AGE-RELATED DIFFERENCES IN POSTURAL ADJUSTMENTS DURING LIMB MOVEMENT AND MOTOR IMAGERY IN YOUNG AND OLDER ADULTS

A KINEMATIC ANALYSIS

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Copyright Statement

Abstract

Motor imagery (MI) shares many of the neurophysiological and behavioural characteristics associated with physical movements, and motor imagery training has been shown to be effective at improving subsequent performance on a given motor task. Jeannerod (2006) proposed that imagined movements are covert internal simulations of the physical counterpart. MI, therefore, provides an ideal setting for studying the anticipatory aspects of posture control.

Recent research has shown that systematic postural adjustments occur during periods of MI in young adults, although the timing and direction of these postural adjustments, relative to individual physical actions or imagery of these actions, is not well understood. Additionally, further research has demonstrated that in an older, aged population, MI fails to induce the same postural response seen in their younger counterparts. Older people exhibited relatively restricted postural sway during periods of imagined reaching movements, whereas young adults increased sway whilst performing the same imagined movements.

This thesis utilises kinematic measures to study anticipatory and compensatory postural motion in the temporal vicinity of physical and imagined forward arm raises. Healthy young and older adult participants performed, or imagined performing, unilateral and bilateral arm raises under self-initiated and externally triggered conditions.

Under bilateral arm raises, when MI was self-initiated, both age groups showed significant forward postural motion during the 1000 ms immediately prior to MI initiation. However, when MI was externally triggered, older participants did not show anticipatory postural motion (APM), whereas this was maintained in the younger participants.

When MI of the dominant arm was self-initiated neither age group showed significant APM in the anteroposterior plane. When MI was externally triggered, older participants did not show APM, whereas the younger participants did. Older participants did show movement in the mediolateral direction in

both externally and self-initiated conditions indicating sensitivity to the weaker, non-dominant side of the body.

Finally, when MI of the non-dominant arm was self-initiated, older participants alone showed forward anteroposterior APM. However, when the same MI movement was externally triggered, there was again no APM observed.

Taken together these data demonstrate that MI is accompanied by APM and suggests that older adults are capable of and sensitive to postural motion planning. However, these data show that the use of APM is disrupted when the timing or onset of the task is not under their own control, and as such they may be particularly vulnerable to unpredictable environmental changes such as those that occur in fall situations. Unlike compensatory postural control, which relies on sensory feedback, the anticipatory component of postural control relies on forward motor planning, and as such these findings suggest that forward motor planning is disrupted by a decreasing ability to predict forthcoming events or a decrease in the ability to correctly judge the required postural change for balance.

As systematic APM was observed for self-initiated MI, this suggests that MI training may be an effective intervention for anticipatory postural control, strengthening corresponding neural networks and improving the ability to anticipate necessary posture changes. Additionally, these may be used to identify weak postural positions and pre-plan balancing strategies in later age.

Declaration

This thesis comprises the candidate's own work and has not been submitted to this or any other University for a degree. All aspects of the thesis were completed by the candidate.

Publications

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List of Abbreviations

ANS	Autonomic Nervous System
AP	Anteroposterior
APA	Anticipatory Postural Adjustment
APM	Anticipatory Postural Motion
CNS	Central Nervous System
COP	Center of Pressure
CPA	Compensatory Postural Adjustment
CPM	Compensatory Postural Motion
EMG	Electromyography
ET	Externally Triggered
MI	Motor Imagery
ML	Mediolateral
SI	Self-Initiated

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CHAPTER 1: Introduction

The safe and effective performance of everyday activities is critically dependant on the individual's ability to maintain standing balance. The postural control system maintains upright stance through the coordination of sensorimotor strategies and muscle synergies to ensure the body's centre of gravity (CG) is kept inside the base of support. Posture control is also critical in aiding in the performance of voluntary movements. Ricco and Stoffregen (1988) argued that the main concern in stance control is the goal of the individual's behaviour, and that posture control also aids in the coordination of the limbs. However, limb movement in upright humans is inherently perturbing and is therefore accompanied by concurrent postural control functions that prepare for and counteract the resulting perturbation to stance (Massion 1992).

This thesis examines the role of posture control in support of voluntary reaching movements and imagery of the arms. The reported empirical work measures and analyses anteroposterior (Chapters 2,3,4) and mediolateral (Chapters 3, 4) postural motion just preceding and following the onset of raising movements of both (Chapter 2) or either arm (Chapters 3, 4). The project's main goals are to investigate (1) whether anticipatory postural motion occurs immediately preceding imagery of arm movements, (2) the effects of ageing on this postural anticipation, and (3) the effects of self-initiated or environmentally controlled movement or imagery onset on the occurrence of anticipatory postural motion in young and older participants. In the following, I first introduce research on anticipatory and compensatory postural adjustments, and the effects of ageing. I then review the literature on motor imagery, its similarity movement execution, and the effects of ageing on imagery. I then introduce the issue of postural anticipation and control over movement (or imagery) initiation. This chapter ends with a brief overview of the experimental work conducted in this project, and the goals the work have sought to achieve.

Anticipatory Postural Adjustments

Early studies on raising the arm while standing showed that leg muscles involved in postural control are the first to be activated 40 to 60ms prior to the prime mover (Belen'kii et al. 1967), and a backward bending of the trunk compensates for a forward motion of the CG caused by forward arm movement (Martin 1967). Bouisset and Zattara's work (1987a, b; 1988) on uni- and bilateral arm raises demonstrated that anticipatory postural adjustments (APA) act in the direction opposite to the reaction forces generated by the arm movement. It was proposed that the central nervous system (CNS) generates APAs prior to an expected perturbation (such as that produced by voluntary limb movement). These changes reflect pre-emptive action to neutralise the destabilising effects of the arm movement.

Cordo and Nashner (1982) showed that forward body sway that would result from a handle pull is counteracted by anticipatory gastrocnemius muscle activity producing backward sway. The higher likelihood of observing APAs prior to fast (Lee et al., 1987) but not slow (Crenna et al. 1987; Horak et al. 1984, 1989) focal movements suggested that the purpose of APAs might be to protect the body's balance from being disrupted by the perturbation caused by limb motion. Thus, a key goal of APAs may be to regulate the CG (Bouisset and Zattara 1981, 1987b, 1988, 1990; Friedli et al. 1988; Ramos and Stark 1990) or its projection on the ground (Mouchnino et al. 1990; Rogers and Pai 1990).

More recently, Bleuse et al. (2006) observed that the counter-clockwise (viewed from above) vertical torque generated by raising the right arm from standing position is counteracted by an anticipatory clockwise torque. They suggested that this APA was produced to assist the arm movement by stabilizing the joints affected by it. The role of APAs in facilitating voluntary limb movements had also been suggested earlier by Lee et al. (1990) in the context of manual pulling movements. Based on the evidence that the duration of APAs increases with the load raised by the arm (Bouisset and Zattara 1988; Brown and Frank 1987; Zattara and Bouisset 1986), they suggested that APAs may provide additional force to focal movements, and therefore should be considered an integral aspect of voluntary movement control. In this respect, there is also evidence that APAs can contribute to movement initiation in the case of large forward movements of the body (Stapley et al. 1998).

The specificity of APA with respect to the associated focal movement suggests that the planning of both is functionally linked (Massion 1992). However, the adaptability of their relative timing also raises the possibility that APA production is a separate process from the control of focal limb movements (Brown and Frank 1987; Cordo and Nashner 1982). The close coordination between APAs and associated focal movements (e.g., APAs can be affected independently by the magnitude of perturbation and the magnitude of action triggering the perturbation) has suggested to some researchers that APAs should be considered integral aspects of focal movement planning (Aruin and Latash 1995, 1996).

The finding that APAs can occur even when there is no focal movement (but a perturbation is predictable) suggests that APAs and corresponding focal movements are planned and controlled through two parallel processes of central origin (Aruin et al. 2001; Massion 1992).

Compensatory Postural Adjustments

Compensatory postural adjustments (CPA) occur post perturbation onset. In contrast to APAs which operate in a feedforward manner and serve to counteract the predicted perturbation, CPAs rely on sensory feedback signals to reorganise posture post perturbation onset. When preceded by a strong APA, CPAs are minimised. Conversely, when an APA is not generated, such as in response to an unexpected perturbation, the CNS utilises CPAs to restore balance (Santos et al. 2010b; Santos et al. 2010a).

Three different balance recovery strategies have been identified in the literature: an ankle strategy, hip strategy and stepping strategy. These strategies are dependent on the postural context and age.

When utilising an ankle strategy, people sway as a flexible inverted pendulum, where posture is stabilised using torque produced at the ankle, with little hip or knee movement. Horak and Nashner (1986) showed that an ankle strategy was predominately utilised to restore balance. In an open stance (feet side-by-side) situation the ankle strategy produces AP sway, whereas ML sway increases as the stance narrows (Gatev et al., 1999) increasing the risk of a fall for older adults.

For the hip strategy, sway is observed as a 2-segment inverted pendulum, with this strategy generating movement of the trunk around the hip joint and generating force on the support surface but with little ankle torque. The hip strategy predominantly produces ML sway (Winter et al., 1996) and so when responding to a larger, faster displacement of support, the primary action to retain balance, in most people, occurs at the hip (Nashner & McCollum, 1985). In situations with a narrower base of support, a further increase in ML sway is observed (Gatev et al., 1999), additionally Horak and Nashner (1986) found that when the length of a support surface was shorter than foot length, the involvement of the hip becomes more pronounced.

When neither of these strategies will suffice, a stepping strategy is typically utilised. By taking a step, the base of support is extended to keep the body’s centre of mass within the support boundaries (Shumway-Cook & Woollacott, 2012). Historically, a stepping action to maintain balance has been considered a strategy of last resort, however, McIlroy and Maki (1993) observed stepping to recover balance was more frequent in participants who were not instructed to keep their feet in place. This suggests that stepping may not be as common as an ankle or hip strategy but is still a commonly used balance strategy none the less.

Ageing and posture control

The literature on APAs preceding physical arm movements has also found important age-related differences. APA preceding self-initiated body perturbations occurs later in older adults (Inglin and Woollacott 1988; Man'kovskii et al. 1980; Rogers et al. 1992), even when the velocities of the focal movements between young and old adults are not significantly different (Woollacott and Manchester 1993). This delay in the onset of APA is thought to necessitate larger compensatory postural activity during focal movements in older adults (Kanekar and Aruin 2014a).

Analysing electromyographic (EMG) activity and centre of pressure (COP), Lee et al. (2015) measured APAs in young and older participants while pushing an object with both hands. They observed delayed anticipatory muscle onset times and delayed COP displacements in older adults, suggesting that older adults show less efficient postural control.

Research has shown that APAs associated with postural control (e.g., displacement of centre of pressure and centre of mass) also occurs later in older adults relative to their younger counterparts. Bleuse et al. (2006) observed APAs during unilateral arm raising in young and older adults. APAs were measured using vertical torque alongside COP displacement and electromyography (EMG). They observed reduced APA durations in older adults during arm movements performed at maximum speed. However, at slow speeds, older adults showed no impairments in APA production compared to younger participants. However, electrical activity occurred earlier than in the Lee et al. study (148ms in older and 256ms in young adults). For Bleuse et al. COP displacement occurred at 148ms in older participants and 256ms in younger participants. This was later than in the Lee et al. experiment, with displacements occurring at 253ms and 322ms for older and younger participants respectively.

Woollacott and Manchester (1993) suggested that inconsistent findings of age-related differences in APA duration may be related to the mechanical characteristics of the movement. When the task involved generating force with the arm against a support, older adults required longer time to generate the forces for postural stabilisation. However, when free standing participants performed arm movements without contact with a support, APA duration was shorter, with this shortened duration appearing across both older and younger adults. Despite these differences, the findings that APAs occur later in older adults is a consistent finding across multiple movements and experimental protocols.

Different compensatory adjustments become preferable as individuals get older. Older adults are more likely to prefer a hip strategy when a perturbation is small and a stepping strategy is not needed. Horak et al. (1989) suggested that an altered internal representation of stability limits leads older adults to use inappropriate hip strategy for correcting balance even when the postural perturbation is small and can be corrected with ankle strategy.

Older adults are also more likely to utilise a stepping strategy to recover balance compared to younger adults, and this is especially the case for older adults with balance problems (Schulz et al., 2005; McIlroy & Maki., 1993). Blaszczyk et al. (2000) suggested asymmetrical limb loading acts as a compensatory postural response to a destabilising situation, and that it is a functional asymmetry in that it shortens the time required for older adults to take a stabilising step should they need to (Rogers & Mille, 2004; Lord et al., 1999). Research has also demonstrated that age related bilateral asymmetries in postural sway and weight distribution occur (Prieto et al., 1993). Using the dual force plate balance platform, Prieto et al showed that in two elderly subjects the body weight was asymmetrically distributed between limbs.

However, these postural strategies can become a problem for older adults as increasing asymmetry can lead to an increasing in postural motion in the mediolateral (ML) direction. It is well known that ageing particularly affects ML postural stability (Brauer et al. 2000; Maki et al. 1994) and the ability to counteract perturbations in the ML direction (Claudino et al 2013; Santos et al. 2016). As older adults spend more time in/rely more on ML posture control, lateral falls grow increasingly likely. Falls in this direction are particularly devastating as they are the most likely to result in a hip fracture (Maki et al., 1996; Nevitt et al., 1993).

Motor imagery

The act of mentally simulating a movement is referred to as motor imagery (MI). MI is defined as a dynamic mental state during which the representation of a movement is rehearsed in working memory without the individual engaging in the corresponding physical action (Decety, 1996; Moran & O'shea, 2020). It is a key feature of human cognitive and allows the individual to predict the consequences of a movement and infer the intentions of actions made by others.

The Simulation Hypothesis

The simulation hypothesis, as put forward by Jeannerod (1994; 2006), suggests that non-physical, imagined movements are in fact covert replicated simulations of the corresponding physical movement being imagined, therefore suggesting that both physical and imagined movements share common neurocognitive mechanisms, and as such common motor rules that govern physical execution are also illustrated and present in imagined movement. This common pathway activation may therefore account for the similarities observed between imagined and physical movement. However, the lack of corresponding physical movement despite similar cortical activation suggests that a downstream inhibitory mechanism is activated to prevent subsequent movement. According to Jeannerod (2006), this proposed inhibitory mechanism is dependent on an early efference copy of motor commands that originate within the motor cortex, and it is a further downstream suppression of motor movement within the brainstem or spinal cord that suppresses the intended physical movement from occurring.

One of the core components of the simulation hypothesis is the concept of internal models. Internal models were first detailed to account for physical movements and how sensorimotor loops are regulated and modelled by the CNS (Wolpert & Ghahramani, 2000). Both inverse and forward models are proposed, representing the generation of motor commands specific to the current context, intention and capability of an individual (inverse model), and involved in anticipation of future physical states relative to returning sensory feedback (forward model). It appears that during imagined movement, these same internal models present in physical movement are activated, suggesting that regardless of movement or mode of execution, the inherent planning of a movement whether physical or not, remains the same. Given the presence of common cognitive pathway activation between imagined and physical movements, it suggests a strong basis for how covert mental rehearsal of movements may subsequently improve physical task performance (Jeannerod, 2006).

Whilst covert simulations of motor function are present in MI tasks, they are not unique to this context. In order to develop a goal directed action, both in terms of viability and preparatory action, a covert stage of motor preparation may occur prior to physically executing the motor task. This suggests that MI may provide comparable covert mechanisms that are either consciously prepared (MI) or unconsciously prepared (physical movement). Therefore, the study of motor imagery may also pertain to, and provide insight into, the processes and development of motor preparation (Jeannerod, 1994). Indeed, conscious or unconscious covert simulations may also occur when viewing the actions of another, particularly in the context of learning, where replication of the action is ultimately the desired outcome, though this may also simply aid in understanding the intention and function of the performed action. A relative comparison between covert rehearsal of the action with internally stored motor commands may provide comparative insight into both the physical implementation of the action and the corresponding necessity for that movement type. Given that the mirror neuron system is activated both during execution and observation of movement, it is thought this neuronal population is important to the simulation process (Jeannerod, 2006).

Similarities with physical movement

Behavioural similarities

Imagined movements exhibit many behavioural characteristics similar to physical movement. Studies investigating the temporal congruence of physical and imagined movements have found isochrony between scaling of their movement time to distance (Decety et al. 1989; Papaxanthis et al. 2002; Sirigu et al. 1996). Decety et al. (1989) used a walking task to compare the time taken for participants to physically or mentally walk to targets at different locations. They found that participants took the same time to achieve the physical and mental task. Also, that in both the mental and physical condition walking time increase with distance covered.

Imagined movements also exhibit similar speed accuracy trade off as is the case with physical movement (Decety & Jeannerod, 1995; Sirigu et al., 1996). Cerritelli et al. (2000) found that both physical and imagined movement times increased as target size decreased in a visually guided pointing task. The incorporation of such trade-offs during MI implies imagined and physical movements are governed by the same programming rules (Jeannerod, 2006). Together this data suggests that physical and imagined movements operates of similar neurocognitive mechanisms.

Imagined movements also appear to avoid impossible or uncomfortable trajectories to reach a final limb position (Frak, Paulignan, & Jeannerod, 2001; Johnson, 2000). Movement trajectories appear to be organised to minimise the discomfort of the final posture of the limb. For example, Rosenbaum et al. (2004) found the final position of a hand movement must be made prior to the initiation of the action, where the action is presented and prepared. Frak et al. (2001) developed this. Participants were shown an object, such as a cup, in different orientations. Some orientations offered an easy grasp of the of the object, and others an awkward one. They found that time taken to respond whether the grasp was easy or difficult was a function of the orientation of the object and that the time taken to make this estimate was similar to the time taken to physically reach and grasp the object when in the same rotation. This suggests that participants simulated the movement of the hand into a appropriate position before they could make the response. Suggesting that MI also incorporates the body’s current position in the simulation of the movement, rather than MI being an isolated process.

Neural substrates of imagined movements

MI also appears to share brain mechanisms for movement representation and execution (Bonnet et al. 1997; Clark et al. 2004; De Lange et al. 2006; Grèzes and Decety 2001; Orr et al. 2008). Neuroimaging studies have provided evidence that cortical (ventral and dorsal parts of the premotor cortex, as well as the supplementary motor area) and subcortical areas (such as the cerebellum and the basal ganglia are active during MI (e.g., Lotze & Halsband, 2006; Guillot et al., 2008; Munzert et al., 2009). The activation of these areas has been consistent across studies and methodologies, from minor movements involving the hand to whole body movements. The activation of these areas during imagery are specific motor imagery, and not visual imagery of non-anatomical objects (Kosslyn et al., 1998; Stevens et al., 2005).

Contribution of the primary motor cortex

While the role of the primary motor cortex is considered to be in the transmission of motor commands, its activation is not systematically observed in MI. Some researchers having not reported any activation of the primary motor cortex during MI (Gerardin et al., 2000; Hanakawa et al., 2008), whereas others have found moderate (Dechent et al., 2004) or even significant involvement (Lotze et al., 1999b; Porro et al., 2000; Solodkin et al., 2004; Guillot et al., 2008; Sharma et al., 2008). With Ehrsson et al. (2003) reporting the content of MI reflected in activation of the primary motor cortex, MI of hand foot and tongue movements activated their respective regions of the motor cortex. The differences observed across studies may be due to methodological differences such as different imaging techniques (Lotze & Zentgraf, 2010), as well as the complexity of the movement (Kuhtz-Buschbeck et al., 2003) and could be influenced by MI instructions, MI ability and motor expertise (Lotze & Zentgraf, 2010). Taken together, research suggests that the primary motor cortex is activated during MI but more weakly than during physical execution, though as imagery is able to be performed without activation of the primary motor cortex, such activation does not appear crucial for MI.

Activation of parietal areas

Activation of parietal areas, including the inferior and superior parietal lobules, as well as the precuneus, are frequently reported during MI (Gerardin et al., 2000; Hanakawa et al., 2003; Guillot et al., 2009; Munzert et al., 2009). Studies in patients with lesions in the superior parietal cortex showed the temporal congruence between physical movement times and MI times was affected (Malouin et al., 2004; Sabate et al., 2007; Sirigu et al., 1996). Sirigu et al. (1996) suggested the parietal cortex might set up an internal model of the forthcoming movement. Furthermore, Schwoebel et al. (2002) found that in bilateral parietal lesions patients expressed a complete unawareness of movement execution during MI. Taken together these studies support the role of the posterior parietal cortex in the generation and guidance of imagined movements.

Peripheral Activation in MI

The CNS generates the motor command, and the autonomic nervous system (ANS) provides the resources needed to execute it (Mogenson, 1977). However, motor actions require planning, and as this is the function of the CNS, motor preparation also needs the ANS to supply the resources necessary for its execution (Collet et al., 2013).

MI has also been found to elicit specific but attenuated EMG activity in muscles involved with performing the physical motor task (Guillot et al., 2009; Lebon et al., 2008), with a number of studies reporting muscular activation during periods of MI that are greater than when at rest, though the degree of activation is not as strong as observed with the physical counterpart (Bonnet et al., 1997; Guillot et al., 2007; Lebon et al., 2008). Guillot et al. (2007) recorded EMG activity both while participants lifted a dumb bell with the dominant arm, and also while they imagined lifting the dumb bell. They found that all nine muscles used for the physical movement, were active during the imagined movement. This shows that the effects of MI are observed at the peripheral level and are not limited to central processes.

However, muscular activity during MI tasks is not consistently seen across the literature. Multiple studies have reported no EMG activation during periods of MI (Hanakawa et al., 2003; Personnier et al., 2010). Collet et al. (2013) suggested that this may be due to methodological differences such as the placement of EMG sensors on the skin, as well as variation in the nature of the movement being imagined, effectively suggesting that a more intense MI task will result in a more detectable or stronger EMG signal in the corresponding muscles involved with the physical counterpart task. The presence of EMG during MI may suggest an incomplete inhibition of the motor command at the level of the CNS, however this does not necessarily discount the activation of muscle fibres during MI as an important component of improving performance on a given motor task (Collet et al., 2013).

Autonomic activation during MI

During physical actions motor preparation involves the ANS to provide resources that make the execution of the movement possible. A few examples are electrodermal activity, heart rate and respiration. Research has shown that such preparatory responses escape inhibition during periods of imagined movements (Decety et al., 1991; Beyer et al., 1990; Bolliet et al., 2005).

Previous research has reported increased heart and respiration rates in participants as they started a MI task session, demonstrated through a significant decrease in participants skin resistance (Oishi and Maeshima, 2004). Similarly, heart and respiration rate were found to not only increase during MI tasks, but also increase proportional to the mental intensity or effort of the imagery task (Wuyam et al., 1995). This evidence further underlies the close relationship between movement preparation and motor imagery.

Inhibition of overt movement

These results suggest that MI involves detailed and specific motor planning (and even some preparatory aspects of motor execution), but no limb motion occurs because an inhibition process of brain stem or spinal origin blocks the focal movement (Collet & Guillot 2009; Jeannerod 2006), before being sent to peripheral effectors.

However, there is also research that speculates inhibition may occur centrally, specifically within the fronto-parietal network. Pathological evidence occurs in a case study of CW, a patient suffering from bilateral parietal damage, wherein CW was asked to imagine performing hand movements and subsequently performed the physical hand movements unknowingly (Schwoebel, Boronat, and Branch Coslett., 2002). This work is further supported by evidence from Brass, Zysset, and von Cramon (2001) who demonstrated that during inhibition of the overt task movement, central activity was measured within the dorsolateral prefrontal cortex, right anterior parietal cortex and precuneus. Despite this evidence an early and centrally mediated inhibitory mechanism is not supported by the presence of increased corticospinal activity during MI (Guillot et al., 2010; Jeannerod, 2006).

If such inhibition exists, it must be incomplete in the sense that it does not block autonomic arousal, EMG activity (Collet et al. 2013; Guillot et al., 2012) or the postural adjustments that arise with motor planning (de Souza et al., 2015).

Posture control during MI

The posture control system is functionally linked to the performance of movement, with adjustments taking place prior to (APAs) and during execution itself (CPAs). The occurrence of postural adjustments has also been studied in the context of motor imagery of limb movements (Boulton and Mitra 2013, 2015; Grangeon et al. 2011; Rodrigues et al. 2010).

Boulton and Mitra (2013) found that participants postural sway while standing upright differed depending on the direction of imagined arm movements. Participants generated greater AP sway during MI of arm movements in the AP direction, and greater ML sway during MI of arm movements in the ML direction. Indicating that imagining goal-directed arm movements elicits postural sway linked to task performance.

In a later study, Boulton and Mitra (2015) observed the possibility that the control of postural sway during MI is of central origin. Participants were asked to imagine wearing a load on the wrist when imagining movement. This imagined loading of the arm was a purely top-down MI task constraint (I.e. the arm was not loaded during MI) but postural adjustments were still observed in response the this task. This indicates that postural adjustments that escape inhibition during MI are of cortical rather than spinal origin.

Boulton and Mitra’s (2013, 2015) studies focused on demonstrating that MI was a cognitive task that could interfere with posture control because of the two tasks’ functional linkage resulting from the characteristics of MI noted earlier (Mitra et al. 2013; Stoffregen et al. 2007). As such, they focused on measuring postural sway during periods of imagined movements under specific MI and postural task conditions. This design allowed them to observe that MI-linked postural sway occurred, but it did not enable identification of the nature or direction of postural motion in the temporal vicinity of individual instances of imagined reaching movements of the arm. Grangeon et al. (2011) suggested that the postural movement observed during MI could indicate unsuppressed APAs.

Boulton and Mitra (2013) considered both the possibility that their participants made APAs (and that these were larger when the imagined movements were expected to have a greater destabilizing effect on stance), and the possibility that postural motion was arranged to assist the reaching arm movements being imagined.

Motor imagery in ageing

Research into motor imagery and ageing have reported that older adults show inconsistencies in the temporal similarities between overt and covert motor actions, such that the length of time taken to complete the MI task often varies significantly from the time taken to complete the corresponding physical action.

In the case of sit-to-stand movements (timed up-and-go), older people report faster times during MI relative to observed time during physical execution (Bridenbaugh et al., 2013). Similarly, in the case of unconstrained walking, despite an increase in the time taken for older people to physically execute the task over longer distances (>20m), movement time during MI fails to increase proportionally (Schott & Munzert, 2007), whereas under conditions of spatial constraint (e.g., a narrow walkway), older people have been shown to overestimate walking time during MI relative to their physical execution time (Personnier et al., 2010).

This research suggests an age-related loss of timing between the feedforward aspect of motor planning that is captured in MI and the combination of feedforward and feedback processes that occur during physical movement execution. This was also reported by Mitra et al. (2016), who studied younger and older adults postural sway during a pointing task. This study found that older participants were slower during the physical task than younger participants, but this difference was not observed in imagined movements and older adults were comparable in their timing to younger adults, suggesting that older adults failed to reflect their motor slowing, as an aspect of ageing, in internal planning during imagery.

Mitra et al. also reported that while younger participants sway increased relative to their baseline, older participants restricted postural sway during MI, a pattern that also occurred during physical movement of the same task. One possibility is that this was a bracing action against an expected postural destabilization due to the planned arm movement, suggesting a conscious or unconscious decrease in physical confidence through aging.

Thinking about physically executing an action has the potential to interfere with concurrent postural control, and this is exacerbated in older adults as ageing brings with it a decline in the efficiency of motor planning (Haaland et al., 1993; Ketcham & Stelmach, 2001; Trewartha et al., 2009), along with the decline of other executive functions, such as working memory, that makes imagery less efficient (Maylor et al., 2007; Raz et al., 1999).

Self-initiated and externally triggered movements in MI

Boulton and Mitra's (2013, 2015) and Mitra et al.'s (2016) experiments triggered physical and imagined reaching movements with an external signal. Their participants' instructions were always to follow the 'go' signal immediately. The literature on APA preceding physical movements was initially thought to suggest that APA occurs only when a voluntary action generates a postural perturbation (Aruin and Latash 1995; Bennis et al. 1996; Dufosse et al. 1985; Johansson & Westling 1988; Massion 1992; Paulignan et al. 1989; Struppler et al. 1993), but Shiratori and Latash (2001) showed that APA can occur in the absence of voluntary limb motion when predictable perturbations are delivered externally. The issue of APA in the context of perturbations initiated by limb motion or an external perturbation is not the same as APA in the context of voluntary limb movements that start at a self-chosen time or are triggered by an environmental cue. However, initiating a movement in response to an expected environmental trigger, but with unpredictable timing, requires a motor plan to be held suspended until externally released, and the results of this process may differ from self-initiated action that does not require coordination with an unpredictable external trigger.

The present project

The purpose of the present project was to investigate patterns of postural motion that occur immediately preceding and following the onset of arm movements. Previous research on postural support for voluntary movements has used the arm raising task (e.g. Bleuse et al., 2006) as it is a simple action that delivers a perturbation to the body in the direction opposite to arm movement and produces a backward shift in COP. In this project, I used the arm raising task to investigate the postural motion that occurs when the arm raises to the front of the body are either executed or imagined. Boulton and Mitra's (2013, 2015) had demonstrated that motor imagery (MI) of reaching arm movements were accompanied by postural actions that appear to counteract the perturbation the imagined movement would cause if executed. However, that work analysed postural motion during periods of manual MI, which did not allow separate investigation of the anticipatory and compensatory postural movement that might occur on either side of arm movement or MI onset.

The first goal of this project was to use the arm raising task to establish whether anticipatory postural motion occurs in advance of MI even though no mechanical perturbation to body posture is impending. The second goal was to document any differences in postural action, particularly anticipatory postural action, between young and older adults in the context of MI. The interest in this age difference, introduced in more detail in the introductions to the empirical chapters, derives from the expectation that MI is a useful context for studying the planning of movements and their postural support. The third goal of the project was to investigate ageing effects associated with the contrast between arm movement (or MI) that are self-initiated at a time of the actor's own choosing, and the occasions when the movement or MI onset is dictated by an environmental event of uncertain timing. It has been noted in the anticipatory postural adjustment literature that these adjustments are most reliably observed in the context of self-initiated movements. That literature contrasts self-initiated movements with unpredictable external perturbations. The case of an expected perturbation that is uncertain only with respect to its timing has not been investigated. This case is important with respect to the effects of ageing, which introduces deficits in sensorimotor integration (Yordanova, 2004) that may challenge the ability to initiate postural support for a movement whose onset is unpredictable.

The experimental work of the project is presented in three chapters. Chapter 2 studies the case of bilateral arm raises and focuses on anteroposterior (AP) postural motion before and after movement (or

MI) onset. Chapters 2 and 3 study unilateral arm raises of the dominant and non-dominant arm, respectively, and analyse AP and mediolateral (ML) postural motion in the temporal vicinity of movement or MI onset. Throughout the reported work, the arm raises studied are to the front of the body. Note that the project plan originally included two further chapters studying unilateral arm raises to the side of the body, which produce a more direct form of mediolateral postural perturbation than unilateral arm raises to the front of the body. This work would have been particularly important with respect to the effects of ageing, given that ageing is particularly associated with postural instability in the ML axis (Brauer et al., 2000; Maki et al., 1994). Unfortunately, the laboratory closures due to the pandemic in 2020-21 made it impossible to conduct those final studies. Finally, Chapter 5 synthesises the results obtained in the project and points to future directions in this research.

Aim 1: Determine a foundational baseline response in postural control with minimal perturbation of posture both in physical and imagined movement, compared between young and old participants.

- **Objective 1**: Validate age differences of similarities in postural control with simple bi-lateral arm arises.
- **Objective 2**: Assess postural control that occurs under motor imagery of bilateral arm raises.

Aim 2: Establish what perturbations of posture occur in young and old participants both physically raising the dominant arm and doing so under MI conditions.

- **Objective 1**: Determine if a unilateral raise of the dominant arm aggravates age dependent differences between young and old participants.
- **Objective 2**: Establish if postural adjustments both before (APA) and after (CPA) MI of the same movement produces comparable postural sway.

Aim 3: Further progress there difficult of the perturbation with nondominant arm raises both physically and as an MI task.

- **Objective 1**: To determine if postural control strategies are conversed between dominant and nondominant arm raises.
- **Objective 2**: Assess if differences between young and old participants postural control is further perturbed by nondominant arm movement or age does not excessively decline nondominant control over dominant control.

Aim 4: Use the data, under progressive posture perturbation, to establish a comprehensive baseline of segmental posture differences and to develop a modified model of posture and movement control (see Mason, 1992)

[1]CHAPTER 2: Physical and imagined bilateral arm raises and posture in young and older adults

INTRODUCTION

Boulton and Mitra’s (2013, 2015) studies focused on demonstrating that MI is a cognitive task that can interfere with posture control because of the two tasks’ functional linkage resulting from the characteristics of MI noted earlier (Mitra et al. 2013; Stoffregen et al., 2007). As such, they focused on measuring postural sway during periods of imagined movements under specific MI and postural task conditions. This design allowed them to observe that MI-linked postural sway occurred, but it did not enable identification of the nature or direction of postural motion in the temporal vicinity of individual instances of imagined reaching movements of the arm. Grangeon et al. (2011) suggested that postural movement during MI could indicate unsuppressed APAs. Echoing the possible dual function of APAs outlined earlier, Boulton and Mitra (2013) considered both the possibility that their participants made APAs (and that these were larger when the imagined movements were expected to have a greater destabilizing effect on stance), and the possibility that postural motion was arranged to assist the reaching arm movements being imagined. The postural stabilization possibility was further supported when Mitra et al. (2016) found that older people restricted postural sway (even relative to quiet standing) where young people increased sway during MI of manual reaching movements. They interpreted this age-related reversal of response to MI as indicating a postural threat response.

The literature on APA preceding physical arm movements has also found important age-related differences. APA preceding self-initiated body perturbations occurs later in older adults (Inglin &

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[1] The experiment described in this chapter has been reported in full in Wider, C., Mitra, S., Andrews, M., & Boulton, H. (2020). Age-related differences in postural adjustments during limb movement and motor imagery in young and older adults. Experimental Brain Research, 238, 771-787.

Woollacott, 1988; Man'kovskii et al., 1980; Rogers et al., 1992), even when the velocities of the focal movements are not different between young and older adults (Woollacott & Manchester, 1993). This delay in the onset of APA is thought to necessitate larger compensatory postural activity during focal movements in older adults (Kanekar & Aruin, 2014a). Although most studies on age-related differences in APA onset have analysed muscle activity, research has also shown that body motion associated with postural control (e.g., displacement of centre of pressure and centre of mass; (Kanekar & Aruin, 2014b) also occurs relatively later in older adults (Bleuse et al. 2006; Lee et al. 2015).

The experiment described in this chapter investigated the postural motion of standing young (Y) and older (O) participants' head and hip in the 1000ms preceding and following the onset of physical and imagined forward arm raising movements (Fig. 1). When postural motion seeks to minimize destabilisation of the CG during the arm's extension forward and up, we would expect to see either the backward motion of the upper and lower body (Fig. 1b), or the backward motion of the upper body only (Fig. 1d), corresponding, respectively, to the ankle and hip strategies (Nashner & McCollum, 1985), or a mixture of the two. If this compensatory postural motion (CPM) moves the body backward, while the arm moves forward, any anticipatory postural motion (APM) preceding the onset of arm motion might be expected to take the body forward (Fig. 1a, c) (Bleuse et al. 2006; Bouisett & Zattara 1987a, b, 1988; Cordo & Nashner 1982). If this is the pattern we observe in the case of physical arm movement, an analogous forward motion of the body preceding imagined raising of the arm will point to APA accompanying MI. This experiment is limited to a kinematic approach as the question of the nature of postural activity during MI arose in the context of kinematic studies (Boulton and Mitra 2013, 2015; Mitra et al. 2016).

In task conditions where the arm raise is imagined, a mechanical postural perturbation (as a result of the planned focal movement) does not in fact occur. Rodrigues et al. (2010) suggested that a mismatch between movement representations evoked by imagery and the subsequent absence of actual peripheral motor activity might have been responsible for the increase in postural sway they had observed in standing participants imagining plantar flexion movements. I predicted, therefore, that if MI elicits

APM (i.e., forward body motion), reactive CPM should occur in the opposite (i.e., backward) direction in the post MI-onset period. Based on Mitra et al. (2016) finding of postural sway restriction in older adults during MI, I predicted that O would show reduced levels of postural motion relative to Y.

The present experiment also tested for age-related differences based on whether the physical or imagined arm movement was triggered by an external event (ET), such as a ‘go’ signal, or initiated at a time of their own choosing by the participants themselves (SI). In experiments reported in Boulton and Mitra (2013, 2015) or Mitra et al. (2016), manual movement (or imagery) was always triggered by an external signal. In all cases, the participants’ instruction was to follow the signal with immediate movement. The APA literature was originally taken to suggest that APAs occur only when a perturbation is produced by a voluntary action (Aruin & Latash, 1995; Bennis et al., 1996; Dufosse et al., 1985; Massion, 1992; Paulignan et al., 1989; Struppler et al., 1993). However, Shiratori and Latash (2001) found that APA can also occur without voluntary limb motion when an externally delivered perturbation is predicted. The question of APA when perturbations are generated by limb motion or externally is different from the question of self-selected movement start time compared to an externally dictated start. However, starting a movement in response to an expected externally trigger of uncertain timing requires a motor plan to be held suspended until it is externally released. The results of this may differ from a process of self-initiated action that does not require coordination with an unpredictable external trigger. To allow the detection of any age-related differences sensitive to this contrast, I carried out the present study under both ET and SI conditions.

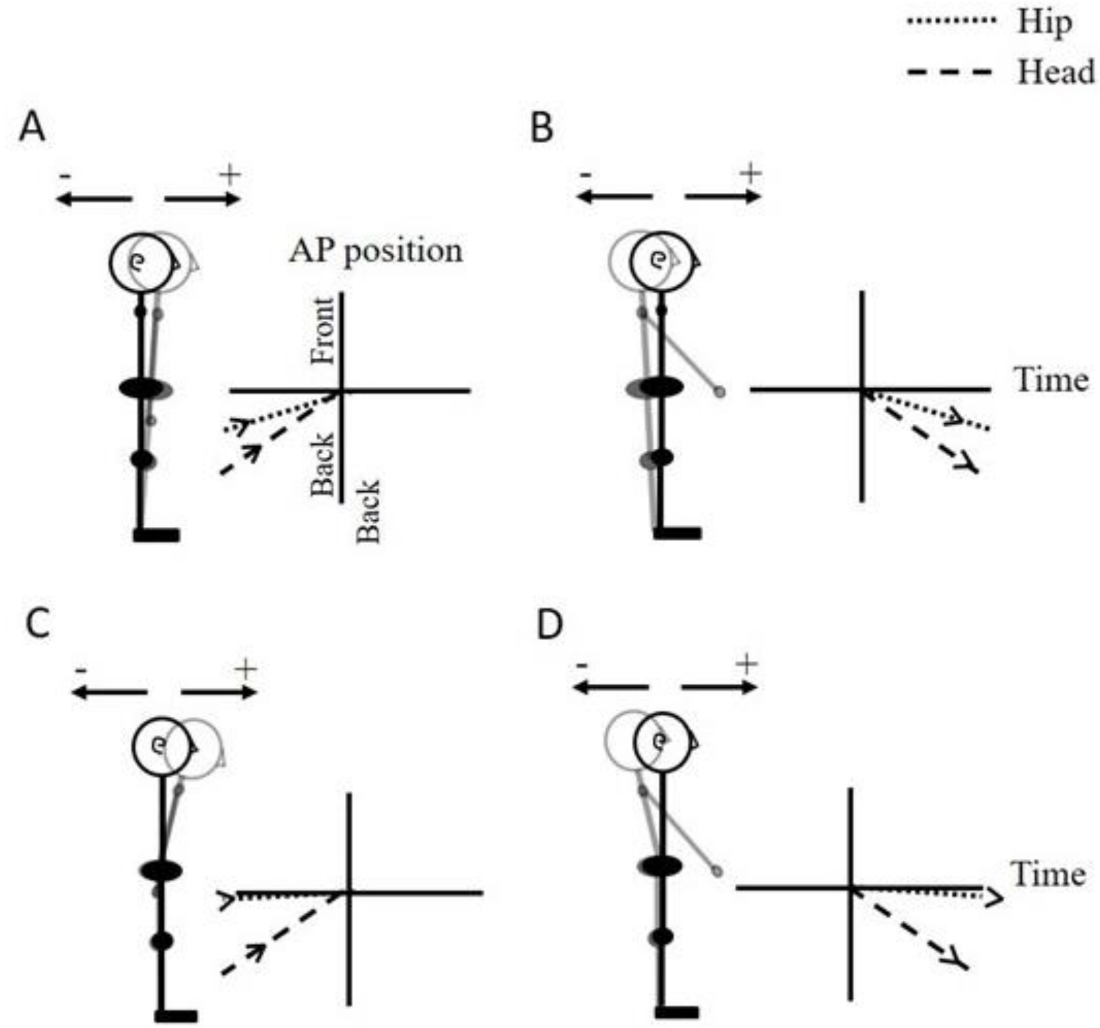

Figure 1. Schematic representation of anticipatory forward postural motion preceding the onset of arm extension (**A, C**) and compensatory backward postural motion during the arm's extension (**B, D**). The vertical axis represents anteroposterior (AP) body position and the horizontal axis represents time. The origin is placed at the point in time the arm movement is initiated, and the hip or head AP position at that time is assumed to have coordinate of zero. Panels **A** and **B** illustrate the expected motion in the case of postural adjustments made at the ankle joint (i.e., both the upper and lower body rotate), and panels **C** and **D** show the expected motion in the case of postural adjustment at the hip joint only (i.e., only the upper body rotates).

METHOD

Participants

Twenty young (8 male, 12 female; age range: 18-29) and 20 older (6 male, 14 female; age range: 65-88) participants were recruited from the university and local communities, respectively, through existing research participant panels. Older participants were recruited through the Trent Ageing Panel.[2] The young adult participants (18-30) were recruited through either NTU's Paid Participant Panel or Research Participation Scheme.[3] Participants recruited from the Trent Ageing Panel and the Paid Participant Panel were given a £10 voucher for their time. Participants recruited through the research participation scheme were given 6 research credits for their time.

Ethical approval for this research was granted by the Nottingham Trent University College of Business, Law and Social Sciences Research Ethics Committee. No physical perturbation was applied during the experiment, and as participants reported no history of falls or balance disorders in the past, fall risk was minimised. Each participant gave written and informed consent and was debriefed at the end of the session.

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[2] The Trent Ageing Panel is a group of 400-500 community-dwelling adults, aged over 60, registered as volunteers for participation in age-based research at Nottingham Trent University. Upon joining, all volunteers in the Trent Ageing Panel complete a health and lifestyle form. Due to the nature of this investigation, only volunteers over 65, who reported no history of balance or neurological disorders, and self-reported as healthy (i.e., not experiencing any form of cognitive impairment) were contacted through email.

[3] The Paid Participant Panel is a group of 500+ members from the university wide community, encompassing both staff and students, that spans all age and role brackets within the university. As with the Trent Ageing Panel, members of the Paid Participant Panel complete a health and lifestyle form. Volunteers in the desired young participant age bracket (18-30), who also reported no history of balance or neurological disorders, were contacted through email for participation. Participants were also recruited through the Psychology department's research participation scheme. The scheme allows a researcher (staff, PhD student or third year undergraduate) to find participants from the student community by offering research credits to first- or second-year undergraduate students. Students are required to earn enough credits to use the scheme themselves to recruit participants for their own projects in the future.

Standardised Tests

Prior to participation in the physical aspects of the experiment, all participants were required to complete standardised tests of cognitive functioning. Formal assessment of cognitive capabilities was required to ensure that all participants had accurately self-reported their cognitive health, such that they were competent to both understand and perform the experiment. Cognitive test scores were also compared to expected outcomes (Salthouse, 2009) for their age bracket to help prevent outlying results.

The Digit Symbol Substitution test (DSST) from the Wechsler Adult Intelligence Scale-Revised (Wechsler, 1981) was used to measure age-related differences in speed of processing. For the DSST the participant is presented with 9 digit-symbol pairs followed by a list of 102 digits (the first eight of which are for practise). Under each digit the participant writes down the corresponding symbol as fast as possible. The number of correct symbols in the allowed time of 90 seconds is measured. The test scales to a maximum score of 94, with higher score indicative of faster processing. The DSST was selected for its efficiency, being easy to understand and quick to complete, and for its sensitivity, as it has been shown to be sensitive to cognitive decline caused by age and is considered a general marker in age-comparative studies (Hoyer et al., 2004).

The multiple-choice section of the Mill Hill vocabulary scale (MHVS) test (Raven et al. 1988) was used to measure vocabulary. The MHVS is a test designed to measure verbal intelligence. For the multiple-choice section, the participant selects the corresponding synonym for a given word from a choice of six. There are 33 words in total and no fixed time is set. Higher scores indicate a higher level of vocabulary. Cognitive skills are known to age at different rates, with vocabulary persisting longer into old age, while other aspects of cognitive performance decline earlier (Hedden & Gabrieli, 2004; Lambrechts et al., 2013). Given that vocabulary accumulates over time, older people are likely to have a better vocabulary than younger people.

The Edinburgh handedness inventory (EHI) (Oldfield, 1971) short form Veale (2014) is a 4-item scale used to determine objectively whether someone is left or right-handed. Scoring uses a -100 to 100 scale, with -100 being always left, 0 both equally and a score of 100 is always right. The EHI is a widely used scale to establish hand dominance, the short form was selected for its simplicity and brevity. With the 4-item scale showing good correlation and reliability with the original 10 item scale. Only right-handed participants were recruited for this experiment (and throughout this project) to isolate age as a dependent variable to as great a degree as possible. While the EHI is not sufficient on its own to determine cerebral laterality establishing cerebral laterality to this extent was beyond the scope of this project.

In the tests of cognitive functioning, Young (Y) and older (O) groups differed as expected, with significantly higher speed of information processing scores but lower vocabulary scores for Y than O (Salthouse, 2010). The participant characteristics are summarized in Table 1.

	Old	Young
Age (yrs)	72.85 *(6.15)*	23.65 *(3.51)*
Height (cm)	164.225 *(9.93)*	168.55 *(9.49)*
Weight (kg)	71.645 *(19.3)*	68.965 *(15.56*
EHI	96.25 *(11.54)*	84.38 *(19.82)*
Mill Hill	22.45*(3.93)*	17.8*(4.44)*
DSS	50.1*(7.92)*	68.2*(11.08)*

Table 1. Participant characteristic means with SD in parentheses. EHI: Edinburgh Handedness Inventory; Mill Hill: vocabulary; DSS: digit symbol substitution test of information processing speed (from WAIS-R). Welch's t-tests showed that Y and O differed significantly in vocabulary (t(37.43) = -3.51, p<.01) and speed of processing (t(34.40) = 5.94, p<.001).

Apparatus

A Codamotion motion-tracking system (Charnwood Dynamics, Rothley, UK) was used to record participants' arm and postural motion. The system uses infrared emission markers (powered by drive boxes) attached to the body, and sensor units consisting of three optical sensors that capture the horizontal, vertical and rotational movements of the markers in real time. The Codamotion ODIN software analyses the sensor data and records each marker's position coordinates at the specified sampling rate (100 Hz in this experiment). Markers positioned at the distal end of the middle metacarpal recorded the motion of the arms, and markers placed on the Codamotion pelvic frame placed horizontally over the posterior superior iliac spine recorded the hip's postural motion. Motion of the head was recorded by markers placed over the zygomatic bone. Ground reaction force measurements were also collected, but subsequent analyses focused on the hip and head motion data.[4]

The experimental protocol was controlled by a script written in OpenSesame (Mathôt et al., 2012). This script delivered all the instructions and sequence of trials to the participants. The script also communicated with ODIN software to start and stop motion data acquisition.

Procedure

For all trials, participants stood barefoot in open stance (heels were approximately 10 cm apart) and held a computer mouse in their right hand. A computer monitor placed at eye-level 2.5m in front of the participant delivered the instructions for the experimental condition, which were presented at the start of each condition.

Once the participant was ready and in the start position, facing forwards, with arms relaxed by their sides, the experimenter initiated the trials. All trials started with a recorded voice saying, “get ready”, which was followed by a random delay of up to 4000ms. Following this, the recorded voice gave the “go” signal to make (or imagine) the arm raise. The instruction for the movement was to raise both arms to the front until it was aligned at shoulder level. Participants were asked to click the handheld mouse just as they started to make the movement (onset mouse click) while their arms were still by their sides, and to click again when they completed the movement (offset mouse click), defined as when arms

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[4] Overall, no significant differences were observed in CoP data between young and old participants. Whilst previous research has shown that CoP perturbations can be significantly different between young and old adults, these papers use more physically and mentally demanding motor tasks, and so it is likely that the simple nature of the motor task used in the current research was insufficient to produce a CoP displacement that displayed a significant difference between young and old participants. Alternatively, the segmental dynamics demonstrated by the kinematic data from this research may counteract each other, preventing a significant displacement or change in CoP. This further highlights the value of kinematic measures of posture as they appear to be more able to detect relatively minor changes in segmental and overall posture. This is also the case for experiment 2 and experiment 3.

reached the horizonal position, then return to the start position. A single trial consisted of one full movement, trials were recorded in sets of three and three trials made up one experimental block. Physical trials were performed with eyes open. Motor imagery trials were performed with eyes closed (more detail on motor imagery trials below).

Self-Initiated condition

In the self-initiated (SI) movement condition, participants were asked to wait at least 1000ms after the "go" signal and then initiate (or imagine initiating) arm movement at a time of their own choosing. Recording of the arm motion was taken as a set of 3 movements. Participants were asked to make (or imagine) three movements at a time of their own choosing, returning to the starting position after each. Once the three movements had been made, and subsequently a total of six mouse clicks had been recorded, the recording of movement data ended, the experiment switched to standby and waited for the experimenter to initiate the next set of three trials/movements. This gave the participant time to move freely and get into position for the next set of trials. This sequence ran 5 times, and therefore were 15 trials in this condition.

Externally triggered condition

For the externally triggered (ET) movement condition, participants moved (or imagined moving) their arm immediately upon hearing the "go" signal. As in the SI condition, movements were recorded in sets of three, however under this condition the "ready-go" signal was made before each movement. Once the participant made one movement, and the software recorded two mouse clicks (the onset and offset mouse click), the experimenter started the next trial, once the participant was in position. After three trials, the recording of movement data ended, the experiment was then left on standby waiting for the experimenter to initiate the next set of three trials/movements. This also ran 5 times, for a total of 15 trials in this condition.

MI trials

The procedure for MI trials was the same as for the physical movement trials, except, instead of physically performing the movement, participants were asked close their eyes and imagine performing the same movement. They clicked the mouse when they imagined the start of the movement (onset mouse click), and again when they imagined their arms were in the horizonal position (offset mouse click), the end of the movement. They then imagined bringing their arms back to the start position. The imagery instruction was to focus on the kinaesthetic aspect of MI. Participants were told to imagine what it feels like to make the movement.

Baseline Sway

Each participant’s baseline sway pattern was recorded separately over a 60 s period while the participant stood quietly with their eyes closed.

Practise Trials

Prior to the start of a physical condition, the participant was given a set of three physical practise trials. At the start of an imagery condition, the participant was asked to perform a set of three physical practise trials, followed by a set of three imagery trials. One intended effect of these practice trials was that participants had a fresh memory of performing the physical movement at the time of the MI trials. Additionally this enhanced the functional equivalence between the physical movement and the one being imagined (Olsson & Nyberg, 2010).

Experimental Block Structure

Trials of physical movement and MI were blocked and blocks were delivered in random order. Experimental blocks were made up of five sets of three trials each. This allowed participants to take breaks frequently if they needed.

In summary, both groups (young and old) were subjected to a total of four conditions. Movements were either physically performed or were imagined (MI). Within both of these conditions physical movements or MI were either self-initiated or were externally triggered by the experimenter.

Data Analysis

For both the SI and ET conditions, only the first physical (or imagined) movement of each set of three was analysed. This was because not all participants waited long enough in the SI condition between the first and second, or second and third movements, for the latter movements to be free of carryover effects. Furthermore, second and third trials could be qualitatively different than the first, even when the participant did leave time, as they were not preceded by the ready go signal. Therefore, 5 trials were analysed per condition.

Measurements of postural sway were made in the window of 1000 ms preceding arm movement (or MI) onset to pick up the effects of both the early (preparatory) and the anticipatory postural activity that have been distinguished in the previous research (Krishnan et al., 2012; Lee et al., 1990). Post-arm movement (or MI) onset, a 1000 ms time window allowed the postural consequences of arm motion (or MI) to play out.

Data analysis focused on the anteroposterior (AP) postural motion of the hip and head segments, and the forward (horizontal) component of arm motion. Motion data were sampled at 100 Hz and extracted for analysis in data structures accessed through MATLAB R2017b (Natick, MA). The raw motion data were smoothed using a moving window average of 10 samples. For physical movements, the onset was taken to occur when the forward velocity of the arm exceeded 1 m/s. Postural motion in the 1000 ms prior to this onset was analysed as anticipatory and motion in the 1000 ms following onset was analysed as compensatory. In the case of MI trials, the participants' mouse-click indicating the start of imagined arm movement was taken as the point of onset. Following the determination of movement (or MI) onset, the time stamps of all coordinate values were shifted such that the time of arm movement (or MI) onset was at t=0 and AP position coordinate of 0 (see Figure 2, 3, 5).

Analysis of APM

As Figures 2 and 3 indicate, APMs in both the physical movement and MI conditions had approximately linear trajectories at the hip and the head. For these cases, I adopted a multilevel linear modelling approach using lme4 v1.06 in R (Bates et al., 2014; Magezi, 2015). I fit Y and O's hip or head position data to a varying slope and varying intercept model with time as a fixed effect and participants as a random effect. This will be referred to as the test model. A positive slope (i.e., positive time coefficient) in the test model indicated forward motion (expected for APMs). If the slope was zero, this indicated no forward motion in the anticipatory period (i.e., no evidence of APM). In this case, the data would fit a baseline version of the test model with the time coefficient excluded. So, my first hypothesis test was to compare the test model with the baseline model (for Y and O separately). If the test model was a better fit to the data, I could conclude that there was significant APM (forward motion).

In the next step, I took Y and O's data and compared the test model to what is referred to as the theoretical model. The theoretical model added age and the interaction between age and time to the test model. If the theoretical model fit the data better (i.e., the time coefficient differed depending on age), I concluded that Y and O showed different levels of APM.

Analysis of CPM

Inspection of Figures 2 and 3 indicates that CPM in both physical movement and MI conditions had backward head and hip motion that was not linear but curved. The CPM trajectories had the shape of order 2 polynomials in the case of MI (right panels). The trajectories in the case of physical arm movements had the shape of order 3 polynomials (left panels). For CPM, I sought to determine only whether the trajectories of Y and O were statistically distinguishable. There was no intention to interpret the biomechanics in terms of model coefficients. Analyses of CPM the same were similar to those for APM except that I fit the second and third order polynomials in time for MI and physical arm movements, respectively. The theoretical model had a varying intercept and slope predicting AP position with age, time, time^2 (and time^3 in the case of physical movements) and the interaction between age and each order of time as fixed effects. Participants were a random effect. I compared this theoretical model to a test model that did not include age and its interactions to test whether Y and O differed in their postural motion in the period following arm movement (or MI) onset.

Comparison of linear mixed effects models

A likelihood ratio test enabled comparisons between the models. First the difference in the log likelihoods of the models is calculated. Where the null hypothesis is that the two models do not differ, -2 x log likelihood difference is distributed as a Chi-squared distribution. The degrees of freedom are the difference in the number of parameters in the models.

Analysis of differences in arm velocity profiles

To be meaningful, any age-related postural differences that were observed in the physical arm movement conditions should not be attributable to differences in the speed of arm movement between Y and O (e.g., reduced postural motion because the arm movement was very slow). Also, in the MI condition, it was important to ascertain whether Y and O were able to keep their arms still to the same extent. Relatedly, it was also important to analyse Y and O's postural motion in the baseline condition (with no arm movement or MI task) to demonstrate that the patterns observed in the physical movement or MI conditions were not also present in the body's natural sway in the experimental conditions.

RESULTS

First, I present the details of the results for anticipatory and compensatory postural motion observed during physical and imagined arm movements in the self-initiated (SI) and externally triggered (ET) arm movement conditions. At the end of the section, I provide a short summary of the main results.

Self-Initiated Condition

Figure 2 summarises the AP postural motion recorded just before and after arm movement (or MI) initiation in the SI condition. I will first present the results for APM and then consider the case of CPM. The regression coefficients are shown in Table 2.

Anticipatory postural motion

AP sway recorded at the head and hip in the 1000 ms prior to physical arm movement (or MI) were analysed separately. For Y and O, I ran the test model first (to test whether there was a significant linear AP displacement prior to arm movement (or MI) onset. I then compared the test model to the baseline model. To test whether age affected AP displacement, I then compared the test model to the theoretical model. The regression coefficients are in Table 2.

Physical arm movements

At the hip (Fig. 2b), O showed significant forward displacement of 0.98 mm ($\chi2(1) = 8.93$, $p<0.01$), but Y's displacement of -0.33 mm was not significantly different from zero ($\chi2(1) = 0.88$, $p=0.35$). The difference between Y and O's displacement was significant ($\chi2(2) = 8.09$, $p=0.02$).

At the head (Fig. 2a), O had significant forward displacement of 2.35 mm ($\chi2(1) = 6.66$, $p<0.01$), but Y's displacement of 1.42 mm was not statistically distinguishable from zero ($\chi2(1) = 2.02$, $p=0.16$). The difference between Y's and O's displacement was not significant ($\chi2(2) = 1.71$, $p=0.43$).

Thus, O exhibited anticipatory forward motion at both the hip and the head, but Y did not. O showed more forward motion than Y at the hip but not at the head.

Imagined arm movements

At the hip (Fig. 2d), both O ($\chi2(1) = 6.23$, $p=0.01$) and Y ($\chi2(1) = 7.75$, $p<0.01$) showed significant forward displacement of 0.93 mm and 0.97 mm, respectively, but the difference between Y and O's displacement was not significant ($\chi2(2) = 0.12$, $p=0.94$).

At the head (Fig. 2c), O ($\chi2(1) = 5.02$, $p=0.03$) and Y ($\chi2(1) = 12.34$, $p<0.01$) showed significant forward displacement of 1.85 mm and 1.66 mm, respectively, but the difference between Y and O's displacement was not significant ($\chi2(2) = 1.38$, $p=0.50$).

Thus, both O and Y exhibited significant anticipatory forward motion at both the hip and head, but there was no difference between the age groups.

Compensatory postural motion

As shown in Figure 2, the compensatory postural motion trajectories were curved and were modelled as order 3 (physical arm movement, Figure 2, left panels) or order 2 (imagined arm movement, Figure 2, right panels) polynomials in time as previously described. The theoretical, test and baseline models were established analogously to the procedure used for the analysis of APMs. The regression coefficients are shown in Table 2 and the postural motion trajectories in Figure 2.

Physical arm movements

At the hip, the theoretical model showed that age, time, time2, time3, and all the interactions terms were significant predictors of AP position (Fig. 2b). When compared with the test model that excluded age and its interactions, the theoretical model provided a significantly better fit ($\chi 2(4) = 133.57$, $p<0.01$).

At the head, the theoretical model showed that age, time, time2, time3, and the interaction between age and time2 were significant predictors (Fig. 2a). The theoretical model provided a significantly better fit to the data than the test model ($\chi 2(4) = 208.36$, $p<0.01$).

These results indicated that O and Y’s postural motion trajectories accompanying physical arm movement differed both at the head and the hip segments. The head showed a similar backward motion in O and Y (velocity was greater in Y), but the significant age x time2 interaction supports visual inspection in that O’s head velocity and displacement were lower than Y’s (Fig. 2a). Y’s hip motion was qualitatively different from O’s in that it showed forward motion following an initial backward motion. O’s hip motion did not show this recovery following initial backward motion (Fig. 2b). Given that the interactions between age and all three orders of time were significant in the test model, we conclude that Y initially had in-phase (backward) motion but switched to anti-phase hip-head motion in the latter part of this time period. O’s hip motion plateaued following the initial in-phase backward motion, but did not reverse direction as for Y.

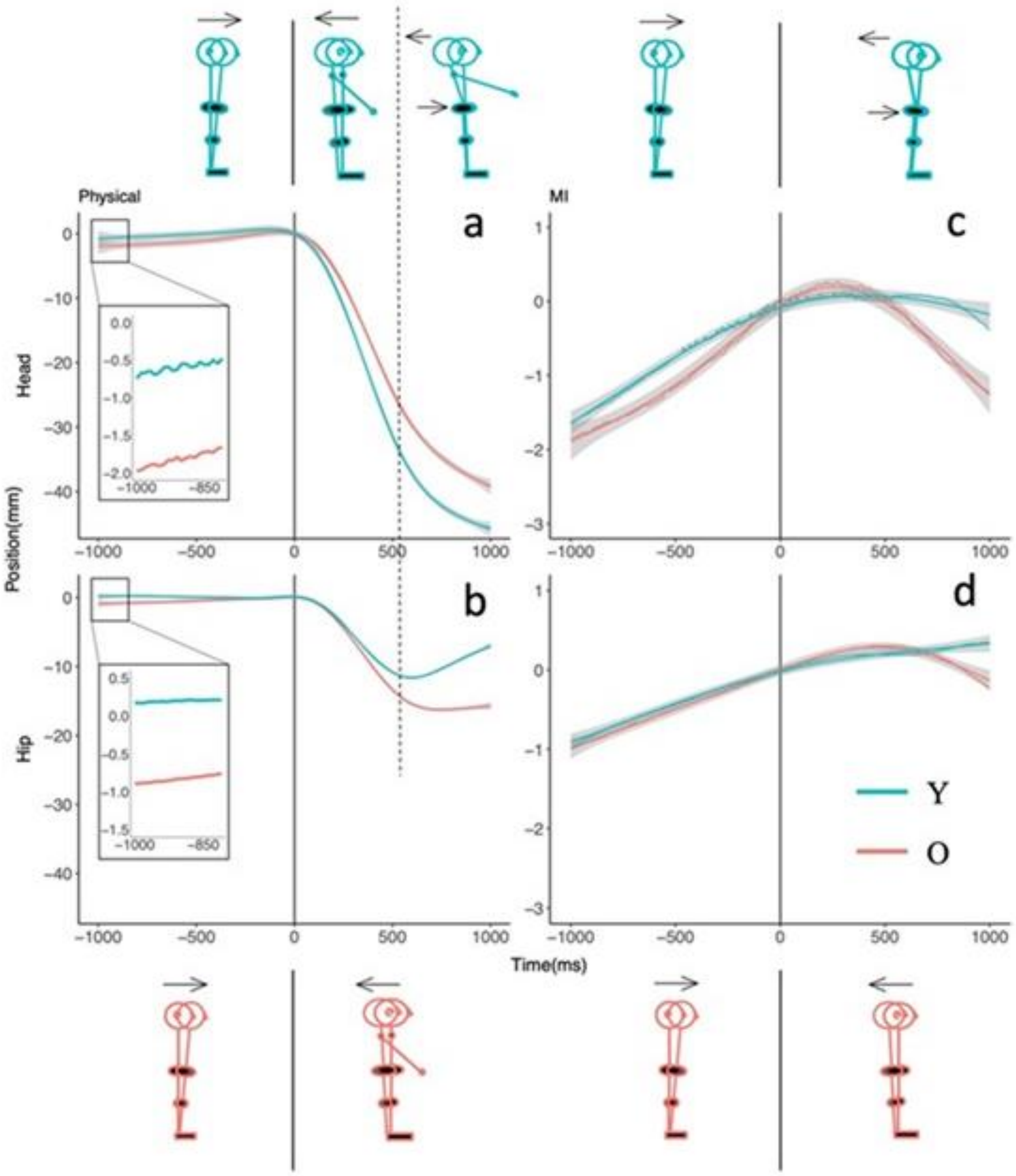

Figure 2. AP Postural motion in the vicinity of physical (a, b) and imagined (c, d) arm raising movements in the self-initiated (SI) conditions during bilateral arm raises. The upper panels show head motion, and the bottom panels show him motion.

Illustrations above and below the panels represent the bodies physical position, in reference to an ankle or hip posture control strategy, as shown by the data reported. Blue illustrations represent Y and red illustrations represent O. Illustrations where the axis of the body rotate at the ankle show an ankle strategy, and where the body rotates around the hip show a hip strategy.

Imagined arm movements

At the hip, the theoretical model showed that time2 and the interaction between age and time2 were significant predictors of AP position (Fig. 2d). When compared to the test model that excluded age and its interactions, the theoretical model provided a significantly better fit ($\chi2(3) = 503.61$, $p<0.01$).

At the head also, the theoretical model showed that time2 and age x time2 were significant predictors of AP position (Fig 2c). Compared to the test model, the theoretical model fit significantly better ($\chi2(3) = 96.66$, $p<0.01$).

These results suggested that O and Y followed parametrically different quadratic curves in their postural motion during imagined arm movement. Inspection of Figure 2 (panels c, d) shows that O’s AP motion reversed direction relative to the forward motion seen in the anticipatory phase. Y’s hip motion continued in the forward direction, albeit at a reduced rate, but Y’s head motion did reverse direction, although not as strongly as O’s.

Fixed Effects	**Anticipatory (SELF-INITIATED)**	**Head**		**Hip**	
		Estimate	**(SE)**	**Estimate**	**(SE)**
Physical	**Intercept**	-1.01	0.65	-0.47*	0.18
	Time	0.69*	0.27	0.29**	0.10
	Age (young)	0.96	0.92	0.54*	0.26
	Time*Age	-0.27	0.38	-0.38**	0.14
MI	**Intercept**	-1.08***	0.30	-0.50**	0.17
	Time	0.54**	0.18	0.28**	0.10
	Age (young)	0.28	0.42	0.06	0.24
	Time*Age	0.06	0.26	-0.01	0.14

	Compensatory (SELF-INITIATED)	**Head**		**Hip**	
		Estimate	**(SE)**	**Estimate**	**(SE)**
Physical	**intercept**	-21.82***	1.79	-10.58***	0.73
	Time	-848.31***	64.36	-359.51***	31.19
	Time^2	114.10***	3.71	121.29***	2.42
	Time^3	97.02***	3.71	50.64***	2.42
	Age (young)	-5.36*	2.52	3.34**	1.03
	Time*Age	-134.01	91.01	179.49***	44.11
	Time^2*Age	75.49***	5.26	34.46***	3.42
	Time^3*Age	7.55	5.26	-14.98***	3.42
MI	**intercept**	-0.24	0.38	0.16	0.24
	Time	-27.77	14.95	-3.05	8.75
	Time^2	-12.67***	0.57	-8.10***	0.25
	Age (young)	0.24	0.53	0.04	0.34
	Time*Age	24.25	21.14	7.88	12.38
	Time^2*Age	7.86***	0.81	8.12***	0.35

Table 2. Regression coefficients of the theoretical model for anticipatory and compensatory AP postural motion recorded at the head and hip segments in the self-initiated arm movement condition (see text for details).

Environmentally Triggered Condition

Figure 3 summarises the AP postural motion recorded before and after arm movement (or MI) initiation in the ET condition. I will first discuss the results for APM and then consider the case of CPM. The regression coefficients are shown in Table 3.

Anticipatory postural motion

Physical arm movements

At the hip (Fig. 3b), O did not show significant forward displacement (0.37 mm) ($\chi 2(1) = 1.36$, p=0.24), but Y's displacement of 0.87 mm was significantly different from zero ($\chi 2(1) = 10.16$, $p<0.01$). The difference between Y and O's displacement was not significant ($\chi 2(2) = 1.65$, p=0.44).

At the head (Fig. 3a), O did not show significant forward displacement (0.51 mm) ($\chi 2(1) = 0.52$, p=0.50), but Y's displacement of 2.02 mm was statistically distinguishable from zero ($\chi 2(1) = 5.94$, $p<0.01$). The difference between Y's and O's displacement was significant ($\chi 2(2) = 6.79$, p=0.03).

Thus, Y exhibited anticipatory forward motion at both the hip and the head but O did not. Y showed more forward motion than O at the head but not at the hip.

Imagined arm movements

At the hip (Fig. 3d), O did not show significant forward displacement (0.35 mm) ($\chi 2(1) = 0.86$, p=0.35), but Y's displacement of 1.99 mm was significantly different from zero ($\chi 2(1) = 17.48$, $p<0.01$). The difference between Y and O's displacement was significant ($\chi 2(2) = 8.84$, p=0.01).

At the head (Fig. 3c), O did not show significant forward displacement (0.36 mm) (χ2(1) = 0.24, p=0.62), but Y’s displacement of 3.00 mm was statistically distinguishable from zero (χ2(1) = 14.78, p<0.01). The difference between Y’s and O’s displacement was significant (χ2(2) = 8.00, p=0.02).

Thus, Y but not O exhibited anticipatory forward motion at both the hip and head, and their difference was significant.

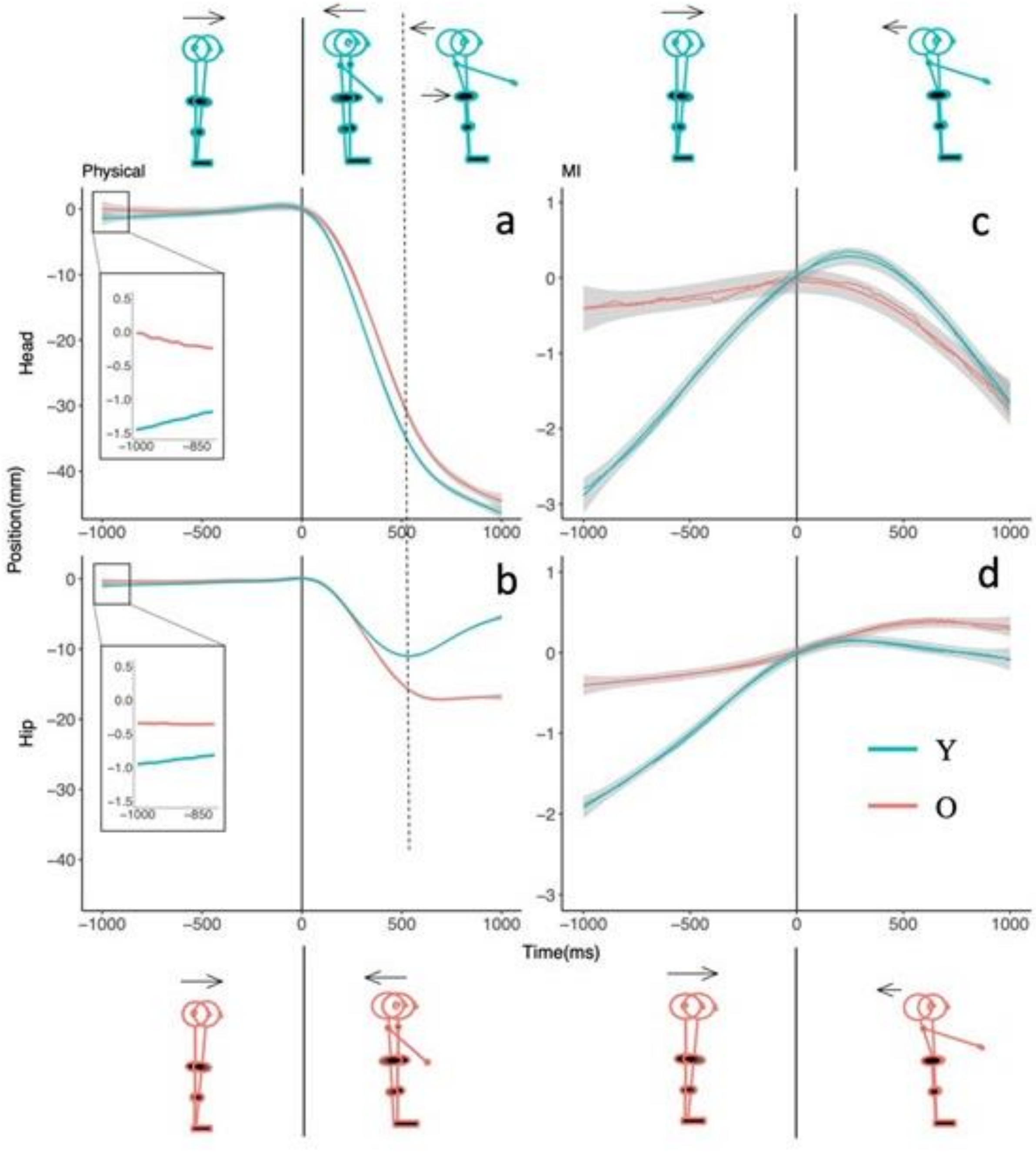

Figure 2. AP Postural motion in the vicinity of physical (a, b) and imagined (c, d) arm raising movements in the externally triggered (ET) conditions during bilateral arm raises. The upper panels show head motion, and the bottom panels show him motion.

Illustrations above and below the panels represent the bodies physical position, in reference to an ankle or hip posture control strategy, as shown by the data reported. Blue illustrations represent Y and red illustrations represent O. Illustrations where the axis of the body rotate at the ankle show an ankle strategy, and where the body rotates around the hip show a hip strategy.

Compensatory postural motion

Physical arm movement

At the hip, the theoretical model showed that time, $time^2$, $time^3$, and the age x $time^2$ and age x $time^3$ interactions were significant predictors of AP displacement (Fig. 3b). When compared with the test model that excluded age and its interactions, the theoretical model provided a significantly better fit ($\chi 2(4) = 223.57$, $p<0.01$).

At the head as well, the theoretical model showed that time, $time^2$, $time^3$, and the age x $time^2$ and age x $time^3$ interactions were significant predictors of AP displacement (Fig. 3a). The theoretical model provided a significantly better fit to the data than the test model ($\chi 2(4) = 228.36$, $p<0.01$).

Thus, O and Y’s postural motion during physical arm movements differed both at the head and hip segments. The head’s backward motion was very similar in O and Y, but the interactions between age and the $time^2$ and $time^3$ terms express O’s lower head velocity and displacement (Fig. 3a). Y’s hip motion differed qualitatively from O’s in that it reversed its initially backward direction to recover. O’s backward hip motion had higher velocity but then plateaued rather than reverse direction like Y’s (Fig. 3b). Considering hip and head motion together, Y initially showed in-phase backward motion, and then switched to anti-phase as hip position began moving forward. O initially showed in-phase hip and head motion but diverged when the hip’s backward motion stopped (without reversing direction).

Imaginary arm movement

At the hip, the theoretical model showed that time^2 and the interaction between age and time^2 were significant predictors of AP position (Fig. 3d). When compared to the test model that excluded age and its interactions, the theoretical model provided a significantly better fit ($\chi 2(3) = 42.75$, $p<0.01$).

At the head also, the theoretical model showed that time^2 and age x time^2 were significant predictors of AP position (Fig. 3c). Compared to the test model, the theoretical model fit significantly better ($\chi 2(3) = 71.30$, $p<0.01$).

These results indicated that O and Y followed different quadratic curves in their hip and head motion during imagined movement. Figure 3 (panels c and d) shows that Y exhibited backward motion at both hip and head, but O showed backward motion only of the head.

Fixed Effects	**Anticipatory (EXTERNALLY TRIGGERED)**				
		Head		**Hip**	
		Estimate	**(SE)**	**Estimate**	**(SE)**
Physical	**Intercept**	-0.14	0.48	-0.25	0.19
	Time	0.15	0.22	0.11	0.08
	Age	-0.44	0.68	-0.31	0.27
	Time*Age	0.44	0.31	0.15	0.12
MI	**Intercept**	-0.25	0.41	-0.25	0.12
	Time	0.11	0.21	0.10	0.11
	Age	-1.16	0.58	-0.74*	0.28
	Time*Age	0.77*	0.29	0.48***	0.16

	Compensatory (EXTERNALLY TRIGGERED)				
		Head		**Hip**	
		Estimate	**(SE)**	**Estimate**	**(SE)**
Physical	**intercept**	-25.57***	1.78	-11.51***	0.72
	Time	-976.06***	66.51	-371.63***	24.28
	Time^2	157.32***	3.88	143.61***	2.62
	Time^3	120.68***	3.88	40.55***	2.62
	Age (young)	-2.83	2.52	4.70***	1.02
	Time*Age	3.62	94.06	253.17***	34.33
	Time^2*Age	72.59***	5.49	32.76***	3.7
	Time^3*Age	-40.49***	5.49	-39.51***	3.7
MI	**intercept**	-0.61	0.52	0.29	0.22
	Time	-34.07	18.59	4.93	8.21
	Time^2	-8.33***	0.70	-4.83***	0.33
	Age (young)	0.33	0.74	-0.23	0.31
	Time*Age	-2.37	26.28	-8.74	11.61
	Time^2*Age	-8.31***	0.99	3.06***	0.47

Table 3. Regression coefficients of the theoretical model for anticipatory and compensatory AP postural motion recorded at the head and hip segments in the externally triggered arm movement condition (see text for details).

Arm Movement Peak Velocity and its Latency

For the experimental conditions in which the arm raise was physically performed, we investigated whether there were any age-related differences in the peak velocity attained by the arm and in the latency at which this occurred (Fig. 4). The theoretical model was a varying intercept and slope model predicting the right hand's peak AP velocity and its latency with age and time as fixed effects and participant as a random effect. We compared this model with a test model that excluded the age coefficient.

In the SI condition, there was no difference between Y and O's peak velocity ($\chi2(1) = 1.01$, p=0.32) or its latency ($\chi2(1) = 1.58$, p=0.21). In the ET condition, there was no difference between Y and O's peak velocity ($\chi2(1) = 1.75$, p=0.18), but O reached peak velocity later (374.00ms, SD=86.29) than Y (326.60ms, SD=73.95) ($\chi2(1) = 4.29$, p=0.04).

For the ET condition, while there was no difference in the absolute peak velocity between Y and O , there was a significant difference in the time to peak velocity with O reaching peak velocity later than Y. This is consistent with previous literature, suggesting a higher contribution of feedback-based control and/or a less prominent ballistic phase (Ketcham & Stelmach, 2004). Despite the time to peak velocity being statistically different between O and Y, this is unlikely to have a significant effect on the movement itself, particularly given that peak velocity not showing any significant differences between Y and O.

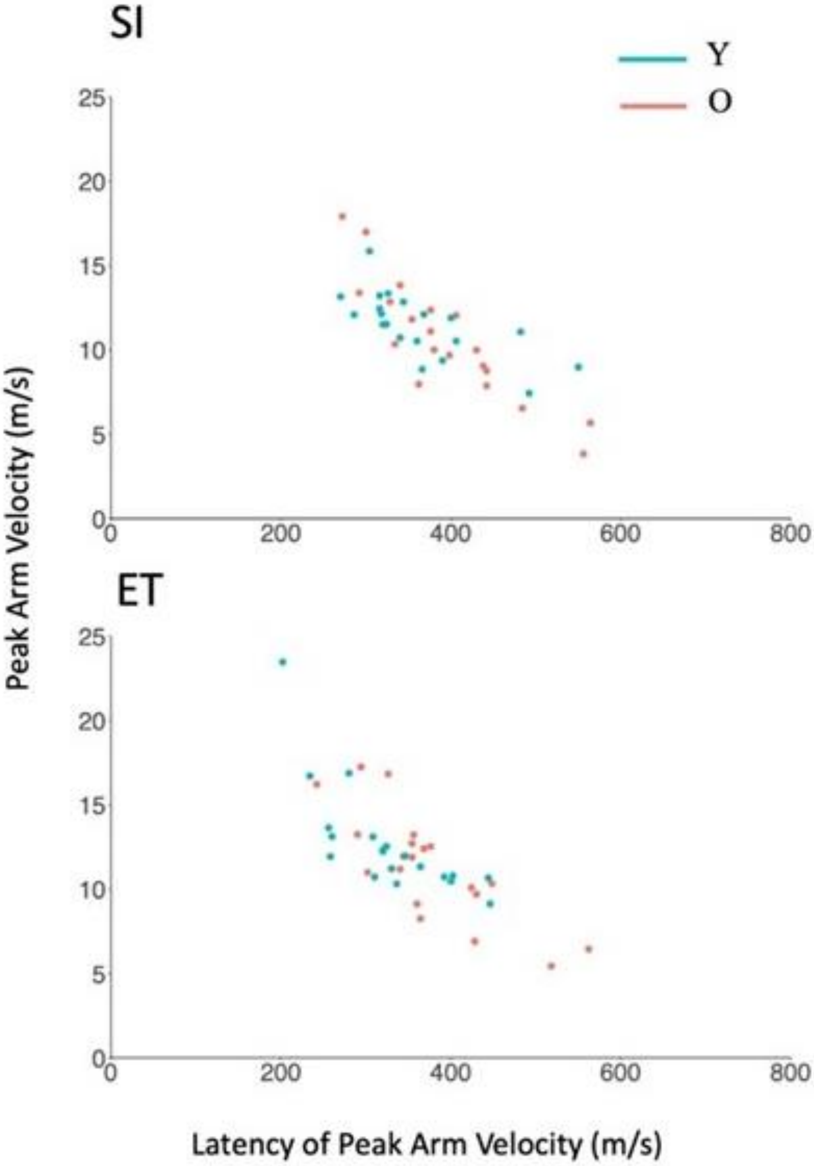

Figure 4. Peak arm velocity and its latency in the self-initiated (SI) and externally triggered (ET) conditions.

Arm Motion during MI

In the experimental conditions in which the arm raise was to be imagined but not performed, I analysed whether the arm exhibited any systematic forward or backward motion in the 1000ms before or after the start of MI (indicated by participants' mouse clicks). I used the same strategy as in the analysis of postural motion - the test model was a varying intercept and slope model predicting the right hand's AP position with time as a fixed effect and participants as a random effect. This model was compared with a baseline model that excluded the time coefficient. I rejected the null hypothesis (no AP displacement in this time period) if the test model fit the data significantly better than the null model.

In the SI condition, O showed no significant arm motion in the pre-MI period ($\chi2(1) = 0.93$, $p=0.33$), and Y also showed no significant ($\chi2(1) = 3.54$, $p=0.06$) forward motion. The magnitudes were 0.52 mm and 0.64 mm, respectively (compared to the 2.35 mm and 1.42 mm of head sway recording during this time period).

During the MI period, O showed no significant arm motion ($\chi2(1) = 3.52$, $p=0.06$) and Y also showed no significant ($\chi2(1) = 1.52$, $p=0.22$) arm motion. Again, the magnitudes of 1.83 mm and 1.22 mm, respectively, were comparable to head motion recorded in this time period.

In the ET condition, O showed significant arm motion in the pre-MI period ($\chi2(1) = 10.38$, $p<0.01$), and so did Y ($\chi2(1) = 22.20$, $p<0.01$). The magnitudes were 1.25 mm and 2.02 mm, respectively, which were comparable to the 0.36 mm and 3.00 mm of head sway recorded during this time period.

During MI, O showed marginally significant arm motion ($\chi2(1) = 3.70$, p=0.05) but Y did not ($\chi2(1) = 0.42$, p=0.52). Again, the magnitudes of 3.17 mm and 0.52 mm, respectively, were comparable to head motion recorded in this time period.

These results show that arm motion was comparable or smaller than postural motion recorded from the upper body. I concluded, therefore, that both O and Y successfully inhibited focal arm movement during 1000ms before and after self-reported MI onset.

Postural sway in the quiet stance baseline condition

Figure 5 shows participants' sway pattern during 1000ms preceding and following the midpoint of the average 2000ms time window during the baseline trial. It can be seen that sway relative to an arbitrary time point during quiet stance has much lower dispersion than was observed around the onset of physical and imagined arm movements in the experimental conditions. We performed the same statistical modelling on this data as in the experimental conditions and found no significant linear trends.

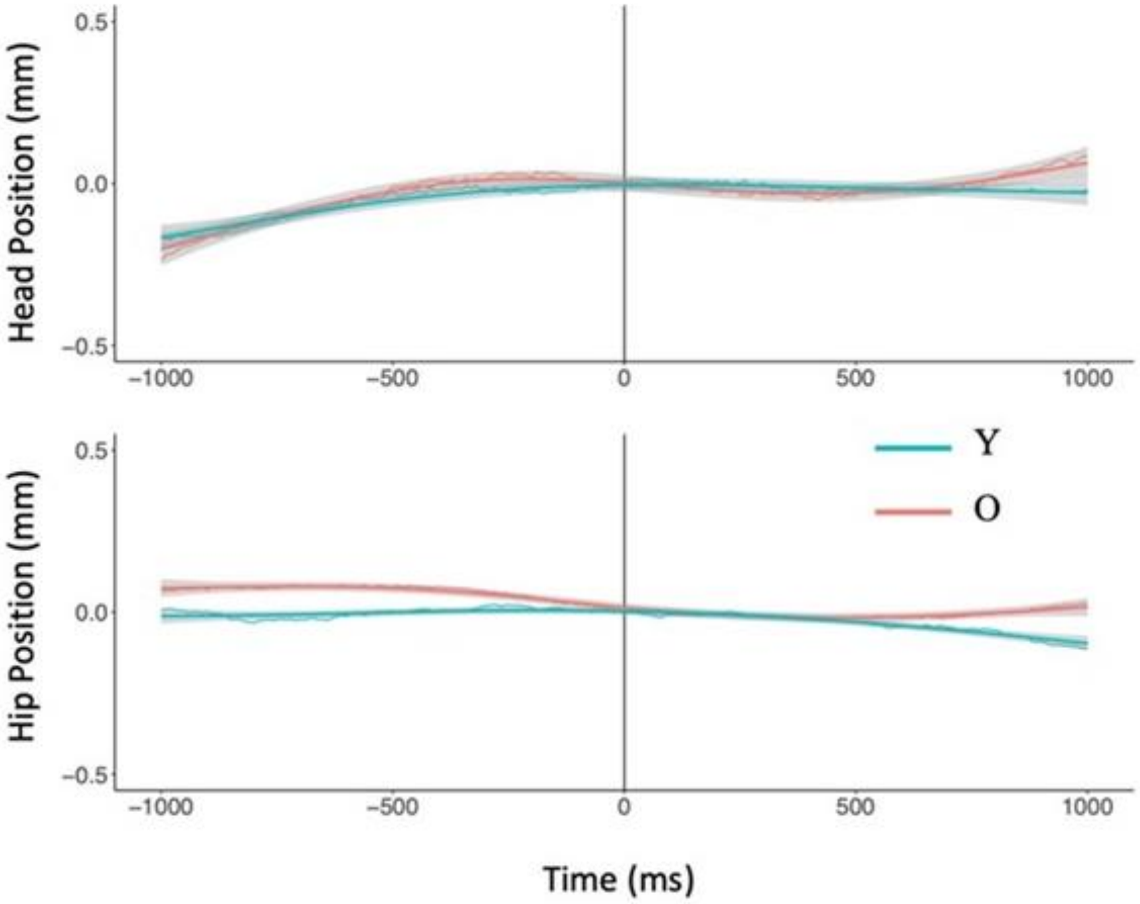

Figure 5. Average AP postural motion over 2000ms time windows during 60 second quiet stance baseline condition.

Results Summary

Self-initiated arm movement

Anticipatory postural motion: Immediately before physically performing the arm movement, O showed significant forward displacement at the hip and head segments, while Y did not. Compared to Y, O showed more forward motion at the hip but not the head. Preceding imagined the arm movement, both age groups showed significant forward motion at the head and hip. O and Y’s head or hip motion did not differ from each other.

Compensatory postural motion: O and Y differed in their postural motion during physical and imagined arm movement at both segments. Y showed greater backward motion and greater reversal of this than O.

Environmentally triggered arm movement

Anticipatory postural motion: Preceding physical arm movements, O did not show forward displacement at the head or hip whereas Y did. O and Y’s head motion but not hip motion differed significantly. Preceding imagined arm movements, O did not show forward motion of the hip or the head, but Y did. The difference between the groups was significant at both the head and the hip.

Compensatory postural motion: Y and O’s hip and head motion followed statistically different quadratic curves during physical and imagined arm movements.

DISCUSSION

The purpose of this experiment was to investigate the spatiotemporal characteristics of the postural motion that accompanies physical and imagined arm movements in standing young and older adults. Y and O executed (or imagined) bilateral, straight-arm raises under SI or ET conditions. Y and O's physical arm movements' velocity profiles were very similar and differed only in O's slower time to peak velocity in the ET condition. I consider CPMs and APMs observed around physical arm movement onset first, and then focus on postural motion observed in the context of manual MI.

In the case of physical arm movements, the forward displacement of the arms moves the body's CG in the forward direction, so a backward CPM would be expected to stabilize the CG as the movement occurs (Bouisset and Zattara 1981, 1987b, 1988, 1990; Friedli et al. 1988; Mouchnino et al. 1990; Ramos and Stark 1990; Rogers and Pai 1990). Martin (1967) specifically observed that a backward bending of the trunk achieved this CG regulation. CPM analysis in this study showed that in both SI and ET conditions, Y and O had backward postural motion in the first 500 ms following arm movement initiation, Y with higher velocity of the hip and the head. In the next 500 ms, the behaviour of Y and O diverged in a similar way in the SI and ET conditions. Y and O's head motion continued in the negative direction (with decreasing velocity), but Y's hip motion reversed direction to move forward, whereas O's hip motion remained unchanged over this period. This pattern suggests that, as noted by Martin (1967), backward bending of the trunk was used to regulate CG as the arms extended forward. The intersegmental phase change was simply more prominent in Y than in O.

If an APM precedes a forward movement of the arms, it ought to be in the forward direction, opposite to the backward CPM accompanying the movement (Bleuse et al. 2006; Cordo and Nashner 1982). In this study, analysis of APM preceding physical arm movement showed that O but not Y moved forward in the SI condition (Fig. 2a, b), whereas Y but not O did so in the ET condition (Fig. 3a, b). The differences between Y and O were subtle in the case of physical movements. In the SI condition, O showed more forward motion than Y at the hip but not at the head, and in the ET condition, Y showed more forward motion than O at the head but not at the hip. The forward direction of APMs (when they occurred) is consistent with expectation, but it is not clear what the age-related differences between the SI and ET conditions indicate.

In the SI condition, the perturbation due to arm motion was predictable, and given that the participants chose when to initiate the movement, so was the timing of movement onset. O’s forward APM was expected, but the absence of APM in Y was not. It could be that Y used a neuromuscular strategy such as co-contraction and so their anticipatory postural adjustment did not generate net forward motion. In the case of MI in the SI condition, both Y and O showed clear APM of similar magnitude in the forward direction. Y and O’s mean APM magnitudes (hip: 0.97 mm and 0.93 mm, and head: 1.66 mm and 1.85 mm, respectively) preceding MI were of the same order as O’s APM magnitude (hip: 0.98 mm, head: 2.35 mm) preceding physical movements. The MI data suggest that forward APM was planned by both Y and O.

For physical movements in the ET condition, Y’s APM in the forward direction was as expected, but O did not show statistically significant APMs. In this condition, it was predictable that arm movement would perturb posture control, but exactly when the go signal for the arm movement would arrive was not predictable due to the randomly variable latency between the ready and go signals. One possibility is that, under these conditions, O did not (or could not) plan and execute APMs. The APM data from the corresponding MI condition support this possibility as Y showed significant APM (hip: 1.99 mm, head: 3.00 mm), whereas O did not. As O did not show APM preceding physical arm movement or MI, it appears that the lack of control over arm movement (or MI) onset impeded O’s ability to prepare for the postural perturbation to come.

This leaves the pattern observed for postural motion following the onset of MI. As the planned arm motion does not in fact occur in the case of MI, any APM preceding MI onset would need to be compensated following MI onset to maintain balance. In the present case of imagined forward arm movement, the CPM would need to be in the backward direction, and this is generally what was observed for Y and O in both the SI and ET conditions. However, there were differences in hip–head phasing that are worth noting. In the SI condition (Fig. 2c, d), Y showed an anti-phase hip–head pattern (the head reversed to moving backwards while the hip continued forward motion), but O showed in-phase backward motion of hip and head. Comparing with the corresponding CPMs in the physical arm movement condition (Fig. 2a, b), both Y and O had the same CPM pattern in the MI condition as in the physical arm movement case. In the ET condition (Fig. 3c, d), Y and O showed a very small amount of hip motion, but their difference was significant; Fig. 3d suggests that Y had a more backward tendency at the hip that counteracted their forward APM prior to MI onset. Y's backward CPM at the head counteracted their forward APM prior to MI onset. O showed the same pattern of backward head CPM as Y (Fig. 3c), but their head CPM followed next to no forward APM prior to MI onset. Thus, O ended the MI trials with a net backward head motion in the absence of forward arm motion, which will have been a destabilizing influence on their balance.

These results clearly demonstrate that APM is a feature of motor behaviour not only in the case of physical limb movement, as previous research has long established, but also, as raised by Boulton and Mitra (2013, 2015) and Grangeon et al. (2011), in the case of MI. In their comparison of the postural motion of Y and O, Mitra et al. (2016) found that sway increased in Y but decreased in O (relative to a quiet standing baseline), while they imagined reaching arm movements under ET conditions. Here, I observed that, unlike in the SI condition, O did not produce APM preceding MI in the ET condition. This absence of APM in the ET condition is consistent with the reduced sway recorded by O in Mitra et al. (2016). The reaching movements imagined in that study had more precisely defined targets, occurred only along the horizontal plane, and had smaller magnitudes than the bilateral arm raise studied here. Those task constraints may have added incentives for O to reduce body sway (e.g., to reduce shoulder motion to improve the precision of arm movement planning), but the absence of APM in O, which we observed here for both physical and imagined movements under ET conditions, appears likely to have contributed to O's reduced sway during MI in Mitra et al. (2016).

The absence of APM preceding O's executed and imagined arm movement in the ET condition has potentially important practical consequences for active and independent living. Limb movements that must be coordinated with environmental events of unpredictable timing are an everyday necessity in navigating civic spaces and interacting socially. Raising the arm while standing upright does not even include the variable spatial constraints that are often added to the temporal uncertainties of coordinating with external events. Take, for example, the active destabilization of body posture that occurs when the trunk must bend as part of the focal movement, resulting in a large change in CG position (e.g., in Stapley et al., 1998). Previous research on postural support for physical movements has shown that O produce weaker and delayed APA (Inglin and Woollacott 1988; Man'kovskii et al. 1980; Rogers et al. 1992; Woollacott and Manchester 1993), and, as a result, larger CPA that can have destabilizing effects (Kanekar and Aruin (2014a). Here, O's absence of APM for physical arm movements and MI in the ET condition suggests that the issue occurs at the level of planning the postural support for the movement that is to be coordinated with external events. Curiously, but potentially significantly, the absence of APMs coexists with intact CPMs even as no focal movement takes place.

[5]CHAPTER 3: Age-related differences in postural control during physical and imagined unilateral raises of the dominant arm

INTRODUCTION

The experiment reported in Chapter 2 studied symmetrical, bilateral arm raises and reported on AP postural motion. Postural adjustment in the case of unilateral arm movement is arguably even more important with respect to the impact of ageing because such manual movements are more likely to perturb posture mediolaterally. It is well known that ageing particularly affects mediolateral (ML) postural stability (Brauer et al. 2000; Maki et al. 1994) and the ability to counteract perturbations in the ML direction (Claudino et al 2013; Santos et al. 2016). As summarised in Chapter 1, research also suggests greater asymmetry in body weight distribution in O and asymmetric leg muscle power in O with a history of falls (Blaszczyk et al., 2000; Skelton, 2002).

The experiment presented in this chapter began my investigation of the effects of unilateral manual reaching and MI on the postural motions measured just before and after movement onset. This chapter focuses on the case of dominant arm raises. The case of the non-dominant arm is addressed in Chapter 4. Y and O participants stood in canonical stance and raised (or imagined raising) their dominant arm to shoulder level in front of them (Fig. 6). As in Chapter 2, arm movements were either self-initiated or externally triggered. This allowed investigation into how controlling the timing of the focal movement affected the postural activity elicited. The participants' arm, hip and head motion were recorded using

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[5] The experiment described in this chapter has been reported in full in Wider, C., Mitra, S., Boulton, H., & Andrews, M. (under review). Age-related asymmetry in anticipatory postural movements during unilateral arm movement and imagery. Experimental Brain Research.

real-time motion tracking. Of interest were the differences in anticipatory and compensatory AP and ML motion accompanying movements of the arm.

Expectations of differences in postural motion associated with dominant arm raises were based on the assumption that the dominant arm is favoured (and more practised) in fast or load-bearing movements that generate greater postural perturbation. The movements studied here, as in Chapter 2, were forward arm raises that produced a backward postural perturbation in the AP plane. In general, anticipatory postural action (moving the body forward) should be more prominent for physical or imagined movements of the dominant arm. Also, unilateral movement of the dominant arm applies a mediolateral postural perturbation to the weaker, non-dominant side. Assuming that this perturbation is more destabilizing than the reverse case (addressed in Chapter 4), and more so in O than Y (as mediolateral stability is more affected by ageing), anticipatory postural action in the mediolateral direction should also be a key feature of the dominant arm's movement or imagery.

Chapter 2's investigation of bilateral arm raises studied a self-initiated and an externally triggered task condition. In the latter, the participants knew that a signal to make (or imagine) the movement was imminent but could not predict its exact timing. A key result was that O (but not Y) failed to show anticipatory postural motion in this externally triggered condition. This pointed to an age-related deficit in planning the postural support for actions that must be coordinated with external events. The present experiment retained these task conditions to observe whether postural support patterns changed in the case of unilateral action. The pattern of age-related differences in AP postural motion in the case of dominant arm movement (or MI) was expected to be similar to that observed in Chapter 2. Of additional interest was the pattern of ML postural motion in Y and O (not studied in Chapter 2).

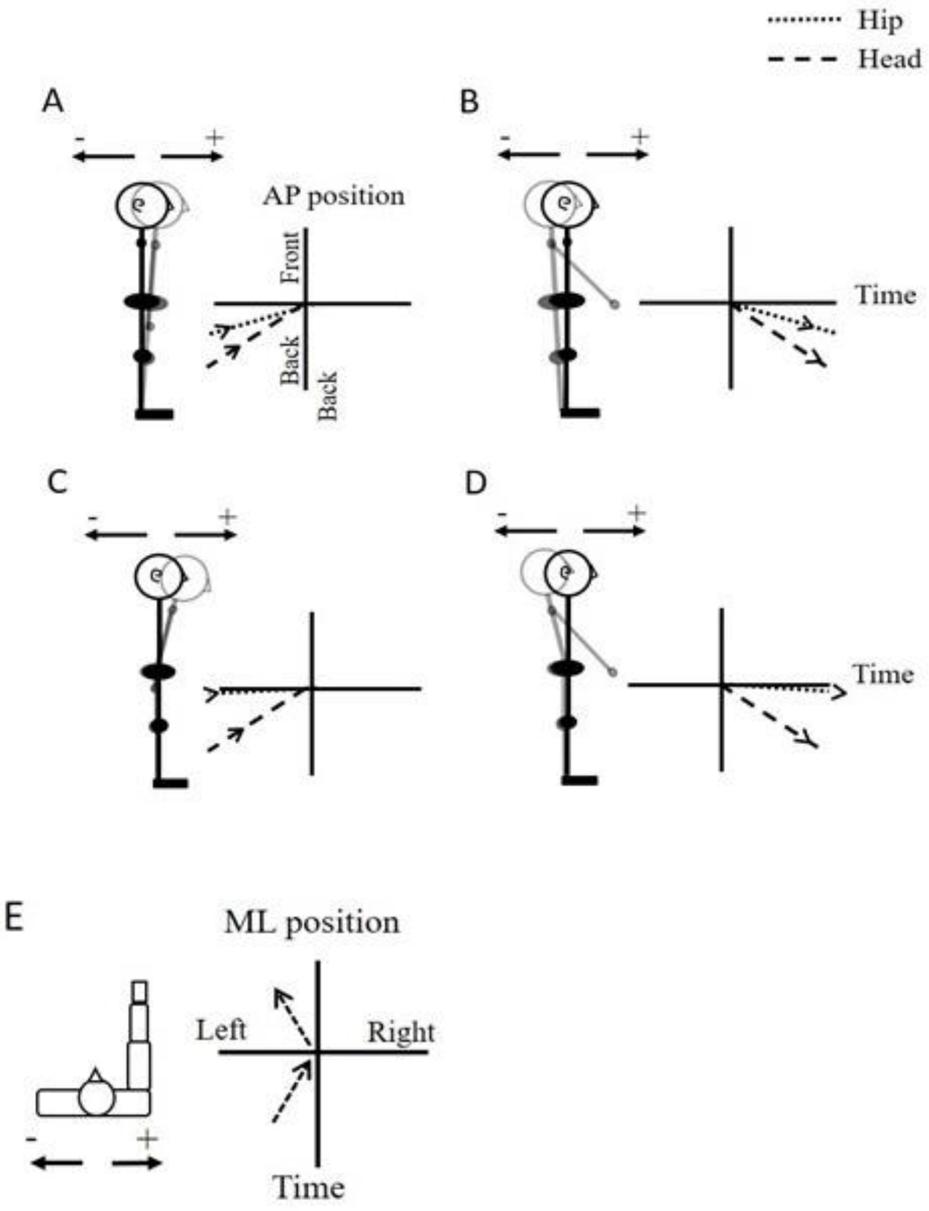

Figure 6. Continuing from Figure 1 in chapter 3. For the forward arm raises studied here, anticipatory postural motion in the anteroposterior plane is expected to be in the forward direction (**A, C**), and compensatory postural motion in the backward direction (**B, D**). Panel E shows the convention used to represent mediolateral postural motion (viewed from above). In this case, the vertical axis represents time, and the horizontal axis the mediolateral hip or head position. Figure 8 uses this convention. When the movement (or imagery) is of the dominant (right) arm, the expected anticipatory postural motion in the mediolateral plane is expected to be to the right, and the compensatory motion to the left (panel E).

METHOD

Participants

Twenty-two young (16 female, 6 male; age range 19-30) and twenty-two older (12 female, 10 male; age range 65–89) participants were recruited from the university and local communities, respectively, through existing research participant panels as described in Chapter 2. The inclusion criteria were the same as for Chapter 2. All were right-handed according to the Edinburgh handedness inventory (Oldfield 1971). Ethical approval for this research was granted by the Nottingham Trent University College of Business, Law and Social Sciences Research Ethics Committee.

All participants completed the standardized tests of cognitive functioning described in Chapter 2. Young (Y) and older (O) groups differed as expected, with significantly higher speed of information processing scores but lower vocabulary scores for Y than O (Salthouse 2010). The participant characteristics are summarized in Table 1.

	Old	Young
Age (yrs)	70.82 *(5.62)*	21.86 *(3.43)*
Height (cm)	170.05 *(8.04)*	168.14 *(10.92)*
Weight (kg)	66.18 *(13.06)*	70.36 *(16.20)*
EHI	95.45 *(9.87)*	94.32 *(8.39)*
Mill Hill	22.86 *(3.20)*	17.36 *(3.97)*
DSS	53.77 *(10.02)*	68.45 *(12.62)*

Table 4. Participant characteristic means with SD in parentheses. Independent t-tests showed younger participants had faster scores for SOP ($t(39.95) = -4.27$, $p < 0.001$) and older participants had better vocabulary scores ($t(40.17) = 5.06$, $p < 0.0001$). EHI Edinburgh Handedness Inventory, Mill Hill vocabulary, DSS digit symbol substitution test of information processing speed (from WAIS-R).

Apparatus

The experimental setup and measurement systems were identical to those used in Chapter 2.

Procedure

The experimental procedure was exactly as described for Chapter 2, except that participants raised (or imagined raising) the dominant arm only, and were asked not to engage the non-dominant arm at all. The onset and offset of movements were recorded by the participants, as described in Chapter 2, with the mouse held in the active (dominant) arm.

Self-initiated condition

The SI condition was conducted as in Chapter 2. The only difference was the manner in which trials were recorded. Each trial was recorded separately and initiated and ended by the experimenter. This was to avoid carry over effects that affected data collection in Chapter 2 (when a series of three movements were made by the participants per trial). For each trial, participants made one movement, with one mouse click when the arm movement started and another when it ended. Once two mouse clicks were recorded and the arm returned to the start position, the experimenter ended the recording before initiating the next trial. This set up allowed all movements to be included in the analysis.

Externally triggered condition

ET trials also followed the same sequence as described in Chapter 2, except that the trials were recorded individually, as described for the SI condition.

The only difference in this experiment between SI and ET trials was the instructions to participants.

Procedure for MI trials

The procedure for MI trials followed the same procedure described in Chapter 2, except that the trials recorded individually rather than in sets of three.

Practise trials

The procedure for practise trials followed the same procedure as in Chapter 2.

Data analysis

Data analysis focused on the anteroposterior (AP) and mediolateral (ML) postural motion of the hip and head segments, and the forward (horizontal) component of arm motion. Data analysis followed the procedure detailed in Chapter 2. In this experiment, a linear model was applied to anticipatory arm motion (APM) in most conditions. One APM trajectory was not linear but notably curved. This APM was in the ML direction under MI in the ET condition at the hip (Fig. 8, panel 2d).

RESULTS

Presented first are the APM and CPM results for postural motion in the AP direction in the self-initiated (SI) and externally triggered (ET) conditions. AP regression coefficients are shown in Table 5 and 6. Following this, results for postural motion in the ML direction are presented. ML regression coefficients are shown in Table 7 and 8. Finally, a summary of the results is presented with reference to figures 7 and 8.

AP Postural Motion

Self-Initiated Physical Movement

Anticipatory Postural Motion. At the hip (Fig. 7, panel 1b), O's movement was not statistically different to zero (χ^2 (1) = 2.56, p = 0.11). Y's forward motion of 1.08mm was significantly different to zero (χ^2 (1) = 5.82, p = 0.02). However, Y and O's displacement was not significantly different (χ^2 (2) = 1.59, p = 0.46). At the head (Fig. 7, panel 1a), O's forward motion of 1.28mm was statistically different to zero (χ^2 (1) = 4.02, p = 0.04). Y's forward motion of 1.04mm was not significantly different to zero (χ^2 (1) = 1.76, $p = 0.18$). Again, Y and O were not significantly different (χ^2 (2) = 0.18, $p = 0.91$).

Thus, O showed anticipatory forward movement at the head but not the hip. Whereas Y showed anticipatory movement at the hip but not the head. However, the two age groups did not differ in APM at either segment.

Compensatory postural motion. At the hip (Fig. 7, panel 1b), age, time, time^2 and the interaction between age and time were significant predictors of AP position. Y and O differed in their motion (χ^2(3) = 19.14, $p < 0.001$). At the head (Fig. 7, panel 1a), time and time^2 were significant predictors of position, but the two age groups did not differ (χ^2 (3) = 1.73, $p = 0.63$).

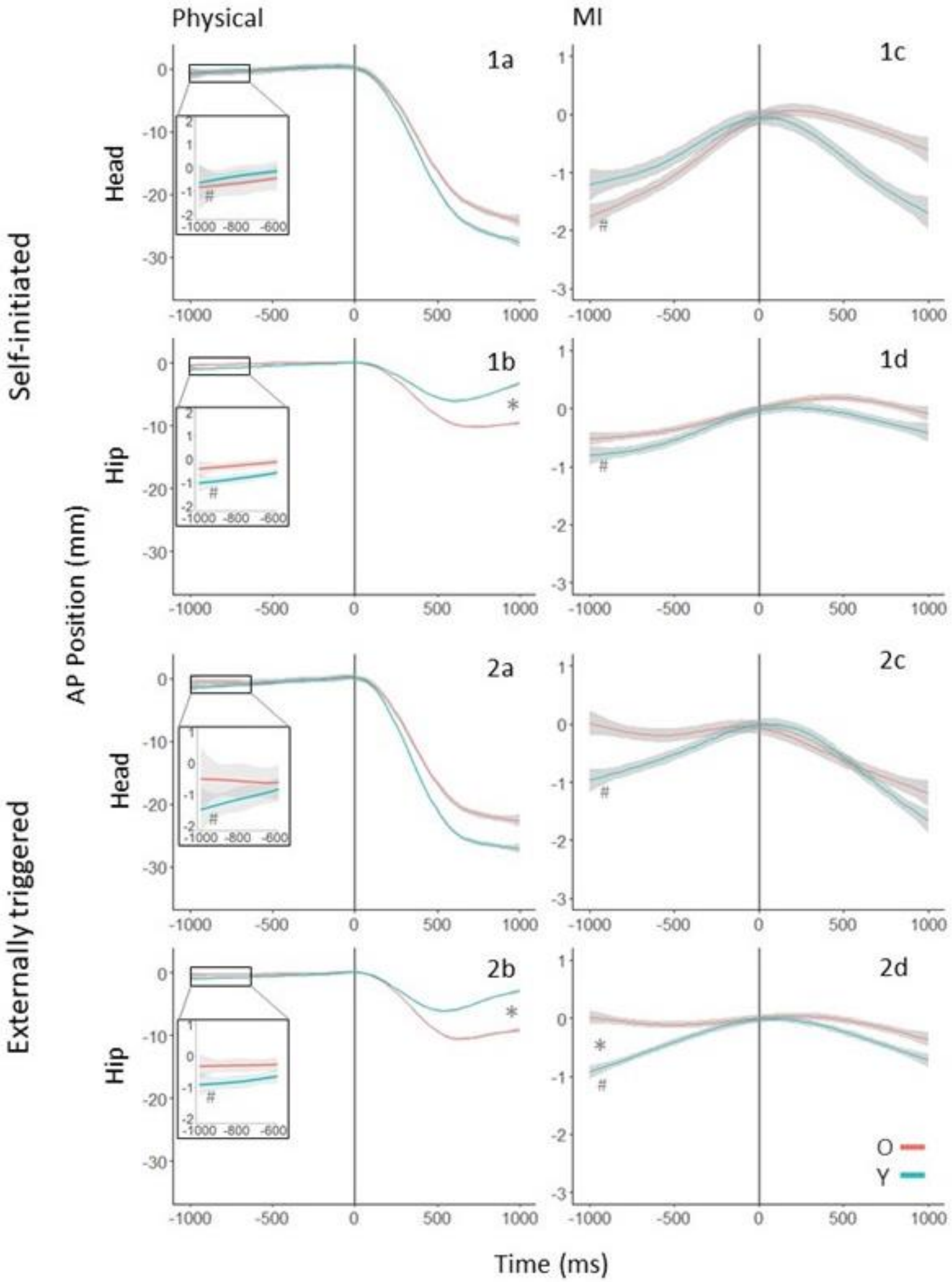

Figure 7. AP postural motion of the dominant (right) arm in the 1000ms preceding and following the onset of physical (a, b) and imagined (c, d) arm raising movements in the self-initiated (1a, 1b, 1c, 1d) and externally triggered conditions (2a, 2b, 2c, 2d). An upward deviation indicates forward movement, and a downward deviation indicates backwards movement. * between Y and O's trajectories indicates a statistically significant difference between the age groups. Trajectories marked with # have slopes significantly different to zero.

Fixed Effects	**Anticipatory (SELF-INITIATED)**				
		Head		**Hip**	
		Estimate	**(SE)**	**Estimate**	**(SE)**
Physical	**Intercept**	0.38*	0.17	0.11	0.08
	Time	0.37	0.21	0.13	0.11
	Age (young)	0.08	0.23	- 0.06	0.11
	Time*Age	- 0.07	0.29	0.18	0.15
MI	**Intercept**	- 0.08	0.15	- 0.06	0.09
	Time	0.53*	0.21	0.16	0.11
	Age (young)	0.06	0.21	- 0.01	0.13
	Time*Age	- 0.14	0.29	0.09	0.16

	Compensatory (SELF-INITIATED)				
		Head		**Hip**	
		Estimate	**(SE)**	**Estimate**	**(SE)**
Physical	**intercept**	- 14.02***	1.34	- 6.54***	0.53
	Time	- 558.56***	52.48	- 234.42***	20.54
	Time^2	100.72***	20.51	81.64***	10.74
	Age (young)	- 2.30	1.89	2.89***	0.75
	Time*Age	- 71.55	74.22	135.75***	29.05
	Time^2*Age	25.60	29.00	3.69	15.19
MI	**intercept**	0.20	0.16	0.16	0.08
	Time	- 0.21	0.21	- 0.04	0.13
	Age (young)	- 0.02	0.23	- 0.06	0.12
	Time*Age	- 0.35	0.30	- 0.10	0.18

Table 5. Regression coefficients of the theoretical model for anticipatory and compensatory AP postural motion recorded at the head and hip segments in the self-initiated condition. Signif. codes: '***' 0.001 '**' 0.01 '*' 0.05

O and Y's compensatory postural motion trajectories accompanying physical arm movement differed at the hip, but not at the head. At the hip, O showed greater backwards displacement than Y. Y moved back towards the pre-movement-onset position following the backwards motion, but O's hip motion did not show this recovery motion within the 1000ms window.

Self-Initiated MI

Anticipatory Postural Motion. At the hip (Fig. 7, panel 1d), O's forward movement of 0.53mm was not statistically different to zero (χ^2 (1) = 1.90, p = 0.17). Y's forward movement of 0.86mm was significantly different to zero (χ^2 (1) = 4.59, p = 0.03). However, Y and O's movement did not differ (χ^2 (2) = 0.37, p = 0.83). At the head (Fig. 7, panel 1c), O's forward movement of 1.80mm was statistically different to zero (χ^2 (1) = 5.72, p = 0.02). Y's forward movement of 1.31mm was not significantly different to zero (χ^2 (1) = 3.49, p = 0.06). Again, the age groups did not differ (χ2 (2) = 0.37, p = 0.83).

As in the physical condition, O showed anticipatory forward movement at the head but not the hip, whereas Y showed anticipatory forward movement at the hip but only slight forward motion at the head. The age groups did not differ from each other in either segment.

Compensatory Postural Motion. At the hip (Fig. 7, panel 1d) and head (Fig. 7, panel 1c), no significant effects were found. O and Y were not distinguishable from each other at either segment.

Externally Triggered Physical Movement

Anticipatory postural motion. At the hip (Fig. 7, panel 2b), O's forward movement of 0.37mm was not statistically different to zero (χ^2 (1) = 1.19, p = 0.28). Y's forward movement of 0.93mm was significantly different to zero (χ^2 (1) = 6.79, p = 0.01). However, Y and O statistically differ in their movement (χ^2 (2) = 1.85, p = 0.40). At the head (Fig. 7, panel 2a), O's forward movement of 0.66mm was not statistically different to zero (χ^2 (1) = 1.43, p = 0.23). Y's forward movement of 1.76mm was significantly different to zero (χ^2 (1) = 13.91, $p < 0.001$). Again, Y and O's movement were not significantly different (χ^2 (2) = 1.59, p = 0.46).

O did not show anticipatory motion at the head or hip, whereas Y did show significant forward motion at both segments. However, O and Y could not be statistically distinguished.

Compensatory postural motion. At the hip (Fig. 7, panel 2b), age, time, time^2, the interaction between age and time and the interaction between age and time^2 were significant predictors of AP position. Y and O's trajectories differed significantly (χ^2 (3) = 19.04, $p < 0.001$). At the head (Fig. 7, panel 2a), age, time and time^2 were significant predictors of position. However, Y and O's motion could not be statistically distinguished from each other (χ^2 (3) = 5.23, p = 0.16).

O and Y's postural motion trajectories accompanying physical arm movement differed at the hip, O showing less recovery than Y. However, the two age groups were not statistically different.

Externally Triggered MI

Anticipatory postural motion. At the hip (Fig. 7, panel 2d.), O’s movement was not statistically different to zero (χ^2 (1) = 0.01, p = 0.93). Y’s forward movement of 0.95mm was significantly different to zero (χ^2 (1) = 10.04, p = 0.002). Age was found to have an effect on anticipatory movement, as Y and O’s displacement was significantly different (χ^2 (2) = 7.07, p = 0.03). At the head (Fig. 7, panel 2c), O’s motion was not statistically different to zero (χ^2 (1) = 0.02, p = 0.90). Y’s forward movement of 1.02 mm was significantly different to zero (χ^2 (1) = 5.11, p = 0.02). However, Y and O’s movements were not statistically distinguishable from each other (χ^2 (2) = 2.17, p = 0.34).

O did not show anticipatory motion at the hip or head. While Y did show forward anticipatory motion at both segments, only at the hip were Y and O statistically different.

Compensatory postural motion. At the hip (Fig. 7, panel 2d) and head (Fig. 7, panel 2c), no significant effects were found. O and Y were not significantly distinguishable from each other at either segment.

Fixed Effects	**Anticipatory (EXTERNALLY TRIGGERED)**				
		Head		**Hip**	
		Estimate	**(SE)**	**Estimate**	**(SE)**
Physical	**Intercept**	- 0.07	0.14	- 0.01	0.07
	Time	0.19	0.14	0.11	0.10
	Age (young)	0.31	0.19	- 0.07	0.10
	Time*Age	0.32	0.20	0.16	0.14
MI	**Intercept**	- 0.08	0.13	- 0.08	0.08
	Time	0.02	0.14	- 0.01	0.08
	Age (young)	0.08	0.18	0.12	0.11
	Time*Age	0.28	0.20	0.29*	0.12

	Compensatory (EXTERNALLY TRIGGERED)				
		Head		**Hip**	
		Estimate	**(SE)**	**Estimate**	**(SE)**
Physical	**intercept**	- 13.85***	1.28	- 6.84***	0.56
	Time	- 526.53***	57.13	- 223.44***	23.49
	Time^2	127.92***	17.66	106.77***	10.55
	Age (young)	- 3.27	1.81	3.16***	0.79
	Time*Age	- 95.66	80.80	151.88***	33.22
	Time^2*Age	47.02	24.98	- 6.55	14.92
MI	**intercept**	- 0.01	0.15	0.13	0.09
	Time	- 0.35	0.22	- 0.12	0.12
	Age (young)	0.30	0.21	- 0.01	0.12
	Time*Age	- 0.20	0.31	- 0.11	0.18

Table 6. Regression coefficients of the theoretical model for anticipatory and compensatory AP postural motion recorded at the head and hip segments in the externally triggered condition. Signif. codes: '***' 0.001 '**' 0.01 '*' 0.05

ML Postural Motion

Self-Initiated Physical Movement

Anticipatory postural motion. At the hip (Fig. 8, panel 1b), O's movement was not statistically different to zero (χ^2 (1) = 0.15, p = 0.70). Y's rightward movement of 1.93mm was significantly different to zero (χ^2 (1) = 12.58, $p < 0.001$). Y and O's movements were significantly different (χ^2 (2) = 8.23, p = 0.02). At the head (Fig. 8, panel 1a), O's movement was not statistically different to zero (χ^2 (1) = 0.15, p = 0.70). Y's movement was also not significantly different to zero (χ^2 (1) = 2.77, p = 0.10). However, Y and O's movements were significantly different (χ^2 (2) = 6.38, p = 0.04).

At the hip, O showed no APM, whereas Y showed APM to the right. This age difference was significant. At the head, O showed a slight leftward tendency, and Y a rightward tendency. Neither of these trajectories was significantly different to zero, but they were significantly different from each other.

Compensatory postural motion. At the hip (Fig. 8, panel 1b) and head (Fig. 8, panel 1a), no significant effects were found. O and Y were not significantly distinguishable from each other at either segment.

Self-Initiated MI

Anticipatory Postural Motion. At the hip (Fig. 8, panel 1d), no significant results were found. At the head (Fig. 8, panel 1c), O's rightward movement of 0.92mm was statistically different to zero (χ^2 (1) = 6.78, p = 0.01). Y's movement was not statistically different to zero (χ^2 (1) = 2.32, p = 0.13). Age was found to have an effect, as Y and O's displacements significantly differed (χ^2 (2) = 8.96, p = 0.01).

O but not Y exhibited anticipatory rightward motion at the head. This difference between O and Y was significant. At the hip, both age groups showed no difference in APM.

Compensatory Postural Motion. At the hip (Fig. 8, panel 1d) and head (Fig. 8, panel 1c), no significant effects were found. O and Y were not significantly distinguishable from each other at either segment.

Fixed Effects	**Anticipatory (SELF-INITIATED)**				
		Head		**Hip**	
		Estimate	**(SE)**	**Estimate**	**(SE)**
Physical	**Intercept**	0.18	0.10	- 0.75**	0.23
	Time	- 0.08	0.19	0.04	0.13
	Age (young)	0.27	0.14	- 0.26	0.32
	Time*Age	0.33	0.27	0.52**	0.18
MI	**Intercept**	0.06	0.06	0.01	0.06
	Time	0.27**	0.09	- 0.07	0.07
	Age (young)	- 0.05	0.09	- 0.02	0.09
	Time*Age	- 0.40**	0.13	- 0.04	0.10

	Compensatory (SELF-INITIATED)				
		Head		**Hip**	
		Estimate	**(SE)**	**Estimate**	**(SE)**
Physical (order 2)	**intercept**	- 1.04	0.64	- 0.64	0.98
	Time	- 22.78	28.25	139.97**	43.92
	Time^2	11.12	12.47	185.37***	22.55
	Age (young)	0.80	0.90	- 1.02	1.38
	Time*Age	59.96	39.95	- 12.42	62.12
	Time^2*Age	7.17	17.63	48.36	31.89
MI (linear)	**intercept**	0.01	0.07	0.12	0.07
	Time	- 0.29*	0.12	- 0.13	0.10
	Age (young)	- 0.05	0.10	- 0.19*	0.09
	Time*Age	0.11	0.16	0.10	0.14

Table 7. Regression coefficients of the theoretical model for anticipatory and compensatory ML postural motion recorded at the head and hip segments in the self-initiated condition. Signif. codes: ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05

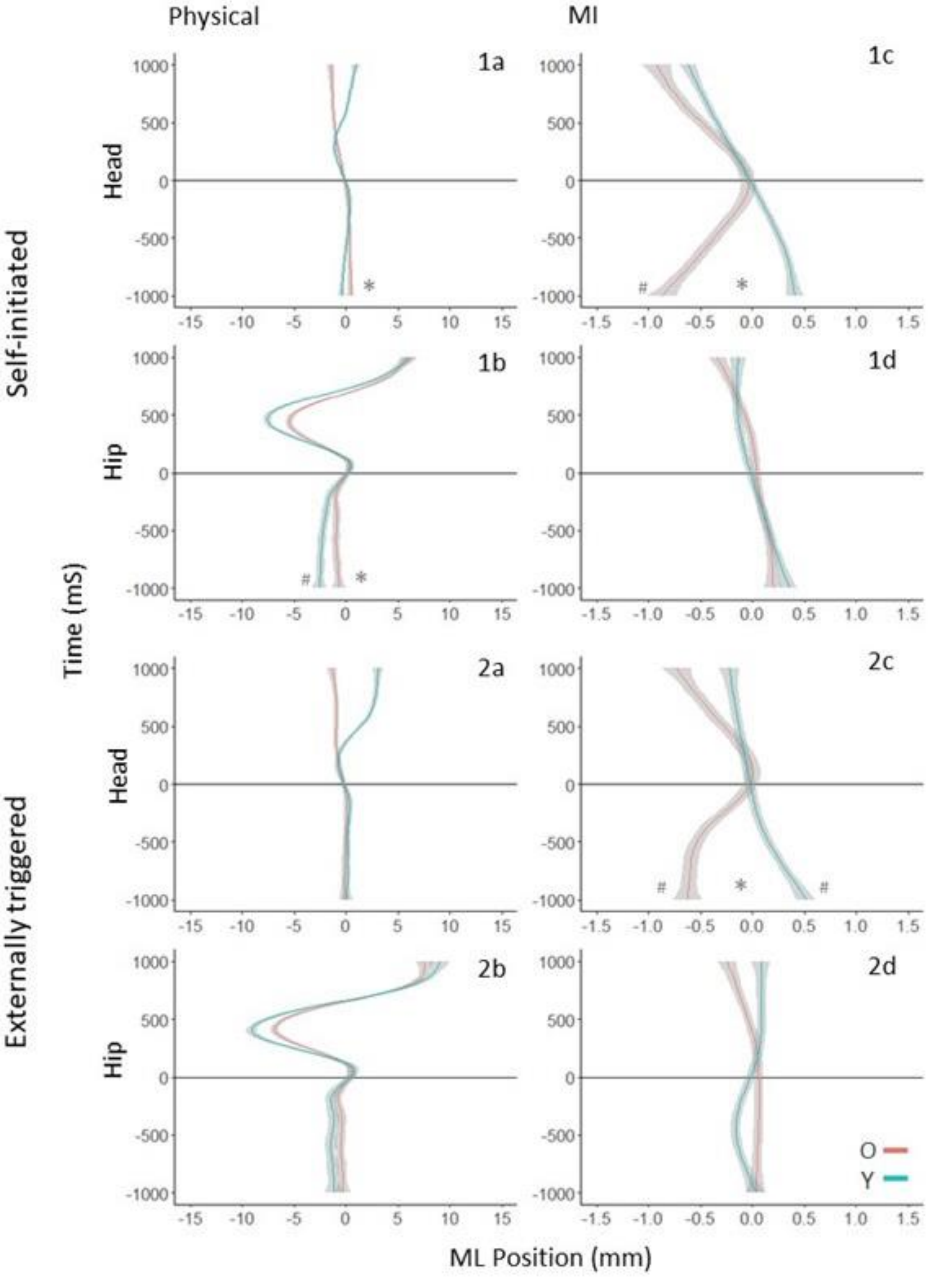

Figure 8. ML postural motion of the dominant (right) arm in the 1000ms preceding and following the onset of physical (a, b) and imagined (c, d) arm raising movements in the self-initiated (1a, 1b, 1c, 1d) and externally triggered conditions (2a, 2b, 2c, 2d). An upward deviation indicates forward movement, and a downward deviation indicates backwards movement. * between Y and O's trajectories indicates a statistically significant difference between the age groups. Trajectories marked with # have slopes significantly different to zero.

Externally Triggered Physical Movement

Anticipatory postural motion. At the hip (Fig. 8, panel 2b) and head (Fig. 8, panel 2a), no significant effects were found. O and Y were not significantly distinguishable from each other or zero at either segment.

Compensatory postural motion. At the hip (Fig. 8, panel 2b) and head (Fig. 8, panel 2a), no significant effects were found. O and Y were not significantly distinguishable from each other at either segment.

Externally Triggered MI

Anticipatory Postural Motion. At the hip (Fig. 8, panel 2d), no significant effects were found. At the head (Fig. 8, panel 2c), O's right trajectory of 0.63mm was statistically different to zero (χ^2 (1) = 3.88, p = 0.049). Y's left movement of -0.58mm was also significantly different to zero (χ^2 (1) = 4.12, p = 0.04). Age was found to have an effect as Y and O's displacement was significantly different (χ^2 (2) = 7.97, p = 0.02).

Both O and Y exhibited significant anticipatory motion, O moving to the right and Y the left. The difference between O and Y was significant.

Compensatory Postural Motion. At the hip (Fig. 8, panel 2d) and head (Fig. 8, panel 2c), no significant effects were found. O and Y were not significantly distinguishable from each other at either segment.

Fixed Effects	**Anticipatory (EXTERNALLY TRIGGERED)**				
		Head		**Hip**	
		Estimate	**(SE)**	**Estimate**	**(SE)**
Physical	**Intercept**	0.14	0.09	- 0.51**	0.17
	Time	0.12	0.11	- 0.03	0.10
	Age (young)	0.14	0.13	- 0.46	0.23
	Time*Age	- 0.06	0.16	0.17	0.14
MI (order 2 polynomial at hip)	**Intercept**	- 0.13	0.08	0.04	0.11
	Time	0.18*	0.09	- 0.34	4.07
	Time^2	n/a		- 1.09	2.52
	Age (young)	0.03	0.11	- 0.14	0.16
	Time*Age	- 0.35**	0.12	- 1.50	5.76
	Time^2*Age	n/a		5.14	3.56

	Compensatory (EXTERNALLY TRIGGERED)				
		Head		**Hip**	
		Estimate	**(SE)**	**Estimate**	**(SE)**
Physical (order 2)	**intercept**	- 0.91	0.86	- 0.22	1.31
	Time	- 12.66	36.72	211.23***	57.87
	Time^2	3.17	10.67	221.99***	23.60
	Age (young)	2.12	1.22	- 0.55	1.85
	Time*Age	110.18*	51.93	34.33	81.84
	Time^2*Age	- 3.96	15.08	59.38	59.38
MI (linear)	**intercept**	0.12*	0.06	0.15*	0.07
	Time	- 0.25	0.12	- 0.12	0.10
	Age (young)	- 0.14	0.08	- 0.10	0.10
	Time*Age	0.18	0.18	0.13	0.14

Table 8. Regression coefficients of the theoretical model for anticipatory and compensatory ML postural motion recorded at the head and hip segments in the externally triggered condition. Signif. codes: ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05

Arm movement peak velocity and its latency

For the experimental conditions in which the arm raise was physically performed, I investigated whether there were any age-related differences in the peak velocity attained by the arm and in the latency at which this occurred. The theoretical model was a varying intercept and slope model predicting the right hand's peak AP velocity and its latency with age and time as fixed effects and participants as a random effect. I compared this model with a test model that excluded the age coefficient.

Figure 9 shows peak arm velocity and it's latency for O and Y. In the SI condition, there was no difference between Y and O's peak velocity ($\chi2$ (1)=0.82, p=0.36) or its latency ($\chi2$ (1)=3.38, p=0.07). In the ET condition, there was no difference between Y and O's peak velocity ($\chi2$ (1)=0, p=0.998) or its latency ($\chi2$ (1)=3.65, p=0.06).

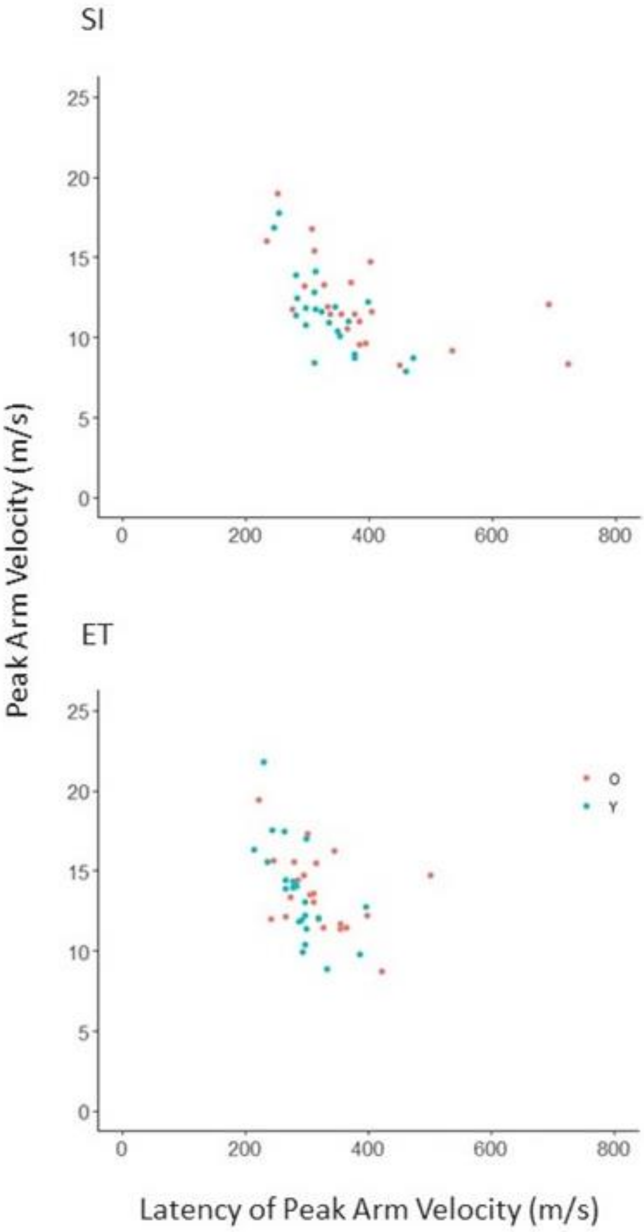

Figure 9. Peak arm velocity and its latency of the dominant arm in the self-initiated (SI) and externally triggered (ET) conditions.

Arm motion during MI

In the experimental conditions in which the arm raise was to be imagined but not performed, I analysed whether the arm exhibited any systematic forward or backward motion in the 1000ms before or after the start of MI (indicated by participants' mouse click). I used the same strategy as in the analysis of postural motion—the test model was a varying intercept and slope model predicting the right hand's AP position with time as a fixed effect and participants as a random effect. This model was compared with a baseline model that excluded the time coefficient. I rejected the null hypothesis (no AP displacement in this time period) if the test model fit the data significantly better than the null model.

In the SI condition, O showed no significant arm motion in the pre-MI period ($\chi2(1) = 1.34$, $p = 0.25$) and Y also showed no significant forward motion ($\chi2(1) = 3.76$, $p = 0.053$). During the MI period, O showed no significant arm motion ($\chi2(1) = 0.01$, $p = 0.90$), and neither did Y ($\chi2(1) = 0.36$, $p = 0.55$).

In the ET condition, O showed no significant arm motion in the pre-MI period ($\chi2(1) = 1.14$, $p = 0.29$). Y did show significant forward motion ($\chi2(1) = 6.89$, $p = 0.01$), however, the magnitude of 1.20mm was comparable to the 1.02mm of head motion recorded in this time period. During the MI period, O showed no significant arm motion ($\chi2(1) = 3.19$, $p = 0.07$), and neither did Y ($\chi2(1) = 1.83$, $p = 0.18$).

These results show that arm motion was comparable to postural motion recorded from the upper body. I concluded, therefore, that both O and Y successfully inhibited focal arm movement during 1000ms before and after self-reported MI onset.

Postural sway in the quiet stance baseline condition

Figures 10 and 11 show participants' sway pattern during 1000ms preceding and following the midpoint of the average 2000ms time window during the baseline trial. This midpoint was shifted such that the coordinate value had a t=0 and an AP and ML position coordinate of zero, as was applied in the main postural analysis for movement onset position.

Under ML sway it can be seen that sway relative to an arbitrary time point during quiet stance has lower dispersion than was observed around the onset of physical and imagined arm movements in the experimental conditions. We performed the same statistical modelling on this data as in the experimental conditions and found no significant linear trends.

Under AP sway Y again show no significant changes in postural sway. O, however, demonstrate a larger sway pattern before the arbitrary time point but only at the head ($\chi2(2) = 6.55$, $p = 0.04$). Whilst this significant difference was seen, this is not entirely unexpected due to the greater variation in baseline sway typically exhibited in older adults (Roman-Liu, 2018).

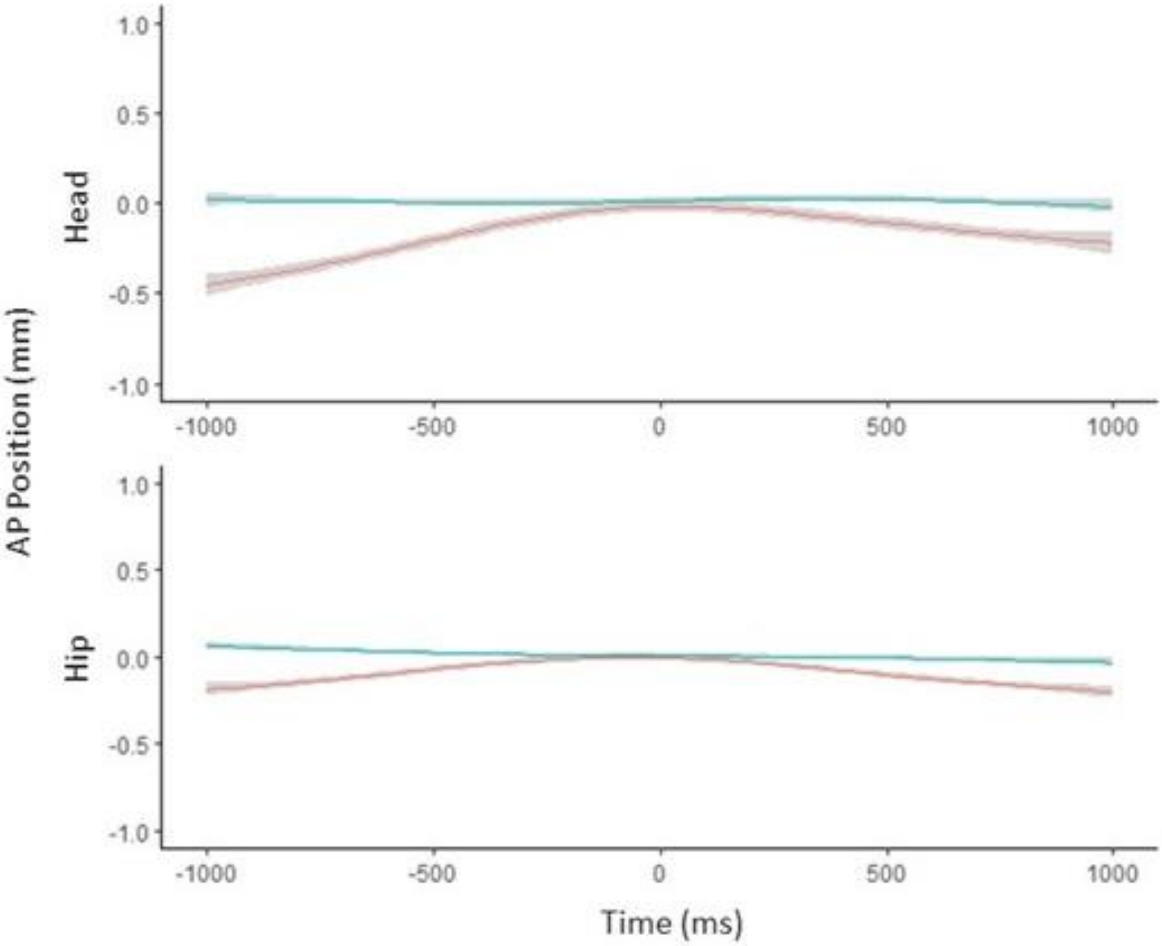

Figure 10. Average AP postural motion over 2000ms time windows during 60 second quiet stance baseline condition.

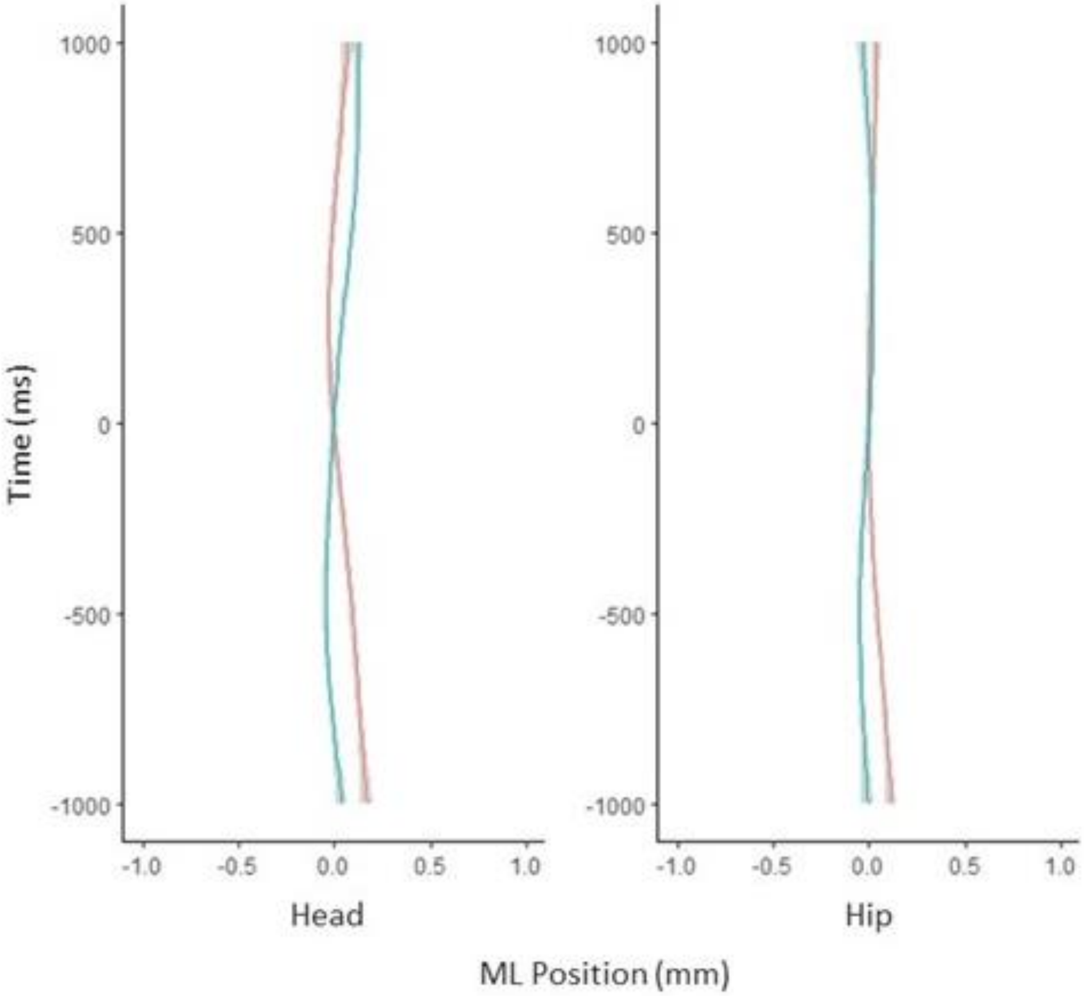

Figure 11. Average ML postural motion over 2000ms time windows during 60 second quiet stance baseline condition.

Results Summary

I consider postural motion in the AP direction first. When making physical movements of the dominant arm in the self-initiated condition, O showed indications of APM in the AP direction (at the head), but this was not the case when they made the movements in the externally triggered condition (compare Fig 7, 1a and 2a). In contrast, Y showed APM in both the task conditions (at the hip). When imagining the movements, both age groups showed APM in the self-initiated condition, but in the externally triggered condition, only Y showed APM (compare Fig 7, 1c/d with 2c/d). In the period following the onset of physical arm movement, in both the self-initiated and externally triggered condition, O showed a larger backward CPM (at the hip) than Y (Fig 7, 1b and 2b). No statistical differences were found in the MI conditions.

Next, I consider postural motion in the ML direction. When making physical movements of the dominant arm in the self-initiated condition, Y showed APM in the ML direction (Fig. 8, 1b). This was not the case for the head or the hip in the externally triggered condition (Fig. 8, 2a and 2b). O did not show any APM at the head or the hip in self-initiated or externally triggered conditions. When imagining the movements, O showed APM in both conditions but only in the head segment. Y did not show APM in either condition or body segment.

Following the onset of physical or imagined arm movement, no significant ML deviations were detected for either age group in any condition or body segment.

DISCUSSION

The purpose of this experiment was to investigate Y and O's postural motion immediately preceding and following the onset of unilateral arm movements and imagery. Y and O performed or imagined straight-arm raises of the dominant under self-initiated and externally triggered conditions. Y and O's arm velocity profiles and times to peak velocity did not differ across experiments and conditions. I will first consider CPM and APM patterns for physical arm movements and then discuss postural motion accompanying manual MI.

When an arm is raised in front of the body, the CG moves forward, necessitating a backward CPM to maintain stability as the movement occurs (Bouisset and Zattara 1981, 1987b, 1988, 1990; Friedli et al., 1988; Mouchnino et al., 1992; Ramos & Stark, 1990; Rogers & Pai, 1990). For forward movements of either arm, CPMs of both Y and O showed backward postural movement in the first 500ms following movement onset in both conditions and experiments (Fig. 7). Following this, Y's but not O's hip motion reversed direction, as head motion continued backwards in both groups. This pattern is consistent with the use of backward bending of the trunk to regulate CG (Martin 1967) in Y, as was also observed in Chapter 2 for bilateral arm raises. In the ML direction, CPMs to the left for dominant (right) arm raises (Fig. 8) were observed at the hip in both task conditions. This suggests that unilateral forward arm raises generate a lateral perturbation that is counteracted by a hip movement to the inactive side.

Any anteroposterior APM that occurs prior to forward arm movements are expected to be in the forward direction, opposite to the backward CPMs observed during the movements themselves (Bleuse et al. 2006; Cordo and Nashner 1982). In the present case of dominant arm movement, Y showed APM at the hip in the SI condition and the head and hip in the ET condition (Fig. 7). O only showed APM at the head in SI, and none in ET. The perturbation due to arm motion was predictable in both occurrence and timing in the SI condition. Thus, a forward APM was expected, as was seen in Y.

O again showed APM at the head in the SI condition, but no APM in the ET condition at the head or hip. This absence of O’s APMs in the ET condition replicated the pattern seen in Chapter 2 in the case of bilateral arm raises. In the ET condition, a random delay between the ready and go signals did not allow participants to predict the exact time of movement onset. O’s lack of APM under these conditions suggests a lack of preparatory postural action in O when an expected movement must be coordinated with an external perceptual event. As discussed shortly, the results of the MI conditions corroborate this.

Any mediolateral APM preceding dominant (right) arm movement would be to the right. The only indication of APM to the right was seen in Y at the hip in the SI condition (Fig. 8, panel 1b). Y did not show lateral APM in the ET condition, and O did not in ET or SI. I return to these results in the context of the MI results discussed next.

I turn next to the postural motions observed when the arm movements were imagined rather than executed. For MI of the dominant arm, Y showed anteroposterior APM at the hip in SI and at the hip and head in ET (Fig. 7, panels 1d, 2c, 2d). O showed APM at the head in SI, but no APM in ET. In the mediolateral direction, Y did not show APM in any MI condition. O, however, showed APM at the head in both conditions (Fig. 8, panels 1c, 2c).

The MI results of anteroposterior APM showed a similar pattern to Chapter 2’s results for bilateral arm raises. As in the case of physical movements in the ET condition, O did not show anteroposterior APM (whereas Y did) when MI onset was triggered by an external signal. This suggests a lack of postural preparation when the planned movement’s onset must be coordinated with an external event. It is likely linked to the sensory integration deficits that characterise postural control in older age (Redfern et al., 2001; Teasdale et al., 1991). Everyday life includes numerous instances in public places or social settings in which a particular movement can be foreseen and planned for, but its execution must await the arrival of an external sensory signal. For example, observing an acquaintance approaching can prime the motor planning of reaching for a handshake. However, the start of the movement must await a comfortable inter-personal distance and facial or linguistic signals. O have been shown previously to produce smaller and more delayed APA (Inglin & Woollacott, 1988; Woollacott & Manchester, 1993). The observed absence of anteroposterior APM during MI suggests that there is a general age-related deficit in the planning of postural support in the ET condition, irrespective of whether both arms or the dominant arm is to be deployed.

I did not observe any indications of mediolateral APM by Y in either of the MI conditions. Y's mediolateral APM preceding physical movement of the dominant arm in the SI condition (Fig. 8, panel 1b) suggests that mediolateral APM is indeed a feature of postural support for unilateral arm raises to the front of the body. This component may be small enough that it was not expressed by Y during MI trials. O, however, did show mediolateral APM for MI of the dominant arm in both the SI and ET conditions (Fig. 8, panels 1c and 2c). This suggests that O planned postural support for a mediolateral perturbation when imagining forward movements of the dominant arm. One reason for this may be that O needed to plan a mediolateral APM when imagining raising the dominant arm because the expected perturbation would be to the weaker, non-dominant side. It is worth noting in this context that the ML direction is considered more important than AP for stepping out in case of falling (Lord et al., 1999; Rogers & Mille, 2003). The anticipatory head (but not hip) motion to the dominant side that was observed in O could indicate the use of a hip strategy to reduce the perceived likelihood of needing to step to the left.

The first of two final points worth noting about the pattern of results is that there were several instances in which O showed APM at the head where Y did not. For anteroposterior APM, these included the physical movement and MI trials in the SI condition. For mediolateral APM, this was seen in the case of MI in both the SI and ET conditions. APM at the head but not the hip, particularly in the case of MI, where the planned postural perturbation does not in fact occur, suggests the use of a hip strategy (Horak and Nashner, 1986), to which O are known to be more prone (Bleuse et al., 2006; Inglin & Woollacott, 1988; Lin et al., 2004), but, in fact, this may be more destabilizing in the context of MI than APM involving a shift of hip position. Further work is needed to closely inspect whether O’s APMs have a greater tendency to incorporate leaning of the upper body consistent with a hip strategy. Also, as noted above, O but not Y showed mediolateral APM preceding MI of the dominant arm. In both these conditions, the expected postural perturbation impacted the weaker, non-dominant side of the body. O appear to have been sensitive to this in their postural planning.

CHAPTER 4: Age-related differences in postural control during physical and imagined unilateral raises of the non-dominant arm

INTRODUCTION

Chapter 3 focused on postural control just before and after the onset of physical and imagined arm movement in the case of unilateral raises of the dominant arm. Because unilateral arm movements are more likely to perturb posture in the ML direction, AP and ML movement trajectories were analysed. In the AP direction results supported findings from Chapter 2. When the movement was performed at the participants' own pace, O and Y both showed forward APM. When participants performed the movement in response to a trigger of uncertain timing, Y did show forward APM, whereas O did not. This suggested that O had deficits in incorporating the timing of the APM into their motor plan. Observations in the ML direction showed further age-related differences in movement planning. During MI in both SI and ET conditions, O showed significant APM to the right at the head, whereas Y did not. This suggests that O's anticipatory postural action adopted a hip strategy along the ML plane.

This Chapter builds on these results by examining the case of raising movements and MI of the non-dominant arm. Previous research suggests that postural strategies that accompany raises of the dominant and non-dominant arm are asymmetrical, but the exact nature of this asymmetry is unclear. There is evidence that movements of the dominant and non-dominant arm differ in the postural adjustments they elicit. Teyssèdre et al. (2000) showed, for example, that asymmetry of postural adjustment during dominant and non-dominant arm movements depends on the body's level of stability. When stable, APAs started earlier, and arm velocity was higher for the dominant arm. When less stable, arm velocities did not differ, but greater postural muscle activity occurred for movements of the non-dominant arm. Hunag (2009) reported that Y and O's APA amplitude and duration were greater for reaches of the dominant arm. Blaszczyk et al. (2000) reported body weight asymmetry during raises of the dominant and nondominant arm in O, but this was not specific to one side of the body or the other. They suggested that this was linked to the need to accommodate a potential stepping action in the case of loss of balance. Sadeghi et al. (2001) suggested that the dominant and non-dominant legs have different functions - the dominant leg's function is to move the body forward and the non-dominant leg's is to ensure safe transfer of body weight.

Considering the posture changes that occurred during MI in Chapter 3, postural changes during non-dominant arm raises should act in a way opposite to the dominant arm. Posture should shift to the left in preparation for compensatory motion to the right (Fig. 12). The movements studied in this chapter were forward arm raises of the non-dominant arm that produced a backward postural perturbation in the AP plane. In general, anticipatory postural action (moving the body forward) should be less prominent for physical or imagined movements of the non-dominant arm than was observed for the dominant arm. In the ML plane, anticipatory postural motion associated with raising the non-dominant arm should generate lateral movement toward the dominant side of the body. As this perturbation would affect the stronger side of the body, the magnitude of this APM should be smaller than that produced by the dominant arm. Assuming that this perturbation may be less destabilizing than in the case of dominant arm raises, and more so in O than Y (as mediolateral stability is more affected in O), anticipatory postural action in the ML direction should also be greater for O than Y, but less prominent than that observed for the dominant arm's movement or imagery.

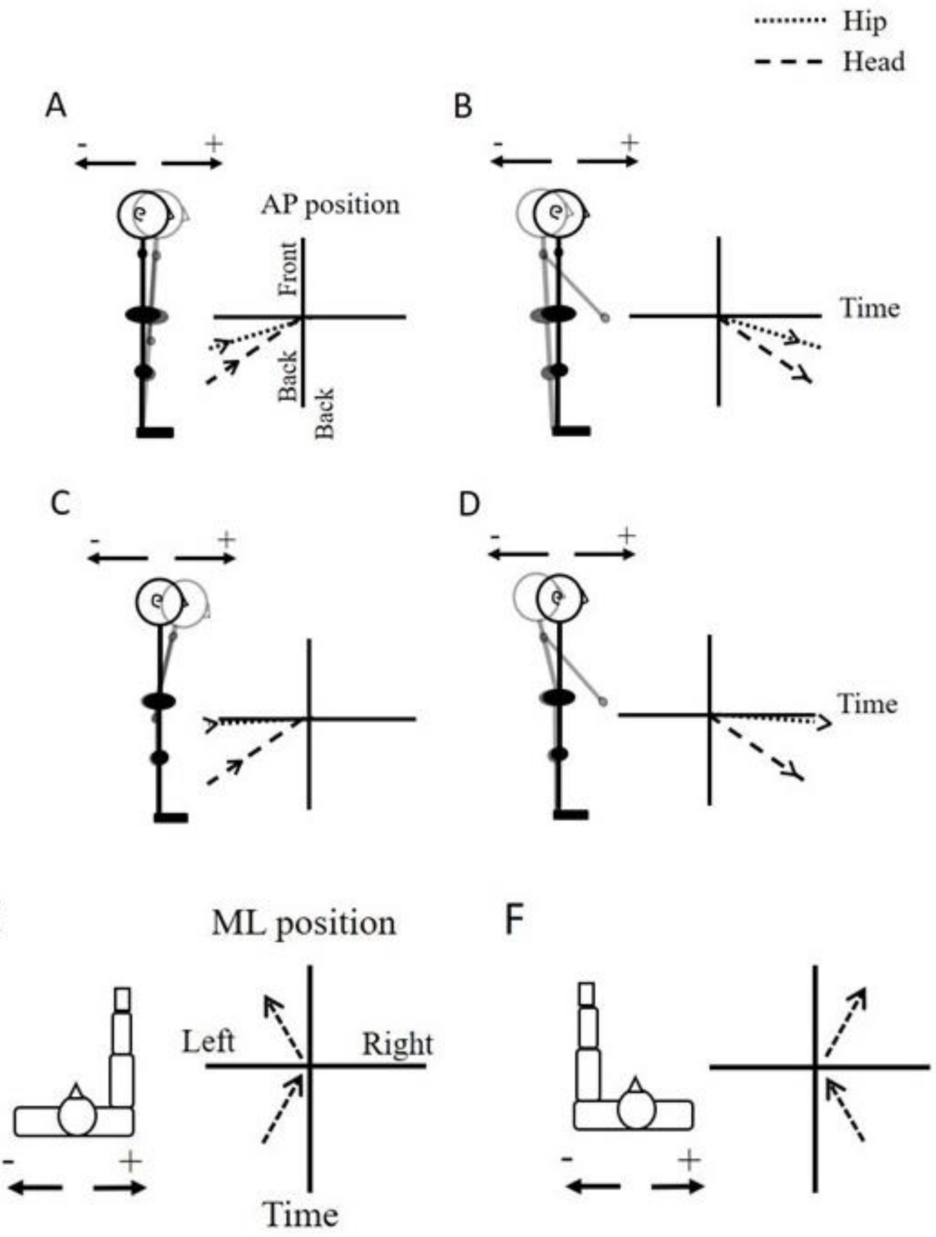

Figure 12. Representation of anticipatory and compensatory postural motion. Panels **A**-**D** show anteroposterior postural motion, where the vertical axis represents anteroposterior (AP) hip or head position and the horizontal axis represents time. The origin is at the onset of arm movement (or imagery). The time and hip and head positions at this moment are set to zero. Figure 10 uses the convention shown in panels **A**-**D**. Panel **A** shows how forward motion made at the ankle joint would be represented, and panel **B** shows the corresponding backward motion. Panels **C** and **D** show the same movements made at the hip. For the forward arm raises, anticipatory postural motion in the anteroposterior plane is expected to be in the forward direction (**A**, **C**), and compensatory postural motion in the backward direction (**B**, **D**). Panels **E** and **F** show the convention used to represent mediolateral postural motion (viewed from above). In this case, the vertical axis represents time, and the horizontal axis the mediolateral hip or head position. Figure 11 uses this convention. When the movement (or imagery) is of the dominant (right) arm, the expected anticipatory postural motion in the mediolateral plane is expected to be to the right, and the compensatory motion to the left (panel **E**). For the movement (or imagery) of the non-dominant (left) arm, the expected anticipatory postural motion in the mediolateral plane is expected to the left, and the compensatory motion to the right (panel **F**).

METHOD

The participants, experimental protocol and set up, as well as data collection and analysis methodology were the same as in Chapter 3, except that the participants raised or imagined raising their non-dominant arm. The onset and offset of movements were recorded by the participants, as described in Chapter 2, with the mouse held in the active (non-dominant) arm.

Data analysis

Data analysis focused on the anteroposterior (AP) and mediolateral (ML) postural motion of the hip and head segments, and the forward (horizontal) component of arm motion. Data analysis followed the procedure detailed in Chapter 2. In this experiment, a linear model was applied to anticipatory arm motion (APM) in most conditions. One APM trajectory was not linear but notably curved. This APM was in the ML direction under MI in the SI condition at the hip (Fig. 14, panel 1d). Here, a second order polynomial was applied. For compensatory postural motion (CPM), in all physical arm movement conditions a second order polynomial was applied to the data. For most MI movement conditions in this period a linear model was applied to the data. One CPM trajectory was notably curved, and so a second order polynomial was applied to the data. This CPM was in the ML direction under MI in the ET condition at the head (Fig. 14, panel 2c).

RESULTS

Presented first are results for APM and CPM in the AP direction in the self-initiated (SI) and externally triggered (ET) conditions. AP regression coefficients are shown in Tables 9 and 10. Following this, results for postural motion in the ML direction are presented. ML regression coefficients are shown in Tables 11 and 12. Finally, I provide a summary of all the results with reference to figures 13 and 14.

AP Postural Motion

Self-Initiated Physical Movement

Anticipatory postural motion. At the hip (Fig. 13, panel 1b), O's forward movement of 0.60mm was statistically different to zero (χ^2 (1) = 4.30, p = 0.04). Y's forward movement of 0.51mm was also significantly different to zero (χ^2 (1) = 4.54, p = 0.03). However, Y and O's movements were not significantly different from each other (χ^2 (2) = 0.47, p = 0.79). At the head (Fig. 13, panel 1a), O's forward movement of 2.19mm was statistically different to zero (χ^2 (1) = 4.77, p = 0.03). Y's movement was not significantly different to zero (χ^2 (1) = 0.01, p = 0.93). Y and O's trajectories were significantly different (χ^2 (2) = 14.74, $p < 0.001$).

O and Y exhibited similar anticipatory forward motion at the hip, and the age difference was not significant. At the head, O showed forward motion while Y did not show any deviation from zero. This age difference was also significant.

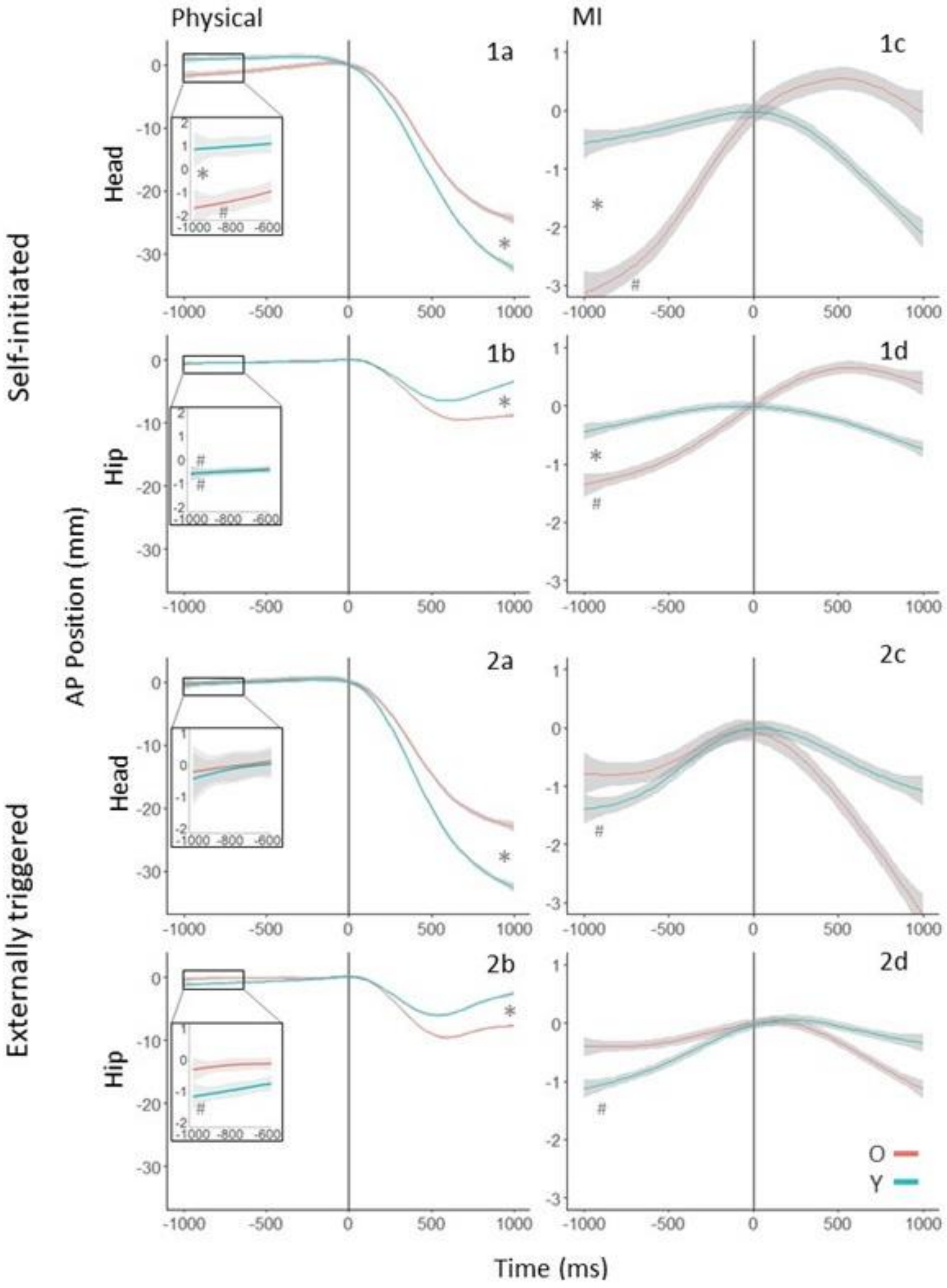

Figure 13: AP postural motion of the non-dominant (left) arm in the 1000ms preceding and following the onset of physical (a, b) and imagined (c, d) arm raising movements in the self-initiated (1a, 1b, 1c, 1d) and externally triggered conditions (2a, 2b, 2c, 2d). An upward deviation indicates forward movement, and a downward deviation indicates backwards movement. * between Y and O's trajectories indicates a statistically significant difference between the age groups. Trajectories marked with # have slopes significantly different to zero.

Fixed Effects	**Anticipatory (SELF-INITIATED)**				
		Head		**Hip**	
		Estimate	**(SE)**	**Estimate**	**(SE)**
Physical	**Intercept**	0.39**	0.14	- 0.01	0.09
	Time	0.64**	0.23	0.18*	0.08
	Age (young)	0.60**	0.20	- 0.08	0.13
	Time*Age	- 0.65*	0.32	- 0.03	0.11
MI	**Intercept**	- 0.17	0.16	- 0.15*	0.07
	Time	0.98***	0.22	0.39**	0.13
	Age (young)	0.18	0.23	0.24*	0.11
	Time*Age	- 0.81*	0.31	- 0.24	0.18

	Compensatory (SELF-INITIATED)				
		Head		**Hip**	
		Estimate	**(SE)**	**Estimate**	**(SE)**
Physical	**intercept**	- 13.28***	1.21	- 6.16***	0.42
	Time	- 562.90***	48.35	- 214.37***	19.61
	Time^2	53.58**	15.54	84.23***	10.23
	Age (young)	- 3.93*	1.71	2.21***	0.59
	Time*Age	- 149.70*	68.38	116.50***	27.73
	Time^2*Age	- 3.73	21.98	12.63	14.47
MI	**intercept**	0.35	0.18	0.33**	0.09
	Time	- 0.01	0.29	0.09	0.16
	Age (young)	- 0.03	0.25	- 0.24	0.13
	Time*Age	- 0.67	0.40	- 0.31	0.23

Table 9. Regression coefficients of the theoretical model for anticipatory and compensatory AP postural motion recorded at the head and hip segments in the self-initiated condition. Signif. codes: '***' 0.001 '**' 0.01 '*' 0.05

Compensatory postural motion. At the hip (Fig. 13, panel 1b), age, time, $time^2$ and the interaction between age and time were significant predictors of AP position. Y and O's trajectories were statistically distinguishable (χ^2 (3) = 16.10, p = 0.001). At the head (Fig. 13, panel 1a), age, time, $time^2$ and the interaction between age and time were significant predictors. Again, Y and O's trajectories were statistically distinguishable (χ^2 (3) = 15.94, p = 0.001).

O and Y's trajectories differed at both the head and hip segments. At the hip, Y showed backwards motion before moving back towards the pre-movement-onset position. O showed more backwards motion than Y, but no tendency return to baseline within the observation window. At the head, O and Y showed similar backwards motion, however Y showed greater backwards displacement than O.

Fixed Effects	Anticipatory (EXTERNALLY TRIGGERED)				
		Head		**Hip**	
		Estimate	**(SE)**	**Estimate**	**(SE)**
Physical	**Intercept**	0.52***	0.10	- 0.01	0.08
	Time	0.20	0.17	0.07	0.09
	Age (young)	0.02	0.14	- 0.05	0.12
	Time*Age	0.05	0.24	0.27*	0.13
MI	**Intercept**	- 0.01	0.12	- 0.07	0.07
	Time	0.29	0.24	0.12	0.13
	Age (young)	0.07	0.16	0.02	0.10
	Time*Age	0.19	0.33	0.22	0.18

	Compensatory (EXTERNALLY TRIGGERED)				
		Head		**Hip**	
		Estimate	**(SE)**	**Estimate**	**(SE)**
Physical	**intercept**	- 12.98***	1.27	- 6.19***	0.56
	Time	- 520.13***	50.87	- 179.95***	25.87
	Time^2	75.86***	18.58	115.48***	9.47
	Age (young)	- 5.07**	1.80	2.62**	0.79
	Time*Age	- 208.39**	71.93	115.18**	36.58
	Time^2*Age	13.05	26.28	- 11.80	13.39
MI	**intercept**	0.29	0.14	0.25**	0.08
	Time	- 0.97**	0.33	- 0.38*	0.16
	Age (young)	- 0.16	0.21	- 0.11	0.12
	Time*Age	0.60	0.46	0.25	0.22

Table 10. Regression coefficients of the theoretical model for anticipatory and compensatory AP postural motion recorded at the head and hip segments in the externally triggered condition. Signif. codes: ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05

Self-Initiated MI

Anticipatory postural motion. At the hip (Fig. 13, panel 1d), O's forward trajectory of 1.35mm was statistically different to zero (χ^2 (1) = 7.17, p = 0.01), but Y's movement was not significantly different to zero (χ^2 (1) = 1.66, p = 0.20). Y and O's displacements were significantly different (χ^2 (2) = 6.31, p = 0.04). At the head (Fig. 13, panel 1c), O's forward trajectory of 3.35mm was statistically different to zero (χ^2 (1) = 11.62, $p < 0.001$), but Y's movement was not significantly different to zero (χ^2 (1) = 1.00, p = 0.32). Again, Y and O's displacements were significantly different from each other (χ^2 (2) = 6.81, p = 0.03).

O and Y were statistically distinguishable in their movement trajectories at the hip and head. At both segments, O showed significant forward motion, whereas Y did not.

Compensatory postural motion. At the hip (Fig. 13, panel 1d) and head (Fig. 13, panel 1c), no significant effects were found. O and Y were not significantly distinguishable from each other at either segment.

Externally Triggered Physical Movement

Anticipatory postural motion. At the hip (Fig. 13, panel 2b), O's movement was not statistically different to zero (χ^2 (1) = 0.85, p = 0.36). Y's forward movement of 1.17mm was significantly different to zero (χ^2 (1) = 9.24, p = 0.002). However, Y and O's displacements were not significantly different (χ^2 (2) = 4.76, p = 0.09). At the head (Fig. 13, panel 2a), no significant effects were found.

O did not show significant motion at the hip or head. Y did show significant forward motion at the hip only, but O and Y did not differ significantly.

Compensatory postural motion. At the hip (Fig. 13, panel 2b), age, time, time^2, the interaction between age and time, and the interaction between age and time^2 were significant predictors of position. Y and O's trajectories differed significantly (χ^2 (3) = 13.47, p = 0.004). At the head (Fig. 13, panel 2a), age, time, time^2, the interaction between age and time, and the interaction between age and time^2 were significant predictors of position. Again, Y and O's trajectories differed significantly (χ^2 (3) = 8.31, p = 0.04).

At the hip, O and Y show backwards motion prior to forward motion bringing the body back to baseline. The head shows similar trajectories for O and Y but Y's displacement was greater.

Externally Triggered MI

Anticipatory postural motion. At the hip (Fig. 13, panel 2d), O's movement was not statistically different to zero (χ^2 (1) = 0.74, p = 0.39). Y's forward movement of 1.17mm was significantly different to zero (χ^2 (1) = 7.70, p = 0.01). However, Y and O's displacements were not significantly different from each other (χ^2 (2) = 1.46, p = 0.48). At the head (Fig. 13, panel 2c), O's movement was not statistically different to zero (χ^2 (1) = 1.14, p = 0.29). Y's forward movement of 1.66mm was significantly different to zero (χ^2 (1) = 6.00, p = 0.01). However, again, Y and O's displacements were not significantly different (χ^2 (2) = 0.45, p = 0.80).

O showed no significant motion at the hip or head, whereas Y did. However, in neither case were O and Y statistically distinguishable.

Compensatory postural motion. At the hip (Fig. 13, panel 2d) and head (Fig. 13, panel 2c), no significant effects were found. O and Y were not significantly distinguishable from each other at either segment.

ML Postural Motion

Self-Initiated Physical Movement

Anticipatory postural motion. At the hip (Fig. 14, panel 1b) and head (Fig. 14, panel 1a), no significant effects were found. O and Y were not significantly distinguishable from each other or zero at either segment.

Compensatory postural motion. At the hip (Fig. 14, panel 1b), no significant effects were found. At the head (Fig. 14, panel 1a), Y and O's trajectories were statistically distinguishable (χ^2 (3) = 14.29, p = 0.003).

Y and O show rightwards motion immediately after the onset of the movement, with Y showing a steeper movement trajectory than O before returning back to baseline. O continue on a steady rightwards trajectory and did not bring themselves back to baseline within the 1000ms time window.

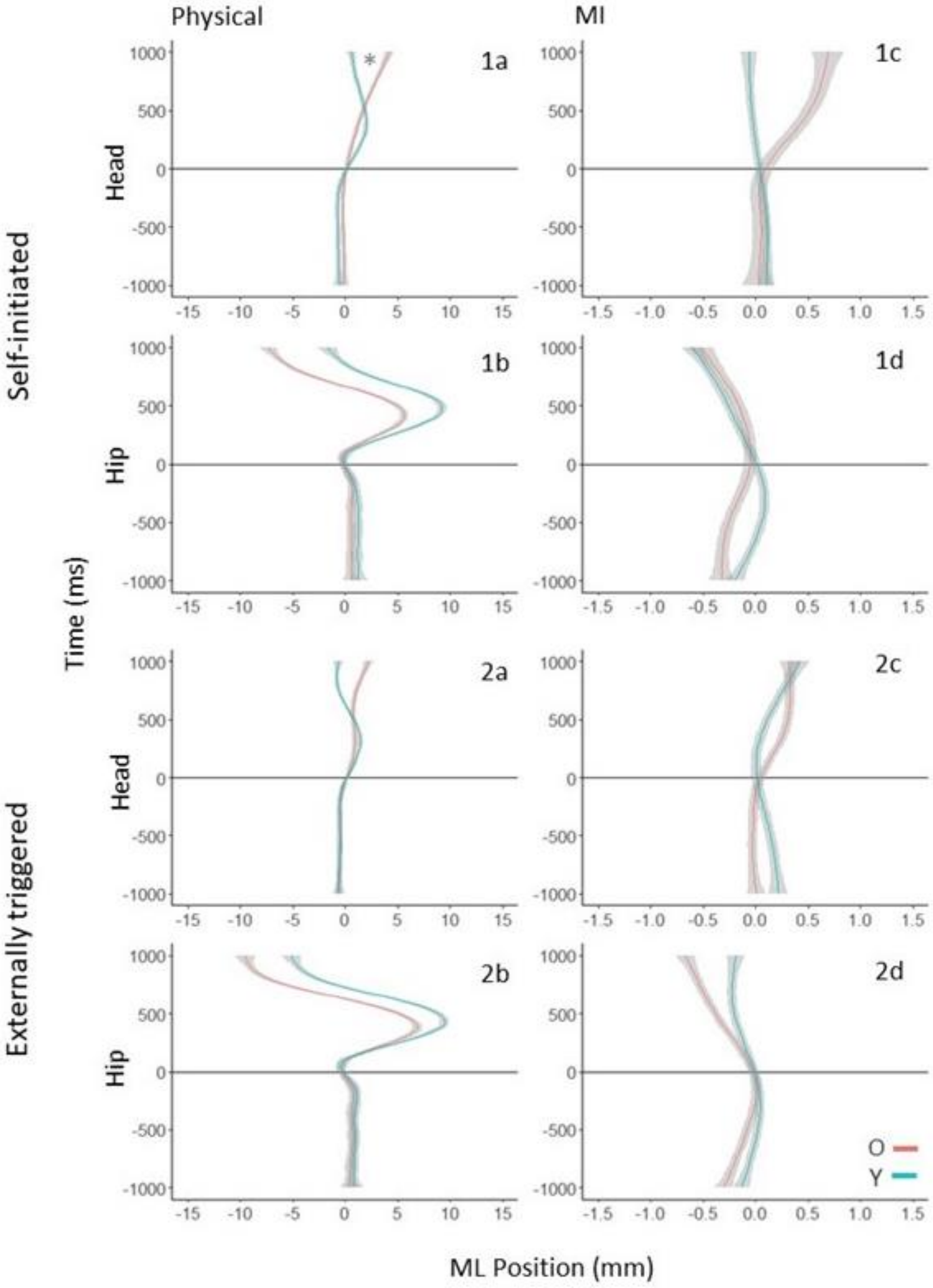

Figure 14: ML postural motion of the non-dominant (left) arm in the 1000ms preceding and following the onset of physical (a, b) and imagined (c, d) arm raising movements in the self-initiated (1a, 1b, 1c, 1d) and externally triggered conditions (2a, 2b, 2c, 2d). An upward deviation indicates forward movement, and a downward deviation indicates backwards movement. * between Y and O's trajectories indicates a statistically significant difference between the age groups. Trajectories marked with # have slopes significantly different to zero.

Fixed Effects	**Anticipatory (SELF-INITIATED)**				
		Head		**Hip**	
		Estimate	**(SE)**	**Estimate**	**(SE)**
Physical	**Intercept**	- 0.24*	0.10	0.44*	0.19
	Time	- 0.05	0.13	- 0.05	0.10
	Age (young)	- 0.27	0.14	0.25	0.27
	Time*Age	0.11	0.18	- 0.17	0.14
MI	**Intercept**	0.02	0.07	- 0.22	0.16
	Time	- 0.01	0.10	6.42	6.22
	Time^2	n/a	n/a	3.39*	1.49*
	Age (young)	0.06	0.10	0.23	0.22
	Time*Age	- 0.00	0.15	- 1.07	8.80
	Time^2*Age	n/a	n/a	- 6.61	2.11**

	Compensatory (SELF-INITIATED)				
		Head		**Hip**	
		Estimate	**(SE)**	**Estimate**	**(SE)**
Physical	**intercept**	1.90*	0.86	0.31	1.21
	Time	79.95*	37.35	- 176.76**	50.35
	Time^2	11.00	10.86	- 194.57***	24.29
	Age (young)	- 0.59	1.22	3.51*	1.71
	Time*Age	- 86.19	52.82	133.94	71.21
	Time^2*Age	- 43.54**	15.36	- 30.53	34.35
MI	**intercept**	0.15	0.08	0.04	0.05
	Time	0.19	0.12	- 0.15	0.11
	Age (young)	- 0.15	0.12	- 0.04	0.07
	Time*Age	- 0.21	0.17	- 0.02	0.15

Table 11. Regression coefficients of the theoretical model for anticipatory and compensatory ML postural motion recorded at the head and hip segments in the self-initiated condition. Signif. codes: ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05

Self-Initiated MI

Anticipatory postural motion. At the hip (Fig. 14, panel 1d) and head (Fig. 14, panel 1c), no significant effects were found. O and Y were not significantly distinguishable from each other or zero at either segment.

Compensatory postural motion. At the hip (Fig. 14, panel 1d) and head (Fig. 14, panel 1c), no significant effects were found. O and Y were not significantly distinguishable from each other at either segment.

Externally Triggered Physical Movement

Anticipatory postural motion. At the hip (Fig. 14, panel 2b) and head (Fig. 14, panel 2a), no significant effects were found. O and Y were not significantly distinguishable from each other or zero at either segment.

Compensatory postural motion. At the hip (Fig. 14, panel 2b) and head (Fig. 14, panel 2a), no significant effects were found. O and Y were not significantly distinguishable from each other at either segment.

Externally Triggered MI

Anticipatory postural motion. At the hip (Fig. 14, panel 2d) and head (Fig. 14, panel 2c), no significant effects were found. O and Y were not significantly distinguishable from each other or zero at either segment.

Compensatory postural motion. At the hip (Fig. 14, panel 2d) and head (Fig. 14, panel 2c), no significant effects were found. O and Y were not significantly distinguishable from each other at either segment.

Fixed Effects	Anticipatory (EXTERNALLY TRIGGERED)				
		Head		Hip	
		Estimate	(SE)	Estimate	(SE)
Physical	**Intercept**	- 0.41***	0.11	0.54***	0.14
	Time	0.04	0.11	- 0.02	0.09
	Age (young)	0.14	0.16	0.20	0.20
	Time*Age	0.07	0.16	- 0.04	0.13
MI	**Intercept**	- 0.02	0.07	0.08	0.05
	Time	- 0.00	0.08	0.10	0.07
	Age (young)	0.05	0.10	0.01	0.07
	Time*Age	- 0.06	0.11	- 0.05	0.09

	Compensatory (EXTERNALLY TRIGGERED)				
		Head		Hip	
		Estimate	(SE)	Estimate	(SE)
Physical	**intercept**	1.00	0.75	- 0.37	1.28
	Time	23.12	31.37	- 263.03***	58.79
	Time^2	11.23	11.69	- 226.81***	27.81
	Age (young)	- 0.65	1.06	2.89	1.81
	Time*Age	- 67.57	44.37	116.78	83.14
	Time^2*Age	- 33.63*	16.54	- 34.02	39.33
MI	**intercept**	0.26	0.16	- 0.04	0.07
	Time	5.24	5.63	- 0.19*	0.08
	Time^2	- 3.79	2.20	n/a	n/a
	Age (young)	- 0.11	0.22	- 0.03	0.10
	Time*Age	4.17	7.97	0.14	0.12
	Time^2*Age	5.81	3.12	n/a	n/a

Table 12. Regression coefficients of the theoretical model for anticipatory and compensatory ML postural motion recorded at the head and hip segments in the externally triggered condition. Signif. codes: ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05

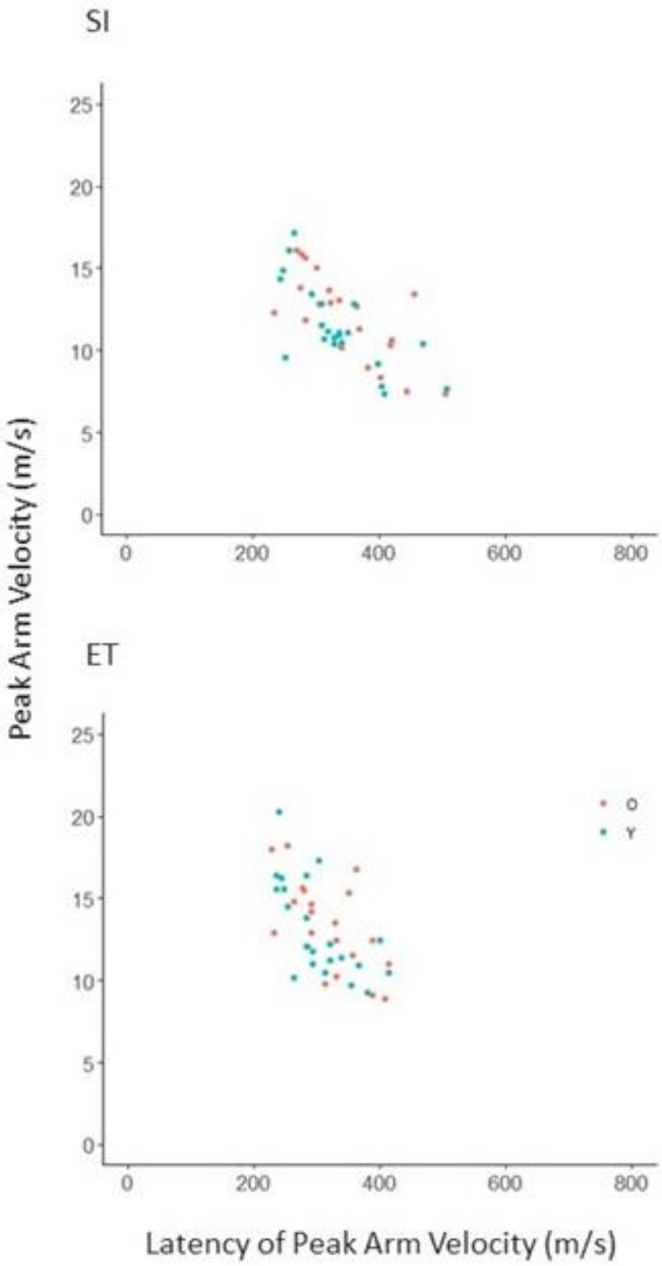

Figure 15. Peak arm velocity and its latency of the non-dominant arm in the self-initiated (SI) and externally triggered (ET) conditions

Arm movement peak velocity and its latency

Figure 15 shows peak velocity of physical arm movement and it's latency in O and Y. In the SI condition, there was no difference between Y and O's peak velocity ($\chi2\ (1)=0.53$, $p=0.47$) or its latency ($\chi2(1)=0.34$, $p=0.56$). In the ET condition, there was no difference between Y and O's peak velocity ($\chi2(1)=0.16$, $p=0.69$), or its latency ($\chi2(1)=1.01$, $p=0.31$).

Arm motion during MI

In the SI condition, O did show significant arm motion in the pre-MI period ($\chi2(1)=8.14$, $p=0.004$), however, the magnitude of 2.38mm was comparable to the 3.35mm of head motion recorded in this period. Y showed no significant arm motion ($\chi2(1) = 2.98$, $p = 0.08$). During the MI period, O showed no significant arm motion ($\chi2(1)=2.89$, $p=0.09$) and neither did Y ($\chi2(1)=1.44$, $p=0.22$).

In the ET condition, O showed no significant arm motion in the pre-MI period ($\chi2(1)=2.69$, $p=0.10$). Y did show significant arm motion ($\chi2(1)=5.48$, $p=0.02$), however, the magnitude of 1.26mm was comparable to the 1.66mm of head sway recorded during this period. During the MI period, O showed no significant arm motion ($\chi2(1)=2.71$, $p=0.10$) and neither did Y ($\chi2(1)=0.48$, $p=0.49$).

These results show that arm motion was comparable or smaller than postural motion recorded from the upper body. I concluded, therefore, that both O and Y successfully inhibited focal arm movement during 1000ms before and after self-reported MI onset.

Postural sway in the quiet stance baseline condition

The baseline measures for this experiment were as reported in Chapter 3.

Results summary

I consider postural motion in the AP direction first. When making physical movements of the non-dominant arm in the self-initiated condition, O showed APM at both segments, but Y did so only at the hip (Fig. 13, 1a and 1b). In the externally triggered condition, O did not show APM at either segment, but Y did at the hip (Fig. 13, 2a and 2b). When imagining the movements, O but not Y showed significant APM in the self-initiated condition (Fig. 13, 1c and 1d). In the externally triggered case, Y but not O showed significant APM at both segments (Fig. 13, 2c and 2d).

Following the onset of physical arm movement, in both the self-initiated and externally triggered conditions, O showed greater backward movement at the hip and less at the head than Y (Fig. 13, panels 1a and 1b). In the MI conditions, O and Y's trajectories did not have statistically significant deviations or mutual differences.

For postural motion in the ML direction, there was no evidence of APM in either condition or body segment in Y or O. The results were the same in the case of CPM after arm movement or MI onset. As shown in Fig. 14, panel 1a, there was a significant difference between Y and O at the head in the case of physical movement under self-initiated conditions. As neither trajectory deviated significantly from zero, I did not interpret this difference.

DISCUSSION

The purpose of the present study was to investigate Y and O’s postural motion immediately preceding and following the onset of unilateral arm movements and imagery of the non-dominant arm. Y and O performed or imagined straight-arm raises of the non-dominant arm under self-initiated and externally triggered conditions. Y and O’s arm velocity profiles and times to peak velocity did not differ across experiments and conditions. I will first consider CPM and APM patterns for physical arm movements and then discuss postural motion accompanying manual MI.

For forward movements, CPMs of both Y and O showed backward postural movement in the first 500ms following movement onset in both conditions (Fig. 13). Following this, Y’s but not O’s hip motion reversed direction, as head motion continued backwards in both groups. This pattern is consistent with the use of backward bending of the trunk to regulate CG (Martin, 1967) in Y, this was also observed in the Chapter 2 studying bilateral arm raises, and Chapter 3 studying unilateral arm raises of the dominant arm.

In the ML direction, CPMs to the right for non-dominant (left) arm raises (Fig. 14) were observed at the hip in both task conditions. This suggests that unilateral forward arm raises generate a lateral perturbation that is counteracted by a hip movement to the inactive side, this was also observed in Chapter 3.

Any anteroposterior APM that occurs prior to forward arm movements are expected to be in the forward direction, opposite to the backward CPMs observed during the movements themselves (Bleuse et al. 2006; Cordo and Nashner 1982). This was the case here, where Y showed forward APM at the hip in both task conditions. O showed APM at the head and hip in the SI condition, but no APM in the ET condition at the head or hip. This absence of O’s APMs in the ET condition replicated the pattern seen in Chapters 2 and 3. Again, O’s lack of APM under these conditions suggests a lack of preparatory postural action in O when an expected movement must be coordinated with an external perceptual event. Any mediolateral APM preceding non-dominant (left) arm movement would be to the left, however, neither group showed any lateral APM.

I turn next to the postural motions observed when the arm movements were imagined rather than executed. In the SI condition in the anteroposterior direction, O showed APM at both head and hip, whereas Y did not (Fig. 13, panels 1c, 1d). In the ET condition, the pattern here was the same as for the dominant arm in Chapter 3. Y showed APM but O did not. In the mediolateral direction, O and Y did not show APM in any MI condition.

The MI results of anteroposterior APM for the non-dominant arm showed a similar pattern to the results from Chapter 2 and 3 of bilateral arm raises and dominant arm raises. As in the case of physical movements in the ET condition, O did not show anteroposterior APM (whereas Y did) when MI onset was triggered by an external signal. This suggests a lack of postural preparation when the planned movement’s onset must be coordinated with an external event.

In the case of mediolateral arm raises, O and Y did not show any APM in any of the MI conditions. In Chapter 3, a large mediolateral APM to the right was observed prior to raising the dominant arm, one reason for this was that O needed to plan a mediolateral APM when imagining raising the dominant arm because the expected perturbation would be to the weaker, non-dominant side. The anticipatory head (but not hip) motion to the dominant side that was observed in O in Exp. 2 could indicate the use of a hip strategy to reduce the perceived likelihood of needing to step to the left. However, when the MI was of the non-dominant arm, the mediolateral perturbation to the stronger, dominant side was expected to be absorbed without the need for APM.

The first of two final points worth noting about the pattern of results is that there were several instances in which O showed APM at the head where Y did not. For anteroposterior APM, these included the physical movement and MI trials in the SI condition. APM at the head but not the hip, particularly in the case of MI, where the planned postural perturbation does not in fact occur, suggests the use of a hip strategy (Horak & Nashner, 1986), to which O are known to be more prone (Bleuse et al., 2006; Inglin & Woollacott, 1988; Lin et al., 2004), but, in fact, this may be more destabilizing in the context of MI than APM involving a shift of hip position. Further work is needed to closely inspect whether O's APMs have a greater tendency to incorporate leaning of the upper body consistent with a hip strategy.

The overall pattern of Y and O's postural motion was similar for the unilateral movements of dominant and non-dominant arms when compared to the bilateral movements studied in Chapter 2. However, O showed stronger anteroposterior APM, involving both head and hip, preceding MI of the non-dominant arm compared to the dominant arm in Chapter 3.

CHAPTER 5: General Discussion

In this final chapter of the thesis, I will first summarise the main findings for each chapter, and then consider the theoretical and practical implications of the set of findings. Finally, I will consider the limitations of the present work and future directions.

Summary of results

Chapter 2

In Chapter 2, the experimental procedure was designed to investigate the spatiotemporal characteristics of the postural motion that accompanies physical and imagined bilateral arm movements in standing young and older adults. Previous research that focused on measuring postural sway during periods of imagined movements was able to observe that postural sway linked to MI occurred, but it did not enable identification of the timing or direction of postural motion in the immediately linked time periods before and after individual instances of imagined reaching movements of the arm (Boulton & Mitra, 2013, 2015; Mitra et al., 2016).

Boulton and Mitra (2013) and Grangeon et al. (2011) suggested that these postural adjustments could indicate uninhibited APAs, therefore understanding the direction and timing of these postural adjustments could provide insight into the postural preparation involved in motor planning. Mitra et al (2016) found that where young people increased sway during MI, older adults restricted sway. This was interpreted as a postural threat response, consistent with the literature of APAs in older adults, where often the APA is delayed, or even restricted (Bleuse et al., 2006; Lee et al., 2015).

In Chapter 2, participants performed physical and imagined movement under self-initiated (SI) and environmentally triggered (ET) task conditions. The movements were forward, bilateral arm raises, creating a measurable forward shift in the participants CG at the time of movement initiation, subsequently generating a backward anticipatory postural motion to counteract the forward shift in movement. COP.

Only anteroposterior postural motion was analysed. Under SI conditions (Fig. 2), only O showed anticipatory postural motion just before physical arm raises, whereas both O and Y showed anticipatory postural motion just before imagined arm raises. Under ET conditions (Fig. 3), Y showed anticipatory postural motion before physical and imagined arm raises, but O did not show anticipation in either task condition. These results showed that anticipatory postural motion does precede MI but this process is absent in O when participants did not have control over the timing of movement onset.

Chapter 3

The findings in Chapter 2 indicated that forward anticipatory postural motion occurred during imagined bilateral arm movements. However, the picture of posture control changes in the case of mediolateral arm movement, particularly with respect to ageing. It is well known that ageing particularly effects posture in the mediolateral direction and the ability to counteract perturbations in the mediolateral direction (Claudino et al., 2013; Santos et al., 2016). As unilateral are movements are more perturbing in the ML direction, the case of unilateral arm movements is arguably more important with respect to the impact of ageing on posture control and balance.

In the case of fast or load bearing movements that can generate greater postural perturbation the dominant arm is favoured, and more practised (Bagesteiro & Sainburg, 2002; Sainburg & Kalakanis, 2000). Therefore, prominent anticipatory postural motion to the right should be expected for physical and imagined movement of the dominant arm (when the dominant arm is the right), particularly as raises of the dominant arm require the body to prepare for mediolateral perturbation to the weaker non-dominant side.

The movements studied in Chapter 3 were unilateral forward, dominant arm raises that produced a backward postural perturbation in the anteroposterior plane. Participants performed physical and imagined raises of the dominant arm under SI and ET task conditions. Anteroposterior and mediolateral postural motion was recorded. Results for anteroposterior (Fig. 7) APM demonstrated a similar pattern to the postural sway results observed in Chapter 2. When the participants arm raise movement was self-initiated, whether physical or imagined, mild forward APM was observed in both age groups, significant for O at the head and significant for Y at the hip. When the movement was externally triggered, only Y showed any APM.

These results suggested that a lack of postural preparation in older participants when the planned movement's onset must coordinate with an external event. In the mediolateral direction (Fig. 8) there were no indications of any APM by Y, expect in the SI condition. This suggests that although mediolateral APM is a feature of postural support for dominant arm raises, it is small enough that it is not expressed by Y during MI trials. On the other hand, O did show mediolateral APM during MI in both SI and ET conditions (Fig. 8, panels 1c, 2c). Suggesting that O planned postural support for a mediolateral perturbation when imagining forward movements of the dominant arm. This conscious or unconscious strategy may be due to the expectation of a perturbation towards the weaker non-dominant side of the body.

Chapter 4

Chapter 3 developed our understanding of postural sway by examining how dominant arm raises affect anteroposterior and mediolateral APMs immediately before and after the onset of movement, physical or imagined. However, there is some evidence to suggest that movements of the dominant and non-dominant arm differ in the postural adjustments they elicit (Teyssdrè et al., 2000; Hunag, 2009). Thus, studying the effect of imagined non-dominant arm raises provides further insight into how the CNS anticipates and protects against postural perturbations.

Based on the results in Chapter 3, if the dominant side impacts the weaker non dominant side of the body, then it theoretically follows that movements of the non-dominant arm would impact the stronger, dominant side of the body. If this is the case, the APM should be smaller as it is absorbed by the stronger side. To assess this question, the movements studied in Chapter 4 were physical and imagined forward non-dominant arm raises during SI and ET task conditions. As with Chapter 3 anteroposterior and mediolateral postural motion were recorded.

Results in the anteroposterior direction (Fig. 13) further followed the pattern of postural sway demonstrated in both Chapter 2 and 3. Y showed APM at the hip in both SI and ET conditions. O showed APM in the SI condition but not in the ET condition. Though it should be noted in the SI condition, while Y did show a significant difference to zero and O did not, these trajectories were not significantly different from each other, unlike the results of similar trajectories from Chapter 2 and 3. Whilst Chapter 4 shows a clear trend similar to that observed previously, there was no significant difference between O and Y. However, O did demonstrate a significant APM in the physical condition at the head and imagined arm movement conditions at both the hip and head, when the movement of the nondominant arm was self-initiated.

O’s posture appeared to be sensitive to the impact of forward arm arises of the non-dominant arm, as significant APMs were observed at the head and hip prior to the onset of movement (Fig. 13). Whereas changes in ML sway were not observed (Fig. 14). This may reflect the dominant side of the body performing a more effective stabilisation of posture in the ML direction, therefore restricting sway.

Forward raises of the non-dominant arm impact AP posture more than ML posture and older adults are sensitive to this in their postural planning.

Theoretical applications

These results raise questions for our understanding of the architecture of motor planning leading to physical or imagined limb movements. Massion (1992) summarized the control of focal movement execution and its postural support as parallel descending pathways of central origin (Fig. 16). The assumption of separate pathways for controlling the focal and postural components was necessitated by the known flexibility of their relative timing depending upon task conditions (Benvenuti et al. 1990; Horak et al. 1984; Lee et al. 1987; Zattara and Bouisset 1986). Based on the evidence that the onset of focal movement can be held back until the required APA is fully developed (Cordo and Nashner 1982), an inhibition on the control of movement from the process that controls postural support was also postulated.

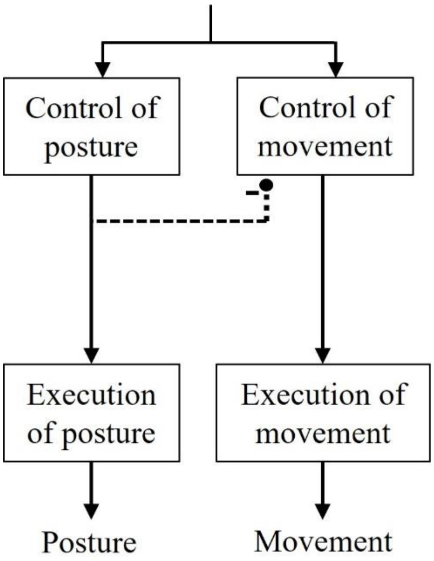

Figure 16. Parallel descending pathways of central origin for the control of focal movement and the postural support for the movement.

Massion did not consider the case of MI, which involves a process that inhibits focal movement (Jeannerod 2006), and only recently has it been demonstrated that postural adjustments (Boulton and Mitra 2013, 2015; Grangeon et al. 2011; Rodrigues et al. 2010) and autonomic preparation (Collet et al., 2013) planned in support of imagined movement can escape this inhibition. Evidence for incomplete inhibition during MI is not confined to postural adjustments, but also includes observations of specific but attenuated EMG activity in muscles that would be activated if the movement was executed (Bonnet et al., 1997; Guillot et al., 2007; Lebon et al., 2008). Massion also did not elaborate the architecture in respect of the anticipatory and compensatory components of posture control. A key purpose of the present set of experiments was to ascertain whether postural movements that accompany MI do have an anticipatory component. The possibility of this was clearly indicated by Boulton and Mitra's (2015) finding that postural movements during periods of MI are sensitive to imagined constraints on the movements being imaged. This suggested that the postural activity that was not being fully inhibited during MI was of central origin as it could incorporate task-specific cognitive constraints. The present project has shown not only that postural movement during manual MI has an anticipatory component, but also that CPM following MI may or may not be preceded by APM before MI onset (as was the case for O in the ET conditions). This pattern of findings reinforces the necessity of expanding the control architecture to address the anticipatory and compensatory components explicitly.

Based on these considerations, I propose that the anticipatory and compensatory elements of the postural control pathway should be considered separable. I have schematised my proposed architecture in Figure 17. Leaving aside the actions associated with imagery intention for the time being, the movement intention aspect proposes parallel focal movement and postural support plans of central origin (as did Massion, Fig. 16). I represent the anticipatory and compensatory components of the postural support plan as parallel processes. The focal movement and compensatory postural support are tightly linked and co-occur in the case of movement execution. The anticipatory component may or may not occur depending upon its necessity and the ability to plan it. Where movement onset is externally triggered, for example, there may not be enough time or information to take anticipatory action. Previous and present results on movement execution, and present results on MI, suggest that old age brings with it a specific deficit in generating the anticipatory postural component when the focal movement's timing must coordinate with an unpredictable external cue. Note that an inhibition pathway is proposed from the anticipatory arm of the postural support plan to the focal movement plan. This is the analogue here of the inhibition depicted in Figure 16, proposed to accommodate observations in the literature that the timing of focal movements can be modulated based on the time requirements of anticipatory postural adjustments (e.g., Cordo and Nashner 1982).

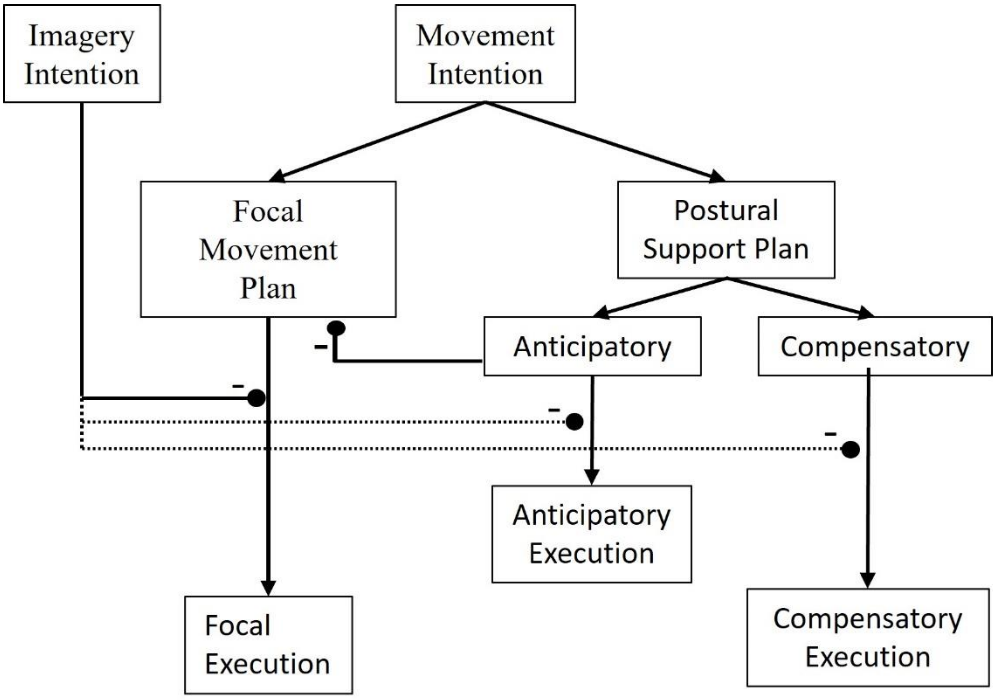

Figure 17. Proposed control architecture for focal movement and postural support during execution and MI.

Next, I consider the case of MI, which I have depicted as the imagery intention process. This view of what occurs during MI is based on the proposal that MI involves an inhibition process that counteracts the focal movement commands before they activate peripheral effectors (Collet & Guillot 2009; Jeannerod, 2006). Any such inhibition is understood to be incomplete, as it does not eliminate autonomic arousal, EMG activity in involved muscles, or the postural adjustments accompanying motor planning (Collet et al., 2013; De Souza et al., 2015; Guillot et al., 2012). Accordingly, an inhibitory influence from imagery intention to the focal movement plan is indicated in Figure 17. This inhibition appears as a solid line as, in many instances, focal movement can be completely absent during MI. Inhibitory influences are also indicated from imagery intention to the anticipatory and compensatory components of the postural support plan, but these are dashed lines to indicate that these pathways do not achieve complete attenuation of postural adjustments, as has been shown in the present experiments and Boulton and Mitra (2013; 2015) and Mitra et al. (2016). Aside, from enabling insights into the postural component of focal movement planning (without contamination from execution processes) the discovery incomplete inhibition of postural adjustments during MI presents potential practical benefits in training and rehabilitation. I turn to these possibilities next.

Practical consequences for independent living

The absence of APM preceding O’s executed and imagined arm movement in the ET condition has potentially important practical consequences for active and independent living. Limb movements that must be coordinated with environmental events of unpredictable timing are an everyday necessity in navigating civic spaces and interacting socially. Raising the arm while standing upright does not even include the variable spatial constraints that are often added to the temporal uncertainties of coordinating with external events.

Take, for example, the active destabilization of body posture that occurs when the trunk must bend as part of the focal movement, resulting in a large change in CG position (e.g., in Stapley et al. 1998). Previous research on postural support for physical movements has shown that O produces weaker and delayed APA (Inglin and Woollacott 1988; Man'kovskii et al. 1980; Rogers et al. 1992; Woollacott and Manchester 1993), and, as a result, larger CPA that can have destabilizing effects (Kanekar and Aruin (2014a).

Here, O's absence of APM for physical arm movements and MI in the ET condition suggests that the issue occurs at the level of planning the postural support for the movement that is to be coordinated with external events. Curiously, but potentially significantly, the absence of APMs coexists with intact CPMs even as no focal movement takes place.

Anticipatory postural actions do not always occur, and in the case of O, they are less likely to occur when the planned movement must coordinate with external events; but are comparatively stronger when the expected postural perturbation impacts the weaker, non-dominant side of the body. The occurrence of APMs during MI, and their modulation based on task conditions suggests MI could be an effective means of providing training in anticipatory postural control. Recent research is showing that MI training may benefit a number of measures of postural stability in O (Nicholson et al., 2019; Oh & Choi, 2021) and neurological patients (Cho et al., 2013). So far, there has not been a specific focus on anticipatory postural control tasks and tests. Developing such focus in rehabilitation studies using MI may augment O's postural support of limb movements, and potentially mitigate the loss of coordination between anticipatory postural control and environmental events.

In a literature review, de Vries & Mulder (2007) conclude that MI has the potential to play a role in the recovery of motor coordination processes after a stroke. This can be applied to healthy older adults with reduced motor coordination/capabilities from a multitude of pathologies. They found that

MI training influences recovery in a positive way. In a study by Mulder et al. (2004) they found that mental practice of a movement (specific movement of a single toe) improved performance of that movement significantly. However, participants who did not have a central representation of that movement showed no significant improvement, suggesting the need for a motor pathway to be embedded prior to its ability for MI to improve it.

The findings of the current project further elucidate the role MI plays in motor planning, particularly in posture control, and demonstrates how these change with ageing, agreeing with the existing literature. This highlights that MI is a tractable target for therapeutic intervention, with further development of MI tasks likely to aid in both the prevention and treatment of degenerative motor conditions.

Further work examining the role of the primary motor cortex and its interaction with covert movement representation, in tandem with how different MI tasks can help to strengthen specific pathways will allow a more bespoke development of intervention tasks that can be used in therapeutic rehabilitation regimes following the onset of degenerative motor conditions. However, as additional tools are developed to identify members of vulnerable populations (e.g., ageing adults) at risk of motor decline, MI tasks may also be used as preventative measures to delay the onset of motor decline or prevent it entirely depending on the pathology of the individual.

These questions will require extensive longitudinal studies in the future to provide a sufficiently solid basis on which to base therapeutic interventions.

Limitations and Future research

Kinaesthetic vs. Visual Motor Imagery

Whilst efforts were made to encourage the use of kinaesthetic imagery over visual imagery, formal assessment of imagery ability was not conducted, additionally participants were not directly questioned about their mode of imagery as part of experiments. The modality of imagery is critical as there is evidence to suggest that kinaesthetic and visual imagery are dissociable at a neuronal level, with significantly greater recruitment of cortical motor areas during kinaesthetic imagery compared to visual imagery (Guillot et al., 2009). This suggests that critical evaluation of the mode of imagery may be significant in dissociating participants accidentally using a visual strategy over a kinaesthetic one.

Previous research has demonstrated that under MI task conditions, a stronger postural response is evoked under a multitude of explicit kinaesthetic task instructions (Rodrigues et al., 2010). This research suggests that measured changes in posture, under imagined arm movement conditions, will be greater when participants are instructed to use a kinaesthetic mode of imagery.

The decision was made to direct participants to use a kinaesthetic mode of imagery, however, as the participants general ability to produce vivid imagery as well as their ability to distinguish and utilise kinaesthetic versus visual imagery were not formally assessed, it remains possible that scales of imagery ability and method may be present within the collected data. However, the difference in imagery method is unlikely to be responsible for the differences observed between Y and O as there is no evidence to suggest that one group would predominantly use one method over another, though variations in method may account for some of the group variability seen.

Given that there is now a body of literature, including the work presented in this thesis, that establishes changes in body posture are related to MI, specifically imagined arm movements, it suggests that further research should aim to experimentally dissociate changes in body posture evoked by kinaesthetic versus visual imagery. Ideally both modalities should be examined in parallel as described previously (Rodrigues et al., 2010), though it would be of immense value to combine these observations with further experimental measures such as EMG activity in related muscles as well as EEG activity in related cortical areas i.e. motor versus occipital visual areas. These experiments may allow us to separate or integrate the components of motor imagery and visual motor feedback into postural sway and ageing.

Imagery ability

Given that there is evidence demonstrating significant differences in the ability of individual to produce mental imagery of any kind, such as is seen with aphantasia (Keogh & Pearson, 2018), it suggests that changes in postural sway evoked by MI tasks may in part be dependent on the participants ability to effectively imagine the task. Therefore, even if participants do use the same visualisation strategy (e.g. kinaesthetic) the magnitude of the observed postural response may differ based on the vividness or completeness of the imagined movement.

Furthermore, previous research has demonstrated that there is an observable age-related decline in vividness of imagery between younger and older adults, with older participants reporting lower scores on mental imagery scales than younger participants (Saimpont et al., 2013). It has been argued that this may be due to higher reliance on sensory feedback as we age, which may be indicative of age-related declines in the ability to plan offline. This data suggests that differences in imagery ability may account for some of the variation between O and Y observed within the research of this thesis.

In order to assess this variability in future experiments, the ability of participants to develop or generate vivid and detailed mental images can be assessed prior to and following experimentation. This can be achieved though use of ordinal scales such as The Movement Imagery Questionnaire, The Vividness of Motor Imagery Questionnaire, and the Kinaesthetic and Visual Imagery Questionnaire (Dickstein &

Deutsch, 2007). Assessment of these mental capacities may allow further understanding of the scale and variability of postural sway that is experimentally observed.

Kinematic and EMG measurement

Throughout this thesis, a careful distinction has been made to distinguish APAs and CPAs, which have been studied in terms of patterns of postural muscle activation, and the APMs and CPMs that feature in our kinematic analysis.

The presence of postural motion implies the presence of postural muscle activity to generate it, or the absence of muscle activity to resist it against gravity. The absence of postural motion, on the other hand, may signal either that no muscular effort was applied or that muscle activity occurred, but did not generate measurable body displacement (e.g., co-contraction of agonist–antagonist systems). Thus, further exploration of the ET task conditions combining kinematic and EMG measurement would be fruitful, although a surface EMG approach may be challenging if MI is associated with level-attenuated postural muscle activity. There seem to be at least two ways of amplifying the postural response accompanying MI.

Additionally, the use of electroencephalography (EEG) measurements would allow a direct measure of how different cortical areas related to motor function are activated during motor imagery tasks. This would also allow a diversification in the motor tasks utilised, with changes in cortical or cerebellar activity likely being directly related to the task performed or imagined. Importantly, the use of EEG would also allow the measurement of cortical areas directly unrelated to motor function, such as the visual cortex, as this may be measurably activated if participants are using a visual imaging strategy compared to a kinaesthetic imaging strategy.

Concluding remarks

The data presented within this thesis provides novel evidence for the presence of postural adjustments occurring before and after imagined movements as well as their physical counterparts. Significantly, these postural changes were shown to be different in older adults compared to the younger cohort when asked to perform motor imagery. This difference in postural control may relate to a decline in aging adults' ability to engage in forward planning of movements such as balance strategies, further demonstrating the importance of motor imagery as a potential method of remediating age-related declines in posture control through established motor imagery tasks.

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