant before entering the scanner room. Rest time was also provided during the scanning session, between movement trials and between the two sessions, so the participant could remain relaxed for the duration of the scan to avoid any unwanted head movement which could lead to the occurrence of artefacts.

Imaging procedures

Prior to fMRI scanning, all participants received verbal instructions on what they should expect in the scanner and how the task was to be completed. Participants were positioned in the scanner in a supine position where they were in a comfortable reaching distance of the MRIbot handle with their right hand. Before scanning started, all participants completed a training session which included familiarisation with the behavioural task within the scanner. This involved approximately one minute of unperturbed movement within a null field block. It also enabled the participants to find the most comfortable position within the scanner where they could reach all points of the behavioural task comfortably with their right hand and arm.

Imaging behavioural task

As outlined in the protocol development, the behavioural task was adapted several times to ensure it would be the most effective during scan acquisition. A final protocol development took place prior to the first scan (figure 1.5).

Figure 1.5. Timeline for protocol development of the behavioural task to be used within fmri scanning. R= Reverse field block, N = Null field block, F= Force field block.

The behavioural task was split into identical sessions (session 1 and session 2) which took place before and after a break occurred (figure 1.5.). Each session lasted approximately 18 minutes and triggered the start of the functional scan once the task was initiated. Each block included four trials rather than five included in the previous protocol, to reduce scan time to ensure the most detailed scan possible was acquired. The break included a five-minute anatomical scan which also acted as a rest for the participants. This protocol meant that both sessions of behavioural and functional data could be compared directly.

Imaging Data Analysis

Functional imaging data was analysed using functional magnetic resonance imaging of the brain software library (FSL) FMRI expert analysis tool (FEAT) FMRI analysis and FSLeyes, in which this analysis was based on general linear modelling (Woolrich *et al.,* 2001). During data pre-processing, high-pass temporal filtering took place to remove certain low frequency trends with a cut off frequency of 100s, along with 5mm spatial smoothing of full-width at half maximum (FWHM) resolution, along with functional magnetic resonance imaging of the brain's (FMRIB) motion correction linear registration tool (MCFLIRT) for motion correction (Jenkinson *et al.,* 2002). The brain extraction tool (BET) provided by FSL was used for brain extraction, and functional scans were normalised to the Montreal Neurological Institute (MNI) template. Following this, statistics were completed to produce a statistical model which included seven regressors as explanatory variables with a convolution of double-gamma haemodynamic response function. Contrasts of movement>rest, force>null, null>force, average deviation and time on target were acquired. Whilst time on target, average deviation, speed and the temporal derivative of speed, acceleration, were also used within the statistical model to account for some motion correction, these were removed from the results. Post statistics used cluster thresholding with a z threshold of 4.0. and a p value of 0.05.

fMRI results

The current study aimed to produce a novel rotary behavioural task, resulting in successful behavioural results which could be replicated within an fMRI scanner where neural correlates of skill learning and motor adaptation could be recorded. Following successfully obtaining behavioural results which differentiated between skill learning and motor adaptation in the mock scanner, the task was transferred to the real fMRI scanner, where similar behavioural results were displayed. Importantly, we have produced a novel motor task which can successfully take place within an fMRI scanner. However, the two data sets which were collected within fMRI scanning, due to large movement artefacts, did not display data of the quality we hope for. The fMRI data collected involved large movement artefacts around the edge of the brain which could potentially be driving all activations. During the completion of first level analysis of the fMRI data, the highest voxel cluster activations did in fact take place in expected neural regions related to motor adaptation. But these cluster activations along with large movement artefacts, observed in the results below, highlight errors and points for improvement within the fMRI scanning protocol and analysis.

fMRI case study one

Figures 3.0., 3.1. and 3.2 represented some neural areas which presented the highest activation during force field trials. These highlighted neural areas, which consisted of voxel clusters, had a significance value of <.001. These areas of neural activation were believed to be the neural correlates relating to force field trials, and therefore motor adaptation. Neural correlates with the highest activation included large areas of the cerebellum (figure 3.0.) and areas of the temporal lobe (figure 3.1.). Additionally, neural correlates of vision were observed within the occipital lobe and visual cortex, which were largely important in observation of the behavioural task. Moreover, the temporal gyrus, cerebral cortex, primary somatosensory cortex, premotor cortex, primary motor cortex and areas of the basal ganglia such as the putamen contained areas of activation (figure 3.2).

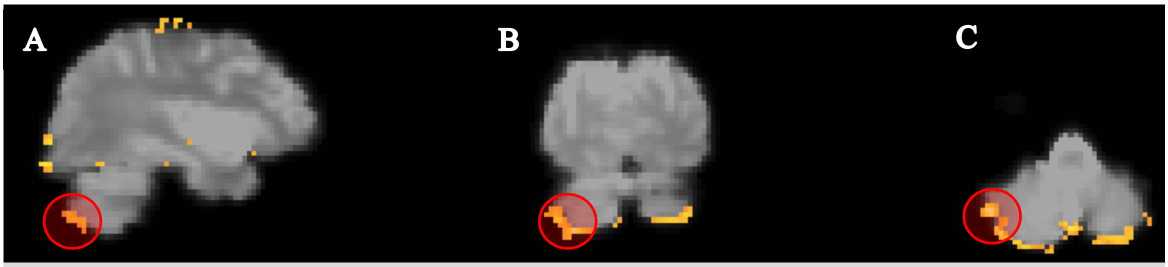

Figure 3.0.
Activation (p<.001) for case study one within **A** sagittal, **B** coronal and **C** axial planes. Statistical contrast of force>null. These image planes, together, outline the greatest activation in areas of the cerebellum. The cluster with the greatest fMRI activation within the cerebellum consisted of 256 voxels.

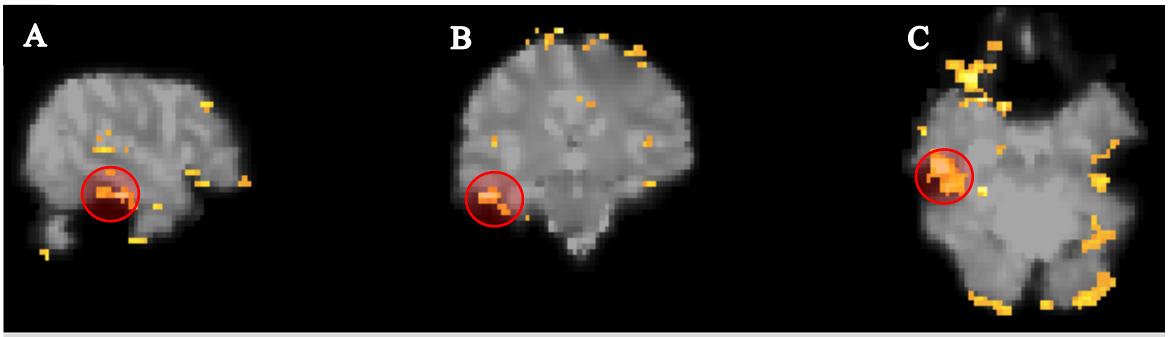

Figure 3.1.
Activation (p<.001) for case study one within **A** sagittal, **B** coronal and **C** axial planes. Statistical contrast of force>null. These image planes together outline the greatest activation, mainly in areas of the temporal lobe. The cluster with the greatest fMRI activation within the temporal lobe consisted of 116 voxels. Within these images, areas of noise activation were observed which did not correlate with a neural atlas.

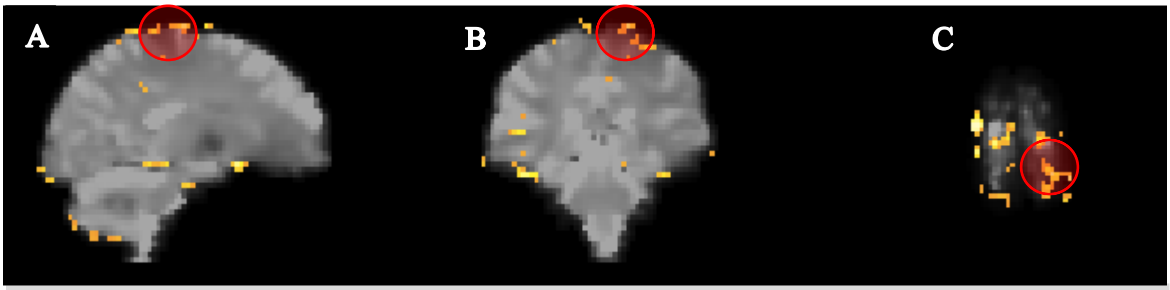

Figure 3.2.
Activation (p<.001) for case study one within **A** sagittal, **B** coronal and **C** axial planes. Statistical contrast of force>null. These image planes, together, outline the greatest activation in areas of the primary somatosensory cortex, premotor cortex and the primary motor cortex. The cluster with the greatest fMRI activation within these neural areas consisted of 68 voxels.

fMRI case study two

In comparison to case study one, which presented the neural correlates of force>null, the second case study (figures 4.0., 4.1. and 4.2.) represented some neural areas which presented the highest activations during movement, using the statistical contrast of movement>rest. During this second case study, statistical data could not be acquired for the contrast of force>null, so could not be compared with case study one. As a result, given this statistical fMRI data was from another individual participant, it was important to present results which highlighted neural areas relating to the behavioural task, in this case, movement. All highlighted neural areas, which consisted of voxel clusters, had a significance value of <.001. Neural correlates with the highest activation include large areas of the pre-motor cortex, the primary motor cortex and the primary somatosensory cortex (figure 4.0.).

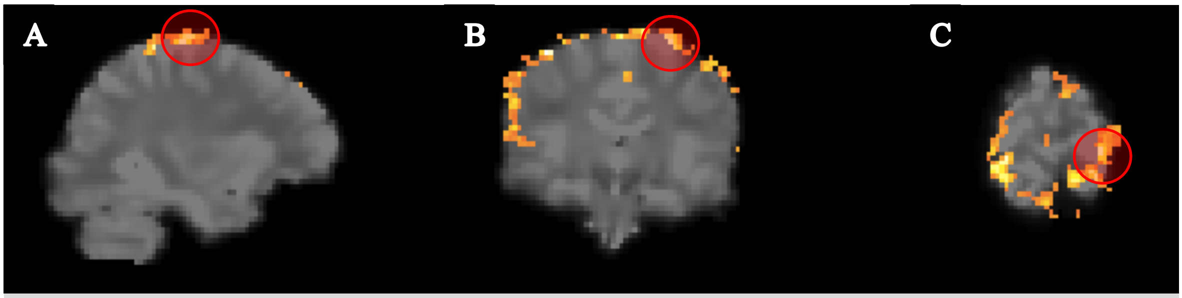

Figure 4.0.
Activation (p<.001) for case study two within **A** sagittal, **B** coronal and **C** axial planes. Statistical contrast of movement>rest. These image planes, together, outline the greatest activation in areas of the pre-motor cortex, the primary motor cortex and the primary somatosensory cortex. The cluster with the greatest fMRI activation within these areas consisted of 1234 voxels.

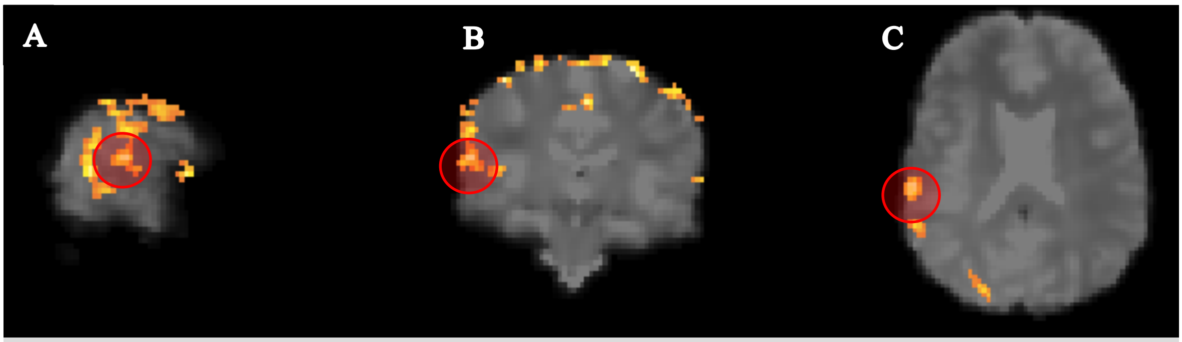

Figure 4.1.
Activation (p<.001) for case study one within **A** sagittal, **B** coronal and **C** axial planes. Statistical contrast of movement>rest. These image planes, together, outline the greatest activation mainly in the parietal and temporal lobes. The cluster with the greatest fMRI activation within the parietal and temporal lobes consisted of 361 voxels.

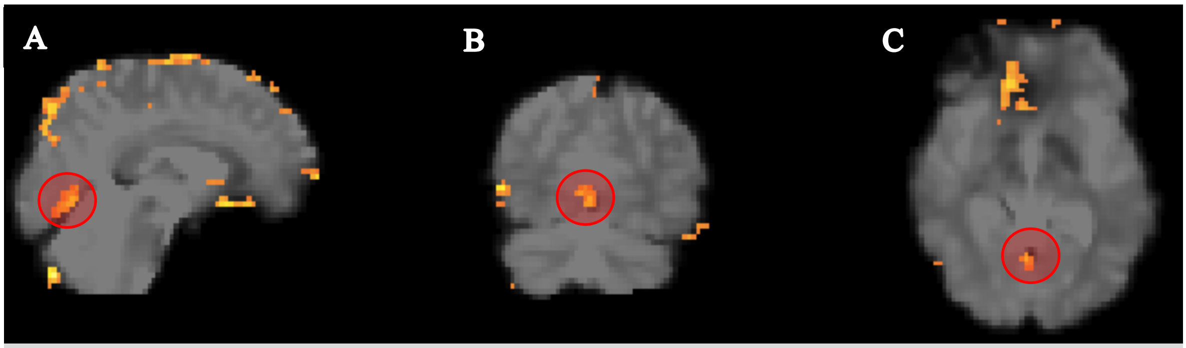

Figure 4.2.
Activation (p<.001) for case study one within **A** sagittal, **B** coronal and **C** axial planes. Statistical contrast of movement>rest. These image planes, together, outline the greatest activation in the occipital lobe and visual cortex. The cluster with the greatest fMRI activation within the parietal and temporal lobes consisted of 78 voxels.

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