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Coordinate Frame for Proprioception Acuity Changes Accompanying Motor Learning

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Abstract

Proprioception is important for skilled motor control. Improvements in proprioception occur in conjunction with motor learning. However, it has not been established whether these improvements occur within intrinsic or extrinsic coordinate frames. In Experiment 1 we gave participants a perceptual test of sensed limb position and a motor learning task in the same location of the workspace or in two different locations of the workspace. Participants performed better on the proprioception test when the motor learning task was completed in the same location as the proprioception test. In Experiment 2 we tested whether this perceptual improvement occurred in an intrinsic or extrinsic coordinate frame. Proprioceptive improvements were observed when participants maintained the same joint angles, but no improvements were found when participants altered their joint angles and maintained the same hand position. This consists with the idea that perceptual changes associated to motor learning occur in an intrinsic coordinate frame.

Keywords: human, proprioception, motor learning, somatosensory cortex, intrinsic coordinate frame, extrinsic coordinate frame, sensory, perceptual

Summary for Lay Audience

How is it that we can touch our nose while simultaneously keeping our eyes closed, or reach for a cup of coffee without taking our focus off our computer screen? The answer is proprioception. Proprioception is described as our ability to know where our limbs are in the external space around us. Without proprioception we may have poor coordination, a lack of body and limb awareness, and loss of motor control. Proprioception changes are suggested to occur in conjunction with motor learning. Motor learning can be defined as improvements in performance through repeated practice, such as becoming a better soccer player through practice. By learning a new motor skill, such as playing soccer, you also use proprioception to coordinate your motor movements. For instance, when you are playing soccer, you look forward to see where to pass or shoot the ball while at the same time kicking the ball. Proprioception allows us to know where our leg and foot are in relation to the soccer ball without having to look down. Proprioception is seen to improve following a motor learning task. The question we are trying to answer in the present study is whether proprioception changes use information from our joint and limb angles or information from the external space around us to improve limb sense. Proprioception is imperative to understand as it plays an important role in our everyday life by informing our central nervous system of our body in space and limb changes.

Acknowledgment

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Chapter 1

Introduction

Proprioception is described as our ability to detect where our limbs are located in space. Our muscle spindles, skin and joint receptors send sensory signals from our peripheral nervous system to our somatosensory cortex to indicate limb position (Goble & Brown, 2008; Goble, 2010). With the use of proprioception, we are better able to plan and then react.

Proprioceptive changes can occur in conjunction with motor learning (Wong et al., 2011). Motor learning can be defined as modifying an already learned skill, in the presence of a perturbation (motor adaptation), or acquiring a new skill through repeated practice, without any perturbation (skill learning). Motor learning is also associated with somatosensory and motor cortex plasticity (Vahdat et al., 2011). It has also been suggested that motor learning is influenced by proprioception (Brodie et al., 2014; Wong et al., 2012). The loss of proprioceptive feedback, such as in patients with neuropathy, results in deficits in motor control (Sainburg et al., 1995; Yousif et al., 2015). Evidence from non-invasive brain stimulation shows how disturbances within the somatosensory cortex in healthy individuals hinders the acquisition of new motor skills (Vidoni et al., 2010).

Work on animal models has also emphasised the important role the primary somatosensory cortex (S1) plays in motor learning (Sakamoto, Arissian & Asanuma., 1989). Compelling physiological evidence by Pavlides et al. (1993) demonstrates that lesions to S1 in non-human primates results in a loss of acquiring new motor skills in the hand contralateral to the lesion. However, it is important to note that impaired proprioceptive feedback or disruptions in the somatosensory cortex do not impede already learned motor skills (Sakamoto et al., 1989; Pavlides et al.,1993).

While past studies have convincingly demonstrated the relationship between the somatosensory and motor brain regions (Burton & Fabri, 1995; Darian-Smith et al., 1993; Stepniewska, Preuss & Kaas, 1993), along with proprioceptive acuity changes associated with motor learning (Mirdamadi & Block, 2020a,b; Wong et al., 2011), it has yet to be investigated, at least to our knowledge, whether proprioceptive acuity changes associated with motor learning occur within an intrinsic or extrinsic coordinate frame. This is the focus of the current study.

1.1 Physiology of proprioception

Proprioception is important for our sense of limb position. Extracellular stimuli are transduced into intracellular signals via mechanoreceptors that are innervated by myelinated afferent fibers (McCloskey 1978; Yousif et al., 2015). Afferent fibers ascend through the dorsal column-medial lemniscus pathway, sending sensory information towards the thalamus. Sensory information is then relayed to the primary somatosensory cortex where sensation is processed (Tuthill & Azim, 2018). Both static and dynamic (passive or active) limb movement are signaled by muscle, joint and cutaneous receptors (Burges et al., 1982; McCloskey, 1978). Joint receptors provide information about joint position during flexion and extension of joints (Burges et al., 1982; Clarke et al., 1975; Grigg & Greenspan, 1977), while cutaneous receptors are more sensitive to skin stretch (Burges et al., 1982). Muscle spindles signal when muscle stretches or the velocity of muscle stretch changes. Spindles have different sensory endings which can be classified as either: primary endings comprised of fast-conducting axons (group 1), which are sensitive to dynamic proprioception, or secondary endings comprised of slow-conducting axons (group 2), that are sensitive to static proprioception (McCloskey, 1978).

Previous findings have suggested that muscle spindles play a greater role in proprioception in comparison to joint and cutaneous receptors (McCloskey, 1978), whereas joint receptors may play a greater role in deep-pressure senses at or close to end range of joints (Burges et al., 1982; Clarke et al., 1975; Grigg & Greenspan, 1977), and cutaneous receptors are primarily activated during passive movements (Han et al., 2016), skin strain associated to movement (Edin & Johansson, 1995), or when the skin is stretched at certain joint angles (Burges et al., 1982). Nonetheless, muscle spindles, joint and cutaneous receptors all play a role in proprioceptive feedback.

1.2 Proprioceptive changes following motor learning

Previous studies have documented interneuronal projections between the somatosensory and motor cortex. Ren et al. (2019) used monosynaptic tracing, an approach allowing one to identify synaptic connections between neurons, and a retrovirus labelling technique to identify neuronal projections from the somatosensory cortex to related brain areas in mice. Neuronal projections from the somatosensory cortex were found to extend to the primary motor cortex. Similar neuronal projections between the somatosensory and motor cortex have also been found in Macaque monkeys (Burton & Fabri, 1995; Darian-Smith et al., 1993) and owl monkeys (Stepniewska, Preuss & Kaas, 1993). As such, short-range cortical connections exist between the somatosensory and motor cortex. It could therefore be suggested that changes in the somatosensory cortex may be influenced by motor cortex changes, and vice versa.

It has been well documented by neuroanatomical and behavioural studies that changes within the somatosensory and motor cortex are modulated by motor learning (Byl et al., 1997; Mirdamadi & Block, 2020a Ohashi et al., 2019; Rossi et al., 2021; Vahdat et al., 2011) where sensory inflow and motor outflow occur together.

Andrew et al. (2015) report somatosensory cortex changes following a motor learning task. Participants were required to perform sequential keyboard presses using only their thumb. Somatosensory evoked potentials (SEPs) were measured and found to be larger following learning when compared to participants' SEPs baseline measure. Similarly, Ohashi et al. (2019) examined excitability changes of the somatosensory cortex by measuring SEP changes using electrophysiological (EEG) signals related to median nerve stimulation in the right wrist, and changes in the motor cortex by measuring motor evoked potential (MEPs) measured via single-pulse transcranial magnetic stimulation (TMS), following learning. Their results clearly demonstrated increases in the magnitude of both SEPs and MEPs following learning indicating somatosensory and motor cortex changes following motor learning.

Additionally, as the somatosensory cortex has been seen to influence motor learning and motor cortex plasticity, lesions to the somatosensory cortex can likewise disrupt motor learning. The removal of somatosensory brain areas in cats has been shown to inhibit their ability to acquire new motor skill (Sakamoto, Arissian & Asanuma., 1989). Pavlides et al. (1993) conducted an experimental study on non-human primates (monkeys) using various motor learning tasks (i.e., food catching task, lever task and a food pick-up task) following lesions to the somatosensory cortex. The monkeys displayed deficits in learning how to catch food, but no deficits were seen for existing motor skills such as picking up food. Their results suggest that projections from the somatosensory cortex to the motor cortex influence learning, where lesions to the somatosensory cortex can affect the acquisition of a new motor skill, but motor skills obtained prior to the lesion are not abolished.

Like the above animal studies, human studies have also reported similar results in which disruptions to proprioceptive feedback can attribute to a loss of motor control. As discussed earlier on in the chapter, the dorsal column media-lemniscus pathway (also referred to as the posterior column media-lemniscus pathway) is an essential pathway for sensory information. Disruptions to the posterior column may therefore influence proprioceptive feedback. For instance, posterior cord syndrome (PCS) is caused by injury done to the posterior column of the spinal cord. Dysfunctions of the posterior column can lead to deficits in proprioceptive feedback. Patients with PCS have displayed deficits in vibration and proprioceptive sense, although temperature and pain sense seem to remain intact (Belen & Weingarden, 1988; McKinley et al., 2007). Additionally, PCS patients show, to some degree, deficits in mobility (e.g., transferring themselves from a bed to a chair, grooming, eating, etc.) (McKinley et al., 2019). Temporary loss of muscle strength have also been reported in patients with PCS (Belen & Weingarden, 1988). As such, disruptions in the afferent pathway of the spinal cord may result in sensory feedback impairments and consequently, disrupt motor control. However, it should be noted that patients with PCS may regain some mobility following rehabilitation.

Vidoni et al. (2010) examined how inhibitory 1 Hz repetitive transcranial magnetic stimulation (rTMS) can disrupt somatosensation and ultimately influence motor skill learning. It should be noted that participants who took part in their study reported no record of any neurological deficits. Participants in the experimental group were given perceptual tests (matching tests) to measure their sensory function prior to and after 1 Hz rTMS was administered. The sham group was given the same perceptual tests, but 1 Hz rTMS was not administered. A motor learning tracking task was also given to both groups of participants.

Participants in the experimental group made more errors during the tracking task in comparison to the sham group who did not make as many tracking errors. The results from Vidoni et al. (2010) clearly demonstrate how disruptions to somatosensory feedback can impair learning.

On the other hand, Brodie et al. (2014) demonstrated how 5 Hz transcranial magnetic stimulation (rTMS) over the somatosensory cortex accompanied by motor learning led to improvements in motor performance in patients who suffered from chronic stroke. A group of healthy participants and patients with chronic stroke were given a perceptual test and a two-point discrimination task, to assess cutaneous somatosensation. This was also paired with a serial tracking task (STT) to assess motor learning. Both groups of participants displayed improved motor performance when 5 Hz rTMS was administered over the somatosensory cortex and paired with motor practice, suggesting that enhanced somatosensory cortex stimulation results in improved motor performance.

As previously discussed, somatosensory changes are also influenced by sensory feedback, specifically proprioception (Burges et al., 1982) meaning that proprioceptive deficits, such as damage to peripheral nerves, negatively impact our somatosensory cortex. Likewise, the loss of proprioception may lead to poor coordination, a lack of body and limb awareness, and loss of motor control (Yousif et al., 2015). Proprioception thus plays an important role in motor learning and developing a new skill. Participants in a previous study have shown greater improvements in motor movements following proprioceptive training in comparison to control participants who did not receive any proprioceptive training (Wong et al., 2012). Thus perceptual input can influence motor output, and vice versa. These studies strengthen the idea that somatosensory and motor cortex strongly influence each other such that plasticity in one domain leads to changes in the other.

1.3 Coordinate frames

Somatotopic representations can be defined as a map of the body in which a specific body part is represented or associated with a specific location in the central nervous system. Receptors in the body send signals, via nerve fibers, to the cerebral cortex and create representations of the body with respect to space (Leoné, 2014). Sensory somatotopic representations have been discovered within the posterior parietal (PPC) and premotor cortex (PM) and the representations within the parieto-frontal cortex are said to be related to various functions such as: imaging movement, when a body part is moved (e.g., hand movements), when a body part is touched, and when attention directed towards a body part (Leoné, 2014; Shadmehr & Wise, 2004).

Specifically, whole-body representations are known to be formed in the somatosensory and motor cortex (Penfield & Boldrey, 1937). For instance, when we move our hand, our peripheral nervous system sends sensory signals to our somatosensory cortex, the somatosensory cortex then forms representations of where our hand is in space. Through neuroimaging, behavioural and neurophysiological studies conducted in humans and monkeys, multiple coordinate frames have been found to play a role not only in forming representations but also in conducting planned motor movements (Cohen & Anderson, 2002; Grefkes & Fink, 2005).

Coordinate frames can be described as either limb-centered (intrinsic) or world-centered (extrinsic). For instance, if information from joint angles or muscle length changes can be used to guide our hand towards a target in the workspace, this would be described as changes occurring in a limb-centered or intrinsic coordinate frame (Shadmehr & Mussa-Ivaldi, 1994). In contrast, if information from perceptual systems (e.g., vision or audition) is used to indicate where a target is located in the workspace, this would be described as changes occurring in a world-centered or extrinsic coordinate frame (Anderson, Snyder, Li & Stricanne, 1993). Within the field of motor learning, coordinate frames have been investigated to better understand if learning improvements occur in intrinsic or extrinsic coordinate frames. If for instance, motor learning improvements occur in intrinsic coordinate frame then it may be suggested that motor learning changes occur in intrinsic coordinate frames, in contrast if learning is improved in extrinsic coordinate frame then motor cortex changes would thus be suggested to occur in extrinsic coordinates frame.

Previous literature suggests that motor learning occurs in either intrinsic or extrinsic coordinate frames influenced by the given task or the goal of the task (Berniker et al., 2014). During motor learning motor cortex cells encode limb state and it is believed that changes to the limb are encoded in limb-centered coordinates of joints and muscles (Orban de Xivry et al., 2011).

Malfait et al. (2002) constructed a motor learning task in which subjects were asked to make point-to-point reaches to different targets positioned in the arm's workspace. They were first given the task on the left side of the workspace and were then required to do the same reaching task on the right side of the workspace. Subjects were asked to either maintain the same joint displacements (testing intrinsic) or maintain the same hand displacement (testing extrinsic) in both parts of the study. Subjects who kept the same joint displacement but had different hand displacement within the trained and novel workspace performed significantly better in comparison to the subjects who had different joint displacements but maintained the same hand displacement. Thus, their results suggest that motor learning occurs in an intrinsic coordinate frame. Their results also correspond to a study conducted by Ghez and colleagues (2000) who also propose that motor learning changes occur in an intrinsic coordinate frame.

In contrast to the findings from Malfait et al. (2002), previous studies have suggested motor adaptation to occur within an extrinsic coordinate frame. Morton et al. (2001) show transfer of adaptation to occur with different limb configurations. Participants were asked to catch a ball with their shoulder at 10º and elbow at 80º (i.e., bent position) or their shoulder at 80º and elbow at 10º (i.e., straight position). During the first experiment, participants were trained to catch a light weight ball in the bent position. During the transfer phase, participants were then asked to catch a heavy weight ball using their contralateral arm with the same joint angle as the training phase. In experiment 2, during training participants were asked to catch a light weight ball in either the bent or straight position and then required to catch a heavy weight ball in the other position during the transfer phase. Their results displayed greater transfer of adaptation control when participants maintained the same hand displacement in comparison to participants who maintained the same joint angles in the contralateral arm. Similarly, Criscimagna-Hemminger et al. (2003) display a transfer of force-field learning during a reaching task within an extrinsic coordinate frame. Participants were trained using their dominate hand and then tested using their nondominant hand or, trained with their nondominant hand and then tested using their dominant hand. Participants were also placed in either the intrinsic or extrinsic group. The intrinsic group maintained the same joint displacement in the contralateral hand during the testing phase, while participants in the extrinsic group maintained the same hand displacement in the contralateral hand during the testing phase. Transfer of learning occurred for participants in the extrinsic group but only when they trained using their dominant hand and then tested using their nondominated hand. As such, these results suggest that motor learning may also occur within an extrinsic coordinate frame.

Proprioceptive changes have also been tested in both intrinsic and extrinsic coordinate frames. Iandolo et al. (2015) tested proprioceptive performance using a bimanual matching task within intrinsic and extrinsic coordinates. Participants were asked to match the position of their right finger to their left finger either by matching them within the same spatial location of the workspace (testing extrinsic coordinates) or mirroring the locations of their right finger to their left finger with respect to their body midline (testing intrinsic coordinates). Participants displayed lower matching errors within the extrinsic condition in comparison to the intrinsic condition, thus suggesting that information of limb position within space may occur within an extrinsic coordinate frame.

Additionally, somatosensory cortex (S1) cells have been measured during various limb configurations in monkeys (Tillery et al., 1996). The objective of the experiment was to observe changes in S1 cell activity in different coordinate frames. The monkeys were trained to hold onto a robotic manipulandum while it guided their hand to different location in the workspace. Cell sensitivity was specific where specific S1 cells were discharged at certain hand location. For instance, some S1 cells dominated during hand movements to a location away and towards the monkeys' midline (posterior-anterior axis) while other S1 cells had greater activity during left and right movements (left-right axis) with the greatest discharge being at the far most left or right boundaries within the workspace. Although their results show that S1 cell activity is altered as the hand is being shifted through different locations in the workspace, it does not confirm whether S1 cells represent these changes as a factor of hand location (extrinsic coordinate) or represent these changes as factor of joint angles (intrinsic coordinates). As such, it is unclear whether somatosensory changes occur within an intrinsic or extrinsic coordinate frame.

In recent years, behavioural studies have investigated proprioceptive improvements and the changes that may occur within the somatosensory cortex following motor learning (Mirdamadi & Block 2020a,b). However, it has not been established, to our knowledge, whether these observed improvements are a result of somatosensory changes occurring within a limb-centered coordinate or world-centered coordinate frame. Previous work done by Wong and colleagues (2011) tested proprioceptive acuity changes following motor learning. Participants were given judgment tests and a reaching task in either the same location of the workspace (i.e., the matched group) or, the judgment tests in the center of the workspace and the reaching task 25 cm to the right of the center (i.e., the unmatched group). Proprioceptive improvements were only seen for participants in the matched group when both the judgments tests and the reaching task were given in the same location of the workspace, suggesting that these improvements were spatially specific. However, when participants in the unmatched group were given the reaching task on the right side of the workspace, both their joint angles and hand displacement were changed. Therefore, it is unclear whether changes in the participants' joint angles (testing them in an intrinsic coordinate frame) or hand displacement (testing them in an extrinsic coordinate frame) influenced the overall results. Given that proprioceptive improvements occur in conjunction with motor learning (Wong et al., 2011), one may therefore question if proprioceptive changes occur within intrinsic or extrinsic coordinate frames.

This gap of scientific knowledge is important to investigate as it would give us a better understanding on how somatosensory representations are formed and whether these changes occur within intrinsic or extrinsic coordinates. Additionally, this question will further deepen our knowledge on the relationship between the somatosensory and motor cortex. As such, the current study was conducted to answer these questions with the hopes to fill the gap in our scientific knowledge of the somatosensory cortex changes that occur following motor learning.

1.4 Current study

The objectives of the present study were to 1) replicate the previous findings by Wong et al. (2011) and see if proprioceptive improvements occur following motor learning and if these improvements are spatially specific, and 2) gain a better understand if somatosensory changes occurred in intrinsic or extrinsic coordinate frames with the use of proprioceptive tests, following motor learning. We hypothesized that somatosensory changes associated with motor learning occur within limb-centered coordinate frame.

In the first experiment we tested if proprioceptive acuity is improved following motor learning. We specifically examined if these improvements are spatially specific. In other words do the proprioceptive tests and motor learning task need to be given within the same location of the workspace to observe proprioceptive improvements? To answer our questions for Experiment 1, the motor learning task was given in either the same location of the workspace as the proprioceptive tests, or in a different location of the workspace. The proprioceptive tests required participants to give judgment responses as to whether they believed their hand was to the right or left of a previously remember reference target.

Past studies have clearly demonstrated perceptual changes following motor learning (Ostry & Gribble, 2016) and these changes have also been suggested to be spatially specific (Wong et al., 2011). As such, we predicted 1) proprioceptive acuity improvements occur following motor learning, and 2) the proprioceptive acuity improvements would only be observed in participants who receive the proprioceptive tests and motor learning task within the center of the workspace but no improvements would be seen for participants who receive the proprioceptive tests in the center of the workspace and the learning task 25 cm to the right of the center.

For the second experiment, we questioned why proprioceptive improvements were only seen in participants who were given both the tests and the learning task in the same location of the workspace. We questioned if these improvements were a result of participants maintaining the same limb and joint angles (i.e., same limb configuration in an intrinsic coordinate frame), or maintaining the same hand displacement (i.e., same position in an extrinsic coordinate frame). Participants were given the same proprioceptive tests and motor learning task as the first experiment. However, after motor learning, participants were given the post proprioceptive test after learning in either the same location of the workspace but their torso was turned 45° from the screen, altering their limb and joint angles but keeping their hand position in the workspace the same, or their whole body was shifted 25 cm to the right of the center, maintaining the same joint angles but with their hand in a different location in the workspace.

Motor learning is suggested to occur within a limb-centered coordinate frame rather than a world-centered coordinate frame (Shadmehr & Mussa-Ivaldi, 1994; Malfait et al., 2002; Haswell et al., 2009) and given the strong neuroanatomical connections between the somatosensory and motor cortex observed in human neurophysiological (Byl et al., 1997;

Mirdamadi & Block, 2020a; Ohashi et al., 2019; Rossi et al., 2021; Vahdat et al., 2011), behavioural (Mirdamadi & Block, 2020b; Wong et al., 2011; Wong et al., 2012) and animal studies (Burton & Fabri, 1995; Darian-Smith et al., 1993; Vogt et al., 1978), we thus predicted that 1) proprioceptive acuity improvements occur in a limb-centered coordinate frame.

We also predicted that 2) participants who maintained the same joint angles during the post proprioceptive tests would display improvements in proprioceptive acuity in comparison to participants who altered their joint angles but maintained the same hand position in the workspace.

Chapter 2

Methods

The goal of Experiment 1 was to replicate the findings from the Wong et al. (2011) study. Their results displayed improvements in proprioceptive acuity only when both the proprioceptive tests and motor learning task were given in the same location of workspace. As such, for our first experiment the proprioceptive tests and the motor learning task were either given in the same location of the workspace (i.e., in the center of the workspace) or, in two different locations in the workspace (i.e., the proprioceptive tests were given in the center of the workspace and the motor learning task was given 25 cm to the right of the center).

For Experiment 2, we wanted to test whether proprioceptive improvements occur within a limb-centered or world-centered coordinate frame. For the second experiment, participants were either asked to maintain the same joint-angles (testing limb-centered) or maintain the same hand displacement (testing world-centered).

2.1 Participants

Sixty healthy participants between 19 and 30 years of age were randomly assigned to one of four groups. All participants had no prior neurological, musculoskeletal or visual disorders. Prior to taking part in the study, all participants filled out a written consent form. Upon completing the experiment, participants were given course credit or compensated for their time. All procedures were approved by the University of Western Ontario Research Ethics Board.

2.2 Apparatus

All participants were seated in front of an end-point robot (KINARM) with a horizontal LCD monitor stationed below their chin as seen in Figure 2.1. The LCD display provided visual feedback of the participant's hand position in real time. A customized air sled was used for participants to rest their right forearm on while they held onto the robotic manipulandum controlled by an experimental protocol. The robotic arm moved participants' passive limb in a horizontal plane across the workspace to each programmed location. A six-axis force transducer (ATI Industrial Automation, Apec, NC; resolution: 0.05 N), located inside the handle, measured forces at the hand.

2.3 Proprioceptive tests

The proprioceptive tests were identical for all the experimental conditions. The method of constant stimuli was used for our tests. This method requires participants to compare their hand's end position to its start position (i.e., comparing current hand position to the original start position within the workspace). The method of constant stimuli presents participants with stimuli in random order, preventing participants from predicting the next stimulus, which ultimately decreases expectancy errors and habituation (Han et al., 2016).

All participants were required to keep their eyes closed as the robotic arm moved their passive limb to the different test locations. The robotic arm first moved participants' arm, aligning their elbow joints at roughly a 90° angle, to the first target called the reference target. Upon arriving at the reference target, participants were given an auditory stimulus (a beep sound). Then, the robotic arm moved their passive limb along a left-right axis at a random direction (left/right), duration (between 1000 and 1500 ms) and distance (up to 15 cm) to a second target, called the distractor target. The distractor targets were used to reduce the possibility of participants using any type of direction or duration cue that would bias their judgment of hand position. From there the robot brought them to a third target, called the judgment target, where participants were given another auditory stimulus (a beep sound that was slightly different from the first beep). The judgment targets were randomly placed in 1 of the 7 different locations (0 ± 0.3, 1.3, 3.7 cm) to the left or right of the reference target. Once they arrived at the judgment location, they were required to give a verbal response as to whether they felt they were to the left or to the right of the reference target. Participants' verbal responses were recorded by the task protocol. Once participants' verbal response was recorded, their hand was taken to another distractor target before returning to the reference location (see Figure 2.2).

Each judgment location was tested 10 times with a total of 70 trials. All participants were given two proprioceptive tests (pre and post-tests) during the experiment. The pre-test was used as baseline measure for participants' proprioceptive acuity and to rule out any outliers. All participants needed to score under a 20 mm threshold in the pre-test in order to continue in the study. Prior to the experimental phase of the study, an abundant amount of data was collected during our pilot study (i.e., a total of 104 participants were tested). Using plot data, we found that roughly 28% of participants had an uncertainty range score below 20 mm. A score above 20 mm also corresponds to more than 50% of the middle 50% of the task. If participants were successful in the pre-test during the experimental study, they were then given the learning task (explained in section 2.5) followed by another proprioceptive post-test. If participants scored above 20 mm during the pre-test, they did not continue in the study and were compensated for their time.

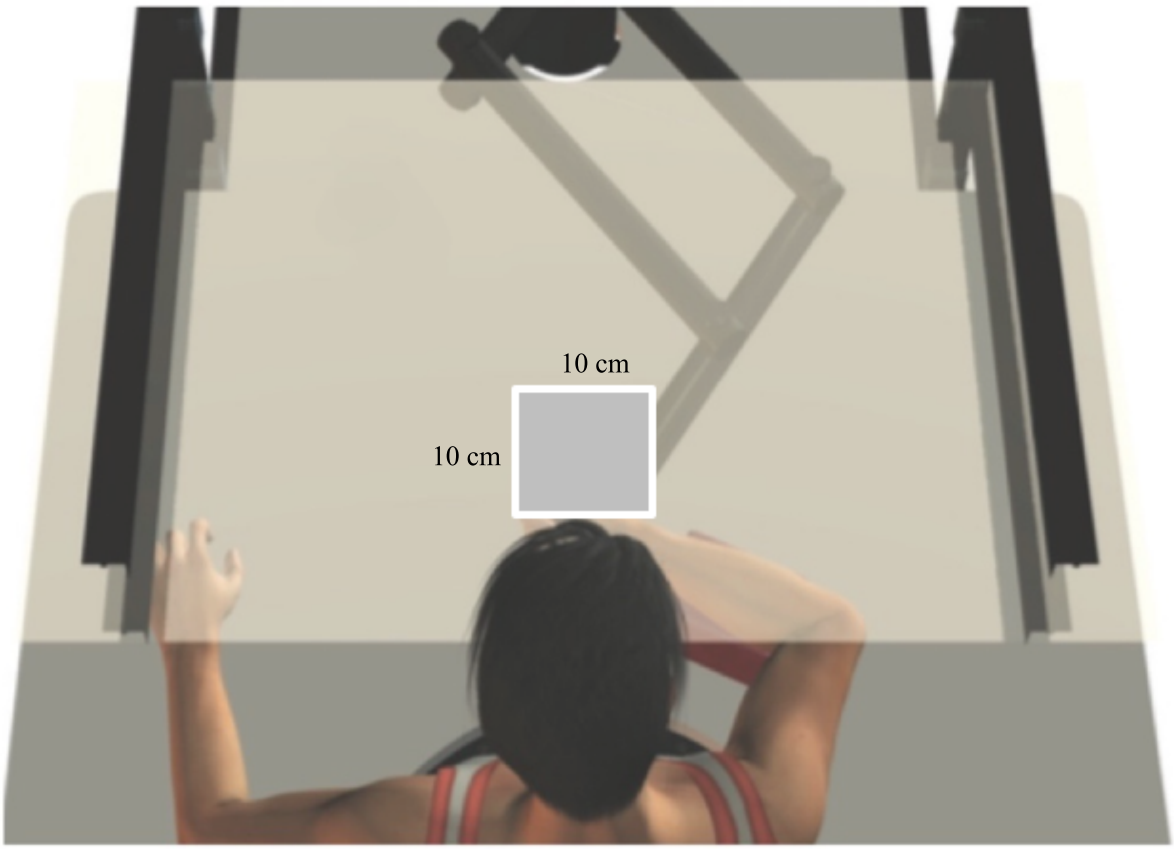

Figure 2.1. Experimental apparatus overhead view. Participants held on to a robotic manipulandum that moved the hand along the surface of the desk in a left-right movement within a 10 by 10 cm patch of the workspace. A custom air sled was placed under the participants forearm for support.

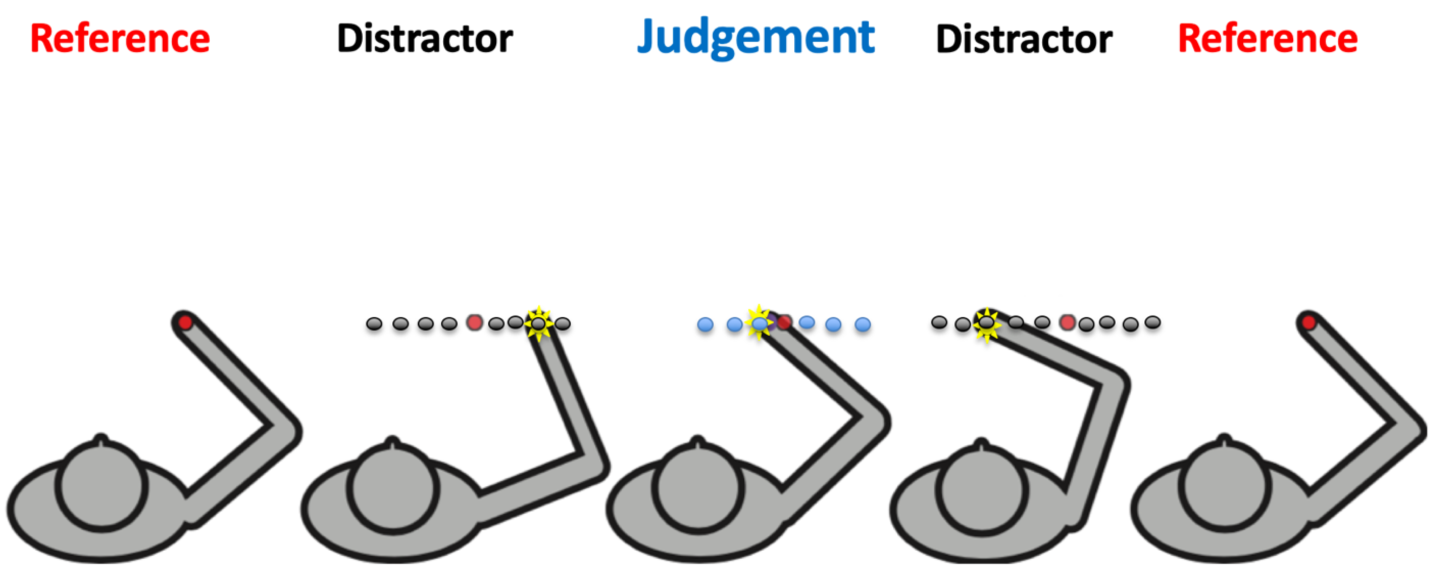

Figure 2.2. Experimental apparatus overhead view: Proprioception test. Participants held on to a robotic manipulandum that moved the hand along the surface of the desk in a left-right movement. Red target illustrates the reference target; black target illustrates the distractor targets placed randomly to the left or right of the reference; blue targets illustrate the 7 judgement targets. All participants performed pre and post judgment tests.

2.3.1 Proprioceptive test group assignment

Participants were randomly assigned to one of four groups, and were directed to keep their eyes closed throughout the tests, regardless of group assignment, whilst facing forward.

For Experiment 1, participants were randomly assigned to groups 1 and 2, which will be referred to as the matched and unmatched groups respectively. Participants in the matched and unmatched groups were given both the pre and post proprioceptive tests in the center of the screen.

For Experiment 2, a new set of participants were randomly assigned to either group 3, referred to as the limb-centered coordinate frame group (LCC) or group 4, referred to as the world-centered coordinate frame group (WCC). Participants in the LCC group were given the pre-test in the center location of the workspace, and the post-test 25 cm to the right of the center (see Figure 2.3A). Participants in the WCC group were also given the pre-test in the center of the workspace. For the post-test, participants in the WCC group were required to hold the robotic handle while their torso was shifted 45° to the left of the table and to keep their head rotated towards the screen. Tape was placed on the floor to indicate how much participants would need to be rotated and a custom protractor was also used to measure participants rotation from the table. Participants were asked to keep their head faced towards the screen and to maintain this position (see Figure 2.3B).

A.

B.

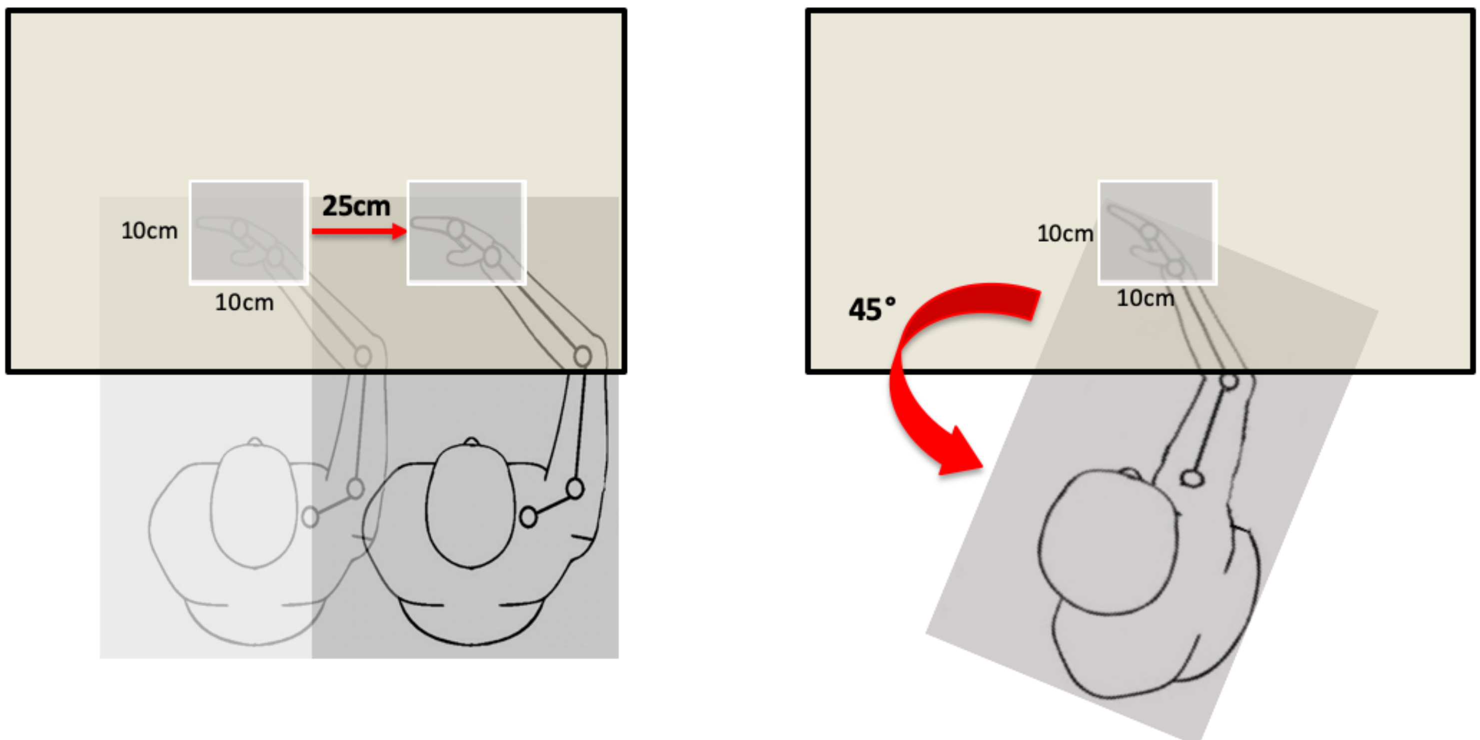

Figure 2.3 (A) Overhead view of experimental apparatus: Coordinate frame. Participants in the limb-centered coordinate frame group held on to the robotic manipulandum while they were shifted to 25cm to the right of center for the post-test. (B) Participants in the world-centered coordinate frame group held on to the robotic manipulandum while their torso was shifted to 45° from the screen while still facing forward for the post-test.

2.3.2 Proprioceptive measurement

To measure proprioceptive improvements, the proportion of trials participants responded "right" at each judgment target was plotted against the actual judgment location using MATLAB software (The Mathworks Inc.). Data sets of binary responses of perceived hand position against actual hand position in the workspace were fitted to and estimated by psychometric functions (Figure 2.4A). From the psychometric function we were able to calculate proprioceptive sensitivity and bias. Proprioceptive bias is defined as the hand position associated with the 50th percentile of the psychometric function. Proprioceptive sensitivity is the distance between the hand positions associated with the 75th and 25th percentiles, defined as the uncertainty range (UR).

The UR is calculated by finding the difference between the participant's hand position at the 75th percentile (p75) when they responded "right" and their hand position at the 25th percentile (p25) when they responded "right":

$$UR = p75 - p25$$

The uncertainty range is thus used as the dependent measure to observe if participants have improved judgment after training (Figure 2.4A). Figure 2.4B shows an example of a participant's uncertainty range for both the pre and post-test where the participant's response is plotted against the actual target location.

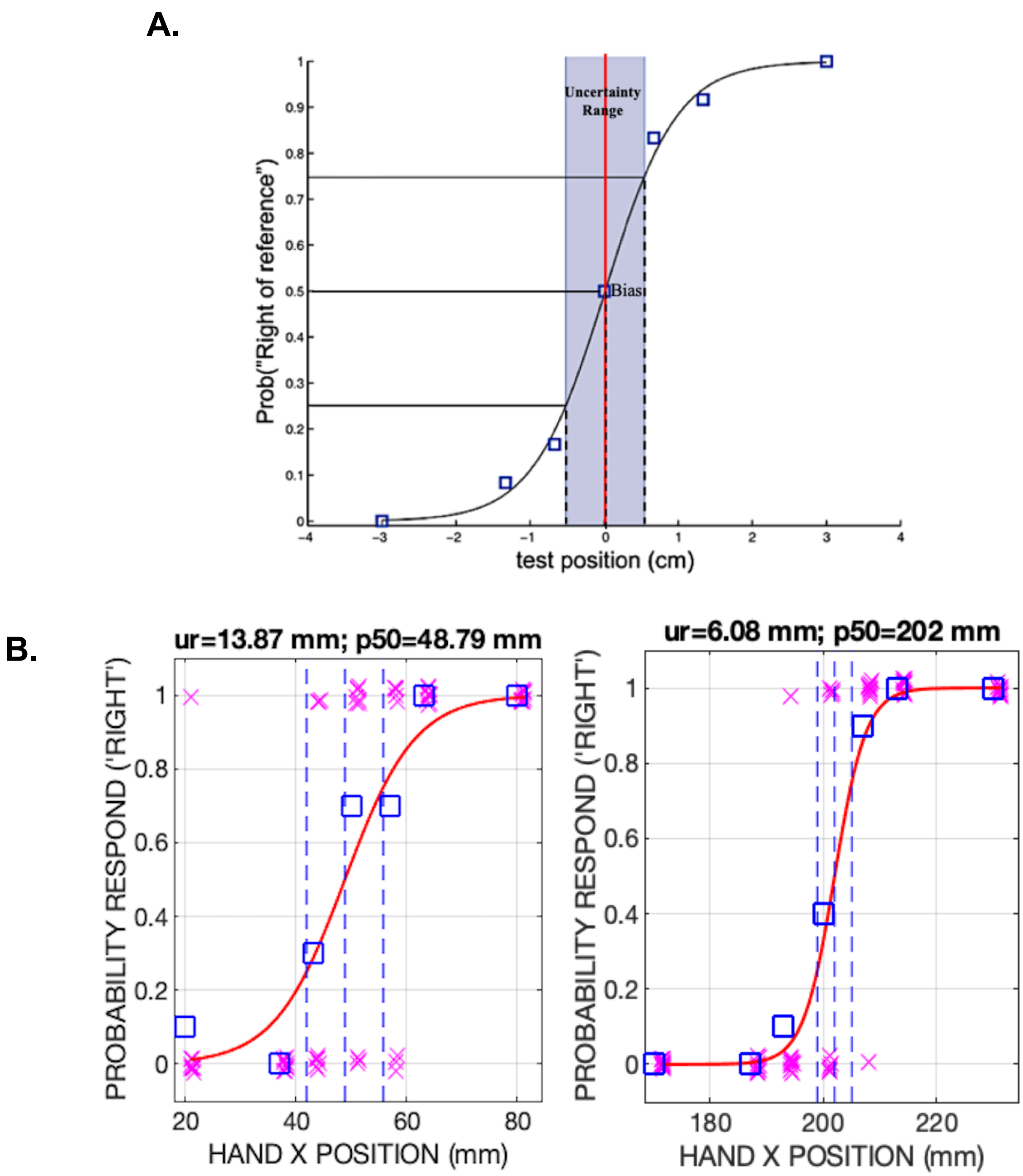

Figure 2.4. (A) Example of psychometric function. The blue squares display the probability of a participants response of their hand position to the right of the reference position. The center of the figure is the uncertainty range. (B) Example of one participant's pre-test (left) and post-test (right) following motor learning. The blue squares denote the target location to the reference and the pink X's illustrate the participant's judgment of hand location to the actual target location. Uncertainty range and proprioceptive bias are represented by ur and p50 respectively.

2.4 Proprioceptive statistical analysis

In both experiments 1 and 2, differences in uncertainty ranges between groups were tested using a mixed (split-plot) design analysis of variance (ANOVA) using JASP software (JASP Inc.). We tested one between subjects factor: group (matched vs. unmatched and limb-centered vs world-centered), and one within-subjects factor: pre-tests vs post-tests. Tukey post hoc tests were then conducted to analyze significant main effects and interactions.

2.5 Motor learning task

We used a reaching task to measure motor learning. The reaching task was identical for all the experimental conditions. Participants were asked to hold the robotic manipulandum with their right hand and reach to 7-mm targets that were displayed randomly within a 10 x 10 cm patch within the workspace. The task consisted of 4 blocks of 100 targets. Participants were instructed to reach towards each target as accurately and fast as possible. Once their hand reached the target the next target immediately appeared. In order to keep participants engaged, they were given verbal feedback on how fast it took them to complete each block (in ms).

2.5.1 Learning task group assignment

Participants were given the learning task in one of two locations based on their group assignment. Participants who were assigned to the matched, limb-centered and world-centered groups were given the learning task in the center of the workspace (see Figure 2.5A). Participants who were assigned to the unmatched group, were given the learning task 25 cm to the right of the center (see Figure 2.5B).

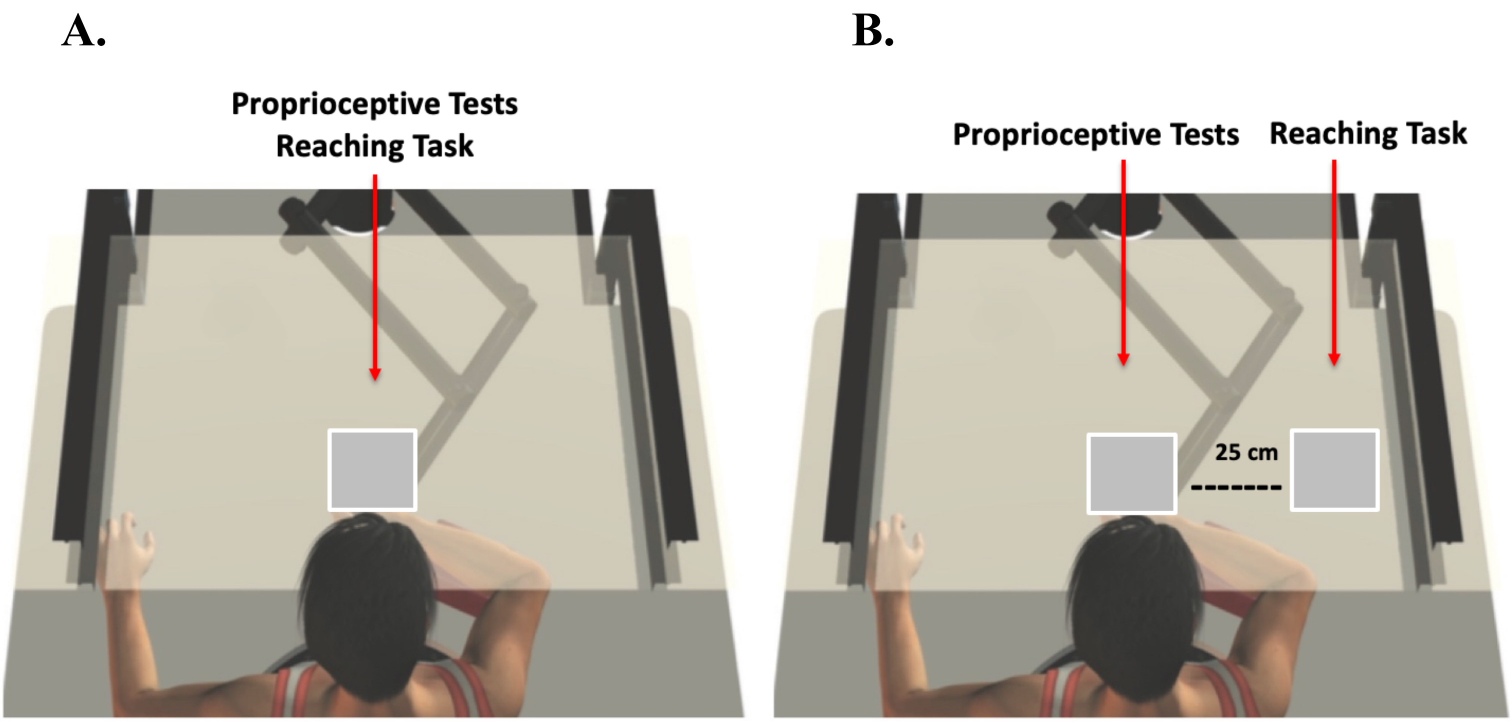

Figure 2.5 (A) Overhead view of experimental apparatus: Participants in the matched, limb-centered and world-centered groups were given the motor learning task in the center of the workspace within a 10 cm by 10 cm patch. (B) Participants in the unmatched group were given the motor learning task 25cm to the right of the center of the workspace within a 10 cm by 10 cm patch.

2.5.2 Learning measurement: Movement time

To assess changes in participants' skill, we looked at total movement time within a block as the dependent measure. Total movement time is defined as how fast it took participants to reach towards 100 targets in each block. If participants' total movement time decreases as they progress through each block, then it would indicate that participants are learning to reach faster towards the targets. Changes in movement time is calculated by comparing mean movement time difference between block 1 and block 4 for each group. For instance, participants were instructed to reach towards targets as "fast as possible" therefore, if participants engaged in motor learning, then their movement time to complete block two would be faster than their movement time to complete block one.

2.6 Movement time statistical analysis

For both Experiment 1 and 2 an analysis of variance was used to observe changes in movement time for each group with one within-subjects factor: block (1 to 4). Tukey post hoc tests were then conducted to analyze significant main effect of block and total movement time.

2.7 Learning measurement: Movement path

Participants were also asked to reach towards the targets as "accurately as possible". We therefore also measured participants accuracy when reaching towards target during motor learning. If participants were learning to reach accurately towards targets, we would expect the distance of their hand path would be equal to or relatively closer to the distance between two targets in block 4 when compared to block 1. For instance, Figure 2.7 shows one participant's hand path for movements towards the first 5 targets in block 1 and the straight line connecting each target. To calculate accuracy, we calculated the ratio (R) of the total movement path from one target to another (Dh) and the distance between each target (Dt):

$$R = Dh/Dt$$

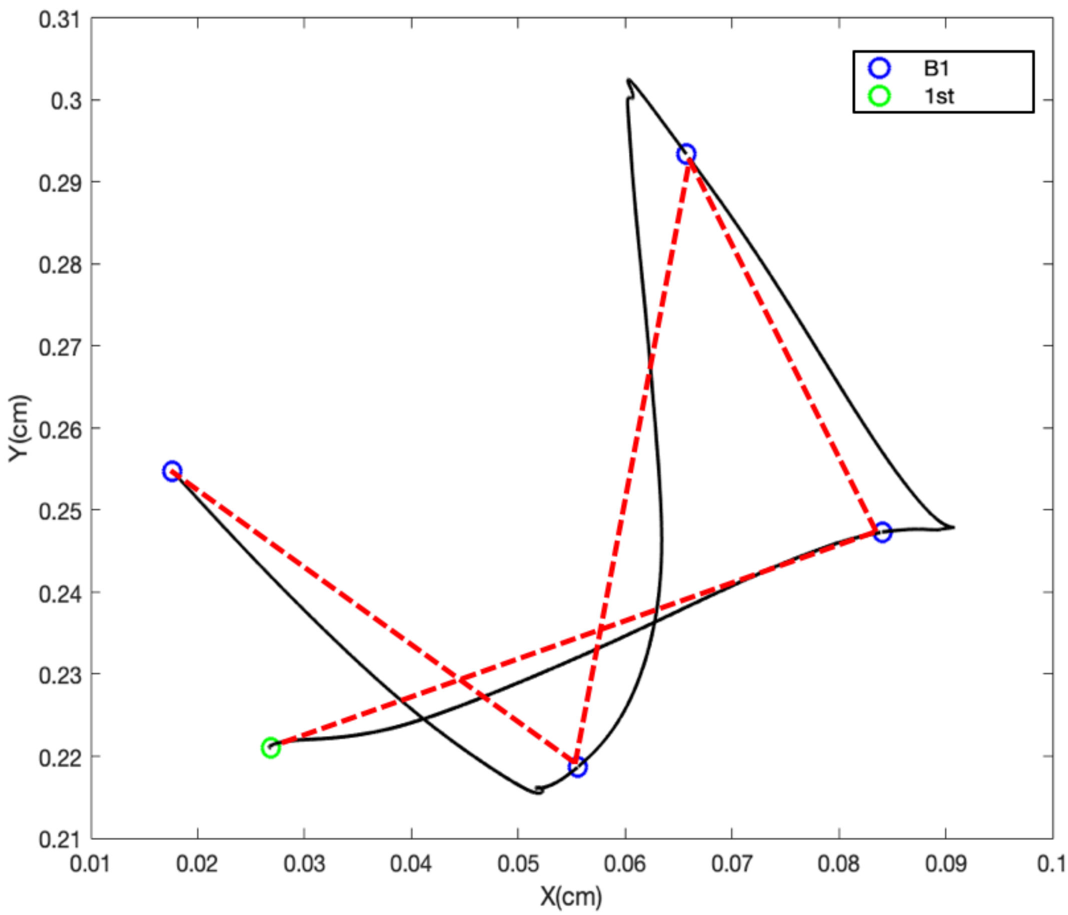

Figure 2.6. Example of one participant's hand path movements during block 1. The green circle represents the first target. The black lines denotes the participant's movements towards each target (Dh), the red dashed lines represent the straight line between each target (Dt).

2.7.1 Accuracy statistical analysis

For both Experiment 1 and 2 an analysis of variance (ANOVA) was used to test for changes in mean accuracy for each group with one within-subjects factor: block (1 through 4). Tukey post hoc tests were then conducted to analyze significant main effect of block and hand path accuracy.

Chapter 3

Results

3.1 Experiment 1

To assess if proprioceptive acuity changes that accompany motor learning are spatially specific, participants were given the proprioceptive tests and learning task in either the same location of the workspace (i.e., center of the screen) or in two different locations of the workspace (i.e., proprioceptive tests in the center of screen and the learning task 25 cm to the right of the center). Difference in post-test uncertainty range was analyzed between groups.

3.1.1 Experiment 1: Uncertainty range

The uncertainty range is inversely proportional to proprioceptive sensitivity. A split-plot analysis of variance (ANOVA) was conducted to determine changes in participants' uncertainty range with one between subjects factor: group (matched vs. unmatched), and one within-subjects factor: pre-tests vs post-tests. Smaller uncertainty ranges during the post-test compared to the pre-test would suggest proprioceptive acuity improvements following motor learning. Mean (± SE) uncertainty ranges for the pre and post proprioceptive tests are displayed in Figure 3.1A for each group. The uncertainty range was used as the dependent measure to test for proprioceptive improvements in the post-test in comparison to the pre-test. Figure 3.1A shows that although the matched group (blue) seems to be improving while the unmatched group (red) does not, there was no significant interaction between groups and block [$F(1, 28) = 0.38$, $p = 0.54$]. However, a significant main effect of test was found for the matched group [$F(1,14) = 5.27$, $p = 0.04$], but no significant main effect of test was found for the unmatched group [$F(1,14) = 0.009$, $p = 0.92$]. Additionally, participants in the matched group displayed significant changes in their mean uncertainty range (mean ± SE) in the post-test in comparison to their pre-test (-2.57 ± 1.12 mm). However, no significant difference between the pre and post-test for participants in the unmatched group was found, as there was no significant change in their mean uncertainty range (-0.12 ± 1.26 mm). The changes in the mean uncertainty range (mean ± SE) for both the matched and the unmatched group can be seen in Figure 3.1B. As such, proprioceptive acuity improved in the part of the workspace where motor learning occurred and not in a location where no motor learning occurred.

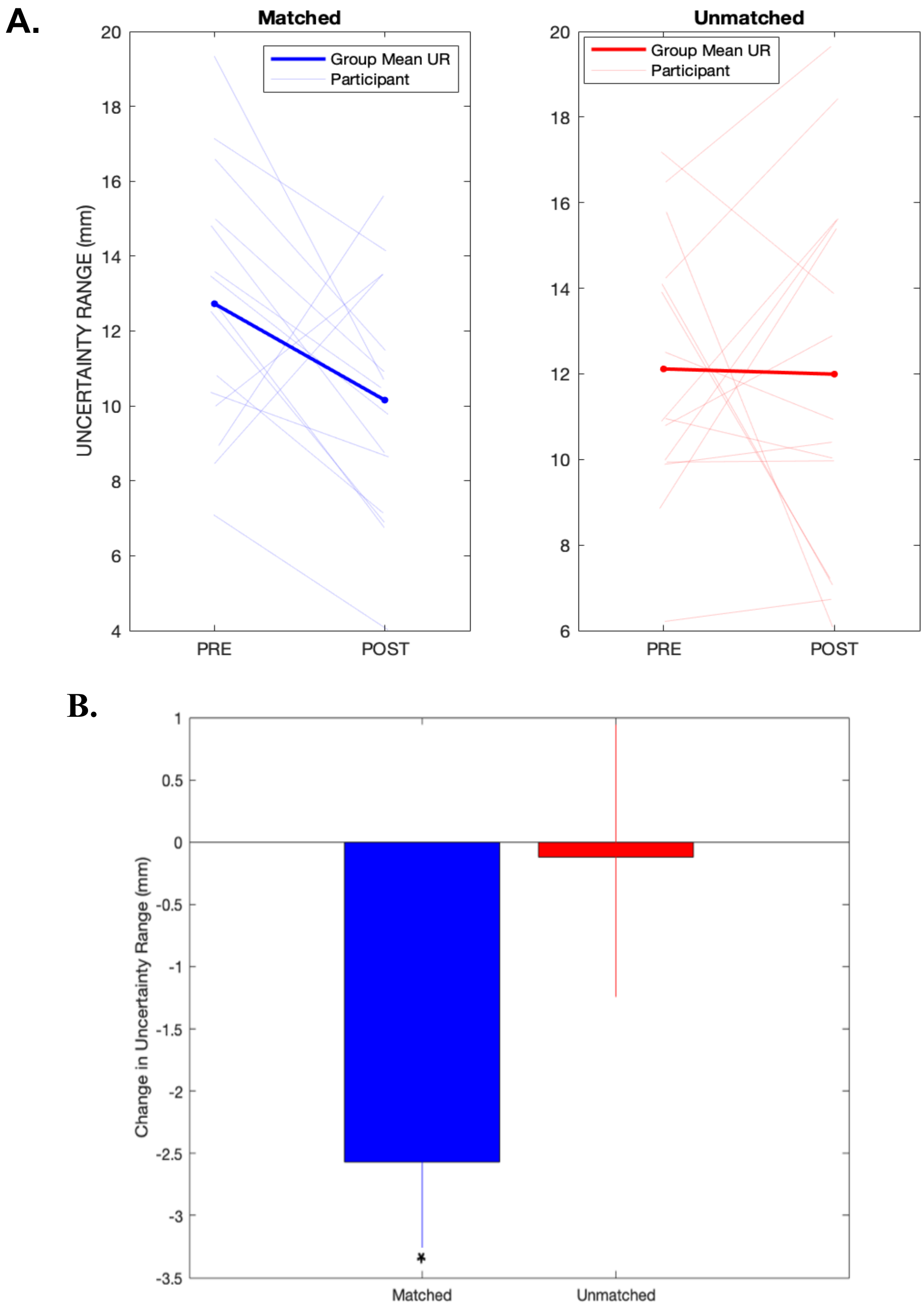

Figure 3.1. Experiment 1: Uncertainty range.(A) Participant's uncertainty range and group mean (± SE) uncertainty range during pre-test and post-test for both matched (left) and unmatched (right) groups. Uncertainty range is used to measure changes in proprioceptive acuity. (B) Change in mean uncertainty range between pre and post-tests. The matched group displays an improvement in proprioceptive acuity in comparison to the unmatched group.

3.1.2 Experiment 1: Movement time

Movement time is used to measure motor learning. Figure 3.2 displays the total time it took participants to reach to 100 targets in each block (4 blocks total). A mixed design analysis of variance (ANOVA) was calculated with one between subjects factor: group (matched vs unmatched), and one within-subjects factors: blocks (1 through 4). No significant interaction was found between groups and block [$F(3,28) = 0.68$, $p = 0.42$]. For the matched group, a significant effect of block was found for movement time [$F(3) = 6.82$, $p < .001$]. Participants in the matched group had faster total movement time in block 4 in comparison to block 1 [$t(14) = 5.65$, $p < .001$, Tukey]. A significant effect of block was found for movement time for participants in the unmatched group who were given the motor learning task 25 cm to the right of center [$F(3) = 20.57$, $p < .001$]. Post hoc tests displayed a significant difference between block 1 and block 4 [$t(14) = 4.12$, $p = 0.002$, Tukey]. Participants' total movement time in the unmatched group was less in block 4 in comparison to block 1. As such, these results display faster total movement times as participants progressed from block 1 to block 4 regardless of the testing location (i.e., center of the screen or 25 cm to the right of the center).

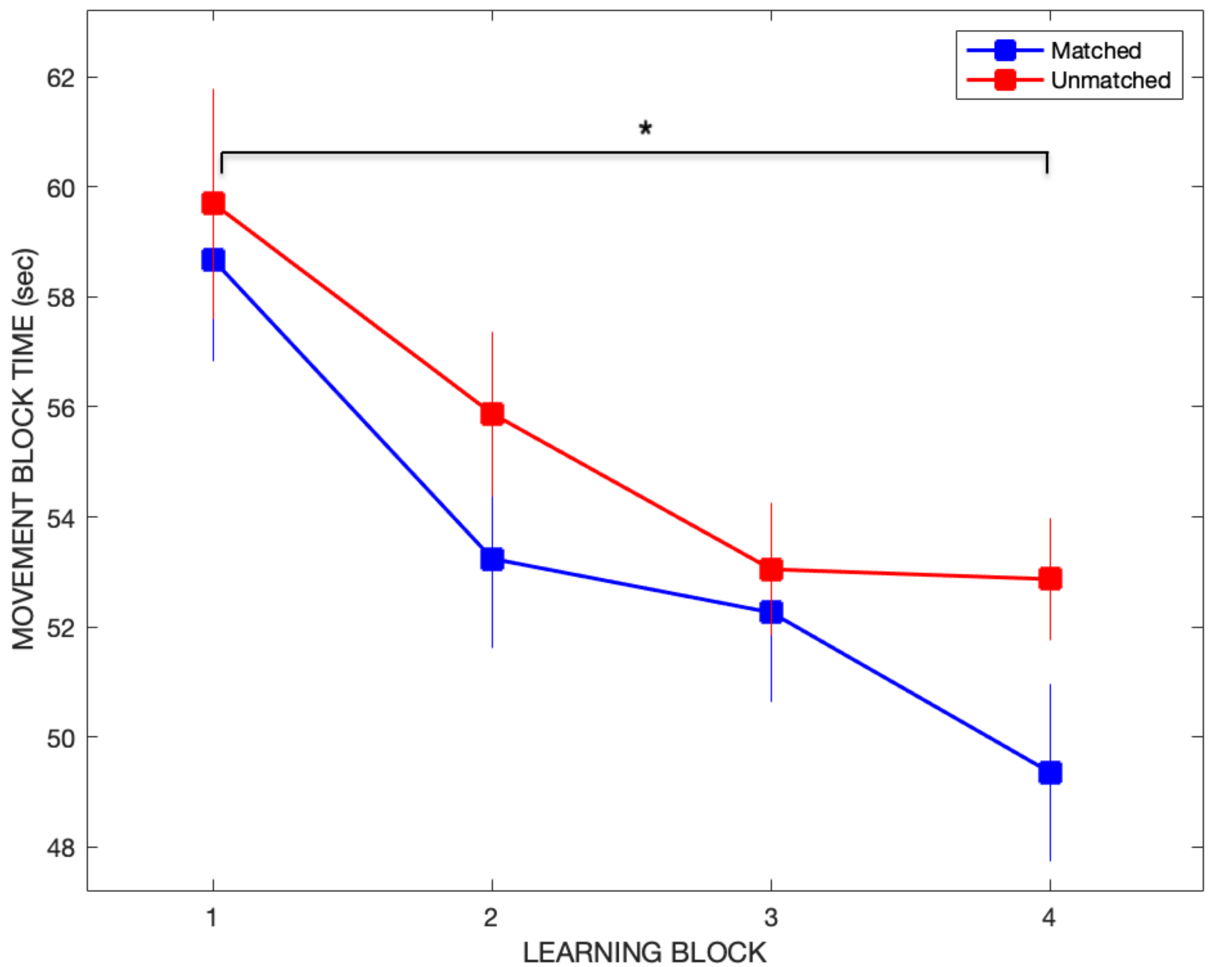

Figure 3.2. Experiment 1: Movement time. The mean (± SE) movement time it took participants to reach towards 100 random targets in each block (4 blocks total). Participants tested in the center of screen (matched group) is denoted by the blue line. Participants tested 25cm to the right of the center (unmatched group) is denoted by the red line.

3.1.3 Experiment 1: Movement path

Movement path ratio was used to measure learning as participants progressed through blocks 1 to 4. A mixed design analysis of variance (ANOVA) was used to assess changes in accuracy with one between subjects factor: group (matched vs unmatched), and one within subjects factor: blocks (block1 through block 4). No significant interaction was found between groups and block [$F(1,28) = 2.17$, $p = 0.15$]. Figure 3.3 illustrates no significant main effect of block for the matched group [$F(3) = 1.81$, $p = 0.16$] or the unmatched group [$F(3) = 1.71$, $p = 0.18$]. Therefore, participants did not change their movement accuracy.

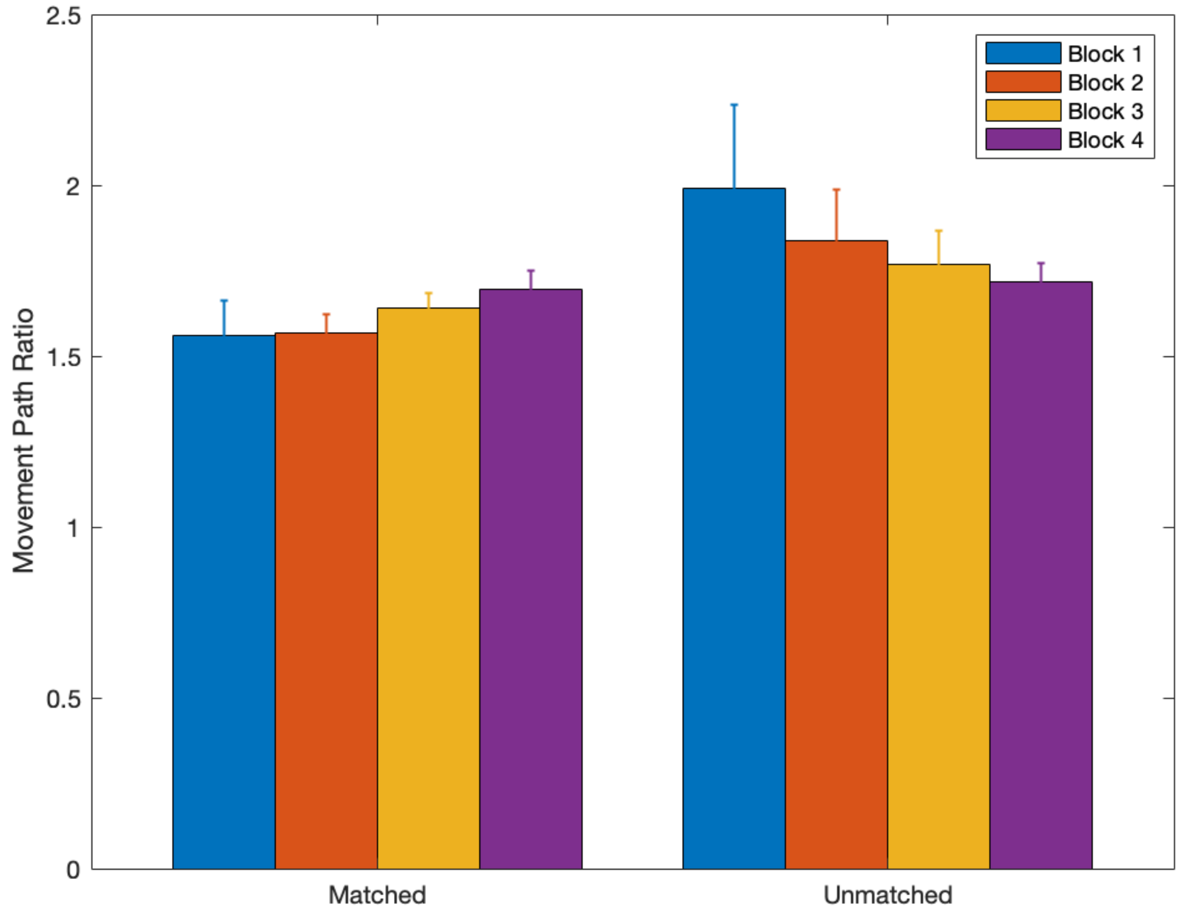

Figure 3.3. Experiment 1: Movement path. Mean (± SE) movement path participants took to reach towards targets. The blue bar represents block 1 and the orange bar represents block 4 for the matched and unmatched groups.

3.2 Experiment 2

Proprioceptive acuity changes were tested in different positions to observe if proprioceptive acuity changes occur in a limb-coordinate frame or world-coordinate frame. Both group of participants, limb-centered and world-centered coordinate frame groups, were given the initial proprioceptive test (i.e., pre-test) in the center of workspace followed by the motor learning task in the same location of the workspace. Participants in the limb-centered coordinate frame group were shifted 25 cm to the right of center and then given the proprioceptive post-test. Participants in the world-centered coordinate frame group were given the proprioceptive post-test in the center of the workspace but rotated their torso 45° from the screen.

3.2.1 Experiment 2: Uncertainty range

A split-plot analysis of variance (ANOVA) was also conducted in Experiment 2 to determine changes in participants' uncertainty range with one between subjects factor: group (limb-centered vs. world-centered coordinate frame group), and one within-subjects factor: pre-tests vs post-tests. Smaller uncertainty ranges during the post-test compared to the pre-test would suggest proprioceptive acuity improvements following motor learning. Figure 3.4A displays a clear significant interaction [$F(1,28) = 8.38$, $p = 0.01$]. A significant within subjects effect was observed within the limb-centered group [$t(14) = 4.88$, $p < .001$, Tukey]. No significant within subject effect was seen in the world-centered group [$t(14) = -0.78$, $p = 0.86$, Tukey]. Figure 3.4B shows a significant difference in mean uncertainty range (mean ± SE) between pre and post-test for participants in the limb-centered group (-4.60 ± 0.87 mm) in comparison to participants in the world-centered group who displayed no significant changes in mean uncertainty range (0.74 ± 1.01 mm). Therefore, participants' proprioceptive acuity improved when maintained the same joint angles.

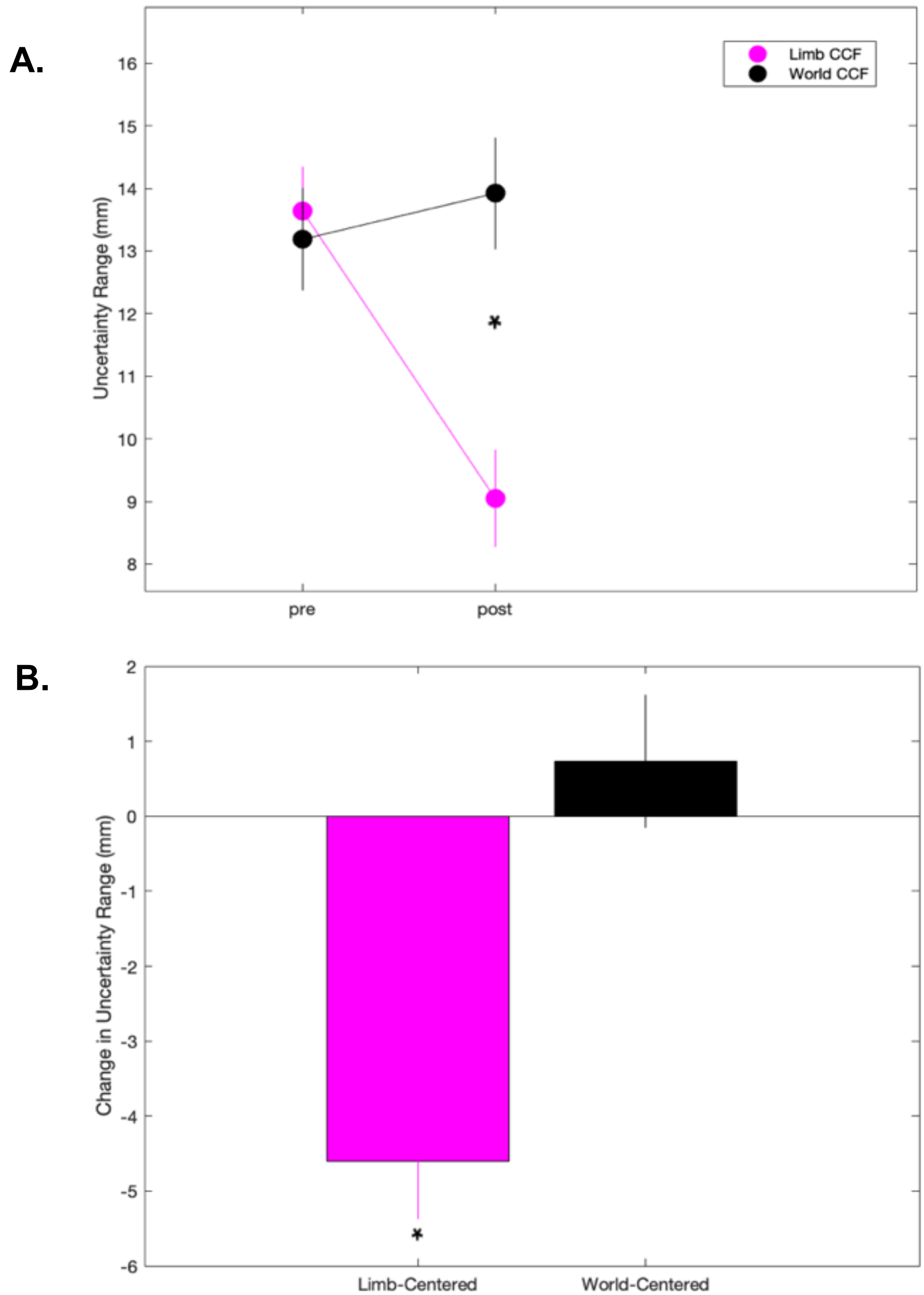

Figure 3.4. Experiment 2 : Uncertainty range.(A) Mean (± SE) uncertainty range during pre-test and post-test following motor learning for both limb-centered and world-centered coordinate frame groups. (B) Change in mean uncertainty range between pre and post-tests. The limb-centered coordinate frame group displays an improvement in proprioceptive acuity in comparison to the world-centered coordinate frame group.

3.2.2 Experiment 2: Movement time

Movement time is used to measure motor learning. Figure 3.5 displays the total time it took participants to reach to 100 random targets in each block (4 blocks total). A mixed design analysis of variance (ANOVA) was calculated with on between subjects factor: group (limb-centered vs world-centered), and one within-subjects factor: blocks (1 through 4). No significant interaction was found between groups and block [$F(3,28) = 2.08$, $p = 0.16$]. For the limb-centered coordinate frame group, a significant main effect of block was found on movement time [$F(3) = 63.26$, $p < .001$]. Post hoc tests were conducted and displayed a significant difference in participants' total movement time in block 4 in comparison to block 1 [$t(14) = 9.64$, $p <.001$, Tukey]. Moreover, participants in the world-centered coordinate frame group who also conducted the motor learning task in the center of workspace displayed similar results. A significant main effect of block was found on movement time for the world-centered coordinate frame group [$F(3) = 40.63$, $p < .001$]. Post hoc tests also displayed a significant difference between block 1 and block 4 [$t(14) = 11.36$, $p <.001$, Tukey]. Participants' total movement time in the world-centered group was less in block 4 in comparison to block 1. As such, these results clearly display that total movement time was decreasing as participants progressed from block 1 to block 4 in both groups (i.e., limb-centered coordinate and world-centered coordinate frame groups).

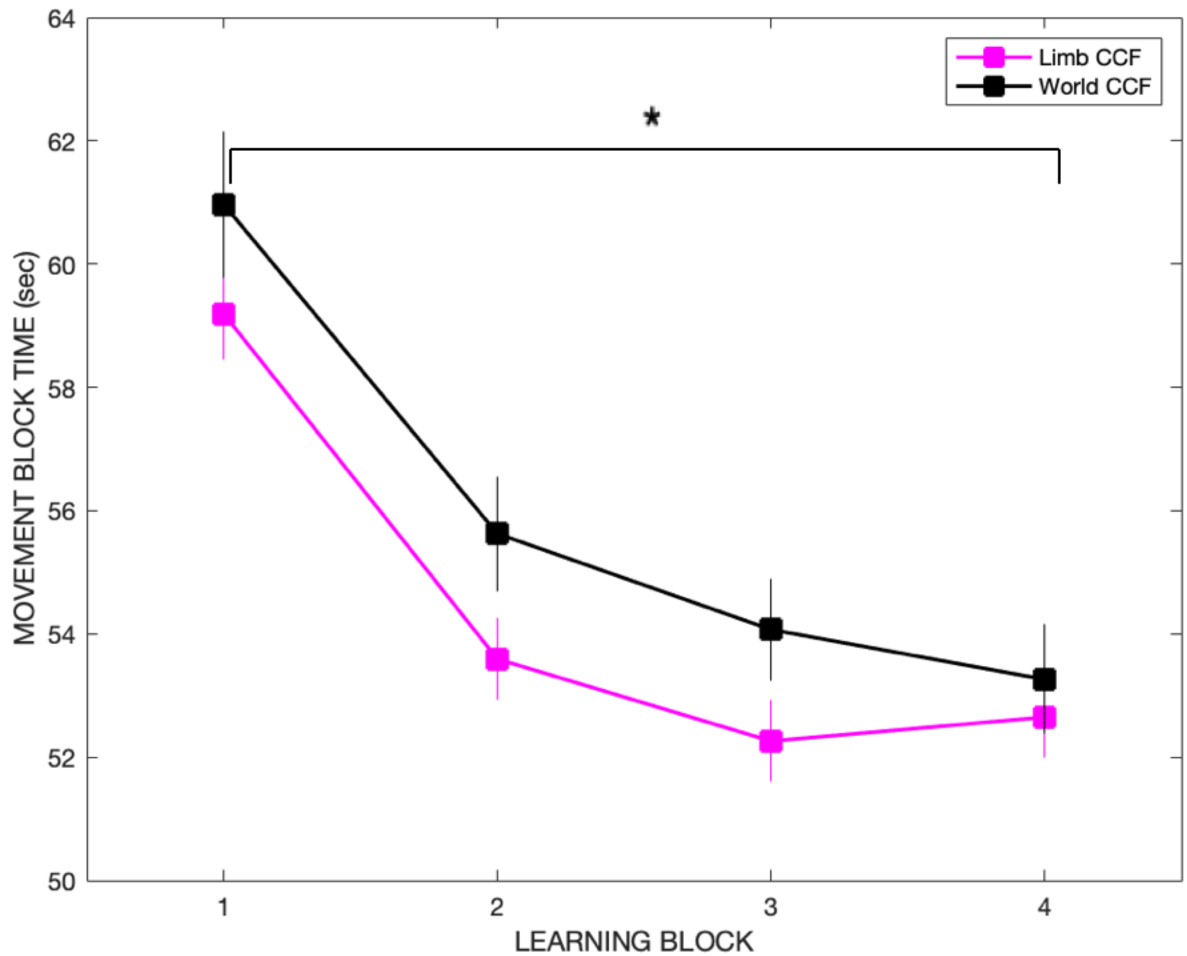

Figure 3.5. Experiment 2: Movement time. The mean (± SE) movement time it took participants to reach towards 100 random targets in each block (4 blocks total). Participants tested in the limb-centered coordinate frame group is denoted by the black line. Participants in the world-centered coordinate frame group is denoted by the purple line.

3.2.3 Experiment 2: Movement path

Movement path ratio was also used to measure learning as participants progressed through blocks 1 to 4 in Experiment 2. A mixed design analysis of variance (ANOVA) was conducted to analyze changes in accuracy with one between subjects factor: group (limb-centered vs world-centered), and one within subjects factor: blocks (block 1 through block 4). No significant interaction was found between groups and block [$F(1,28) = 0.07$, $p = 0.80$]. Figure 3.6 displays no significant main effect of block for the limb-centered group [$F(3) = 1.20$, $p = 0.32$] or the world-centered group [$F(3) = 1.52$, $p = 0.22$]. Therefore, participants did not change their movement accuracy.

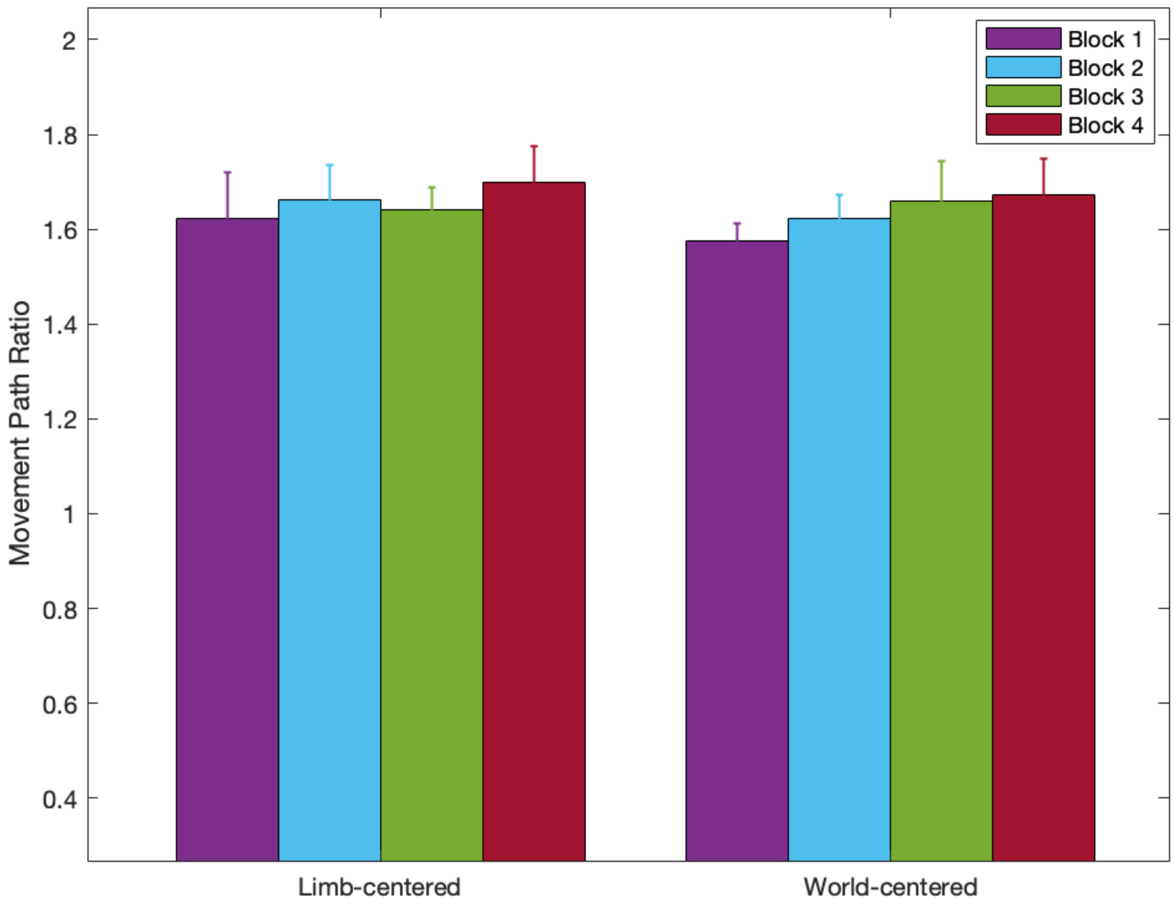

Figure 3.6. Experiment 2: Movement path. Mean (± SE) movement path participants took to reach towards targets. The purple bar represents block 1 and the red bar represents block 4 for the limb-centered and world-centered groups.

Chapter 4

Discussion

The present study investigated somatosensory changes following motor learning using proprioceptive judgment tests and a motor learning task. Experiment 1 and 2 tested proprioceptive acuity changes following motor learning within different workspace locations or within different coordinate frames.

The objective of the first experiment was to understand if proprioceptive improvements were spatially specific to motor learning. In other words, are proprioceptive acuity improvements only observed when both the perceptual tests and motor learning task are given within the same location? Significant post-test improvements were seen for participants who were given both the proprioceptive tests and learning task within the same patch of the workspace (i.e., matched group: center of the workspace) in comparison to their pre-test. As such, the results suggested that proprioceptive acuity improvements are spatially specific with motor learning.

The results from Experiment 1 led to the investigation of understanding why improvements were only seen in the matched group and not the unmatched group who were given the proprioceptive tests in the center of the workspace and the learning task 25 cm to the right of the center. Experiment 2 thus investigated whether proprioceptive acuity changes occurred within an intrinsic or extrinsic coordinate frame following learning. The results displayed significant proprioceptive improvements for participants who maintained the same joint angles, following learning (i.e., limb-centered coordinate frame group). In contrast, no improvements were observed for participants who maintained the same hand displacement but altered their joint angles (i.e., world-centered coordinate frame group). Therefore, from these results we can suggest that improvements in proprioceptive acuity occur in a limb-coordinate frame of joints and muscles, following motor learning.

4.1 Proprioceptive improvements following learning

The results from Experiment 1 align with the idea that motor learning results not only in changes in our motor cortex but also changes in our sensory system (Ostry et al., 2010). Participants in

Experiment 1 were given the motor learning task following the initial proprioceptive test given at the beginning of study as a baseline measure. Participants displayed significant improvements in proprioceptive acuity following motor learning within the matched group in comparison to the unmatched group who did not display proprioceptive improvements. Experiment 1 results therefore suggest that proprioceptive acuity is improved following learning.

Similarly to the current study, participants in a study conducted by Wong et al. (2011) were given a reaching task and displayed significant improvements in proprioceptive acuity in comparison to the control group. The control group in their study were given a proprioceptive test at the beginning of the study as a baseline measure and then a post proprioceptive test at the end of the study, but they were not given the learning task (instead they were asked to read for the duration of a given time). Their results thus suggested that proprioceptive acuity improvements were associated with motor learning, consisting with the results from Experiment 1 of our study.

Improvements in proprioceptive acuity following learning can be explained by the strong intercortical connection between the motor cortex and somatosensory cortex. Vahdat et al. (2011) indicated changes within the somatosensory cortex following motor learning using functional magnetic resonance imagining (fMRI) in which participants were given a reaching task and then scanned during a resting state followed by a perceptual test. Functional connectivity changes were displayed in motor and sensory brain areas that occurred in conjunction with motor learning. Changes within the sensory networks following learning reported by Vahdat et al. (2011) have also been shown to play a role in perception during a sensory learning task (Bernardi, Darainy & Ostry, 2015; de Lafuente & Romo 2006).

Proprioceptive sense of limb position has also been observed within force field adaptation studies in which somatosensory changes are seen to be associated to motor learning (Nasir et al., 2013). These studies give a neurophysiological outlook on the association between proprioception and motor learning and further strengthen the observed results from Experiment 1 of our study in which participants within the matched group displayed proprioceptive acuity improvements.

In support of the evidence stated above, Mirdamadi and Block (2020b) displayed changes in somatosensory function following a complex motor learning task. Mirdamadi and Block (2020b) described a motor learning task as complex when it requires participants to make changes in their joint angles during the execution of a movement pattern, thus making it kinematically harder, in comparison to a straight reaching task that does not require participants to make changes in their joint angles as they reach towards targets. Participants' judgment of hand position in relation to a reference target improved following learning thus behaviourally, proprioceptive acuity improvements were found to be associated to motor learning. With the use of transcranial magnetic stimulation (TMS) they were also able to report enhanced connections between the motor and somatosensory cortex. This suggests that proprioceptive improvements may be modulated by somatosensory changes, following learning. In sum, the results strongly suggest proprioceptive improvements occur following motor learning which defends our claim that proprioceptive improvements are associated to motor learning as also seen by our results from Experiment 1 of our study.

4.2 Spatially Specific Improvements

In Experiment 1 of the current study, proprioceptive improvements were only seen within the matched group following motor learning. Participants only displayed improvements in sensing limb position when both the proprioceptive tests and motor learning task were given within the same location of the workspace. In contrast, improvements were not seen within the unmatched group (i.e., given the proprioceptive tests in the center of the workspace and the learning task 25 cm to right of the center). As such it may be argued that proprioceptive improvements are not associated to motor learning. However, the unmatched group was given the motor learning task within a different location of the workspace than the proprioceptive test. We can thus infer from these results that proprioceptive acuity improvements are spatially specific to motor learning.

Previous studies have displayed similar results in which proprioceptive acuity improvements were seen when both the proprioceptive tests and motor learning task were given within the same patch of the workspace. The study mentioned earlier conducted by Mirdamadi and Block (2020b) displayed proprioceptive changes following motor learning. However, it should be noted that the complex reaching task and proprioceptive tests were given within the same location of the workspace. As such, spatial specificity may have been a contributing factor to their observed improvements.

Experiment 1 of the current study is a replication of the Wong et al. (2011) study who first suggested proprioceptive acuity improvements to be spatially specific to motor learning. The study conducted by Wong and colleagues (2011) uses almost an identical judgment and motor learning task. Participants within the Wong study (2011) were given the proprioceptive tests and motor learning task within the same location of the workspace (i.e., matched groups) or the proprioceptive tests in a different location than the motor learning task within the workspace (i.e., unmatched groups).

The results from Wong et al. (2011) displayed significant proprioceptive acuity improvements when the judgment tests and learning task were given within the same location of the workspace which suggests proprioceptive changes and motor learning are spatially specific, consisting with the results from Experiment 1 of our study. However, it should be noted that participants in the unmatched group in the current study and in the Wong et al. (2011) study, had altered both their hand displacement and joint angles. As such, the unobserved improvements within the unmatched group may be explained by other contributing factors such as changes in coordinate frames, which is discussed below. Nonetheless, we can still suggest that motor learning is associated to improvements in proprioceptive acuity.

4.3 Speed-accuracy trade-off

In both Experiment 1 and 2 participants displayed faster movement times in which their reaches towards 100 targets were much faster in block 4 in comparison to block 1.

Fitts (1954) first suggested that the distance between targets and the width of the targets contribute to movement time. For instance, larger targets that are relatively closer to each other require shorter movement times. However, to counteract this, the targets within motor learning of the current experiment were randomly placed within a 10 by 10 cm patch of the workspace, 7mm in size and were at least 5cm apart from each other. As such, faster movement times seen in both

Experiment 1 and 2 were a result of participants learning to reach faster towards the targets and not due other factors such as bigger targets or shorter distance between the targets.

It has previously been suggested that faster movement speeds may be associated with a loss in movement accuracy which is described as speed-accuracy trade-off (Fitts, 1954; Nagengast, Braun & Wolpert, 2011). The speed-accuracy trade-off idea may explain the results that were seen in both Experiment 1 and 2 in which participants displayed faster movement times (i.e., speed), but no changes in their hand path movements (i.e., accuracy).

Dean et al. (2007) examined speed-accuracy trade-off using a goal directed task in which participants were either rewarded for their movement time towards a target (i.e., faster time means greater reward) or their accuracy (i.e., better accuracy means greater reward). They found that participants speed-accuracy trade-off was dependent on the goal of the condition. In other words, it likely that when gain is higher for speed, accuracy is decreased and vice versa. This may also explain the results from the current study. Although there was no difference in gain between speed and accuracy as participants were simply directed to reach "as accurately and fast as possible towards each target", participants were only given verbal feedback about their movement time but no feedback about their accuracy. Giving participants feedback about their movement time but not their accuracy may have influenced participants to focus more on reaching faster towards the targets rather than reaching fast and accurately towards the targets. Ultimately this may have led to a speed-accuracy trade-off, explaining the findings of our study.

It can however, still be argued that participants were learning as improvements in movement time have been used as clear indication of motor learning (Wong et al., 2011) and these improvements were seen in both Experiment 1 and 2 of our study (i.e., block 4 movement times were faster than block 1 movement times).

4.4 Somatosensory changes within coordinate frames

In Experiment 2 we measured proprioceptive improvements following motor learning within intrinsic and extrinsic coordinate frames. Participants who maintained the same joint angles during the post proprioceptive test (i.e., limb-centered coordinate frame group) displayed proprioceptive acuity improvements in comparison to their baseline proprioceptive measure.

However, participants who shifted their joint angles (i.e., world-centered coordinate frame group) during the post proprioceptive test did not display proprioceptive improvements in comparison to their baseline proprioceptive measure. We therefore can suggest that proprioceptive acuity may be attributed to changes within the somatosensory cortex occurring within an intrinsic coordinate frame, following motor learning.

Our findings from Experiment 2 may be supported by the idea that proprioceptive improvements are accompanied by motor learning (Mirdamadi & Block, 2020a,b; Wong et al., 2011) and that these improvements occur in limb-centered coordinate frame since motor learning is believed to occur in limb-centered coordinate frame (Scott & Kalaska, 1997; Hwang & Shadmehr, 2005; Orban de Xivry et al., 2011).

Kakei et al. (2003) recorded neuronal activity in trained monkeys during a motor learning task in both the motor cortex (M1) and the ventral premotor cortex (PMv) and both brain regions are believed to play a part in sensorimotor transformation (i.e., transforming sensory input into motor output). Wrist movements were tested in intrinsic coordinate frame (by observing the activity of muscles and wrist joint) and extrinsic coordinate frame (observing movement in space). The monkeys were instructed to reach towards eight different targets evenly spaced in the workspace. Their results revealed that PMv neurons were primarily activated during movement in space, suggesting that these neurons were strongly associated to extrinsic coordinate frame. In contrast, M1 neurons varied in activity throughout the task; some M1 neurons were activated in extrinsic coordinate frame while other M1 neurons were activated in intrinsic coordinate frame. Their results therefore suggest that M1 neurons may encode motor movements in both types of coordinate frames. However, this would not explain the results from Experiment 2 of our study. As discussed earlier, proprioceptive acuity improvements are observed following motor learning (Wong et al., 2011), and this may be a result of somatosensory changes being modulated by increased activity of M1 neurons (Haswell et al., 2009), thus from Kakei et al (2003) study one may assume that proprioceptive improvements would also occur in both coordinate frames. But this was not the case in our study as participants in the limb-centered group displayed proprioceptive improvements and participants in the world-centered group did not. It could therefore be assumed that the proprioceptive improvements observed in Experiment 2 may have been associated to changes in the somatosensory cortex that were modulated by specific M1 neurons that are activated in intrinsic coordinate frame.

In contrast to Kakei et al. (2003) findings, increased motor cortex cell activity has been suggested to occur within intrinsic rather than extrinsic coordinate frames. Scott and Kalaska (1997) investigated M1 cell activity in rhesus monkeys during a reaching task. The task required the trained monkeys to make reaching movements towards eight different visual guided targets within the workspace. The reaches were either performed in a natural arm orientation in which the hand, elbow and shoulder were all aligned during the movements, or in an abducted arm orientation in which the joint angles were altered during the reaching movements. It should be noted that the hand paths of these reaches were similar and only orientation of the arm was different. Throughout the experiment they measured motor cortex (M1) cell activity changes, electromyographic (EMG) signals and hand trajectories. Their results displayed significantly increased activity of M1 cells during and even after reaching movements. Greater M1 cell discharge was also found when the arm would change its orientation during the movements (i.e., natural to abduction). The evidence from their study therefore suggests that motor cortex changes occur as a result of increased M1 cell activity during reaching movements in an intrinsic coordinate frame. The findings from their study bolsters the idea that motor cortex changes occur in an intrinsic coordinate frame, rather than extrinsic, which may further suggest that proprioceptive acuity improvements accompanied by motor learning may also occur within intrinsic rather extrinsic coordinate frames. This idea also aligns with results found in Experiment 2 of the current study.

Somatotopic representations of the whole-body within space occur within the somatosensory and motor cortex and the somatosensory cortex receives information from joint and muscle afferents which also project to the motor cortex (McCloskey, 1978; Burges et al., 1982). Representations of the whole-body may be encoded by different reference frames when coding motor and sensory spaces. With respect to the current study, participants' hand and arm position was shifted across the workspace (left and right axis), and the arm muscles originate within the shoulder. It is thus possible that during motor learning and the proprioceptive tests, sensory and motor spaces were coded in the coordinates of the shoulder muscles and joint angles. This idea would align with the results of current study since improvement were observed when participants maintained the same joint angles (i.e., limb-centered coordinate group) in contrast to participants who had altered their joint angles (i.e., world-centered coordinate group).

4.5 Passive vs active proprioception

During both Experiment 1 and 2, participants were given proprioceptive tests such that their passive limb was moved from the reference target to a distractor target and then to a judgment target on a horizontal axis (left-right). During passive limb movements the muscle is relaxed and therefore fusiform activity from muscle spindles may be diminished (Han et al., 2016; McCloskey, 1978). As a result, during passive movements sensory feedback may not rely on muscle spindles or joint receptors but rather cutaneous receptors (Han et al., 2016). In contrast, active proprioception (e.g., matching task) uses muscle spindles and greater fusimotor drive and thus active movements result in better proprioceptive acuity (Gandevia, McCloskey & Burke, 1992). It may therefore be argued that during our study participants may have relied more on cutaneous receptors rather than joint receptors and muscle spindles.

Although passive movements are posed as more reliant on cutaneous receptors rather than joint receptors and muscles spindles (Han et al., 2016; McCloskey, 1978), this may not be completely true. Specifically, during our proprioceptive tests participants are moved to random distractors that are at least 6 cm away from the reference target. This would lead to participants stretching their muscles as the robotic handle moves their limb from the reference to a distractor target. When the muscle is being stretched spindle firing is increased, and spindle firing is especially influenced by greater joint angle changes (McCloskey, 1978). The stretch would therefore utilize both their muscle spindles and joint receptors. Likewise, the judgment targets were also placed at close (0.3 cm) and further distances (1.3 cm and 3.7 cm) to left or right of the reference. The judgement targets further from the reference would have also stretched, to a certain degree, the participants muscles, in turn signalling muscle spindles and joint receptors. Closer judgement targets may have resulted in utilizing more cutaneous receptors but this cannot be concluded due to no physiological changes being measured.

Additionally, in Experiment 2 results only displayed significant proprioceptive improvements for participants who maintained the same limb and joint angles (limb-centered group) but no improvements were found with participants who had altered their limb and joint angles (world-centered group). If cutaneous receptors were the primary source of sensory feedback during the proprioceptive tests, then both groups would have displayed improvements, regardless if their limb and joint angles remained the same or were altered, but this was not the case. Therefore, although the proprioceptive tests used passive limb movements, muscle spindles and joint receptors must have also played a role in sensory feedback.

4.6 Additional contributing factors

As the current study investigates somatosensory changes within different coordinate frames and is measured proprioceptive tests and a learning task, factors that may influence task outcome should also be discussed.

In both Experiment 1 and 2, participants were required to verbally state the position of their hand (i.e., left or right) with respect to the reference target. Since participants were also required to keep their eyes closed, the task did not use any visual stimuli and thus was dependent on proprioception but also on working memory. Working memory is one's ability to first process and then recall information (Goble, Mousigian & Brown, 2011), during the task participants needed to remember where their hand position started and in which direction (left or right) it was shifted from the reference target. Working memory changes throughout our lifespan, specifically as we get older, and the decline of memory may also play a role in decreased proprioceptive sense (Goble et al., 2009; Goble, Noble & Brown, 2010). It is thus difficult to conclude that performance error was solely the result of proprioceptive estimation and not memory recall. Future studies may therefor consider using memory tests as an independent assessment of memory.

The present study displayed an association between our sensory and motor networks for which proprioceptive acuity improvements were observed following motor learning and these improvements were significant within a limb-centered coordinate frame when compared to world-centered coordinate frame. However, the current study is based on behavioural tests, future studies may conduct similar experiments using neurophysiological evidence (e.g., EEGs).

This would further deepen our understanding of sensory changes within different coordinate frames on a cortical level, giving more specific conclusions.

Additionally, no improvements were seen for the world-centered coordinate group as they were rotated 45° from the screen which altered their limb and joint angles. We could therefore conclude that somatosensory changes must occur within a limb-centered coordinate frame. One question may arise is, were improvements not seen due to the degree the limb and joint angles were rotated? Given that joint and muscle receptors play an important role in proprioceptive limb sense (Burges et al., 1982; Clark et al.,1975), an interesting investigation may be to rotate participants at different limb and joint angles (e.g., 25°, 45°, 90°, etc.) and observe whether there are differences in proprioceptive performance within different coordinate frames. For instance, if performance is improved at a 25° rotation but not seen at a 45° rotation it could suggest that somatosensory changes may possibly also occur in extrinsic coordinates but were not seen within the current study due to greater rotations of joints and stretch of the muscles. Future studies may therefore test joint and limb changes within different coordinate frames to disassociate whether these changes influence proprioceptive performance.

4.7 Limitation

In both Experiment 1 and 2 the same motor learning task was given to participants. Movement time was used as a dependent measure for learning. Participants were required to reach towards different targets within each block, although participants displayed faster movement times, only 4 blocks were given. The limited number of blocks given may not show an accurate representation of learning. For instance, if participants were given a 5th block would we observe faster movement times or would participants stay at the same speed? If participants stay at the same speed (i.e., their movement time does not progress), it would suggest that they have reached their peak movement time and cannot physically reach faster. This can be seen as a limitation for future replication studies. If we, or any other study, wanted to replicate the current findings of the present whilst also observing changes in learning within different coordinate frames movement time may not be a display an accurate representation of changes in learning because, as discussed previously, participants may have reached their peak.

Additionally, during the proprioceptive tests in both experiments, participants were presented with a reference target and held stationary at the reference target for only 2 seconds. Previous findings have suggested that proprioceptive acuity is influenced by the duration of target presentation. Globe et al. (2010) conducted a study using a memory based joint position matching. Participants' right elbow were passively moved to a target 20º or 40º from the start position and were held at the target for a long (12 seconds) or short (3 seconds) period of time. Participants passive elbow was then brough back to the starting position, and were then asked to match the previously remembered joint angle. Regardless of the target position (i.e., 20º or 40º), participants who were in the long condition (i.e., held at the target for 12 seconds) displayed less error matching in comparison to participants in the short condition (i.e., held at the target for 3 seconds). Their overall result suggests that longer delays at a target contribute to more accurate representations of limb position. In the current study, participants were presented with the reference target for a short period of time (2 seconds), as such the error in proprioceptive acuity may have been attributed by target presentation time.

In Experiment 2 of the study, we rotated participants' torso 45° from the screen in the world-centered coordinate group. As explained within the methods section, we used a customized protractor and lined tape on the floor to measure the rotation. This can be seen as a limitation as we cannot confidently concluded that participants maintained the exact position when they were given the post proprioceptive test. However, participants angles were re-measured following the completion of the proprioceptive test to make sure they did not completely shift back to their original position. An alternative way to measure rotations is by using a motion tracker (e.g., OptiTrack, flock-of-birds, etc.). Due to the time constraints of the study (i.e., COVID) we were unable to use a motion tracker but it would be advised for future studies to use this technique as it would provide better measures.

4.8 Implications

Proprioception is imperative to understand as it plays an important role in our everyday life by informing our central nervous system of our body in space and limb changes. Sensory feedback is vital for neural plasticity and proprioception is suggested to be the most informative and important sensory feedback involved in neural plasticity (Burges et al., 1982; Goble, 2010). Loss of proprioception (e.g., peripheral neuropathy) leads to deficits in attaining new motor skills (Pavlides et al., 1993; Sakamoto, 1989; Vidoni et al., 2010) and motor movements (Yousif, Cole, Rothwell & Diedrichsen, 2015).

The findings from our study are important as it aids in understanding the role of proprioception and how it is influenced by motor learning. A key, more novel finding, from our study is how different coordinate frames attribute to changes within our somatosensory cortex. Our understanding of the changes that occur within the somatosensory cortex in different coordinate frames, intrinsic vs extrinsic, is limited and not clearly understood. The results from this study gives us a better understanding on the how our somatosensory cortex builds different sensory representations in intrinsic and extrinsic coordinate frames.

References

Andersen, R. A., Snyder, L. H., Li, C.-S., & Stricanne, B. (1993). Coordinate transformations in the representation of spatial information. *Current Opinion in Neurobiology*, *3*(2), 171–176. https://doi.org/10.1016/0959-4388(93)90206-e

Andrew, D., Haavik, H., Dancey, E., Yielder, P., & Murphy, B. (2015). Somatosensory evoked potentials show plastic changes following a novel motor training task with The thumb. *Clinical Neurophysiology*, *126*(3), 575–580. https://doi.org/10.1016/j.clinph.2014.05.020

Belen, J. G., & Weingarden, S. I. (1988). Posterior central cord syndrome following a hyperextension injury: Case report. *Spinal Cord*, *26*(3), 209–211. https://doi.org/10.1038/sc.1988.33

Bernardi, N. F., Darainy, M., & Ostry, D. J. (2015). Somatosensory contribution to the initial stages of Human Motor Learning. *Journal of Neuroscience*, *35*(42), 14316–14326. https://doi.org/10.1523/jneurosci.1344-15.2015

Berniker, M., Franklin, D. W., Flanagan, J. R., Wolpert, D. M., & Kording, K. (2014). Motor learning of novel dynamics is not represented in a single global coordinate system: Evaluation of mixed coordinate representations and local learning. *Journal of Neurophysiology*, *111*(6), 1165–1182. https://doi.org/10.1152/jn.00493.2013

Brodie, S. M., Meehan, S., Borich, M. R., & Boyd, L. A. (2014). 5 Hz repetitive transcranial magnetic stimulation over the ipsilesional sensory cortex enhances motor learning after stroke. *Frontiers in Human Neuroscience*, *8*. https://doi.org/10.3389/fnhum.2014.00143

Burgess, P. R., Wei, J. Y., Clark, F. J., & Simon, J. (1982). Signaling of kinesthetic information by peripheral sensory receptors. *Annual Review of Neuroscience*, *5*(1), 171–188. https://doi.org/10.1146/annurev.ne.05.030182.001131

Burton, H., & Fabri, M. (1995). Ipsilateral intracortical connections of physiologically defined cutaneous representations in areas 3b and 1 of macaque monkeys: Projections in the vicinity of the Central sulcus. *The Journal of Comparative Neurology*, *355*(4), 508–538. https://doi.org/10.1002/cne.903550404

Byl, N. N., Merzenich, M. M., Cheung, S., Bedenbaugh, P., Nagarajan, S. S., & Jenkins, W. M. (1997). A primate model for studying focal dystonia and repetitive strain injury: Effects on the primary somatosensory cortex. *Physical Therapy*, *77*(3), 269–284. https://doi.org/10.1093/ptj/77.3.269

Caminiti, R., Johnson, P. B., & Urbano, A. (1990). Making arm movements within different parts of space: Dynamic Aspects in the primate motor cortex. *The Journal of Neuroscience*, *10*(7), 2039–2058. https://doi.org/10.1523/jneurosci.10-07-02039.1990

Clark, F. J., & Burgess, P. R. (1975). Slowly adapting receptors in cat knee joint: Can they signal joint angle? *Journal of Neurophysiology*, *38*(6), 1448–1463. https://doi.org/10.1152/jn.1975.38.6.1448

Cohen, Y. E., & Andersen, R. A. (2002). A common reference frame for movement plans in the posterior parietal cortex. *Nature Reviews Neuroscience*, *3*(7), 553–562. https://doi.org/10.1038/nrn873

Criscimagna-Hemminger, S. E., Donchin, O., Gazzaniga, M. S., & Shadmehr, R. (2003). Learned dynamics of reaching movements generalize from dominant to nondominant arm. *Journal of Neurophysiology*, *89*(1), 168–176. https://doi.org/10.1152/jn.00622.2002

Darian-Smith, C., Darian-Smith, I., Burman, K., & Ratcliffe, N. (1993). Ipsilateral cortical projections to areas 3A, 3B, and 4 in the macaque monkey. *The Journal of Comparative Neurology*, *335*(2), 200–213. https://doi.org/10.1002/cne.903350205

Dean, M., Wu, S.-W., & Maloney, L. T. (2007). Trading off speed and accuracy in Rapid, goal-directed movements. *Journal of Vision*, *7*(5), 10. https://doi.org/10.1167/7.5.10

de Lafuente, V., & Romo, R. (2006). Neural correlate of subjective sensory experience gradually builds up across cortical areas. *Proceedings of the National Academy of Sciences*, *103*(39), 14266–14271. https://doi.org/10.1073/pnas.0605826103

Edin, B. B., & Johansson, N. (1995). Skin strain patterns provide kinaesthetic information to the human central nervous system. *The Journal of Physiology*, *487*(1), 243–251. https://doi.org/10.1113/jphysiol.1995.sp020875

Fitts, P. M. (1954). The information capacity of the human motor system in controlling the amplitude of movement. *Journal of Experimental Psychology*, *47*(6), 381–391. https://doi.org/10.1037/h0055392

Gandevia, S., McCloskey, D., & Burke, D. (1992). Kinaesthetic signals and muscle contraction. *Trends in Neurosciences*, *15*(2), 62–65. https://doi.org/10.1016/0166-2236(92)90028-7

Ghez, C., Krakauer, J.W., Sainburg, R.L., Ghilardi M-F (2000). Spatial representations and internal models of limb dynamics in motor learning. *The new cognitive neurosciences,* 501-514

Goble, D. J., & Brown, S. H. (2009). Dynamic proprioceptive target matching behavior in the upper limb: Effects of speed, task difficulty and arm/hemisphere asymmetries. *Behavioural Brain Research, 200*(1), 7-14. doi:10.1016/j.bbr.2008.11.034

Goble, D. J. (2010). Proprioceptive acuity assessment via joint position matching: From basic science to general practice. *Physical Therapy*, *90*(8), 1176–1184. https://doi.org/10.2522/ptj.20090399

Goble, D. J., Mousigian, M. A., & Brown, S. H. (2011). Compromised encoding of proprioceptively determined joint angles in older adults: The role of working memory and attentional load. *Experimental Brain Research*, *216*(1), 35–40. https://doi.org/10.1007/s00221-011-2904-8

Goble, D. J., Noble, B. C., & Brown, S. H. (2010). Where was my arm again? memory-based matching of proprioceptive targets is enhanced by increased target presentation time. *Neuroscience Letters*, *481*(1), 54–58. https://doi.org/10.1016/j.neulet.2010.06.053

Grefkes, C., & Fink, G. R. (2005). Review: The Functional Organization of the intraparietal sulcus in humans and Monkeys. *Journal of Anatomy*, *207*(1), 3–17. https://doi.org/10.1111/j.1469-7580.2005.00426.x

Grigg, P., & Greenspan, B. J. (1977). Response of primate joint afferent neurons to mechanical stimulation of knee joint. *Journal of Neurophysiology*, *40*(1), 1–8. https://doi.org/10.1152/jn.1977.40.1.1

Han, J., Waddington, G., Adams, R., Anson, J., & Liu, Y. (2016). Assessing proprioception: A critical review of methods. *Journal of Sport and Health Science*, *5*(1), 80–90. https://doi.org/10.1016/j.jshs.2014.10.004

Haswell, C. C., Izawa, J., Dowell, L. R., Mostofsky, S. H., & Shadmehr, R. (2009). Representation of internal models of action in the autistic brain. *Nature Neuroscience*, *12*(8), 970–972. https://doi.org/10.1038/nn.2356

Hwang, E. J., & Shadmehr, R. (2005). Internal models of limb dynamics and the encoding of Limb State. *Journal of Neural Engineering*, *2*(3). https://doi.org/10.1088/1741-2560/2/3/s09

Iandolo, R., Squeri, V., De Santis, D., Giannoni, P., Morasso, P., & Casadio, M. (2015). Proprioceptive bimanual test in intrinsic and extrinsic coordinates. *Frontiers in Human Neuroscience*, *9*. https://doi.org/10.3389/fnhum.2015.00072

Kakei, S., Hoffman, D. S., & Strick, P. L. (2003). Sensorimotor transformations in cortical motor areas. *Neuroscience Research*, *46*(1), 1–10. https://doi.org/10.1016/s0168-0102(03)00031-2

Kargo, W. J., & Nitz, D. A. (2004). Improvements in the signal-to-noise ratio of motor cortex cells distinguish early versus late phases of Motor Skill Learning. *Journal of Neuroscience*, *24*(24), 5560–5569. https://doi.org/10.1523/jneurosci.0562-04.2004

Leoné Frank. (2014). *Mapping sensorimotor space: Parieto-frontal contributions to goal-directed movements*. Uitgever niet vastgesteld.

Malfait, N., Shiller, D. M., & Ostry, D. J. (2002). Transfer of motor learning across arm configurations. *Journal of Neuroscience*, *22*(22), 9656-9660. doi.org/10.1523/JNEUROSCI.22-22-09656.2002

McCloskey, D. I. (1978). Kinesthetic sensibility. *Physiological Reviews*, *58*(4), 763–820. https://doi.org/10.1152/physrev.1978.58.4.763

McKinley, W., Santos, K., Meade, M., & Brooke, K. (2007). Incidence and outcomes of spinal cord injury clinical syndromes. *The Journal of Spinal Cord Medicine*, *30*(3), 215–224. https://doi.org/10.1080/10790268.2007.11753929

McKinley, W., Hills, A., & Sima, A. (2019). Posterior cord syndrome: Demographics and rehabilitation outcomes. *The Journal of Spinal Cord Medicine*, *44*(2), 241–246. https://doi.org/10.1080/10790268.2019.1585135

Mirdamadi, J. L., & Block, H. J. (2020a). Somatosensory changes associated with motor skill learning. *Journal of neurophysiology*, *123*(3), 1052-1062. doi.org/10.1152/jn.00497.2019

Mirdamadi, J. L., & Block, H. J. (2020b). Somatosensory versus cerebellar contributions to proprioceptive changes associated with Motor Skill Learning: A theta burst stimulation study. https://doi.org/10.1101/2020.08.06.239707

Morton, S., Lang, C., & Bastian, A. (2001). Inter- and intra-limb generalization of adaptation during catching. *Experimental Brain Research*, *141*(4), 438–445. https://doi.org/10.1007/s002210100889

Nagengast, A. J., Braun, D. A., & Wolpert, D. M. (2011). Risk sensitivity in a motor task with speed-accuracy trade-off. *Journal of Neurophysiology*, *105*(6), 2668–2674. https://doi.org/10.1152/jn.00804.2010

Nasir, S. M., Darainy, M., & Ostry, D. J. (2013). Sensorimotor adaptation changes the neural coding of somatosensory stimuli. *Journal of Neurophysiology*, *109*(8), 2077–2085. https://doi.org/10.1152/jn.00719.2012

Ohashi, H., Gribble, P. L., & Ostry, D. J. (2019). Somatosensory cortical excitability changes precede those in motor cortex during Human Motor Learning. *Journal of Neurophysiology*, *122*(4), 1397–1405. https://doi.org/10.1152/jn.00383.2019

Orban de Xivry, J.-J., Marko, M. K., Pekny, S. E., Pastor, D., Izawa, J., Celnik, P., & Shadmehr, R. (2011). Stimulation of the human motor cortex alters generalization patterns of motor learning. *Journal of Neuroscience*, *31*(19), 7102–7110. https://doi.org/10.1523/jneurosci.0273-11.2011

Ostry, D. J., Darainy, M., Mattar, A. A., Wong, J., & Gribble, P. L. (2010). Somatosensory plasticity and motor learning. *Journal of Neuroscience*, *30*(15), 5384–5393. https://doi.org/10.1523/jneurosci.4571-09.2010

Ostry, D. J., & Gribble, P. L. (2016). Sensory plasticity in human motor learning. *Trends in neurosciences*, *39*(2), 114-123. doi.org/10.1016/j.tins.2015.12.006

Pavlides, C., Miyashita, E., & Asanuma, H. (1993). Projection from the sensory to the motor cortex is important in learning motor skills in the monkey. *Journal of Neurophysiology*, *70*(2), 733–741. https://doi.org/10.1152/jn.1993.70.2.733

Penfield, W., & Boldrey, E. (1937). Somatic motor and sensory representation in the cerebral cortex of man as studied by electrical stimulation. *Brain*, *60*(4), 389–443. https://doi.org/10.1093/brain/60.4.389

Ren, S.-Q., Li, Z., Lin, S., Bergami, M., & Shi, S.-H. (2019). Precise long-range microcircuit-to-microcircuit communication connects the frontal and sensory cortices in the mammalian brain. *Neuron*, *104*(2). https://doi.org/10.1016/j.neuron.2019.06.028

Rossi, C., Bastian, A. J., & Therrien, A. S. (2021). Mechanisms of proprioceptive realignment in Human Motor Learning. *Current Opinion in Physiology*, *20*, 186–197. https://doi.org/10.1016/j.cophys.2021.01.011

Sainburg, R. L., Ghilardi, M. F., Poizner, H., & Ghez, C. (1995). Control of limb dynamics in normal subjects and patients without proprioception. *Journal of Neurophysiology*, *73*(2), 820–835. https://doi.org/10.1152/jn.1995.73.2.820

Sakamoto, T., Arissian, K., & Asanuma, H. (1989). Functional role of the sensory cortex in learning motor skills in cats. *Brain Research*, *503*(2), 258–264. https://doi.org/10.1016/0006-8993(89)91672-7

Scott, S. H., & Kalaska, J. F. (1997). Reaching movements with similar hand paths but different arm orientations. I. Activity of individual cells in motor cortex. *Journal of Neurophysiology*, *77*(2), 826–852. https://doi.org/10.1152/jn.1997.77.2.826

Shadmehr, R., & Wise, S. P. (2004). *The computational neurobiology of reaching and pointing: A Foundation for Motor Learning*. MIT.

Stepniewska, I., Preuss, T. M., & Kaas, J. H. (1993). Architectionis, somatotopic organization, and ipsilateral cortical connections of the primary motor area (M1) of Owl Monkeys. *The Journal of Comparative Neurology*, *330*(2), 238–271. https://doi.org/10.1002/cne.903300207

Tillery, S. I., Soechting, J. F., & Ebner, T. J. (1996). Somatosensory cortical activity in relation to arm posture: Nonuniform spatial tuning. *Journal of Neurophysiology*, *76*(4), 2423–2438. https://doi.org/10.1152/jn.1996.76.4.2423

Tuthill, J. C., & Azim, E. (2018). Proprioception. *Current Biology*, *28*(5). https://doi.org/10.1016/j.cub.2018.01.064

Vahdat, S., Darainy, M., Milner, T. E., & Ostry, D. J. (2011). Functionally specific changes in resting-state sensorimotor networks after Motor Learning. *Journal of Neuroscience*, *31*(47), 16907–16915. https://doi.org/10.1523/jneurosci.2737-11.2011

Vidoni, E. D., & Boyd, L. A. (2009). Preserved motor learning after stroke is related to the degree of proprioceptive deficit. *Behavioral and Brain Functions*, *5*(1), 1-10. doi.org/10.1186/1744-9081-5-36

Vidoni, E. D., Acerra, N. E., Dao, E., Meehan, S. K., & Boyd, L. A. (2010). Role of the primary somatosensory cortex in motor learning: An RTMS study. *Neurobiology of Learning and Memory*, *93*(4), 532–539. https://doi.org/10.1016/j.nlm.2010.01.011

Vogt, B. A., & Pandya, D. N. (1978). Cortico-cortical connections of somatic sensory cortex (areas 3, 1 and 2) in the rhesus monkey. *The Journal of Comparative Neurology*, *177*(2), 179–191. https://doi.org/10.1002/cne.901770202

Wong, J. D., Kistemaker, D. A., Chin, A., & Gribble, P. L. (2012). Can proprioceptive training improve motor learning? *Journal of Neurophysiology*, *108*(12), 3313–3321. https://doi.org/10.1152/jn.00122.2012

Wong, J. D., Wilson, E. T., & Gribble, P. L. (2011). Spatially selective enhancement of proprioceptive acuity following motor learning. *Journal of Neurophysiology, 105*(5), 2512-2521. doi:10.1152/jn.00949.2010

Yousif, N., Cole, J., Rothwell, J., & Diedrichsen, J. (2015). Proprioception in motor learning: Lessons from a deafferented subject. *Experimental Brain Research*, *233*(8), 2449–2459. https://doi.org/10.1007/s00221-015-4315-8

Appendix A: Ethics approval form

Date: 28 April 2021
To: Dr. Paul Gribble
Project ID: 118242
Study Title: Coordinate Frame for Proprioceptive Acuity Changes Accompanying Motor Learning **Short Title:** Coordinate Frame for Proprioceptive Acuity Changes Accompanying Motor Learning **Application Type:** NMREB Initial Application

Review Type: Delegated
Full Board Reporting Date: May 7 2021 **Date Approval Issued:** 28/Apr/2021 12:57 **REB Approval Expiry Date:** 28/Apr/2022

Dear Dr. Paul Gribble

The Western University Non-Medical Research Ethics Board (NMREB) has reviewed and approved the WREM application form for the above mentioned study, as of the date noted above. NMREB approval for this study remains valid until the expiry date noted above, conditional to timely submission and acceptance of NMREB Continuing Ethics Review.

This research study is to be conducted by the investigator noted above. **All other required institutional approvals and mandated training must also be obtained prior to the conduct of the study.**

Documents Approved:

Document Name	Document Type	Document Date	Document Version
DEBRIEFING FORM	Debriefing document		
Email Script - SONA	Recruitment Materials	07/Apr/2021	
Email Script- OurBrainsCAN	Recruitment Materials	07/Apr/2021	
Information About The Study- OurBrainsCAN	Recruitment Materials	07/Apr/2021	
Letter of Information and Consent Forms	Written Consent/Assent	07/Apr/2021	

No deviations from, or changes to the protocol should be initiated without prior written approval from the NMREB, except when necessary to eliminate immediate hazard(s) to study participants or when the change(s) involves only administrative or logistical aspects of the trial.

The Western University NMREB operates in compliance with the Tri-Council Policy Statement Ethical Conduct for Research Involving Humans (TCPS2), the Ontario Personal Health Information Protection Act (PHIPA, 2004), and the applicable laws and regulations of Ontario. Members of the NMREB who are named as Investigators in research studies do not participate in discussions related to, nor vote on such studies when they are presented to the REB. The NMREB is registered with the U.S. Department of Health & Human Services under the IRB registration number IRB 00000941.

Please do not hesitate to contact us if you have any questions.
Sincerely,
Kelly Patterson , Research Ethics Officer on behalf of Dr. Randal Graham, NMREB Chair

Note: This correspondence includes an electronic signature (validation and approval via an online system that is compliant with all regulations).

Curriculum Vitae

Name:	Heba Hussian
Post-secondary Education and Degrees:	University of Western Ontario London, Ontario, Canada 2015-2020 B.Sc. (Hon.)
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