ELSEVIER



# **Experimental Gerontology**





# Older adults rely on somatosensory information from the effector limb in the planning of discrete movements to somatosensory cues



Rachel Goodman<sup>a,b,\*</sup>, Luc Tremblay<sup>a,b</sup>

<sup>a</sup> Perceptual Motor Behaviour Laboratory, Faculty of Kinesiology and Physical Education, University of Toronto, Canada
<sup>b</sup> Centre for Motor Control, University of Toronto, Canada

#### ARTICLE INFO

Sensorimotor transformation

Section Editor:

Somatosensory

Tendon vibration

Keywords:

Reaching

Aging

Visual

## ABSTRACT

While younger and older adults can perform upper-limb reaches to spatial targets with comparable endpoint accuracy (i.e., Helsen et al., 2016; Goodman et al., 2020), movement planning (i.e., reaction time) is significantly longer in older versus younger adults (e.g., Pohl et al., 1996; Goodman et al., 2020). Critically relevant to the current study, age-related differences in reaction time are even greater when older adults plan movement towards somatosensory versus visual or bimodal targets in the absence of vision of the moving limb (e.g., Goodman et al., 2020). One proposed explanation of these lengthened reaction times to somatosensory targets is that older adults may be experiencing challenges in implementing sensorimotor transformations when planning discrete movements of their unseen limb. To test this idea and assess the contributions of somatosensory information to these motor planning processes, tendon vibration was applied to the muscles of the effector limb between reaching movements made towards visual, somatosensory, or bimodal targets. The results revealed that older adults show the greatest increases in reaction times when vibration was applied during the preparation of movements to somatosensory targets. Further, both older and younger adults exhibited decreased movement endpoint precision when tendon vibration was applied. However, only older adults showed significantly lower movement endpoint precision due to tendon vibration when making movements to somatosensory targets, versus both visual and bimodal targets. These results corroborate previous evidence that older adults have difficulties planning upper-limb movements to somatosensory targets. As well, these results yielded novel evidence that such motor planning processes in older adult rely on somatosensory cues from the effector limb.

## 1. Introduction

The ability to initiate voluntary movement involves an intricate network of sensorimotor processes. For individuals with a healthy nervous system, planning voluntary action appears to integrate reliable sources of sensory information to execute safe and efficient movements (e.g., Elliott et al., 2010). Specifically, visual and somatosensory information are important to localize both limb and target positions for any voluntary goal-directed upper-limb movement (e.g., Henriques et al., 2002; Sober and Sabes, 2005). As humans age, it appears that the reliance on sensory information for movement production is altered (e.g., Chaput and Proteau, 1996). For example, older adults appear to rely more on visual than somatosensory feedback. Specifically, in more recent work, it has been shown that the time to initiate a voluntary reaching movement without vision of the limb is lengthened in older versus younger adults when planning movements to somatosensory versus visual or bimodal targets (Goodman et al., 2020). While these results could be an outcome of the visual dominance observed in older adults (e.g., Seidler-Dobrin and Stelmach, 1998; Brodoehl et al., 2016), an alternative or complementary explanation involves age-related differences in the sensorimotor transformation processes that occur when planning a limb movement towards targets of different modalities (e.g., Bernier et al., 2007). In the current study, dual-muscle muscle tendon vibration was employed between upper-limb movements towards visual, somatosensory, or bimodal target presentations, to further explore the age-related differences of somatosensory information utilization for voluntary movement planning.

#### 1.1. Planning voluntary movement in younger adults

Planning voluntary movement largely relies on the capability to integrate, transform, and use sensory information to prepare a motor

https://doi.org/10.1016/j.exger.2021.111310

Received 24 April 2020; Received in revised form 16 February 2021; Accepted 8 March 2021 Available online 17 March 2021 0531-5565/© 2021 Elsevier Inc. All rights reserved.

<sup>\*</sup> Corresponding author at: 55 Harbord Street, Toronto, Ontario M5S2W6, Canada. *E-mail address:* r.goodman@mail.utoronto.ca (R. Goodman).

response (e.g., Sober and Sabes, 2005; Sarlegna and Sainburg, 2007). The central nervous system (CNS) combines and integrates various sources of available sensory information (e.g., Ernst and Bülthoff, 2004), and subsequently creates an effective motor plan (e.g., Elliott et al., 2004; Todorov and Jordan, 2002). The motor plan is then sent to implement the movement. As previously mentioned, both visual and somatosensory information are important for these upper-limb motor planning processes. The contributions of visual and somatosensory feedback utilization to preparing these movement plans have been extensively explored in the literature. However, very few studies have directly perturbed somatosensory feedback for assessment (cf., use of visual-proprioceptive mismatch paradigms: see Sober and Sabes, 2005; Bagesteiro et al., 2006; Bernier et al., 2007), and even fewer employed somatosensory targets (e.g., Cuppone et al., 2016; Mikula et al., 2018). Thus, previous conclusions regarding visual information are based on tangible findings, whereas conclusions regarding somatosensory information are typically inferred. Although perhaps less applicable to everyday life, studying how sensorimotor mechanisms are altered as a function of cues from a somatosensory spatial target (e.g., Bernier et al., 2007), can reveal the underlying cross-modal sensorimotor transformations taking place during voluntary movement planning.

Sensory information from different modalities is likely spatially mapped in the CNS onto one common reference frame or coordinate system (see Alais et al., 2010 for more details). For example, when making a reach towards a door knob, visual information regarding both the location of the reaching arm and the location of the door knob must be combined and mapped with somatosensory information about the head, neck, and reaching arm to make an appropriate estimation of the movement parameters (e.g., Ernst and Bülthoff, 2004; Tremblay and de Grosbois, 2015). It has been observed that, in isolation, visual information can be mapped in a different coordinate system than somatosensory information (i.e., retinotopically versus somatotopically, respectively; see Gardner and Johnson, 2013). Thus, sensory combinations and transformations allow the CNS to compare and utilize sensory information in the same coordinate system (e.g., Ernst and Bülthoff, 2004). Evidence for such sensorimotor transformations between visual and somatosensory information partially stems from studies where perceived visual information is manipulated and the behavioural outcomes are observed (e.g., with a visual-proprioceptive mismatch paradigm: e.g., Bagesteiro et al., 2006; Bernier et al., 2007). Studies involving such methods have shown that, when performing upper-limb movements to somatosensory targets, visual feedback of the reaching limb does not yield significant influences on the movement direction (i. e., Sober and Sabes, 2005; Sarlegna and Sainburg, 2007). Alternatively, in cases where perceived visual shifts of the reaching limb are presented to a participant before a reaching movement, there are observable significant influences on movement direction, at least when participants make movements to visual targets (i.e., Sarlegna and Sainburg, 2007). Thus, sensory transformation processes appear to depend on the sensory information available and the modality of the spatial target.

Humans can use different sensory coordinate systems when executing movements to visual versus somatosensory targets (e.g., Blouin et al., 2013; Manson et al., 2019). In Manson et al. (2019), participants performed leftward upper-limb reaching movements with their right limb to either a stationary or perturbed target location. Specifically, participants reached to a visual target (i.e., LED) or a somatosensory target (i.e., their left index fingertip), without vision of the reaching limb. On the perturbation trials, the target location was shifted 3 cm either away or towards the participant (i.e., perpendicular to the primary movement axis), 100 ms or 200 ms into the movement. Visual perturbations were implemented using additional LEDs below and above the original target, while the somatosensory perturbations were implemented by shifting the location of the left index fingertip via a robotic end-effector manipulandum. Participants were told to complete their movements to the presented target as accurately as possible. Participants exhibited earlier and more accurate corrections for

somatosensory target perturbations, when reaching to somatosensory versus visual targets. Thus, participants were able to make better amendments to their limb trajectories when moving to somatosensory targets, when visual feedback about the moving limb information was not available. Manson et al. (2019), suggested that information regarding the somatosensory target position (i.e., left index fingertip) may have not been transformed into a visual reference frame to produce the corrections to the somatosensory targets. Accordingly, it was suggested that movements to somatosensory targets may have been planned without the use of cross-modal transformations. That is, somatosensory information did not need to be transformed into another reference frame (i.e., visual reference frame, e.g., Bernier et al., 2007), because both the target and limb information were already in a somatosensory coordinate system. Overall, it is evident that younger adults reaching to somatosensory targets without vision of the moving limb may implement fewer sensorimotor transformation processes than when reaching to visual targets. Also, reaching to visual targets in the absence of vision of the reaching limb may require more elaborate and longer sensorimotor mapping processes (i.e., to a visual reference frame), as this task would involve both visual and somatosensory cues. This outcome is at least the case for the above-cited studies, which exclusively involved younger adults.

## 1.2. Effects of aging

It is also important to consider how older adults perform sensory transformations, as they may have reduced motor abilities due to the neuronal degradation that accompanies natural aging processes (e.g., Yang et al., 2015). Also, movements may be altered and slowed by deterioration of white matter and/or loss of contractile fibers in the muscle tissue. Reports from EMG studies with older adults have demonstrated reduced antagonistic activity (e.g., reduced force) during voluntary movements (e.g., Darling et al., 1989; Seidler and Stelmach, 1996). While these changes are likely a result of muscle atrophy and reduced motor unit activations (e.g., Lexell et al., 1988), is it also possible that the reduced quality and quantity of somatosensory feedback leading to transformation processes also plays a role with the movement planning and execution in older adults. Further, as humans age, it appears that sensorimotor processes associated with voluntary movement are also altered.

Older adults typically display movements that are slower, less coordinated, and more unpredictable than their younger counterparts. For example, it has been suggested that compared to younger adults, older adults plan voluntary movements differently and adopt strategies to compensate for their reduced sensory acuity (e.g., Skinner et al., 1984). More specifically, older adults shift to more time spent after peak limb velocity, to allow for longer proportions of movement in the later phases of the trajectory when the limb is approaching the target (e.g., Pratt et al., 1994; Haaland et al., 1993; Pohl et al., 1996). It is in these later phases of a reaching movement that online trajectory amendments are implemented (i.e., Multiple Processes Model, see Elliott et al., 2017 for review). However, it is not yet clear whether these age-related changes could be linked with motor planning processes.

In a recent study, age-related differences in motor planning were compared across movements to targets of varying sensory modality. Older and younger adults performed upper-limb reaches to visual, somatosensory, or bimodal targets (Goodman et al., 2020). Movements were performed without vision of the reaching limb and participants were told to be as accurate as they could within a movement bandwidth of 300–700 ms. Results revealed that older adults took more time to initiate their movements (i.e., longer reaction times than younger adults), and this difference was significantly greater for movements towards the somatosensory versus visual or bimodal targets. Participants from the aforementioned study planned reaching movements in the absence of visual feedback from the environment, including the moving limb. As a result, they were likely relying more heavily on somatosensory information to plan and execute the movement to the somatosensory targets (see also Manson et al., 2019).

It appears that regardless of potential age-related neural delays in processing, older adults are still able to perform reaching movements with comparable endpoint accuracy to that of younger adults (e.g., Helsen et al., 2016, Goodman et al., 2020). This is particularly important as much of the current evidence about age-related sensorimotor processes for the planning and control of voluntary movements involved movements to visual targets only. Further, the results of Goodman et al. (2020) would suggest that older adults experience challenges in using somatosensory information to plan a voluntary movement. Thus, it is important and relevant to explore the possibility that the effects of aging alter sensorimotor transformation processes.

#### 1.3. Purpose

The purpose of the current study was to further evaluate the use of somatosensory information for the planning of voluntary action in younger and older adults. Tendon vibration was applied to the effector limb to investigate the impact that somatosensory information from the reaching limb has on planning movements to visual, somatosensory, or bimodal targets (see Methods). Based on previous results from older adults (i.e., Goodman et al., 2020), it was expected that if different sensorimotor transformation processes are taking place for somatosensory than for visual targets then movement to somatosensory targets would elicit longer reaction times than movements to visual targets. Furthermore, if the age-related reaction time differences are a result of reduced sensorimotor processes when planning movements of an unseen limb to somatosensory targets in older adults (i.e., conversion to a visual reference frame), applying tendon vibration to the reaching limb was expected to exacerbate these reaction time effects with older adults only, or to a greater extent in older than younger adults. Alternatively, if tendon vibration does not induce significant age-related differences in reaction time, then somatosensory specific processing and transformations may be preserved in healthy older adults. Additionally, the application of tendon vibration between movements to somatosensory targets was expected to elicit greater movement endpoint variability than movements to somatosensory targets without vibration (i.e., Goodman and Tremblay, 2018), for all participants. Alternatively, if the tendon vibration has no effect on endpoint variability, it is possible that participants are not using somatosensory information from the effector limb to control the precision of their movements. Lastly, it was also predicted that all participants would achieve comparable endpoint accuracy, at least when reaching to visual targets (i.e., Rand et al., 2013; Helsen et al., 2016).

## 2. Materials and methods

Two groups of participants were recruited from the University of Toronto community, including 18 younger adults (mean age 23.6 years, standard deviation 4.0; 11 women) and 18 older adults (mean age 73.1 years, standard deviation 4.6; 12 women). The protocol for this research was approved by the University of Toronto Research Ethics Board (REB). To be included in the study, participants had to be right-handed and have normal or corrected-to-normal visual acuity. Handedness was confirmed with a 5-item questionnaire (i.e., Edinburgh handedness questionnaire, adapted from Oldfield, 1971). Participants were excluded if they were unable to give informed consent or had any self-reported history of chronic back, neck, or arm pain. Participants were also given an opportunity to adjust themselves in the set-up to see if any discomfort was felt before the start of the experiment. All participants also completed a brief neurological questionnaire, to ensure they could provide informed consent and understand the demands of the task and tendon vibration perturbations. The questionnaire also included items related to sensory and motor limitations, such as numbness, tingling, tremor, or any other sensory impairment. Both visual and

somatosensory acuity were tested before each experiment. Visual acuity was assessed with a visual orientation test (i.e., FrACT, Landot C 8-point acuity test; see Bach, 1996), while somatosensory acuity was evaluated with a tactile discrimination task. In the tactile discrimination task, participants were seated in a dark room with their three middle fingers on vibro-tactile tactors (see below). In a random fashion, each finger was vibrated three times and participants had to verbally identify which finger was stimulated. All participants performed the tactile discrimination task with 100% accuracy.

The study was conducted using a custom aiming console (66 cm imes38 cm  $\times$  12.8 cm), equipped with a Plexiglas  $^{\rm TM}$  translucent surface. Participants were seated in front of the console in a kneeling chair, to minimize over flexion of the spine and to maintain an ergonomic posture during the experimental protocol. The room was dark, and participants could not see their limbs nor the experimental set-up. The console enclosed three green Light Emitted Diodes (LEDs), and three vibrotactile tactors (C3 Tactors, Engineering Acoustics Inc., Casselberry, FL). The tactors were embedded in the console 3 cm apart and were accessible to the participant by reaching their supine hand under the tinted surface (see Fig. 1A). The tactors delivered vibration at 250 Hz for 40 ms. These values have been used in previous works (e.g., Goodman et al., 2020 (Goodman et al., 2020)) and were intended to stimulate the Pacinian corpuscles in the fingertips, which are sensitive to higher frequencies of vibration (i.e., 60-300 Hz). The use of tactors has been shown effective to implement somatosensory spatial target locations (e. g., Cuppone et al., 2016, Mikula et al., 2018). A LED was located directly above each embedded tactor, and below the aiming surface, which was only visible when illuminated (see Fig. 1B).

Participants were asked to place their right limb atop the board, with their hand in a pointing position, and the index finger extended. Participants were instructed to make medio-lateral movements from a home position to one of three targets locations: 27, 30 and 33 cm leftward from the home position (see Fig. 1A & B). A custom MATLAB program (The Mathworks Inc., Natick, MA) was used to elicit experimental cues and outputs, as well as gather data from the Optotrak motion tracking system (Northern Digital Inc., Waterloo, ON). Trials began with a warning tone (i.e., single tone, 40 ms; piezoelectric buzzer, 2900 Hz; SC628 Mallory Sonalert Products Inc., Indianapolis, IN), informing the participants that the trial was about to begin. After a variable fore period (500–1200 ms), a target stimulus was elicited (40 ms in duration), which signaled the participant to begin their movement. A target could appear at one of the three target locations, and comprised of either visual information (i.e., from a LED), somatosensory information (i.e., from a tactor), or bimodal information (i.e., simultaneous presentation of visual and somatosensory information). The bimodal targets were always spatially compatible. Participants were told to move as quickly and as accurately as possible to the target, and keep their right index finger on the perceived target location until another auditory tone was sounded (i.e., a double tone), signaling the participants to return their finger to the home position and await the start of the next trial. The home position was texturized with Velcro™, so that participants could find the exact location in the dark room.

Participants were affixed with two cylindric tendon vibration devices (Dynatronic VB100, 30 mm in diameter, 75 mm in length, 125 g) on their distal right biceps brachii and distal right triceps brachii tendons (i. e., the primary agonist and antagonist movers of the reaching task). Tendon vibration has been used widely in the literature to perturb activity of the somatosensory receptors (e.g., Cordo et al., 1995; Redon et al., 1991; Roll and Vedel, 1982; Roll et al., 1989). Specifically, vibrating muscle tendons at specific frequencies (i.e., 100 Hz), can increase the firing rate of Type 1a muscle fibers, which provide information about muscle length (i.e., Gardner and Johnson, 2013). Vibrating a single muscle in a static condition can create the illusion that the muscle is lengthening (see Goodwin et al., 1972 for a review). Tendon vibration has been implemented widely in the literature to assess somatosensory feedback utilization (e.g., Cordo et al., 1995; Roll et al., 1989, Goodman



**Fig. 1.** Front (A) and over-the-shoulder (B) views of experimental set-up. Panel A portrays the experimenter/front view of the participant, who placed the right index finger on atop the aiming surface and the index, middle, and ring fingers of the left hand underneath the board equipped with the somatosensory tactors. Panel B portrays an over-the-shoulder view of the aiming surface, with a display of the textured home position for the right index finger and all three potential visual target locations.

and Tremblay, 2018), as it has been shown to induce endpoint biases (e. g., Roll and Vedel, 1982; Redon et al., 1991) and variability in voluntary limb trajectories (e.g., Goodman and Tremblay, 2018). To avoid directional biases (i.e., perception of flexion or extension at the elbow), application of tendon vibration was applied to both the agonist and antagonist muscle (e.g., Roll and Vedel, 1982; Goodman and Tremblay, 2018). Furthermore, tendon vibration, has been shown to create aftereffects on the muscle fiber activation, lasting up to 30 s. That is, after the removing of muscle tendon vibration, a large proportion (i.e., ~73%) of muscle spindles exhibit a reduction in firing rates for at least 6 s and up to 30 s, with the peak of depression of spindle responsiveness occurring around 3 s (Ribot-Ciscar et al., 1998). Thus, presenting tendon vibration between movements was expected to have an impact on the signals relayed by the sensory fibers of the effector limb. Furthermore, tendon vibration presented between movements also allows for avoiding reflexive behaviours of antagonistic muscles that could occur when presented during voluntary movements (e.g., Eklund and Hagbarth, 1966). In sum, tendon vibration applied to both the antagonist and agonist muscle between movement trials was deemed to be an effective way to perturb somatosensory feedback from the moving limb (see also Goodman and Tremblay, 2018). In the current study, vibration was applied at 100 Hz (i.e., to stimulate Type 1a receptors) to both the biceps and triceps brachii muscles for 5 s before movement onset. After the 5 s of vibration, the variable fore period began (see above), and thus movement onset was anywhere between 5.5 and 6.2 s after the onset of vibration. The tendon vibrations were worn by the participant for the entire duration of the experiment to reduce any inconsistencies of the skin receptors and compression on the arm (i.e., during both no vibration and vibration trials).

Participants performed two blocks of trials, one block with vibration presented between movements, and one block without vibration. The order of the blocks was counter-balanced between participants. A mandatory 15-min break was taken between blocks to ensure that the aftereffects of the vibration were significantly depleted (see Ribot-Ciscar et al., 1998). Before the first trial in the vibration block, the vibrators were activated for 60-s. Additionally, 5 s of tendon vibration was delivered before each trial in the vibration block. Such an approach has already been shown to be effective in increasing limb trajectory and endpoint variability (e.g., Goodman and Tremblay, 2018). Within each vibration block, three subsets of trials were employed in a blocked

fashion, each presenting targets of different sensory modality. The targets could be visual, somatosensory, or bimodal (see below), and the presentation order of subsets was also counterbalanced across participants. While the sensory information used to elicit the target was blocked within each subset, the location of target presentation was randomized within each subset for the three possible target locations (i. e., 27, 30 and 33 cm, see above).

### 2.1. Data analysis

The dependent variables were reaction time (RT), movement time (MT), endpoint location (i.e., movement accuracy), and endpoint variability (i.e., movement precision). Both endpoint variables were both measured in the primary movement axis (see Fig. 1A). Movement onset and offset times were captured when the horizontal limb velocity of the reaching finger (i.e., movement along the primary movement axis) rose above and fell below 0.03 m/s, respectively. RT was defined as the time between stimulus onset and offset. Endpoint location was defined as the time between movement onset and offset. Endpoint location was defined as the as the average trajectory endpoint. Endpoint variability was the standard deviation of movement endpoints.

Data from each dependent variable was submitted to a 2 Age Group (younger, older) by 3 Target Modality (visual, somatosensory, bimodal) by 2 Vibration (no vibration, vibration) mixed analysis of variance (ANOVA). All post-hoc analyses were performed using Tukey's HSD procedure. When the sphericity assumption was violated, Huynh-Feldt corrected statistics were used for calculations, with the degrees of freedom reported to the nearest decimal. Significance was set at p = 0.05 for all statistical contrasts. All inferential statistics were calculated (see Table 1). If a main effect was superseded by an interaction or more, only the highest level of interaction(s) were discussed in in the text.

## 3. Results

Analysis of RT revealed significant Age Group differences, superseded by a significant Age Group by Target Modality interaction, *F* (2,56) = 4.58, p = 0.01,  $\eta_p^2 = 0.14$ . Post-hoc analyses (HSD = 88 ms) revealed that older adults took more time to initiate movements than younger adults in the somatosensory target condition only (541 and 440 ms, respectively, see Fig. 2). Further, only older adults took more time to

#### Table 1

Inferential statistics.

		Reaction time	Movement time	Endpoint	Variable error
Age	F ratio P-	18.75 0.00	11.56 0.01	13.46 0.00	11.01 0.00
	value				
	Effect size	0.40	0.29	0.32	0.28
Target modality	F ratio	47.05	3.02	6.08	13.59
	<i>P</i> -	0.00	0.06	0.00	0.00
	value				
	Effect size	0.63	0.09	0.18	0.33
Vibration	F ratio	63.52	0.23	14.20	8.93
	<i>P</i> -	0.00	0.64	0.00	0.01
	value				
	Effect	0.65	0.01	0.33	0.24
	size				
Age group * target modality	F ratio	4.59	0.45	0.72	0.27
	P-	0.01	0.64	0.49	0.76
	value				
	Effect size	0.14	0.02	0.03	0.01
Age group * vibration	F ratio	2.08	0.01	0.79	1.16
	<i>P</i> -	0.16	0.93	0.38	0.29
	value				
	Effect	0.07	0.00	0.03	0.04
	size				
Target modality * vibration	F ratio	9.14	0.54	0.64	0.95
	P-	0.00	0.59	0.53	0.39
	value				
	Effect size	0.25	0.02	0.02	0.03
Age Group * target modality * vibration	F ratio	1.51	2.55	0.07	3.71
	<i>P</i> -	0.23	0.09	0.93	0.03
	value				
	Effect size	0.05	0.08	0.00	0.12

Note. All significant effects are denoted by bold text. Effect size values are partial Eta-square's generated from the ANOVA analyses.

initiate movements to somatosensory targets (541 ms) than bimodal targets (448 ms). The analysis also revealed a significant main effect of Target Modality, *F*(2,56) = 47.05, *p* < 0.001,  $\eta_p^2$  = 0.627 and a main effect of Vibration, *F*(1,28) = 63.52, p < 0.001,  $\eta_p^2$  = 0.694, which was superseded by a significant interaction between Target Modality and Vibration, *F*(2,56) = 9.14, *p* < 0.001,  $\eta_p^2$  = 0.246. Post-hoc analyses (HSD = 76.0 ms) revealed that both age groups took longest to initiate movements in the somatosensory condition, 524 ms) compared to visual (452 ms) and bimodal (438 ms) conditions, only in the presence of vibration. In contrast, there was only a significant main effect of Age Group for Movement Time, *F*(1,29) = 11.56, *p* = 0.001,  $\eta_p^2$  = 0.290, with older adults taking more time to complete their movements than younger adults (Fig. 3).

Analyses of movement endpoint location revealed a main effect of Age Group, F(1,29) = 13.46, p = 0.001,  $\eta_p^2 = 0.317$ , Target Modality, F(2,56) = 6.08, p = 0.004,  $\eta_p^2 = 0.178$ , and Vibration, F(1,29) = 14.20, p < 0.001,  $\eta_p^2 = 0.330$  (see Fig. 4). Post-hoc testing on the effect of Target Modality (HSD = 12.2 mm) revealed that movement to somatosensory targets yielded shorter terminal movement amplitudes (288 mm) than movements to either visual (295 mm) and bimodal targets (293 mm). Finally, endpoint locations were overall closer to the starting position for movements in the vibration versus no vibration block (288 mm and 295 mm, respectively).

The analyses of endpoint variability revealed significant main effects of Age Group, F(1,28) = 11.01, p = 0.003,  $\eta_p^2 = 0.282$ , Target Modality, F(2,56) = 13.58, p < 0.001,  $\eta_p^2 = 0.327$ , and Vibration, F(1,28) = 8.93, p = 0.006,  $\eta_p^2 = 0.242$ . These main effects were compounded by a threeway interaction between all factors, F(2,56) = 4.71, p = 0.031,  $\eta_p^2 = 0.117$ . Post-hoc analysis revealed that in the vibration condition, older adults exhibited greater endpoint variability than younger adults on movements towards somatosensory targets (12 mm and 9 mm, respectively, see Fig. 5). Further, only the older adults had significantly larger endpoint variability in the somatosensory targets in the vibration (14 mm) than in the no vibration condition (10 mm). Lastly, in the vibration condition, only the older adults had larger endpoint variability in the somatosensory target condition (14 mm), than in either the visual (10 mm) or bimodal conditions (9 mm) (Fig. 5).

#### 4. Discussion and conclusions

The current study investigated how younger and older adults prepare and perform upper-limb movements towards visual, somatosensory, or bimodal targets, in the absence of visual feedback from the environment. Additionally, on one block of the movement trials, tendon vibration was applied to the effector limb between the trials. The vibration was used to assess the participants' ability to prepare movements with disrupted somatosensory feedback from the moving limb. Results revealed that, while younger adults exhibited no significant differences in reaction times across all target modalities, older adults exhibited longer reaction times with somatosensory targets versus the visual and bimodal targets (see also Goodman et al., 2020). Critically, this effect of target modality on older adults' reaction time was exacerbated when tendon vibration was applied to the effector limb between movement trials. Furthermore, the application of tendon vibration resulted in only the older adults displaying larger movement endpoint variability when reaching to the somatosensory targets. These novel findings provide further evidence that older adults are likely engaging in different sensorimotor processes and/or transformations than younger adults when moving to somatosensory targets, at least when vision of the moving limb is not available. These results were considered with respect to motor planning in natural aging, sensory utilization and dominance, and then hypothetical agerelated differences in sensory weighting.

Age-related reliance on visual feedback has been thought to be associated with deteriorated planning abilities (e.g., Stelmach et al., 1987; Goodman et al., 2020). Based on this idea and the previouslyreported reduced strength and physiological changes that occur with age (e.g., Lexell et al., 1988), the current study investigated how somatosensory information from the effector limb is used as a function of target modality to plan voluntary action. The results replicated previous results, such that when older adults planned movements to somatosensory targets, they took more time to initiate their movements than vounger adults (see also Goodman et al., 2020). Furthermore, when somatosensory information of the effector was perturbed, the initiation times and endpoint variability were further increased. Thus, perturbing somatosensory feedback appeared to induce movement planning delays. One may suggest that these observed outcomes are a result of decreased quality and quantity of peripheral receptors (e.g., Lexell et al., 1988; Seidler and Stelmach, 1996), or perhaps increased neural noise from the degraded somatosensory signals (e.g., Skinner et al., 1984). However, it has recently been shown that older adults can perceive visual and somatosensory stimuli in a similar in a comparable fashion to younger adults when identifying stimuli for detection purposes (Goodman and Tremblay, submitted). Thus, while the results of the current study could reflect the degradation of somatosensory perception and transmission, an alternate or complementary explanation is related to sensorimotor transformation processes.

One idea that could explain the increased difficulty employing sensorimotor transformations may be a result of visual dominance typically displayed by older adults (e.g., Diaconescu et al., 2013). Thus, older adults may predominantly use visual reference frames to perform voluntary movements. In the absence of visual feedback, older adults took more time implementing sensorimotor transformations when only a somatosensory target was available. The idea that somatosensory information can be transformed into a visual reference frame for movement control is supported by the work of Reichenbach et al. (2009), who



Fig. 2. Reaction time results across all experimental conditions. Conditions are presented by cue of the target, as well as vibration block. Reaction time is plotted in milliseconds (ms) and error bars denote standard deviation values.



Fig. 3. Movement time results across all experimental conditions. Conditions are presented by cue of the target, as well as vibration block. Movement time is plotted in milliseconds (ms) and error bars denote standard deviation values.

examined the effect of visual feedback of the reaching limb on the latency of online corrections. In their study, younger adults made movements to visual targets using a haptic manipulandum, which allowed perturbations on the reaching limb (i.e., 10 N of force applied to the left or right from the original target). Further, visual perturbations were induced by shifting the target position 7.5 degrees to the left or to the right of the original target. Either perturbation could occur early or late in the movement (i.e., 1 cm or 5 cm from the starting position, respectively). Results indicated that limb trajectory corrections in response to visual target perturbations were longer when movements were made without vision of the limb than when they were performed with vision of the limb. Furthermore, when provided with vision of the reaching limb, corrections were not significantly affected. Reichenbach et al. (2009) concluded that the increase of correction time was a result of the



Fig. 4. Endpoint location results across all experimental conditions. Conditions are presented by cue of the target, as well as vibration block. Endpoint location is plotted in millimeters (mm) and error bars denote standard deviation values.



Fig. 5. Endpoint variability results across all experimental conditions. Conditions are presented by cue of the target, as well as vibration block. Endpoint variability is plotted in millimeters (mm) and error bars denote standard deviation values.

remapping/transformation of somatosensory feedback into a visual reference frame before the corrections take place. Likewise, the older adults in the current study, may have also mapped somatosensory information about the target and moving limb into a visual reference frame when planning their reaching movement. This effect could explain the longer movement initiation times seen only in the older adults towards somatosensory targets.

Further evidence for greater reliance on visual information in older than in younger adults arises from adaptation research. To better understand which aspects of visuomotor adaptation is influenced by age, Buch et al. (2003) recruited two groups of participants (younger and older) to perform reaches in either a quickly-adapting visual perturbation (i.e.,  $90^{\circ}$  rotation from onset of exposure), or a slowly-adapting visual perturbations (i.e.,  $11.25^{\circ}$  increments, up to  $90^{\circ}$ ). When comparing the aftereffects of reach adaptations, Buch et al. (2003) found that final reach adaptation achieved was lower in the older participants compared to younger participants when the  $90^{\circ}$  visual-proprioceptive mismatch was introduced on the first trial. Thus, older adults could not correct for the abrupt visuo-proprioceptive perturbations. Alternatively, when the mismatch was presented gradually, older and younger

adults could adapt their movement with similar correction amplitudes (see also Cressman et al., 2010). These studies help to support the hypothesis of age-related decreases in somatosensory feedback utilization for movement planning. Alternatively, it is also possible that older adults do not weigh visual and somatosensory cues appropriately, leading to different effects on movement planning processes. Further, these effects may be worsened in older versus younger adults.

The contributions of visual and somatosensory information have been shown to influence movement planning in different ways for younger adults. Sober and Sabes (2005) had young adult participants perform a reaching task to both visual and somatosensory targets, while manipulating both somatosensory and visual feedback about the position of the effector limb. The results showed that, with visual information, the difference between the target and seen fingertip position for aiming movements was more accurately predicted for visual targets, while somatosensory information had a stronger error predictive value for movements to somatosensory targets (see Sober and Sabes, 2005). In the current study, older adults were more affected by the tendon vibration than the younger adults for movements towards the somatosensory targets. Thus, the different age groups may be using different sensorimotor processes or transformations. Based on the results of Sober and Sabes (2005) and Manson et al. (2019), it appears that younger adults can plan and amend limb trajectories using only somatosensory processes, while the current results suggest that these capabilities are limited and/or delayed in a healthy older population. Additionally, the current study found that both older and younger adults planned movements with comparable reaction times to bimodal targets. Thus, the inclusion of visual feedback alleviated the effects of tendon vibration and reduced the inefficiencies displayed by the older adults in the somatosensory only target conditions. While it is not possible to comment about the relative reliance on each sensory system for the two age groups in the bimodal target condition, the longer initiation times displayed by older adults to the somatosensory targets indicates that using somatosensory information for movement planning did significantly differ between older and younger adults.

The results from the current study can also be interpreted in accordance to the neural frameworks such as the Vector Integration to End model (i.e., VITE, Cisek et al., 1998). In this model, somatosensory feedback is used to explain how the central nervous system represents sensory information for the completion of movement. According to the model, a difference vector between the estimated position of the limb and the estimated position of the limb at the target is created when preparing a reaching movement. These predictions are made with information from somatosensory inputs in Brodmann area 5, which is based on parietal inputs. The parietal areas, which are thought to receive input from the visual system (e.g., Churchland et al., 2006), contribute to the estimation of the intended target. Concurrently, the actual position of the limb is monitored by somatosensory feedback in area 5, via muscle spindle fibers and 1 tendon organs. The output of the movement is regulated by a velocity vector, characterized by cortical activity in area 4. Furthermore, and most relevant to the current work, the neurons that send the velocity vector project to motor neurons of the limb, which control the muscles of the effector. When the signal is sent, information is immediately received from the sensory fibers of the same limb to ensure the vector is in line with the difference vector predicted. The results of the current experiment showed that perturbed somatosensory feedback of the effector limb elongated reaction time to a greater extent in older than in younger adults. Furthermore, the somatosensory perturbation caused an increase in endpoint variability only in the older adults, likely caused by increased variability in these cortical firing patterns. Thus, the somatosensory feedback from the moving limb may have caused instability of the predicted vectors to the point that the older adults could not adjust their movements to the intended target, as further seen by the decreased endpoint precision. One omission of the VITE model is the influence of visual inputs, and the current study offers some challenges to the model by exposing the implications of somatosensory cue information with both visual and non-visual targets. Thus, the age-related differences in reaction time appear to be associated with the sensorimotor processes between sensory (i.e., area 5) and motor (i.e., area 4) cortical areas for the planning of movement. Furthermore, the processes indicated in the VITE model could be different in older than younger adults.

In conclusion, perturbing somatosensory information of the effector limb lengthened the time older adults took to plan a movement to somatosensory targets and worsened the endpoint precision of their reaching movement. Specifically, the observed effects of lengthened reaction times and larger endpoint variability with tendon vibration of the reaching limb were significantly greater for older than for younger adults, suggesting that somatosensory information from effector also contributes to planning movements to a somatosensory target. Based on the current results and the previously reported evidence, it is likely that older adults do not perform the same sensorimotor processes as younger adults, at least when integrating somatosensory information.

## Funding

This work was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC), the University of Toronto, Ontario Research Fund (ORF) and Canada Foundation for Innovation (CFI).

#### References

- Alais, D., Newell, F.N., Mamassian, P., 2010. Multisensory processing in review: from physiology to behaviour. Seeing Perceiving 23 (1), 3–38. https://doi.org/10.1163/ 187847510X488603.
- Bach, M., 1996. The Freiburg Visual Acuity Test-automatic measurement of visual acuity. Optom. Vis. Sci. 73 (1), 49–53. https://doi.org/10.1097/00006324-199601000-00008.
- Bagesteiro, L.B., Sarlegna, F.R., Sainburg, R.L., 2006. Differential influence of vision proprioception on control of movement distance. Exp. Brain Res. 171 (3), 358. https://doi.org/10.1007/s00221-005-0272-y.
- Bernier, P.-M., Gauthier, G.M., Blouin, J., 2007. Evidence for distinct, differentially adaptable sensorimotor transformations for reaches to visual and proprioceptive targets. J. Neurophysiol. 98 (3), 1815–1819. https://doi.org/10.1152/ in.00570.2007.
- Blouin, J., Saradjian, A.H., Lebar, N., Guillaume, A., Mouchnino, L., 2013. Opposed optimal strategies of weighting somatosensory inputs for planning reaching movements toward visual and proprioceptive targets. J. Neurophysiol. 112 (9), 2290–2301. https://doi.org/10.1152/jn.00857.2013.
- Brodoehl, S., Klingner, C., Witte, O.W., 2016. Age-dependent modulation of the somatosensory network upon eye closure. Behav. Brain Res. 298, 52–56. https://doi. org/10.1016/j.bbr.2015.10.035.
- Buch, E.R., Young, S., Contreras-Vidal, J.L., 2003. Visuomotor adaptation in normal aging. Learn. Mem. 10 (1), 55–63. https://doi.org/10.1101/lm.50303.
- Chaput, S., Proteau, L., 1996. Modifications with aging in the role played by vision and proprioception for movement control. Exp. Aging Res. 22, 1–21. https://doi.org/ 10.1080/03610739608253994.
- Churchland, M.M., Byron, M.Y., Ryu, S.I., Santhanam, G., Shenoy, K.V., 2006. Neural variability in premotor cortex provides a signature of motor preparation. J. Neurosci. 26 (14), 3697–3712.
- Cisek, P., Grossberg, S., Bullock, D., 1998. A cortico-spinal model of reaching and proprioception under multiple task constraints. J. Cogn. Neurosci. 10 (4), 425–444.
- Cordo, P., Gurfinkel, V.S., Bevan, L., Kerr, G.K., 1995. Proprioceptive consequences of tendon vibration during movement. J. Neurophysiol. 74 (4), 1675–1688. https:// doi.org/10.1152/jn.1995.74.4.1675.
- Cressman, E.K., Salomonczyk, D., Henriques, D.Y., 2010. Visuomotor adaptation and proprioceptive recalibration in older adults. Exp. Brain Res. 205 (4), 533–544.
- Cuppone, A.V., Squeri, V., Semprini, M., Masia, L., Konczak, J., 2016. Robot-assisted proprioceptive training with added vibro-tactile feedback enhances somatosensory and motor performance. PLoS One 11 (10). https://doi.org/10.1371/journal. pone.0164511.
- Darling, W.G., Cooke, J.D., Brown, S.H., 1989. Control of simple arm movements in elderly humans. Neurobiol. Aging 10 (2), 149–157. https://doi.org/10.1016/0197-4580(89)90024-9.
- Diaconescu, A.O., Hasher, L., McIntosh, A.R., 2013. Visual dominance and multisensory integration changes with age. Neuroimage 65, 152–166. https://doi.org/10.1016/j. neuroimage.2012.09.057.
- Eklund, G., Hagbarth, K.E., 1966. Normal variability of tonic vibration reflexes in man. Exp. Neurol. 16 (1), 80–92. https://doi.org/10.1016/0014-4886(66)90088-4.
- Elliott, D., Hansen, S., Mendoza, J., Tremblay, L., 2004. Learning to optimize speed, accuracy, and energy expenditure: a framework for understanding speed-accuracy relations in goal-directed aiming. J. Mot. Behav. 36 (3), 339–351. https://doi.org/ 10.3200/JMBR.36.3.339-351.

- Elliott, D., Hansen, S., Grierson, L.E., Lyons, J., Bennett, S.J., Hayes, S.J., 2010. Goaldirected aiming: two components but multiple processes. Psychol. Bull. 136 (6), 1023. https://doi.org/10.1037/a0020958.
- Elliott, D., Lyons, J., Hayes, S.J., Burkitt, J.J., Roberts, J.W., Grierson, L.E., Bennett, S.J., 2017. The multiple process model of goal-directed reaching revisited. Neurosci. Biobehav. Rev. 72, 95–110. https://doi.org/10.1016/j.neubiorev.2016.11.016.
- Ernst, M.O., Bülthoff, H.H., 2004. Merging the senses into a robust percept. Trends Cogn. Sci. 8 (4), 162–169. https://doi.org/10.1016/j.tics.2004.02.002.
- Gardner, E.P., Johnson, K.O., 2013. Sensory coding. In: Kandel, E.R., Schwartz, J.H., Jessell, T.M., Siegelbaum, S.A., Hudspeth, A.J. (Eds.), Principles of Neural Science, 5th ed. McGraw Hill, New York, pp. 449–474.
- Goodman, R., Tremblay, L., 2018. Using proprioception to control ongoing actions: dominance of vision or altered proprioceptive weighing? Exp. Brain Res. 236 (7), 1897–1910. https://doi.org/10.1007/s00221-018-5258-7.
- Goodman, R., Tremblay, L., 2021. Out of touch? The challenge of initiating voluntary movements to somatosensory targets in older adults. Neurosci. Lett. (in preparation).
- Goodman, R., Manson, G.A., Tremblay, L., 2020. Age-related differences in sensorimotor transformations for visual and/or somatosensory targets: planning or execution? Exp. Aging Res. https://doi.org/10.1080/0361073X.2020.1716153.
- Goodwin, G.M., McCloskey, D.I., Matthews, P.B.C., 1972. Proprioceptive illusions induced by muscle vibration: contribution by muscle spindles to perception? Science 175, 1382–1384. https://doi.org/10.1126/science.175.4028.1382.
- Haaland, K.Y., Harrington, D.L., Grice, J.W., 1993. Effects of aging on planning and implementing arm movements. Psychol. Aging 8 (4), 617. https://doi.org/10.1037/ 0882-7974.8.4.617.
- Helsen, W.F., Van Halewyck, F., Levin, O., Boisgontier, M.P., Lavrysen, A., Elliott, D., 2016. Manual aiming in healthy aging: does proprioceptive acuity make the difference? Age 38, 45. https://doi.org/10.1007/s11357-016-9908-z.
- Henriques, D.Y., Medendorp, W.P., Khan, A.Z., Crawford, J.D., 2002. Visuomotor transformations for eye-hand coordination. Prog. Brain Res. 140, 329–340. https:// doi.org/10.1016/S0079-6123(02)40060-X.
- Lexell, J., Taylor, C.C., Sjöström, M., 1988. What is the cause of the ageing atrophy?: Total number, size and proportion of different fiber types studied in whole vastus lateralis muscle from 15-to 83-year-old men. J. Neurol. Sci. 84 (2), 275–294. https:// doi.org/10.1016/0022-510X(88)90132-3.
- Manson, G.A., Blouin, J., Kumawat, A.S., Crainic, V.A., Tremblay, L., 2019. Rapid online corrections for upper limb reaches to perturbed somatosensory targets: evidence for non-visual sensorimotor transformation processes. Exp. Brain Res. 237 (3), 839–853. https://doi.org/10.1007/s00221-018-5448-3.
- Mikula, L., Sahnoun, S., Pisella, L., Blohm, G., Khan, A.Z., 2018. Vibrotactile information improves proprioceptive reaching target localization. PLoS One 13 (7), 1–13. https://doi.org/10.1371/journal.pone.0199627.
- Oldfield, R.C., 1971. The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9, 97–113.
- Pohl, P.S., Winstein, C.J., Fisher, B.E., 1996. The locus of age-related movement slowing: sensory processing in continuous goal-directed aiming. J. Gerontol. Ser. B Psychol. Sci. Soc. Sci. 51 (2), 94–102. https://doi.org/10.1093/geronb/51B.2.P94.

- Pratt, J., Chasteen, A.L., Abrams, R.A., 1994. Rapid aimed limb movements: age differences and practice effects in component submovements. Psychol. Aging 9 (2), 325. https://doi.org/10.1037/0882-7974.9.2.325.
- Rand, M.K., Wang, L., Müsseler, J., Heuer, H., 2013. Vision and proprioception in action monitoring by young and older adults. Neurobiol. Aging 34 (7), 1864–1872. https:// doi.org/10.1016/j.neurobiolaging.2013.01.021.
- Redon, C., Hay, L., Velay, J.L., 1991. Proprioceptive control of goal-directed movements in man, studied by means of vibratory muscle tendon stimulation. J. Mot. Behav. 23 (2), 101–108. https://doi.org/10.1080/00222895.1991.9942027.
- Reichenbach, A., Thielscher, A., Peer, A., Bülthoff, H.H., Bresciani, J.-P., 2009. Seeing the hand while reaching speeds up on-line responses to a sudden change in target position. J. Physiol. 587 (19), 4605–4616. https://doi.org/10.1113/ jphysiol.2009.176362.
- Ribot-Ciscar, E., Rossi-Durand, C., Roll, J.P., 1998. Muscle spindle activity following muscle tendon vibration in man. Neurosci. Lett. 258 (3), 147–150. https://doi.org/ 10.1016/S0304-3940(98)00732-0.
- Roll, J.P., Vedel, J.P., 1982. Kinaesthetic role of muscle afferents in man, studied by tendon vibration and microneurography. Exp. Brain Res. 47 (2), 177–190. https:// doi.org/10.1007/bf00239377.
- Roll, J.P., Vedel, J.P., Ribot, E., 1989. Alteration of proprioceptive messages induced by tendon vibration in man: a microneurographic study. Exp. Brain Res. 76 (1), 213–222. https://doi.org/10.1007/bf00253639.
- Sarlegna, F.R., Sainburg, R.L., 2007. The effect of target modality on visual and proprioceptive contributions to the control of movement distance. Exp. Brain Res. 176, 267–280. https://doi.org/10.1007/s00221-006-0613-5.
- Seidler, R.D., Stelmach, G.E., 1996. EMG patterns: age differences in a speed-constrained, self-initiated task. In: Society for Neuroscience–Abstract, vol. 22, p. 1638. https:// doi.org/10.4322/rbeb.2013.029.
- Seidler-Dobrin, R.D., Stelmach, G.E., 1998. Persistence in visual feedback control by the elderly. Exp. Brain Res. 119 (4), 467–474. https://doi.org/10.1007/ s002210050362

Skinner, H.B., Barrack, R.L., Cook, S.D., 1984. Age-related decline in proprioception. Clin. Orthop. Relat. Res. (184), 208–211.

- Sober, S.J., Sabes, P.N., 2005. Flexible strategies for sensory integration during motor planning, Nat. Neurosci. 8 (4), 490. https://doi.org/10.1038/nn1427.
- Stelmach, G.E., Goggin, N.L., García-Colera, A., 1987. Movement specification time with age. Exp. Aging Res. 13 (1), 39–46. https://doi.org/10.1080/03610738708259298. Todorov, E., Jordan, M.I., 2002. Optimal feedback control as a theory of motor

coordination. Nat. Neurosci. 5 (11), 1226. https://doi.org/10.1038/nn963.

- Tremblay, L., de Grosbois, J., 2015. Why encode limb and body displacements in the velocity domain? Neurophysiological and behavioral evidence. Adv. Visual Percept. Res. 279–292.
- Yang, Y., Bender, A.R., Raz, N., 2015. Age related differences in reaction time components and diffusion properties of normal-appearing white matter in healthy adults. Neuropsychologia 66, 246–258. https://doi.org/10.1016/j. neuropsychologia.2014.11.020.