THE CONTRIBUTION OF PROPRIOCEPTIVE ACUITY TO UPPER LIMB MOTOR PERFORMANCE IN OLDER AND YOUNGER ADULTS

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Abstract

As we get older there is an increase in the variability of upper limb movements which typically require greater reliance on online corrective mechanisms. However, the relative contribution of proprioceptive loss to the development of these impairments in the upper limb is not well understood. The work in this thesis aimed to address this by presenting a novel method of measuring upper limb proprioception using a 2D-robotic manipulandum with older and younger adults. We show that this task provides distinct measures from traditional methods, and that despite physically inactive older adults having larger systematic errors in judging limb position, this was not related to motor performance during rapid target reaching. Furthermore, there was also a null relationship with the extent of motor adaptation to novel field dynamics even when only proprioceptive information regarding the perturbation was available. We were unable to measure robust effects of ageing on proprioceptive acuity throughout the thesis, and suggest that the level of impairment may have been previously over-inflated due to task and population specific limitations as a result. Collectively, we found a limited role of proprioceptive loss in the presentation of age-related impairments in motor control.

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CHAPTER 1

Characterisation and Causation of Sensorimotor Performance In Later Life

1.1 – Overview

In the UK, it is thought that the population of adults aged 65 years and over will outweigh those below the age of 17 by 2023, with the overall population of these older adults (OAs) expected to increase by almost 170% by 2037 (Figure 1.1; House of Lords, 2013; Office for National Statistics, 2013). In a recent report from the House of Lords, the potential impact of this increase on the social and economic welfare of the country was outlined in detail (House of Lords, 2013). They projected that the growth of this high risk population will be met with a corresponding rise in demand for healthcare, which will place greater strain on existing services, including the NHS. As such, improving the understanding of the biological and functional changes associated with normal ageing will be critical to help guide methods to reduce this strain in the future.

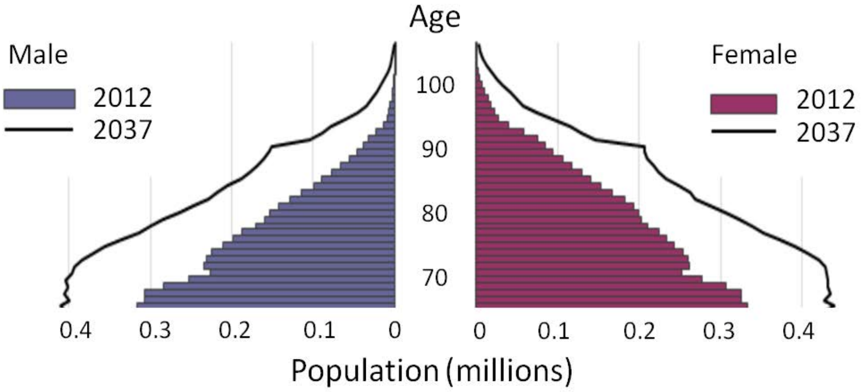


Figure 1.1. – Diagram depicting projected population of adults aged 65 and over by 2037. Adapted from figure supplied by Office for National Statistics (2013)

In the UK, 20-30% of people aged over 65 years old need help with at least one activity of daily living (ADLs; Age UK, 2017) indicating a reduced independence for this population. An important aspect of maintaining independence for older OAs is the ability to control movements, which allows safe and successful performance of ADLs without assistance. In cases where movements are not controlled as intended, attempting daily tasks can increase the risk of injury, including those incurred by trips and falls which have a high incidence in the older population (World Health Organisation, 2007). These injuries can cause long-term disabilities which further limit independence and increase the need for assistive care. Ultimately this leads to a poorer quality of life and equally increases demand on public healthcare services. As such, investigating the underlying processes which cause the development of movement disorders with ageing could be highly beneficial to reduce public cost and improve quality of life for OAs.

Currently, research has shown there are several physiological changes in the motor system which may contribute to age-related movement deficits. These occur both peripherally in terms of neuromuscular function (Morley, Baumgartner, Roubenoff, Mayer, & Nair, 2001; Taylor, 1984; Valdez et al., 2010) and centrally as a consequence of brain structural and connectivity changes (Mattay et al., 2002; Raz et al., 2005; Salat et al., 2004). This is likely to have a profound effect on the ability to generate and execute motor commands, which could partially explain characteristic declines in spatial and temporal movement regularity, particularly when task difficulty is increased (Christou & Enoka, 2011; Contreras-Vidal, Teulings, & Stelmach, 1998; Ketcham, Seidler, Van Gemmert, & Stelmach, 2002; Wishart, Lee, Murdoch, & Hodges, 2000; Yan, Thomas, & Stelmach, 1998). But aside from the changes in motor physiology, we also know that sensation plays a critical role in the regulation and adaptation of movements (Miall, Christensen, Cain, & Stanley, 2007; Miall & Wolpert, 1996; Shadmehr, Smith, & Krakauer, 2010), and that sensory acuity declines in normal healthy ageing (Goble, Coxon, Wenderoth, Van Impe, & Swinnen, 2009; Thornbury & Mistretta, 1981; Wright, Adamo, & Brown, 2011). In particular, there is growing evidence from a range of different methods to show that upper limb proprioceptive sensation is diminished during later life (Adamo, Alexander, & Brown, 2009; Adamo, Martin, & Brown, 2007; Cressman, Salomonczyk, & Henriques, 2010; Helsen et al., 2016), which is why we choose to focus on upper limb function as the focus of this thesis. Considering the severe movement deficits which are caused in cases of chronic proprioceptive loss (Gordon, Ghilardi, & Ghez, 1995; Sainburg, Ghilardi, Poizner, & Ghez, 1995), it follows that this loss in sensory acuity may contribute to age-related movement deficits of the upper limb, however this relationship is still poorly understood. Following this, we see a need for the investigation of this relationship to guide future training, exercise or lifestyle recommendations that could optimise motor function in ageing. This could help improve independence and quality of life for OAs, whilst equally relieving healthcare pressures which are projected for this rapidly growing population.

In order to assess this relationship effectively, we use this chapter to first outline and review the literature which characterises sensorimotor ageing and some of the known physiological causes of its development. This initially includes peripheral and central changes to sensorimotor physiology with advanced age, before identifying typical upper limb motor performance in laboratory settings. We then review the current evidence showing upper limb proprioceptive decline and include a critical appraisal of the methods used to measure this. Finally, we summarise this research in justification of the work completed for this thesis, and briefly outline our approach by summarising the experimental chapters.

1.2 – Physiology of Sensorimotor Ageing

1.2.1 – Peripheral Physiology

There are several age-related changes which occur in the physiology of the peripheral sensorimotor system which reduce its capacity to function normally. Age-related loss of skeletal muscle mass is one such change, which typically affects strength and force production, contributing to an increase in frailty (Lindle et al., 1997; Morley et al., 2001). Termed "sarcopenia", this process is characterised by a disproportional loss of fast-twitch Type II fibres over slow-twitch Type I fibres so that dynamic force production, or "power", is significantly reduced (Lexell, 1995). Rodent models have also shown there to be a degradation of the neuromuscular junction, which includes denervation of acetylcholine (Ach) receptor sites as well as axon thinning and fragmentation (Valdez et al., 2010). This means the neural commands sent to muscles may be disrupted as well as degradation of the muscle itself.

In addition to neuromuscular degeneration, human post-mortem examinations have shown there to be an increase in the capsular thickness of muscle spindles with age, as well as a reduction in the total number of intrafusal fibres (Swash & Fox, 1972). More recently, age-related loss of spindle diameter and number of intrafusal fibres was only found in specific muscles (Kararizou, Manta, Kalfakis, & Vassilopoulos, 2005), but is still thought to occur as a result of denervation processes, potentially following remodelling of extrafusal muscle towards a higher proportion of Type I fibres with increasing age (Shaffer & Harrison, 2007). In rodent models, primary spindle endings have been shown to become less spiral and more physiologically similar to secondary endings, which may affect the dynamic response to muscle stretch (Kim, Suzuki, & Kanda, 2007). Collectively, this will affect the quality or acuity of proprioceptive sensory information in advanced age.

Peripheral sensorimotor nerves also undergo considerable degradation with ageing, resulting in disrupted signalling through processes involving oxidative stress and altered cell metabolism (Kihara, Nickander, & Low, 1991; Sims-Robinson et al., 2013). In fact, during normal ageing the peripheral nervous system (PNS) is thought to lose 30% of myelinated fibre density and approximately 50% for unmyelinated fibres (Ceballos, Cuadras, Verdu, & Navarro, 1999; Jacobs & Love, 1985). These degenerative processes may also explain the loss of conduction velocity which is observed in both sensory and motor nerves of the PNS with advanced age (Taylor, 1984). Interestingly, when an efferent nerve fibre degenerates, there is a loss of input to the muscle fibres it innervates which will ultimately lead to the muscle fibre's death. In order to salvage these fibres, neighbouring motor neurons sprout axons to innervate them through a process known as collateral reinnervation (Slack, Hopkins, & Williams, 1979). However, whilst this ameliorates overall loss of muscle fibres, it leads to larger motor units of mixed fibres type which can affect precision of force production (Hepple & Rice, 2016; Power, Dalton, & Rice, 2013) and further impair movement control as a more maladaptive process. Taken together, this evidence indicates a limited ability of OAs to reliably carry out intended motor commands or receive accurate sensory information from receptors due to these changes in sensorimotor physiology.

It is, however, important to note that these effects can be delayed in ageing by participating in regular physical activity (PA). This has been shown to increase anti-oxidant responses and reduce accumulation of damage from oxidative stress (Bo, Jiang, Ji, & Zhang, 2013; Ristow & Zarse, 2010), as well as increase levels of circulating neutrophins (Coelho et al., 2012) which may help remodel damaged PNS fibres and lead to the observed preservation of muscle motor unit numbers (Power et al., 2012).

1.2.2 – Central Physiology

Oxidative stress and other degenerative mechanisms are also thought to affect central nervous system physiology with advanced age (Mattson & Magnus, 2006) which can similarly place limits on sensorimotor performance (for review see Seidler et al., 2010). Ageing induces a stereotypical reduction in grey matter volume in which prefrontal cortex appears to show the greatest susceptibility (Ge et al., 2002; Giorgio et al., 2010; Good et al., 2001). However, sensorimotor regions are also subjected to grey matter atrophy with cortical thinning observed in both primary motor and somatosensory cortices (Good et al., 2001; Salat et al., 2004). These declines naturally reduce the ability to execute movement and perceive sensory stimuli, which is apparent from correlations in grey matter atrophy of these areas and indices of gait impairments in advanced age (Rosano et al., 2008).

In addition to grey matter atrophy, OAs also experience an overall reduction in white matter volume (Ge et al., 2002; Good et al., 2001). Diffusion tensor imaging (DTI) allows detailed structural analysis of white matter fibres and has revealed compromised white matter integrity in the posterior limb of the internal capsule which carries corticospinal tract (CST) projections from primary motor cortex (Salat et al., 2005). As such, this compromises the direct pathway from central to peripheral motor circuits, highlighted by the fact these losses have been correlated with both unimanual and bimanual control of object manipulations (Sullivan, Rohlfing, & Pfefferbaum, 2010). Other, more recent evidence examined magnetic resonance imaging (MRI) data from over 3,000 participants where age was associated with higher mean diffusivity of white matter in sensorimotor thalamic radiations, indicating reduced structural integrity of the fibres (Cox et al., 2016). OAs exhibit accelerated degradation of the corpus callosum as indicated by reduced white matter fibre density and size, in which degeneration occurs along an anterior-posterior gradient (Hou & Pakkenberg, 2012; Ota et al., 2006). Since this is the primary commissural structure connecting left and right hemispheres, loss of fibre integrity reduces interhemispheric communication efficiency which affects performance of coordinated bimanual tasks (Bangert, Reuter-Lorenz, Walsh, Schachter, & Seidler, 2010; Sullivan, Pfefferbaum, Adalsteinsson, Swan, & Carmelli, 2002).

Sub-cortical structures such as the cerebellum are also subjected to accelerated loss of volume with age, with atrophy observed in adults as young as 50 years old (Raz et al., 2005; Terribilli et al., 2011). This is likely to place limits on the coordinated guidance of movements. Ageing is also associated with physiology changes to the basal ganglia, specifically a reduction in striatal dopaminergic activity, which has been associated with cognitive deficits as well as impaired movement control in simple reaction time tasks (Kaasinen & Rinne, 2002; van Dyck et al., 2008).

These degenerative losses in central sensorimotor physiology can be delayed by increased participation in PA. This includes reduced loss of grey matter and preserved white matter structural integrity (K. I. Erickson, Leckie, & Weinstein, 2014; Gow et al., 2012) and appears to occur in a non-specific fashion in cortical and sub-cortical structures alike.

An interesting observation is that during performance on sensorimotor tasks there is typically wider, more diffuse brain activity in older than younger adults (YAs; Heuninckx, Wenderoth, Debaere, Peeters, & Swinnen, 2005; Heuninckx, Wenderoth, & Swinnen, 2008; Wu & Hallett, 2005). And whilst there remains debate about whether the nature of this widespread activity represents compensation for age-related degeneration, or a loss of brain activation specificity (Bernard & Seidler, 2012; Heuninckx et al., 2008; Morcom & Henson, 2017), it is interesting that the additionally recruited areas often include prefrontal cortex, where there is paradoxically the highest susceptibility to age-related physiological decline (Ge et al., 2002; Giorgio et al., 2010; Good et al., 2001; Heuninckx et al., 2005; Heuninckx et al., 2008; Morcom & Henson, 2017). As such, this means that there are reduced cognitive resources in brain areas which are recruited to a greater extent during sensorimotor performance, thus increasing the overall cognitive demand of sensorimotor control. This relationship is epitomised by Figure 1.2, adapted from a review by Seidler et al. (2010), and is captured functionally in OAs by impairments on sensory and motor based tasks performed with a concurrent cognitive task (Goble, Mousigian, & Brown, 2012; Li & Lindenberger, 2002; Voelcker-Rehage & Alberts, 2007).

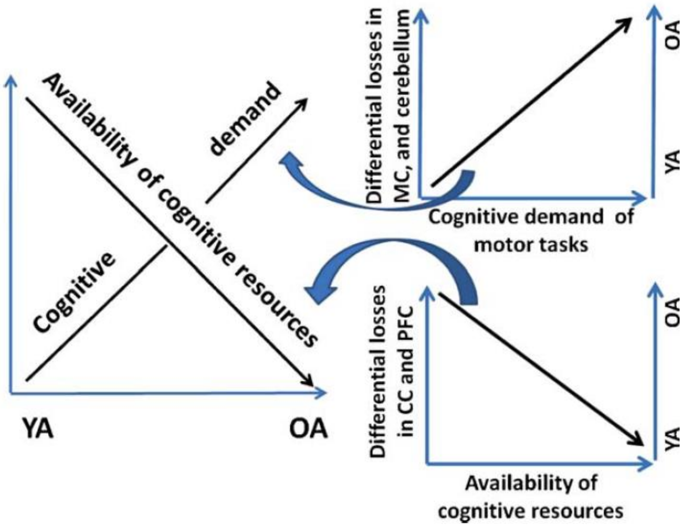


Figure 1.2. – Depiction of concurrent reduction in availability of cognitive resources through prefrontal cortex (PFC) and corpus callosum (CC) degeneration, and increase in cognitive demand of motor control due to degradation of motor cortex (MC) and cerebellum. Adapted from Seidler et al. (2010)

1.2.3 – Summary

There is a great deal of evidence to show that both peripheral and central sensorimotor systems are degraded with ageing, and can be spared to an extent by engagement in PA. This demonstrates that declines in motor function and sensory acuity have multi-factorial causes, and are likely expressed differently based on individual differences as we age. Compensatory or reactive processes may have short term benefits, but at the cost of impaired function in other respects or a general depletion of resources.

1.3 – Characteristic Movement Control of the Older Adult

1.3.1 – Basic Upper Limb Movements

The effects which ageing have on motor system physiology have profound influences on the ability to control basic movements. In the upper limb, this has been studied extensively in reaching and pointing tasks, particularly with respect to the kinematic profile of movements and both spatial and temporal reliability.

A number of studies have found impaired spatial and temporal performance in continuous, point-to-point movements along pre-defined 2D-directions as a result of advanced age (Contreras-Vidal et al., 1998; Lee, Fradet, Ketcham, & Dounskaia, 2007; Yan et al., 1998; Yan, Thomas, Stelmach, & Thomas, 2000). Yan et al. (1998) used a continuous pointing task to show OAs increased variation of timing between movements as well as extending movement duration. With a broader range of movement directions, Lee et al. (2007) also noted prolonged duration of continuous point-to-point movements which was thought to be a mechanism by which OAs maintained spatial accuracy comparably top YAs. However, when comparing single and repeated point-to-point movements, Yan et al. (2000) noted OAs increased movement duration for both tasks as well as showing increased movement jerk which suggests that spatial and temporal variations with ageing may not work in a simple speed-accuracy trade-off. In addition to these findings, OAs have exhibited more varied peak velocity and duration to peak velocity (sometimes termed “primary sub-movement”), coupled with increased jerk and straightness errors too (Contreras-Vidal et al., 1998). Ultimately, evidence from these types of continuous movement tasks provides clear indication that the kinematic and temporal profile of movements becomes more unreliable with increasing age.

More commonly, upper limb motor performance is assessed by discrete movements towards a target or specific goal, and has shown similar motor control deficits with advanced age (Coats & Wann, 2011; Darling, Cooke, & Brown, 1989; Helsen et al., 2016; Ketcham et al., 2002; Seidler-Dobrin & Stelmach, 1998; Seidler, Alberts, & Stelmach, 2002). During ballistic movements, Ketcham et al. (2002) found that OAs were unable to proportionally scale primary sub-movements or velocity profiles to changes in target size or reach amplitude which resulted in slower, more variable movements. They also observed a general age-dependent shortening of the primary sub-movement, with increased incidence of secondary sub-movements, reflecting a greater reliance on online sensory feedback which may be how they were able to achieve comparable endpoint accuracy to YAs. Using a greater range of movement directions, Seidler et al. (2002) found comparable performance accuracy between age groups when movements were isolated to the elbow, which was thought to occur via age-dependent increases in muscle co-activation. However, as movements required increasing involvement of the shoulder in addition to the elbow, endpoint errors and jerk scores for OAs became significantly higher. Thus, coordinating multi-joint movements may further challenge motor performance with advanced age. Whilst muscle co-activation at the elbow appears to reduce motor variation (Seidler et al., 2002), unreliable (ant)agonist muscle activity timing during different phases of elbow joint movements have also been shown in OAs, leading to greater trajectory variation (Darling et al., 1989) which suggests this strategy may be task-dependent. During targeted movements of the wrist, Helsen et al. (2016) reported longer reaction times, movement durations and "relative homing in phase" of movement for OAs, as well as more corrective sub-movements. In a similar fashion to Ketcham et al. (2002), this was thought to be the mechanism which allowed them to maintain a similar level of endpoint accuracy to YAs. With this in mind, it is interesting to note that both OAs and YAs shorten the primary sub-movement when visual feedback is removed (Coats & Wann, 2011; Helsen et al., 2016; Seidler-Dobrin & Stelmach, 1998) but only YAs are able to lengthen it again after extensive training where visual feedback is provided (Seidler-Dobrin & Stelmach, 1998). This shows a specific reliance on online visual feedback with increasing age but also an inability to update motor programs based on previous experience.

Collectively, these studies illustrate an increase in kinematic variation of upper limb movement control with ageing, which is likely influenced by increased noise from compromised motor system physiology. However, movement accuracy is often maintained in spite of this (Helsen et al., 2016; Lee et al., 2007; Seidler-Dobrin & Stelmach, 1998), which may reflect a preference towards accuracy over speed in ageing, such that movement duration and corrective sub-movements are increased to compensate for the impaired consistency. These findings also suggest OAs rely more on online sensory feedback, particularly visual, rather than on internally regulated control mechanisms. This topic is explored in more detail in the next sub-section.

1.3.2 – Sensorimotor Adaptation

The ability to control and adapt movements is dependent on sensory feedback. Online control refers to the process where sensory feedback is processed in real-time to guide and update motor commands towards a desired outcome. However, this process involves considerable delays in processing of sensory feedback and limits the speed at which we can perform movements, as well as adapt them to changing contextual environments. As such, a widely accepted theory of how movements are controlled by sensory feedback is through internal forward models (Miall & Wolpert, 1996; Shadmehr et al., 2010). Thought to occur in the cerebellum (Miall et al., 2007), this centrally driven process uses previous sensorimotor experience to predict or estimate the sensory 'state' of the limb based on the efference copy of a given motor command. By estimating the sensory state of the limb, appropriate subsequent movements can be implemented rapidly to overcome normal delays in online sensory feedback. When the sensory consequences of a movement do not match the predicted state, a sensory prediction error signal updates the forward model so that it will be more accurate in predicting sensory states of future movements of a similar nature and or context. The efficiency of this process therefore limits the rate and extent to which movements can be learned and adapted and has been a topic of high interest in the research community as a result. In a controlled laboratory setting, the most common method of studying sensorimotor adaptation is by observing performance of goal-directed movements before, during and after exposure to a sensory displacement or perturbation. More rapid and complete compensation for the displacement is thought to indicate improved ability to utilise sensory feedback and update motor programs for internally regulated movement control (see Figure 1.3).

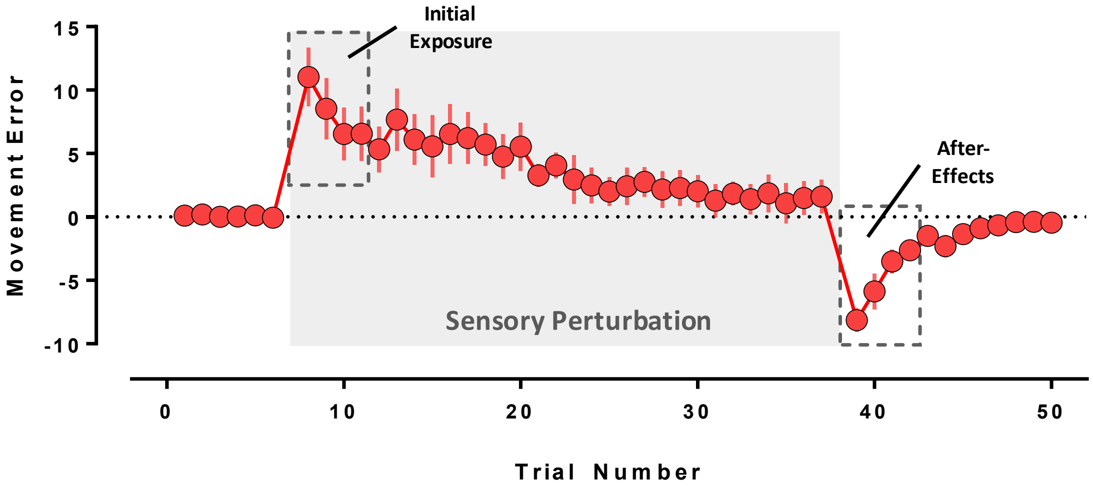


Figure 1.3 – Example progression in performance of a sensorimotor adaptation task. Initially, performance errors are small, but when the sensory perturbation is introduced (grey shaded region) errors become larger. Over increased exposure to the perturbation errors are gradually reduced, but when the perturbation is removed after-effects of the adaptation are apparent from errors in the opposite direction. Over time, performance returns to baseline showing that learning in this case is relatively transient. This performance profile is demonstrated with empirical data in Chapter 6

1.3.2.1 – Visual Feedback Manipulations

One well-established, low-cost and relatively easy to implement method of investigating sensorimotor adaptation is by asking participants to wear prism goggles which distort the visual feedback of movements (Fernández-Ruiz, Hall, Vergara, & Díaz, 2000; Nemanich & Earhart, 2015; Roller, Cohen, Kimball, & Bloomberg, 2002; Uresti-Cabrera, Diaz, Vaca-Palomares, & Fernandez-Ruiz, 2015). Nemanich & Earhart (2015) noted no difference between older and younger adults in the rate or extent of prism adaptation during target reaching. For ball throwing, there are mixed results of adaptation being independent of age (Roller et al., 2002) as well as OAs exhibiting slower adaptation rates but with increased after-effects (Fernández-Ruiz et al., 2000). Uresti-Cabrera et al. (2015) also used a ball throwing task to examine adaptation to 2 strengths of prism goggles, noting impaired adaptation for OAs but with age-independent after-effects. Interestingly, they also noted that extent of adaptation was correlated with spatial working memory (SWM), which may reflect an impaired ability to memorise localised throwing errors and hence use them to update internal models in this task. Larger movement variation was also typically reported for OAs in these studies (Fernández-Ruiz et al., 2000; Nemanich & Earhart, 2015), reinforcing the characteristics of OA movement control identified earlier in this chapter. Data from these experiments therefore show mixed effects of ageing on sensorimotor adaption. However, this may partially be explained by differences in the nature of the movement task and other methodological discrepancies.

An alternative method of studying visuomotor adaptation is by manipulating the relationship between hand or arm position and a visually presented cursor, which can be achieved by altering the cursor gain (Contreras-Vidal, Teulings, Stelmach, & Adler, 2002; Hegele & Heuer, 2010; Seidler, 2006; Teulings, Contreras-Vidal, Stelmach, & Adler, 2002). Seidler (2006) used this paradigm to show that OAs had a reduced adaptive response to the introduction of a 1.5x gain perturbation during centre-out joystick movements. In a slightly different approach, Teulings et al. (2002) examined how handwriting was performed in both increased and reduced visual feedback gain, which was constrained to the y-axis only to reduce awareness of its introduction. Here, OAs showed a mild impairment in the ability to scale writing to the gain distortions, but in a follow-up study where vision of the digitising pen and hand were occluded, this effect was abolished (Contreras-Vidal et al., 2002). This could imply that the sensory conflict in visual feedback of hand and cursor position disrupts adaptation in OAs, potentially through increased attentional capture which reduces explicit attention to performing the task. With this in mind, Hegele & Heuer (2010) found mild adaptive impairment in OAs when moving in a complex direction-dependent gain perturbation, but also noted reduced explicit awareness of the perturbation. This indicates explicit knowledge of the perturbation is an influential factor in OA sensorimotor adaptation performance of these tasks. Together, these gain perturbation studies also present a slightly mixed view on sensorimotor adaptation capacity for OAs, though they do highlight the role of explicit perturbation knowledge as a potentially limiting factor for adaptation.

The final and most common means of manipulating visual feedback is by rotating the cursor's path relative to the hand or limb, typically referred to as a visuomotor rotation (Anguera, Reuter-Lorenz, Willingham, & Seidler, 2010; Bock, 2005; Buch, Young, & Contreras-Vidal, 2003; McNay & Willingham, 1998; Seidler, 2006). Using both 30 and 45 deg rotations of a joystick controlled cursor, Seidler (2006) found age-independent movement errors at peak-velocity, but that errors after this stage of the movement were typically larger and more poorly adapted with advanced age. Similarly, Anguera et al. (2010) noted both reduced rate and extent of adaptation according to direction error for OAs performing a 30 deg visuomotor rotation task in an MRI scanner. They were also able to identify that early adaptation was correlated with SWM capacity for older, but not younger, adults, and that OAs were unable to engage brain areas associated with SWM during adaptation in the same way as YAs, which therefore limited performance. McNay & Willingham (1998) used a centre out line tracing task with a larger 90 deg rotation, and found OAs were worse at adapting to the displacement. However, when visual feedback was intermittently removed in "test" blocks, performance became comparable to YAs. This was also seen by Bock (2005) who reported a diminished adaptive response for OAs to a 60 deg rotation in a target pointing task, but age-independent performance when visual feedback was removed. Interestingly, when visual feedback was restored again the age-dependent deficits were once again apparent and similar to previous reports, fewer OAs reported explicit knowledge of the visual distortion or use of an explicit strategy. This may also explain why adaptation is independent of age when the visual rotation is introduced gradually (Cressman et al., 2010) and is not consciously attended to, but OAs adapt worse when it's introduced abruptly and high explicit attention is necessary for successful adaptation (Buch et al., 2003).

Collectively, the data presented here show a limited ability of OAs to adapt their movements to visual displacements when the perturbation salience is high and more explicit strategies are necessary to adapt the movements. Failure to engage SWM also appears to limit adaptation which could reflect an inability to consolidate previous sensory prediction errors and update internal models. These effects could stem from the fact OAs see the greatest deterioration in frontal brain areas (Ge et al., 2002; Giorgio et al., 2010; Good et al., 2001; Heuninckx et al., 2005; Heuninckx et al., 2008; Morcom & Henson, 2017) and that they are recruited to a greater extent than YAs during movement control (Heuninckx et al., 2005; Wu & Hallett, 2005), leaving fewer resources to explicitly attend to the task.

1.3.2.2 – Novel Field Dynamics

In addition to visual feedback distortions, another commonly used method of examining sensorimotor adaption is by modifying the dynamics of the field in which the movements are made. This creates an unexpected physical perturbation of the limb and can be achieved by using a robotic manipulandum where forces are imposed by a motor (Shadmehr & Mussa-Ivaldi, 1994), by applying constant loads to the manipulandum (Krakauer, Ghilardi, & Ghez, 1999) or with coriolis forces imposed by rotating chairs (Sarlegna, Malfait, Bringoux, Bourdin, & Vercher, 2010). As such, these tasks involve sensory prediction errors of both visual and proprioceptive feedback. Although this is a well researched paradigm, there are relatively few published instances in which it is used to examine the effects of ageing specifically, all of which use motor-imposed forces on a manipulandum as their method (Cesqui, Macri, Dario, & Micera, 2008; Huang & Ahmed, 2014; Trewartha, Garcia, Wolpert, & Flanagan, 2014). For example, Cesqui et al. (2008) used a velocity-dependent, clock-wise force-field with a centre out, 8-target reaching task to demonstrate that OAs are able to adapt and de-adapt successfully, though to a lower extent than YAs. However, adaptation here was measured in terms of kinematic profile only and gives little indication of the extent to which the perturbation was actually compensated for during movements. Huang & Ahmed (2014) were interested in whether OAs were able to adapt movements in a similar clockwise velocity-dependent force-field, but during target reaching movements along a single linear path. They found effects on some performance indices for force-field compensation to show reduced adaptation with ageing. Additionally, they reported higher muscle co-activation in OAs which was negatively correlated with extent of adaptation. Due to a similar baseline performance of OAs and YAs in the null-field, this co-contraction was thought to reflect a strategy to compensate for higher age-related motor noise, similar to previous reports (Seidler et al., 2002). However, the negative correlation with adaptive performance in the force-field shows this may be maladaptive in sensorimotor learning. As a final point, they noted higher reliance on online sensory feedback control due to prolonged deceleration phases of movement, in a similar fashion to previous reports with OAs (Helsen et al., 2016; Ketcham et al., 2002; Yan et al., 2000). Trewartha et al. (2014) found that adaptation to a novel clock-wise field was similar between age groups during similar linear reaching movements. In their experiment, Trewartha et al. (2014) used an interesting design that included a block of trials with reversed force-field direction (making it counter-clockwise) and an “error-clamp” phase where visual feedback was occluded and movements were constrained in a tight linear trajectory to target. This allowed them to decompose the reaching behaviour into slow and fast adaptive processes (M. A. Smith, Ghazizadeh, & Shadmehr, 2006). Following this, they identified a significant correlation between explicit memory performance and the fast retention factor for OAs only, thus indicating a more rapid decay of the fast adapted behaviour with reduced memory capacity.

These findings provide mixed evidence for the effects of ageing on adaptation to novel field dynamics and therefore need corroboration from further study. It seems the findings of Trewartha et al. (2014) parallel those of visuomotor perturbations by indicating a memory correlate of adaptive behaviour. However, this association occurs in retention phases for novel field dynamics and in the adaptation phase for visual displacements, perhaps reflecting differential learning processes between the two tasks which could be influenced differently by ageing. Additional themes of age-related increases in co-contraction to reduce movement variability and greater reliance on online sensory feedback control are also reported in these tasks.

1.3.3 – Summary

Taken together, the evidence provided here indicates a strong age-related increase in movement variability. It appears that it is possible to maintain accuracy in spite of this by utilising online sensory corrective mechanisms and increasing the duration of movements which may also reflect a shift towards favouring accuracy over speed in advanced age. Increasing reliance on online over centrally driven movement control could reflect the reduced reliability of predictive internal models due to increased sensorimotor noise (Boisgontier & Nougier, 2013). Increasing muscle co-activation also appears to help reduce the effects of motor variability, but the success of this is task-dependent. Age-related impairments of sensorimotor adaptation appear to be dependent on the saliency of the perturbation during visual displacements. This appears to reflect the necessity to engage explicit adaptive strategies in these tasks, which may be impaired in ageing due to increases in prefrontal cortex recruitment for movement control, as well as age-related decline in cortical physiology. Associations with working memory may partially reflect this use of explicit strategy, but perhaps also indicate a diminished ability to consolidate sensory prediction errors to update and regulate internal models. The effects of memory also appear to differ between types of sensorimotor perturbation for OAs, which may reflect task-dependent differences in the processes needed to adapt to them.

1.4 – Effects of Ageing on Proprioceptive Acuity

1.4.1 – Proprioception in Movement Control

As well as deficits in movement control, ageing of the sensorimotor system equally affects the acuity of sensation. This includes proprioception, which is known as the static and dynamic sensation of body and limb position in space, in the absence of vision (Goble et al., 2009; Proske & Gandevia, 2012). Proprioception is of particular interest here because of its close relationship with movement control which is most apparent from experiments studying rare cases of individuals who are proprioceptively deafferented (Gordon et al., 1995; Lajoie et al., 1996; Sainburg et al., 1995). For these people, essentially all tactile and proprioceptive sensation is absent from the neck down due to a selective neuropathy of large myelinated sensory fibres, whilst leaving motor fibres intact. This provides a unique model in which the relative contribution of proprioception to human movement control can be studied in a laboratory based setting. Indeed, when visual feedback of moving limbs is removed, these individuals experience drastically impaired movements (Figure 1.4; Gordon et al., 1995; Lajoie et al., 1996; Sainburg et al., 1995). In neurologically intact humans, proprioception can be disrupted by vibrating muscle spindles which similarly disturbs motor performance, though to a lesser extent (Verschueren, Swinnen, Cordo, & Dounskaia, 1999; Verschueren, Swinnen, Desloovere, & Duysens, 2002). Collectively, this illustrates the importance of proprioceptive sensation for movement control. In the ageing population, there have been several reports showing loss of this sensation in the lower limb with respect to the incidence of trips and falls (Hurley, Rees, & Newham, 1998; Lord, Clark, & Webster, 1991a, 1991b; Wingert, Welder, & Foo, 2014).

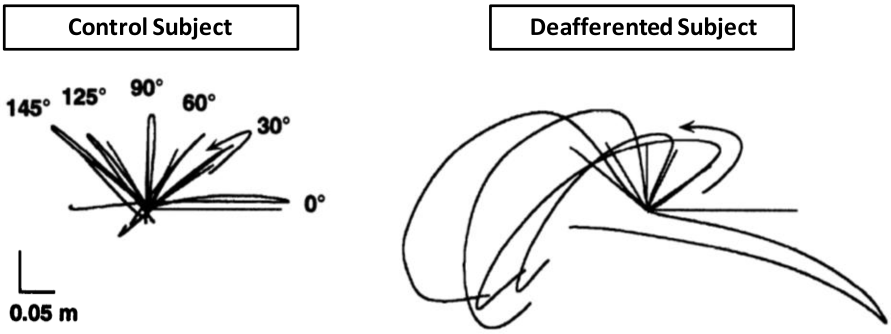


Figure 1.4 – Example of the extent to which simple movements are disrupted for deafferented patients when visual feedback is removed. Figure shows hand paths from a task that required movement from a home position to the end of a linear template and back again (arrows show reversal error). Adapted from Sainburg et al. (1995)

But the question of how this sensation changes with age in the upper limb has only more recently gained interest (for review see Goble et al. 2009). Here, we review the reports of age-effects on upper limb proprioceptive acuity and critically appraise the choice of methods for its assessment of the OA population specifically.

1.4.2 – Common Proprioceptive Assessment Methods

One commonly used method for measuring proprioceptive sensation is limb position matching (Adamo et al., 2009; Adamo et al., 2007; Goble, Mousigian, et al., 2012; Herter, Scott, & Dukelow, 2014). In these tasks, an unseen limb is passively moved to a reference position before the participant has to make an active movement to match it. The magnitude of error between the matched and reference position is then used to indicate the extent of proprioceptive loss or impairment. Although there are fine variations in methodology, most types of position matching task fall under one of three categories: ipsilateral remembered, contralateral concurrent or contralateral remembered (see Figure 1.5). During ipsilateral remembered tasks, the reference position is memorised and actively matched in the same limb. In contralateral concurrent tasks, one limb is moved to the reference position where it remains whilst it is mirror-matched contralaterally. Contralateral remembered tasks are then the same as contralateral concurrent, except the reference is memorised before contralateral mirror-matching. For a summary of these tasks see Figure 1.5.

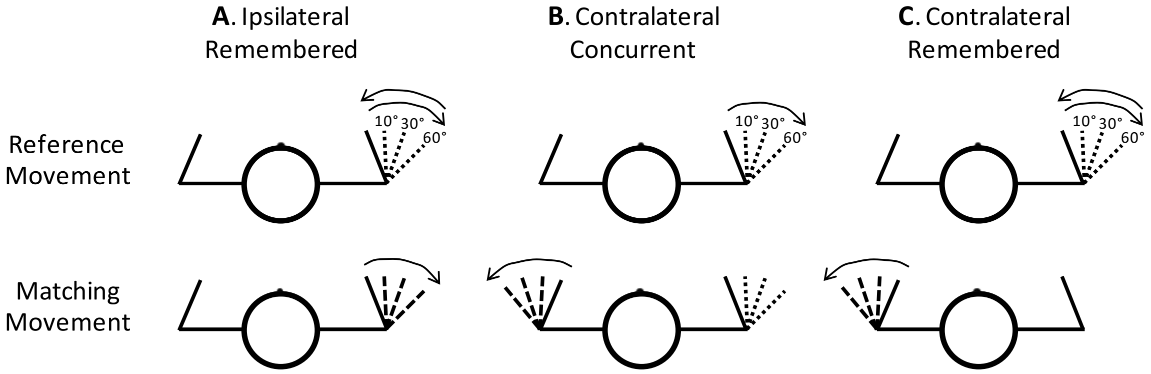


Figure 1.5 – Different categories of proprioceptive position matching tasks, shown here for matches constrained to the elbow joint. Reference movements are typically performed passively by machine or experimenter, with participants actively moving to match them. Reference positions here are 10, 30 and 60 deg from the home position, for remembered tasks the limb is returned to the home position before matching occurs **A.** Reference position is memorised and matched ipsilaterally **B.** Reference position is held whilst mirror-matched contralaterally **C.** Reference position is memorised and mirror-matched contralaterally. Adapted from Adamo et al. (2007)

Adamo et al. (2007) used all three of these position matching tasks to assess the effects of ageing on proprioceptive acuity. They found that OAs had larger absolute matching errors than YAs, and that this became more exaggerated as the task moved from ipsilateral remembered to contralateral remembered matching. These effects were later replicated with a similar three-task paradigm at the wrist (Adamo et al., 2009), but with the additional finding that matching errors were larger in sedentary OAs than physically active ones. A proposed limitation of matching tasks for ageing research is that they involve memorised limb positions, which means age-effects on matching accuracy may be confounded by normal age-related cognitive decline in memory function. To address this, Adamo et al. (2009) also included a verbal working memory assessment in their experiment but found no associations in memory capacity with matching errors, suggesting this may not be a limiting factor in these tasks. Goble, Mousigian, et al. (2012) were also interested by this potential confound, so sub-grouped OAs according to high or low verbal working memory score and assessed their performance on an ipsilateral elbow matching task. Typical age-related increases in matching error were observed, but there was no difference between the OA low and high working memory groups. However, when an additional attentional load task was performed concurrently, the low memory group had distinct increases in matching errors compared to both the high memory OA group and YAs. This may indicate a potentially confounding role of working memory in these types of proprioceptive assessment, and further highlights how limitations in explicit cognitive resources influence sensorimotor control in ageing. In a multi-joint context, Herter et al. (2014) tested contralateral concurrent matching performance of the upper limb using 2 robotic manipulanda and 9 spatial reference positions in the 2D workspace. Similar to the elbow joint tasks, they noted some modest age-effects across a range of different performance indices which included systematic shifts, replication variability and spatial contraction or expansion in both hand and joint based terms. Helsen et al. (2016) used a slightly different variation of an ipsilateral matching task at the wrist. They used a passive displacement for both reference and matching movements, with participants indicating the perceived reference position by pressing a button to halt the passive displacement. Physically inactive OAs were found to have larger matching errors compared to both active OAs and YAs, which again indicates an influential role of PA on proprioceptive acuity in ageing. In their experiment, Helsen et al.

(2016) also included a different method of proprioceptive assessment known as a passive movement detection task. This involves participants indicating the point at which they first detect movement at a joint which is very slowly passive displaced. Helsen et al. (2016) found that sedentary OAs took longer to detect the wrist displacement than active OAs or YAs which indicated reduced joint position sensitivity. This was also observed by Wright et al. (2011), where the angular displacement of the wrist at detection was highest for physically inactive OAs. This evidence outlines loss of proprioceptive sensation with ageing which may be limited by participation in regular PA. However, data from remembered matching tasks may be subject to confound by working memory if the attentional loading of the procedure is too high.

1.4.3 – Limitations of Common Assessments and Alternative Methods

In addition to the age-specific limitation of working memory for these tasks, one general flaw is that they use passive reference movements. This is important in proprioceptive sensation since joint position sense can be biased by sense of effort or corollary discharge (J. L. Smith, Crawford, Proske, Taylor, & Gandevia, 2009). Since the signals of limb position used to regulate movement in daily living are heavily based on active, voluntary movement, these tests may therefore have poor ecological validity. Similarly, the proprioceptive sensation perceived during a passive reference movement may be different to that during voluntary replication, which may exaggerate matching errors in these tasks. Indeed, the use of participant-defined, active reference positions has been shown to reduce matching errors compared to traditional, passive methods in both YAs and OAs separately (R. I. Erickson & Karduna, 2012; Langan, 2014; Lonn, Crenshaw, Djupsjobacka, Pederson, & Johansson, 2000).

As a direct comparison between age-groups with actively defined reference positions, Schaap, Gonzales, Janssen, & Brown (2015) used multi-joint position matching in a 3D workspace with both older and younger adults. Interestingly, they found no difference in absolute matching error between age groups during ipsilateral matching, but age-dependent increases in errors for contralateral matching. Although this still demonstrates a decline of proprioceptive sensation with ageing, the use of active over passive reference movements appears to make this less pronounced. This should therefore be a consideration when evaluating reports of age-effects on proprioceptive sensation.

As well as limitations of passive movements in the experiments discussed here, there are several issues with the use of contralateral matching tasks specifically which may make them unreliable, especially for an ageing population. Firstly, differences in the thixotropic states of the muscle and relative spindle firing rates between limbs have been shown to affect contralateral matching errors, and may therefore be a confounding factor in these tasks if not suitably controlled (Tsay, Savage, Allen, & Proske, 2014). Secondly, proprioceptive acuity asymmetries between right and left limbs have been reported (Goble & Brown, 2009; Goble, Lewis, & Brown, 2006) with similar asymmetries in the influence of efference copy or effort on perception (Scotland, Adamo, & Martin, 2014), both of which could further limit the reliability of contralateral matching paradigms. But perhaps more importantly for research with an ageing population, contralateral matching tasks require interhemispheric transfer of sensory information in order to transform it into a motor command to replicate the reference positions. This transfer is dependent on the corpus callosum which (as noted previously) has been shown to degenerate with advanced age (Hou & Pakkenberg, 2012; Ota et al., 2006), and as such, may explain why errors in this particular paradigm appear to be more pronounced for OAs than ipsilateral matching tasks (Adamo et al., 2009; Adamo et al., 2007; Schaap et al., 2015). Whilst efficiency in assessing one limb position with respect to another may be important in coordinating some bimanual movements, the confounding effects of degraded interhemispheric communication in ageing may limit the reliability of these tasks as a pure, non-task-specific measure of limb proprioception. As such, they may not be suitable for assessing the contribution of proprioceptive sensation to age-related unimanual motor performance.

As an alternative, paradigms which make use of adaptive staircase procedures and psychometric curve fitting have also been reported which aim to measure the acuity of limb position sense more precisely (Cressman & Henriques, 2009; Cressman et al., 2010; Hoseini, Sexton, Kurtz, Liu, & Block, 2015; Ostry, Darainy, Mattar, Wong, & Gribble, 2010). These types of procedure alter stimulus magnitude on a trial-by-trial basis based on the response to a 2-alternative forced choice decision. For proprioceptive tasks, the stimulus is typically the distance of limb position relative to a reference position of some description. Responses are then pooled together and fitted with a logistic function to gain two measures of proprioceptive acuity: a systematic proprioceptive error known as the bias, and a variable proprioceptive error known as the uncertainty range. The use of these adaptive procedures is typically more flexible than the use of discrete values and have been found as more reliable than traditional position matching or detection tasks (Elangovan, Herrmann, & Konczak, 2014; Hoseini et al., 2015). In an ageing population, a version of this task involved a static hand position, but judgements were made about finger position relative to a visually displayed white bar (Hoseini et al., 2015). The angular displacement of the white bar from the actual finger position was then altered using a staircase procedure, with the resultant data showing age-dependent increases in bias but not uncertainty range. Although reliable, this only provides an indication of static position sense and not kinaesthesia, which is more relevant to studying the relationship with motor control in aging. With this in mind, an early report of an active version of this task was presented by Cressman & Henriques (2009) in which active movements of an ipsilateral limb were tightly constrained to a specific pathway that deviated hand position from a visually presented target. Judgements in this task were regarding final limb position relative to the target, with the size of the deviation altered by an adaptive staircase procedure. When tested with OAs, Cressman et al. (2010) found that OAs had larger uncertainty ranges, but not biases, than YAs. This is in line with the increased sensorimotor noise which accompanies normal healthy ageing, and the difference in findings to Hoseini et al. (2015) may reflect age-dependent differences in static and dynamic limb position sense. Since the task proposed by Cressman et al. (2009; 2010) involves active movements of an ipsilateral limb and instantaneous perceptual judgements, it works well to address the limitations outlined presently with more traditional proprioceptive assessments. As such, use of these tasks may be important for adding to the knowledge of proprioceptive acuity loss with ageing and its relationship with motor control.

1.4.4 – Summary

Although there are relatively few reports of upper limb proprioceptive assessments across the lifespan, they all seem to indicate a general loss of acuity with age. This deterioration appears to be ameliorated by participation in regular physical exercise, but the reliability of measures may be ecologically limited. In addition to this, there appear to be several age-specific limitations to some of the reported tasks which may equally limit their validity. There is, however, promise for the use of adaptive staircase based procedures, particularly those using active movements, for the reliable estimation of upper limb proprioceptive acuity of OAs. As such, they may be the most suitable choice for investigating the relationship of proprioceptive sensation with upper limb movement control in the ageing population.

1.5 – Chapter Summary and Outline of Thesis

1.5.1 – Chapter Summary

The ageing population is expanding rapidly and developing the understanding of ways to improve health and wellbeing in later life is of critical importance, both to improve quality of life for ageing individuals and to relieve associated social and economic pressures. Movement control is one such aspect of ageing which is necessary to maintain independence and as such, understanding contributors to its decline is of critical importance. The evidence presented in this chapter shows clear motor system physiology decline with ageing. This likely contributes to the characteristic slowing and variability of upper limb movement control observed in OAs. However, concurrent degeneration in sensory system physiology contributes to a loss of proprioceptive sensation in a similar way. Since the role of proprioception in movement control is well-established, it then stands to reason that a further contributor to age-related movement impairment could be loss of proprioceptive acuity. However, only recently have there been efforts to examine this directly, with passive methods of measuring proprioception showing little association with motor impairments in ageing (Helsen et al., 2016). Even with dynamic proprioceptive measurement techniques, loss of acuity does not seem to affect visuomotor adaptation or the ability to recalibrate hand position in response to learning with advanced age (Cressman et al., 2010). Yet with such few reports, we see a need to explore this in more detail with the use of currently under-examined paradigms with OAs, including adaptive staircase, ipsilateral reaching measures of proprioception and adaptation to novel field dynamics. Following this, we may better understand the relative contribution of proprioceptive sensation to upper limb motor performance in ageing to help guide future recommendations and further research to support healthy later life. Together, this formed the basis for the work outlined in this thesis.

1.5.2 – Thesis Outline

In Chapter 2 we began our investigation by pilot testing a novel task to measure dynamic upper limb proprioceptive acuity, similar to Cressman et al. (2010), on a small group of older and younger adults. Since there are few published reports of these tasks, especially with OAs, this allowed us to identify key aspects of the protocol which could be optimised for use throughout the rest of the thesis. Contrary to Cressman et al. (2010), we found an age-dependent increase in proprioceptive bias, but not uncertainty range, which was associated with PA level. However, with only a small sample size and several task limitations we were interested to test this further.

In Chapter 3, we used an optimised version of the dynamic task to examine the relationship between proprioceptive acuity and rapid, target-based movement control in physically (in)active OAs and YAs. We replicated the findings from Chapter 2 by showing physically inactive OAs had larger biases than YAs, but did not find any evidence of an association between proprioception and either systematic or variable motor performance. We suggested that this may have been due to the ballistic nature of movements requiring little online sensory feedback to perform. As such, we saw the need for further experimentation with motor tasks where proprioceptive feedback is emphasised in motor task performance to examine this relationship in more detail.

To test the extent to which the limitations we identified in previous methodology (Section 1.4.3) influenced estimates of proprioceptive acuity, in Chapter 4, we used the same set of participants from Chapter 3 and compared performance on our dynamic task with a more commonly used elbow position matching paradigm. Despite observing age-dependent effects on measures from both proprioceptive assessment methods, we did not find a relationship between the two. This confirmed that passive and active methods of measuring proprioception give rise to different estimates of proprioceptive acuity, which we suggest strengthens the basis for using the dynamic task specifically to investigate the relationship of proprioception with motor control in ageing.

In light of the unexpected bias effect reported in Chapters 2 and 3, and its contradiction to Cressman et al. (2010), we were interested in investigating the basis of these observations in Chapter 5 and whether they could be explained by variants in the parameters of our dynamic task. We identified reach distance as the most influential parameter to affect measures of proprioception, followed by trajectory of constrained movement and visual feedback of target, but no specific interactions involving age group. Furthermore, we did not replicate either our own findings or those of Cressman et al. (2010), which suggested the age-effects on dynamic proprioceptive acuity may not be as robust as initially predicted.

In order to examine motor control under conditions where proprioceptive feedback is emphasised for successful performance, we examined the relationship between dynamic proprioceptive acuity and sensorimotor adaptation to novel field dynamics in Chapter 6. In order to maximise this dependency further, we also included a condition in which visual feedback of the perturbation’s nature was occluded, which we hypothesised would see the strongest relationship with proprioceptive acuity. Similar to previous work (Trewartha et al., 2014), we reported a lack of adaptation effects with age, regardless of visual feedback, which we suggest reflects reduced use of explicit control strategies for novel field adaptation. Furthermore, baseline proprioceptive bias was larger for physically inactive participants regardless of age but critically, we found that proprioceptive acuity did not predict adaptive motor performance. As such, it seems that although proprioceptive feedback is necessary for novel field adaptation, it may be used offline, between trials which may have limited the extent to which online proprioceptive control of movement was tested, similar to Chapter 3. This means the relationship under such conditions remains unknown.

In order to collectively understand the findings presented in Chapters 2-6, we explored explanations for thesis wide observations and the open-ended questions that remain in Chapter 7. In this chapter, we suggest the reality of age-related proprioceptive impairment may be smaller and hence harder to empirically measure than previous reports indicate, perhaps due to the limitations in their methodology which are addressed with the dynamic task. Furthermore, it seems the basis and occurrence of the proprioceptive bias needs greater attention in future research since it is strongly predicted by physical activity and partially by age in our work. As a final line of investigation, experimentation with motor tasks involving continuous shape or position tracking movements may maximise online proprioceptive feedback, allowing the relationship between proprioceptive loss and motor control in ageing to be concluded more definitively.

CHAPTER 2

Dynamic Proprioceptive Acuity in Ageing: A Pilot Study

Chapter Abstract

In this chapter, we pilot tested a dynamic proprioceptive acuity task which sought to address some of the limitations with previous work that were highlighted in Chapter 1. The task involved making judgements regarding the position of an unseen limb relative to a visual reference position following an active, but constrained, reaching movement. The main aim of the experiment was to highlight any potentially confounding limitations of the task or its different parameters so that it could be optimised for future use. However, we still predicted that the small sample of older adults (OAs) we tested would demonstrate increased uncertainty ranges, but not biases, when compared to younger adults (YAs). Following completion of the experiment we identified that the parameters of the adaptive staircase sequence used to alter the stimulus magnitude were too conservative to converge on a stimulus value that gave sensitive indices of proprioceptive acuity. Contrary to predictions, OAs were found to have larger proprioceptive biases (specifically at inward reaching targets 5 and 6) than YAs, yet comparable uncertainty ranges. Furthermore, bias scores were correlated with physical activity (PA) levels in OAs. However, due to the low sample size and potentially confounding effects of the staircase parameters, we are cautious to make strong conclusions or interpretations of these findings. By addressing the issues highlighted with the task from this experiment, future study will benefit from more sensitive measures of proprioceptive acuity from which to draw conclusions more confidently.

2.1 – Introduction

In Chapter 1, we outlined the experiments which used passive position matching and detection tasks to show age-related declines in upper limb proprioceptive sensation (Section 1.4.2; Adamo, Alexander, & Brown, 2009; Adamo, Martin, & Brown, 2007; Goble, Mousigian, & Brown, 2012; Helsen et al., 2016; Herter, Scott, & Dukelow, 2014; Wright, Adamo, & Brown, 2011), and that this loss is ameliorated by participation in regular physical activity (Adamo et al., 2009; Helsen et al., 2016; Wright et al., 2011). Similarly, we highlighted several limitations of these tasks for representing proprioception in normal, active day-to-day movements (Scotland, Adamo, & Martin, 2014; Tsay, Savage, Allen, & Proske, 2014) and for use with OAs specifically (Goble et al., 2012; Hou & Pakkenberg, 2012). As such, we identified the need for further experimentation of upper limb proprioceptive acuity in the ageing population that makes use of novel measurement tasks involving dynamic, multi-joint movements and instantaneous judgements of an unseen ipsilateral limb (Cressman & Henriques, 2009; Cressman, Salomonczyk, & Henriques, 2010; Ostry, Darainy, Mattar, Wong, & Gribble, 2010).

In this chapter, we pilot tested a similar, but novel version of this task which combined different elements of paradigms published in previous reports (Cressman & Henriques, 2009; Cressman et al., 2010; Ostry et al., 2010), and extended them to include 6 reference target locations in the 2D workspace. The main purpose of this was to examine how the task performed and whether we could identify ways to optimise it before it was implemented with a larger cohort of participants. Based on the evidence of increased proprioceptive noise associated with age-related sensory system degeneration (Ceballos, Cuadras, Verdu, &

Navarro, 1999; Seidler et al., 2010; Swash & Fox, 1972) and findings from a single previous report of a similar nature (Cressman et al., 2010), we predicted that OAs would have increased proprioceptive uncertainty, but not bias, and that this would be dependent on their level of PA.

2.2 – Methods

2.2.1 – Participants

There were 9 OAs (5 male, 74.7 ± 5.3 yrs [mean ± SD, presented in text throughout thesis, with SE presented in tables and figures]) and 7 YAs (3 male, 19.3 ± 1.0 yrs) who were right-hand dominant (laterality quotient 30 or above, [10-item Edinburgh Handedness Inventory; Oldfield, 1971]) that participated in the experiment. All OAs were screened for history of neurological illness and carpal tunnel syndrome, arthritis or similar movement pains or limitations in the arm, wrist or fingers. All participants read an information sheet and were given the opportunity to ask any questions before they signed consent forms and began the experiment. PA estimates for the OAs were attained using the CHAMPS questionnaire (Stewart et al., 2001), which was also completed prior to participation.

2.2.2 – Experimental Set-Up (vBOT)

Participants were seated in front of a 2D-planar robotic manipulandum (vBOT; Howard, Ingram, & Wolpert, 2009) which provided a low-friction means of recording simple reaching movements in a 40x64cm workspace. With their foreheads resting against a padded metal frame approximately 10cm behind the edge of the workspace, participants grasped the manipulandum handle with their right hand and were asked to look down onto a mirrored surface (Figure 2.1). This blocked any vision of the hand or arm directly and reflected projected images from a large, horizontally mounted monitor display directly above. Target locations and visual feedback of hand position were presented in this way, with the cursor (when displayed) spatially coincident with the centre of the vBOT handle. Recordings of the vBOT handle position were sampled at 1kHz with translational torque forces updated at the same rate. All recorded data was stored for future offline analysis following experiment completion.

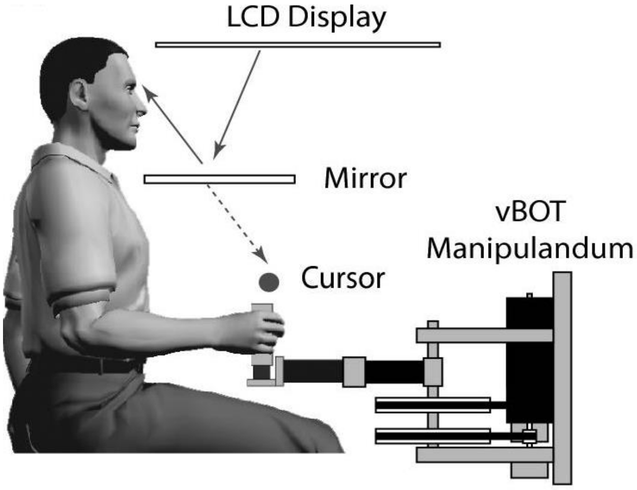


Figure 2.1. – Example set-up of vBOT adapted from Ahmed & Wolpert (2009). LCD display projects image onto mirrored surface to give visual feedback of hand location on robot handle. Mirror occludes any direct vision of the reaching arm

2.2.3 – Procedure

Participants made reaching movements towards targets 15cm from a start position with target and hand position visual feedback occluded after initial 3cm outward movement (see Figure 2.2). These movements were constrained to a pre-defined minimum jerk path using stiff virtual walls (imposed by vBOT motors) and guided movements through a path that laterally deviated the hand away from the target. At the end of the movement, the hand was held at the final position and a blue and red cross appeared at a constant position clockwise (CW) and counter-clockwise (CCW) of the target, respectively. The participant was then instructed to verbally indicate the cross colour (red or blue) which represented the side of the target that they felt they had been guided to. With visual feedback of hand position still occluded, participants were actively guided back to the start position before a new target appeared and the next trial began. The magnitude and direction of the lateral deviation from the target was manipulated throughout ongoing trials by 2 randomly interleaved PEST sequences (see Section 2.2.6), which were reset at the start of each new block. Each block of channel trials was also preceded with several unconstrained, null-field, target reaching trials where full visual feedback of hand position was provided with a small circular cursor.

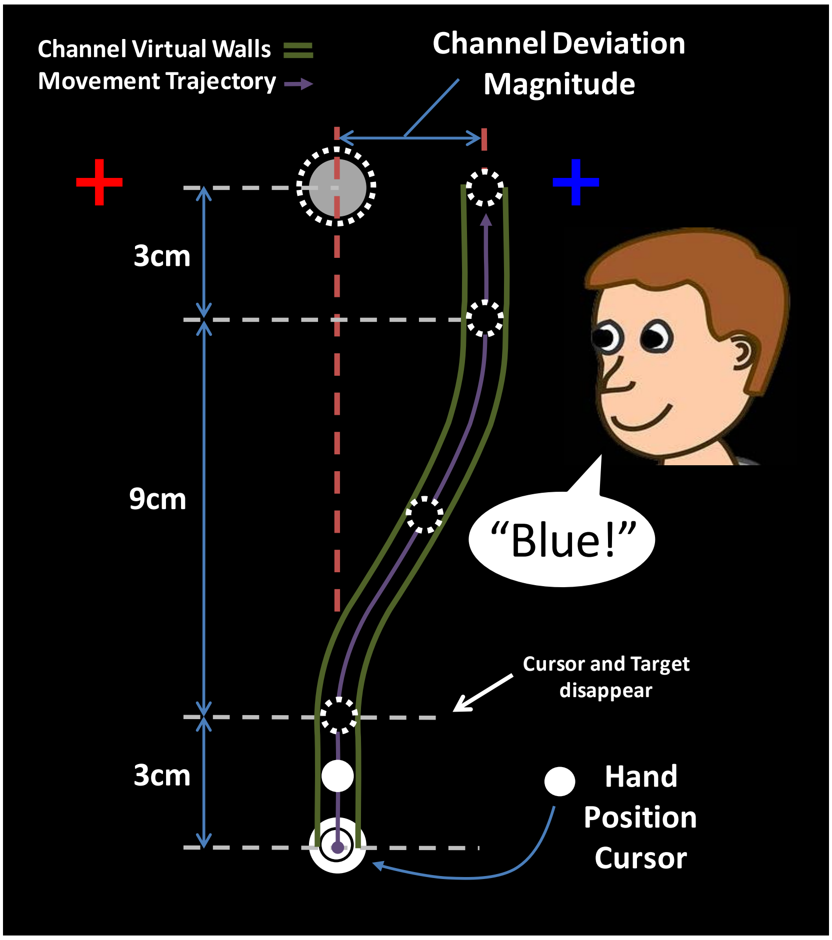


Figure 2.2. – Perceptual channel trajectory. Initial 3cm are straight, then minimum jerk profile deviates hand laterally (pre-defined channel deviation magnitude) over next linear 9cm reach, finishing with a further straight 3cm before verbal response was given. The first 3cm include the hand position cursor feedback and target before they are both removed for the remainder of the trial (denoted by dashed circles)

The complete procedure was repeated for a set of 3 distal targets and 3 proximal targets. The order of completion (distal or proximal first) was randomised to counterbalance order effects across participants.

2.2.4 – Targets and Visual Feedback

When available, visual feedback of hand position was given as a 0.5cm radius white marker which updated on a real-time basis with limb movement on the manipulandum handle. Targets were always presented as 1cm radius grey markers and the start position as a 1cm radius white marker. For channel trials, visual feedback of hand position was provided for the first 3cm of movement, after which the cursor disappeared along with the grey target. Both then remained occluded for the rest of the trial. When the movement ended the red and blue crosses (1cm width) appeared on the counter-clockwise (CCW) and clockwise (CW) side of the target (which remained visually occluded) respectively.

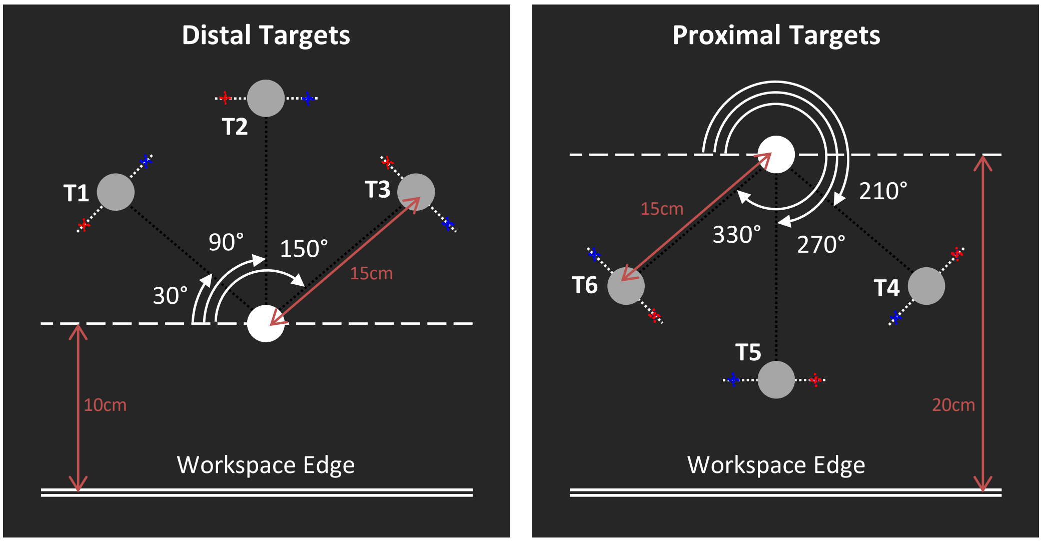


Figure 2.3. – Workspace locations of distal (left panel) and proximal (right panel) target sets

Targets had varied angular elevation but in all cases were 15cm from the start position which remained visible throughout the entirety of the task.

The 6 targets were divided into 2 sets of 3, proximal and distal, each with their own start positions to ensure that reach distance was easily manageable within the constrained workspace. The start position for the distal targets was 10cm into the workspace (approximately 30cm from the participant's torso) with the targets arranged at 30°, 90° and 150° elevation. The start position for the proximal targets was 20cm into the workspace (approximately 40cm from the participant's trunk) with the targets arranged at 210°, 270° and 330° elevation (Figure 2.3). For both channel and null-field trials, targets were presented in a pseudorandom order such that each target would be presented at least once every 3 trials. Null-field trials, where the hand position cursor was always visible, were intended to reduce the likelihood of proprioceptive drift confounding perceptual results as the experiment progressed. Proximal and distal target locations remained the same for these trials. Furthermore, participants were given accuracy feedback in null-field trials based on the lateral endpoint error from the target where they intersected a virtual wall. This was provided in the form of an explosion graphic (whose size and colour varied with error) and the colour of the target (yellow for a 'hit' and red for a 'miss').

2.2.5 – Channel Virtual Walls and Trajectory

The forces participants experienced during the channel trials always acted orthogonally to the pre-defined movement trajectory according to Equation 2.1, which has previously been described by Ostry et al. (2010) and Scheidt, Reinkensmeyer, Conditt, Rymer, & Mussa-Ivaldi (2000).

$$f_x = 2000\delta_x - 10v_x \tag{2.1}$$

Here, f_x refers to the lateral resistive force (N) imposed by the channel wall, δ_x represents the lateral distance between the current hand position and centre of the channel (m) and v_x represents the lateral velocity of the hand (m/s). The wall stiffness was given as 2000 N/m and the viscosity as 10 Ns/m. No forces were applied in the y-direction of the channel trajectory as movement in this plane was freely dictated by the participant. The channel itself remained in a straight line towards the target for 3cm at which point the channel deviated hand path laterally through a minimum jerk profile for a further 9cm before it finally continued straight again for the remaining 3cm (Figure 2.2). Hand position was locked at the end of the channel until the verbal response had been made. The robot then actively assisted the participants back to the start position through a similar minimum jerk profile before a new trial began.

2.2.6 – PEST Staircase Procedure

The size and direction of the lateral deviation imposed by the virtual channels was dictated by two randomly interleaved PEST sequences (Taylor & Creelman, 1967) spanning across all 3 targets (proximal or distal). One sequence started from the CW (or blue cross) side of the targets and the other from the CCW (or red cross) side. Each deviation size was repeated a minimum of 6 times (2 per target), with sequences always beginning at a magnitude of 3cm (±0.05cm added noise) and initial step size of ±1cm. To determine whether the participant was reliably responding correctly or incorrectly to a given deviation size, one of two equations needed to be satisfied. They included the total number of responses at that deviation size (R_{tot}), the PEST sequence weight (W_{PEST}) which was fixed at 1 and the number of correct responses (R_{cor}) as follows...

$$R_{cor} \geq (R_{tot} / 2) + W_{PEST} \tag{2.2}$$

$$R_{cor} \leq (R_{tot} / 2) - W_{PEST} \tag{2.3}$$

This means that for the minimum 6 repeats at each deviation size, R_{cor} either needed to be greater than or equal to 4 (Equation 2.2), or less than or equal to 2 (Equation 2.3) for the responses to that deviation size to be deemed reliably correct or incorrect respectively. In the case where neither of these equations were met after the initial 6 repeats (i.e. $R_{cor} = 3$), the sequence continued to repeat itself at the same deviation size until either equation was eventually satisfied. The deviation size reduced if the responses were correct and Equation 2.2 was satisfied and increased if they were incorrect and Equation 2.3 was satisfied. This meant that the sequence direction would reverse if there were consecutive correct and incorrect overall responses (or vice-versa). If the sequence reversed at any time, the new step size was always half of the previous one i.e. from 1cm to 0.5cm at the first reversal. Otherwise, the step size would remain the same for the first 3 steps and double on the 4th (i.e. from 1cm to 2cm) in order to optimise convergence of the sequence to the bias value.

2.2.7 – Experimental Design

All participants performed both the proximal and distal target tasks, with the order of completion of the two tasks randomized to counterbalance any potential effects of learning or fatigue. In both instances, testing was divided into 5 blocks, each block beginning with 12 null-field trials followed by 48 channel trials (PEST sequences were reset at the start of each new block).

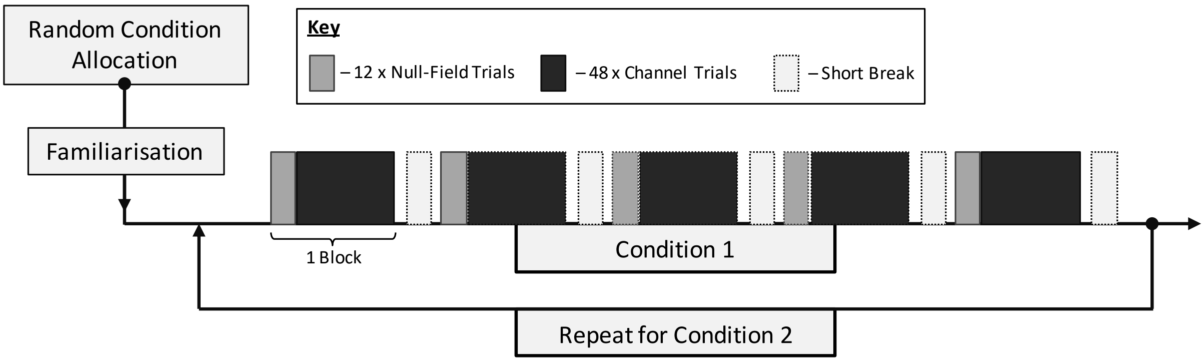


Figure 2.4. – Summary of experimental design. Random allocation was to proximal or distal targets as condition 1 or 2 to counterbalance any potential order effects

This was preceded by brief familiarisation blocks of 6 null-field and 9 channel trials for both the proximal and distal target sets, performed in the same order as was randomly allocated. This was to ensure participants fully understood the task and the data was not included in the final analysis. A summary of the experimental design can be seen in Figure 2.4.

2.2.8 – Outcome Measures

The participant’s verbal responses from each of the 6 targets were binarized (“blue” = 1, “red” = 0) and plotted against their respective channel deviation size and direction. A logistic function was then fitted to the data using the Matlab glmfit function which provided estimates of response probabilities across the range of lateral deviations.

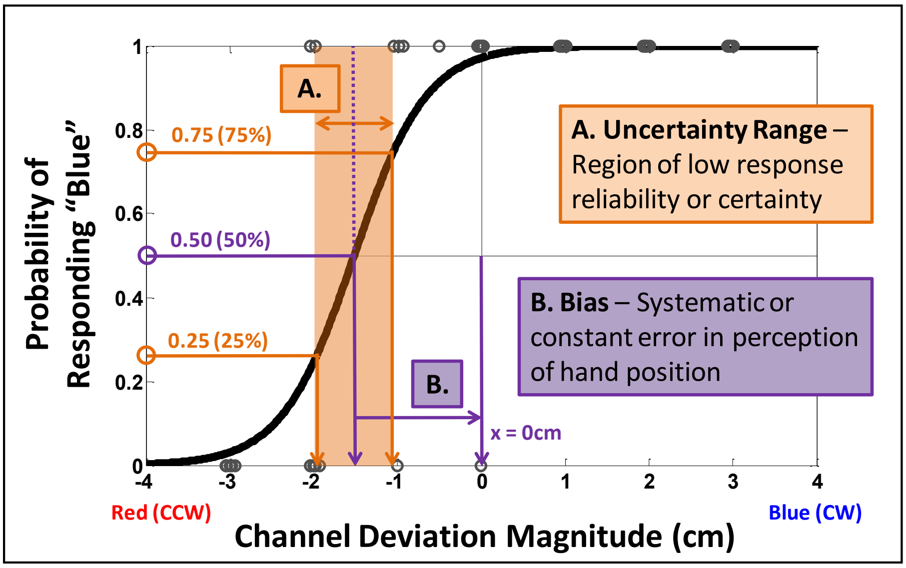


Figure 2.5. – Verbal responses plotted as binary 1s (“blue”) or 0s (“red”) shown as grey open circles. Fitted logistic function (black line) gives rise to Bias (purple) and Uncertainty Range (orange) as proprioceptive outcome measures

From these curves, two proprioceptive outcome measures were extracted for each of the 6 different targets: the bias and uncertainty range. The bias represents the systematic or constant error in perception of hand position, and is defined as the negative of the channel deviation corresponding to the 50th percentile of the logistic function. This is such that a positive bias represents perception of hand position shifted towards the blue cross (CW direction), and a negative bias represents perception of hand position shifted towards the red cross (CCW direction). The uncertainty range represents the region of low response reliability or confidence (perceptual acuity) and is defined as the difference between the channel deviations for the 25th and 75th percentile of the logistic function. This is such that a small uncertainty range represents increased perceptual acuity, where sensitivity to small step changes around perceived hand location (bias) is high. The annotated curve in Figure 2.5 illustrates how both of these measures are obtained. In order to diminish the effects of outlying responses on the curve's profile, data points which had a Pearson residual value which was more than 2 standard deviations away from the mean of the logistic regression residuals were excluded from the analysis. Pearson residuals are an approximately normally distributed set of residual values for logistic regression analyses, and as such, allow outlying values to be excluded in this fashion.

The forces imposed against the channel walls were calculated for the first 2cm of the final straight portion of the movement (i.e. 12-14cm of reach) to investigate their influence on perception of hand position. Average self-selected movement speed was also recorded for the channel trials to investigate its relationship with perceptual acuity. This was recorded for each target from the portion of the movement where the participant first reached 1cm from the start position to 1cm short of the final deviated position. Since the purpose of the null field trials was to reduce the likelihood of proprioceptive drift across a long block of trials without visual feedback (Brown, Rosenbaum, & Sainburg, 2003a, 2003b), their associated trajectory and kinematic data was not analysed. Physical activity estimates were acquired using the CHAMPS questionnaire (Stewart et al., 2001) for OAs only and were collected on the basis of a previously demonstrated relationship with proprioceptive acuity (Wright et al., 2011).

2.2.9 – Statistical Analysis

To assess age group differences in task performance across the different targets, three separate 6 x 2 mixed-design ANOVAs: (Target; 1-6) x (Age Group; older vs. younger adults), were performed for proprioceptive (bias and uncertainty range) and kinematic (average movement speed) measures. In all cases where the sphericity assumption was violated a Greenhouse-Geisser correction was used, with significance being assessed at the $p < .050$ level. However, in order to reduce family-wise Type I error, a False Discovery Rate (FDR) analysis was used to define a critical *p*-threshold at which to assess significance during the follow-up multiple pair-wise comparisons (Benjamini & Hochberg, 1995). Since the FDR analysis makes use of observed *p*-values to calculate an adjusted critical *p*-threshold, it can be used in a range of different test statistics (Curran-Everett, 2000) and typically has higher power (the proportion of the false hypotheses which are correctly rejected) and is less conservative than other more commonly used methods, such as the Bonferroni correction (Benjamini & Hochberg, 1995). As such, it is gaining more popularity in the field of sensorimotor research (Boisgontier et al., 2014; Helsen et al., 2016).

FDR analysis for a set of multiple comparisons (*k*) is calculated according to the following 3 steps where *i* refers to the i^{th} comparison, with p_i as its corresponding observed *p*-value:

1) Organise the *k* observed p_i values by descending magnitude.
2) For $i = k, k - 1, k - 2, \ldots, 1$, calculate the critical significance value (p^*_i) for each observed p-value (p_i) as is given by Equation 2.4, where α is set to .050.

$$p^*_i = (i/k) \cdot \alpha \tag{2.4}$$

3) Starting with the largest p_i (where $i = k$), continue to assess whether $p_i \leq p^*_i$ in a stepwise fashion. Once this criterion is satisfied, reject the null hypotheses associated with the remaining *i* comparisons where FDR adjusted *p*-threshold (p_{FDR}) = p^*_i.

Comparison (*i*)	Observed *p*-value (p_i)	Critical *p*-value (p^*_i)
12	0.742	0.050
11	0.457	0.046
10	0.329	0.042
9	0.156	0.038
8	0.046	0.033
7	**0.024**	**0.029**
6	**0.019**	**0.025**
5	**0.009**	**0.021**
4	**0.008**	**0.017**
3	**0.0012**	**0.013**
2	**0.0011**	**0.008**
1	**< .001**	**0.004**

Table 2.1. – A set of fictional observed *p*-values (p_i) for $k = 12$ multiple comparisons and their associated critical *p*-values (p^*_i) according to FDR adjustment analysis (Equation 2.4). First significant comparison at $i = 7$ (bold, underlined) according to $p_i \leq p^*_i$ such that the null hypothesis is rejected for comparisons $i = 7\text{-}1$ (bold) and $p_{FDR} = .029$

For example, look at the fictional set of observed *p*-values for a set of 12 multiple comparisons in Table 2.1. Note here that p_{FDR} = .029 is found at the *i* = 7 observation and thus we can reject the null hypothesis for ranked comparisons 7-1. It is worth noting that based on this analysis, if the largest observed *p*-value (where *i* = *k*) is less than .050, then all comparisons are deemed to be significant and the critical *p*-threshold is reported as p_{FDR} = .050 (see Table 2.2). In situations where no comparisons are found to be significant (i.e. $p_i \leq p^*_i$ is false for all observations) the smallest observed *p*-value (p_{min}) and its associated critical significance value (still denoted as p_{FDR}) is reported. All *p*-values for multiple comparisons are therefore reported as uncorrected (Least Significant Difference; LSD) values in the Results section but assessed at FDR adjusted *p*-thresholds (as noted). This is both for sets of tests which correspond to follow-up comparisons of significant ANOVA effects, and also associative relationships assessed by bivariate correlations.

Comparison (*i*)	Observed *p*-value (p_i)	Critical *p*-value (p^*_i)
<u>6</u>	<u>0.043</u>	<u>0.050</u>
5	**0.033**	**0.046**
4	**0.031**	**0.042**
3	**0.012**	**0.038**
2	**0.003**	**0.033**
1	**0.002**	**0.029**

Table 2.2. – A set of fictional observed *p*-values (p_i) for *k* = 6 multiple comparisons and their associated critical *p*-values (p^*_i) according to FDR adjustment analysis (Equation 2.4). In this case, the first significant comparison is at *i* = *k* (bold, underlined) according to $p_i \leq p^*_i$ such that the null hypothesis is rejected for all comparisons (bold) and p_{FDR} = .050

2.3 – Results

2.3.1 – Proprioceptive Measures

Group average results can be seen in Figure 2.6, where perceptual responses were grouped in 1cm bins along the x-axis at each of the 6 targets before logistic functions were fitted to the data. However, all statistical analyses were performed on outcome measures from raw, binary logistic functions which are summarised in Table 2.3 and Figure 2.7.

The uncertainty range (Figure 2.7, Panel A) was unaffected by Age Group (F[1, 14] = .17, p = .691) and there was no interaction between Age Group and Target (F[2.8, 38.9] = 1.37, p = .268). Uncertainty range was significantly affected by Target (F[2.8, 38.9] = 4.01, p = .016, η^2_p = .22); however follow-up pair-wise comparisons showed no differences between any of the 6 targets (15 paired t-tests, p_{min} = .006; p_{FDR} = .003).

For the bias (Figure 2.7, Panel B), there was a main effect of Age-Group (F[1, 14] = 5.06, p = .041, η^2_p = .27) such that OAs had larger systematic errors in limb perception than YAs. The interaction of Target and Age-Group on bias was also significant (F[5, 70] = 2.94, p = .018, η^2_p = .17), and when followed up with simple effects analysis (6 independent t-tests) it was found that OAs had significantly larger biases than YAs at Targets 5 (p = .002; p_{FDR} = .017) and 6 (p = .001) after correcting for multiple comparisons. However, there was no overall main effect of Target on bias (F[5, 70] = 1.07, p = .384).

Although slightly larger for OAs, the statistically comparable uncertainty range between age groups contradicts original predictions. The age-dependent increase in proprioceptive bias was equally unexpected and both findings are explored in more detail in the discussion.

Measure	Group	Target 1	2	3	4	5	6	**Overall**
Uncertainty Range (cm)	*Older*	1.27 *(± .31)*	.78 *(± .12)*	.63 *(± .13)*	1.41 *(± .35)*	.69 *(± .12)*	1.05 *(± .19)*	.97 *(± .16)*
	Younger	.93 *(± .15)*	.90 *(± .11)*	.96 *(± .21)*	1.13 *(± .15)*	.60 *(± .22)*	.79 *(± .20)*	.88 *(± .14)*
Bias (cm)	*Older*	.07 *(± .43)*	.63 *(± .26)*	1.56 *(± .45)*	.64 *(± .21)*	****1.12 *(± .18)***	****1.04 *(± .17)***	***.84 *(± .15)***
	Younger	.51 *(± .34)*	.73 *(± .25)*	.26 *(± .25)*	.56 *(± .24)*	.32 *(± .11)*	.19 *(± .11)*	.43 *(± .08)*
Movement Velocity (cm/sec)	*Older*	12.1 *(± 1.7)*	12.0 *(± 2.0)*	13.9 *(± 2.4)*	13.1 *(± 1.3)*	13.3 *(± 1.8)*	13.8 *(± 1.8)*	13.0 *(± 1.8)*
	Younger	15.6 *(± 2.0)*	15.6 *(± 2.1)*	16.9 *(± 2.1)*	16.5 *(± 2.3)*	15.2 *(± 2.3)*	17.3 *(± 2.0)*	16.2 *(± 2.0)*

Table 2.3 – Group average proprioceptive (uncertainty range and bias) and kinematic (movement velocity) data for older and younger adults. Values are given as means ± standard error where significantly different from younger adults is indicated by * ($p < .05$) and ** ($p < .010$). Multiple comparisons subjected to FDR adjusted p-threshold

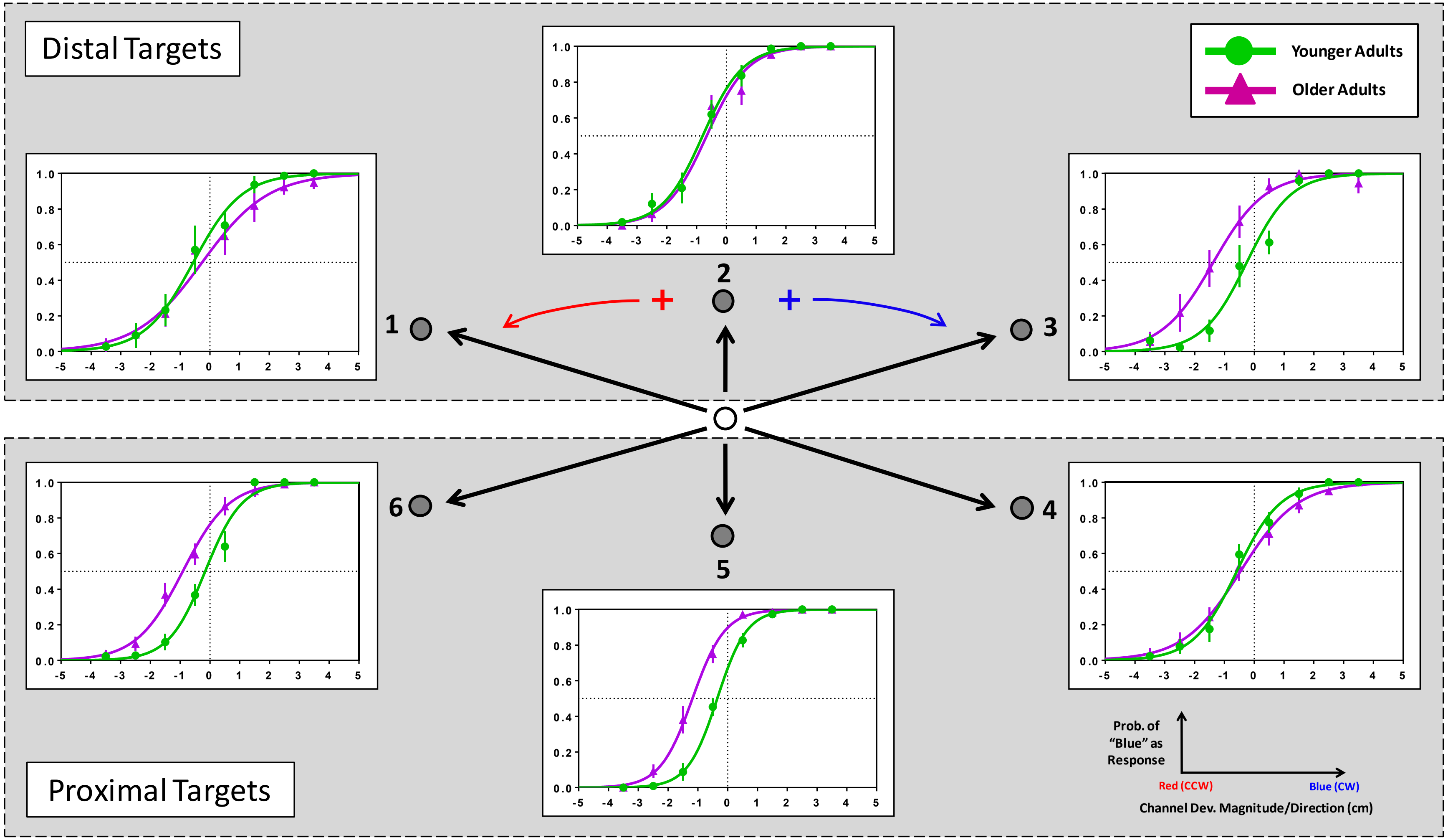


Figure 2.6. – Group average logistic functions for older (purple) and younger (green) adults for the 3 proximal (bottom panel) and 3 distal (top panel) target groups. Symbols represent group average mean (± standard error) response probabilities across 1cm x-axis bins. Note that these fitted curves are for visualisation purposes only and unlike this figure, the actual start position differed for the two sets of targets (see Figure 2.3)

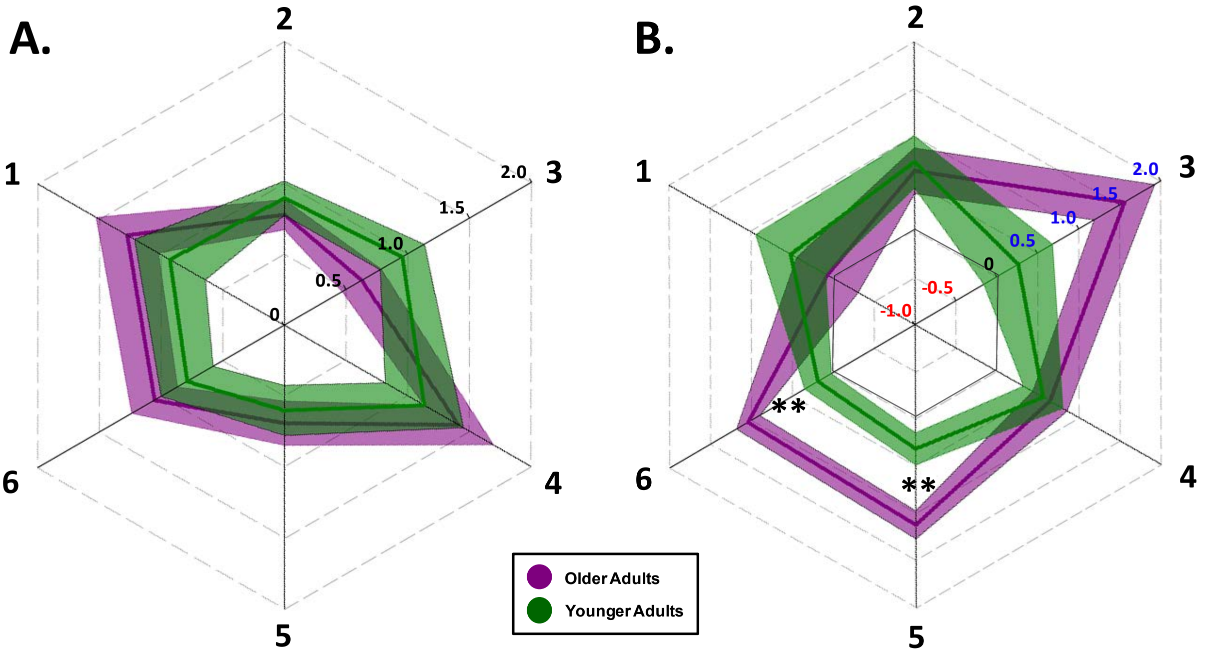


Figure 2.7. – Group average proprioceptive measures data (both in cm) for older (purple) and younger (green) adults, thick coloured line represents group average with shaded region as ± standard error **A.** Uncertainty Range, no significant age group differences were found, larger uncertainty range represents poorer perceptual acuity **B.** Bias where positive values represent tendency to perceive hand as further towards blue cross (i.e. clockwise to target) and negative values as perceived further towards red cross (counter-clockwise of target). Significant age group differences were found here at Targets 5 and 6 as indicated by ** (*p* < .010; multiple comparisons subjected to FDR adjusted *p*-threshold)

2.3.2 – Kinematic Measures

Due to unforeseeable data loss, we did not have analysable kinematic data for 3 older participants (whilst the proprioceptive responses remained valid). For this reason, kinematic data presented here is n = 6 for OAs.

Movement velocity data is summarised in Table 2.3. OAs tended to move more slowly than YAs, though this difference was not statistically significant (F[1, 11] = 1.37, *p* = .267). Similarly, movement speed was not affected by Target (F[1.8, 19.5] = 2.02, *p* = .163) and there was no interaction between Target and Age Group (F[1.8, 19.5] = .38, *p* = .662). To investigate whether the self-selected movement speed was associated with perceptual performance on the task, we correlated average hand velocity with both bias and uncertainty range for the older and younger adults at each of the 6 targets (uncertainty range and bias Pearson correlations for 2 [Age Group] x 6 [Target] relationships). It was found that there were no significant correlations between movement speed and uncertainty range (p_{min} = .151; p_{FDR} = .004) or bias (p_{min} = .010; p_{FDR} = .004) at any of the targets, confirming that perceptual judgements were independent of movement speed during the task.

To examine whether perceptual judgements were influenced by sense of effort or corollary discharge (Smith, Crawford, Proske, Taylor, & Gandevia, 2009) we correlated individuals' biases with the mean of their orthogonal forces applied to the channel walls during the last portion of the movement. This was again performed separately for older and younger adults at each of the 6 different targets and it was found that there were no significant relationships in any case (Pearson correlations for 2 [Age Group] x 6 [Target] relationships; p_{min} = .011; p_{FDR} = .004). This confirms that systematic errors in limb position sense were independent of the effort exerted during task performance.

2.3.3 – Physical Activity

To examine the influence of PA on proprioceptive acuity in OAs, we collapsed uncertainty range and bias across all 6 targets and correlated these average measures with the CHAMPs score. The analysis showed that bias was significantly correlated with CHAMPs score (r = .69, *p* = .040) but uncertainty range was poorly associated with this PA measure (r = .14, *p* = .716). This similarly contradicted our predictions of proprioceptive uncertainty, but not bias, having an association with physical activity status in advanced age.

2.4 – Discussion

The aim of this experiment was to pilot test a novel method of measuring dynamic upper limb proprioceptive acuity and to guide its design for future experimental implementation. Although we only tested a small sample of participants, we were able to successfully collect and analyse datasets which indicate its feasibility. However, in completing this experiment we noted several limitations to the methods which may have reduced the reliability of the findings. As such we focus mainly on discussing these limitations here and how to address them in future implementations, with fewer comments aimed at interpreting the results which may have been confounded by these issues.

Firstly, although the use of adaptive staircase procedures have been evaluated as more reliable than other common methods of measuring proprioception (Elangovan, Herrmann, & Konczak, 2014; Hoseini, Sexton, Kurtz, Liu, & Block, 2015), the parameters we used for the PEST sequence appeared to perform poorly within the confines of the 48 trial blocks. This was apparent from the 2 sequences often not converging onto a similar deviation magnitude and direction by the end of a block, and sometimes with multiple repeats needed before either Equations 2.2 or 2.3 were satisfied. As such, it seems the parameters of the PEST sequence used here may have been too conservative to gain sensitive measures of proprioceptive acuity. In future, altering both the PEST sequence weight and reducing the number of repeats per level (in a similar fashion to Ostry et al., 2010) may therefore improve the sensitivity of measures without having to increase the number of trials.

This may be important considering that in its current form, the entire experiment took roughly 30-40 mins to complete which may make it difficult to implement alongside other tasks in a single visit for future experiments, and extending the number of trials will exacerbate this. In addition to this, there were some anecdotal reports of fatigue from older adults (OAs) on experiment completion which suggests the length of the task should be reduced, not extended. This reduction could be achieved by limiting the number of spatial reference locations to the outward reaching targets (1-3) only. Although we saw significant age-effects on bias at targets 5 and 6, the functional relevance of these movements are lower than outward reaches and is likely why the latter are studied more frequently in ageing (Goble et al., 2012; Ketcham, Seidler, Van Gemmert, & Stelmach, 2002; Seidler, Alberts, & Stelmach, 2002). Other beneficial modifications to the methodology may include changing the nature of the 2-alternative forced choice symbols to reflect shape and not colour since the latter can differentially capture visual attention (Becker, 2010). This could influence the 2-alternative forced choice and may have confounded the estimates of bias measured here as a result.

Despite these limitations of the task, we did measure age-dependent increases in bias, but not uncertainty range, which were most apparent at targets 5 and 6 as well as being associated with physical activity (PA) which was in line with previous reports (Adamo et al., 2009; Helsen et al., 2016; Wright et al., 2011). This was contrary to our predictions and to the findings of Cressman et al. (2010) who reported age-dependent increase in uncertainty range only. Although it is unclear to what extent the limitations outlined here influenced our findings, task-dependent differences between the present report and Cressman et al. (2010) may somewhat account for this discrepancy. It may be that by using minimum jerk perceptual channels here (as opposed to straight channels used in Cressman et al., 2010), additional proprioceptive cues from the changes in trajectory direction may have helped to detect the direction of the lateral deviations. If OAs did in fact have greater proprioceptive noise, this may have disproportionally benefitted them over younger adults (YAs) and allowed them to perform comparably. This would also explain why the typical uncertainty range measured presently (approximately 0.5-1.5cm) was lower than that measured by Cressman et al. (2010; approximately 9-16° which translates to roughly 1.6-2.9cm). Interestingly, Cressman et al. (2010) did not include inward reaching movements (targets 4-6 in this experiment) in their experiment which is where we observed the largest age-dependent increases in bias. As such, this may be why they did not report an effect for this proprioceptive measure. Other task-dependent features including the visual representation of reference target, reach distance and block design differed between our experiment and Cressman et al. (2010). These may have influenced the proprioceptive acuity measures and partially explained the different results, but since their specific effects are not well understood this could therefore be a focus of future research.

In summary, we were able to successfully implement a novel task to measure upper limb proprioceptive acuity with a small group of older and younger adults. The completion of this experiment was important for identifying limitations in the task so that it can be optimised for future application with larger cohorts of participants. Since the size of the sample was small and the limitations identified likely reduced the sensitivity and reliability of the measures we reported, firm conclusions regarding the reported effects cannot be made with confidence. As such, further experimentation with an optimised version of this task is necessary to better understand the effects of ageing on dynamic upper limb proprioceptive acuity.

CHAPTER 3

Proprioceptive Acuity Does Not Predict Motor Performance in Older or Younger Adults

Chapter Abstract

This experiment aimed to investigate the relationship of dynamic proprioception, as measured by an optimised task that addressed limitations identified in Chapter 2, and basic movement control. Since the increased proprioceptive bias result for older adults (OAs) in Chapter 2 was unexpected and it is unclear to what extent the limitations of the dynamic task caused this finding, we chose to again keep the prediction that older, physically inactive adults would have larger proprioceptive uncertainty ranges. We also expected OAs would have slower, more varied profiles of movement whilst maintaining endpoint accuracy. Furthermore, we expected that proprioceptive uncertainty would be related to motor error variation in OAs. Physically inactive OAs were found to have larger proprioceptive biases than younger adults (YAs), whilst there were no differences between physically inactive OAs, active OAs or YAs in uncertainty range. OAs moved and reacted more slowly than YAs, regardless of physical activity (PA) status, however, they maintained absolute endpoint accuracy as predicted, which was partially explained by the reduction in movement speed. Finally, neither proprioceptive bias nor uncertainty were able to predict motor accuracy or variation in motor accuracy for either age group, contrary to predictions. We suggest that these unexpected age and PA-dependent increases in proprioceptive bias may be related to selective intrafusal fibre loss or more lateralised sensory priors biasing perception. Moreover, we suggest the rapid nature of the motor task may have minimised dependency

on online proprioceptive feedback and reduced the likelihood of measuring an association between the two. We therefore propose future work focus towards motor tasks which emphasises use of proprioceptive feedback such as continuous position tracking or sensorimotor adaptation to novel field dynamics.

3.1 – Introduction

In Chapter 1 (Section 1.3) we highlighted reports of characteristic changes in upper limb movement control with ageing, which included increased movement duration (Contreras-Vidal, Teulings, & Stelmach, 1998; Helsen et al., 2016; Ketcham, Seidler, Van Gemmert, & Stelmach, 2002), as well as increased spatial (Darling, Cooke, & Brown, 1989; Seidler, Alberts, & Stelmach, 2002) and temporal (Contreras-Vidal et al., 1998; Yan, Thomas, & Stelmach, 1998; Yan, Thomas, Stelmach, & Thomas, 2000) variations which have been reported during a range of different movement tasks. Similarly, there are age-dependent increases in movement duration as well as observed reductions in primary sub-movement duration (Helsen et al., 2016; Ketcham et al., 2002; Seidler-Dobrin & Stelmach, 1998) and an increased number of secondary sub-movements (Helsen et al., 2016; Ketcham et al., 2002) which are thought to represent an increase in online sensory feedback mechanisms to control movement in advanced age. These changes are thought to compensate for increased movement variability as a means to maintain endpoint accuracy (Helsen et al., 2016; Ketcham et al., 2002; Lee, Fradet, Ketcham, & Dounskaia, 2007).

We also identified reports of age-related changes in motor physiology which may contribute to these movement deficits (Section 1.2), including changes to both the peripheral neuromuscular system (Ceballos, Cuadras, Verdu, & Navarro, 1999; Morley, Baumgartner, Roubenoff, Mayer, & Nair, 2001; Slack, Hopkins, & Williams, 1979; Valdez et al., 2010) and more central structures too (Good et al., 2001; Rosano et al., 2008; Salat et al., 2005). Ultimately, these degenerative processes introduce more noise into the motor system which makes it harder to use internal models to accurately predict consequential sensory states of movements (Miall & Wolpert, 1996; Shadmehr, Smith, & Krakauer, 2010). As such, movements become more variable and this could explain why there appears to be a shift with ageing towards online sensory feedback control over internally driven mechanisms (Seidler-Dobrin & Stelmach, 1998). However, there are also deteriorations in peripheral and central sensory physiology with advanced age which may further contribute to this process (Kim, Suzuki, & Kanda, 2007; Salat et al., 2004; Swash & Fox, 1972). Specifically, we highlighted several experiments reporting age-related decline in upper limb proprioceptive acuity (Section 1.4; Adamo, Alexander, & Brown, 2009; Adamo, Martin, & Brown, 2007; Helsen et al., 2016; Wright, Adamo, & Brown, 2011) which has been shown as essential for basic control of movement (Sainburg, Ghilardi, Poizner, & Ghez, 1995). As such, the extent of proprioceptive loss with ageing may limit movement control, but the nature of this relationship is poorly understood.

One key publication aimed at examining this issue in more detail assessed performance on two passive proprioception tasks and a rapid target-based movement task at the wrist (Helsen et al., 2016). Although they found no relationship between proprioceptive and motor performance for either older or younger adults, their proprioceptive assessment techniques suffer from several limitations which reduce their ability to assess limb position sense as it occurs in day-to-day movements (see Section 1.4.3 for detailed review). These limitations include use of passive movement, single joint constraints and aspects of memory which may explain why they were unable to measure a relationship in their experiment. As such, there is a need to re-examine this relationship with more functionally relevant methods of measuring active proprioception and motor control, which are better matched with their use in everyday multi-joint, dynamic movement.

In Chapter 2, we successfully pilot tested a novel method of measuring dynamic proprioception and subsequently highlighted limitations in its protocol. In this chapter, we used a modified version of this task which addresses these limitations to more sensitively assess upper limb proprioception at 3 spatial locations in the 2D-workspace. We also assessed the profile of rapid, multi-joint reaching movements to spatially coincident targets which allowed us to closely examine the relationship between proprioception and motor control in older and younger adults. Since the reliability and sensitivity of data collected in Chapter 2 may be confounded by task limitations and sample size, we again used the reports of increased proprioceptive system noise from physiological degeneration and the findings from Cressman, Salomonczyk, & Henriques (2010) to predict that OAs would exhibit larger uncertainty ranges than YAs in this experiment, and that this would depend on PA levels. We also predicted OAs would have slower, more varied profiles of movement but that absolute endpoint accuracy would be maintained. Finally, we predicted that the extent of motor error variation would be positively associated with proprioceptive uncertainty in OAs.

3.2 – Methods

3.2.1 – Participants

There were 36 OAs (15 male, 71.2 ± 4.4 yrs), defined as 65 years or older, and 20 YAs (11 male, 20.4 ± 2.0 yrs), defined as 18-25 years old, who participated in the experiment. However, only data for 31 OAs (11 male, 71.2 ± 4.5 yrs) was included in the analysis and presented in this chapter due to unforeseeable data loss resulting in incomplete datasets for 5 older participants. All participants were right-hand dominant as defined by a laterality quotient of 30 or higher on the 10-item Edinburgh Handedness Inventory (Oldfield, 1971). Participants were excluded from participation if they had any history of neurological illness or carpal tunnel syndrome, arthritis or similar movement pains or limitations in the arm, wrist or fingers. All participants were asked to read an information sheet prior to participation and given the opportunity to ask any questions before they signed a written consent form. OAs also completed the Montreal Cognitive Assessment (MoCA) and were only included in the analysis if they scored 26 or above out of 30, which is considered to indicate "normal" cognitive functioning (Nasreddine et al., 2005).

3.2.2 – Physical Activity Measures

3.2.2.1 – Younger Adults

Self-reported PA measures were recorded using the IPAQ-Short questionnaire (Craig et al., 2003) for YAs, and was used predominantly to exclude highly physically active participants. As such, those individuals with a score considered as "Health Enhancing Physical Activity" were excluded from participation.

3.2.2.2 – Older Adults

After completing the experiment, OAs were given wrist-worn accelerometers (Philips Actiwatch 2) to wear for 5 days (120 hours), where "activity count" data was logged in 30 second epochs. If an epoch had 40 activity counts or higher then it was deemed to be physically "active", with the sum of all activity counts in these "active" epochs over the 5 days providing a metric for each older participant. The median value of the scores between participants was then used as a threshold to define "Inactive" and "Active" sub-groups of OAs for further analysis (demographic details for these groups are detailed in the Results section).

3.2.3 – Working Memory

In order to see whether working memory capacity influenced the ability to remember and replicate unseen limb positions, working memory was measured by using the backward digit span test (Adamo et al., 2009; Goble, Mousigian, & Brown, 2012). In this task, participants were required to memorise a sequence of random numbers (ranging 1-9; read out to them at a rate of approximately 1 number per second), and then recite them in reverse order. The task began with two trials at a sequence length of 2. If participants could correctly recite the sequence on at least 1 out of the 2 attempts at that sequence length level, the sequence length would increase by one. The task then incremented in this fashion until both attempted recitals were incorrect. The highest sequence length which the participant could correctly recite at least 1 out of the 2 attempts was recorded as their verbal working memory score (similar to the method used by Goble, Mousigian, et al., 2012).

3.2.4 – Experimental Set-Up

The experimental set-up was identical to that used in Chapter 2, with both the dynamic proprioceptive and rapid motor tasks completed on the vBOT 2D robotic manipulandum (Howard, Ingram, & Wolpert, 2009). Participants grasped the manipulandum handle with their right hand and viewed a reflected monitor display of targets and hand position (spatially coincident with the vBOT handle), which occluded vision of the hand and arm.

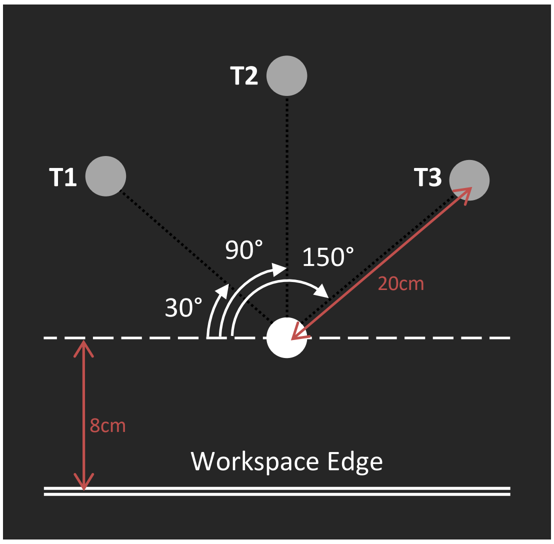


Figure 3.1. – Workspace locations and relative distances of the 3 targets used in both the dynamic proprioception and rapid motor tasks

In both the dynamic proprioceptive and rapid motor reaching tasks, participants made reaching movements from a white 1cm radius start position located 8cm into the workspace (approximately 28cm from the participant's torso). Participants made reaching movements to one of three 1cm radius grey targets which were located 20cm from the start position at 30°, 90° and 150° elevation (Figure 3.1). These targets were spatially similar to the distal targets used in Chapter 2, however the start position was nearer to the workspace edge and targets were 20cm away. When made available, hand position feedback was provided on a real-time basis as a 0.5cm radius white cursor.

3.2.5 – Dynamic Proprioception

3.2.5.1 – Procedure

Unless otherwise stated the key details for this task are identical to those used in Chapter 2, and will only be summarised briefly here. Participants made guided reaching movements towards visually presented targets before making a verbal judgement to indicate the side of the target they felt they had been guided to. Reaching movements were made to one of three pseudo-randomly presented targets 20cm from the start position, and the symbols used for verbal hand perception judgements were a 1cm width white square (counter-clockwise side of target; “Square”) and 1cm diameter white circle (clockwise side of target; “Circle”). The magnitude and direction of lateral deviations were altered on a trial-by-trial basis by two randomly interleaved PEST sequences with some key parameter alterations in light of findings from Chapter 2 detailed in the following sections. Each block of the dynamic proprioceptive trials were preceded by several unconstrained, null-field reaching trials with full visual feedback of hand position represented by a 0.5cm white position cursor. These trials were performed to the same spatially located targets and coloured feedback (an “explosion” graphic) was provided at the target location, with its size inversely proportional to the lateral error to the target.

3.2.5.2 – Channel Virtual Walls and Trajectory

The channel virtual walls used in the perceptual trials were controlled in an identical manner to that which was outlined in Chapter 2, such that forces experienced by participants always acted orthogonally to the pre-defined movement path according to Equation 2.1. The specific trajectory constrained by these walls was also defined similarly to Chapter 2; however, to reflect the increased reach distance of 20cm, the straight portions at the start and end of the movement spanned 5cm with the middle, minimum jerk deviation section occurring over 10cm (Figure 3.2). Participants were actively guided back to the start position through a similar minimum jerk profile following trial termination.

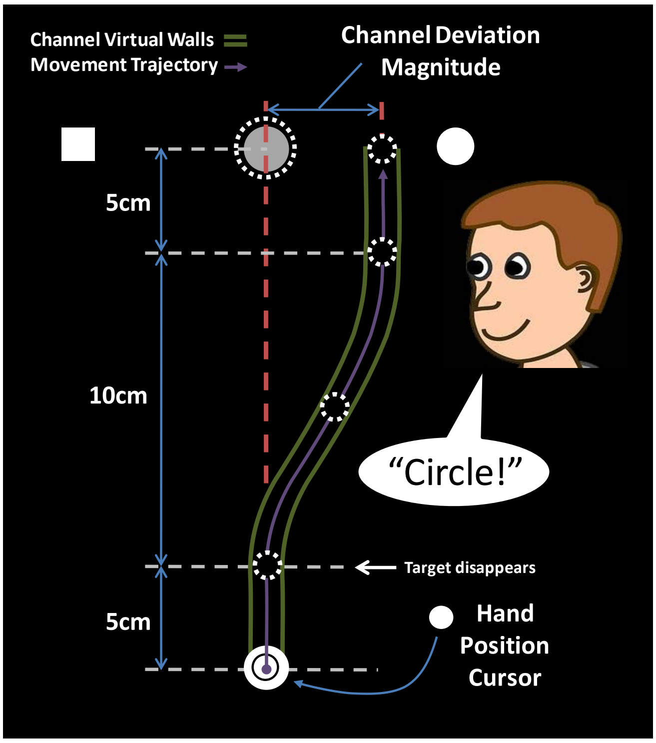


Figure 3.2. – Perceptual channel trajectory. Initial 5cm are straight, then minimum jerk profile deviates hand laterally (pre-defined channel deviation magnitude) over next linear 10cm reach, finishing with a further straight 5cm before verbal response was given. Target is visible for first 5cm before it disappears for remainder of trial (denoted by dashed circles). Hand position cursor remains occluded for all channel trials in a given block (unlike Chapter 2)

3.2.5.3 – PEST Sequence

To address the limitations identified in Chapter 2, some key changes were made to the PEST sequence for this experiment. The two interleaved sequences were applied across all 3 targets, as before, with one starting each from the counter clockwise (CCW; “Square”) and clockwise (CW; “Circle”) sides of the target. Initial deviation magnitude again began at 3cm (±0.05cm added noise) with an initial step size of ±1cm. However there were only 3 repeats per deviation size or ‘level’ which equated to 1 repeat per target.

To determine the step change in deviation magnitude following these 3 repeats, the sequence used Equations 2.2 and 2.3 in an identical way to Chapter 2 but with an altered PEST sequence weight (W_{PEST}) of 0.5. Since there were only 3 repeats per level (R_{tot}) for the present experiment, this meant that the total number of correct responses (R_{cor}) needed to be greater than or equal to 2 (i.e. 2 or 3 out of 3 correct) to satisfy Equation 2.2 and deem the responses reliably correct, leading to a reduction in the deviation size. Conversely, R_{cor} needed to be less than or equal to 1 (i.e. 1 or 0 out of 3 correct) to satisfy Equation 2.3 and deem the responses reliably incorrect, thus increasing the deviation size. This meant that the sequence step direction would reverse if there were consecutive sets of reliably correct or incorrect responses (or vice-versa), at which point the new step size would be half of the previous one i.e. from 1cm to 0.5cm at first reversal. Unlike Chapter 2, this was the only rule employed to alter step size.

3.2.5.4 – Task Design

All participants were given a short practice block to familiarise themselves with the task before completing 5 blocks of 6 null-field reaching trials followed by 48 perceptual channel trials. Participants were given the opportunity for a brief break between these blocks. The PEST sequence reset at the start of each new block such that the entire task included 5 PEST ‘runs’ and totalled 80 perceptual judgements per target. Null-field trials were intended to reduce occurrence of proprioceptive drift during prolonged periods of occluded vision and, as such, were not analysed. A summary of the task design can be seen in Figure 3.4 (left panel).

3.2.5.5 – Outcome Measures and Analysis

The perceptual responses were analysed in an identical way to Chapter 2, where responses were binarized (“Circle” = 1, “Square” = 0) and plotted against respective channel deviation size and direction following outlier removal (Pearson residual values greater than 2 standard deviations away from the mean). Proprioceptive outcome measures (uncertainty range and bias) were then extracted from the resulting logistic regression function. Average self-selected movement speed was recorded for the portion of movement where the participant first reached 1cm from the start position to 1cm short of the final position. Forces imposed against the channel walls were also recorded for the middle 3cm of the final straight, 5cm portion of movement (i.e. 16-19cm from the start; see Figure 3.2 for trajectory details).

3.2.6 – Rapid Motor Reaching

3.2.6.1 – Procedure

Participants began each reaching trial by moving the visible hand position cursor to the start position, which then turned blue. After a random wait time of between 2 and 3 seconds, one of the three targets appeared, and this was the participant's cue to move towards, and come to a stop on, the target as quickly and as accurately as possible. As soon as the cursor was moved outside of the start position it disappeared so that the participant had no visual feedback of hand position during the movement. The trial was terminated once hand velocity fell under 4cm/sec at which point an animated "explosion" appeared at the target whose size and colour was based on absolute Euclidean distance from trial termination position to the target location (absolute endpoint error [AE]). There was a small red explosion if this endpoint error was greater than 4cm, a medium-sized orange explosion if it was greater than 1.5cm but less than or equal to 4cm, and a large green explosion if it was less than or equal to 1.5cm. Once the explosion animation had finished, the hand position cursor reappeared, the target disappeared, and the participant was actively guided back towards the start position for the next trial.

3.2.6.2 – Task Design

To familiarise themselves with the task, participants initially performed 9 practice trials (3 per target) which were not included in the analysis. For the main task performance, target presentation order was randomised across 3 blocks of 20 movements such that there were a total of 20 movements to each target. Due to the relatively short nature of these blocks participants did not take breaks in between (a summary of the task design is shown in Figure 3.4, right panel).

3.2.6.3 – Outcome Measures and Analysis

Kinematic performance was quantified by calculating reaction time, peak hand velocity and duration to peak velocity. Movement initiation and termination were defined as the points where hand velocity first exceeded and then fell below 4cm/sec respectively. Reaction time was therefore defined as the duration of time between the target appearing (i.e. movement initiation cue) and movement initiation. Trials where reaction time was less than 0.1sec or greater than 1sec were excluded from analysis to avoid confounds of anticipatory movements and delayed responses, respectively. Duration to peak hand velocity was expressed as a percentage of total movement duration (time between movement initiation and termination) to examine the speed profile of the movement independently of its actual duration. Motor performance accuracy was quantified both by the AE at endpoint (movement termination position) and by the lateral deviation at endpoint (LE; Both accuracy measures shown in Figure 3.3). The LE was calculated as the orthogonal distance from the linear path between start position and target, to endpoint.

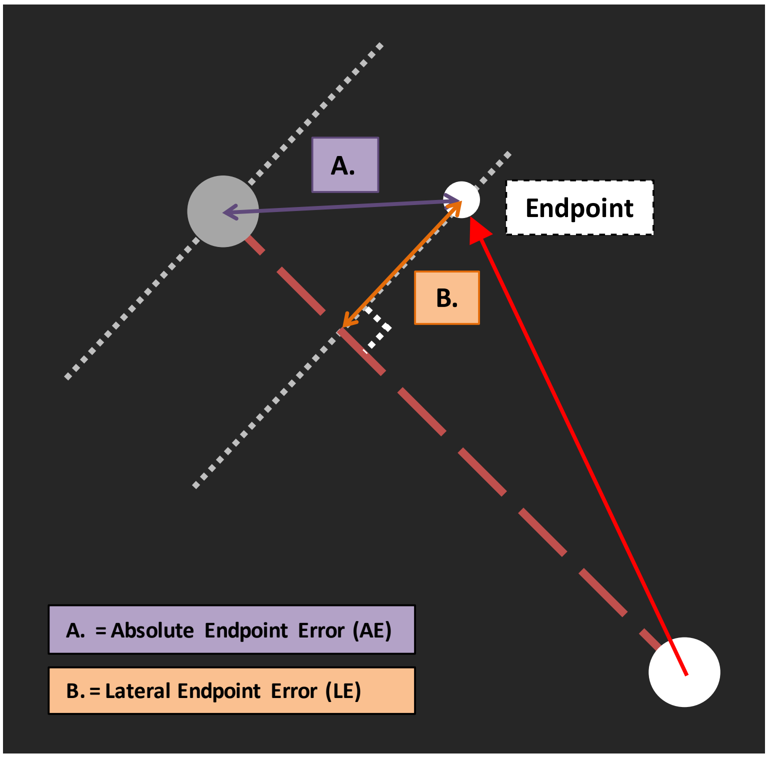


Figure 3.3. – Motor performance accuracy measures. Red line shows the movement path from start position to terminal hand position (endpoint). Euclidean distance from endpoint to target is absolute endpoint error (AE; purple arrow, **A.**) and orthogonal deviation from optimal or shortest path to target from start position is lateral endpoint error (LE; orange arrow, **B.**). LE represents motor error on parallel axis to dynamic perceptual judgements (indicated by grey dashed line intersecting target).

This indicated the lateral deviation from optimal or shortest hand path and was included in analysis so as to improve the predictive validity of the regression analyses against the proprioceptive measures, which use a similar lateral deviation measure according to perceptual judgements on an axis orthogonal to the start-target vector.

For all motor performance measures, the average and standard deviation was calculated for each participant so that systematic motor performance and motor variability measures could be recorded for each participant individually.

3.2.7 – Experimental Design and Statistical Analysis

All participants performed the dynamic proprioceptive task first to remove any likelihood that the feedback associated with rapid motor reaching may alter or improve proprioceptive acuity to the same spatially located targets. Participants were given a short break between tasks. A full summary of the experimental design is shown in Figure 3.4.

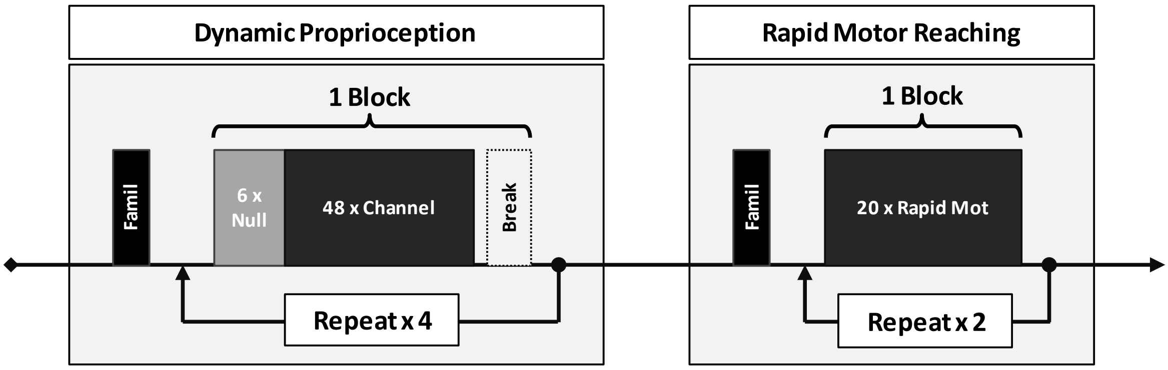


Figure 4. – Summary of experimental design. Dynamic proprioception task was always performed first, and began with a familiarisation block followed by 5 blocks of 6 x null and 48 x channel trials (total 240 channel trials, 80 per target). This was followed by the rapid motor reaching task which similarly began with a familiarisation block followed by 3 blocks of 20 trials (total 60 trials, 20 per target)

Figure 3.4. – Summary of experimental design. Dynamic proprioception task was always performed first, and began with a familiarisation block followed by 5 blocks of 6 x null and 48 x channel trials (total 240 channel trials, 80 per target). This was followed by the rapid motor reaching task which similarly began with a familiarisation block followed by 3 blocks of 20 trials (total 60 trials, 20 per target)

Values which were greater than 2.5 standard deviations away from the group mean were removed as outliers from analysis. The remaining data were analysed in separate 3 x 3 mixed-design ANOVAs: (Group; inactive OAs, active OAs, YAs) x (Target; 1, 2, 3), with a Greenhouse-Geisser correction used in all cases where the sphericity assumption was violated, and significance assessed at the $p < .050$ level. In the case of follow-up multiple comparisons, uncorrected (Least Significant Difference; LSD) values are reported but assessed for significance using a False Discovery Rate (FDR) analysis which is described in detail in Chapter 2. This applies to sets of comparisons performed to follow up significant ANOVA main effects (typically sets of 3 independent [group effects] or paired [target effects] t-tests), but also to assess associative relationships tested with bivariate correlations and linear regression models. FDR adjusted *p*-thresholds (p_{FDR}) are noted in the results section as necessary; when there were no significant comparisons observed (i.e. $p < p_{\text{FDR}}$ was not found) the smallest observed p-value (p_{min}) is reported with its associated critical significance value (still denoted as p_{FDR}) (see Chapter 2 for details).

3.3 – Results

3.3.1 – Physical Activity Grouping

The 31 older adults (OAs) were divided into either a physically inactive or physically active sub-group according to a threshold median value of 1.68 x 10^6 activity counts from the 5-day accelerometer data. This left 16 OAs in the inactive group (1.29 ± .31 x 10^6 counts; 7 male, 72.9 ± 5.1 yrs) and 15 in the active group (1.96 ± .26 x 10^6 counts; 4 male, 69.3 ± 2.7 yrs). Following this group allocation, it was found that those in the inactive group were significantly older than those in the active group (t[22.9] = 2.52, $p = .019$). This difference is addressed directly as needed for cases where it could be deemed to have a confounding effect on multiple comparisons.

3.3.2 – Dynamic Proprioception

3.3.2.1 – Proprioceptive Measures

A summary of the proprioceptive outcome measures can be seen in Figures 3.5 (bias in Panel A, and uncertainty range in Panel B) and 3.6 (full scale summary of both measures) with a full list of results presented in Table 3.1. The ANOVA revealed a significant main effect of Group on bias (F[2, 47] = 4.11, $p = .023$, $\eta^2_p = .15$) with follow up comparisons between groups revealing significantly larger biases for inactive OAs than younger adults (YAs; $p = .009$; $p_{\text{FDR}} = .017$). To test whether this effect was truly due to physical inactivity of OAs and not their increased age (see 3.3.1 – Physical Activity Grouping) we correlated age and bias (averaged across all 3 targets) for the entire OA sample. Since the correlation was non-significant (r = .005, $p = .977$) we conclude that the bias effect is due to the physical inactivity of OAs, and not to their increased age. Target also had a significant effect on bias (F[1.7, 78.6] = 3.84, $p = .032$, $\eta^2_p = .08$) but there were no differences found between specific pairs of targets ($p_{\text{min}} = .023$; $p_{\text{FDR}} = .017$). The interaction of Target and Group on bias was non-significant (F[3.3, 78.6] = 0.28, $p = .861$).

Group did not have a significant effect on uncertainty range (F[2, 45] = .31, $p = .733$) although Target did (F[2, 90] = 4.78, $p = .011$, $\eta^2_p = .10$), such that uncertainty range was larger at target 3 than target 2 ($p = .006$; $p_{\text{FDR}} = .017$). There was no interaction effect of Group and Target on uncertainty range (F[4, 90] = .51, $p = .730$).

Contrary to predictions, but similar to Chapter 2, these findings show that physically inactive OAs have larger proprioceptive biases but not uncertainty ranges than YAs.

Measure	Group	Target			Overall
		1	**2**	**3**	
Uncertainty Range (cm)	*Inactive Older*	1.55 *(± .20)*	1.23 *(± .18)*	1.60 *(± .26)*	1.46 *(± .18)*
	Active Older	1.31 *(± .13)*	1.25 *(± .17)*	1.54 *(± .20)*	1.36 *(± .15)*
	Younger	1.25 *(± .08)*	1.24 *(± .13)*	1.47 *(± .11)*	1.32 *(± .11)*
Bias (cm)	*Inactive Older*	1.00 *(± .13)*	.90 *(± .13)*	.77 *(± .16)*	**.89 (± .13)
	Active Older	.81 *(± .13)*	.79 *(± .15)*	.73 *(± .17)*	.78 *(± .14)*
	Younger	.51 *(± .13)*	.42 *(± .10)*	.33 *(± .14)*	.42 *(± .11)*
Movement Velocity (cm/sec)	*Inactive Older*	13.9 *(± 1.6)*	14.1 *(± 1.7)*	15.7 *(± 1.4)*	**14.6 (± 1.6)
	Active Older	15.1 *(± 1.2)*	15.4 *(± 1.2)*	17.8 *(± 1.5)*	16.1 *(± 1.3)*
	Younger	19.7 *(± 1.2)*	19.7 *(± 1.4)*	21.1 *(± 1.4)*	20.2 *(± 1.3)*

Table 3.1. – Group average proprioceptive (uncertainty range and bias) and kinematic (movement velocity) data for inactive older adults, active older adults, and younger adults. Values are given as means ± standard error where significantly different values from younger adults indicated by ** (*p* < .010, multiple comparisons subjected to FDR adjusted *p*-threshold)

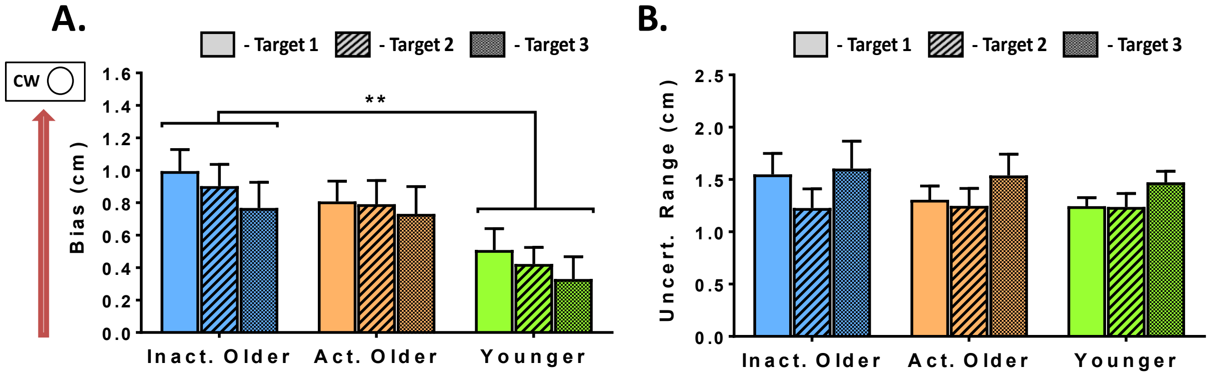


Figure 3.5. – Group average data from dynamic proprioceptive task (mean ± standard error bars) **A**. results for bias, where inactive older adults had significantly larger, positive biases than younger adults (** *p* < .010, multiple comparisons subjected to FDR adjusted *p*-threshold). Note all groups have positive biases which represents perception of hand position towards the clockwise ("Circle") side of the targets **B**. results for uncertainty range where there were no significant differences observed between any of the 3 groups

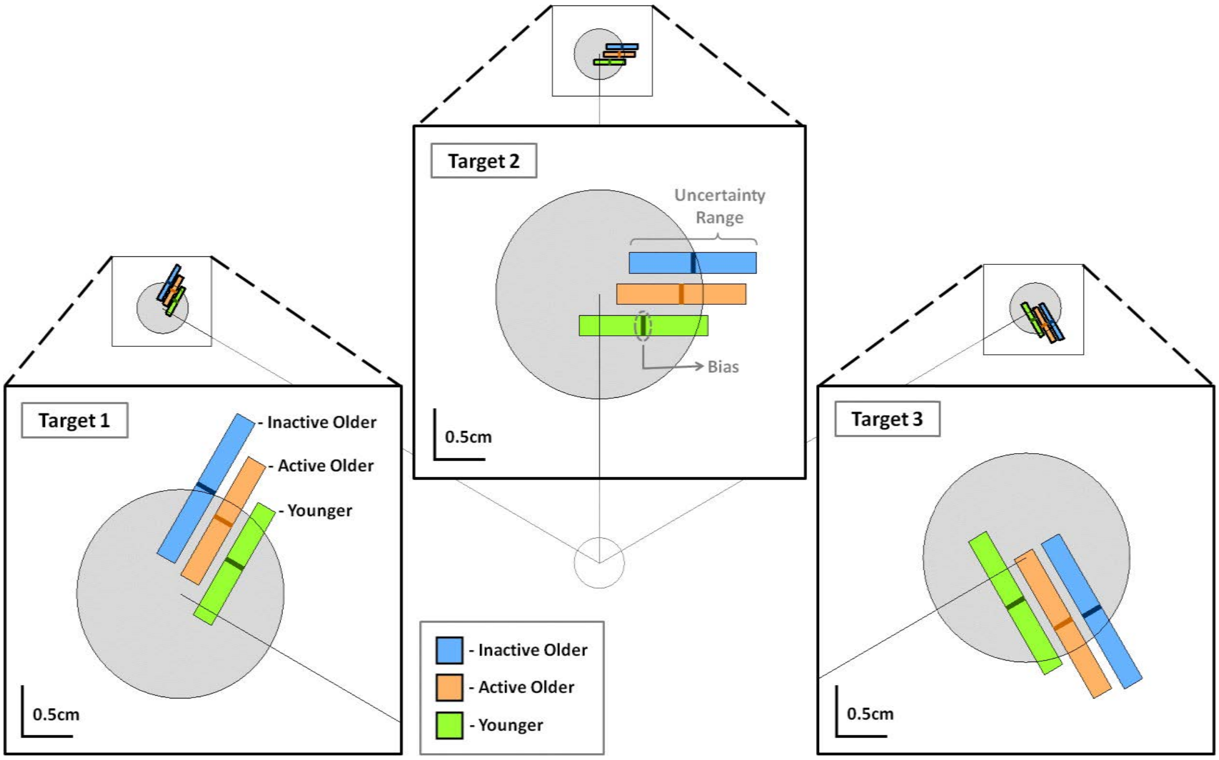


Figure 3.6. – Group average data from dynamic proprioceptive task scaled and superimposed over targets. Thick coloured line represents the bias and on average shows participants perceived their hand to be more towards the clockwise ("Circle") side of the target. This was significantly greater across targets for inactive older adults than younger adults (*p* = .009). The length of the coloured bar represents the uncertainty range and was similar between groups (*p* = .733)

3.3.2.2 – Kinematic Measures

Due to unforeseeable data loss, we had only partial kinematic data which was non-analysable (whilst perceptual judgement data remained valid) for 4 OAs in the physically inactive group. For this reason kinematic data here was analysed as n = 12 for inactive OAs. This data is summarised in Table 3.1. Group had a significant effect on average movement velocity (F[2, 43] = 4.6, p = .015, η^2_p = .18) such that inactive OAs moved significantly slower than YAs (p = .007; p_{FDR} = .017). Target also had a significant main effect on movement velocity (F[1.7, 71.7] = 18.3, p < .001, η^2_p = .30), where multiple post-hoc comparisons revealed that movements were faster at target 3 than targets 1 and 2 (both p < .001; p_{FDR} = .034). However, the Group by Target interaction was not significant (F[3.3, 71.7] = .729, p = .552).

To examine how self-selected movement speed was related to perceptual performance in this task, both bias and uncertainty range were correlated with movement velocity for each of the different groups at each target (bias and uncertainty range Pearson correlations for 3 [Group] x 3 [Target] relationships). We found that none of the relationships were significant (bias, p_{min} = .286; uncertainty range, p_{min} = .028; p_{FDR} = .006) which demonstrates that perception was independent of movement speed for this task.

As noted previously in Chapter 2, limb position sense has been shown to be influenced by corollary discharge or sense of effort (Smith, Crawford, Proske, Taylor, & Gandevia, 2009). To ensure this phenomenon wasn't confounding the perceptual outcome measures reported presently, the mean orthogonal force exerted on the channel walls in the last portion of the channel trial movement was correlated with bias. Similar to movement speed, there were no significant relationships observed (Pearson correlations for 3 [Group] x 3 [Target] relationships; $p_{\text{min}} = .028$; $p_{\text{FDR}} = .006$) demonstrating systematic perceptual errors were also independent of direction of effort exerted during task performance.

3.3.3 – Rapid Motor Reaching Performance

3.3.3.1 – Performance Accuracy Measures

A summary of the lateral motor accuracy results are summarised in Figure 3.7 (lateral error [LE] in Panel A and lateral error variation [LE Var] in Panel B) with all motor accuracy data summarised in Table 3.2. The spatial distribution of individuals' average end-positions and the 95% confidence interval ellipses for the groups are shown in Figure 3.8 for each target.

Measure	Group	Target			**Overall**
		1	**2**	**3**	
LE (cm)	*Inactive Older*	.25 *(± .13)*	-1.24 *(± .16)*	-1.31 *(± .20)*	-.77 *(± .12)*
	Active Older	.48 *(± .15)*	-1.42 *(± .21)*	-.97 *(± .30)*	-.64 *(± .15)*
	Younger	-.40 *(± .22)*	-1.47 *(± .17)*	-1.08 *(± .26)*	-.98 *(± .15)*
LE Var (cm)	*Inactive Older*	.79 *(± .06)*	.86 *(± .06)*	.74 *(± .05)*	.80 *(± .04)*
	Active Older	.94 *(± .09)*	.79 *(± .07)*	.95 *(± .08)*	.89 *(± .07)*
	Younger	1.03 *(± .08)*	.91 *(± .05)*	.99 *(± .07)*	.98 *(± .05)*
AE (cm)	*Inactive Older*	1.57 *(± .08)*	2.12 *(± .19)*	2.03 *(± .20)*	1.91 *(± .13)*
	Active Older	1.94 *(± .13)*	2.34 *(± .16)*	2.19 *(± .20)*	2.16 *(± .13)*
	Younger	2.14 *(± .11)*	2.24 *(± .14)*	2.32 *(± .18)*	2.23 *(± .12)*
AE Var (cm)	*Inactive Older*	.88 *(± .06)*	.94 *(± .07)*	.96 *(± .07)*	.92 *(± .05)*
	Active Older	1.06 *(± .08)*	.94 *(± .07)*	1.09 *(± .15)*	1.03 *(± .09)*
	Younger	1.08 *(± .08)*	1.00 *(± .06)*	.99 *(± .06)*	1.02 *(± .06)*

Table 3.2. – Group average motor performance accuracy measures for inactive older adults, active older adults, and younger adults. Values are given as means ± standard error, there were no significant group effects observed. LE = Lateral Endpoint Error, AE = Absolute Endpoint Error, in both cases Var = intra-subject standard deviation (variation) in either measure

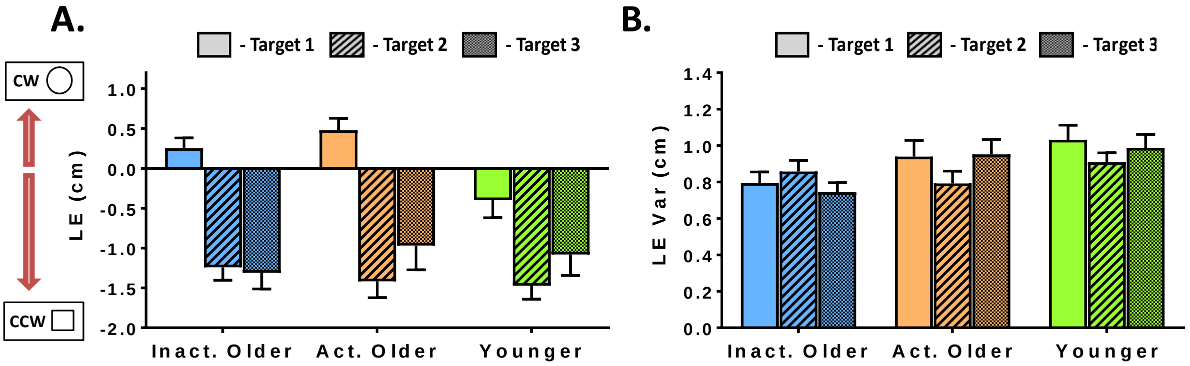


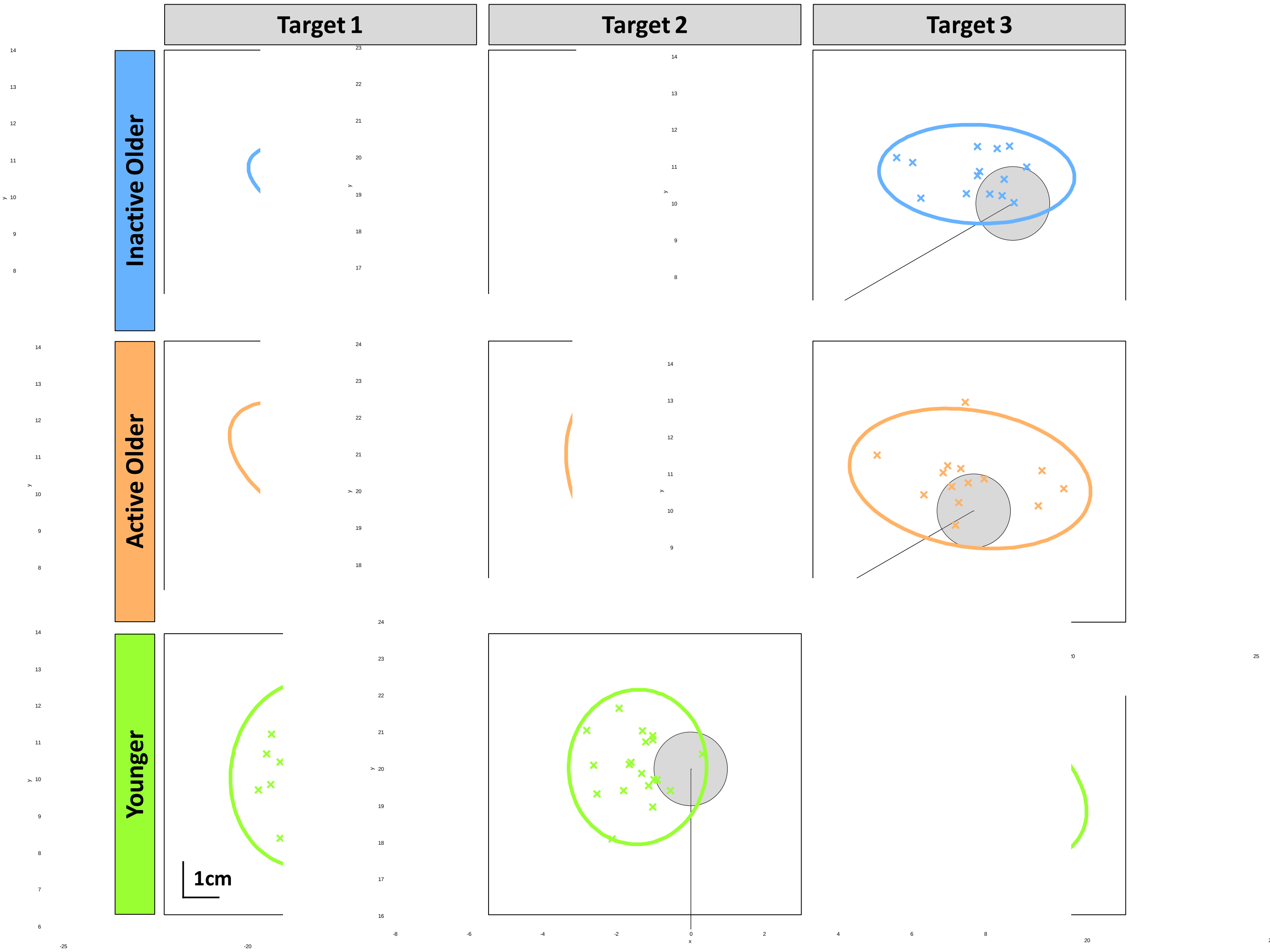
Figure 3.7. – Group average motor performance accuracy measures (mean ± standard error bars) to be used in linear regression models with proprioceptive outcomes **A**. results for lateral endpoint error (LE), where negative error represents an end-position which deviated laterally in the counter-clockwise ("Square" from the proprioceptive task) direction and vice versa **B**. results for the intra-subject variation (standard deviation) of the LE (LE Var). There were no significant differences between groups for either measure

Absolute endpoint error (AE) was unaffected by Group (F[2,44] = 1.8, *p* = .181) but was affected by Target (F[2, 88] = 7.6, *p* = .001, η^2_p = .15) with errors being significantly larger at targets 2 (*p* < .001; p_{FDR} = .033) and 3 (*p* = .008) than at target 1. The Group x Target interaction was non-significant (F[4, 88] = 1.11, *p* = .356). Neither Group (F[2, 44] = .78, *p* = .471) nor Target (F[1.7, 76.7) = .93, *p* = .389) had an effect on intra-subject variation in AE (standard deviation across trials; AE Var), with the interaction of Target and Group also being non-significant (F[3.5, 76.7] = 1.4, *p* = .260). Thus, all groups had similar systematic and variable endpoint errors in accuracy of their movements.

Moreover, there was a non-significant effect of Group (F[2, 48] = 1.6, *p* = .218) on LE but a significant effect of Target (F[1.4, 68.8] = 51.2, *p* < .001, η^2_p = .52). Post-hoc comparisons showed that LE was significantly different between all targets (target 1 vs. 2, *p* < .001; target 1 vs. 3, *p* < .001; target 2 vs. 3, *p* = .038; p_{FDR} = .050) such that lateral errors were smallest and more positive at target 1, and largest and most negative at target 2. The interaction of Group and Target on LE was non-significant (F[2.9, 68.8) = 2.3, *p* = .091). There were no significant effects on LE Var for Group (F[2, 45] = 2.8, $p = .072$), Target (F[2, 90] = 1.2, $p = .308$) or their interaction (F[4, 90] = 1.8, $p = .180$).

Collectively, this demonstrates a similar level of systematic and variable lateral error between groups during these rapid, target-reaching movements. This therefore supports the prediction of maintained endpoint accuracy in motor performance with advanced age.

Since participants were provided with accuracy feedback during the motor task, an additional ANOVA was performed on the accuracy measures. We compared early (first 10 trials) vs. late (last 10 trials) errors to examine whether there were significant improvements in performance (motor learning) during the task. For these purposes we focus on, and report, only the factors of Time-Point (early or late in the task) and Group x Time-Point interaction effects from the 3 x 3 x 2 ANOVAs: (Group: inactive older, active older or younger) x (Target) x (Time-Point). There was a significant effect of Time-Point on LE (F[1, 47] = 6.0, $p = .018$, $\eta^2_p = 0.11$), AE (F[1, 42] = 6.2, $p = .017$, $\eta^2_p = .13$) and AE Var (F[1, 42] = 7.0, $p = .012$, $\eta^2_p = .14$) such that lateral errors, absolute errors and variation in absolute errors respectively were larger in the early stages of the task than the late. However, there were no significant Group x Time-Point interaction effects on any of the motor accuracy measures (all $p > .050$). This shows that although there were improvements in performance over the duration of the task, the extent of these improvements did not differ between any of the 3 groups.



95% confidence ellipses for each of the different groups and targets (figure generated for visualisation purposes only)

3.3.3.2 – Kinematic Performance Measures

The kinematic measures for the rapid motor task kinematic measures are summarised in Table 3.3. There was a significant effect of Group on reaction time (RT; F[2, 47] = 11.5, $p < .001$, $\eta^2_p = .33$) whereby both inactive and active OAs (both $p < .001$; $p_{FDR} = .033$) had slower reaction times than YAs (Figure 3.9, Panel A). Likewise there was a significant effect of Target on RT (F[2, 94] = 15.0, $p < .001$, $\eta^2_p = .24$) whereby participants reacted faster at target 1 compared to both target 2 and 3 (both $p < .001$; $p_{\text{FDR}} = .033$). The interaction effect of Group and Target on RT was not significant (F[4, 94] = 2.0, $p = .102$). There was also a Group effect on the intra-participant variability of reaction time (RT Var; F[2, 45] = 8.2, $p = .001$, $\eta^2_p = .27$) where both inactive ($p = .001$; $p_{\text{FDR}} = .033$) and active ($p = .002$) OAs had more variable reaction times than YAs (Figure 3.9, Panel B). There was also a significant Target effect on RT Var (F[1.7, 76.4) = 5.3, $p = .010$, $\eta^2_p = .11$) where reaction time variation was lower at target 1 compared to target 2 ($p = .015$; $p_{\text{FDR}} = .033$) and target 3 ($p = .003$). The interaction of Group and Target on RT Var was also significant (F[3.4, 76.4] = 3.2, $p = .024$, $\eta^2_p = .12$) and simple effects analysis showed that both inactive and active OAs had more variable reaction times at targets 2 and 3 than YAs (3 [Group] x 3 [Target] comparisons, all significant at $p_{\text{FDR}} = .028$). However at target 1, only the inactive OAs had significantly greater RT Var than YAs ($p = .017$).

Group had a significant effect on peak hand velocity (Peak Vel; F[2, 46] = 18.8, $p < .001$, $\eta^2_p = .45$), where both inactive and active OAs were significantly slower than YAs ($p < .001$ in both cases; $p_{\text{FDR}} = .033$; Figure 3.9, Panel C). Target also had a significant effect on Peak Vel (F[2, 92] = 32.8, $p < .001$, $\eta^2_p = .55$), with multiple comparisons showing each target was significantly different from one another ($p < . 001$ in all cases; $p_{\text{FDR}} = .050$) such that target 3 movements were fastest and target 1 movements were slowest. The interaction effect of Group and Target on Peak Vel was also significant (F[4, 92] = 3.5, $p = .011$, $\eta^2_p = .13$) with simple effects analysis reflecting the main effect of Group, in that both inactive and active OAs were significantly slower than YAs at all 3 targets (3 [Group] x 3 [Target] comparisons; all significant at $p < .003$; $p_{\text{FDR}} = .033$).

Measure	Group	Target			**Overall**
		1	**2**	**3**	
RT (sec)	*Inactive Older*	.44 (± .02)	.46 (± .02)	.47 (± .02)	***.46 (± .02)
	Active Older	.42 (± .02)	.46 (± .02)	.46 (± .03)	***.45 (± .02)
	Younger	.35 (± .01)	.37 (± .01)	.36 (± .01)	.36 (± .01)
RT Var (sec)	*Inactive Older*	*.072 (± .010)	**.074 (± .006)	**.079 (± .008)	**.075 (± .007)
	Active Older	.057 (± .006)	**.082 (± .010)	**.077 (± .009)	**.072 (± .007)
	Younger	.045 (± .004)	.048 (± .004)	.043 (± .003)	.046 (± .003)
PeakVel (cm/sec)	*Inactive Older*	***48.1 (± 3.2)	***51.2 (± 3.9)	**57.6 (± 3.9)	***52.3 (± 3.6)
	Active Older	***53.0 (± 3.7)	***56.8 (± 3.5)	**58.1 (± 4.1)	***55.9 (± 3.7)
	Younger	81.4 (± 4.0)	84.3 (± 4.8)	85.3 (± 4.7)	83.7 (± 4.5)
¥ Peak Vel Var (cm/sec)	*Inactive Older*	7.04 (± .55)	8.12 (± .90)	8.21 (± .95)	7.79 (± .74)
	Active Older	6.75 (± .59)	7.52 (± .78)	8.11 (± 1.00)	7.46 (± .73)
	Younger	9.18 (± .66)	9.82 (± .68)	10.56 (± .98)	9.85 (± .73)
DPV (% Move Duration)	*Inactive Older*	42.5 (± 1.2)	43.6 (± 1.3)	47.4 (± 1.5)	44.5 (± 1.2)
	Active Older	41.1 (± 1.3)	42.7 (± 1.7)	44.6 (± 1.5)	42.8 (± 1.4)
	Younger	42.9 (± .5)	44.2 (± .6)	46.0 (± .6)	44.4 (± .5)
¥ DPV Var (% Move Dur.)	*Inactive Older*	6.42 (± .55)	6.69 (± .52)	6.79 (± .64)	6.64 (± .48)
	Active Older	6.41 (± .62)	6.93 (± .58)	7.40 (± .70)	6.91 (± .56)
	Younger	5.35 (± .44)	5.83 (± .41)	5.24 (± .36)	5.47 (± .29)

Table 3.3. – Group average motor performance kinematic measures for inactive older adults, active older adults and younger adults (means ± standard error). Significant differences from younger adults are indicated by ** (*p* < .010) and *** (*p* < .001; multiple comparisons subjected to FDR adjusted *p*-threshold). Significant group effects which did not have significant follow-up multiple comparisons indicated by ¥ (*p* < .050). RT = Reaction Time, Peak Vel = Peak Hand Velocity, DPV = Duration to Peak Velocity (expressed as percentage of total movement duration). In all cases Var = intra-subject standard deviation (variation) of the respective measure

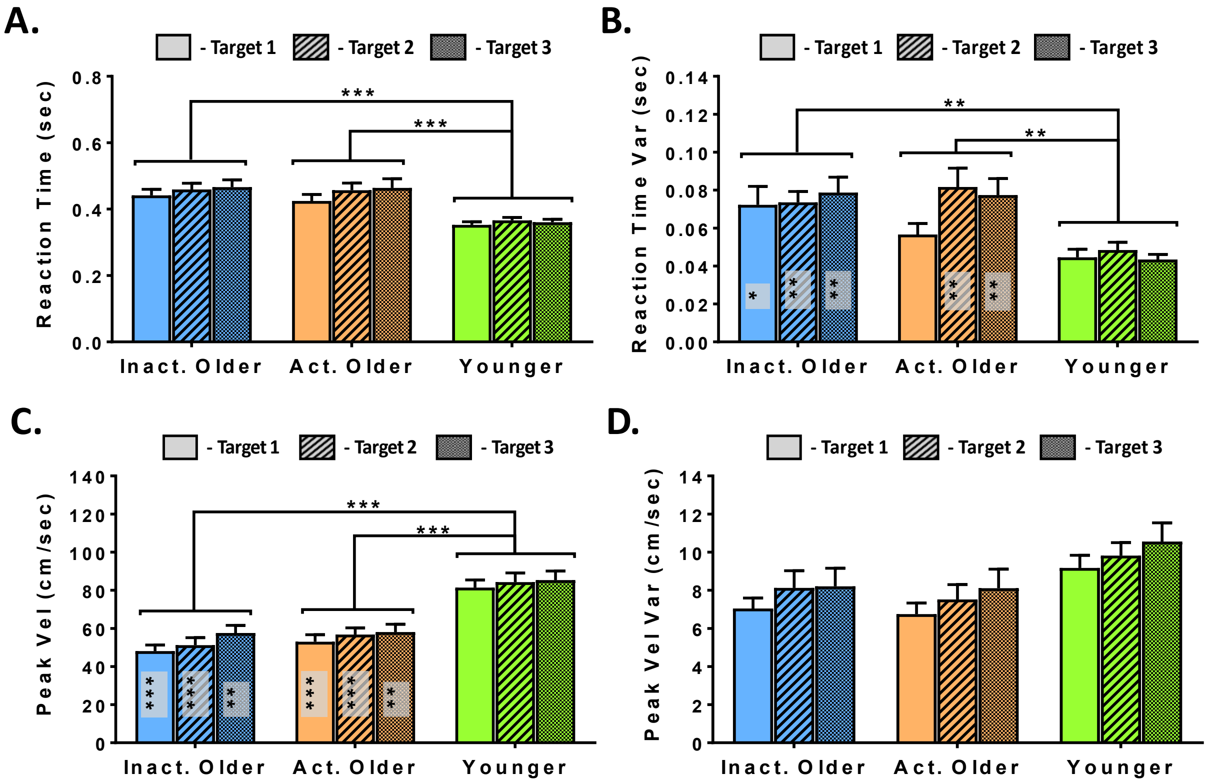


Figure 3.9. – Group average motor performance kinematic measures (mean ± standard error bars) results are shown as **A**. reaction time **B**. intra-subject reaction time variation **C**. peak hand velocity and **D**. intra-subject peak velocity variation. Significant differences from younger adults are indicated by ***** ($p < .050$), ****** ($p < .010$), ******* ($p < .001$) with multiple comparisons subjected to FDR adjusted *p*-threshold. Asterisks within bars denote significant difference from younger adults at same target, asterisks above brackets represent significant group level differences

There was an effect of Group on the intra-subject variation in Peak Vel (Peak Vel Var; Figure 3.9, Panel D; F[2, 47] = 3.3, $p = .046$, $\eta^2_p = .12$) however multiple comparisons did not show specific differences between groups ($p_{\text{min}} = .025$; $p_{\text{FDR}} = .017$).There was also a main effect of Target on Peak Vel Var (F[2, 94] = 7.8, $p = .001$, $\eta^2_p = .14$), with target 1 showing a significantly reduced variation in peak velocity compared to target 2 ($p = .006$; $p_{\text{FDR}} = .033$) and 3 ($p = .001$). However the Group x Target interaction was not significant (F[4, 94] = .95, $p = .945$).

The main effect of Group on duration to peak hand velocity (DPV; Table 3.3) was not significant (F[2, 47] = .77, p = .473). However, there was a main effect of Target (F[2, 94] = 33.7, p < .001, η^2_p = .42) whereby DPV was significantly different between all 3 targets (target 1 vs. 2, p = .002; target 1 vs. 3 p < .001; target 2 vs. 3, p < .001; p_{FDR} = .050) such that peak velocity occurred latest in movements to target 3 and earliest to target 1. There was no interaction of Group and Target on DPV (F[4, 94] = 1.1, p = .382). Group had a significant effect on intra-subject variation of DPV (DPV Var; F[2, 48] = 3.3, p = .044 η^2_p = .12). However multiple comparisons did not reveal any differences in DPV Var between specific groups (p_{min} = .022; p_{FDR} = .017). Finally, neither Target (F[2, 96] = 1.3, p = .287) nor the Group by Target interaction (F[4, 96] = .76, p = .553) had an effect on DPV Var.

Together, the results from these kinematic measures shows that OAs tend to react and move more slowly than YAs, regardless of PA level. However, the speed profile of movements was similar between all groups. These findings partially support the prediction that OAs would have a slower more varied profile of movements for this task.

3.3.3.3 – Errors Controlled for Peak Velocity

Since there were significant differences in peak hand velocity between older and younger groups, we wanted to see whether movement errors were influenced by this in a potential speed-accuracy trade-off. Specifically, whether OAs were slowing their movements to become comparatively accurate to YAs during task performance. In order to do this, we divided both LE and AE by corresponding average peak hand velocity for each target to create lateral and absolute errors which were controlled for by movement speed. These velocity controlled error measures (LE_{PVCont}; AE_{PVCont}) were analysed by similar 3 x 3 mixed-design ANOVAs: (Group; inactive OAs, active OAs, YAs) x (Target; 1, 2, 3).

This group average data for these measures is summarised in Table 3.4. There was no effect of Group on LE_{PVCont} (Figure 3.10, Panel A; F[2, 46] = .19, p = .826) but the main effect of Target was significant (F[1.6, 73.7] = 58.1, $p < .001$, $\eta^2_p = .56$), where velocity controlled lateral errors were all significantly different between targets (target 1 vs. 2, $p < .001$; target 1 vs. 3, $p < .001$; target 2 vs. 3, $p = .018$; $p_{FDR} = .050$) with smallest most positive errors at target 1 and largest most negative errors at target 2. The Group x Target interaction LE_{PVCont} was also significant (F[3.2, 73.7] = 4.8, $p = .004$, $\eta^2_p = .17$) however simple effects analysis did not reveal any specific differences between groups at any of the 3 targets, though there was a trend towards active OAs having more positive velocity controlled lateral errors than YAs at target 1 ($p = .0063$; all other relationships $p_{min} = .015$; $p_{FDR} = .0056$) .

The Group effect on AE_{PVCont} was significant (F[2, 42] = 4.2, p =.021, $\eta^2_p = .17$) such that both inactive ($p = .027$; $p_{FDR} = .033$) and active ($p = .014$) OAs had larger velocity controlled absolute errors than YAs (Figure 3.10, Panel B). There was also a significant main effect of Target (F[2, 84] = 4.2, p =.023, $\eta^2_p = .09$) where velocity controlled absolute errors were larger at target 2 than target 1 only ($p = .012$; $p_{FDR} = .017$). The Group x Target interaction on AE_{PVCont} was not significant (F[4, 84] = .73, p =.574).

Collectively, this additional analysis shows that the maintenance of absolute endpoint accuracy in OAs can be partially explained by movement slowing. However, lateral errors appear to be independent of age regardless of movement speed, suggesting a different mechanism may be responsible for this.

Measure	Group	Target			**Overall**
		1	**2**	**3**	
$\mathrm{LE}_{\mathrm{PVCont}}$ x 10^{-3} (sec)	*Inactive Older*	5.6 *(± 2.8)*	-24.3 *(± 3.2)*	-23.8 *(± 4.1)*	-14.1 *(± 2.4)*
	Active Older	7.5 *(± 2.8)*	-25.6 *(± 4.5)*	-16.8 *(± 5.6)*	-11.5 *(± 3.2)*
	Younger	-5.7 *(± 3.2)*	-19.3 *(± 3.1)*	-14.0 *(± 3.6)*	-13.0 *(± 2.6)*
$\mathrm{AE}_{\mathrm{PVCont}}$ x 10^{-3} (sec)	*Inactive Older*	35.0 *(± 2.6)*	43.3 *(± 4.0)*	38.8 *(± 4.9)*	***39.0 *(± 3.3)***
	Active Older	38.5 *(± 3.5)*	43.5 *(± 3.9)*	38.8 *(± 4.1)*	***40.2 *(± 3.1)***
	Younger	27.7 *(± 2.3)*	29.3 *(± 4.3)*	28.9 *(± 3.2)*	28.6 *(± 3.1)*

Table 3.4. – Group average motor accuracy measures divided by peak hand velocity for inactive older adults, active older adults, and younger adults. Values are given as means ± standard error (x 10^{-3}) where significantly different from younger adults indicated by ***** (*p* < .050, multiple comparisons subjected to FDR adjusted *p*-threshold). $\mathrm{LE}_{\mathrm{PVCont}}$/$\mathrm{AE}_{\mathrm{PVCont}}$ = lateral and absolute error controlled for by peak velocity respectively

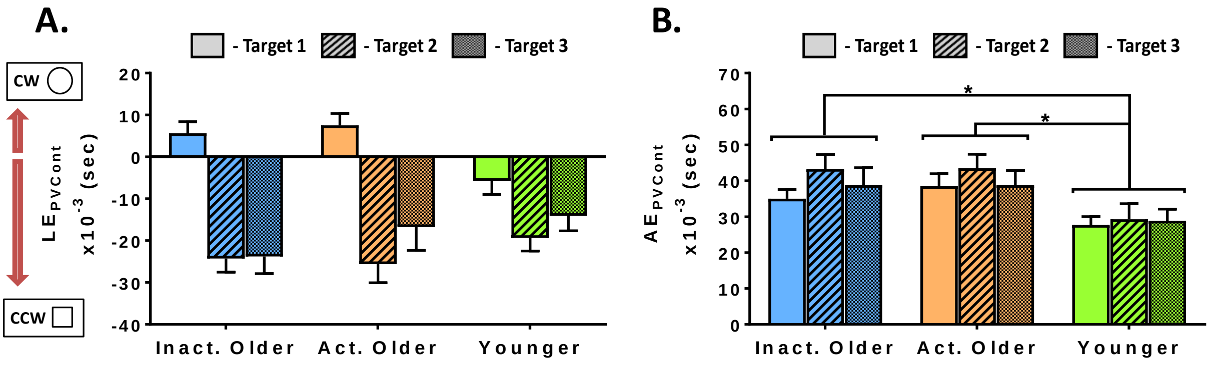


Figure 3.10. – Group average motor accuracy measures controlled peak hand velocity (means ± standard error x 10^{-3}) for inactive older adults, active older adults, and younger adults. **A.** Lateral error divided by peak hand velocity ($\mathrm{LE}_{\mathrm{PVCont}}$) where more positive values represent errors to the clockwise (or "Circle" from proprioceptive task) side. **B.** Absolute errors divided by peak hand velocity ($\mathrm{AE}_{\mathrm{PVCont}}$). Significantly different values from younger adults indicated by ***** (*p* < .050, multiple comparisons subjected to FDR adjusted *p*-threshold)

3.3.4 – Working Memory Capacity

All groups had similar working memory capacity scores, as indicated by a non-significant one-way ANOVA (F[2, 48] = .16, *p* = .854). Inactive OAs had the lowest score (5.5 ± 1.3 numbers in sequence) followed by active OAs (5.7 ± 1.4 numbers in sequence) and YAs (5.8 ± 1.6 numbers in sequence). To see how working memory was related to proprioceptive performance, we correlated the bias and uncertainty range averaged across all 3 targets with working memory score. There were no significant relationships found for any of the 3 groups for either measure (all |r| < .38, p_{min} = .106; p_{FDR} = .008), showing proprioceptive performance was independent of working memory.

3.3.5 – Predicting Motor Performance from Proprioceptive Acuity

An important objective of this experiment was to examine the extent to which proprioceptive acuity could predict motor performance in older and YAs, which we investigated with a series of linear regression models. But in order to minimise the number of these tests and keep the analysis meaningful, it is important to consider a hypothesis led approach to decide which measures should be analysed in this way. For dynamic proprioception measures, the bias gives a systematic proprioceptive error whilst the uncertainty range indicates variable errors, but both are made according to judgements of limb position along an axis orthogonal to start-target vector. Because of this, we assume that if either measure was related to motor control this would be most apparent with motor errors along a similar orthogonal axis. Thus, LE and LE Var (intra-subject standard deviation of LE) were chosen as the motor performance measures to include in the regression models. Specifically, bias was used to predict LE (i.e. systematic proprioceptive error to predict systematic motor error) and uncertainty range used to predict LE Var (i.e. variable proprioceptive error to predict variable motor error).

Since there were some significant target effects for these measures which did not always occur in a linear fashion, separate linear regression models were used for each of the different targets. However, to increase power of this analysis, all OAs were included in the same models with PA level (accelerometer counts) used as an additional predictor to control for its effects. Self-reported PA (IPAQ-score) was used in the regression models for YAs. Since LE appeared to be independent of peak hand velocity (see 3.3.3.3 – Errors Controlled for Peak Velocity), we decided against including it as an additional predictor in the models.

Predicting LE from Bias and Physical Activity

Measure	Group	Target		
		1	**2**	**3**
Model R^2	*Older*	.07	.07	.02
	Younger	.21	.13	.05
Bias β-Coeff.	*Older*	-.04	-.21	-.10
	Younger	-.45	-.36	-.20
PA β-Coeff.	*Older*	.26	-.18	.10
	Younger	.02	-.15	-.10

Table 3.5. – Summary of linear regression model statistics with bias and physical activity (PA) measures (younger adults = IPAQ-Short score, older adults = total activity counts of 5-day accelerometer data) as predictors of lateral endpoint error (LE). None of the models were significant (p_{min} = .073; p_{FDR} = .008)

Predicting LE Var from Uncertainty Range and Physical Activity

Measure	Group	Target		
		1	**2**	**3**
Model R^2	*Older*	.03	.07	.09
	Younger	.01	.04	.04
UncR β-Coeff.	*Older*	.10	-.16	-.24
	Younger	.03	-.19	-.2
PA β-Coeff.	*Older*	-.12	-.17	.22
	Younger	-.09	.04	.09

Table 3.6. – Summary of linear regression model statistics with uncertainty range (UncR) and physical activity (PA) measures (younger adults = IPAQ-Short score, older adults = total activity counts of 5-day accelerometer data) as predictors of intra-subject variation (standard deviation) in lateral endpoint error (LE Var). None of the models were significant (p_{min} = .210; p_{FDR} = .008)

This meant a total of 6 models were generated for each proprioceptive-motor measure pairing, giving 12 models overall. The R^2 values and standardised beta coefficients for these models are summarised in Tables 3.5 and 3.6 but ultimately, neither the bias and LE (OAs, $R^2 < .08$; YAs, $R^2 < .21$; $p_{\text{min}} = .073$; $p_{\text{FDR}} = .008$) nor the uncertainty range and LE Var (OAs, $R^2 < .09$; YAs, $R^2 < .05$; $p_{\text{min}} = .210$; $p_{\text{FDR}} = .008$) models were significant. We did observe that the systematic proprioceptive errors were negatively associated with systematic motor errors regardless of age (See Table 3.5, middle two rows of negative bias coefficients), showing that limb perception was consistently in the opposite direction to motor errors. However, the lack of variable proprioceptive and motor error relationship in advanced age contradicts our original prediction, and does not appear to consistently occur as a positive association in spite of this as we might expect (Table 3.6, middle two rows of uncertainty range coefficients).

3.4 – Discussion

This experiment aimed to determine the relationship between dynamic proprioceptive acuity and motor control in the upper limb in advanced age. Based on previous research, we predicted older adults (OAs) would have larger uncertainty ranges and that this would be dependent on physical activity (PA). We also predicted this would be positively associated with variation in motor accuracy. However, we found the opposite in that physically inactive OAs had larger proprioceptive bias, but not uncertainty range, which somewhat replicated our finding from the pilot study in Chapter 2. Proprioceptive uncertainty was not related to motor accuracy variation which also did not match our predictions, and although physically inactive OAs had larger proprioceptive biases, these were not related to systematic motor errors either. Finally, in line with previous reports we observed comparable endpoint motor accuracy in older and younger adults, which was partially explained by age-dependent slowing of movements. We discuss these issues point by point.

Here, we showed that physically inactive OAs have larger proprioceptive biases than younger adults (YAs) which partially replicates our finding from Chapter 2. Interestingly, this was without including the 3 inward reaching reference targets (targets 4-6, see Figure 2.3) where the largest age effects on bias were observed in that experiment. The dependency on PA for proprioceptive acuity in ageing has been shown to be limb specific (Adamo et al., 2009). Since we measured PA for OAs using wrist-worn accelerometers, the effects measured on bias are similarly specific to activity of the dominant upper limb. Since naturalistic limb movements are concentrated to a small volume of lateralised space around the body (Howard, Ingram, Kording, & Wolpert, 2009), reduced upper limb activity could confine this further and so reduce exposure to a wider range of limb sensory states. From optimal control theory, it is thought that if there is increased uncertainty regarding a sensory state, such as when vision is removed, then there will be greater reliance on prior experience for sensorimotor control (Gritsenko, Krouchev, & Kalaska, 2007; Kording & Wolpert, 2006). As such, physically inactive OAs may have more lateralised proprioceptive errors in this task because of their reliance on sensory priors which are biased towards a smaller, lateralised range of previous sensory experience. Similarly, spindle afferents are directionally tuned to specific movements (Bergenheim, Ribot-Ciscar, & Roll, 2000; Jones, Wessberg, & Vallbo, 2001) and loss of intrafusal fibres with age has been shown to be muscle specific (Kararizou, Manta, Kalfakis, & Vassilopoulos, 2005). Therefore if movements are limited to a smaller range, loss of intrafusal fibres may be selective to those directionally tuned to the less frequent movements or limb positions in a use-dependent manner. As such, perception would be biased towards positions tuned to the muscles in which the most intrafusal fibres remain. However, since the accelerometer data did not provide spatial information of activity in this experiment, a low activity count could still be achieved through a range of sensory states and movements. As such, this theory remains speculative.

Since visual feedback of hand position was occluded across the entire block, an alternative theory may be that the biases arose from proprioceptive drift (Brown, Rosenbaum, & Sainburg, 2003a, 2003b; Desmurget, Vindras, Gréa, Viviani, & Grafton, 2000). However, this is typically observed during repetitive, unconstrained movements and has been attributed more to persistence of motor errors rather than proprioceptive fading (Brown et al., 2003b). Similarly, since the extent of proprioceptive drift has been associated with movement speed (Brown et al., 2003b) we would expect there to be an association between bias and movement velocity during task performance, however this was not the case. As such, this is less likely to have been the basis for our findings.

Our findings regarding the increased bias were not observed by Cressman et al. (2010) who used a highly similar proprioceptive task. However, Hoseini et al. (2015) also reported age effects on bias and not uncertainty range, using a static finger position task with an adaptive staircase procedure. Although these psychometric procedures are thought to be more reliable than other traditional methods of measuring proprioception (Elangovan, Herrmann, & Konczak, 2014; Hoseini et al., 2015), it may be that the proprioceptive measures they produce are only reliable within the confines of the same task, with the effects of altering proprioceptive task parameters being unclear. Reach distance is one such task dependency which may explain the differences between our findings and those presented by Cressman et al. (2010). Specifically, the movements made here were twice the distance of Cressman et al. (2010), and considering that judgements of static limb position further from the body have been shown to have reduced acuity estimates in YAs (van Beers, Sittig, & Denier van der Gon, 1998; Wilson, Wong, & Gribble, 2010), this increased reach distance may have affected our measurements. Furthermore, the minimum jerk channels used here involve more distinct, albeit smooth, changes of direction than the straight channels used by Cressman et al. (2010) and may provide greater proprioceptive cues to help detect the nature of deviations. This could reduce sensitivity to the age-effects on proprioceptive uncertainty which were observed by Cressman et al. (2010). Another consideration is that by only presenting the visual reference target in the first portion of the movement (unlike Cressman et al. [2010] who presented it at the end of movement only) the perceptual judgement could have involved a memory component and hence proprioceptive errors could have been limited by cognitive function. However, the 2-alternative choice symbols (square and circle) were always presented at constant, evenly spaced positions at the end of each movement, which should have minimised the need to memorise the reference position. But perhaps more importantly, we found that there was no association between working memory capacity and either proprioceptive measure for any of the groups, indicating cognition did not limit performance in this task. On a separate note, although verbal working memory capacity has been measured in conjunction with studying proprioceptive ageing previously (Adamo et al., 2009; Goble, Mousigian, et al., 2012), spatial working memory has been more frequently associated with sensorimotor adaptation and retention in ageing (Anguera, Reuter-Lorenz, Willingham, & Seidler, 2010; Trewartha, Garcia, Wolpert, & Flanagan, 2014; Uresti-Cabrera, Diaz, Vaca-Palomares, & Fernandez-Ruiz, 2015) and may be more appropriate to use in the future as a cognitive correlate for dynamic proprioceptive acuity. Further to this, smaller variable errors are reported for YAs when the presentation time of the reference position is increased (Goble, Noble, & Brown, 2010), which has been correlated with spatial working memory capacity in clinical populations too (Goble, Aaron, Warschausky, Kaufman, & Hurvitz, 2012).

In the rapid motor task, we observed characteristically slower movements in OAs, as well as them being slower and more varied in time taken to react to the initiation cue, which is line with similar previous reports (Helsen et al., 2016; Ketcham et al., 2002; Yan et al., 2000). As a means of trying to examine the unique contribution of proprioceptive acuity to motor control, we removed visual feedback during rapid reaching movements. As in previous experiments, we found both older and younger adults have similar duration to peak velocity (similar to a primary sub-movement), which is shortened during visual feedback occlusion in an age-independent manner (Helsen et al., 2016; Ketcham et al., 2002; Seidler-Dobrin & Stelmach, 1998). More typically, age-effects are found during the second decelerating phase of movement, with OAs increasing corrective adjustments or duration of “homing-in” on the target, despite scaling these similarly to YAs when visual feedback is removed (Helsen et al., 2016; Ketcham et al., 2002; Seidler-Dobrin & Stelmach, 1998). However, when we attempted a similar analysis by assessing additional sub-movements with minimum peak detection, we found that the vast majority of participants made an average of only 1 movement, which we suggest may have been due to the relatively coarse trial termination criteria (< 4cm/sec). As such, statistical analysis was somewhat redundant and so we excluded sub-movements as a variable. In line with previous work, our OAs displayed endpoint movement accuracy at a similar level as YAs (Helsen et al., 2016; Ketcham et al., 2002; Lee et al., 2007). However, once we controlled for movement speed, we found that OAs make larger absolute, but not lateral, endpoint errors compared to YAs, suggesting movement slowing with advanced age contributes to maintenance of accuracy. This may reflect a tendency to favour accuracy over speed with advanced age, but also perhaps a general limitation in the speed at which movements can be made due to motor system degeneration (Lexell, 1995).

One of the key findings from this experiment was that we did not find an association between proprioceptive sensation and motor control in either age group. This replicates the findings from Helsen et al. (2016) and extends them further, since the procedure we used to measure proprioception gives a better representation of sensory acuity likely to occur during normal movement, as well as comparing performance on both tasks in the same spatial locations. Specifically, we did not observe any relationship between bias and systematic motor errors along the same linear axis. This is in spite of observing larger biases in inactive

OAs and lateral motor errors which were typically in the opposite direction of their sensed hand position, in a similar fashion to previous reports (Vindras, Desmurget, Prablanc, & Viviani, 1998). However, as work with sensorimotor adaptation tasks has shown us, participants are able to account for constant or systematic sensory disturbances to maintain accurate motor performance (Cressman & Henriques, 2009; Cressman et al., 2010; Huang & Ahmed, 2014; Trewartha et al., 2014) so systematic proprioceptive errors are unlikely to be related to basic movement control. On the other hand, since variable sensory errors are inherently harder to predict and account for (Tan, Wade, & Brown, 2016) they are more likely to have an influence on movement control, thus making the non-significant relationship between uncertainty range and motor variability more surprising.

One explanation could be that since we did not measure age-effects on uncertainty range or motor variation we did not have the range of responses necessary to measure such an association between the two. However, in stroke patients where sensorimotor deficits are typically much worse, no direct relationship between upper limb position sense and reaching performance has been identified (Dukelow, Herter, Bagg, & Scott, 2012) which suggests this null relationship may be robust. On the other hand, it could be that during these types of ballistic, rapid movements the use of online sensory feedback is reduced, with performance relying more on feedforward, predictive mechanisms of motor control (Miall & Wolpert, 1996; Shadmehr et al., 2010; Wolpert, Ghahramani, & Jordan, 1995). As such, this relationship may become more apparent in motor tasks which rely more heavily on proprioceptive sensory feedback to achieve a specific task or goal, and thus force its utility. Adaptation to novel field dynamics, an under-researched paradigm in ageing, may fit this description since trial to trial performance requires use of proprioceptive feedback to successfully adapt movements. Previous work has shown that the proprioceptive bias can be shifted after reaching in a novel dynamic field, in a manner proportional to the extent of adaptation (Ostry, Darainy, Mattar, Wong, & Gribble, 2010). Considering the bias effects we measured in this experiment, it could therefore be interesting to see if this is paralleled with OAs, and also to see whether proprioceptive uncertainty contributes to adaptive performance. As such, we may gain a better understanding of the relationship between proprioceptive acuity and motor control in ageing.

In conclusion, we did not find evidence to suggest that dynamic, multi-joint proprioceptive acuity is related to rapid, goal-orientated movement control in either older or younger adults. While we found some characteristic features of movement control for OAs compared to YAs, our finding of age-dependent increase in proprioceptive bias, but not uncertainty range, is novel and may be related to task-dependent effects on these measures. Since the relative contributions of different task parameters to variations in proprioceptive acuity reports are unknown, further investigation may be necessary to better understand the basis of our novel findings. Similarly, further experimentation with movement control tasks which place greater emphasis on proprioceptive feedback may help to identify a relationship between proprioceptive acuity and motor function in ageing.

CHAPTER 4

The Association of Dynamically and Passively Derived Measures of Proprioceptive Acuity

Chapter Abstract

In this experiment, we sought to compare proprioceptive acuity estimates from the dynamic task we developed in Chapter 2 with a more commonly used ipsilateral elbow position matching task. This was to indirectly assess the extent to which the limitations of position matching tasks identified in Chapter 1 (Section 1.4.3) influenced estimates of proprioceptive acuity. Due to these limitations, we predicted that the measures from the two tasks would be poorly associated regardless of age. Furthermore, we expected inactive older adults (OAs) to have larger position matching errors than younger adults (YAs). The same set of participants from Chapter 3 completed an ipsilateral elbow position matching task following the dynamic proprioception and rapid motor tasks. For the position matching task, OAs had larger more positive (tend to overshoot the reference position) matching errors than YAs regardless of physical activity (PA) status. However, absolute matching errors were comparable between age groups contrary to predictions and previous reports. Despite age-dependent effects on measures from both proprioceptive tasks, they were poorly associated as predicted. Although we could not replicate previous findings of age-dependent increases in absolute matching error, we conclude that the poor association between proprioceptive tasks indicates and influential role of the position matching task limitations outlined in Chapter 1. Moreover, the poor relationships between performance on these

tasks strengthens the basis for the continued use of the dynamic task top investigate the relationship between proprioception and motor control in ageing throughout this thesis.

4.1 – Introduction

In Chapter 1, we outlined research which has demonstrated an age-related decline in upper limb proprioceptive acuity. Many of these studies made use of position matching tasks (see Figure 1.5) to report this, in which a passively defined reference position is matched with an actively moved limb, typically constrained around a single joint (Adamo, Alexander, & Brown, 2009; Adamo, Martin, & Brown, 2007; Goble, Mousigian, & Brown, 2012; Herter, Scott, & Dukelow, 2014). We also identified several limitations for these types of tasks which reduce their generalisation to perception in daily living and for use with OAs specifically. In brief, since normal movement is voluntary and often involves multiple joints, these tasks poorly mimic the type of sensations likely to occur in typical movements. Likewise proprioception is influenced by sense of effort or corollary discharge (Smith, Crawford, Proske, Taylor, & Gandevia, 2009) which also limits the generalisation of measures from passive tasks. Indeed, the use of actively defined reference positions has been shown to reduce matching errors in both OAs and YAs (Erickson & Karduna, 2012; Langan, 2014; Lonn, Crenshaw, Djupsjobacka, Pederson, & Johansson, 2000) but still indicate some loss of proprioceptive acuity with ageing (Schaap, Gonzales, Janssen, & Brown, 2015). In addition to this, working memory capacity can confound matching errors when attentional load of the task is high (Goble, Mousigian, et al., 2012) and is often not considered or controlled for in reports of age-related proprioceptive loss.

Although these limitations formed the rationale for using the dynamic proprioception task detailed in Chapters 2 and 3, these types of tasks have not previously been compared directly within the ageing population. As such, we were interested to see the extent to which the measures they produced differed and whether these measures were associated with one another. We therefore asked the same group of participants from Chapter 3 to perform a single joint, ipsilateral elbow position matching task following the completion of the dynamic proprioception and rapid motor tasks, all in the same visit. Previous reports have typically found reduced magnitude of the effect of ageing on ipsilateral position matching than contralateral matching tasks (Adamo et al., 2009; Adamo et al., 2007; Schaap et al., 2015) which may be due to declines in central physiology (see Section 1.4.3; Hou & Pakkenberg, 2012; Ota et al., 2006). But since the dynamic proprioceptive task was constrained to the right arm only, we wanted to use the same constraint for the position matching task here. Since there are still age effects reported for ipsilateral matching tasks (Adamo et al., 2009; Adamo et al., 2007; Goble, Mousigian, et al., 2012; Helsen et al., 2016), we predicted OAs would make larger matching errors than YAs. However, due to the difference in movement type for the two proprioceptive tasks, we predicted there would be no relationship across the participants between measures derived from the dynamic and passive assessments.

4.2 – Methods

4.2.1 – Participants, Physical Activity Grouping and Working Memory

Participants were identical to those described in Chapter 3; 31 OAs (15 Male, 71.2 ± 4.4 yrs) and 20 YAs (11 Male 20.4 ± 2.0 yrs). For a full detailed description of the inclusion criteria refer back to Chapter 3. The PA measures used for both the younger and older adults are also described in detail in Chapter 3. YAs completed the IPAQ-Short (Craig et al., 2003) and were excluded if PA was deemed to be high. PA levels for OAs were measured using wrist-worn accelerometers and the data was used to group them into either a physically active (1.96 ± .26 x 10^6 counts; n = 15, 4 male, 69.3 ± 2.7 yrs) or inactive (1.29 ± .31 x 10^6 counts; n = 16, 7 male, 72.9 ± 5.1 yrs) sub-group. Working memory capacity scores as presented in Chapter 3 were used as a correlate for position matching errors to examine how cognitive function influenced performance on the task.

4.2.2 – Dynamic Proprioception

The experimental set-up for the dynamic proprioceptive task (vBOT) is described in detail in Chapters 2 and 3. Target locations, procedure and parameters of perceptual trials for this specific version of the task are outlined in Chapter 3 (Section 3.2.5). In brief, participants made reaching movements towards visually presented targets in the absence of hand position visual feedback. These movements were constrained to a specific pathway which deviated hand position laterally from the target. Participants then made a perceptual judgement to indicate the side of the target they thought they had been guided to by verbally selecting one of 2 symbols (“Square”, counter-clockwise side of target or “Circle”, clock-wise side of target). Size and direction of lateral deviation was altered on a trial-by-trial basis by an adaptive algorithm, and blocks of 48 of these trials were interleaved with blocks of 6 unconstrained, null-field reaching trials where full visual feedback of hand position was provided. The verbal response data was used to generate a systematic (bias) and variable (uncertainty range) proprioceptive error measure at each target (full details of outcome measures and analysis are also found in Chapters 2 and 3).

4.2.3 – Passive Proprioception

4.2.3.1 – Experimental Set-Up

The apparatus for this task was a custom-built padded, plastic forearm cradle which moved freely in the horizontal plane about a single pivot point. Movements were made with minimal frictional resistance between a fabric pad on the underside of the cradle and a highly polished surface below it. Velcro straps held the participant's forearm in position such that their elbow was spatially coincident with the pivot axis and movements were limited to a 90 deg range of motion (from full elbow extension to 90 deg flexion) by end-position blocks. Participants were asked to grip a small piece of padded, wooden dowelling with their hand so that the wrist was maintained in a neutral position (0 deg flexion/extension and 0 deg pronation/supination) throughout the task. Seat height was adjusted so that there was an approximately 20 deg elevation of the shoulder above the level of the workspace, and participants were seated so that at full elbow extension of the shoulder, forearm and wrist were aligned orthogonally to the workspace edge and participant's chest. A single 6 degree-of-freedom position sensor (Polhemus Liberty, sampling at 240Hz) was attached to the underside of the cradle and was used to record and display the angular position of the cradle on a real-time basis through a computer monitor and bespoke matlab algorithm. This allowed the experimenter to accurately move the limb to pre-defined elbow angles with a high degree of accuracy. During the entirety of the trials, vision of the forearm and apparatus was occluded using customised eye goggles. The set-up for this experiment is summarised in Figure 4.1.

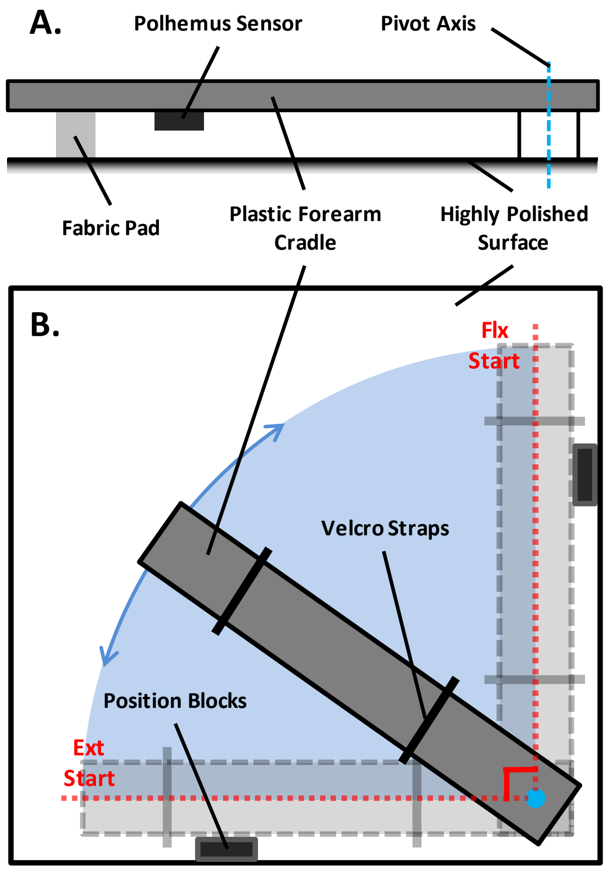


Figure 4.1. (left) – Experimental set-up for passive proprioception task **A.** Shows the cross-sectional view of the plastic forearm cradle with the fabric pad and polhemus sensor attached to its underside. The pad moves with minimal friction across the highly polished surface about the pivot axis (blue dashed line) **B.** Top down view of the set-up showing the 90 deg range of motion of the cradle limited by position blockers. Dashed red lines show extreme limits in range of motion, and form start positions for flexion movements (Flx Start) and extension movements (Ext Start). Participant's right forearms were placed so the pivot axis was spatially coincident with the elbow joint and held down with velcro straps. Vision was occluded for the entirety of the task

4.2.3.2 – Procedure

The full procedure is summarised in Figure 4.2. Participants started from one of the extreme limits in the cradles range of motion (Ext Start or Flx Start; see Figure 4.1), then had their unseen arm passively moved to a reference position by the experimenter where it was held for approximately 3 seconds. The arm was then passively returned back to the start position and following a short pause, participants were instructed to actively move their arm at a self-selected speed to try and match the remembered reference position. Once they had come to a complete stop, the experimenter passively moved the forearm through the remaining range of motion (i.e. to the furthest point from start position) and then returned it to the start position ready for the next trial.

4.2.3.3 – Task Design and Reference Positions

There were 3 reference positions that were 20, 40 and 60 deg from the start position. These were pseudo-randomly presented across 2 blocks of 6 matches for each of the two start positions to give a total of 4 blocks of 6 matching movements (4 matches per reference position and movement direction). Start position was dependent on whether the active movements were elbow extensions (Ext Start; Figure 4.1) or elbow flexions (Flx Start; Figure 4.1). The order of completion (i.e. elbow extension or flexion blocks first) was counterbalanced between participants to control for potential order effects (a summary of the task design is shown in Figure 4.3).

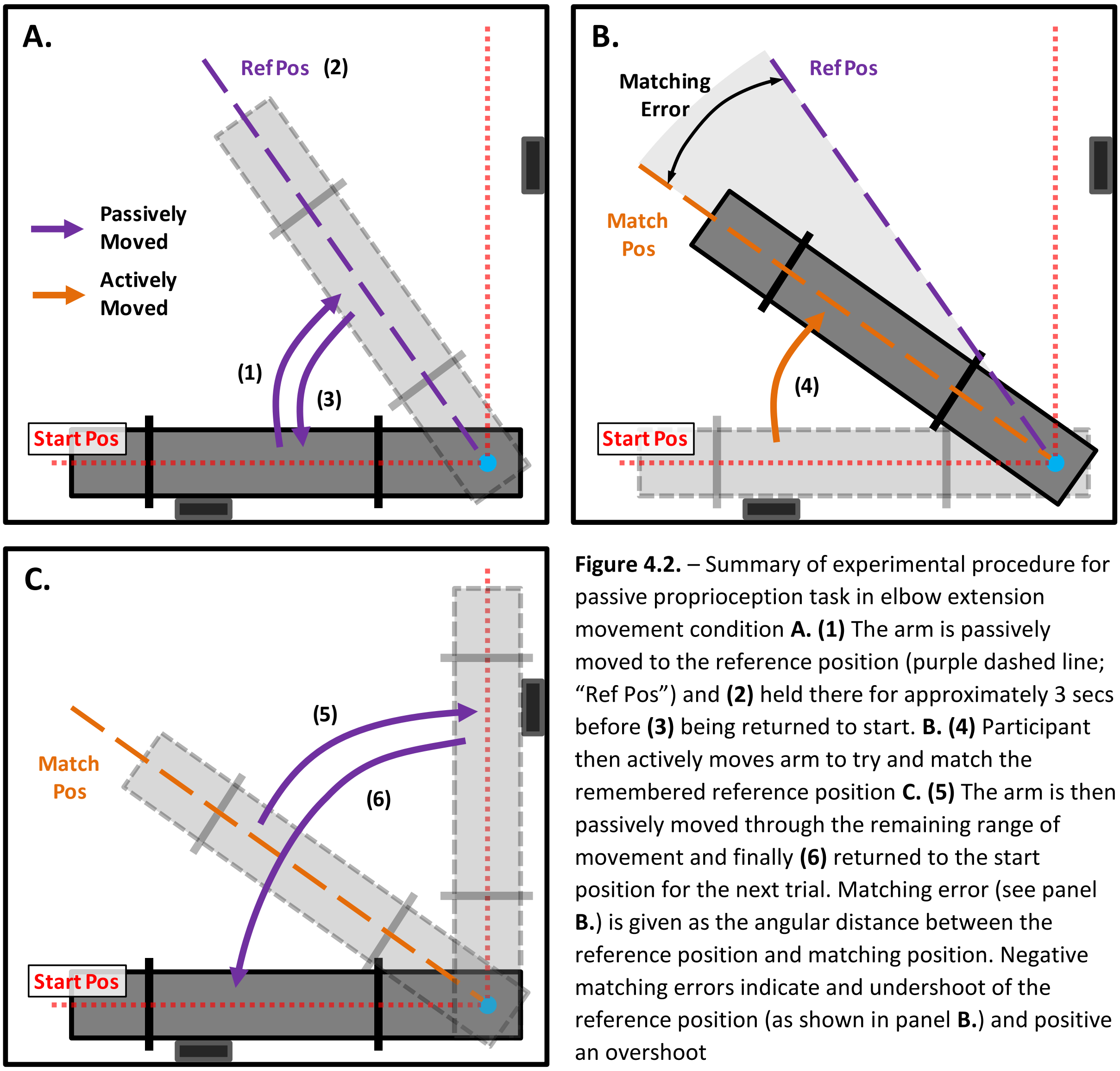


Figure 4.2. – Summary of experimental procedure for passive proprioception task in elbow extension movement condition **A. (1)** The arm is passively moved to the reference position (purple dashed line; “Ref Pos”) and **(2)** held there for approximately 3 secs before **(3)** being returned to start. **B. (4)** Participant then actively moves arm to try and match the remembered reference position **C. (5)** The arm is then passively moved through the remaining range of movement and finally **(6)** returned to the start position for the next trial. Matching error (see panel **B.**) is given as the angular distance between the reference position and matching position. Negative matching errors indicate and undershoot of the reference position (as shown in panel **B.**) and positive an overshoot

4.2.3.4 – Outcome Measures and Analysis

A velocity profile for the active movement was obtained by using a 10Hz low pass filter on the derivative of the recorded angular position data. This allowed calculation of 3 kinematic measures which included peak angular arm velocity, total number of movements and active movement duration. The number of velocity “peaks” was used to examine number of movements in a trial made prior to stopping on the perceived reference position. Velocity peaks were defined as having minimum peak height of either 4 deg/sec or 20% peak velocity for the trial, and were only counted if they had a prominence of 5% of the neighbouring velocity peaks. Movement initiation was defined as the point where angular velocity first exceeded 4 deg/sec, with movement termination being the point where it fell below 4 deg/sec after the final recorded velocity peak. Active movement duration was then given as the time elapsed between movement initiation and termination (and therefore encapsulates total duration for completion of all counted movements).

Matching errors were defined as the angular difference between the final position of the active movement (i.e. position at movement termination) and the reference position. Negative matching errors represented a matching position which undershot or had a smaller angle than the reference position (see Figure 4.2, Panel B. for example), whereas positive errors reflected an overshoot or larger angle than the reference. To examine overall magnitude of errors for these trials, absolute matching error was also recorded.

Since the passive movement to the reference position was made by the experimenter, we also wanted to make sure there were no systematic biases between participants regarding the passive movement profile which could affect the ability to match it. We therefore also recorded the duration of the passive movement to the reference position and the duration which the arm was held at the reference position by the experimenter. The passive movement duration was calculated using the same criteria as the active movement duration, i.e. the time elapsed between movement initiation (point where angular velocity first exceeded 4 deg/sec) and movement termination (point where it fell below 4 deg/sec after the final recorded velocity peak). Reference hold duration was calculated as the time between passive movement termination and when angular velocity first exceeded 4deg/sec again thereafter.

4.2.4 – Experimental Design and Statistical Analysis

Participants performed the passive proprioception task following completion of the dynamic proprioception and rapid motor reaching tasks described in Chapter 3 (see Figure 3.4; details of the number of trials and blocks for the dynamic proprioception task can also be found there). They had a brief familiarisation with the equipment and two practice trials to ensure they fully understood the necessary stages of the task.

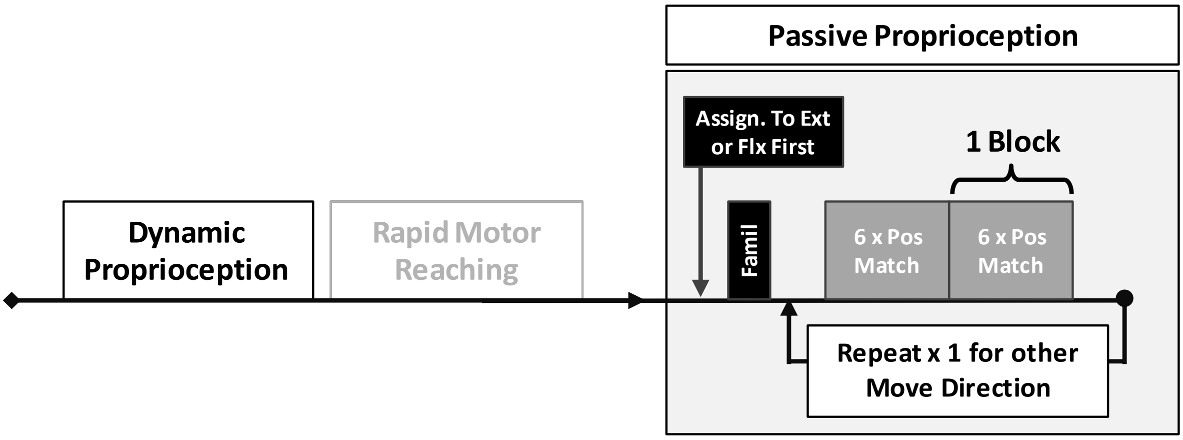


Figure 4.3. – Experimental design for passive proprioception task which followed dynamic proprioception (described in detail in Chapter 3, Figure 3.2) and rapid motor reaching tasks (shown as faded here since not relevant for this Chapter). Participants were pseudo-randomly assigned to perform either the elbow extension (Ext) or elbow flexion (Flx) blocks first

Values which were greater than 2.5 standard deviations away from the group mean were excluded from analysis as outliers. The remaining data was analysed using separate 3 x 2 x 3 mixed-design ANOVAs: (Group; inactive OAs, active OAs and YAs) x (Movement Direction; elbow extension or flexion) x (Reference Position; 20, 40 or 60 deg). In all cases where the sphericity assumption was violated a Greenhouse-Geisser correction was used, with significance being assessed at the $p < .050$ level. Similar to previous chapters, follow-up multiple comparisons are reported as uncorrected (Least Significant Difference; LSD) values but were assessed for significance using a False Discovery Rate (FDR) analysis (for detailed description see Chapter 2). This included post-hoc pair-wise comparisons to follow-up on ANOVA effects, but also for bivariate correlations for associative analyses. The FDR-adjusted p-thresholds (p_{FDR}) are denoted for sets of comparisons throughout the results, and where no significant relationships were found (i.e. $p < p_{\mathrm{FDR}}$ was not observed) the smallest observed p-value (p_{min}) is reported with its associated critical significance value (still denoted as p_{FDR}) (see Chapter 2 for details).

4.3 – Results

4.3.1 – Passive Proprioception

4.3.1.1 – Matching Errors

All matching error data are summarised in Table 4.1 and Figure 4.4. There was a significant main effect of Group on matching error (F[2, 47] = 7.66, p = .001, η^2_p = .25) where follow-up pair-wise comparisons showed that both inactive (p = .011; p_{FDR} = .033) and active (p < .001) OAs had larger, more positive errors (overshooting the reference position) than YAs (Figure 4.4, Panel A). There was also a main effect of Reference Position (F[1.5, 70.0] = 8.47, p = .002, η^2_p = .15) such that errors at the 20 deg reference position were larger and more positive than both 40 deg (p = .001; p_{FDR} = .033) and 60 deg (p = .003) reference positions. The main effect of Movement Direction was not significant (F[1, 47] = 2.89, p = .176) and neither were the remaining two- and three-way interactions (p > .128).

The main effect of Group on absolute matching error (Figure 4.4, Panel B) was not significant (F[2, 45] = .41, p = .663) and neither were the main effects of Reference Position (F[2, 90] = 1.40, p = .251) or Movement Direction (F[1, 45] = 2.47, p = .123). The two-way interaction of Group x Reference Position was significant (F[4, 90] = 3.66, p = .008, η^2_p = .14); however, simple effects analysis did not reveal any specific differences between groups at any of the different reference positions (3 [Group] x 3 [Reference Position] comparisons; p_{min} = .040; p_{FDR} = .006). The remaining interactions were not significant (p > .153).

Collectively, these data demonstrate a tendency for OAs to overshoot the reference position during matching to a greater extent than YAs who slightly undershoot it. Errors also appear to be independent of movement direction (elbow extension or flexion) but depend on amplitude, typically overshooting more in 20 deg reference matches compared to the 40 and 60 deg conditions. The unsigned, absolute magnitude of matching errors appears to be unaffected by age, movement direction or reference position. These findings partially support the prediction that larger matching errors would be observed in older participants.

4.3.1.2 – Movement Kinematics

The kinematic data is summarised in Table 4.2 and Figure 4.5. There was no effect of Group on peak angular arm velocity (Peak Vel; F[2, 47] = .87, p = .427; Figure 4.5, Panel A). However, the main effect of Reference Position on Peak Vel was highly significant (F[1.5, 69.3] = 350.5, $p < .001$, $\eta^2_p = .88$) where peak velocity of matching movements was significantly different between all reference positions (all $p < .001$; $p_{FDR} = .050$) such that movements were fastest at 60 deg matching and slowest at 20 deg.

Measure	Group	Elbow Extension			Elbow Flexion			**Overall**
		20 deg	**40 deg**	**60 deg**	**20 deg**	**40 deg**	**60 deg**	
Error (deg)	*Inactive Older*	4.07 *(± .83)*	2.31 *(± 1.1)*	0.86 *(± 1.2)*	2.20 *(± .90)*	.07 *(± 1.1)*	-.10 *(± .84)*	****1.57 *(± .66)***
	Active Older	4.47 *(± 1.2)*	3.50 *(± .93)*	1.38 *(± 1.2)*	3.52 *(± 1.2)*	1.61 *(± .69)*	1.08 *(± .94)*	*****2.59 *(± .59)***
	Younger	-1.07 *(± .51)*	-1.41 *(± .86)*	-.57 *(± .89)*	.55 *(± .78)*	-.78 *(± 1.1)*	-.78 *(± 1.1)*	-.68 *(± .59)*
Absolute Error (deg)	*Inactive Older*	4.70 *(± .63)*	4.73 *(± .51)*	5.25 *(± .56)*	4.35 *(± .53)*	5.00 *(± .48)*	4.55 *(± .43)*	4.76 *(± .29)*
	Active Older	5.78 *(± .96)*	5.23 *(± .85)*	4.53 *(± .45)*	4.77 *(± .73)*	3.72 *(± .28)*	3.97 *(± .32)*	4.67 *(± .42)*
	Younger	3.25 *(± .36)*	5.62 *(± .44)*	4.14 *(± .33)*	3.78 *(± .32)*	5.14 *(± .63)*	4.54 *(± .51)*	4.41 *(± .21)*

Table 4.1. – Group average matching accuracy data for both movement directions (elbow extension and flexion) and all reference positions (20, 40 and 60 deg). Negatively signed errors indicate a matching movement which fell short of (undershot) the reference position, whilst positive errors indicate an overshoot. Values given as means ± standard error, with significantly different values from younger adults indicated by ** (p < .010) and *** (p < .001; multiple comparisons subjected to FDR adjusted p-threshold)

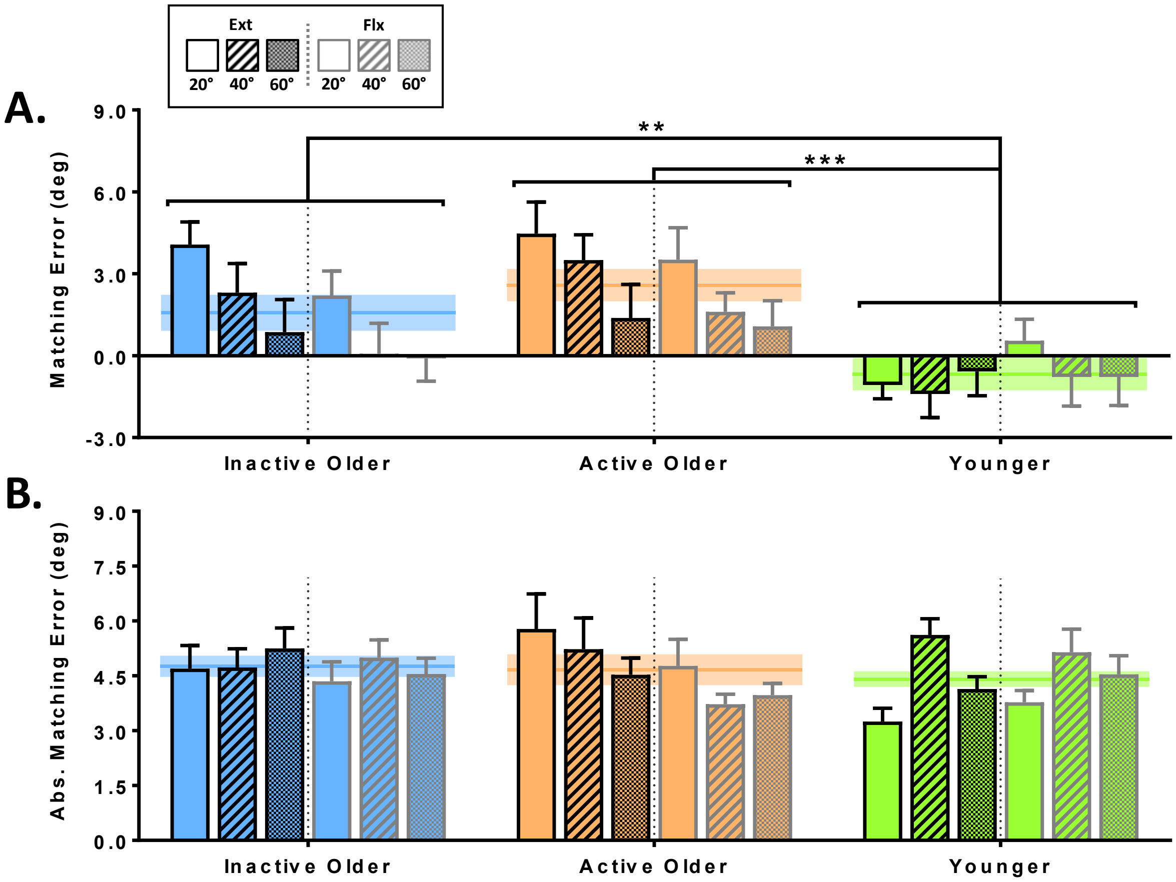


Figure 4.4. – Group average matching accuracy data for extension (solid black outlined bars) and flexion (solid grey outlined bars) movements for all reference positions (20, 40 and 60 deg). In both panels, thick horizontal lines represent group mean values across all conditions, with shaded region indicating ± standard error **A.** Signed matching errors, where negative values indicate a matching movement which fell short of (undershot) the reference position, whilst positive values indicate an overshoot. Inactive and active older adults made larger, more positive errors than younger adults **B.** Absolute matching errors, which were not different between groups. Vertical bar values are given as means ± standard error bars where significantly different values from younger adults are indicated by ** (*p* < .010) and *** (*p* < .001; multiple comparisons subjected to FDR adjusted *p*-threshold)

There was no effect of Movement Direction on Peak Vel (F[2, 47] = .53, *p* = .472) and the two-way interactions of Group x Reference Position (F[3.0, 69.3] = .13, *p* = .939) and Group x Movement Direction (F[2, 47] = 2.23, *p* = .118) were also non-significant. The Reference Position x Movement Direction interaction had an effect on Peak Vel (F[2, 94] = 5.32, *p* = .006, η^2_p = .10), although this appeared to be largely driven by the main effect of Reference Position: simple effects analysis provided identical outcomes when examining reference position differences for extension or flexion in isolation (2 [Movement Direction] x 3 [Reference Position] comparisons; all $p < .001$; $p_{FDR} = .050$). The three-way interaction of Group x Reference Position x Movement Direction was not significant (F[4, 94] = .39, $p = .816$).

The main effect of Group on active movement duration was not significant (F[2, 42] = .05, $p = .951$; Figure 4.5, Panel B), however there was a main effect of Reference Position (F[1.4, 62.4] = 308.2, $p < .001$, $\eta^2_p = .87$) where active movement duration was significantly different between all reference positions (all $p < .001$; $p_{FDR} = .050$), such that active movement duration was longest when matching to 60 deg reference positions and shortest when matching to 20 deg. The main effect of Movement Direction on active movement duration was also significant (F[1, 46] = 14.11, $p < .001$, $\eta^2_p = .24$) with movements taking longer to complete during flexion matches than extension ones. The remaining interactions were not significant ($p > .211$).

There was no main effect of Group on the number of movements (Num Move; F[2, 42] = .05, $p = .949$; Figure 4.5, Panel C) but there was a an effect of Reference Position (F[1.7, 69.5] = 10.5, $p < .001$, $\eta^2_p = .20$) such that the number of movements was greater for 60 deg reference position trials compared to both the 20 deg ($p = .022$; $p_{FDR} = .033$) and 40 deg ($p < .001$) positions. The main effect of Movement Direction on Num Move was also significant (F[1, 42] = 8.03, $p = .007$, $\eta^2_p = .16$) where more movements were made during flexion matching trials than extension ones. The remaining two- and three-way interactions were not significant ($p > .168$).

Measure	Group	Elbow Extension			Elbow Flexion			**Overall**
		20 deg	**40 deg**	**60 deg**	**20 deg**	**40 deg**	**60 deg**	
Peak Vel (deg/sec)	*Inactive Older*	30.1 *(± 2.2)*	41.7 *(± 2.9)*	49.0 *(± 3.0)*	28.1 *(± 1.7)*	40.8 *(± 2.8)*	49.6 *(± 3.3)*	39.9 *(± 2.3)*
	Active Older	32.1 *(± 2.1)*	43.2 *(± 2.5)*	50.1 *(± 2.7)*	27.8 *(± 2.0)*	38.9 *(± 2.5)*	48.6 *(± 2.7)*	40.1 *(± 2.1)*
	Younger	26.8 *(± 1.3)*	37.1 *(± 1.5)*	44.6 *(± 1.7)*	26.2 *(± 1.3)*	38.9 *(± 1.7)*	49.0 *(± 2.9)*	37.1 *(± 1.4)*
Number of Movements	*Inactive Older*	1.34 *(± .21)*	1.29 *(± .15)*	1.52 *(± .20)*	1.32 *(± .13)*	1.36 *(± .12)*	1.50 *(± .14)*	1.39 *(± .10)*
	Active Older	1.19 *(± .06)*	1.12 *(± .05)*	1.33 *(± .10)*	1.62 *(± .12)*	1.44 *(± .15)*	1.54 *(± .10)*	1.37 *(± .07)*
	Younger	1.19 *(± .04)*	1.22 *(± .06)*	1.49 *(± .09)*	1.56 *(± .11)*	1.28 *(± .07)*	1.69 *(± .16)*	1.41 *(± .06)*
Active Movement Duration (sec)	*Inactive Older*	1.21 *(± .06)*	1.63 *(± .12)*	2.07 *(± .16)*	1.34 *(± .11)*	1.78 *(± .13)*	2.13 *(± .13)*	1.69 *(± .10)*
	Active Older	1.12 *(± .05)*	1.56 *(± .09)*	2.01 *(± .15)*	1.35 *(± .08)*	1.82 *(± .11)*	2.22 *(± .12)*	1.68 *(± .09)*
	Younger	1.11 *(± .04)*	1.61 *(± .05)*	2.14 *(± .08)*	1.28 *(± .05)*	1.70 *(± .07)*	2.12 *(± .10)*	1.66 *(± .05)*

Table 4.2. – Group average matching kinematic data for both movement directions (elbow extension and flexion) and all reference positions (20, 40 and 60 deg). Values given as means ± standard error, there were no significant differences between groups for any of the measures ($p > .050$)

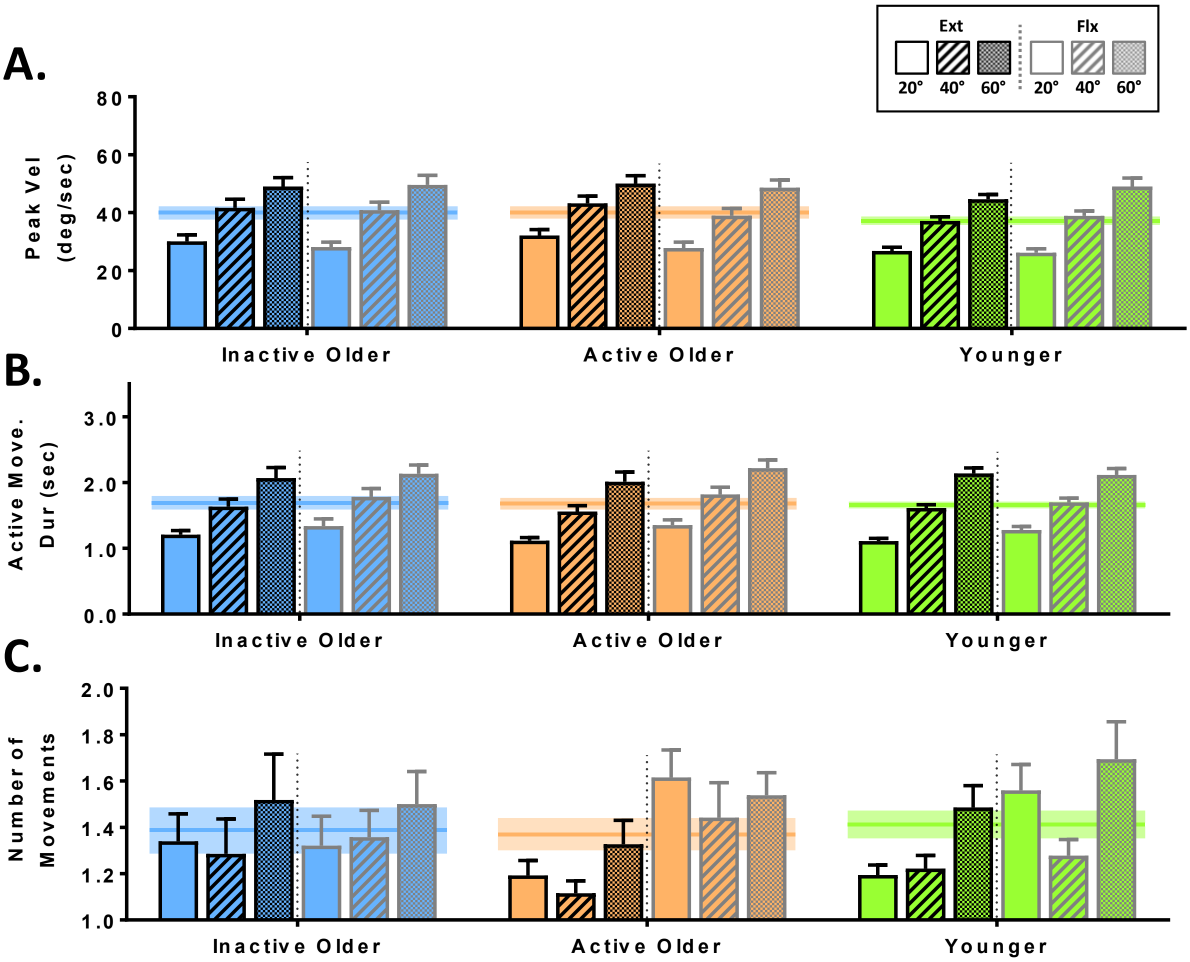


Figure 4.5. – Group average matching kinematic data for extension (solid black outlined bars) and flexion (solid grey outlined bars) movements for all reference positions (20, 40 and 60 deg). In both panels, thick horizontal lines represent group mean values across all conditions, with shaded region indicating ± standard error **A.** Peak angular arm velocity **B.** Whole trial active movement duration **C**. Number of movements. Vertical bar values are given as means ± standard error bars, there were no significant differences found between groups for any of the 3 measures (*p* > .050)

These results show that both older and younger adults had comparable kinematic performances during matching movements. Somewhat predictably, the speed and duration of movements was higher for those reference positions which were further away. But perhaps more interestingly, trials took longer, with a greater number of movements, in flexion matches than extension ones.

In order to examine whether the magnitude and direction of perceptual errors were related to the speed of matching movements, peak angular velocity and matching error were correlated individually for each of the 3 groups at each reference position and for both movement directions (Pearson correlations for 3 [Group] x 2 [Movement Direction] x 3 [Reference Position] relationships). It was found that matching speed was positively correlated with error at only the 20 deg reference position for elbow flexions in both inactive (r = .678, p = .005; p_{FDR} = .006) and active (r = .882, p < .001) OAs. This means that OAs who moved faster in this condition tended to overshoot the reference position to a greater extent. Due to the positive, linear nature of this relationship it is not possible to simply divide these errors by the peak angular velocity and re-analyse the data to control for the effects of movement speed (as in Chapter 3). Specifically, this was possible in Chapter 3 since both positive and negative errors increased with speed, but that does not apply here. However, with a significant effect only present in 1 out of the 6 conditions, and there being no overall group differences in movement speed, this is not likely to have had a notable effect on the results. This finding should still be considered in relation to future tests of a similar nature.

4.3.1.3 – Experimenter Passive Movement Kinematics

The purpose of including the reference movement measures was to ensure there was no difference between groups for any of the reference position or movement direction combinations which might bias the ability to make accurate active matches. As such, we only report the main effects of Group and their interactions here from the 3 x 2 x 3 mixed-design

ANOVAs: (Group; inactive OAs, active OAs and YAs) x (Movement Direction; elbow extension or flexion) x (Reference Position; 20, 40 or 60 deg).

There was no effect of Group on passive movement duration (F[2, 47] = .57, *p* = .570), nor were there any significant interactions involving Group (*p* > .070). There was also no effect of Group on reference position hold duration (F[2, 44] = .39, *p* = .680) and the Group interactions were also all non-significant (*p* > .169). This shows that the passive movement to the reference position was comparable between groups across the 6 conditions.

4.3.2 – Working Memory Capacity

There were no group effects on working memory capacity as outlined in Chapter 3 (*p* = .854). Here, the scores were correlated with absolute matching errors to see how working memory influenced performance on the task (Pearson correlations for 3 [Group] x 2 [Movement Direction] x 3 [Reference Position] relationships). It was found that working memory was unrelated to the magnitude of matching errors in any condition for either inactive older (all |r| < .41; p_{min} = .120; p_{FDR} = .003), active older (all |r| < .44; p_{min} = .135) or younger adults (all |r| < .28; p_{min} = .241), showing that perceptual errors were unaffected by cognitive ability.

4.3.3 – Dynamic and Passively Measured Proprioceptive Acuity Relationship

In this experiment we wanted to compare the proprioceptive measures from the dynamic proprioception task we developed in this thesis to a more traditional, passively referenced, position matching task. Since there was no straightforward way to associate the measures within specific sub-conditions (i.e. to compare specific targets for the dynamic task with reference positions or movement directions for the passive task), we used the mean bias and uncertainty range from the dynamic task (for detailed group results see Chapter 3, Section 3.3.2) as well as error and absolute error from the passive task for each participant, across all conditions. Similarly, there was not a strong theoretical basis to predict performance on one task from the other so it was hard to justify multiple linear regression models with PA as an additional predictor (as in Chapter 3). As such, we correlated the measures from the different tasks separately for each of the 3 groups (Pearson correlations for 3 [Group] x 4 [Bias vs. (Absolute) Error, Uncertainty Range vs. (Absolute) Error] relationships).

The analysis showed that there was no relationship between any of the 4 measures for either inactive older (p_{min} = .052; p_{FDR} = .004), active older (p_{min} = .081) or younger adults (p_{min} = .088) as summarised in Table 4.3. This confirms our predictions and shows that the nature of the movements and joints involved in dynamic and passive based tasks can considerably affect proprioceptive acuity estimates.

		Group	Passive Proprioception	
			Error	**Abs. Error**
Dynamic Proprioception	**Uncert. Range**	*Inact. Older*	**r = -.009** *(p = .974)*	**r = .041** *(p = .885)*
		Act. Older	**r = -.050** *(p = .865)*	**r = -.142** *(p = .661)*
		Younger	**r = -.194** *(p = .440)*	**r = -.064** *(p = .800)*
	Bias	*Inact. Older*	**r = .368** *(p = .161)*	**r = .494** *(p = .052)*
		Act. Older	**r = -.166** *(p = .554)*	**r = -.502** *(p = .081)*
		Younger	**r = .414** *(p = .088)*	**r = .084** *(p = .739)*

Table 4.3. – Pearson correlation coefficients and *p*-values for associations between measures of proprioception generated from passive and dynamic tasks, averaged across conditions. No significant relationships were found (p_{min} = .052; p_{FDR} = .004)

4.4 – Discussion

In this chapter we aimed to compare measures from passively and dynamically based proprioceptive assessments to indirectly examine the limitations of position matching tasks. We predicted older adults (OAs) would have larger matching errors than younger adults (YAs), but that they would be poorly associated with measures collected from the dynamic proprioceptive task, regardless of age. We found that OAs tended to overshoot the reference position whilst YAs slightly undershot it and that this was independent of physical activity (PA) level in OAs, reference position and movement direction. Absolute matching error was unaffected by age, a finding contrary to previous reports and to our predictions.

The finding of age-independent absolute matching errors is opposed to several previous reports (Adamo et al., 2009; Adamo et al., 2007; Helsen et al., 2016). One reason for this may be that in our procedure we tried to remove any influence of spindle conditioning effects or the “thixotropic state” of the muscle (Proske & Gandevia, 2009; Tsay, Savage, Allen, & Proske, 2014) which has been shown to bias errors in proprioceptive sensation (Gregory, Wise, Wood, Prochazka, & Proske, 1998; Winter, Allen, & Proske, 2005). By moving the limb through the full range of motion between matches we attempted to normalise any potential prior spindle state effects which may have occurred between successive trials. Since other reports have not taken this into account and age-related degeneration of muscle physiology is well-documented (Morley, Baumgartner, Roubenoff, Mayer, & Nair, 2001; Slack, Hopkins, & Williams, 1979; Valdez et al., 2010), it may be that the muscle thixotropy differentially affects older and younger adults to provide a further limitation in these tasks. Since muscle conditioning experiments seem to be focused towards the younger population

(Gregory et al., 1998; Winter et al., 2005), further investigation as to how the effects of muscle thixotropy contribute to position sense in ageing may be important for interpreting previous reports which use these types of tasks.

Following this, it is interesting to note that a common change in muscle physiology with ageing is that the muscle-tendon complex seems to become more compliant (Goldspink, 2012; Narici & Maganaris, 2006). As such, this may create a muscle spindle which is typically more “slack” in nature and could contribute to a reduced dynamic stretch response (Kim, Suzuki, & Kanda, 2007). We found that OAs tended to overshoot the reference position, which represents a perception of limb position as behind its physical position in the path of motion. This may arise from a perception of the muscle being less stretched than it actually is and as such, would fit with a slacker spindle and diminished dynamic response with ageing, which could partially explain these observations.

Similar to previous reports we found that working memory capacity was not associated with matching errors (Adamo et al., 2009; Goble, Mousigian, et al., 2012). However, unlike these previous reports, we did not find age-effects on working memory capacity either. This may be due to an above average working memory capacity of our OA sample. Indeed, the average scores for the two OA groups place them roughly in the 80th percentile for their age group (Iverson & Tulsky, 2003) with only 8 out of 32 older participants qualifying as having “Low” working memory (score of less than 5 remembered digits) according to the threshold used by Goble, Mousigian, et al. (2012). This may have limited the potential for us to measure the effects of this potential confound on matching performance, and may have contributed to the null effect we observed on absolute errors. As mentioned in Chapter 3, since sensorimotor adaptation tasks have implicated spatial working memory as a performance limiting factor in ageing (Anguera, Reuter-Lorenz, Willingham, & Seidler, 2010; Trewartha, Garcia, Wolpert, & Flanagan, 2014; Uresti-Cabrera, Diaz, Vaca-Palomares, & Fernandez-Ruiz, 2015), it may also be a more relevant correlate for the coding of spatial limb location, such as with proprioceptive assessment tasks, than verbal working memory capacity as used here. Moreover, increased presentation time of the reference position has been shown to reduce variable errors in ipsilateral position matching tasks in YAs (Goble, Noble, & Brown, 2010), and has been correlated with spatial working memory capacity in subjects with cerebral palsy (Goble, Aaron, Warschausky, Kaufman, & Hurvitz, 2012). It may therefore be important to assess spatial working memory in relation to these tasks in the future.

As predicted, we did not find an association between passively and dynamically derived measures of proprioception. In the dynamic task, proprioceptive biases were typically positive which indicated the perception of limb position to be further to the right (or clockwise) of the reference positions, which could roughly translate as a perception of increased elbow extension. If the two tasks were correlated, we might then predict that position matching errors for the extension condition would be seen as undershoots, similarly indicating perception of the elbow being more extended than it is. Whilst this was generally the case for YAs, OAs overshot the reference considerably and in fact, the errors were consistent across flexion and extension movements but occurred in opposite directions for the two age groups. This may highlight differences in these tasks, and the limitations of using passive position matching tasks outlined in the introduction. Furthermore, we also observed that in the 20 deg flexion condition OAs overshot the reference position proportionally to their movement speed, indicating that the faster they were going the further they perceived their arm to be behind its actual position in the path of motion. This represents the inverse relationship you might expect if predictions of limb position were to be scaled appropriately to movement speed, and as such, may represent a particular disparity between passive and active perception at these small angular deviations. In any case, the fact that we did not find an association between measures from the two tasks further supports the use of the dynamic procedure throughout this thesis. Specifically, since the dynamic task has a higher specificity to normal, voluntary motor control and was unrelated to passively derived measures, it seems that passive position matching tasks may not be suitable for investigating the relationship between proprioceptive sensation and motor performance in ageing.

Unlike the dynamic proprioception task, we could only gain measures of systematic, and not variable, proprioceptive errors from the position matching task. In previous chapters we had enough trials to validly examine the intra-subject performance variability (Chapter 3, Rapid Motor Reaching Task), but with only 4 trials per condition presently this was not possible. This meant we did not have a strong correlate for uncertainty range and it may be that variable proprioceptive errors of the two tasks are associated but could not be measured here. Moreover, the reliability of the dynamic proprioceptive task may be higher since it was performed first and therefore was unlikely to be influenced by any order effects (fatigue, learning etc.) which the position matching task may have been subjected to. Finally, dynamic measures were calculated from 80 trials per target rather than 4 for the matching task, and may be more robust. With this in mind, it may be beneficial to corroborate these findings by conducting a similar experiment but constrained to the 2 proprioceptive tasks in the protocol only. However, it is interesting to note that previous reports of position matching tasks only tend to use around 3-12 trials per condition in order to assess position matching performance (Adamo et al., 2009; Adamo et al., 2007; Goble, Mousigian, et al., 2012; Helsen et al., 2016). As such, it may be that the dynamic protocol we have developed more reliably measures proprioceptive acuity compared to position matching paradigms, as well as more accurately capturing proprioception as it is perceived in normal voluntary movement.

In summary, we did not observe age-related increases in absolute matching errors, contrary to previous reports, which may be a result of our considerations for muscle thixotropy or the relatively high cognitive functioning of our OA sample. However, direction specific errors were age-dependent and may be due to specific age-related changes in muscle physiology. Importantly, we found no relationship between passively and dynamically derived proprioceptive acuity measures in older or younger adults. Since estimates of proprioceptive acuity acquired from the dynamic task have higher specificity to voluntary movement and may be more reliable than previous reports with passive tasks, this further supports the use of the dynamic task for experimentation in this thesis.

CHAPTER 5

The Effects of Altered Task Parameters on Measures of Dynamic Proprioceptive Acuity

Chapter Abstract

Since the finding of age and physical activity dependent effects on bias in Chapter 3 were unexpected, we were interested to examine the extent to which manipulating parameters of the dynamic task influenced the proprioceptive acuity estimates they produced. Specifically we noted 3 parameters of interest which were reach distance (10 or 20cm), shape of constrained channel trajectory (straight or minimum jerk) and target visibility (remain visible or disappear). We predicted the largest systematic and variable proprioceptive errors would occur when reach distance was largest, channel trajectory was straight and target visibility was removed. Furthermore, we predicted we would replicate the bias effects from Chapter 3 and uncertainty range effects from Cressman, Salomonczyk, & Henriques (2010) in conditions where task parameters had the highest similarities to the respective experiments. In addition to completing blocks of the dynamic task corresponding to all combinations of the different task parameters, older and younger participants also performed tasks to measure spatial working memory (SWM) and proprioceptive drift as additional correlates of dynamic task performance. Contrary to predictions there were no effects of age on either bias or uncertainty range in any of the conditions, including those corresponding to Chapter 3 and the report by Cressman et al. (2010). Regardless of age, reaching further increased both types of proprioceptive error, with straight channels increasing just bias compared to minimum jerk, partially supporting predictions. However, having the target remain visible

increased bias in the 20cm reaches, which was unexpected. Despite age-dependent loss of SWM capacity there were no significant correlations with proprioceptive measures, but younger adults (YAs) saw a correlation between bias and proprioceptive drift in the corresponding 20cm, target disappear reaching condition. Based on inability to replicate findings, we conclude that the effects of ageing on dynamic proprioceptive acuity may not be robust and that more sensitive methodology with larger sample sizes (such as those used in Chapter 3) may therefore be necessary to capture them empirically.

5.1 – Introduction

In Chapter 3, we presented data to show an increased bias, but not uncertainty range, for physically inactive older adults (OAs) compared to YAs. In contrast, a previous study by Cressman et al. (2010) used a similar dynamic task to show age-dependent increases in uncertainty range but not bias. Since the number of experiments using these types of tasks with the older population is limited, we speculated that differences in task design may have contributed to these contrasting findings. Specifically, we highlighted reach distance as a potentially influential task parameter which has been shown to affect measures of upper limb proprioceptive acuity in YAs (van Beers, Sittig, & Denier van der Gon, 1998; Wilson, Wong, & Gribble, 2010). We also noted the possible role of enhanced proprioceptive cues with minimum jerk over straight perceptual channels, and finally the role of visual feedback of the reference target position, all of which have unknown effects between age groups in these types of tasks.

Additionally, we discussed the idea that SWM capacity may be a more relevant correlate for dynamic proprioceptive acuity measures than verbal working memory since it has been associated with OA performance in sensorimotor adaptation tasks (Anguera, Reuter-Lorenz, Willingham, & Seidler, 2010; Trewartha, Garcia, Wolpert, & Flanagan, 2014; Uresti-Cabrera, Diaz, Vaca-Palomares, & Fernandez-Ruiz, 2015) and with reduced variable errors in position matching tasks (Goble, Aaron, Warschausky, Kaufman, & Hurvitz, 2012; Goble, Noble, & Brown, 2010). Finally, we briefly mentioned that proprioceptive drift may have contributed to proprioceptive biases since movements were performed with prolonged visual occlusion and systematic errors were consistent with the direction of drift reported elsewhere (Brown, Rosenbaum, & Sainburg, 2003a, 2003b; Desmurget, Vindras, Gréa, Viviani, & Grafton, 2000). Although it was noted that this phenomenon typically occurs during unconstrained continuous movements, we were interested in the extent to which this may influence the proprioceptive measures in our task and whether they could partially explain the age-dependent bias effects we measured.

Following this, the study reported in this chapter was designed to look at how the different combinations of reach distance, perceptual channel trajectory and reference target presentation influenced measures of bias and uncertainty range for a group of older and younger adults. In addition, we measured SWM capacity and proprioceptive drift to see how they contributed to the magnitude of proprioceptive deficits measured by our task. Following the observed differences between the task used in Cressman et al. (2010) and our own data reported in Chapter 3, we predicted larger systematic and variable proprioceptive errors during task conditions with larger reach distances, with straight channels and with restricted visual feedback of the reference position. In the task conditions which were identical to those in Chapter 3, we expected to replicate the age-effects on bias and not uncertainty range. And although there were still some slight methodological discrepancies, we expected to replicate the age-effects on uncertainty range but not bias reported by Cressman et al. (2010) when using similar task conditions of straight channels, shorter reach distance and visual presentation of reference position at endpoint.

5.2 – Methods

5.2.1 – Participants

A total of 18 OAs (6 male, 73.2 ± 5.2 yrs) and 16 YAs (3 male, 19.4 ± .72 yrs) participated in the experiment. Participant inclusion criteria were similar to those which are described in previous chapters. Participants were excluded from participation if they had any upper limb or wrist pain or movement limitations, and read information sheets before giving written consent to participate. All participants were right-hand dominant according to a laterality quotient of 30 or higher on the 10-item Edinburgh handedness inventory (Oldfield, 1971), with YAs being between age 18-25 years and OAs being 65 years and older. All OAs included in the analysis had a Montreal Cognitive Assessment (MoCA) score of 26 or above out of 30, which shows normal cognitive functioning (Nasreddine et al., 2005).

5.2.2 – Physical Activity Measures

Due to time, equipment and recruitment limitations it was not possible to measure physical activity (PA) for OAs using accelerometers as in previous chapters, nor was it possible to sub-group a meaningful number of OAs into separate high and low PA groups. As such, PA levels were measured using self-report measures for both older (Physical Activity Scale for the Elderly [PASE]; Washburn, Smith, Jette, & Janney, 1993) and younger (IPAQ-Short questionnaire; Craig et al., 2003) adults and used as a correlate with proprioceptive outcome measures. In this way it was possible to see whether the PA effect on bias reported in Chapter 3 could be replicated, and whether there was a similar relationship within the younger population.

5.2.3 – Fatigue and Attention

To monitor the extent to which participation in the experiment might fatigue participants or cause them to lose concentration over time, they were asked to fill out an additional questionnaire assessing their levels of fatigue and attention at the time of participation. Participants used a 7 point Likert scale both before and after the experiment to rate themselves between least (1) and maximally (7) attentive and least (1) and maximally (7) fatigued. In addition, they reported the number of hours of sleep they had the night before, and rated the quality of the sleep on a similar 1-7 point scale (poor to excellent), with participants reporting 4 hours of sleep or less excluded from analysis.

5.2.4 – Spatial Working Memory

To assess SWM capacity we used a modified version of a task recently reported with OAs and cognitively impaired patient populations (Kessels, Meulenbroek, Fernandez, & Olde Rikkert, 2010; van Asselen, Kessels, Wester, & Postma, 2005). In this task, participants were presented with a series of blue tiles on a computer monitor which they were instructed to click on one at a time using a mouse. They continued to click on these tiles until they selected one which briefly revealed a green tick symbol, before it turned back to blue (a sequence we term a “search”). The task was then to remember the location of this search target and to then continue searching the remaining tiles for a new target which might appear on any of the remaining tiles. Searches continued until a green tick had been found under each tile, at which point the trial terminated. In any given search, if the participant clicked on a tile which they had previously selected, a red cross symbol briefly appeared; this was defined as a within-search error. Similarly, if participants selected a tile which they had previously found a green tick under in an earlier search, they saw a similar red cross; this was a between-search error. The purpose of the task was therefore to find all of the green ticks whilst minimising the number of search errors (red crosses). All participants completed 2 trials at each of 4, 6, 8 and 10 tiles and were given 2 trials at 4 tiles as a familiarisation to ensure they fully understood the task instructions. Participants also wore headphones so they could hear distinct audio feedback tones associated with clicking on a blue tile for the first time in a search, revealing a green tick, and revealing a red cross (error). Between and within search errors were averaged across the 2 attempts at each number of boxes, then compared between age groups and used as correlates with proprioceptive acuity measures to see if this aspect of cognitive function confounded or was related to performance of the task. A summary of this task is shown in Figure 5.1 for a 4-tile trial.

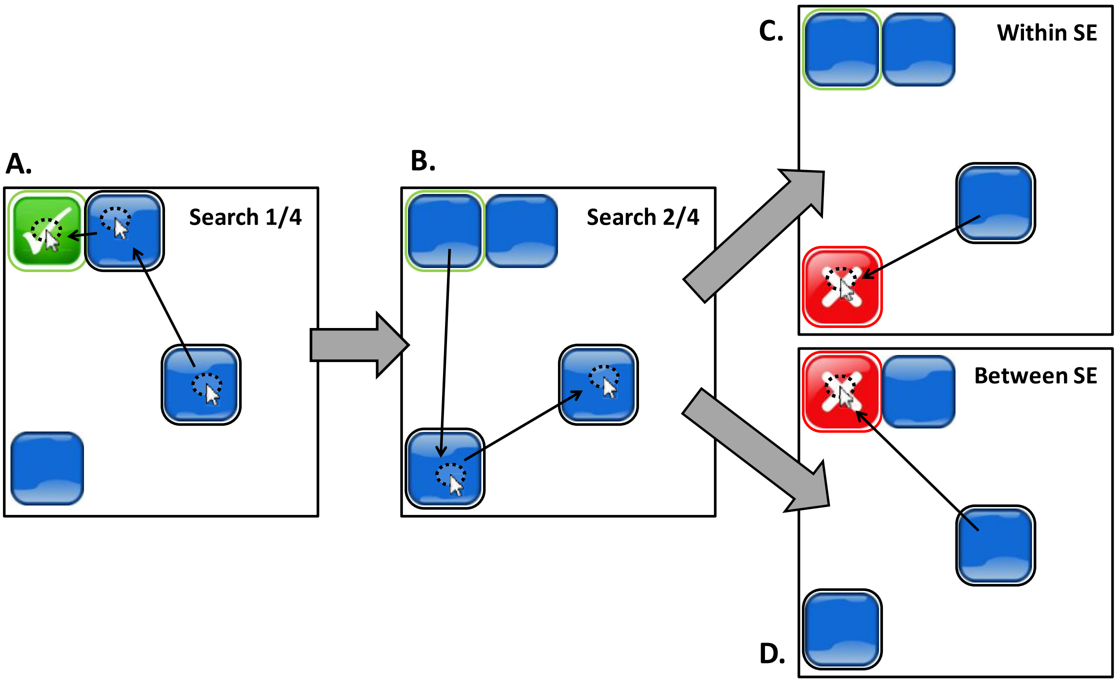


Figure 5.1. – Summary of spatial working memory task and different types of search error (SE). Black outlined tiles show those which have been searched without finding a tick and green outlined tiles are those where a tick has been found. Participants had to memorise this information as these outlines were not displayed during task performance. **A.** Shows an initial successful search, where tiles are sequentially clicked on until green tick appears **B.** shows part of the following search, note green outlined tile is the target of the previous search **C.** A within search error where the tile has already been searched (i.e. in Panel B) **D.** A between search error where a tile is selected that was the target of a previous search (i.e. in Panel A.).

5.2.5 – Experimental Set-Up

The dynamic proprioception and proprioceptive drift tasks in this experiment were performed on the vBOT, was described in detail in Chapter 2. The start position was always displayed as a white 1cm radius marker located 8cm into the workspace (approximately 28cm from the participant's torso), with targets displayed as grey 1cm radius markers and the hand position cursor as a 0.5cm radius marker (when it was provided). For all tasks and conditions the targets were located along a sagittal axis through the participant's mid-line with its distance from start position dependent on the specific task or condition in question.

5.2.6 – Proprioceptive Drift Task

5.2.6.1 – Procedure and Design

Participants made unconstrained reaching movements to a target which was presented 20cm directly ahead of the start position, and were instructed to keep movements as straight as possible. The task was performed with restricted visual feedback by using a horizontal white bar as a hand position cursor, which was displayed orthogonally to the axis linking start position to target and spanned the entire width of the workspace. This meant that participants had visual information regarding the linear distance they had travelled between the start position and the target, but not regarding lateral deviations from this axis during movements. When participants moved the white bar as far as the target, they felt resistance from a soft virtual wall before being actively guided back to the start position ready for the next trial (see Figure 5.2 for procedure summary). Participants performed 2 blocks of 40 of these reaching movements; one where the target was visible for the entire block, and the other where it disappeared after the initial 5cm of each forward reach (in a similar fashion to the dynamic proprioceptive task which has been used in previous chapters). The target 'disappear' trials allowed us to test whether direct visual-proprioceptive comparisons contributed to reaching accuracy. Each block was preceded by 10 unconstrained, null-field target reaching trials where full hand position cursor feedback was provided. These trials were aimed at reducing any potential carry over effects of proprioceptive drift between the two conditions. The order of performance was counterbalanced between participants to eliminate any potential order effects (full summary of the experimental design is shown in Figure 5.4).

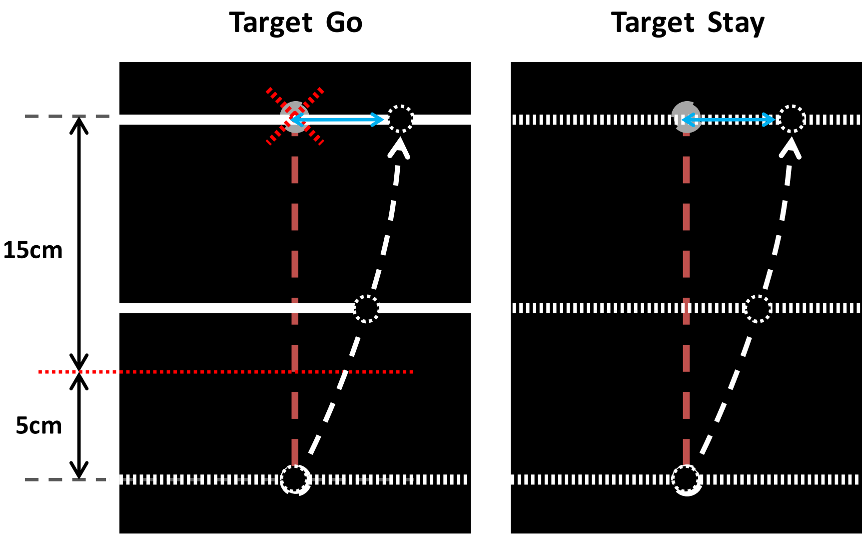


Figure 5.2 – Proprioceptive drift task procedure for the target disappear ("go") or remain ("stay") conditions. Thick white horizontal bar shows the visual feedback provided to participants during movements which gives information regarding linear distance travelled only (dashed circles show progressive position of unseen hand). Blue arrows show the final deviated position which was used to calculate drift index (average lateral deviation for first 10 trials subtracted from the average for the last 10 trials). Horizontal red dashed line shows point at which target disappeared in target "go" condition.

5.2.6.2 – Outcome Measures and Analysis

In order to measure the extent of proprioceptive drift, the average lateral deviation from the target was calculated for the first and last 10 of the 40 trials in the block. The difference between these 2 values then gave an index of limb position drift for that block, with a larger value indicating greater drift. Peak hand velocity was also recorded since it has previously been reported to influence the extent of proprioceptive drift in these types of tasks (Brown et al., 2003b).

5.2.7 – Dynamic Proprioception Tasks

5.2.7.1 – Procedure and Design

A detailed description of the general task procedure is outlined in Chapters 2 and 3, with only the key variations detailed in this section. Participants performed separate blocks of perceptual channel trials where the target distance, target visibility and shape of perceptual force channel were manipulated (Figure 5.3). For the reach distance blocks, movements were made to a target 10cm or 20cm directly ahead. For the manipulation of target visibility, either the target disappeared after the first portion of the movement (as it has done in previous chapters) or remained for the entire movement. And for the perceptual channel parameter, channels were either shaped according to a minimum jerk (MJ) trajectory (as in previous chapters) or in a straight line connecting the start position to the final, laterally deviated position. The different combinations of these manipulations gave a total of 8 different experimental conditions, which are summarised in Figure 5.3. One of these 8 conditions was also repeated twice at set intervals between the other conditions to see how reproducible the measures of proprioceptive acuity were, and whether there was a time-dependent effect. This increased the total number of blocks to 10, with the repeated condition (20cm reach, target staying visible and MJ channels; white asterisk in Figure 5.3) performed in the fixed positions of first, fifth and last (tenth). The remaining 7 conditions were performed in between, where the order of completion was pseudo-randomised between participants.

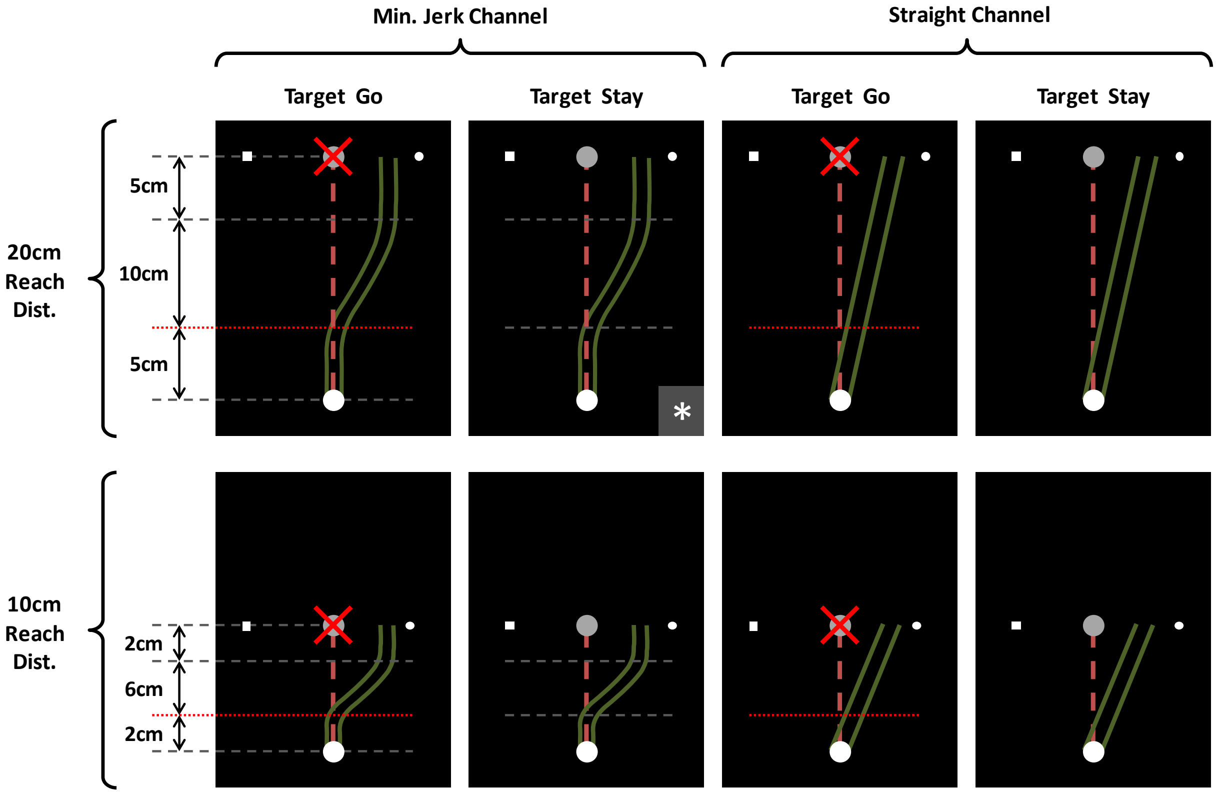


Figure 5.3 – Diagram of 8 different experimental conditions based on manipulation of reach distance (20 or 10cm), target visibility (disappear [“Go”] or remain [“Stay”]) and perceptual channel shape (minimum jerk or straight trajectory). Perception of deviated limb position was indicated by verbal response of “Square” or “Circle” (left- and right-hand side of target respectively). Red dotted lines show the threshold point at which the target disappeared for the target “go” conditions, with grey dashed lines showing the relative components of the minimum jerk trajectories. Solid green lines show the shape of the respective channel type which was used. The repeated condition (20cm reach distance, target “stay”, minimum jerk channel condition) is indicated by the white asterisk

The task used identical PEST sequence parameters to those described in Chapter 3, with the only difference being that the 2 interleaved sequences repeated each deviation magnitude twice, since the task was performed to a single target. Each test block consisted of 40 perceptual channel trials and was preceded by 5 unconstrained, null-field target reaching trials with full visual feedback of hand position, designed to avoid proprioceptive drift in a similar fashion to previous chapters. Participants gave verbal responses to indicate the side of perceived hand path deviation similar to responses described in Chapter 3 (“Square” for left of target and “Circle” for right of target).

5.2.7.2 – Outcome Measures and Analysis

As with previously described analysis of this task, responses were binarized and fitted with a logistic function to gain two measures of proprioceptive acuity; the bias and uncertainty range. In addition to this, the average movement velocity and orthogonal forces exerted against the channel walls in the last portion of the movement (16-19cm of 20cm reach and 8.5-9.5cm of 10cm reach) were also recorded for each condition.

5.2.8 – Experimental Design and Statistical Analysis

The full experimental design is summarised in Figure 5.4. Participants always performed the SWM task first, followed by the proprioceptive drift task (two target visual feedback conditions counterbalanced) and then the dynamic proprioception task blocks (10 conditions pseudorandomised apart from the repeated condition; blocks 1, 5 and 10). There was a short familiarisation block for the dynamic proprioception task which consisted of 5 null-field and 5 perceptual channel trials, and used the same task conditions as would be presented in the first trial.

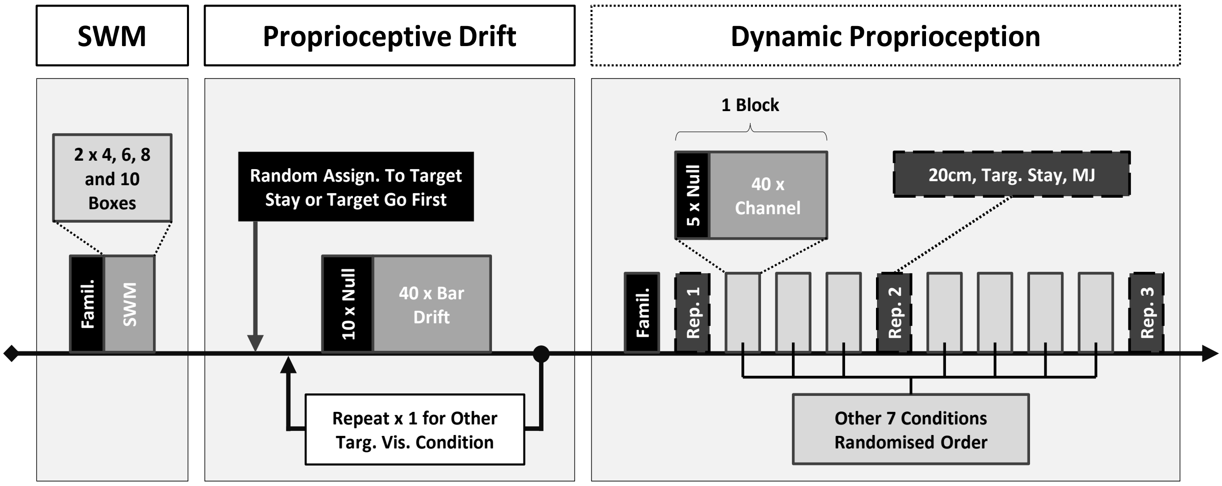


Figure 5.4 – Experimental design summary. Spatial working memory (SWM) was performed first, with 2 trials at each of 4, 6, 8 and 10 blue boxes to search through. Random assignment to either target "stay" (remains visible) or "go" (disappears) preceded proprioceptive drift trials with horizontal bar hand position cursor. There were 10 blocks of dynamic proprioception trials (with 5 null-field preceding each block of 40 channel trials), where the 20cm, target stays, minimum jerk (MJ) channel condition (dark grey, black dash outline) was performed 3 times at fixed positions (1st, 5th and 10th), with other conditions randomly assigned to the remaining 7 positions.

All values which were 2.5 standard deviations away from the group mean were excluded as outliers. The proprioceptive task data was analysed in a 2 x 2 x 2 x 2 mixed-design ANOVA: (Age Group; older or younger adults) x (Channel Type; straight or MJ) x (Reach Distance; 10 or 20cm) x (Target Visibility; target remains visible ["stay"] or disappears ["go"]) , in which the first performance ("Rep. 1" in Figure 5.4) of the 20cm, target stay, MJ channel condition was used. The further repeats of this condition were normalised to values obtained from the first performance, and analysed separately in an additional 2 x 2 mixed-design ANOVA: (Age Group; older or younger adults) x (Repeat; 2nd or 3rd performance) to see how they changed across the course of the experiment. The SWM data was analysed in a separate 2 x 4 mixed-design ANOVA: (Age Group; older or younger adults) x (Number of Tiles; 4, 6, 8 or 10), and proprioceptive drift index was analysed in a 2 x 2 mixed-design ANOVA: (Age Group; older or younger adults) x (Target Visibility; target remains visible ["stay"] or disappears ["go"]). SWM capacity was correlated with performance data corresponding to the target stay and go conditions (collapsed across channel type and reach distance), since target visibility was thought to affect attentional load during task performance to the greatest extent and hence most likely to see a relationship with SWM (Goble, Mousigian, & Brown, 2012). Proprioceptive drift data was correlated with measures from the corresponding target visibility conditions (collapsed across channel type) for the 20cm reach distance. A Greenhouse-Geisser correction was used in all cases where the sphericity assumption had been violated and all main effects and interactions were assessed at the $p < .050$ level. Where multiple comparisons were performed (i.e. to follow-up significant ANOVA effects or with correlations and linear regression models), uncorrected, Least-Significant Difference (LSD) *p*-values are reported but were assessed for significance using a False Discovery Rate (FDR) analysis which is described in detail in Chapter 2. FDR-adjusted *p*-thresholds (p_{FDR}) are reported throughout the results section as necessary, and when there were no significant comparisons observed (i.e. $p < p_{\mathrm{FDR}}$ was not found) the smallest observed p-value (p_{min}) is reported with its associated critical significance value (still denoted as p_{FDR}) (see Chapter 2 for details).

5.3 – Results

5.3.1 – Dynamic Proprioception Parameter Manipulation

5.3.1.1 – Proprioceptive Measures

A summary of the proprioceptive measures data can be seen in Table 5.1. Uncertainty range data is displayed in Figure 5.5. There was no effect of Age Group on uncertainty range (F[1, 27] = .27, p = .608) and Channel Type showed only a trend towards significance (F[1, 27] = 3.96, p = .057, η^2_p = .13) where larger uncertainty ranges were typically measured with straight than MJ channels. The effect of Reach Distance was significant (F[1, 27] = 24.03, p < .001, η^2_p = .47) with larger ranges of uncertainty at the further 20cm reach distance than 10cm. Target Visibility did not have effect on uncertainty range (F[1, 27] = .49, p = .492). All two-, three- and four-way interactions were also non-significant (p > .090). This replicated the findings from previous chapters showing a non-significant difference in uncertainty range between older and younger adults. The only task parameter which seems to strongly influence this measure is reach distance, where reaching further increases uncertainty range, with straight channels showing a trend towards creating larger ranges of uncertainty than MJ. This supports predictions of increased proprioceptive uncertainty with larger reach distances, yet contradicts predictions that reduced visual feedback and straight channels would also have a similar effect. Furthermore, we were not able to replicate the effects of age-dependent increase in uncertainty range from Cressman et al. (2010) in the 10cm, straight channel, target stay condition as we predicted.

Measure	Group	Straight Channel				Minimum Jerk Channel				**Overall**
		20cm Reach		***10cm Reach***		***20cm Reach***		***10cm Reach***		
		Target Go	Target Stay	Target Go	Target Stay	Target Go	Target Stay	Target Go	Target Stay	
Uncertainty Range (cm)	*Older*	.79 *(± .15)*	.78 *(± .09)*	.50 *(± .06)*	.61 *(± .08)*	.49 *(± .05)*	.58 *(± .10)*	.37 *(± .07)*	.37 *(± .06)*	.56 *(± .04)*
	Younger	.73 *(± .10)*	.67 *(± .12)*	.43 *(± .09)*	.58 *(± .08)*	.71 *(± .10)*	.70 *(± .15)*	.50 *(± .06)*	.44 *(± .10)*	.60 *(± .05)*
Bias (cm)	*Older*	1.20 *(± .16)*	1.45 *(± .25)*	.88 *(± .11)*	.84 *(± .15)*	.80 *(± .22)*	.85 *(± .13)*	.47 *(± .09)*	.74 *(± .16)*	.90 *(± .12)*
	Younger	.80 *(± .19)*	.99 *(± .20)*	.64 *(± .16)*	.59 *(± .14)*	.61 *(± .09)*	.89 *(± .18)*	.43 *(± .12)*	.33 *(± .10)*	.66 *(± .09)*
Movement Velocity (cm/sec)	*Older*	15.5 *(± .89)*	15.6 *(± .74)*	10.8 *(± .69)*	10.6 *(± .76)*	15.1 *(± 1.0)*	14.0 *(± .87)*	10.8 *(± .54)*	10.2 *(± .61)*	****12.8 *(± .61)***
	Younger	20.2 *(± 1.4)*	21.2 *(± 1.5)*	14.3 *(± .83)*	14.6 *(± .85)*	20.1 *(± 1.1)*	18.3 *(± 1.4)*	14.3 *(± .86)*	14.8 *(± 1.1)*	17.2 *(± 1.0)*

Table 5.1. – Group average results for all combinations of the manipulated task parameters in the dynamic proprioception task. The 20cm, target stay, minimum jerk condition presented here is the first performance of the three repeats. Values given as means ± standard error, with significant differences from younger adults indicated by ** ($p < .010$)

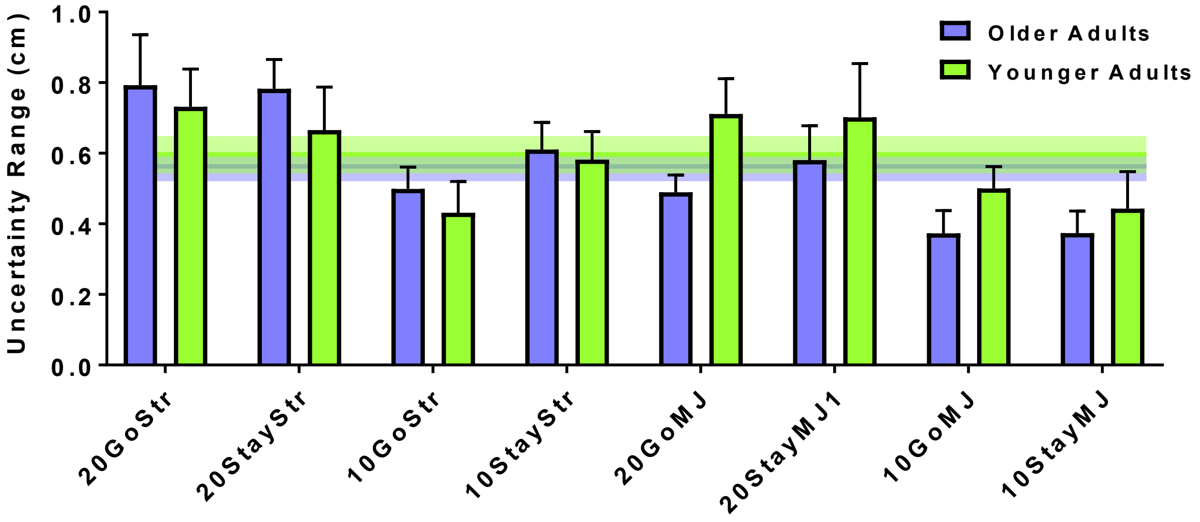


Figure 5.5. – Group average uncertainty range data for all combinations of the different manipulated task parameters. “20” or “10” refers to reach distance in cm, “Stay” or “Go” refers to target visibility, and “Str” and “MJ” refer to straight or minimum jerk force channels respectively. The additional “1” on “20StayMJ” indicates that data presented in this figure is for the first performance of three repeats for this condition. Vertical bars are given as means ± standard error bars, with group means across all conditions shown as solid horizontal bars ± standard error shaded region. There were no significant differences observed between older and younger adults.

Group results for the bias is shown in Figure 5.6. There was no effect of Age Group on bias (F[1, 28] = 2.54, *p* = .122). However, both Channel Type (F[1, 28] = 17.65, *p* < .001, η^2_p = .39) and Reach Distance (F[1, 28] = 14.56, *p* = .001, η^2_p = .34) had strong effects on bias, where 20cm and straight channel reaches caused larger, more positive biases (“Circle” or right-hand side of target) than 10cm and MJ channel reaches respectively. There was no effect of Target Visibility on bias (F[1, 28] = 2.82, *p* = .105). All two-way interactions were non-significant (*p* > .169) except for Reach Distance x Target Visibility which was marginally significant (F[1, 28] = 4.27, *p* = .048, η^2_p = .13). Follow-up pair-wise comparisons showed that when Target Visibility was held constant, the 20cm reaches induced larger biases than the 10cm (target go, *p* = .015; target stay, *p* < .001; p_{FDR} = .038) reflecting the main effect of Reach Distance. However, an additional finding was that for 20cm reaches only, biases were larger and more positive for the target stay than target go condition (*p* = .022, p_{FDR} = .038). All three- and four-way interactions were non-significant (*p* > .106). This shows that age did not affect bias significantly, but there were strong effects of both channel type and reach distance where larger, more positive shifts (towards “Circle” or right-hand side of target) were measured in 20cm reaches and with straight channels. It is also interesting to note that when the 20cm performance data was collapsed across age group and channel type, biases were larger when the target remained than when it disappeared. These findings are in line with predictions that increased reach distance and straight channels would increase systematic proprioceptive errors, but contradicts the prediction that reduced visual feedback of the reference target would also increase errors in this way. Furthermore, we did not replicate the age-dependent bias increase reported Chapter 3 for the 20cm, MJ channel, target go condition as predicted.

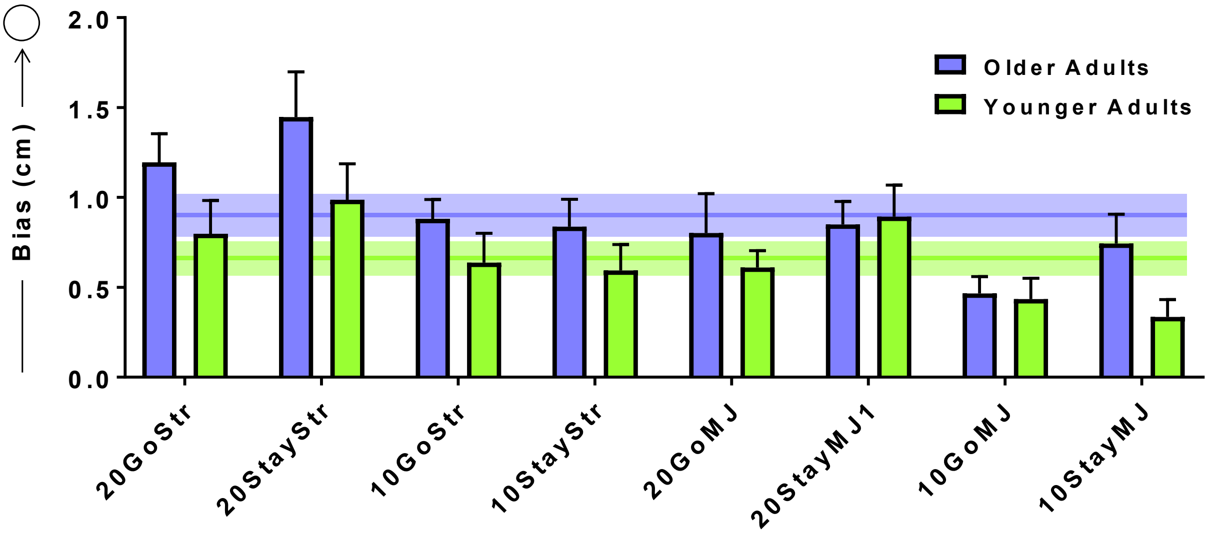


Figure 5.6. – Group average bias data for all combinations of the different manipulated task parameters. "20" or "10" refers to reach distance in cm, "Stay" or "Go" refers to target visibility, and "Str" and "MJ" refer to straight or minimum jerk force channels respectively. The additional "1" on "20StayMJ" indicates that data presented in this figure is for the first performance of three repeats for this condition. Vertical bars are given as means ± standard error bars, with group means across all conditions shown as solid horizontal bars ± standard error shaded region. Despite the separation of the bars, the differences observed between older and younger adults were not statistically significant.

5.3.1.2 – Kinematic Measures

A summary of the movement velocity data can be seen in Table 5.1. There was a significant effect of Age Group on mean movement velocity (MeanVel; F[1, 31] = 14.20, $p = .001$, $\eta^2_p = .31$) such that OAs made slower movements than YAs. There was no effect of Channel Type on MeanVel (F[1, 31] = 3.55, $p = .069$). However, there was a highly significant effect of Reach Distance (F[1, 31] = 278.57, $p < .001$, $\eta^2_p = .90$) where movements were faster during 20cm reaches than 10cm. There was no effect of Target Visibility on MeanVel (F[1, 31] = .72, $p = .402$). All two-, three- and four-way interactions were non-significant ($p > .067$). This replicates our previous findings that OAs typically move slower than YAs during performance of this task, but also shows that movements were faster during 20cm than 10cm reaches.

To see whether the bias was influenced by orthogonal force applied to the channel walls in the last portion of the movements, we correlated the 2 variables for each condition for both older and younger adults (Pearson correlations for 2 [Age Group] x 2 [Channel Type] x 2 [Reach Distance] x 2 [Target Visibility] relationships). There were no significant relationships found for either older (p_{min} = .044; p_{FDR} = .003) or younger (p_{min} = .036) adults for any of the conditions which shows bias was independent of the directed efforts exerted during movements in the force channels. It was also important to see whether movement speed influenced proprioceptive acuity during performance of these different conditions, so both the uncertainty range and bias were correlated with the average movement velocity, calculated for their respective conditions, for older and younger adults too (uncertainty range and bias Pearson correlations for 2 [Age Group] x 2 [Channel Type] x 2 [Reach Distance] x 2 [Target Visibility] relationships). It was similarly found there were no significant relationships for either older (uncertainty range, p_{min} = .099; bias, p_{min} = .066; p_{FDR} = .003) or younger (uncertainty range, p_{min} = .178; bias, p_{min} = .009) adults between perceptual measures and movement speed, showing their independence for this task.

5.3.1.3 – Repeated Performance and Order Effects on Proprioceptive Measures

To compare repeated performance of dynamic proprioception blocks, the bias and uncertainty range values obtained for the 2nd and 3rd repeat were normalised to the values obtained from the 1st performance for each participant. The main effect of Age Group on normalised bias (Figure 5.7, Panel A) was not significant (F[1, 32], = 2.60, *p* = .117) and neither was the effect of Repeat (F[1, 32] = .13, *p* = .719) or their interaction (F[1, 32], = 2.60, *p* = .117). Similarly, there was no effect of Age Group, (F[1, 30] = 2.97, *p* = .095), Repeat (F[1, 30] = .07, p = .799) or their interaction (F[1, 30] = .05, p = .834) on normalised uncertainty range (Figure 5.75.7, Panel B). As an additional means of assessing how these measures changed across the timecourse of the experiment, we also correlated uncertainty and bias for the remaining 7 conditions with the order in which they were performed, for both older and younger adults (uncertainty range and bias Pearson correlations for 2 [Age Group] x 7 [Condition] relationships). There were no significant relationships measured for either older (uncertainty range, p_{min} = .187; bias, p_{min} = .550; p_{FDR} = .004) or younger (uncertainty range, p_{min} =.016; bias, p_{min} = .345) adults, which shows there was no linear change in proprioceptive acuity measures due to order effect.

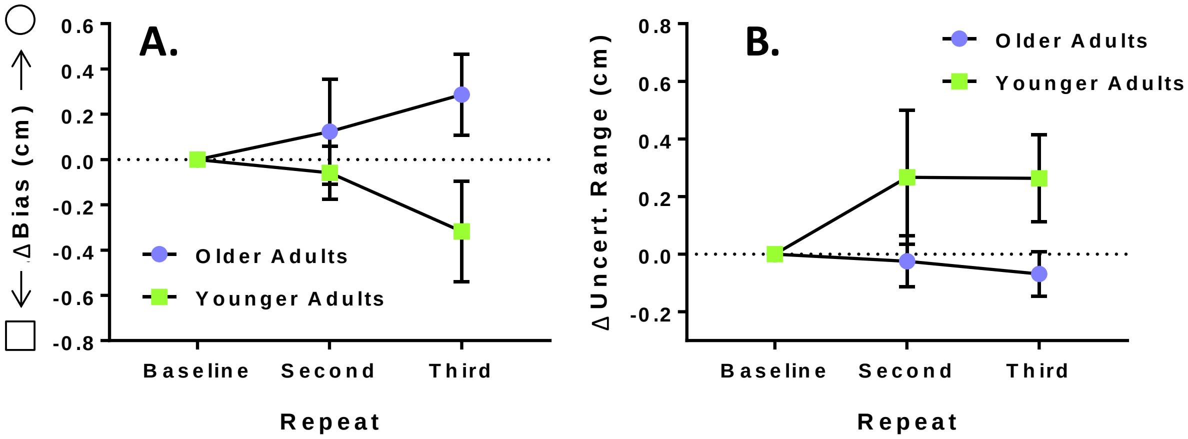


Figure 5.7. – Group average bias (**A.**) and uncertainty range (**B.**) data for the repeated performance of the 20cm, target stay, minimum jerk channel condition. Values for the second and third repeat are normalised to the baseline values for each participant, and therefore show how the measures changed across the timescale of the experiment. Values are given as means ± standard error, there were no significant changes across the repeated performances or between age groups.

Collectively, this demonstrates that proprioceptive estimates remain relatively stable over time and across repeated performance of additional dynamic proprioception blocks. However, whilst the changes may not have been statistically significant, a review of Figure 5.7 shows there is a tendency for a shift in both the bias and the uncertainty range with time, and this should be considered for future applications of the task.

5.3.2 – Spatial Working Memory

All participants were able to complete the task with 4 tiles without incurring any within or between search errors, and as such, this condition was not included in the analysis. This then meant that the remaining data was analysed in a 2 x 3 mixed-design ANOVA: (Age Group; older or younger adults) x (Number of Tiles; 6, 8 or 10).

All data for this task is summarised in Table 5.2. There was a main effect of Age Group on within search errors (WSEs; F[1, 32] = 6.54, $p = .015$, $\eta^2_p = .17$) such that OAs made more WSEs than YAs (Figure 5.8, Panel A). Number of Tiles also had an effect on WSE (F[1.3, 41.1] = 12.72, $p < .001$, $\eta^2_p = .28$) with pair-wise comparisons showing that WSEs at 10 tiles were significantly greater than at 6 tiles and 8 tiles (both $p = .001$; $p_{FDR} = .033$). The Age Group x Number of Tiles interaction was not significant (F[1.3, 41.1] = 1.95, $p = .168$).

Measure	Group	Number of Tiles			**Overall**
		6	**8**	**10**	
Within Search Errors	*Older*	.31 *(± .13)*	.78 *(± .23)*	1.81 *(± .45)*	***.72 *(± .16)***
	Younger	.16 *(± .11)*	.06 *(± .04)*	.78 *(± .27)*	.25 *(± .08)*
Between Search Errors	*Older*	.81 *(± .28)*	*****4.69 *(± .78)***	***7.97 *(± 1.12)***	*****3.37 *(± .40)***
	Younger	.44 *(± .24)*	1.00 *(± .38*	4.19 *(± .74)*	1.41 *(± .18)*

Table 5.2. – Group average within and between search errors for the spatial working memory task. All participants scored 0 errors for the 4 tile condition and it was therefore excluded from analysis. Values are given as means ± standard error, with significantly different values to younger adults indicated by ***** ($p < .050$) and ******* ($p < .001$; multiple comparisons subjected to FDR adjusted *p*-threshold)

OAs also made a greater number of between search errors (BSEs) than YAs (F[1, 32] = 18.45, $p < .001$, $\eta^2_p = .37$; Figure 5.7, Panel B). Number of Tiles also had a significant effect on BSE (F[1.5, 46.6] = 34.33, $p < .001$, $\eta^2_p = .52$) where errors at each of the different number of boxes were significantly different from one another (all $p < .001$, $p_{\text{FDR}} = .050$), such that the most errors were at 10 tiles and the fewest at 6. The Age Group x Number of Tiles interaction was significant (F[1.5, 46.6] = 4.32, $p = .029$, $\eta^2_p = .12$) with follow-up pair-wise comparisons showing that OAs made a greater number of BSEs during task performance at 8 tiles ($p < .001$; $p_{\text{FDR}} = .033$) and 10 tiles ($p = .010$).

This data shows that OAs have impaired SWM which becomes particularly dissociable from YAs when trying to memorise information related to the entire trial (i.e. BSE) and when the task is more complex.

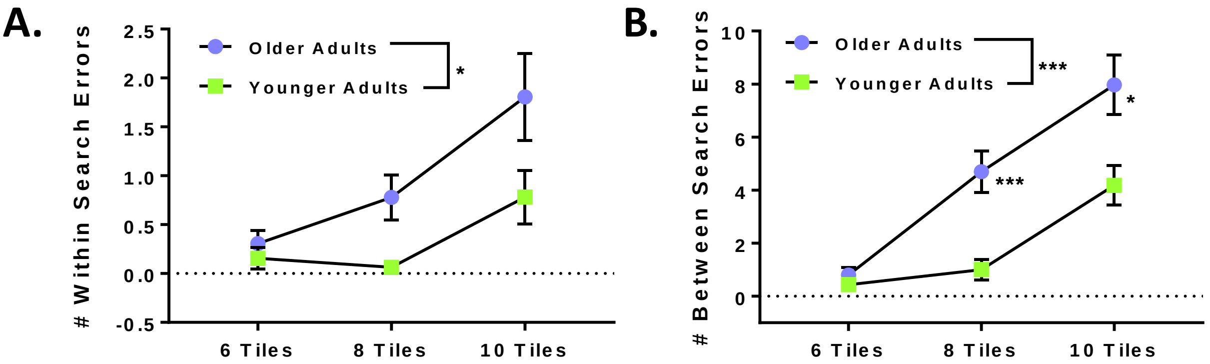


Figure 5.8. – Group average search errors for the spatial working memory task for 6, 8 and 10 tiles. Since all participants got 0 errors for the 4 tile condition, it was not included in analysis. **A.** shows the number of within search errors for each condition and **B.** shows number of between search errors. Values are given as means ± standard error, with significantly different values from younger adults indicated by * ($p < .050$) and *** ($p < .001$; multiple comparisons subjected to FDR adjusted *p*-threshold)

To see whether cognitive function had any influence on proprioceptive acuity measures in this experiment, we correlated the average BSE and WSE with uncertainty range and bias for the target stay and go conditions separately, collapsing data across channel type and reach distance (bias and uncertainty range Pearson correlations for 2 [Age Group] x 2 [Search Error; WSE and BSE] x 2 [Target Visibility; target go or stay] relationships). There were no significant relationships found for OAs, with only a trend towards significance between average bias in the target go condition and average BSE after adjusting for multiple comparisons ($r = .64$, $p = .008$; $p_{FDR} = .006$, all other relationships $p > .093$). Similarly, there were no significant associations for YAs, but a trend towards significance for the correlation between average target go uncertainty range and average WSE after correction for multiple comparisons ($r = .69$, $p = .007$; $p_{FDR} = .006$, all other relationships $p > .090$).

This suggests that performance on these tasks is independent of cognitive ability as measured by this task. However, the trends towards significance with both younger and older adults when target visibility was removed suggest this may be a less reliable paradigm than when the target remains.

5.3.3 – Proprioceptive Drift

There was no effect of Age Group on drift index (F[1, 30] = .28, p = .603), nor of Target Visibility (F[1, 30] = .43, p = .519), or their interaction (F[1, 30] = .1.71, p = .201; Figure 5.9). Peak hand velocity was also unrelated to proprioceptive drift for both older (target stay, r = .39, p = .137; target go, r = -.21, p = .409; p_{FDR} = .013) and younger adults (target stay, r = .05, p = .848; target go, r = -.56, p = .031).

To see whether proprioceptive biases were caused, or influenced, by limb position drift, we correlated the bias for the 20cm target go and stay conditions (straight and MJ channels separately) with the respective target visibility drift indices (target go drift index Pearson correlations for 2 [Age Group; older or younger] x 2 [20cmGo Condition; straight or MJ channel] relationships; target stay drift index Pearson correlations for 2 [Age Group; older or younger] x 2 [20cmStay Condition; straight or MJ channel] relationships). These conditions for bias measurements were chosen specifically because they used the same reach distance parameter (20cm) as in the proprioceptive drift task and therefore had the highest task relevance. All correlations with target stay conditions were non-significant regardless of age (all |r| < .57, p_{min} = .018; p_{FDR} = .013). However, correlation of drift with bias from the straight channel, target go condition was significant in YAs only (r = -.76, p = .002; p_{FDR} = .013) with all other correlations for target go conditions being non-significant (all |r| < .41, p_{min} = .127). The significant, negative relationship in YAs was such that the further their limb drifted to the left of the target (“Square” side), the further they biased perceived hand position to the right of it ("Circle" side; which would be consistent with them aiming to locate the perceived hand position on target). This suggests that when target visibility is removed during task performance with straight channels, proprioceptive biases may be influenced by limb position drift.

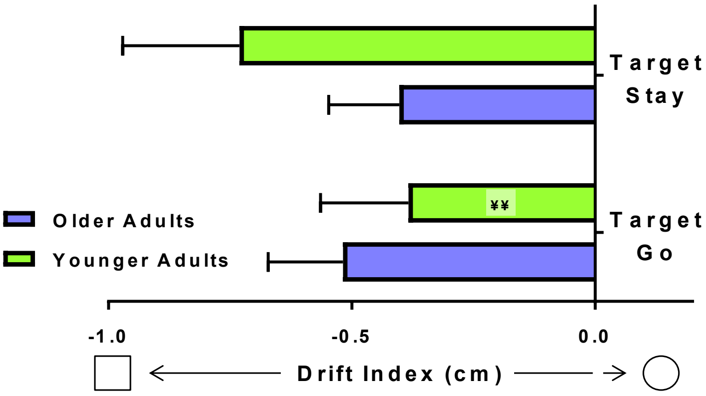


Figure 5.9. – Group average drift index data for the target stay and target go conditions. Horizontal bars are given as means ± standard error, there were no significant differences between older and younger adults. Significant correlation between drift index for target go and bias for 20cm, target go, straight channel condition indicated by ¥¥ (*p* < .010; multiple comparisons subjected to FDR adjusted *p*-threshold)

5.3.4 – Physical Activity

In light of the effect of PA on bias that we measured for OAs in Chapter 3, we were interested to see whether either bias or uncertainty range measured in this experiment were associated with PA. We took the average uncertainty range and bias values across all 10 conditions and correlated these with self-report PA scores for older (PASE score) and younger (IPAQ score) adults, in separate analyses. There were no significant correlations between PA score and uncertainty range (OAs, r = -.09, *p* = .763; YAs, r = -.32, *p* = .270; p_{FDR} = .013) or bias (OAs, r = -.05, *p* =.849; YAs, r =-.001, *p* = .996) for either age group. This means we were not able to observe a similar effect to Chapter 3, and that PA appears to be unrelated to proprioceptive acuity measures in this experiment.

5.3.5 – Attention and Fatigue

The results of an additional 2 x 2 mixed-design ANOVA: (Age Group; older or younger) x (Timepoint; pre- or post-experiment), showed there to be no effect of Age Group on fatigue (F[1, 32] = 2.97, *p* = .097), nor of Timepoint (F[1, 32] = .72, *p* = .403) or their interaction (F[1, 32] = .1.07, *p* = .309). In addition to this, there was no difference between older and younger adults in either number of hours (t[26.0] = .35, *p* = .728) or rated quality (t[32] = -1.59, *p* = .122) of sleep reported.

There was, however, a significant effect of Age Group on attention (F[1, 32] = 7.99, *p* = .008, η^2_p = .20) such that YAs reported having lower attention levels than OAs. There was also a significant effect of Timepoint on attention (F[1, 32] = 19.87, *p* < .001, η^2_p = .38) where attention was reported as lower following the completion of the experiment. The Age Group x Timepoint interaction was not significant (F[1, 32] = .31, *p* = .581).

These data show that whilst participants appear not to have become more tired as a result of participation in the experiment, it has affected their ability to concentrate, with YAs reporting poorer attention than OAs regardless of when it was measured. The absence of any significant interactions shows that participation did not differentially affect attention or fatigue between age groups.

5.4 – Discussion

This experiment assessed how altering the parameters of our dynamic proprioceptive acuity task affected its outcome measures to better understand the basis of our findings in Chapter 3. We found that altering the reach distance had the strongest effects on proprioceptive measures, followed by channel type and then target visibility, but all of these effects were independent of age. We were unable to replicate either our own age-dependent bias effects from Chapter 3 or the opposing age-effects on uncertainty range reported by Cressman et al. (2010). Although older adults (OAs) had worse spatial working memory (SWM) capacity, it was not related to proprioceptive performance. Proprioceptive drift was also unrelated to proprioceptive measures for the OAs, but was correlated with bias for straight channels when target visibility was removed for younger adults (YAs). This effect survived corrections for the multiple comparisons involved.

Similar to previous work, we found that both systematic and variable proprioceptive errors are increased during further reach distances (van Beers et al., 1998; Wilson et al., 2010). This is thought to occur through increased noise in hand localisation as it involves increasing rotation around the relevant joints in the arm (van Beers et al., 1998). Since the hand's distance from the shoulder is larger than from the elbow, it may be that proprioceptive noise from the shoulder joint is the main contributor to decreased acuity as reach distance increases here (van Beers et al., 1998). Considering motor errors have been shown to increase in OAs during movements which involve greater use of the shoulder (Seidler, Alberts, & Stelmach, 2002) the expectation might be of an age-dependent increase in proprioceptive error during further reaches. Yet the effect of reach distance we measured here was independent of age which suggests this observation may be limited to movement control. Similar to predictions, straight channels increased bias, with a trend towards increasing uncertainty range too (*p* = .057). This follows the idea that the changes in direction during minimum jerk (MJ) channels provides increased proprioceptive cues over straight channels to help localise hand position relative to the reference position. Previous reports which use either straight or MJ channels were typically concerned with the extent to which proprioceptive judgements change with sensorimotor learning tasks (Mattar, Darainy, & Ostry, 2013; Ostry, Darainy, Mattar, Wong, & Gribble, 2010) and often used passive methodology (Bernardi, Darainy, & Ostry, 2015; Darainy, Vahdat, & Ostry, 2013). As such, it is difficult to examine whether the effect of channel type seen here is common with other reports. However, similar to reach distance, channel type did not interact with age group which suggests the differences outlined between Cressman et al. (2010) and our data in Chapter 3 may not be due to these parameters.

Finally, we found that the removal of target visual feedback only reduces proprioceptive bias during the longer, 20cm reaches, regardless of age. Since increasing reach distance appears to induce greater proprioceptive noise (van Beers, Sittig, & Gon, 1999) there may be a greater reliance or weighting of perceptual judgements to a more reliable sensory modality, such as vision (Kording & Wolpert, 2006). As such, it is odd that by increasing visual information and keeping the reference position visible, there is actually a shift towards increased systematic proprioceptive error. One explanation for this could be that the constant presence of the reference position captures attentional resources during the movements, such that fewer resources remain for attending to proprioceptive feedback (Goble, Mousigian, et al., 2012). This could then cause inaccurate judgements and increase proprioceptive error. However, if there was greater recruitment of attentional resources in this way, the expectation would be that performance in the target stay conditions would be limited by working memory capacity. This would be particularly true for OAs who had reduced SWM capacity in this experiment, yet there was no such relationship measured. In fact, the only trend towards a significant correlation was with YA bias in a target go condition which contradicts this prediction further and leaves the basis of this finding unclear.

Although we were able to measure the systematic effects of these key parameters on estimates of proprioceptive acuity, an important finding is that they did not differentially affect older or younger adults. As such, this makes them an unlikely basis for the discrepant findings between Cressman et al. (2010) and the data we presented in Chapter 3. Alternatively, it may be that these contrasting findings are related to the reliability or strength of the respective age effects on dynamic proprioception. For example, the age-dependent increase in proprioceptive uncertainty reported by Cressman et al. (2010) only just reached statistical significance (F[1, 17] = 4.28, p = .050) in a sample of 9 OAs with no reported effect size. As such, the weakness of this effect may have limited the ability to replicate it in this experiment, as well as detecting any contributing effects of altering task parameters to its presentation. In contrast, the age and PA effects on bias we measured in Chapter 3 were more statistically reliable (F[2, 47] = 4.11, p = .023, η^2_p = .15; post-hoc pairwise comparisons between inactive OA and YA groups, p = .009) than Cressman et al. (2010) and based on a much larger sample size, suggesting these findings are more robust. Yet in spite of this, we were also unable to replicate this effect in this experiment. With this in mind, it may be that the effects of ageing on dynamic proprioception are smaller than initially expected and methodological approaches which are more sensitive in nature, similar to Chapter 3, are therefore necessary to capture them. Specifically, increasing statistical power with larger sample sizes that are sub-grouped according to PA status, and measuring PA more reliably through accelerometry (Murphy, 2009) may be necessary to measure these effects empirically. This should be taken into consideration when designing future experiments.

Following completion of the experiment participants reported significantly reduced attention, regardless of age, in addition to anecdotal reports from both age groups indicating the same lack of motivation. This may partially be explained by the number of repeated blocks of the task that participants had to complete in order to test each combination of the different parameters. Without any performance feedback throughout such a high number of perceptual judgement trials it may be difficult for participants to remain motivated throughout the experiment. While we presented evidence to suggest the measures were not subject to order effects and were stable over the timecourse of the experiment, it is more difficult to exclude shorter, potentially block-wise, lapses in concentration which may confound results in this way. As such, future experiments may generate more reliable outcome measures if limited to fewer blocks of this task.

Since we were unable to measures any effects of age on verbal working memory in Chapter 3, the correlations of memory capacity with proprioceptive measures were somewhat limited. However, similar to previous reports (Kessels et al., 2010) we measured age-dependent declines in SWM capacity in this experiment, which were also independent of the proprioceptive measures gathered across all conditions. This provides good support for the notion that this dynamic task is not confounded by age-related cognitive decline. With this in mind, it is still worth noting that there were trends towards significant associations of SWM with target go conditions in both older and younger adults. This suggests it may be better to have the target remain visible throughout the task in its future applications to avoid this potential confound. This is further supported from the significant correlation we measured in YAs between proprioceptive drift and bias from a target go condition. Specifically, it was a target go condition with straight channels in which this relationship was measured, which also offers support for the use of MJ channels in the future as well.

In conclusion, we were unable to identify any specific task parameters which could account for the discrepant age-dependent findings presented in Chapter 3 and by Cressman et al. (2010). Considering we were unable to replicate either of the reported effects, it could be that age-related impairments on dynamic proprioception are not as robust as initially expected. However, it may be possible to capture them empirically with more sensitive methodology, at least with respect to the effects on bias we measured in Chapter 3. Finally, performance on our dynamic task was found to be largely independent of proprioceptive drift and cognitive capacity, but we also identified that it may be beneficial to have the target remain visible in future experiments to avoid these potential confounds.

CHAPTER 6

Motor Adaptation to Novel Field Dynamics is not Associated with Proprioceptive Acuity in Older or Younger Adults

Chapter Abstract

Since we found no association between proprioception and rapid movement control in Chapter 3, we were interested to follow this up with a motor task where proprioceptive sensation is more heavily emphasised. This experiment therefore aimed to investigate the association of proprioceptive acuity with sensorimotor adaptation to a novel perturbing forcefield in older and younger adults. To further emphasise the use of proprioceptive feedback, a version of the task which limited visual feedback of the perturbation was included. Additional correlates of adaptive motor performance were spatial working memory (SWM) capacity and physical activity (PA), as well as the extent to which the bias was recalibrated as a result of adaptation. We predicted that adaptive performance would only be impaired by age in the limited visual feedback condition. Furthermore, we expected both age groups to recalibrate limb position but that the extent of recalibration would be more strongly associated with adaptation in the limited visual feedback condition. Finally, we predicted baseline proprioceptive uncertainty would predict adaptation and that SWM capacity would be associated with persistence of the learned behaviour. Contrary to these predictions, we found no difference between age groups on motor adaptation performance, regardless of visual feedback condition. Moreover, there was a poor association of bias recalibration and adaptation in both visual feedback conditions and SWM was unrelated to

persistence. Additionally, we found baseline bias was larger for physically inactive participants regardless of age. Critically, baseline proprioceptive uncertainty was not predictive of motor adaptation. We suggest these findings support the notion that motor performance is most impaired in ageing when explicit control strategies are necessary for performance, which may be minimised in this form of sensorimotor adaptation. Furthermore, although proprioceptive feedback is necessary for adaptation in this experiment (specifically when visual feedback is limited), it may be used offline between trials, and thus the relationship under conditions where online feedback is necessary for motor performance remains unknown and should be investigated further.

6.1 – Introduction

In Chapter 3 we were able to demonstrate that proprioceptive acuity did not predict rapid reaching performance in either older or younger adults. Since the motor task used in that chapter involved ballistic movements which typically require little online sensory feedback, we suggested that by using a motor task in which proprioceptive feedback for performance is emphasised, this relationship may become apparent. An example of this could be a sensorimotor adaptation task, where an unexpected sensory perturbation drives an internal forward model to adapt the movement and maintain performance accuracy (see Section 1.3.2 for detailed review). In ageing, sensorimotor adaptation tasks have commonly used visual sensory perturbations, with older adults (OAs) showing impaired adaptive behaviour that appears to be dependent on their explicit strategy use and working memory capacity (Anguera, Reuter-Lorenz, Willingham, & Seidler, 2010; Buch, Young, & Contreras-Vidal, 2003; Hegele & Heuer, 2010; Uresti-Cabrera, Diaz, Vaca-Palomares, & Fernandez-Ruiz, 2015; see

Section 1.3.2.1 for detailed review). However, sensory prediction errors in these tasks are only apparent in the visual domain so performance is less dependent on acuity of proprioceptive feedback. Equally, OAs have been shown to rely more heavily on visual feedback for motor control than younger adults (YAs; Seidler-Dobrin & Stelmach, 1998), potentially making these tasks even less sensitive to proprioceptive feedback for older participants. This is partially demonstrated by Cressman, Salomonczyk, & Henriques (2010) who showed that both older and younger adults recalibrated proprioceptive bias similarly in response to visuomotor adaptations, but that the size of the proprioceptive "shift" only accounted for around 20% of adaptation. As such, this may not be an ideal paradigm to examine the influence of proprioceptive acuity on motor adaptation.

An alternative is a task using sensorimotor adaptation to novel field dynamics where a physical perturbation is applied to the limb which participants have to learn to overcome in order to maintain performance accuracy (Cesqui, Macri, Dario, & Micera, 2008; Huang & Ahmed, 2014; Ostry, Darainy, Mattar, Wong, & Gribble, 2010; Trewartha, Garcia, Wolpert, & Flanagan, 2014; see Section 1.3.2.2 for detailed review). Unlike visual perturbations, these paradigms also induce proprioceptive sensory prediction errors and may therefore require increased proprioceptive feedback to improve adaptive performance. But performance on these tasks in ageing is less commonly reported, with mixed findings regarding the ability of OAs to adapt (Cesqui et al., 2008; Huang & Ahmed, 2014; Trewartha et al., 2014). Similar to visual perturbations (Anguera et al., 2010; Uresti-Cabrera et al., 2015), it seems SWM plays a role in adaptation to novel fields in ageing (Trewartha et al., 2014) but in limiting the ability to retain the learned behaviour, rather than adapt it in the first place, which may highlight different cognitive processes associated with performing these tasks. Additionally, whilst

Cressman et al. (2010) found proprioceptive recalibration accounted for around 20% of visuomotor adaptation, Ostry et al. (2010) found recalibration could account for slightly higher percentage of learning (around 33% in YAs) during novel force field adaptation which suggests proprioception may be more important for adaptive performance in these tasks. However, one important note is that in all reports of adaptation to novel fields in ageing full visual feedback of hand position is provided which means that it is not possible to dissociate the contribution of visual and proprioceptive sensory feedback to motor adaptation. Although visual feedback is not necessary to adapt movements in novel fields (Franklin, So, Burdet, & Kawato, 2007; Krakauer, Ghilardi, & Ghez, 1999; Mackrous & Proteau, 2015), the unique contribution of proprioceptive acuity and perceptual recalibration to motor adaptation under these conditions in advanced age is unknown.

As such, this chapter aimed to investigate whether dynamic proprioceptive acuity or proprioceptive recalibration was related to motor adaptation to novel field dynamics, under conditions with full and limited visual feedback of hand position in older and younger adults. We predicted that adaptive performance would be similar between age groups when visual feedback of hand position was available but that OAs would have greater difficulty adapting when it was limited. We also predicted that both older and younger adults would recalibrate proprioceptive bias in response to moving in the novel field, but this would be more strongly associated with adaptation when visual feedback of hand position was limited. Finally we predicted that individual’s proprioceptive uncertainty would predict adaptive performance and that SWM would be related to persistence of the learned behaviour.

6.2 – Methods

6.2.1 – Participants and Self-Report Measures

There were 34 OAs (13 male, 75.6 ± 7.2 yrs) and 35 YAs (3 male, 19.1 ± 0.9 yrs) who participated in this experiment. The inclusion criteria for older and younger participants were identical to those described in previous chapters. The only additional stipulation was that participants could not have previously taken part in a force-field adaptation task of any kind, so as not to unfairly advantage their performance. As in Chapter 5, self-reported PA levels were measured using the Physical Activity Scale for the Elderly (PASE; Washburn, Smith, Jette, & Janney, 1993) and the IPAQ-Short questionnaire (Craig et al., 2003) for older and younger participants respectively. Similar to Chapter 5, participants also used a 7 point Likert scale to report attention and fatigue levels before and after participation in the experiment. The number of hours of sleep they had during the previous night as well as quality of sleep (1-7 scale) was also recorded, with those participants reporting fewer than 4 hours of sleep being excluded from analysis.

6.2.2 – Spatial Working Memory

SWM capacity was measured using the task which is described in detail in Chapter 5 (Figure 5.1). Using a computer mouse to click on blue tiles presented via computer monitor, participants had to search for, and remember the location of hidden green tick symbols. Errors were recorded when selecting a blue tile which had previously revealed a green tick (between search error), or when unsuccessfully selecting the same blue tile more than once (within search error). The task started with 4 tiles but the difficulty was gradually increased by incrementing the number of tiles to 6, 8 and 10. The numbers of errors were averaged across the 2 trials performed at each level before they were compared between age groups and used as correlates for motor adaptation. Previous research has shown OAs who have poorer SWM have worse retention of the adapted motor behaviour (Trewartha et al., 2014). Here, we were also interested in whether SWM capacity was associated with learning, particularly when visual feedback was limited and perception of limb position may decay over time.

6.2.3 – Experimental Set-Up

The main tasks were performed on the vBOT, which has been described in detail in Chapter 2. Briefly, the start position and target were displayed as white and grey 1cm radius markers respectively, with full hand position visual feedback displayed as a white 0.5cm radius marker when made available. Start position was located 8cm into the workspace (roughly 28cm from participant's chest) with the single target located 20cm directly ahead along a sagittal axis through the participant's mid-line. The start position and target remained in the same position for all tasks and were kept visible at all times during task performances.

6.2.4 – Dynamic Proprioception Task

This task has been described in previous chapters, with key details of the general task procedure outlined in Chapters 2 and 3. The parameters used in this experiment are identical to the 20cm reach, target stay, minimum jerk channel condition described in Chapter 5, as are the parameters of the PEST sequence and number of repeats per lateral deviation level. Unlike Chapter 5, blocks contained 50 trials and did not start with unconstrained, null-field target reaching trials. However, in the familiarisation block there were 20 null-field trials with full visual feedback of hand-position followed by 8 channel trials. Overall there were 4 blocks of 50 channel trials which were interleaved between reaching trials for the force-field adaptation task. The full experimental design is shown in Figure 6.3. The verbal responses indicating perceived limb position relative to the target (“Square” for left of target or “Circle” for right of target) were binarized in a similar fashion to previous chapters and fitted with a logistic function to generate two proprioceptive acuity measures, the bias and uncertainty range. Average movement velocity was also measured, as well as the orthogonal forces applied to channel walls during the last 16-19cm of the 20cm movement.

6.2.5 – Force-Field Adaptation

6.2.5.1 – Overview

For this task, participants made a series of reaching movements towards a single target with and without the presence of a novel, perturbing, velocity-dependent force-field applied to the vBOT handle. Participants were required to adapt the kinematic profile of their movements when the force-field was imposed in order to continue to keep their movements as straight and accurate as possible towards the target. Coloured visual feedback regarding movement duration was provided to try and maintain movement speed to a similar range between participants, and hence exposure to a similar magnitude of perturbing force. Participants performed this task in 1 of 2 visual feedback conditions; full hand cursor position feedback throughout (Vision+) or limited visual feedback to only linear distance moved (Vision-). Participants were allocated to either 1 of these conditions to create a further 2 sub-groups within the older and younger participant groups. Catch trials were pseudorandomly interleaved between normal target reaching trials, where movements were tightly constrained in a linear path to the target using stiff virtual walls. These were used to examine the lateral forces participants were exerting during movement and were performed with visual feedback of distance provided by a 180-degree arc (see Section 6.2.5.3 – Visual Feedback and Sub-Grouping).

6.2.5.2 – Procedure

To begin, participants first moved to the start position, which turned orange, and then made a reaching movement towards the target. Once they had moved the required 20cm ahead, they intersected a soft virtual wall which ran orthogonally through the target. Regardless of whether the target was hit or not, it then changed colour and displayed an 'explosion' graphic which provided participants with feedback regarding the speed of their movement. If the target turned red and displayed a small explosion the participant had moved too slowly (movement duration > 450ms), if it was blue with a large explosion they were too fast (movement duration < 350ms) and if it was green with a medium explosion (movement duration between 350-450ms) they were within the desired speed range. Once the explosion graphic had finished, the target turned grey again and participants were actively guided back to the start position for the next trial.

For null-field trials, these movements were completely unconstrained. However, force-field trials were performed in the presence of a velocity-dependent force-field applied to the vBOT handle as described by Equation 6.1.

$$\begin{bmatrix} f_x \\ f_y \end{bmatrix} = FS \,.\begin{bmatrix} 0 & 1 \\ -1 & 0 \end{bmatrix} \cdot \begin{bmatrix} v_x \\ v_y \end{bmatrix} \tag{6.1}$$

Where f_x and f_y refer to the imposed forces on the vBOT handle, *FS* refers to the field strength which was held constant at 15N/m/s, and v_x and v_y refer to the velocity of the vBOT handle. This force-field acted to perturb movements in a clockwise direction which participants perceived as rightward. This meant that they were required to apply leftward compensatory forces to the handle in a velocity-proportional manner to successfully perform straight and accurate movements in these trials. See Figure 6.1 for details of null-field and force-field trials.

Catch trials were pseudorandomly presented (randomly within the final 3 of every set of 5 trials) within blocks of null-field and force-field trials whereby hand position was constrained to a linear path between start position and target using stiff virtual walls (see Equation 2.1, Chapter 2). These walls restricted any orthogonal movements from the pre-defined pathway, and made it possible to measure the lateral forces imposed against them during reaching movements. We could then use these data to examine the extent to which participants compensated for the expected force-field during the course of progressive adaptation trials. To reduce awareness of the nature of these trials, visual feedback of hand position was presented as a hollow white arc whose radius increased proportionally to the linear distance travelled towards the target. When the target was reached, it changed colour to give feedback regarding movement speed (as previously but without an explosion) and then participants were actively guided back to the start position ready for the next trial (see Figure 6.2 for catch trial summary). The order of null-field and force-field trial blocks is shown as part of the full experimental design in Figure 6.3.

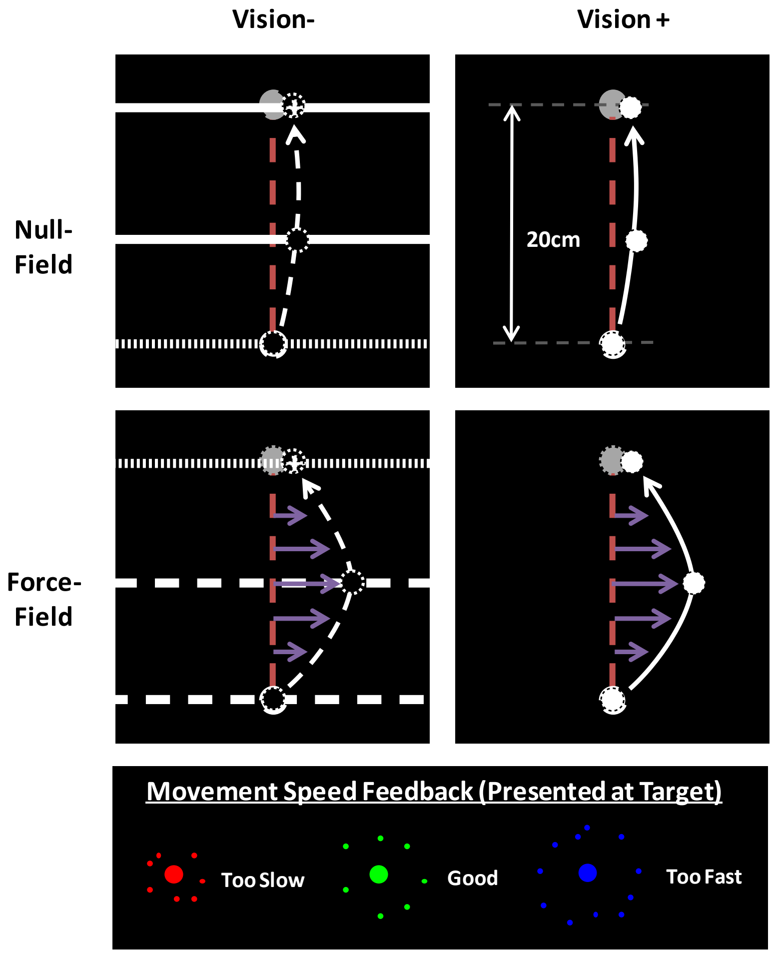


Figure 6.1. – Force-field task summary showing Vision- (left column) where lateral hand position visual feedback was limited using horizontal white bar cursor, and Vision+ (right column) where full visual feedback of hand position was provided. White cross terminal position feedback (pictured) was provided for Vision- participants. Purple arrows show forces imposed by velocity-dependent force-field (middle row), contrasting to null-field trials which were unconstrained (upper row). After reaches, target 'explosion' size and colour gave feedback on movement speed (lower row)

6.2.5.3 – Visual Feedback and Sub-Grouping

Typically, force-field adaptation paradigms are performed with full visual feedback of hand position (usually circular cursor or similar; Figure 6.1 right upper and middle panels) which means that participants receive both visual and proprioceptive sensory information regarding the nature of the perturbation. As such, it makes the relative contribution of either sensory modality to adaptation difficult to distinguish. With this in mind, we included an additional form of visual feedback for this experiment which limited the extent of visual feedback regarding lateral hand position (and hence features of the perturbation) during movements (Figure 6.1, left upper and midle panels). This was achieved by presenting a horizontal, flat white bar as a hand position cursor which spanned the width of the display, identical to that used for the proprioceptive drift task in Chapter 5 (see Figure 5.2 for details). However, unlike the proprioceptive drift task, we wanted participants to try and maintain target accuracy across trials, so terminal position feedback (location at which participant intersected the endpoint orthogonal soft wall) was also provided in the form of a 1cm width white cross (Figure 6.1, left upper and middle panels) at the end of each movement. Movement speed feedback (coloured explosion) was provided normally and the return to the start position between trials was easily achieved despite the lack of visual feedback through vBOT active guidance. Furthermore, catch trials were still presented with white arc feedback to keep awareness of their nature similar across all participants and groups.

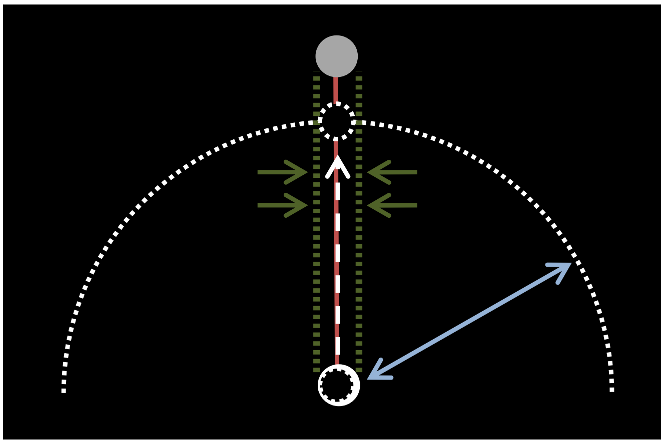


Figure 6.2. – Catch trial diagram. Green vertical bars show walls of channel constraining movement tightly along linear path to target. Visual feedback is provided by the white arc whose radius (blue arrow) increases proportionally with progression along channel. Target still changed colour when reached to indicate movement speed (not pictured here)

Repeated performance of different visual feedback conditions by the same participants was not possible due to the difficulty of controlling the extent of savings between sessions (Caithness et al., 2004). As such, older and younger adults were randomly allocated to groups either having full visual feedback (Vision+) or limited visual feedback (Vision-) during performance of the experiment. This gave a total of 4 distinct groups; 17 OAs in Vision+ (5 male, 75.2 ± 8.3 yrs), 17 OAs in Vision- (8 male, 75.9 ± 6.2 yrs), 17 YAs in Vision+ (1 male, 18.9 ± 0.8 yrs) and 18 YAs in Vision- (2 male, 19.4 ± 1.0 yrs). The visual feedback sub-groups were well matched for age in both older (t[32] = -.28, *p* = .780) and younger (t[33] = -1.69, *p* = .101) adults.

6.2.5.4 – Outcome Measures and Analysis

The extent to which participants were deviated by the force-field was measured by the lateral hand deviation from the linear path connecting start position and target, at peak hand velocity. Smaller deviations indicate straighter movements and thus better compensation for the perturbing forces. As an additional measure of how well movements were adapted within the force-field, we used data collected in the catch trials to calculate an adaptation index (Huang & Ahmed, 2014; Trewartha et al., 2014). This is found from the slope of a least-squared linear regression model (without an intercept) comparing observed and optimal orthogonal compensatory forces across each trial. Observed compensatory forces refer to those imposed by the participant against the walls of the catch trial channel, and optimal compensatory forces refer to the negative of those calculated according to participant velocity (v_y) as they moved along the channel (see Equation 6.1). If the forces were well compensated for, the observed and optimal forces would be similar and the regression coefficient (which we term adaptation index) would be close to 1. However, if they were poorly matched the adaptation index would be closer to 0 indicating worse compensatory orthogonal force production.

To examine the kinematic performance of participants, we also recorded peak hand velocity, total movement duration and the duration to peak velocity (expressed as a percentage of total movement duration). Movement duration was defined as the time taken to move between the middle 18cm of the 20cm reach distance (from 1cm beyond start position to 1cm before target). Trials where total movement duration was greater than 1.5 seconds were not included in the analysis. The intra-subject variation (within subject standard deviation across trials) of peak hand velocity and duration to peak velocity were also used as correlates for motor adaptation. This was to test whether varying the movement velocity (potentially reflecting an exploratory strategy within the velocity dependent force-field) had any benefits for motor adaptation (Wu, Miyamoto, Gonzalez Castro, Olveczky, & Smith, 2014).

To see how performance changed as the experiment progressed, these measures were averaged across the first and last 20 trials in a given block which we term “early” or “late” respectively (this excluded the additional 20 null and 20 force-field trials at the start of the Adaptation and Washout blocks respectively; see Figure 6.3 for details). Extent of adaptation was then defined as the difference between early and late performance in the Adaptation block, with what we termed “persistence” as the difference between early and late in Washout. We use persistence here rather than retention, since the latter typically refers to maintenance of learned behaviour in error-clamped conditions (Trewartha et al. 2014), yet we de-adapted participants with null-field trials in the Washout block for this experiment, similar to Ostry et al. (2010).

6.2.6 – Experimental Design

Participants began with a proprioceptive familiarisation block of 20 null-field trials (self-selected speed, without coloured movement speed feedback) and 8 perceptual channel trials. The null-field trials were in the presence of full hand position cursor feedback regardless of whether the participant was allocated to Vision+ or Vision-, and were intended to normalise baseline performance between participants, providing familiarity of how hand position was aligned to the cursor. This was particularly important for Vision- participants since this was the only time they were provided with this extent of visual feedback throughout the entirety of the experiment. Following the proprioceptive familiarisation, participants performed the first of four blocks of 50 dynamic proprioception trials (P1), followed by a block of 48 null-field trials interleaved with 12 catch trials (‘Null’; movement speed constrained by coloured ‘explosion’ feedback) before another proprioceptive block (P2). There was then a short break before the main adaptation block of 16 null-field trials (interleaved with 4 catch) and 120 force-field trials (interleaved with 30 catch trials; ‘Adaptation’). This was followed by the third proprioceptive block (P3), a washout block which consisted of 16 force-field trials (interleaved with 4 catch) and 48 null-field trials (interleaved with 12 catch; ‘Washout’) and then the fourth and final proprioceptive block (P4). To examine how the proprioceptive tests that were interleaved between blocks affected reaching performance, we used the additional 20 null and force-field trials at the start of the Adaptation and Washout blocks respectively to compare reach performance measures immediately before and after the proprioceptive test blocks P2 and P3. The main intention of the initial Null block was to train participants to moving within the desired speed range and as such, only the late stage of this block was analysed and used in statistical analyses. The full experimental design is shown in Figure 6.3. Participants were informed that they may experience some forces at the vBOT handle during target reaching movements, but that throughout the entirety of the force-field task blocks their objective was to try and keep movements as straight as possible, as accurate as possible (keeping the white cross on target for Vision- and hand position cursor on target for Vision+) and to try to achieve the green explosion movement speed feedback.

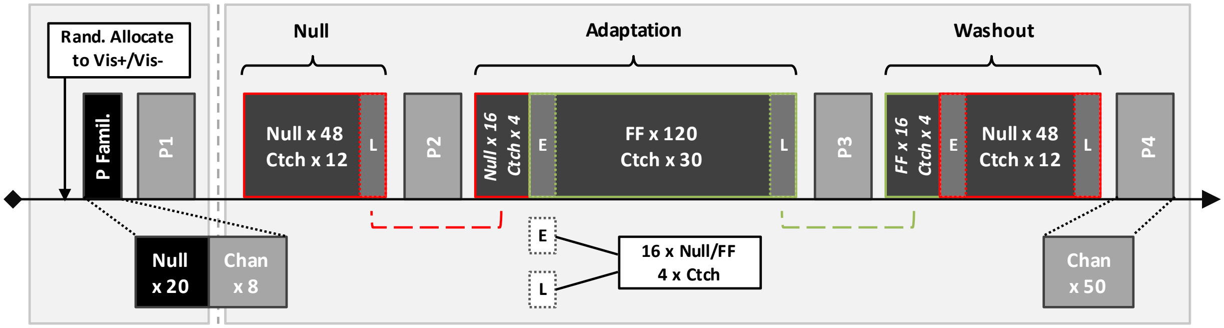


Figure 6.3. – Experimental design summary, excluding spatial working memory task at start (see Figure 5.4, Chapter 5 for block details of this task). Blocks titled ‘P1-4’ represent dynamic proprioception blocks of 50 perceptual channel trials (noted as ‘Chan’) and are interleaved between blocks of reaching trials for force-field task. ‘P Famil.’ represents proprioceptive familiarisation block comprising 20 null-field trials with full hand position visual feedback and 8 perceptual channel trials. All participants performed ‘P. Famil’ identically regardless of Vision+ (‘Vis+’) or Vision- (‘Vis-‘) random allocation. Vertical dashed grey line represents point at which the experiment diverges in terms of visual feedback for the Vis+ and Vis- groups. Red outlined boxes indicate blocks of null-field trials (labelled ‘Null’) and green outlined boxes represent force-field trials (‘FF’), with ‘Ctch’ indicating the number of catch trials pseudo-randomly presented in a given block. The ‘E’ and ‘L’ represent early and late stages of a block respectively in which trials are averaged and used in statistical analyses (Late Null referred to as “Baseline”). Additional trials before early Adaptation and Washout are used to compare effects of proprioception blocks on reaching performance (comparisons indicated by dashed red and green lines).

6.2.7 – Statistical Analysis

All values which were 2.5 standard deviations away from the group mean were excluded from analysis as outliers. Proprioceptive data was compared between groups in separate 2 x 2 x 4 mixed-design ANOVAs: (Age Group; older or younger adults) x (Visual Feedback; Vision+ or Vision-) x Repetition (first, second, third or fourth), to see how they changed in correspondence with different force-field task blocks.

Performance data from the late Null, Adaptation and Washout blocks was first analysed in separate 2 x 2 x 5 mixed-design ANOVAs: (Age Group; older or younger adults) x (Visual Feedback; Vision+ or Vision-) x (Block Progression; late Null, early/late Adaptation and early/late Washout). The late portion of the Null block was then compared to the first 20 null-field trials of the Adaptation block in separate 2 x 2 x 2 mixed-design ANOVAs: (Age Group; older or younger adults) x (Visual Feedback; Vision+ or Vision-) x (PrePost; pre or post proprioceptive block), to see whether the P2 block affected reaching performance. A similar analysis was used to compare the late portion of the Adaptation block with the first 20 force-field trials of the Washout block to see how P3 affected reaching performance in the force-field (both comparisons are indicated by red and green dashed connecting lines in Figure 6.3).

SWM search errors were analysed in separate 2 x 2 x 4 mixed-design ANOVAs; (Age Group; older or younger adults) x (Visual Feedback; Vision+ or Vision-) x (Number of Tiles; 4, 6, 8 or 10), and used as correlates for the extent of adaptation and persistence. Motor variation (peak velocity and duration to peak velocity intra-subject variation) in early Adaptation was also used to predict both extent of adaptation and persistence in a similar fashion. The change in bias before and after the Adaptation block (P3 – P2) was used as a correlate for extent of adaptation, and the change in bias before and after the Washout block (P4 – P3) was used as a correlate for extent of persistence. Baseline proprioceptive acuity was also used as a correlate for extent of adaptation to see whether increased perceptual acuity was advantageous to performance.

In all cases where the sphericity assumption was violated a Greenhouse-Geisser correction was used, with significance assessed at the $p < .05$ level. Multiple comparisons are reported as uncorrected (Least Significant Difference; LSD) values but were assessed for significance using an FDR-analysis which is described in detail in Chapter 2. FDR-adjusted p-thresholds (p_{FDR}) are reported throughout the results section as necessary, and when there were no significant comparisons observed (i.e. $p < p_{\mathrm{FDR}}$ was not found) the smallest observed p-value (p_{min}) is reported with its associated critical significance value (still denoted as p_{FDR}) (see Chapter 2 for details).

6.3 – Results

6.3.1 – Force-Field Adaptation

6.3.1.1 – Measures of Motor Adaptation

Adaptation performance measures are summarised in Table 6.1, with block wide performance summaries shown in Figure 6.5 (peak velocity lateral deviation; PVLD) and Figure 6.6 (adaptation index; AdInd). There was a highly significant effect of Block Progression on PVLD (F[2.7, 156.1] = 196.3, $p < .001$, $\eta^2_p = .77$) with all measurement stages being significantly different from one another ($p < .001$; $p_{\mathrm{FDR}} = .045$) apart from between late Null ("Baseline") and late Washout ($p = .319$). This indicated that participants were significantly perturbed, adapted their movements, showed after-effects and finally recovered back to baseline levels during the progression of the experiment (see Figure 6.4, Panel A for summary). However, there was no overall main effect of Age Group on PVLD (F[1, 58] = .38, $p = .542$) nor of Visual Feedback (F[1, 58] = 2.06, $p = .157$) or their interaction (F[1, 58] = .006, $p = .936$). The Age Group x Block Progression interaction was significant (F[2.7, 156.1] = 4.48, $p = .006$, $\eta^2_p = .07$), however follow-up pair-wise comparisons did not reveal any significant differences between older or younger adults at any of the measurement stages ($p_{\mathrm{min}} = .048$; $p_{\mathrm{FDR}} = .010$). The Visual Feedback x Block Progression interaction was also significant (F[2.7, 156.1] = 2.28, $p = .039$, $\eta^2_p = .05$) but follow-up comparisons also failed to reveal any differences between visual feedback groups at any of the 5 measurement stages.

Measure	Visual Feedback Group	Age Group	**Baseline**	**Adaptation**		**Washout**	
				Early	Late	Early	Late
Peak Velocity Lateral Deviation (cm)	Vision+	*Older*	-.41 *(± .09)*	1.79 *(± .22)*	.62 *(± .18)*	-1.66 *(± .20)*	-.48 *(± .12)*
		Younger	-.62 *(± .06)*	2.26 *(± .36)*	.55 *(± .21)*	-1.38 *(± .13)*	-.60 *(± .08)*
	Vision-	*Older*	-.60 *(± .20)*	1.35 *(± .23)*	-.20 *(± .20)*	-1.34 *(± .17)*	-.33 *(± .14)*
		Younger	-.73 *(± .13)*	2.35 *(± .24)*	-.06 *(± .36)*	-1.56 *(± .34)*	-.67 *(± .15)*
	Overall		**-.59** ***(± .06)***	*****1.95** ***(± .14)***	*****.24** ***(± .13)***	*****-1.49** ***(± .11)***	**¥¥¥-.53** ***(± .06)***
Adaptation Index	Vision+	*Older*	.003 *(± .008)*	.502 *(± .048)*	.763 *(± .036)*	.181 *(± .024)*	.019 *(± .012)*
		Younger	-.009 *(± .006)*	.539 *(± .069)*	.755 *(± .033)*	.091 *(± .013)*	.017 *(± .007)*
	Vision-	*Older*	.046 *(± .015)*	.567 *(± .071)*	.870 *(± .057)*	.128 *(± .055)*	.038 *(± .036)*
		Younger	-.007 *(± .009)*	.560 *(± .071)*	.871 *(± .057)*	.109 *(± .038)*	.002 *(± .009)*
	Overall		**.009** ***(± .006)***	*****.542** ***(± .032)***	*****.815** ***(± .024)***	*****.127** ***(± .018)***	**¥¥¥.019** ***(± .010)***

Table 6.1. – Summary of findings for measures of motor adaptation for older and younger adults in both the Vision+ and Vision- conditions. Baseline here refers to the late portion of the Null block. Values are given as means ± standard error, with ******* indicating significantly different value from Baseline and all other measurement stages ($p < .001$) and ¥¥¥ indicating significantly different value from all other measurement stages except Baseline ($p < .001$; multiple comparisons subjected to FDR adjusted p-threshold).

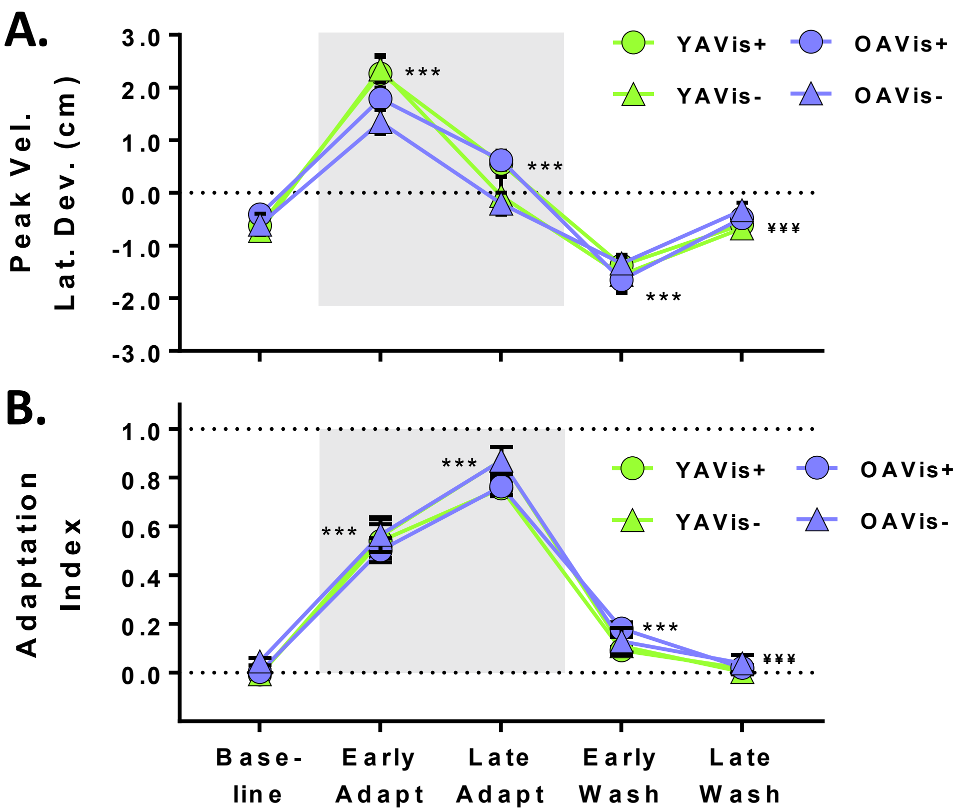


Figure 6.4. – Summary of motor adaptation measures for older (purple symbols) and younger (green symbols) in the Vision+ (circles) and Vision- (triangles) conditions. Shaded region shows the presence of the force-field **A.** Shows data for the lateral deviation at peak where values closer to 0 indicate better performance and **B.** shows the adaptation index where a value closer to 1 indicates better compensation for the imposed force-field. There was a main effect of Block Progression, where ******* indicates different from baseline and all other measurement stages (*p* < .001) and $^{¥¥¥}$ indicates different from all other measurement stages except Baseline (*p* < .001; multiple comparisons subjected to FDR adjusted *p*-threshold).

However, there was a trend towards the Vision- participants having smaller, more negative PVLD in late Adaptation than Vision+ after correcting for multiple comparisons (*p* = .015; all other comparisons *p* > .158; p_{FDR} = .010). The three-way interaction of Age Group x Visual Feedback x Block Progression was not significant (F[2.7, 156.1] = 1.17, *p* = .320).

The main effect of Block Progression on AdInd was once again highly significant (F[2.3, 135.8] = 419.5, $p < .001$, $\eta^2_p = .88$) with all measurement stages being significantly different from one another ($p < .001$; $p_{FDR} = .045$) except between Baseline and late Washout ($p = .314$) mirroring the results for PVLD (for summary see Figure 6.4, Panel B). However, the main effect of Age Group on AdInd was not significant (F[1, 58] = .503, $p = .481$) and neither was the effect of Visual Feedback (F[1, 58] = 1.49, $p = .227$) or their interaction (F[1, 58] = .02, $p = .879$). The other two- and three-way interactions were all non-significant (all $p > .131$).

These data show that participants were able to adapt their movements to compensate for the force-field, with the adaptation persisting early after the force-field was removed before returning to baseline performance levels by the end of the experiment. This partially supports predictions since performance was comparable between age groups with full visual feedback of hand position, but contradicts the prediction that an OAs would be impaired when visual feedback was limited.

6.3.1.2 – Movement Kinematics

A summary of the movement kinematic results can be seen in Table 6.2. The main effect of Age Group on peak hand velocity (PeakVel) was not significant (F[1, 64] = 1.27, $p = .264$) nor was the effect of Visual Feedback (F[1, 64] = .99, $p = .323$) or their interaction (F[1, 64] = .56, $p = .456$; for summary see Figure 6.7, Panel A). The main effect of Block Progression was not significant (F[3.1, 200.0] = 1.97, $p = .100$) and neither were the remaining two- and three-way interactions (all $p > .164$).

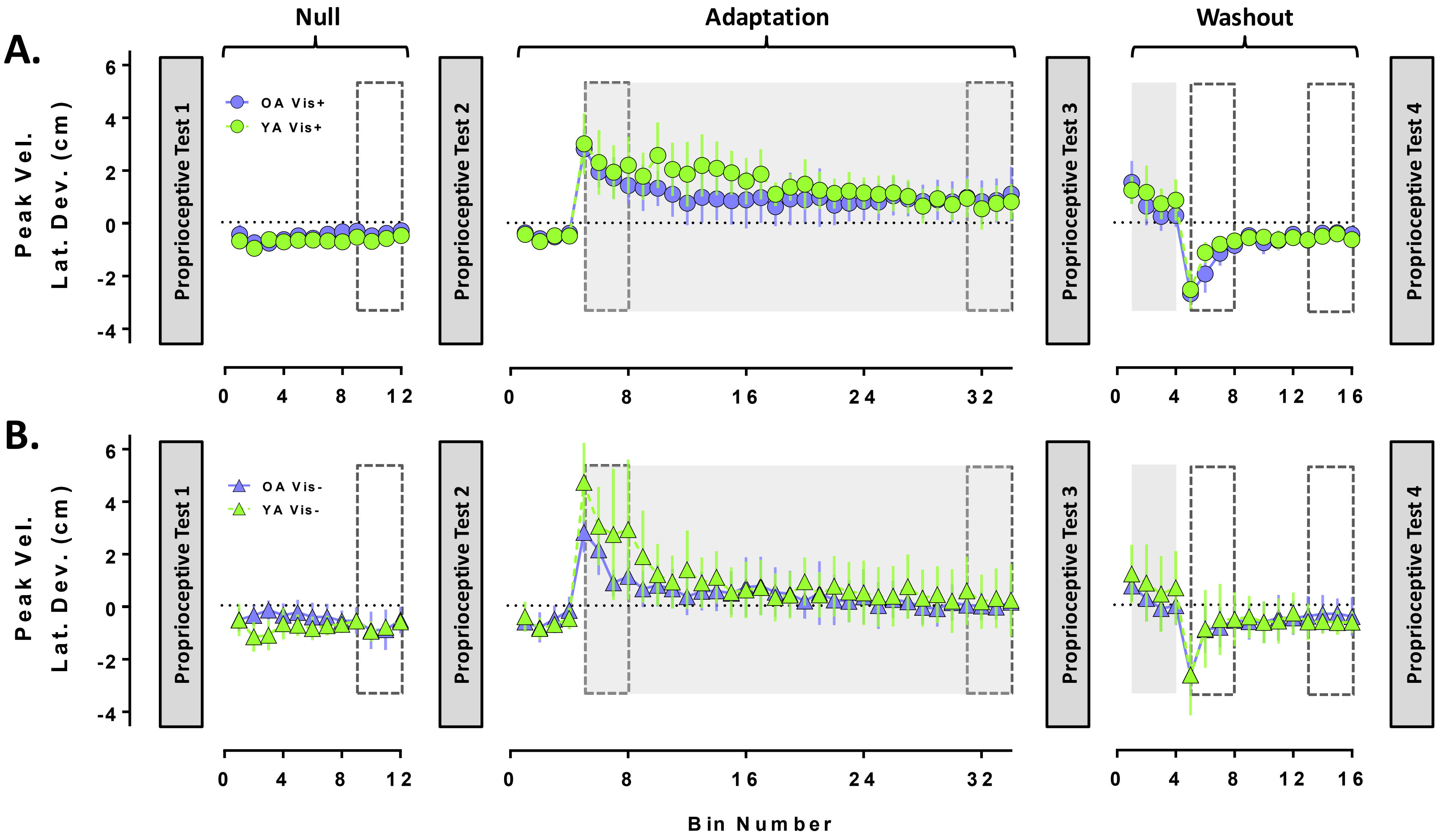


Figure 6.5. – Experiment wide summary of reaching performance for the force-field adaptation task in terms of lateral deviation at peak velocity. Plotted values represent binned averages of 4 trials, with vertical lines indicating ± 1 standard error. Shaded region indicates where the velocity-dependent force-field was imposed and dashed rectangles show regions which were averaged for statistical analyses. Better performance is indicated by values closer to 0cm **A.** Shows the results for the Vision+ older (purple circles) and younger (green circles) adults **B.** Shows the results for the Vision- older (purple triangles) and younger (green triangles) adults.

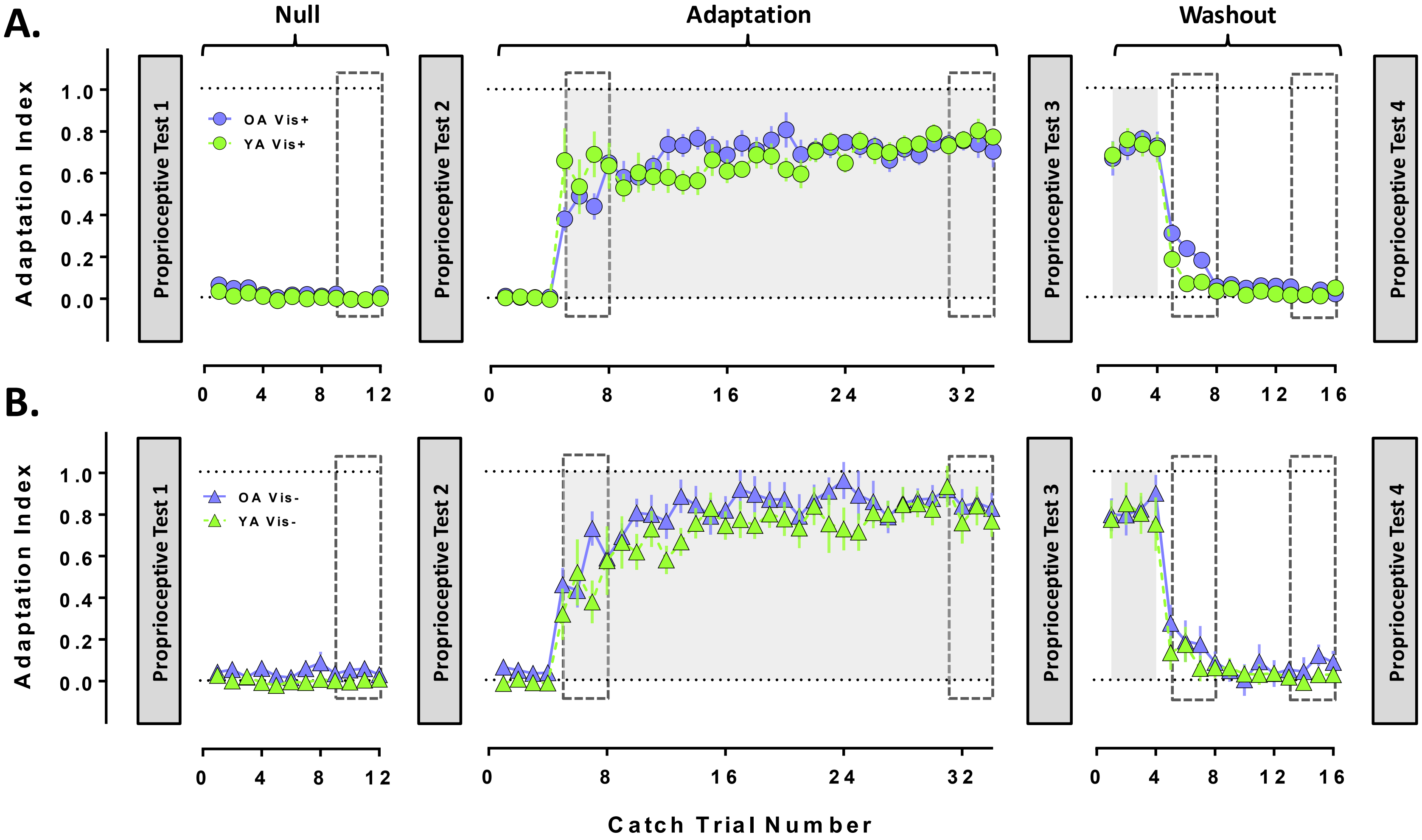


Figure 6.6. – Experiment wide summary of reaching performance for the force-field adaptation task in terms of adaptation index. Plotted values represent single catch trials, with vertical lines indicating ± 1 standard error. Shaded region indicates where the velocity-dependent force-field was imposed and dashed rectangles show regions which were averaged for statistical analyses. Better compensation for forcefield is indicated by values closer to 1 **A.** Shows the results for the Vision+ older (purple circles) and younger (green circles) adults **B.** Shows the results for the Vision- older (purple triangles) and younger (green triangles) adults.

There was a significant effect of Block Progression on movement duration (MoveDur; F[2.26, 137.9] = 26.1, $p < .001$, $\eta^2_p = .30$), such that movements were longer in early Adaptation compared to all other measurement stages (all $p < .001$; $p_{\text{FDR}} = .035$) and movements were shorter in late Washout compared to all other measurement stages (all $p < .001$), with MoveDur remaining stable between Baseline, late Adaptation and early Washout (all $p > .559$; see Figure 6.7, Panel B for summary). There was no effect of Age Group on MoveDur (F[1, 62] = 1.23, $p = .272$). However there was a significant main effect of Visual Feedback (F[1, 62] = 6.03, $p =.017$, $\eta^2_p = .09$) whereby those in the Vision+ group tended to make movements which were shorter in duration than the Vision- group. All other two- and three-way interactions were non-significant (all $p > .343$).

There was a strong, significant effect of Block Progression on duration to reach peak velocity (DPV; F[2.8, 174.7] = 29.6, $p < .001$, $\eta^2_p = .32$), where all measurement stages were significantly different from one another (all $p < .020$; $p_{\text{FDR}} = .040$) except for Baseline vs. early Washout ($p = .049$) and early Washout vs. late Washout ($p = .287$; see Figure 6.7, Panel C for summary). There was no effect of Age Group on DPV (F[1, 63] = .13, $p = .721$) nor of Visual Feedback (F[1, 63] = .46, $p = .498$) or their interaction (F[1, 63] = .20, $p = .659$). The remaining two- and three-way interactions were non-significant (all $p > .161$).

Measure	Visual Feedback Group	Age Group	**Baseline**	**Adaptation**		**Washout**	
				Early	Late	Early	Late
Peak Velocity (cm/sec)	Vision+	_Older_	72.14 _(± 2.63)_	70.69 _(± 3.49)_	67.28 _(± 1.61)_	71.26 _(± 2.79)_	70.11 _(± 2.00)_
		Younger	70.27 _(± 1.09)_	68.01 _(± 1.64)_	68.27 _(± 1.28)_	70.81 _(± 1.55)_	71.41 _(± 1.09)_
	Vision-	_Older_	69.33 _(± 2.06)_	67.00 _(± 2.14)_	71.72 _(± 1.75)_	70.94 _(± 1.77)_	70.72 _(± 1.90)_
		Younger	67.76 _(± .83)_	66.37 _(± 2.13)_	66.98 _(± 1.50)_	66.63 _(± 1.23)_	68.56 _(± .76)_
	Overall		69.87 _(± .91)_	68.02 _(± 1.21)_	68.56 _(± .79)_	69.91 _(± .97)_	70.20 _(± .76)_
Movement Duration (sec)	Vision+	_Older_	.351 _(± .008)_	.400 _(± .021)_	.367 _(± .007)_	.358 _(± .012)_	.340 _(± .006)_
		Younger	.347 _(± .003)_	.396 _(± .011)_	.349 _(± .005)_	.346 _(± .007)_	.336 _(± .003)_
	Vision-§	_Older_	.387 _(± .017)_	.423 _(± .021)_	.360 _(± .011)_	.373 _(± .014)_	.351 _(± .009)_
		Younger	.366 _(± .008)_	.420 _(± .015)_	.362 _(± .009)_	.372 _(± .006)_	.342 _(± .004)_
	Overall		.363 _(± .005)_	***.410 _(± .009)_	.359 _(± .004)_	.363 _(± .005)_	***.342 _(± .003)_
Duration to Peak Velocity (% Movement Duration)	Vision+	_Older_	65.10 _(± 3.26)_	48.63 _(± 3.71)_	54.17 _(± 2.90)_	62.42 _(± 3.31)_	60.79 _(± 3.20)_
		Younger	61.56 _(± 2.03)_	53.33 _(± 2.29)_	56.31 _(± 1.66)_	61.44 _(± 1.83)_	59.49 _(± 1.58)_
	Vision-	_Older_	65.59 _(± 3.03)_	56.29 _(± 3.95)_	58.84 _(± 3.46)_	62.15 _(± 3.04)_	61.81 _(± 2.95)_
		Younger	61.16 _(± 1.98)_	54.51 _(± 3.06)_	57.08 _(± 1.83)_	60.71 _(± 2.12)_	61.54 _(± 1.88)_
	Overall		63.38 _(± 1.32)_	**53.19 _(± 1.67)_	**56.60 _(± 1.28)_	61.68 _(± 1.31)_	$^{¥¥}$60.93 _(± 1.24)_

Table 6.2. – Summary of motor kinematics measures for older and younger adults in both the Vision+ and Vision- conditions. Baseline here refers to the late portion of the Null block. Values are given as means ± standard error, with significantly different values from Baseline and all other measurement stages indicated by *** ($p < .001$) and ** ($p < .020$). Significantly different values from all other measurement stages except early Washout indicated $^{¥¥}$ ($p < .010$; multiple comparisons subjected to FDR adjusted p-threshold), and significant main effects indicated by § ($p < .050$).

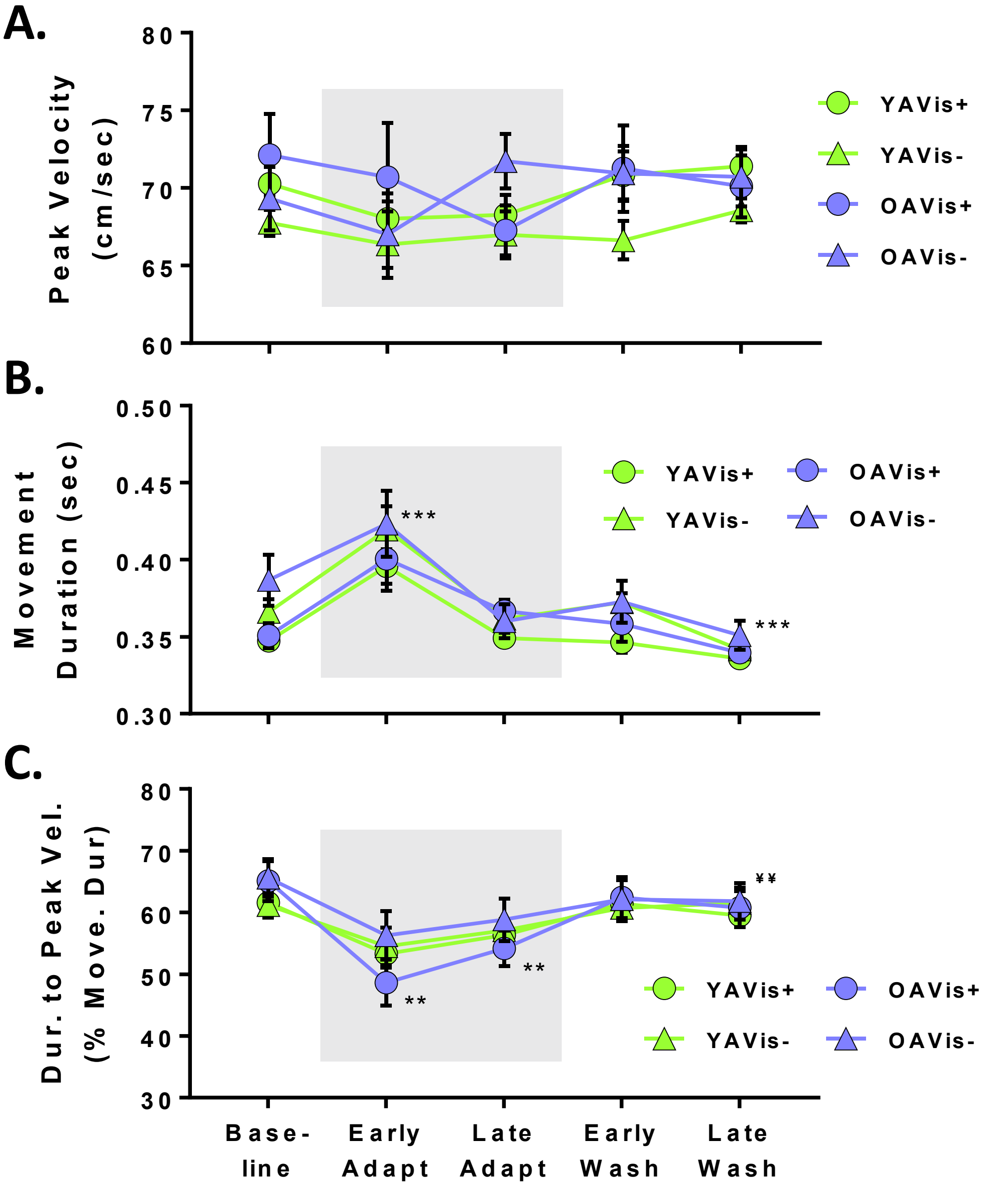


Figure 6.7. – Summary of motor kinematic measures for older (purple symbols) and younger (green symbols) in the Vision+ (circles) and Vision- (triangles) conditions. Shaded region shows the presence of the force-field **A.** Peak hand velocity **B.** movement duration **C**. Duration to reach peak velocity (expressed as percentage of total movement duration). Values are given as means ± standard error, with significantly different values from Baseline and all other measurement stages indicated by ******* (*p* < .001) and ****** (*p* < .020). Significantly different values from all other measurement stages except early Washout indicated ¥¥ (*p* < .010; multiple comparisons subjected to FDR adjusted *p*-threshold). Those in the Vision- also made significantly longer duration movements than those in the Vision+ condition (*p* < .050, not pictured).

Collectively, these results show that the coloured feedback cues successfully regulated speed between groups and that movement kinematics were comparable between them. Movements became longer, with peak velocity occurring earlier in the movements during early adaptation; however peak velocity itself remained relatively stable across the experiment. The extent of visual position feedback did not affect the kinematic performance of the movements for either older or younger adults. These data therefore allow us to examine changes in dynamic proprioception and adaptation performance between groups without serious confounds of differences in movement kinematics or perturbation exposure.

6.3.1.3 – Performance Across Proprioceptive Blocks

To assess the impact of proprioceptive blocks on reaching performance, we compared 20 trials of similar nature across P2 and P3 (see Figure 6.3 for details). Since we are only interested in the change in the measures across the proprioceptive blocks, we only report the main effect and interactions of the PrePost factor from the mixed-design ANOVAs here (see 6.2.7 – Statistical Analysis for details).

For the comparison across P2 (null-field trials between late null and start of Adaptation blocks), the main effects of PrePost on both lateral deviation at peak velocity (PVLD; F[1, 63] = .98, p = .329) and adaptation index (AdInd; F[1, 63] = .02, p = .878) were not significant, and neither were any of the two- or three-way interactions involving PrePost for either measure (all p > .275). For the comparison across P3 (force-field trials between late Adaptation and start of Washout blocks), there were no effects of PrePost on either PVLD (F[1, 60] = 1.71, p = .196) or AdInd (F[1, 61] = .93, p = .339). Furthermore, all other interactions were non-significant for both measures too (all p > .121). These findings suggest that performing blocks of proprioceptive trials did not disrupt reaching performance for either null-field (across P2) or force-field (across P3) reaching trials.

6.3.1.4 – Predicting Adaptation from Motor Kinematic Variation

Since the force-field was velocity-dependent, and participants had no prior experience of moving in the novel environment, we were interested to see whether participants moving with a more exploratory strategy would show improved ability to compensate for the novel field dynamics. To examine this, we correlated the intra-subject standard deviation of peak hand velocity (PeakVel Var) and duration to peak velocity (DPV Var) during early exposure to the force-field (early Adaptation) with the extent of adaptation as quantified by PVLD and AdInd. This was performed separately for all 4 independent groups which gave a total of 16 Pearson correlations: 2 (Age Group) x 2 (Visual Feedback) x 2 (early Adaptation PeakVel Var or DPV Var) x 2 (extent of adaptation measured by PVLD or AdInd). It was found that none of the relationships were significant (all $|r| < .52$; $p_{\text{min}} = .031$; $p_{\text{FDR}} = .003$) which indicates no adaptive performance benefits arose from a strategy with more varied movement within the novel dynamic environment.

As a follow-up to this, we wanted to see whether a more exploratory strategy had any relationship to the extent to which the adapted behaviour persisted during Washout. As such, we performed a similar correlational analysis but used extent of persistence for PVLD and AdInd instead. Once again, there were no significant relationships (all $|r| < .50$; $p_{\text{min}} = .041$; $p_{\text{FDR}} = .003$) which shows that varying the velocity of movements during early exposure to the force-field did not help participants to persist with the learned behaviour or reacquire the baseline behaviour.

6.3.2 – Dynamic Proprioception

6.3.2.1 – Proprioceptive Acuity Measures

Proprioceptive acuity measures are summarised in Table 6.3. The effect of Age Group on uncertainty range (UncR) was not significant (F[1, 62] = 1.80, *p* = .673) nor was the main effect of Visual Feedback (F[1, 62] = .51, *p* = .478) or their interaction (F[1, 62] = .41, *p* = .525; see Figure 6.8, Panel A for summary). There was a marginally significant effect of Repetition (F[3, 186] = 2.68, *p* = .048, η^2_p = .04) with follow-up pair-wise comparisons showing that UncR significantly increased between P1 and P2 (i.e. across the Null Block; *p* = .005; p_{FDR} = .008). The two- and three-way interactions were all non-significant (all *p* > .261).

The effect of Age Group on bias was also not significant (F[1, 61] = 1.44, *p* = .236) and neither was the effect of Visual Feedback (F[1, 61] = .27, *p* = .609) or their interaction (F[1, 61] = 2.33, *p* = .132; see Figure 6.8, Panel B for summary). The main effect of Repetition was also non-significant (F[2.5, 153.8] = 1.47, *p* = .224) with the Age Group x Repetition interaction showing a trend towards significance (F[2.5, 153.8] = 2.77, *p* = .053). The remaining interactions were all non-significant (*p* > .433).

Together, this suggests that early exposure to the null-field reaching task reduced perceptual acuity (UncR) but that it then remained stable for the rest of the experiment, and most important, there was no effect of the adaptation phase on acuity. Adaptation to the novel force-field environment also seems to be independent of the systematic changes in sensed limb perception (bias), which remained unchanged across the whole experiment.

6.3.2.2 – Kinematic Measures

The average movement velocity (MoveVel) data for the dynamic proprioceptive task is summarised in Table 6.3. There was a main effect of Age Group on MoveVel in the dynamic proprioception task (F[1, 64] = 9.25, p = .003, η^2_p = .13) such that YAs tended to move faster than OAs during these trials. The effect of Visual Feedback was not significant (F[1, 64] = 2.34, p = .131), however the Age Group x Visual Feedback interaction was significant (F[1, 64] = 8.05, p = .006, η^2_p = .11) with follow-up pair-wise comparisons showing that OAs in the Vision- condition were significantly slower than those in the Vision+ condition (p = .013; p_{FDR} = .025). There was a strong effect of Repetition on MoveVel (F[2.5, 161.2] = 39.8, p < .001, η^2_p = .38) with all perceptual blocks being significantly different from one another (all p < .001, except P3 vs P4 where p = .012; p_{FDR} = .042) apart from between P2 and P3 where speed remained stable (p = .076). This occurred such that movements were slowest during P1 and fastest during P4. The remaining two- and three-way interactions were all non-significant (all p > .339).

Measure	Visual Feedback Group	Age Group	P1	P2	P3	P4
Uncertainty Range (cm)	Vision+	*Older*	.59 *(± .06)*	.93 *(± .12)*	.86 *(± .08)*	.66 *(± .10)*
		Younger	.61 *(± .07)*	.78 *(± .11)*	.74 *(± .12)*	.86 *(± .12)*
	Vision-	*Older*	.68 *(± .07)*	.66 *(± .09)*	.67 *(± .10)*	.71 *(± .10)*
		Younger	.60 *(± .08)*	.77 *(± .09)*	.81 *(± .11)*	.79 *(± .14)*
	Overall		***.62 (± .03)***	§§***.79 (± .05)***	***.77 (± .05)***	***.76 (± .06)***
Bias (cm)	Vision+	*Older*	.76 *(± .16)*	.69 *(± .18)*	.69 *(± .19)*	.81 *(± .14)*
		Younger	.95 *(± .17)*	.67 *(± .17)*	.72 *(± .14)*	.75 *(± .14)*
	Vision-	*Older*	.74 *(± .18)*	.77 *(± .17)*	.95 *(± .11)*	.97 *(± .13)*
		Younger	.71 *(± .15)*	.52 *(± .12)*	.36 *(± .15)*	.49 *(± .11)*
	Overall		***.79 (± .08)***	***.66 (± .08)***	***.67 (± .08)***	***.75 (± .07)***
Movement Velocity (cm/sec)	Vision+	*Older*	20.1 *(± 1.9)*	26.0 *(± 2.5)*	25.3 *(± 2.2)*	25.8 *(± 2.2)*
		Younger	21.2 *(± 1.3)*	24.4 *(± 1.3)*	25.6 *(± 1.4)*	27.2 *(± 1.6)*
	Vision-	*Older*	15.1 *(± 1.2)*	17.2 *(± 1.5)*	19.2 *(± 1.6)*	20.4 *(± 1.5)*
		Younger	22.9 *(± 1.4)*	26.3 *(± 1.3)*	27.7 *(± 1.2)*	29.3 *(± 1.0)*
	Overall		**19.9 *(± .81)***	$^{¥¥}$**23.6 *(± .95)***	$^{¥¥}$**24.6 *(± .87)***	****25.8 *(± .88)***

Table 6.3. – Summary of findings for dynamic proprioception for older and younger adults in both the Vision+ and Vision- conditions. P1-4 indicates the first to fourth repeated blocks of task performance (see 6.2 – Methods for details). Values are given as means ± standard error, with significantly different values from P1 only, given as §§ ($p < .010$), different from P1 and all other repeats as ** ($p < .010$) and different from P1 and P4 only $^{¥¥}$ ($p < .010$; multiple comparisons subjected to FDR adjusted p-threshold. Main effects and interactions of Age Group on movement velocity are not pictured.

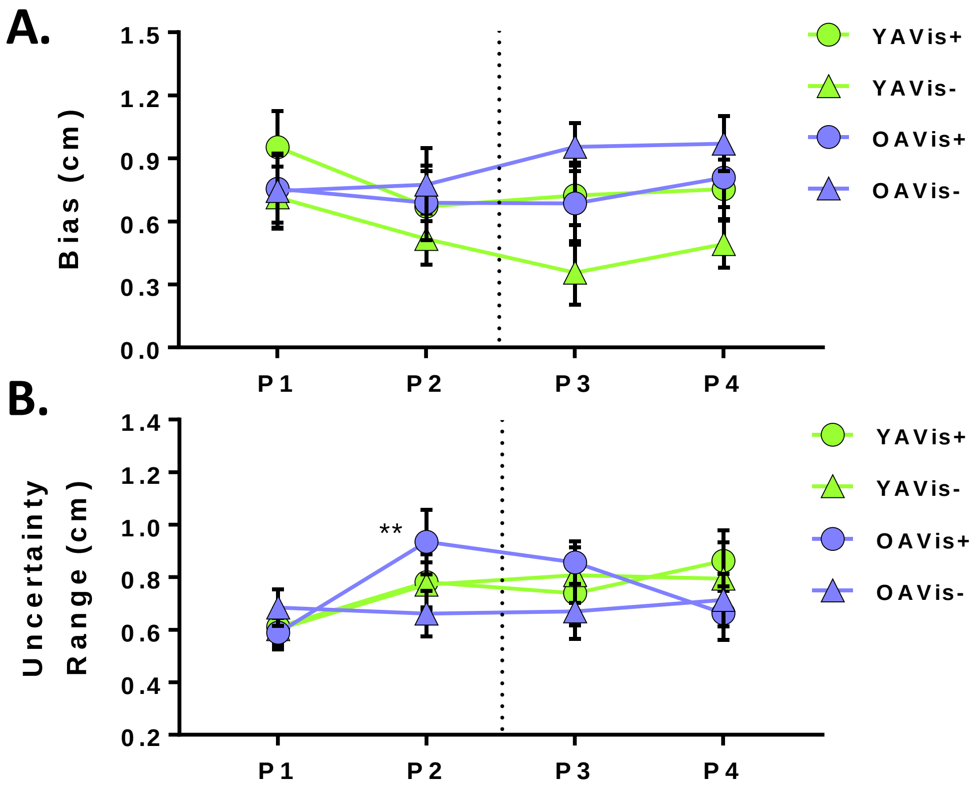


Figure 6.8. – Summary of proprioceptive acuity measures for older (purple symbols) and younger (green symbols) in the Vision+ (circles) and Vision- (triangles) conditions. P1-4 indicates the four repeats of proprioceptive blocks, with the dashed vertical line indicating the occurrence of the Adaptation block in the force-field adaptation task. **A.** shows the results for the uncertainty range and **B.** shows results for the bias. Values are given as means ± standard error, with ** indicating value significantly different from P1 only ($p < .010$; multiple comparisons subjected to FDR adjusted *p*-threshold)

There were no significant correlations between movement velocity and either UncR or bias for any of the 4 groups at any of the repetitions (UncR and bias Pearson correlations for 2 [Age Group] x 2 [Visual Feedback] x 4 [Repetition] relationships; bias, all $|r| < .24$, $p_{\text{min}} = .373$, $p_{\text{FDR}} = .003$; UncR, all $|r| < .35$, $p_{\text{min}} = .182$, $p_{\text{FDR}} = .003$). There were also no significant correlations between the lateral force imposed on the channel walls in the last portion of the movement and the bias for any of the 4 groups or repetitions (all $|r| < .43$, $p_{\text{min}} = .100$, $p_{\text{FDR}} = .003$).

Collectively, this shows that OAs in the Vision- group were systematically slower than other groups but generally movement speed increased across the repeated performances of the perceptual task. Perhaps more importantly, this was not related to estimates of perceptual acuity and even following adaptation to the force-field, the forces imposed against the channel walls during movements were not related to systematic perceptual errors.

6.3.3 – Association Between Limb Proprioception and Motor Adaptation

One of the main purposes of this experiment was to see whether the extent of motor adaptation was related to a change in sensed limb position. As such, we looked at the association between extent of adaptation and the shift in bias between P2-P3 (AdaptShift), and also the extent of persistence and the bias shift between and P3-P4 (PersistShift).

As such, both PVLD and AdInd were correlated with AdaptShift across the 4 different groups, which gave a total of 8 correlations: 2 (Age Group) x 2 (Visual Feedback) x 2 (adaptation measured by PVLD or AdInd). However, there were no significant relationships measured (all $|r| < .38$, $p_{\min} = .129$), indicating no relationship between proprioceptive shift and extent of adaptation. For the relationship with persistence, we performed a similar analysis but with PersistShift and the extent of persistence as measured by PVLD and AdInd. There were again no significant correlations for any of the groups (all $|r| < .19$, $p_{\min} = .467$; $p_{\mathrm{FDR}} = .006$) showing an equally poor association between proprioceptive shift and persistence of learned motor behaviour. These findings refute the prediction that proprioceptive shifts would be most strongly associated with adaptation when visual feedback of hand position was limited.

Finally, to examine the relationship between proprioception and motor adaptation, we correlated the UncR and bias at baseline (P1) with extent of adaptation, but again found no relationships (UncR; $|r| < .32$, $p_{\text{min}} = .232$, $p_{\text{FDR}} = .006$; bias; $|r| < .44$, $p_{\text{min}} = .103$, $p_{\text{FDR}} = .006$) suggesting that these measures are also independent of one another in this experiment, contrary to our predictions.

6.3.4 – Spatial Working Memory

As in Chapter 5, there were essentially no errors during task performance at 4 tiles (one participant made a single within-search error [WSE] on 1 out of the 2 attempts only) so this condition was not included in the main analysis. This left a mixed design ANOVA with Number of Tiles as a 3-level factor (6, 8, or 10 tiles).

The main effect of Age Group on WSE showed a trend towards significance (F[1, 65] = 3.91, $p = .052$) with OAs making a larger number of WSEs than YAs overall (see Figure 6.9, Left Panel for summary). The main effect of Visual Feedback group on WSE was not significant (F[1, 65] = .11, $p = .738$) and neither was the Age Group x Visual Feedback interaction (F[1, 65] = .45, $p = .504$). Number of Tiles had a significant effect on WSE (F[1.5, 94.8] = 18.46, $p < .001$, $\eta^2_p = .22$) with all different levels of difficulty being significantly different from one another (all $p < .001$, except 8 vs. 10 tiles, $p = .004$; $p_{\text{FDR}} = .050$) such that WSEs were highest at 10 tiles and lowest at 6 tiles. All other interactions were non-significant (all $p > .181$).

There was an effect of Age Group on between-search errors (BSEs; F[1, 65] = 20.9, $p < .001$, $\eta^2_p = .24$) where OAs made a greater number of BSEs than YAs across the entire task (see Figure 6.9, Right Panel for summary). There was no effect of Visual Feedback on BSE (F[1, 65] = .24, $p = .629$) or interaction of Age Group x Visual Feedback (F[1, 65] = .25, $p = .620$).

Number of Tiles had a significant effect on BSE (F[1.3, 85.0] = 96.2, *p* < .001, η^2_p = .60) with all levels of difficulty being significantly different from one another (all *p* < .001; p_{FDR} = .050), such that errors were highest at 10 tiles and lowest at 6 tiles. The Age Group x Number of Tiles interaction was also significant (F[1.3, 85.0] = 8.48, *p* = .002, η^2_p = .12), with pair-wise comparisons showing that OAs made more BSEs than YAs during searches of 8 and 10 tiles (both *p* < .001; p_{FDR} = .033). The remaining interactions were not significant (all *p* > .346).

The finding of greater BSEs for OAs matches those reported from Chapter 5, however unlike the findings reported for that chapter, there was only a trend for increased WSEs for OAs measured here. This shows that the OAs tested in this experiment still had impaired cognitive function comparing to younger participants, albeit to a lesser extent than we previously reported. Importantly, there were no differences in spatial working memory (SWM) between the sub-groups defined by the visual feedback conditions.

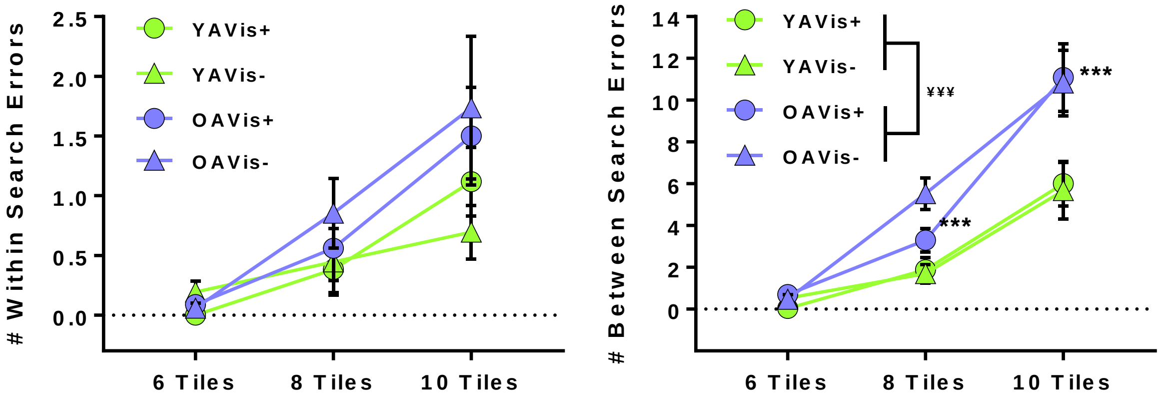


Figure 6.9. – Summary of within (left) and between (right) search errors for the spatial working memory task, for older (purple symbols) and younger (green symbols) adults in the Vision+ (circles) and Vision- (triangles) conditions. Values are given as means ± standard error, with ¥¥¥ indicating significant difference between older and younger adults as main effect (*p* < .001) and ******* as age group difference at specific numbers of tiles (*p* < .001; multiple comparisons subjected to FDR adjusted *p*-threshold). Main effect of number of tiles not pictured.

In addition to age group differences in performance of this task, we were interested to see whether SWM capacity was related to the extent of adaptation and its persistence during the Washout block. We therefore correlated the average within and between search errors with adaptation as measured by both PVLD and AdInd for all 4 groups (Pearson correlations for 2 [Age Group] x 2 [Visual Feedback] x 2 [WSE/BSE] x 2 [PVLD/AdInd Adaptation] relationships). No significant relationships were found ($|r| < .35$, $p_{\min} = .346$, $p_{FDR} = .003$), showing adaptation was not enhanced by SWM capacity. Contrasting to predictions, this was also true for extent of persistence ($|r| < .41$, $p_{\min} = .103$, $p_{FDR} = .003$), suggesting SWM capacity has little influence on this either.

As in Chapter 5, we were also interested to see whether our proprioceptive acuity estimates were related to SWM. This was to assess whether bias or UncR arose from decay in the memory of limb position during prolonged occlusion of visual feedback in the task. For this correlational analysis, we used the baseline (P1) performance of the task, at which point all participants had been exposed to the same task conditions, regardless of their visual feedback group allocation. This meant we were able to collapse across Vision+ and Vision- groups and run the correlations with larger sample sizes for older and younger adults only, increasing the power of the analysis. This gave a total of 8 Pearson correlations: 2 (Age Group) x 2 (WSE/BSE) x 2 (UncR/Bias) relationships. It was found that all the correlations were non-significant (all $|r| < .42$, $p_{\min} = .018$; $p_{FDR} = .006$), apart from for between UncR and BSE for OAs ($r = .47$, $p = .0059$) which just reached significance following correction for multiple comparisons.

This analysis shows that although SWM capacity is unrelated to the extent to which learned motor behaviours persist during de-adaptation, there may be a relationship with perceptual acuity measures from the dynamic proprioception task. It may be that this effect was not detected in Chapter 5 because of the weaker power for that test, and this warrants further discussion.

6.3.5 – Self-Report Measures

6.3.5.1 – Physical Activity

Following the relationship between PA and bias found for OAs in Chapter 3, we were interested in whether self-reported PA levels (PASE for OAs; IPAQ-Short for YAs) were associated with baseline proprioceptive measures. As such, it was also possible to collapse data across visual feedback groups, which meant group sizes were large enough to further sub-divide into high and low PA groups, similar to Chapter 3. To do this, we used a median threshold value of IPAQ score (1988 MET-min per week) to group YAs into physically inactive (n = 18, 1082.7 ± 546.5 MET-min per week) and active (n = 17, 3763.9 ± 1291.7 MET-min per week) groups. We also used a median threshold value for the PASE (score of 155.4) to group OAs into inactive (n = 17, 108.7 ± 42.0) and active (n = 17, 219.4 ± 63.8) groups. Following this we performed 2 separate 2 x 2 univariate ANOVAs: (Age Group) x (PA Status; inactive or active) to analyse baseline (P1) UncR and bias.

There was no effect of either Age Group (F[1, 63] = .11, *p* = .743), PA Status (F[1, 63] = .30, *p* = .584) or their interaction (F[1, 63] < .01, *p* = .935) on baseline UncR. For the bias, there was also no effect of Age Group (F[1, 65] =.07, *p* = .788) but the effect of PA Status was significant (F[1, 65] = 6.30, *p* = .015, η^2_p = .09) such that inactive participants had larger, more positive biases than active ones (Figure 6.10). The interaction of Age Group x PA Status was not significant (F[1, 65] = .13, *p* = 717).

As a final analysis of the PA score, we looked at its association with extent of adaptation and persistence (measured by both PVLD and AdInd) within the 4 independent groups, which gave correlations for 2 (Age Group) x 2 (Visual Feedback) x 2 (adaptation or persistence) x 2 (measured by PVLD or AdInd) relationships. Again, there were no significant correlations found ($|r| < .46$, $p_{min} = .063$, $p_{FDR} = .003$) which suggests that adaptive motor performance was independent of PA.

This shows that PA was associated with increased systematic, but not variable proprioceptive errors recorded at baseline but that this was independent of age. However, we did not measure any association between PA and adaptation or persistence, indicating that these are independent.

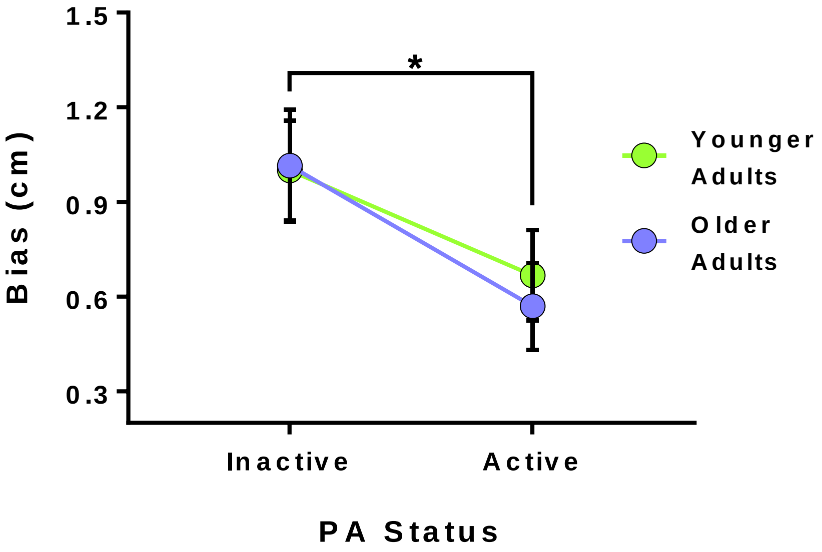


Figure 6.10 – Proprioceptive biases for baseline task performance (P1) of older (purple) and younger (green) adults sub-divided into physically active and inactive according to self-report measures. Values are given as means ± standard error, with ***** indicating significant main effect of physical activity (PA) status ($p < .050$)

6.3.5.2 – Attention and Fatigue

Finally, we looked at how participating in the experiment affected self-reported levels of attention and fatigue (scale of 1-7) in a similar manner to Chapter 5, analysing scores in 2 x 2 x 2 mixed-design ANOVAs: Age Group x Visual Feedback x Timepoint (pre- or post-experiment).

There was no main effect of Age Group on fatigue, nor of Visual Feedback or of their interaction (all $p > .121$). However, there was an effect of Timepoint (F[1, 65] = 27.9, $p < .001$, $\eta^2_p = .30$) such that fatigue levels increased from before (3.01 ± 1.25 out of 7) to after the experiment (3.96 ± 1.38 out of 7) across all participants. The remaining interactions were all non-significant (all $p > .086$). A 2 x 2 univariate ANOVA: Age Group x Visual Feedback, also revealed that YAs had a small but significantly greater number of hours of sleep than OAs (7.23 ± 1.37 hrs vs. 6.59 ± 1.35 hrs; F[1, 65] = 4.03, $p = .049$, $\eta^2_p = .06$), with no other significant effects observed (all $p > .579$). In a similar analysis, quality of sleep (rated 1-7) was comparable between groups (all $p > .110$). For attention, there was an effect of Age Group (F[1, 65] = 7.30, $p = .009$, $\eta^2_p = .10$) such that YAs (4.56 ± 0.99 out of 7) had lower overall reported attention than OAs (5.10 ± 1.09 out of 7). There were no other significant main effects or interactions (all $p > .074$).

In summary, this shows that all participants were fatigued by participating in the experiment but their attention appeared to be unaffected. Similar to Chapter 5, YAs also had lower reported overall attention. Critically, the lack of Age x Timepoint interactions shows both older and younger adults were not differentially affected.

6.4 – Discussion

This experiment aimed to examine the contribution of proprioception to sensorimotor adaptation in a novel dynamic field, in both older and younger adults. Contrary to predictions, older and younger adults were able to adapt their movements comparably regardless of whether visual feedback was limited or not. In fact, restricting visual feedback of hand position had no effect on the ability to adapt to the novel field for either age group. Despite age-dependent reductions in memory capacity, spatial working memory (SWM) was not related to persistence of adapted behaviour, nor was the extent of adaptation predicted by proprioceptive uncertainty. In addition to this we did not see any proprioceptive recalibration at the group level in response to learning, which was also unrelated to extent of adaptation.

As predicted, we found that that ageing does not affect the ability to adapt to novel field dynamics when visual feedback is provided, similar to reports by Trewartha et al. (2014). However, considering previous reports showing greater visual dependency for motor control in ageing (Seidler-Dobrin & Stelmach, 1998) we expected adaptation to become disrupted when visual feedback was removed, yet this wasn't the case. Instead, it may be that the most important factor for motor adaptation in ageing is the extent to which task performance requires explicit cognitive resources, which is most apparent from salient visuomotor adaptation tasks and their associations with working memory in older adults (OAs; Anguera et al., 2010; Uresti-Cabrera et al., 2015). Following this, it could be that the lack of age-effects here indicates that novel field adaptation is more dependent on implicit adaptive processes, which may be spared in ageing to allow preservation of performance

(Cressman et al., 2010). Indeed, there is evidence to suggest that adaptation to novel field dynamics depends more heavily on an implicit, proprioceptive-dependent mechanism of learning with a weaker contribution of an explicit, visual-dependent component (Hwang, Smith, & Shadmehr, 2006) which supports this idea. Moreover, the comparable performance between visual feedback conditions in this experiment suggests there is a negligible benefit to adaptation of added visual information regarding the perturbation, which also indicates a weak contribution of explicit visual learning mechanisms to performance. Finally, in a similar manner to Trewartha et al. (2014), we did not detect any relationship between adaptation and SWM capacity in this experiment, despite age-dependent impairments in memory capacity, indicating no limiting involvement of SWM on adaptive performance. As such, these findings could support the notion that motor control is most impaired in ageing when cognitive demand or attention to the task is high (Seidler et al., 2010).

Contrary to our predictions and previous reports (Cressman & Henriques, 2009, 2010; Cressman et al., 2010; Ostry et al., 2010) we did not find evidence of proprioceptive bias recalibration after motor adaptation. Previous studies had reported proprioceptive recalibration accounted for around 20-30% of the perturbation which we had assumed we would replicate, and perhaps even exceed in the restricted visual feedback condition where adaptation was predominantly proprioceptive based. Yet this was not the case. An alternative view is that the process of proprioceptive recalibration is less indicative or necessary for motor adaptation, and is instead a product of cross-modal sensory integration processes. To elaborate, visual sensory feedback typically dominates perception (Ernst & Banks, 2002; Ernst & Bulthoff, 2004) and can shift perception of other, noisier sensations towards it in what is sometimes termed a cross-modal bias (Bertelson & Aschersleben, 1998;

Hairston et al., 2003; Pick, Warren, & Hay, 1969). With visuomotor displacements there is a large discrepancy between visual and proprioceptive feedback of hand position. This means proprioceptive recalibration may simply arise from the noisier, proprioceptively perceived hand position shifting towards the (normally) more reliable, visually determined hand position in a cross-modal bias. Furthermore, since proprioceptive recalibration is possible even during passive exposure to a visual displacement (Cressman & Henriques, 2010) and is seen in cerebellar patients despite their impaired sensorimotor adaptation (Block & Bastian, 2012), this additionally indicates these shifts in perception are unrelated to active visuomotor adaptation. On the other hand, during adaptation to novel fields there is no discrepancy between visual and proprioceptive sensation of hand position and so cross-modal sensory integration is unchanged, eliminating its contribution to the magnitude of observed proprioceptive recalibration. Indeed, the reported perceptual shifts after adapting to novel field dynamics (around 0.2cm in Ostry et al., 2010) is around 5-10 times smaller than those consistently measured in visuomotor displacement tasks (around 6° equating to roughly 1cm after cursor rotation in Cressman & Henriques, 2009, 2010; Cressman et al., 2010; and around 2cm after cursor translation in Cressman & Henriques, 2009); this may have made these shifts hard to measure empirically in the present experiment. Interestingly, whilst proprioceptive recalibration is possible with passive exposure to visual perturbations (Cressman & Henriques, 2010), it is the process of active motor adaptation to novel fields that drives these shifts, which also accounts for a greater proportion of the perturbation (Ostry et al., 2010). As such, the recalibration induced by these tasks may be more closely related to the adaptation process and less a product of cross-modal bias. However, the fact the proprioceptive bias shift only accounted for at most 33% of adaptation (Ostry et al., 2010) shows that there are other processes which also occur in parallel.

The ability to adapt movements to novel field dynamics involves the use of proprioceptive sensory feedback, and as such, we predicted that the acuity of this sensation would limit adaptation. However, even in conditions where there was no visual feedback regarding the perturbation, we found that proprioceptive acuity was unrelated to adaptive performance for either age group. This may be partially explained by the relatively low level of proprioceptive impairment we measured in this sample of participants, which likely reduced the magnitude of its impact on adaptive performance. Furthermore, since motor adaptation is a multi-factorial process involving sensory feedback processing and updating of motor commands (Bastian, 2008; Wolpert, Diedrichsen, & Flanagan, 2011), this creates other sources of noise which could equally contribute to variance across the groups. Perhaps more importantly, just being exposed to a sensory prediction error is sufficient to drive the adaptation process with corrective movements made in response to the perturbation having a lesser effect (Mattar & Gribble, 2005; Tseng, Diedrichsen, Krakauer, Shadmehr, & Bastian, 2007). This suggests that sensory feedback is utilised for adaptation in a predominantly offline manner between trials, with less involvement of online proprioceptive feedback corrections for performance, potentially explaining why we did not measure an association between the two. It seems then, that this type of task may not be sensitive to the use of of online proprioceptive motor control (similar to Chapter 3) and therefore further experimentation may be warranted to assess this more directly.

Although we found a null effect of ageing on adaptation, similar to Trewartha et al. (2014), we were not able to replicate the finding that SWM was related to persistence of the learned behaviour. However, this can be attributed to the fact that Trewartha et al. (2014) looked at retention of learned behaviour across an “error-clamp” phase (block of repeated catch trials) rather than with null-field trials to washout behaviour as we did. Furthermore, the experimental design they used allowed them to model the fast and slow components of motor learning (Smith, Ghazizadeh, & Shadmehr, 2006) from which they derived a coefficient for retention quite different from the index of persistence used in this experiment. As such, this could account for the reason we were unable to replicate this effect in this experiment. However, similar to Trewartha et al. (2014), we were able to control movement speed between age groups, which means all participants were exposed to a comparable magnitude of force in the velocity-dependent field. Interestingly, in the report by Huang & Ahmed (2014), OAs moved significantly slower than younger adults (YAs), and so their age-dependent effects on adaptation (which differed from both the present report and that of Trewartha et al., 2014) could be explained by differences in perturbation magnitude between age groups. Since we were able to control movement speed between age groups in this experiment, we can more confidently conclude there were no age-dependent effects on novel field adaptation. Furthermore, the importance of controlling movement speed in velocity-dependent force-field tasks may be why these types of tasks are less commonly reported in an ageing population who tend to move more slowly (Contreras-Vidal, Teulings, & Stelmach, 1998; Helsen et al., 2016; Ketcham, Seidler, Van Gemmert, & Stelmach, 2002), thereby making regulation of speed between age groups more difficult.

As in Chapter 5, we were unable to show similar findings to Chapters 2 and 3 of age and physical activity (PA) dependent bias effects. However, by sub-grouping participants based on self-reported PA, we did see that inactive participants had larger systematic proprioceptive errors in detecting hand position at baseline. In Chapter 3, we suggested the age-dependent bias increase may have been due to a use-dependent sparing of intrafusal fibres which caused biased tuning of sensed limb position (Bergenheim, Ribot-Ciscar, & Roll, 2000; Jones, Wessberg, & Vallbo, 2001). Although loss of intrafusal fibres in low activity YAs is unlikely, it may be that reduced PA biases their experience of limb movements to a more laterally constrained region than is typically seen in naturalistic, active settings (Howard, Ingram, Kording, & Wolpert, 2009). As such, perception may be drawn towards the position of highest or most frequent sensory experience as a prior (Gritsenko, Krouchev, & Kalaska, 2007; Kording & Wolpert, 2006), increasing systematic proprioceptive biases during periods of sensory uncertainty (as in the perceptual test). Despite this PA effect on bias, we did not detect an interaction with age as we did in Chapter 3. This could reflect the quality of the self-report measures we used in this experiment, which are typically thought to be less sensitive and reliable than accelerometer data, as used in Chapter 3 (Murphy, 2009). Since the relationship between increased PA and spared proprioception in ageing is typically demonstrated in passive movement tasks (Adamo, Alexander, & Brown, 2009; Helsen et al., 2016; Wright, Adamo, & Brown, 2011) it may be that this relationship is weaker for dynamic proprioceptive acuity in which limitations of passive methodology are addressed. As such, more sensitive measures may be needed to accurately detect it.

In Chapter 5 we found a trend towards a confounding effect of SWM on proprioceptive measures in task versions where the target became visually occluded. In addition to this, by using a version of the task where the target remained visible throughout (20cm reach, target stay, minimum jerk channel), we found statistically stable proprioceptive measures between intermittent repeats across the experiment (Figure 5.7). As such, we decided to use the same version of the dynamic proprioceptive task in the present experiment. However in spite of these considerations, we found that SWM was correlated with baseline uncertainty range for OAs, and that it significantly increased after “Null” block reaching performance as a main effect. This correlation with SWM is unfortunate as this is one of the confounds thought to affect performance on position matching tasks (Goble, Mousigian, & Brown, 2012) which we were trying to avoid with this dynamic task. Although we did not find an association with working memory in previous experiments, it may be that SWM is indeed important in these tasks with ageing, but we lacked the statistical power to measure such an effect in Chapter 5. However, we suggest this association is unlikely to have had a serious confounding effect in this experiment, as although we measured a significant loss of SWM capacity with age, we did not detect a corresponding increase in proprioceptive uncertainty. As such, whilst this finding is novel, we do not consider it as a limitation in our findings. As for the shifts in uncertainty range between P1 and P2, although there was no significant interaction, this effect appears to be driven most prominently by participants in the OA Vis+ group (Table 6.3, Figure 6.8, Panel B). Since these participants also saw the largest increase in movement velocity of all groups between P1 and P2 (around 6cm/sec) it may be this increased movement speed led to increased proprioceptive noise. However, we did not measure any significant associations between movement speed and proprioceptive acuity in the present experiment. Moreover, Ostry et al. (2010) did not measure any changes in uncertainty range between any of the different phases of task performance. As such, the basis for the finding remains unclear.

In conclusion, we show here that OAs are able to adapt movements in novel dynamic fields to a similar extent to YAs regardless of whether visual feedback of the perturbation is provided. We speculate that this may be due to the limited dependency on explicit control strategies needed for this type of sensorimotor adaptation task, which is evidenced by the lack of influence of SWM capacity on adaptation in the older group. In addition to this, we did not detect proprioceptive recalibration in spite of clear evidence of adaptive motor behaviour, and we suggest that previous reports of this effect with visuomotor perturbations may have been amplified by cross-modal sensory biases, and that it is perhaps not indicative of adaptive processes. Finally, we report further evidence of PA effects on proprioceptive bias, but that proprioceptive acuity did not predict adaptation to the novel field. This may be due to the relatively small effect that online proprioceptive motor control has on offline sensorimotor adaptation. This means further experimentation with tasks where online sensory feedback is required may be necessary to conclude the proprioceptive-motor control relationship in ageing.

CHAPTER 7

General Discussion

7.1 – Introduction

The aim of this thesis was to improve our understanding of how proprioceptive acuity contributes to upper limb motor performance in ageing. The hope was to add to knowledge of the factors that contribute to motor impairment so that better recommendations and efforts can be made to reduce their impact on life in advanced age. Ultimately this would help improve quality of life through prolonged independence, and reduce the rapidly increasing burden on public health services. In order to investigate this we used a novel, active method of measuring upper limb proprioception that addresses limitations of previously reported methods with older adults (OAs). Through comparison of performance on this task with target based reaching movements we were able to assess the relationship between proprioceptive acuity, motor performance and learning. In this Chapter, we summarise the findings from these experiments and discuss their collective implications, as well as future directions for research, and highlight some remaining open-ended questions.

7.2 – Summary of Results

Through pilot testing in Chapter 2 we were able to develop a dynamic, upper limb proprioceptive task by identifying methodological limitations which could be altered to improve the reliability and sensitivity of its outcome measures. This allowed us to optimise the task and strengthened the basis for its use in the chapters which followed. Although limited in sample size and with some need for improvement, we showed with this task an age and physical activity (PA) dependent effect on proprioceptive bias.

In Chapter 3 we then used the improved version of this task to replicate this effect, showing that physically inactive OAs had larger proprioceptive biases but not uncertainty ranges, than younger adults (YAs). We also found some distinct characteristics of OA motor performance on a rapid reaching task, including prolonged reaction times and maintained endpoint accuracy of target reaching, which was partially explained by movement slowing. However, we did not find an association of proprioception and motor performance in terms of either systematic or variable errors for older or younger adults.

In Chapter 4, we found that the proprioceptive measures obtained from the dynamic task were distinct from a more commonly used ipsilateral position matching paradigm. This was in spite of increased dynamic proprioceptive bias and overshoot of elbow position matching for OAs. This showed that task methodology does affect estimates of proprioceptive acuity, and that passive movement based paradigms may therefore only give a poor indication of proprioceptive sensation in normal active movement control, further supporting the continued use of our dynamic task.

Since the age-dependent increase in bias we had measured in Chapters 2 and 3 was inconsistent with a notable previous report (Cressman, Salomonczyk, & Henriques, 2010), we probed the basis of its occurrence in Chapter 5 by measuring dynamic task performance with different combinations of task parameters. Despite identifying influential effects of reach distance, perceptual channel type and target visibility on our measures of dynamic proprioception, they did not differentiate between performance of older and younger adults. Furthermore, we saw limited evidence to suggest that either spatial working memory (SWM) capacity or proprioceptive drift contributed to our findings from Chapters 2 and 3. Of most importance, we did not replicate either our own age-dependent effect on bias from previous chapters, or the age-dependent effect on uncertainty range reported by Cressman et al. (2010). This demonstrated that the effects of ageing on dynamic proprioceptive acuity may not be as reliable as initially thought.

Finally in Chapter 6, we examined the relationship between dynamic proprioception and adaptation to novel field dynamics, a task we proposed would emphasise the use of proprioceptive feedback for motor performance above that of the rapid reaching task in Chapter 3. This was further emphasised by including a condition in which on-line visual feedback of the movement was limited. Both older and younger adults adapted similarly regardless of visual feedback, and performance was not related to SWM, which we suggest is indicative of reduced explicit control strategies for this type of task. Interestingly, we did see that physically inactive participants had larger proprioceptive biases, but that this effect was independent of age. However, neither baseline proprioceptive acuity nor recalibration with learning was related to their adaptive motor performance.

Collectively these findings showed little evidence of a strong relationship between dynamic proprioception and motor control in ageing, with only a small or unreliable age-dependent loss of proprioceptive acuity itself. We will discuss these points in more detail in the following sections.

7.3 – Measuring Proprioception Across the Lifespan

In Chapter 1, we outlined the existing evidence to show that upper limb proprioceptive acuity declines with age (Adamo, Alexander, & Brown, 2009; Adamo, Martin, & Brown, 2007; Helsen et al., 2016; Herter, Scott, & Dukelow, 2014; Wright, Adamo, & Brown, 2011; see Section 1.4 for detailed review). From this evidence we hypothesised that OAs would have impaired proprioception when tested throughout this thesis, yet this finding was not consistent across our experiments.

One explanation for the lack of consistent age effects on proprioception could be that we have a particularly high functioning, physically active cohort of OAs which diminished any contrasting effects with YAs. Whilst we cannot directly compare our PA accelerometer data from Chapters 3 and 4 with a typical OA population, there is a publication with a large sample for the OA self-report measure of PA which we used in Chapters 5 and 6 (Physical Activity Scale for the Elderly [PASE]; Logan, Gottlieb, Maitland, Meegan, & Spriet, 2013). In this report, around 300 OAs aged 60-88 were tested and found to have an average PASE score of 155 ± 66 which is close to the range we collected from both Chapter 5 (157.6 ± 85.6) and Chapter 6 (164.1 ± 77.4) which were also not significantly different from each other (t[50] = -.28, p = .785). This suggests these older participants are a good representation of the wider OA population with respect to PA and consistently similar between chapters. We noted slightly above average verbal working memory score for our population of OAs in Chapters 3 and 4 (same cohort) compared to a large scale sample of around 200 participants in each 9 year age band (Iverson & Tulsky, 2003). The number of within search errors the OAs in Chapters 5 and 6 made in our test of SWM capacity were slightly higher than a previous report (Kessels, Meulenbroek, Fernandez, & Olde Rikkert, 2010), indicating worse cognitive function. However, the between search errors were slightly lower. Following these comparisons, it seems our OA sample are within the norms expected for the wider population with regard to factors which may limit estimates of proprioceptive acuity (Adamo et al., 2009; Adamo et al., 2007; Goble, Mousigian, & Brown, 2012; Helsen et al., 2016; Wright et al., 2011; see Section 1.4.2 for detailed review). It is therefore unlikely that these factors explain any of the limited effects of age on proprioception we measured throughout this thesis.

An alternative explanation is that the limitations of previous work outlined in Chapter 1 (see Section 1.4.3 for detailed review) over-inflated reports of age-related proprioceptive deficits, when in reality the level of impairment is much smaller. Specifically, the nature of many previously reported position matching tasks and their reliance on central processes such as memory (Goble, Mousigian, et al., 2012) and interhemispheric transfer may amplify proprioceptive deficits with ageing (Goble, Coxon, Wenderoth, Van Impe, & Swinnen, 2009; Hou & Pakkenberg, 2012; Ota et al., 2006). In addition, the use of passive movements in both matching and detection tasks can also affect performance and limits the generalisation of these findings to sensation in normal voluntary movement (Smith, Crawford, Proske, Taylor, & Gandevia, 2009). This has been shown in experiments where proprioceptive errors were reduced with active compared to passive reference movements, in either older or younger adults (Erickson & Karduna, 2012; Langan, 2014; Lonn, Crenshaw, Djupsjobacka, Pederson, & Johansson, 2000). It has also been directly compared across age groups in a recent study by Schaap, Gonzales, Janssen, & Brown (2015) who reported no age-effects on ipsilateral matching error in 3D space when the reference position was actively determined.

Moreover, in Chapter 4 we found no association between the scores from the dynamic task we used throughout the thesis and performance on a traditional position matching task, highlighting the difference in the nature of these tasks and the proprioceptive measures they provide. Taken together, this suggests that by developing and using a dynamic task aimed at addressing the age-specific limitations of previous work, the resultant age-related proprioceptive impairments are less prominent, even when measured through careful empirical assessment. This is evidenced through our inability to measure consistent and significant proprioceptive deficits with advanced age across the course of the thesis.

In spite of the mixed effects we presented of ageing on proprioception, we did appear to find a more consistent effect of PA on proprioceptive bias when we had the statistical power to sub-group participants in Chapters 3 and 6, but also through correlation in the pilot study conducted in Chapter 2. The cause of this systematic proprioceptive bias is not well understood despite commonly being reported in a range of different dynamic (Cressman & Henriques, 2009; Cressman et al., 2010; Mattar, Darainy, & Ostry, 2013; Ostry, Darainy, Mattar, Wong, & Gribble, 2010), passive (Bernardi, Darainy, & Ostry, 2015; Wilson, Wong, & Gribble, 2010; Wong, Wilson, & Gribble, 2011) and static tasks (van Beers, Sittig, & Denier van der Gon, 1998; van Beers, Sittig, & Gon, 1999). In Chapter 3 we argued that the age and PA dependent increase in bias may have been a result of use-dependent sparing of intrafusal fibres causing a biased directional tuning of limb position (Bergenheim, Ribot-Ciscar, & Roll, 2000; Jones, Wessberg, & Vallbo, 2001; Kording & Wolpert, 2006). However, since we measured a PA, but not age, dependent effect on proprioceptive bias in Chapter 6 it seems less likely that loss of intrafusal fibres contribute to this, as we would expect fibre loss to be more prominent in the elderly, regardless of PA. However, we also suggested that this proprioceptive bias might be driven by greater reliance on sensory priors which may be more lateralised through inactivity. To elaborate, the most frequent naturalistic limb movements are typically lateralised within a relatively small volume of space (Howard, Ingram, Kording, & Wolpert, 2009) which may be further confined with lower activity. As such, during task performance when limb position uncertainty is high and visual feedback is deprived, perception may be drawn towards the prior state of high or frequent sensory experience (Gritsenko, Krouchev, & Kalaska, 2007; Kording & Wolpert, 2006). If, as we suggest, this prior is constrained to a more lateralised region for inactive individuals then this could lead to higher proprioceptive biases. Although we showed evidence in Chapter 5 to demonstrate that proprioceptive drift was relatively unrelated to bias, it is conceivable that a dependence on lateralised priors increases gradually over the duration of the task. As such, further research into proprioceptive drift in physically inactive individuals may help to elucidate this in future.

However, an alternative to discuss is that by using self-report measures in Chapter 6 instead of the accelerometer data (Chapter 3), we reduced the sensitivity of our PA assessment (Murphy, 2009) which may have limited our ability to detect an age and PA interaction on proprioceptive bias. Furthermore, in Chapter 3 we excluded highly physically active YAs in order to control activity of the sample and did not sub-group them according to PA status as we did for the OAs. In spite of this, we were still able to measure differences in bias between inactive OAs and the YA sample. This argues for a loss of proprioceptive quality that is particularly evident in physically inactive OAs. If, as we argue here, the effects of ageing on dynamic proprioception are in fact smaller than previously thought, then it may be they can only be reliably captured when statistical power is increased through sub-grouping participants according to more sensitive measures of PA. Whilst this wouldn't necessarily explain the findings in Chapter 2, the lack of a PA measure for YAs in that Chapter means that the effect of the interaction between age and PA on bias is still unknown.

The closest report to which we can compare our findings is by Cressman et al. (2010) who used a dynamic task to show age effects on uncertainty range, but not bias, contrary to the work of this thesis. We established in Chapter 5 that measures from these dynamic tasks are sensitive to certain experimental parameters, but this sensitivity does not affect the estimates for the two age groups differently. Hence this cannot explain the discrepancy of our results from Cressman et al.'s (2010). In addition, we were unable to replicate the findings they reported in a very similar version of their task (Chapter 5), which suggests the age effect on uncertainty may not be robust. Indeed, the effect reported by Cressman et al. (2010) only marginally reached significance ($p = .050$), with a sample of only 9 OAs (average age 66.3 ± 6 yrs) and no reported effect size. In contrast, we have tested over 80 different OAs in this thesis (typically aged 70 years or above) on a range of different tasks without finding any indication of age-related increase in proprioceptive uncertainty. Instead, we have measured somewhat mixed findings of age, and more reliable effects of PA, on proprioceptive bias which may therefore be more important to pursue in further research.

7.4 – Proprioceptive Control of Movement

In Chapter 1 we outlined independent reports of proprioceptive and motor impairments with ageing as well as the evidence showing proprioception is important for basic motor function. From this, we hypothesised that those participants with the greatest proprioceptive deficits would show the biggest motor impairments. However we did not find evidence to support this hypothesis. In Chapter 3 we detected some stereotypical indices of ageing on motor performance, which included prolonged reaction times and movement slowing which partially contributed to the maintenance of endpoint accuracy. Although previous work had indicated no relationship between passive proprioception and motor control of the wrist in ageing (Helsen et al., 2016), we predicted that by using a dynamic, multi-joint proprioceptive task we would be able to detect this relationship, due to the increased task specificity of our measures. However, in spite of this we were unable to measure an association between proprioceptive acuity and motor performance in older or younger adults, which we suggested may have been due to the choice of the motor control task we used. Since the movements were made rapdily towards visual targets, their control was likely more reliant on predictive, forward model-based processes which overcome the delays associated with online sensory feedback (Miall & Wolpert, 1996; Shadmehr, Smith, & Krakauer, 2010; Wolpert, Ghahramani, & Jordan, 1995). Since the predicted states generated by these models are dependent on previous multimodal sensorimotor experience (Shadmehr et al., 2010), it is unlikely that the accuracy of the rapid movements we tested were heavily dependent on online proprioceptive sensory feedback. This may explain why we were unable to measure a relationship between motor performance and proprioceptive acuity in Chapter 3.

Following these observations, we attempted to measure this relationship again in Chapter 6, but with a task requiring motor adaptation to novel field dynamics, which we chose to emphasise use of proprioceptive feedback. Previous research into sensorimotor adaptation with ageing indicated that performance was dependent on working memory capacity and was most impaired when visual perturbations were salient or introduced abruptly (Anguera, Reuter-Lorenz, Willingham, & Seidler, 2010; Buch, Young, & Contreras-Vidal, 2003; Uresti-Cabrera, Diaz, Vaca-Palomares, & Fernandez-Ruiz, 2015). This was thought to indicate a dependency on explicit control strategies, and the combination of reduced cognitive resources and a greater recruitment of their associated brain regions (Figure 1.2; see Section 1.2.2 for detailed review) limiting performance with old age. Considering we found no differences in adaptive performance between older and younger adults in Chapter 6, we suggested that dependence on explicit control strategies for our novel field adaptation task may be lower than for visuomotor adaptation paradigms. This was further supported from previous work (Trewartha, Garcia, Wolpert, & Flanagan, 2014) which we replicated, where adaptation and SWM capacity were not associated, despite age-dependent increases in search errors on the SWM task. Likewise, we saw no performance benefits of including visual feedback of the perturbation, which suggests little involvement of a visual, explicit component of learning in this sensorimotor paradigm, and greater reliance on a separate implicit, proprioceptive mechanism instead (Hwang, Smith, & Shadmehr, 2006). We concluded that the reduced dependence on explicit control strategies in this task meant performance remained unimpaired with ageing. Moreover, these findings offer further indirect support to the idea that impaired explicit movement control is the predominant cause of poor adaptation in advanced age (Seidler et al., 2010).

Based on the argument that these tasks have greater reliance on proprioceptive-dependent, implicit learning processes, it might be expected that there would be a strong relationship between extent of adaptation and proprioceptive acuity, yet we did not find evidence to support this. However, whilst this might be true in populations where proprioceptive acuity is significantly impaired, the level of sensory loss we measured in the participant sample from Chapter 6 – and other chapters – may not be sufficient to provide a measurable impact on performance (see Section 7.2 for comments on diminished ageing effects on proprioceptive acuity in this thesis). Furthermore, the process of updating forward models of motor commands in adaptive movement control has multiple dependencies (Bastian, 2008; Wolpert, Diedrichsen, & Flanagan, 2011) which may also explain some of the variance in our performance of data. But perhaps more critically, it appears that exposure to a sensory prediction error alone, either through direct experience or via observation, is all that is necessary to drive adaptation, with online movement corrections made in response to perturbations appearing to play a lesser role (Mattar & Gribble, 2005; Tseng, Diedrichsen, Krakauer, Shadmehr, & Bastian, 2007). This suggests that sensorimotor adaptation is based on use of accumulated sensory feedback in an offline, trial-by-trial manner with little involvement of online proprioceptive feedback for movement control, similar to the task used in Chapter 3. Therefore, creating a task specifically dependent on online sensory feedback based motor control may help to elucidate more clearly the relationship of proprioception and movement in ageing.

With this in mind, greater attention to motor control tasks in which there is no discrete goal or target and also involve slower, repeated movements may be an interesting line of research to investigate. This follows from early work proposing that forward models contribute to motor control during short duration movements (around 1 second) as a predictive, feedforward mechanism, with a shift towards increased reliance on online proprioceptive feedback as the movement duration increased (Wolpert et al., 1995). Although there are previous reports of age effects in performance of continuous point-to-point movements (Contreras-Vidal, Teulings, & Stelmach, 1998; Lee, Fradet, Ketcham, & Dounskaia, 2007; Yan, Thomas, & Stelmach, 1998; Yan, Thomas, Stelmach, & Thomas, 2000), these likely involve discrete target-based control mechanisms, similar to those used in the tasks throughout this thesis, which are distinct from mechanisms involved in more continuous, open-ended movement control (Schaal, Sternad, Osu, & Kawato, 2004). Instead, there may be benefit of using shape or position tracking tasks in which a continuous goal or target is pursued. This has been tested with sinusoidal tracking tasks, where OAs tend to have slower more varied movements (Ao, Song, & Tong, 2015; Jagacinski, Liao, & Fayyad, 1995), which is typical of age-related motor control. More recently, OAs have been shown to increase movement size and speed to a greater extent than YAs when visual feedback is removed in a continuous circular movement task (Levy-Tzedek, 2017). This was thought to be consistent with a mechanism to enhance proprioceptive signals for motor control due to age-related sensory decline and as such, suggests these types of movement tasks may be best suited to examine a relationship with dynamic proprioceptive acuity in ageing.

7.5 – Conclusions

In this thesis we have presented data to suggest that dynamic, upper limb proprioceptive acuity does not contribute to either ballistic or adaptive motor performance in advanced age. Based on previous reports we predicted there to be a strong effect of increasing age on proprioceptive loss, yet we did not observe this with our novel dynamic task. Since this task addresses age-specific limitations in previous methodology, we suggest our data gives a truer representation of the level of proprioceptive impairment which occurs in advanced age, and the manner in which it contributes to normal voluntary movement. When we did capture the effects of ageing on proprioception, it was with respect to increased systematic proprioceptive errors, contrary to previous reports. Furthermore, it was most prominent in our experiments with larger sample sizes or more sensitive measures of PA, and it is PA rather than age which appears to be the stronger predictor of systematic proprioceptive errors. Although we speculate about the basis of these effects on proprioceptive bias, concluding its exact cause is beyond the scope of this thesis and we suggest it should therefore be the focus of future research.

In addition to these observations, we saw stereotypical effects of ageing on fast, discrete reaching movements and we replicated findings of preserved motor adaptation to novel field dynamics in older age. We suggest this may highlight a reduced dependence on explicit motor control strategies for these tasks, which means the loss of cognitive resources with ageing does not confound performance as it does with explicit adaptation to visual perturbations. However, proprioceptive acuity was not related to performance in either of these tasks. Since we conclude that the extent of online proprioceptive control may not be high in ballistic and adaptive motor tasks, a final line of investigation for future research on this topic may be to study longer, continuous movements which are less reliant on predictive feedforward control mechanisms. Ultimately, this will help to fully conclude the extent to which dynamic proprioceptive acuity influences upper limb motor control across the lifespan.

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