Increased upper-limb sensory attenuation with age

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Abstract

The pressure of our own finger on the arm feels differently than the same pressure exerted by an external agent: the latter involves just touch, whereas the former involves a combination of touch and predictive output from the internal model of the body. This internal model predicts the movement of our own finger and hence the intensity of the sensation of the finger press is decreased. A decrease in intensity of the self-produced stimulus is called sensory attenuation. It has been reported that, due to decreased proprioception with age and an increased reliance on the prediction of the internal model, sensory attenuation is increased in older adults.

In this study, we used a force-matching paradigm to test if sensory attenuation is also present over the arm and if aging increases sensory attenuation. We demonstrated that, while both young and older adults overestimate a self-produced force, older adults overestimate it even more showing an increased sensory attenuation. In addition, we also found that both younger and older adults self-produce higher forces when activating the homologous muscles of the upper limb.

While this is traditionally viewed as evidence for an increased reliance on internal model function in older adults because of decreased proprioception, proprioception appeared unimpaired in our older participants. This begs the question of whether an age-related decrease in proprioception is really responsible for the increased sensory attenuation observed in older people.

New and Noteworthy

Forces generated externally (by the environment on the participant) and internally (by the participant on her/his body) are not perceived with the same intensity. Internally-generated forces are perceived less intensely than externally generated ones. This difference in force sensation has been shown to be higher in elderly participants when the forces were applied on the fingers because of their impaired proprioception. Here we replicated this finding for the arm but suggest that it is unlikely linked to impaired proprioception.

Introduction

The position of one's arm is monitored by sensory organs such as skin receptors or muscle proprioceptors. This information is then processed in light of a top-down organization where expectations and prior knowledge influence how the stimulus is perceived (Kok et al. 2012; de Lange et al. 2018). In essence, sensorimotor integration is a process in which the central nervous system integrates different sources of information (sensory and prior information) and transform them into motor actions (Machado et al. 2010). This processing allows humans to differentiate between internal (produced by our own movement) and external stimuli (Blakemore et al., 1998). As a result, our body perceives the sensory consequences of its own movements less intensely than the same stimulus produced by the external environment. This decrease in intensity of the perception of the self-produced stimuli is called sensory attenuation (Blakemore et al. 2000; Brown et al. 2013; Wolpert et al. 1995a) and relies on the connection between sensorimotor areas and the cerebellum (Kilteni and Henrik Ehrsson 2020).

Sensory attenuation (also termed sensory cancellation) is a widespread phenomenon that applies to different types of movements (saccades, vestibuloocular reflex, force, etc.) and to perception (Cao et al. 2017; Klever et al. 2019; Niziolek et al. 2013). Sensory attenuation occurs when the internal prediction of the consequences of our own actions is compared to the actual sensory input in order to cancel the resultant self-generated signal (Cullen 2004). Sensory attenuation is observed in many species (Sillar and Roberts 1988; Webb 2004). For instance, there is evidence of attenuation of responses to self-generated sounds in mice (Rummell et al. 2016). Flying insects need to be able to distinguish self-induced stimulation (such as rotation of the visual field caused by tracking a target) from externally imposed stimulation (such as visual rotation due to air disturbances) if they are to use the latter for flight stabilization (Dickinson and Muijres 2016; Webb 2004) . Electric fish need to distinguish between perturbation of the surrounding electric field is due to a predator or due to their own movements (Kirk 1985; Sawtell 2017). Sensory attenuation might also explain why humans cannot tickle themselves (Blakemore et al. 2000; Wolpert et al. 1995b), and why sounds produced by an external agent always seem louder than sounds produced by us (Klaffehn et al. 2019).

Another consequence of sensory attenuation is the tendency to underestimate the force that individuals produce in force matching tasks (Palmer et al. 2016; Shergill et al. 2003; Wolpe et al. 2016). In such tasks, participants are asked to reproduce an external force applied on one hand (target force, e.g. 2N) with their other hand. They typically produce more force that they should (self-produce force, e.g. 3N) while judging that the target and the self-produced forces have the same intensity. This process of producing more force than intended is referred to as over-compensation and is a behavioral consequence of sensory attenuation.

To capture the causal relationships between our actions and their sensory consequences, the brain makes use of an internal forward model (Blakemore et al. 2000; Franklin and Wolpert 2011; Shadmehr et al. 2010; Sommer and Wurtz 2008; Wolpert et al. 1995a; Wolpert and Miall 1996). Such internal model takes a copy of the motor commands sent to the muscles (efference copy or corollary discharge) as input and outputs the predicted sensory consequences. When a sensation is internally generated (e.g. by our own movement), the internal model predicts its sensory consequences (Blakemore et al. 2000; Bubic et al. 2010; Cullen et al. 2011; Wolpert et al. 1995a) and uses this internal prediction to attenuate the sensory effects of the produced movement (Blakemore et al. 2000; Sato 2008; Wolpert et al. 1995). Externally generated sensations are not associated with any efference copy and are therefore perceived differently. Studies have shown that there is no sensory attenuation detected during passive movements and such movements are perceived as strong as external sensations (Kilteni 2020).

By attenuating the sensory consequences that are due to self-produced movement it is possible to accentuate the sensation of events caused by external agents (Moore et al. 2009). The sense of agency, which refers to the ability to perceive that a movement is controlled by the participant and not by an external agent, has been linked to sensory attenuation (Garrido-Vásquez and Rock 2020). Sensory attenuation and sense of agency together yield to the perception that the observed movement has been internally generated (Kilteni and Ehrsson 2017; Moore et al. 2009). The sense of agency is also based on the comparison between the expected sensory consequences of the movement and the actual sensations of it (Brown et al. 2013; Moore et al. 2009; Weiss et al. 2011). If these match, the movement will be considered as controlled by the brain.

Studies have shown that sensory attenuation increases with age (Klever et al. 2019; Wolpe et al. 2016). For instance, in force matching tasks, when young and old participants experience an external force on their finger, older participants applied higher self-produced forces than younger participants. This increased overcompensation with aging might stem from age-related changes in one of the two sources of information used for sensory attenuation: sensory feedback or internal model predictions. Furthermore, the balance between these two streams of information has been shown to rely on Bayesian integration (Ernst and Banks 2002). That is, both streams are weighted in function of their relative reliability (Körding et al. 2004;

Orban de Xivry et al. 2013). Given that the reliability of somatosensory and proprioceptive acuity (measured as haptic recognition and discrimination, sense of position, motion or dynamic position), decreases with aging (Dunn et al. 2015; Goble et al. 2009; Ranganathan et al. 2001), it has been suggested that older adults rely more on the predictive stream (i.e. on their internal model) (Wolpe et al. 2016). In addition, some studies point to the fact that internal model function might be not be affected by aging (Heuer et al. 2011; Vandevoorde and Orban de Xivry 2019), but this is still debated (Bernard and Seidler 2014).

To our knowledge, the only two studies that evaluated age-related changes in the motor domain did so at the fingers (Klever et al. 2019; Wolpe et al. 2016). Yet, sensory attenuation has been reported for upper limbs as well (Logan et al. 2019). In this study, we want to investigate whether a larger sensory attenuation in older participants can be detected in other limbs and decided to focus on the upper limbs. We hypothesized that older adults will have a higher sensory attenuation over the arm due to increased reliance on internal models. Furthermore, we wanted to test the widespread hypothesis that the higher sensory attenuation in older people was linked to an age-related decline in proprioceptive abilities. Finally, we also tested the possibility that sensory attenuation is modulated by the group of muscles sensing and producing the force. The use of two different direct conditions (mirror and parallel) took advantage of what is not possible with the fingers. In a finger force matching task, homologous muscles are always tested (flexor of the index finger) and we were wondering whether sensory attenuation was specific to the activated muscle (homologous and non-homologous in our case) or not. To do so, we compared the amount of overcompensation when homologous or non-homologous muscles are involved in sensing and producing the forces as network controlling homologous muscles have a particular connection as evidenced by mirroring activity during unilateral movements (Beaulé et al. 2012). We hypothesized that this connection would increase with age (Shinohara et al. 2003).

Methods:

Thirty-five young adults aged 18-35 years and thirty-five older adults aged 55-75 years, participated in experiment 1. Thirty-one young adults aged 18-35 years and thirty older adults aged 53-75 years participated in experiment 2. Both experiments were approved by the Ethics Committee of the University Research UZ/KU Leuven (Study number: S61179) and performed according to the guidelines of the Declaration of Helsinki. All subjects provided their written consent prior to their participation. The Edinburgh handedness questionnaire (Oldfield 1971) was used to confirm self-reported right-handedness. All participants were screened with a general health and consumption habits questionnaire (frequency of any use of drugs, tobacco or alcohol beverages). The exclusion criteria were no history of neurological disorders or any addictions or habits (such as drug use) that will alter behavior.

Older adults were assessed using the Mini-Mental State Examination (Folstein et al. 1975) for general cognitive functions. All older adults scored within normal limits (score>= 26).

We did not perform an a-priori power analyses as we did not know what sample size to expect. For experiment 1, we chose 35 people per group as this is larger than most behavioral studies on age related difference in motor control.

Experiment 2 was performed in the context of a master thesis while the data of experiment 1 was being analyzed. Hence, the sample size was planned as N=30 in each group. In the young adults, one extra participant was tested unintentionally. As this did not fit any criteria for data exclusion, we have included all tested participants making sample size N=31 for this group.

Setup

Participants were asked to grab the handles of a robotic manipulandum (KINARM End-Point Labs™, BKIN Technologies, Kingston, ON Canada). Their hands were hidden from view and reflected as two white cursors. These cursors were displayed on a screen placed tangentially above a mirror and were reflected by it. Because the mirror was halfway between the handle and the screen, the cursors appeared to be positioned at the same position in space as the hands. All experimental conditions were programmed in MATLAB-Simulink (Mathworks, Natick, MA, US). The force exerted on the handles were measured by built-in force transducers. Position and force data were sampled at 1000 Hz.

Experimental paradigm

The Force Matching task implements the Method of Adjustment, in which participants adjust the level of the stimulus to match a previously presented stimulus (Wolpe et al., 2016). Two red circles appeared on the screen and participants had to reach to them and to maintain their hand position inside them. The color of the circles turned green to indicate that the hand cursors were positioned inside them. The right handle was then locked at that position in order to eliminate movements of the right handle throughout the experiment. The left circle turned then blue to indicate the start of force perception period. During the force perception period, the left hand (reference arm) was pushed rightward (+X direction) by the robot with a force of 4, 6 or 8N (target force). Three target forces of 4, 6 and 8 N were presented in pseudorandom order. Ten trials were provided for each level of force.

The force was ramped up over 1s, maintained constant during 2s and then ramped down during 1 second. Participants were asked to resist the force with the left hand and stay inside the blue circle. A safety region was included between the two hands. If participants did not resist the force enough and if, as a consequence, the left hand went above half the distance between the two targets (i.e., between the original positions of the left and right hands), the force was turned off and the trial was restarted. We realized during the experimental sessions that there was no clear signal that the trial was restarted. The absence of a clear signal confused the participants. As a consequence, we excluded these trials from further analyses.

At the end of this phase, the right circle (above the right hand) turned blue to indicate the start of force reproduction period. In this phase, the participants had to control the robot with their active right hand in order to produce a force on the left hand that matched the force experienced during the force perception period. The reproduction phase differed in function of the condition.

In the slider condition, the right circle became a rectangular shape of 20 cm of height and 2 cm of length. Participants could produce a force on the left hand (reference arm) by moving the dot (with the active right hand) located within the rectangle in the upward or downward direction. The position on the slider was mapped to the force on the left handle (Fig 1A 2a. Slider). For one block of trials (slider up condition), participants had to move the slider up from the start position in order to produce a force in the +X direction on the left hand. In a separate block of trials (slider down condition), participants had to move the slider down in order to produce a force in the -X direction on the left hand. Results for the slider condition were calculated as the average between the slider up and slider down conditions.

In experiment 1, subjects were given a maximum of 6 seconds to match the perceived force and were asked to apply the matched force until the end of the reproduction phase. In experiment 2, they had unlimited time but had to signal verbally to the experimenter when they had matched the target force. The experimenter ended then the reproduction phase by clicking on a button.

The slider condition serves as control condition for the active conditions (mirror and parallel conditions, see below) but was also used to estimate proprioceptive abilities and evaluate sensory biases in the force-matching task as the movement of the right hand was only indirectly matched to the force produced on the left hand. In contrast, there were two other conditions (active conditions: mirror and parallel where the force exerted by the right hand was directly mapped to the force felt in the left hand. The direct and slider conditions were counterbalanced across participants for both experiments. In experiment 1, the order of the mirror and parallel conditions was also randomized.

In the mirror condition, participants had to match the target force by exerting a force with the active right hand on the right handle, in the –X direction. This produced force was transmitted to and felt on the left handle in the +X direction. We checked that the force recorded by the right hand was effectively felt by the left hand by analyzing the force transducer data from both robotic arms. This applies to the parallel condition as well. In experiment 1, subjects were given a maximum of 6 seconds to match the target force and were asked to apply the matched force until the end of the reproduction phase. In experiment 2, they had unlimited time but had to signal verbally to the experimenter that they had matched the target force. The experimenter ended then the reproduction phase by clicking on a button. This condition required the activation of non-homologous muscles of the arm (biceps for the right arm to produce the force and triceps for the left arm to resist the force). The objective of this condition was to test if activation of non-homologous muscles of both arms had an effect on the perception of self-produced forces.

The parallel condition differed from the mirror condition in the mapping between the force produced on the active right hand and the force felt in the left hand and in the instructions. In the parallel condition, the produced and felt forces were in the same direction. That is, if the right hand produced a force in the –X direction, the force produced on the left hand was also in the –X direction (Fig 1A 2c. Parallel). Furthermore, while the target force was felt in the +X direction, the participants were instructed to match the force in the –X direction. This condition was only used in experiment 1. The parallel condition requires the activation of homologous muscles of the arm.

Before experiment 1, participants were given 9 practice trials, in each condition. In experiment 2, we programmed further instructions for each stage of the task on the screen for participants and increased the number of training blocks. First, there was a practice block where participants only felt the target forces. Next, a “play” block was provided where participants could apply the force on the right handle and feel it on the left one. The third block was a practice block that involved all stages of the task. In both experiments, subjects were also ensured breaks in between conditions and blocks in order to prevent fatigue.

FIG1 HERE

The position matching task.

To assess proprioceptive abilities, we also tested N=69 participants from experiment 1 (34 young and 35 old) and N=56 participants from experiment 2 (30 young and 26 old) on an arm position matching task (Dukelow et al. 2010; Fuentes and Bastian 2010). Subjects were instructed to relax and let the robot move the right arm to 1 of 9 different spatial locations. When the robot stopped moving, subjects were asked to move their left hand to the mirror location in space i.e mirror-match the position of the robot. Subjects notified the examiner when they completed each trial and the examiner then triggered the next trial. Target locations were randomized within a block. Each subject completed 6 blocks for a total of 54 trials. Participants were not blindfolded in this task but their arms were hidden from the view, by a black-colored cover. There were no explicit instructions provided to the participants on where to look, rather they were simply asked to focus on matching the arms.

The motivation for performing the task was to test for proprioceptive differences in the age groups. Wolpe et al. hypothesized that the larger sensory attenuation observed in elderly people was linked to their poorer proprioceptive abilities. Therefore, it makes sense to test for proprioceptive acuity in our group of participants. To do so, we used a bimanual position matching task (Dukelow et al., 2010). Together with the outcome of the slider condition, the outcomes of the position matching task will allow us to evaluate age-related difference in proprioception.

Note that the role of the left and right arm in the position matching task differed from their role in the force matching task. In the force matching task, the left arm was the reference passive arm while the right arm was the active arm. In contrast, in the position matching task, the right arm was passively moved by the robot and served as reference.

Data processing

Force matching task

All the data collected were analyzed in MATLAB (Mathworks, Natick, MA, US). For experiment 1, produced forces were calculated as the average of the force measured by the force transducer of the left handle (which is identical to the force produced by the participant on the right handle in direct conditions) between 1s and 3s after the start of matching phase (Fig 2.1). We chose the time window of 1 to 3 seconds from the start of the matching phase as this was the closest to the perceived force phase (2 seconds of linear force).

In experiment 1, the matching time provided was limited (5s). Based on previous studies, we also analyzed the data from other time windows in order to check the robustness of our results in function of the chosen time window. Specifically, we used a time window between 2 and 2.5 seconds (Wolpe et al., 2016) and between 2.5 and 3 seconds after start of matching as used in previous studies (Wolpe et al., 2016, Palmer at al., 2016). Both of these time windows are situated around the peak force. We also used a later time window, between 2 and 4 seconds after start of the matching phase, as the produced force is potentially more stable later on compared to our first time window.

For experiment 2, the produced forces were calculated between 1s after the start matching phase and until the verbal cue of the participant when the Go button was pressed. Target forces were taken as 4, 6 and 8 N which were same as the commanded forces from the robot. Since the subject resisted the forces, the actual forces perceived during the force perception were very slightly higher or lower than the target forces of 4, 6 and 8 N.

For each trial separately, we computed the force error as the difference between the produced force and the target force. This quantity was expressed in Newton. We then computed the normalized overcompensation as the difference in force error between the direction condition (mirror or parallel) and the slider condition. In other words, we used the slider condition as the control condition.

For an exploratory analysis, we looked at the maximum deviation of the left hand in order to study the ability of each age group to resist the force applied by the robot when the force was externally produced (force perception phase) or when it was internally produced (slider or active conditions). In order to compute the maximum deviation, we computed the maximum horizontal distance between the left hand cursor that the participants were instructed to maintain inside the circular target and the center of the circular target. The calculation was done separately for the force perception phase and the force matching phase

Position matching task

For this task, we used two standardized parameters to assess the results of the task: Absolute error XY and Variability XY (Dukelow et al., 2010; Herter et al., 2014). VariabilityXY was calculated by using the standard deviation for each of the nine target locations for x and y direction separately. Next, the mean of these standard deviations of all nine target locations was taken and the variability was obtained for the x and y direction ($Varx$, $Vary$). The following formula was used:

$$Var_{xy} = \sqrt{{Var_x}^2 + {Var_y}^2}$$

Absolute error was calculated for each of the nine target locations for x and y direction separately. Then the mean of these absolute errors of all nine target locations resulted in the absolute error for the x and y direction (*AbsErrorx*, *AbsErrory*). Absolute errors XY was finally calculated as:

$$AbsError_{xy} = \sqrt{AbsError_x{}^2 + AbsError_y{}^2}$$

Data Analysis

All values (calculated average force and force error values used in our statistical analyses) were those averaged across valid trials. Trials where the forces were not resisted enough and where the hand went into the safety region were excluded. The trials where the hand crossed half the distance from the two circles were rejected. We rejected 6.7 % of trials in the slider condition and 3% in the direction conditions for experiment 1. In experiment 2, these percentages amounted to 6.8% and 1.3%, respectively.

For slider conditions, we calculated the average between the slider up and slider down trials. In experiment 1, there was no slider down condition for one older subject. In experiment 2, there was no slider down condition for 12 older subjects.

In the paper, we report the mean (across trials) of the average force value computed between 1s and 3s after the start of the matching phase from each trial. In the supplementary material, we also report the median (across trials) of the average force values from each trial (supplementary information document Table 2) and the mean (across trials. Supplementary information Table 1) of the maximum force value from each trial (supplementary information Table 3) for each participant, condition, and experiment. The analyses related to different time windows are also reported in the supplementary information Table 4, 5 and 6.

We also performed the analyses using the force applied by the participants during the perception phase as target force instead of the reference values of 4, 6 or 8N. This applied force was then subtracted from the matched forces to obtain the force error. There was no statistical difference in the results with the forces applied during the perception phase vs. the original results. The statistical results have been added to supplementary information Table 7 and 8.

Analysis 1:

To test for differences between the two age groups across all three force levels and all three conditions in experiment 1, we used a 3-way analysis of variance (ANOVA) with the age as the between-subject factor and levels of forces (4, 6 and 8N) and conditions as within-subject factor, with the force level as the dependent variable. These ANOVAs were followed up by post-hoc t-tests with Bonferroni-Holm correction.

Analysis 2:

To test for differences between the normalized overcompensation in the two age groups across all three force levels and mirror and parallel conditions in experiment 1, we used a 3-way analysis of variance (ANOVA) with the age as the between-subject factor and levels of forces and conditions (mirror vs. parallel) as within-subject factor.

Analysis 3:

We performed a one-sample t-test against zero for each condition (mirror and parallel) of experiment 1, to test whether mean normalized overcompensation was higher or lower than zero.

Analysis 4:

To test for differences between the two age groups across all three force levels and both conditions in experiment 2, we used a 3-way analysis of variance (ANOVA) with age group as the between-subject factor and levels of forces and conditions as within-subject factor.

Analysis 5:

To test for differences between the normalized overcompensation in the two age groups across the mirror condition in experiment 2, we used a 1-way analysis of variance (ANOVA) with the age as the between-subject factor.

Analysis 6:

We performed a one-sample t-test against zero for the mirror condition of experiment 1 to test whether mean normalized overcompensation was higher or lower than zero.

Analysis 7:

To investigate the effect of age on proprioceptive abilities, we measured the ability of the participant to scale the produced force with the target force during the slider condition such as done by Wolpe et al. 2016. To do so, we computed the slopes and intercept from a linear regression model fitted on the three target forces (4,6, and 8 N) in the X axis and average forces in the slider condition in the Y axis, for both experiments separately. To assess difference in slope between age groups, we performed permutation tests (10,000 iterations) on the slopes across all participants for both experiment 1 and 2 separately.

Analysis 8:

Unpaired two-tailed t-tests were used to compare Variability XY and Absolute Error XY between the two age groups.

Analysis 9:

We performed a correlation between the slopes obtained from the slider condition and the outcomes of the position matching task. To take the two different age groups into account, we used a robust regression technique robustfit (Huber 1981) where the outcome of the position matching task (C = Absolute Error or Variability of Error), a binary vector for group (G=-1 for young participants and G=1 for older adults) and their interaction (C*G) were used as independent variables and where the slope computed from the slider condition (S) was used as dependent variable. The variables C and S were z-scored before being used in the following regression:

$$S = a + b*C + c*G + d*(C*G)$$

In this case, the coefficient 'b' gives us an estimate of the correlation coefficient across groups and the coefficient 'd' provides us an estimate of the difference in correlations between the two age groups.

Analysis 10:

To test for differences between the two age groups across all three force levels and all three conditions in experiment 1 or 2 for the maximum deviation data, we used a 4-way analysis of variance (ANOVA) with the age as the between-subject factor and levels of forces (4, 6 and 8N), conditions (slider, mirror, parallel for experiment 1 and slider, mirror for experiment 2) and phase (perception and matching) as within-subject factor, with the maximum deviation as the dependent variable. These ANOVAs were followed up by post-hoc t-tests with Bonferroni-Holm correction.

Analysis 11:

To test for differences between the two age groups across all three force levels and all three conditions in experiment 1 or 2 for the maximum deviation data during the matching phase, we used a 3-way analysis of variance (ANOVA) with the age as the between-subject factor and levels of forces (4, 6 and 8N), conditions (slider, mirror, parallel for experiment 1 and slider, mirror for experiment 2) as within-subject factor, with the maximum deviation as the dependent variable. These ANOVAs were followed up by post-hoc t-tests with Bonferroni-Holm correction.

Fig 2 here

Results

In the force-matching task, participants had to reproduce with their right arm a target force that they perceived earlier with their left arm. During the force perception period, participants experienced the target force for 2 seconds, with a force ramp up and ramp down for 1 second while trying to maintain their hand in a given position (Fig.2). During the force reproduction period, they exerted a force against the right handle of the robotic manipulandum, which was transmitted and felt on the left arm (direct condition, Fig 2, C, D, E, F). In the slider condition (Fig 2, A and B), participants produced the force on the left arm by moving the right handle up or down like a slider. As shown in Fig.2 for an average across all participants, the produced forces were generally higher than the target forces in most of the trials. In addition, this was observed across all levels of forces (Fig 2, red, green and blue lines). The level of produced force in the direct condition was compared to the control condition where the action of the right arm was indirectly linked to the force transmitted to the left arm.

FIG 3 HERE

Across all participants, in the slider condition, we observed that both older and young adults were able to scale the forces that they produced with the level of target force but systematically undershot the target forces across all three levels of forces. (Fig 3A and 3B). This contrasts with the observation that older participants exerted higher forces than young adults in the direct conditions (Fig 3D-E, G-H). While younger participants produced less force than the target force during the reproduction phase (Fig. 3D and 3G), the average reproduced force of older participants in the mirror and parallel conditions was higher than the target force in all but one case (8N target force in the mirror condition, Fig 3E and 3H). In addition, the produced forces appear to be larger in the parallel than in the mirror condition for both the young (Fig.3D vs. Fig.3G) and the older participants (Fig.3E and 3H).

Force errors are lower in older than younger adults in the Slider condition

To quantify these differences between age groups, we analyzed the mean force errors (difference between produced and target force, see data processing) between young and old participants across the three levels of forces for each condition separately, starting with the slider condition.

Participants from both age groups produced a force lower than the target force in the slider condition, leading to negative force errors (Fig 3C). Force errors were closer to zero in older (Fig 3C, represented by orange dots) than young adults. That is, their undershoot was smaller than that of young adults (main effect age, $F(1,68)=4.8$, $p=0.03$, $\eta^2_p=0.1402$).

In addition, participants exhibited increasing negative force errors with increasing levels of forces (main effect level of force, $F(2, 136)= 137.5$, $p<0.0001$, $\eta^2_p=0.857$). This was consistent in young and older participants, as we did not detect a between-group difference in the scaling of the force errors with increasing target force (level of force x age, $F(2, 136)= 0.311$, $p=0.73$, $\eta^2_p=0.0019$). If anything, the undershoot became larger with increasing levels of target force in young compared to old participants (Fig.3C). That is, this group of older participants performed at least as good if not better than their young counterparts in the slider condition.

Wolpe et al., 2016 quantified the ability of their participants to scale the force produced to the target force by fitting a regression line on the produced force data and by extracting the slopes of this regression line. They took this parameter as a measure of proprioceptive acuity in their participants with a slope of 1 corresponding to a perfect scaling of the produced force with the target force. Similarly to Wolpe et al. we found a significantly higher slopes in younger participants (Analyses 7 mean= 0.5422 and CI = [0.4 0.585]) compared to older ones (Analyses 7 mean=0.498 and CI = [0.38 0.6]). Yet, we did not find any statistical evidence that the slopes of the older adults were shallower than those of the young adults (Analysis 7: p=0.53). There exists a small difference in slope between the two age groups but this difference is tiny compared to the width of the confidence intervals.

FIG 4 HERE

As Wolpe et al. argued, the slider condition is linked to integrity of proprioception. We also used the arm position matching task as another measure of proprioceptive abilities in our population. In our sample, we did not find any evidence for an age-related differences in proprioception. In the position matching task (Fig 4) for experiment 1, we did not find any evidence for an age-related differences in absolute error (Analyses 8: $t(67)=0.81$, $p=0.4203$, $d = 0.195$) or in variability (Analyses 8: $t(67)=0.375$, $p=0.7$, $d = 0.09$).

We found a significant negative correlation between the variability of error in the position matching task and the slopes computed from the slider condition (Analyses 9: $b=-0.3$, $p=0.016$). In other words, the higher the slope was (better scaling of force with target force in the slider), the lower the variability in the position matching task was. We did not find any evidence for a difference in correlation across age groups, (Analyses 9: $d=-0.19$, $p=0.1$). We also found a significant negative correlation between the absolute position error in the position matching task and the slope from the slider data (Analyses 9: $b=-0.39$, $p=0.0057$). In this case, the relationship differed across age groups (Analyses 9: $d=-0.346$, $p=0.01$). Together, these results suggest that a better scaling of the produced force to the target force in the slider condition was linked to better performance in the arm position matching task.

Older participants exert higher forces in direct conditions than younger participants

The results from the slider condition and from the position-matching task suggest that our two age groups had similar proprioceptive abilities. We then looked at differences in the direct conditions where sensory attenuation is supposed to happen.

In the mirror condition (Fig.3F), force errors in the young group were consistently more negative than those in the older group of participants. Mean force error of older participants was even positive for 4 and 6 N, indicating that the older participants produced more force than they should. Therefore, both young and older adults performed differently in the mirror condition with the magnitude of force errors being higher in the older adults.

With increasing levels of forces, the forces errors became more negative in the young participants and transitioned from positive to more negative in older ones. We could not find any evidence for a different scaling of force error with target force between the two age groups.

In the parallel condition (Fig 3I), the force errors of young group were positive for 4 N but negative 6 and 8N target forces. The mean force errors in older group were consistently positive for all levels of forces and was therefore higher (i.e. more positive) than the force errors of younger participants, indicating once again that the overshoot was larger in old compared to young participants

The force errors were again scaled with target force, becoming more negative with increasing levels of forces, the force errors became more negative in similar ways for both age groups. In this condition too, we could not find any evidence for a different scaling of force error with target force between the two age groups.

In each age group separately, the participants produced different amount of forces in the different conditions, with force errors being more positive in parallel, followed by mirror and by slider. This difference across conditions suggests that both groups exhibited some level of sensory attenuation. Similarly, the force errors became more negative with increasing level of target force for both groups. The scaling of the force errors with target force appeared to vary slightly across condition in both age groups

We then directly compared the force errors between the two age groups directly. In addition to the influence of condition (Analysis 1, main effect condition F (2,136)=19.67, p<0.001, η^2_p =0.345), level of force (main effect level of force, F (2,136)=150.7, p<0.001, η^2_p =0.261) and interaction (Analysis 1, level x condition, F (4,272)=3.02, p=0.018, η^2_p =0.006) that we already highlighted above for both groups separately, we found that the difference in force errors between the slider condition and the two direct conditions (mirror and parallel) was larger for old than for young participants (Analysis 1, age x condition, F (2,136)=4.17, p=0.017 η^2_p =0.0733). In other words, while participants from both groups undershot the target force in the slider condition with younger adults exhibiting a higher undershoot (Analysis 1: Post-hoc pairwise t-test: t(68)=-2.21, p=0.03, *d* =0.52). Older participants exhibited an overshoot in the mirror (Analyses 1: Post-hoc pairwise t-test: t(68)=-2.06, p=0.046, *d* =0.51) and parallel conditions (Analyses 1: Post-hoc, pairwise t-test: (t(68)=-3.458, p=0.0015, d =0.78) for most target force levels (positive force errors) while younger participants kept undershooting the target force (negative force errors).

FIG 5 HERE

Higher overcompensation in parallel than in the mirror condition.

To quantify the amount of sensory attenuation more accurately, we decided to take into account inter-subject difference in proprioception (measured by the performance in the slider condition). To do so, we computed the normalized overcompensation by subtracting force errors measured in the slider condition from the force-errors observed in the direct conditions (Fig.5).

The mean normalized overcompensation was higher than zero in each direct condition for older adults but only in the parallel condition for younger adults (Analyses 3 Young mirror: $t(34)=1.359$, $p=0.1831$; young parallel: $t(34)=2.7278$, $p=0.01$,; older mirror: $t(34)=3.2181$, $p=0.0028$; older parallel: $t(34)=5.286$, $p<0.001$).

Older adults exhibited more sensory attenuation than young adults as shown by their higher mean normalized overcompensation (Analysis 2, main effect age: $F(1,68)=5.168$, $p=0.0262$, $\eta^2_p=0.71$). In the mirror condition, there was no age-related difference seen (Analyses 2: Post-hoc pairwise t-test: $t(68)=-1.5$, $p=0.142$, $d=0.37$). In the parallel condition, there was indeed an age-related difference where older adults showed a higher normalized overcompensation than young adults did (Analyses 2: Post-hoc pairwise t-test: $t(68)=-2.9$, $p=0.006$, $d=0.64$).

In addition, normalized overcompensation allows us to compare the amount of sensory attenuation between both direct conditions. The overcompensation was higher in the parallel than in the mirror condition (Analysis 1, main effect condition $F(1,68)=10.02$, $p=0.0023$, $\eta^2_p=0.2$). However, we did not find any evidence that this difference between conditions was different for the two age groups (Analysis 1, age x condition $F(1,68)=1.96$, $p=0.166$, $\eta^2_p=0.04$).

The above results were obtained when the forces were averaged between 1s and 3s after the start of the matching period. In order to assess the robustness of our results, we tested time windows used by previous investigators (between 2 and 2.5 seconds (Wolpe et al., 2016) and between 2.5 and 3s after the start of the matching period (Wolpe et al., 2016, Palmer at al., 2016). In addition, we also tested a later time window (2-4s after the start of the matching period). For each of these three time windows, we obtained the same statistical results as with the original 1 to 3 seconds time window. The statistical results are provided in the supplementary information tables 4, 5 and 6.

Replication of higher sensory attenuation with age in the mirror condition despite no difference in proprioceptive abilities across age groups.

FIG 6 HERE

Explaining the task to the participants in experiment 1 was much harder than anticipated. We were therefore worried that some of the effects could be driven by the fact that the older participants did not understand the instructions correctly. Therefore, we redesigned the task training and design (see methods) and performed a replication of our mirror and slider conditions (Figure 6). In contrast to Experiment 1, we did not find any evidence that the older adults performed slightly better than the younger participants in the slider condition (Fig.7, main effect of age: $F(1, 59)=0.0068$, $p=0.92346$, $\eta^2_p=0.0002$).

FIG 7 HERE

The force errors varied across the three levels of forces as they become more negative with increasing levels of target forces (Fig. 7a, $F(2,118)=100.98$, $p<0.0001$, $\eta^2_p=0.99$). For this group of participants, the results of the position-matching task (see methods) did not reveal any differences between the two age groups in the proprioceptive abilities (Fig 8). Again, we did not find any evidence for an age-related differences in absolute error (Analyses 8: $t(55)=0.36$, $p=0.71$, $d = 0.09$) or in variability (Analyses 8: $t(67)=-1.07$, $p=0.28$, $d = 0.28$). Similarly, when analyzing the slopes of the regression line obtained from the slider condition data, we found a small difference in slopes between the older adults (Analyses 7 mean=0.58, CI= [0.535 0.73]) and the young adults (Analyses 7 mean=0.64, CI= [0.54 0.71]). This small difference in slope (compared to the wide confidence intervals) did not reach significance (Analyses 7: $p=0.4$).

FIG 8 HERE

In this dataset, we failed to confirm the correlation between the outcomes of the position matching task and the slope from the slider condition (Fig. 8c and 8d). We did not find any evidence that the scaling of the produced force in the slider condition to the different target forces correlated with either the variability of the hand in the position matching task (Analyses 9: $b=0.2274$, $p=0.13$; $d=0.16$, $p=0.25$) or the absolute error (Analyses 9: $b=-0.13$, $p=0.38$; $d=-0.09$, $p=0.54$. Together, these results suggest that the sample of participants recruited for experiment 2 did not exhibit more age-related differences in proprioception than the sample recruited for experiment 1. In all aspects, the proprioceptive abilities of the older adults were similar to that of the younger ones.

Despite similar proprioceptive abilities, in the mirror condition, young and older participants exhibited different pattern of force error (Fig.7b) than in the slider condition (Fig.7a). Older participants were mostly overshooting the target force (positive force error) while the younger participants undershot it.

The difference in force errors across the two conditions (mirror vs. slider) was larger in older participants compared to their younger counterparts (Fig.7, Analysis 4, age x condition, $F(1,59)=4.55$, $p=0.037$, $\eta^2_p=0.09$, In addition, young adults exhibited less undershoot in the mirror than in the slider condition (Analyses 4: Post-hoc pairwise comparisons: ($t(59)=-2.01$, $p=0.053$, $d=0.5$). The older participants even exhibit an overshoot in the mirror condition while they also undershot the target force in the slider condition (mirror vs slider for young adults).

As a result, the normalized overcompensation was positive for both young and old participants (Fig.9, Analyses 6 young: $t(30)=2.47$, $p=0.019$; old: $t(29)=4.04$, $p<0.0001$). Furthermore, this normalized overcompensation was larger for older compared to younger participants (Analysis 5, main effect age, $F(1, 59)=4.53$, $p=0.037$, $\eta^2_p=0.973$). This confirms the results from our first experiment that sensory attenuation was higher in older than younger adults.

FIG 9 HERE

Motion of the left hand provides hint of better prediction of sensory consequences across hands in older participants

For an exploratory analysis, we looked at the motion of the left hand caused by the force produced by the robot during the perception and matching phase. During the perception phase, this force is externally produced. During the matching phase, it is produced by the right hand of the participant in the direct conditions (mirror and parallel) and internally produced but indirectly mapped via the slider in the slider condition. We reasoned that participants who could predict the sensory consequences of the force produced by the right hand on the left hand should be better able to reduce the motion of their left hand compared to those that are less able to make these predictions. To measure this, we computed the maximum horizontal deviation of the left hand from the target.

For experiment 1 (Fig 10), maximum deviation was larger during the perception phase than during the matching phase (Analyses 10 main effect of phase: $F(1,68)=21.42$, $p<0.001$) and there was a main difference across condition (Analyses 10 main effect of condition: $F(2,136)=12.85$, $p<0.001$) with the slider condition being higher than in the other conditions in both phases. Zooming in the matching phase, the maximum deviation was larger for the slider condition than for the direct conditions (Analyses 11 main effect of condition: $F(1,68)=48.4$, $p<0.001$). Post-hoc pairwise comparisons showed that deviations in the slider condition were larger than those in the mirror condition (Analyses 11 $t(68)=8.02$, $p<0.0001$, $d=1.2$) and in the parallel condition (Analyses 11 $t(68)=6.3$, $p<0.001$, $d=0.95$). Furthermore, hand deviation in the parallel condition was also larger than in the mirror condition (Analyses 11 $t(68)=-2.8$, $p=0.006$, $d= 0.12$). We did not find large differences across age groups. If anything, older participants did better in the matching phase:

FIG 10 HERE

In experiment 2 (Fig 11), the average maximum deviation across participants was higher in the slider condition than in the mirror condition (Analyses 10: main effect of condition: $F(1,59)=83.19$, $p<0.001$) and higher during the perception phase than during the matching phase (Analyses 10: $F(1,59)=48.76$, $p<0.001$). Interestingly, while there was no difference between the old and young people in many cases, older participants were better able to compensate for the force on the left arm in the mirror condition (Analyses 10: age x condition x phase: $F(1,59)=15.9$, $p<0.001$). Indeed, the deviation resulting from the force during the matching phase in the mirror condition was lower for the older participants than for the younger ones ($t(58)=4.5$, $p<0.001$).

FIG 11 here

Discussion

In our study, we found that both young and old participants exerted higher forces in the direct conditions (self-produced forces) than in the slider condition but this overcompensation was even higher in older participants. We did not find any evidence that force reproduction in the slider condition or accuracy in a position-matching task (which were our proxies for proprioception) were affected by age. While an increase in sensory attenuation with age (Klever et al. 2019; Wolpe et al. 2016) had been observed for the fingers, we confirm that this phenomenon generalized to another effector: the arm.

Higher reliance on internal forward models with aging

By normalizing our data with respect to the slider condition, we were able to remove the influence of the proprioceptive component and to isolate sensory attenuation. Our findings show that older participants had a higher sensory attenuation than younger adults did. Reduced sensory attenuation has been linked to impaired awareness of action and disorders such as schizophrenia and psychogenic movement disorders (Shergill et al. 2003; Wolpe et al. 2016).

The observed increase in sensory attenuation from this study together with their supposed age-related decline in sensory function (Dunn et al., 2015, Goble et al. 2009) suggests that elderly adults might rely more on the internal models (Wolpe et al. 2016). When a perceived force is self-produced, the sensation is a combination of sensory information with the predicted sensory consequences of the force generation (coming from the internal model). These signals are combined via Bayesian integration in function of their reliability (Körding et al. 2004; Orban de Xivry et al. 2013). Given that proprioceptive input becomes less reliable with increasing age, the weight of the internal model (which is shown not to be impaired by aging) becomes larger (Wolpe et al. 2016). In other words, there is a higher weighting on the internal model during the parallel processes involving both the internal model and sensory system when making a prediction (Bubic et al. 2010). Many studies have shown aging changes weighting on sensorimotor predictions during movements (Klever et al. 2019; Moran et al. 2014). Studies also have shown internal forward model function does not change with aging (Heuer et al. 2011; Vandevoorde and Orban de Xivry 2019).

While there is a shift towards higher sensory attenuation with aging, a shift in the opposite direction is observed in cerebellar patients or in people with schizophrenia (Knolle et al. 2013; Shergill et al. 2005). This shows that sensory attenuation is the outcome of an adaptable combination between sensory and predictive signals in function of their reliability such as been observed in different contexts (Deravet et al. 2018; Ernst and Banks 2002; Orban de Xivry et al. 2013). The increase in sensory attenuation with aging shows that the reliability of the sensory signal decreases faster with aging than the reliability of the internal model signal (Wolpe et al. 2016).

We did not observe an age-related decrement in proprioception

It remains to be understood why older participants assign a higher weight to their internal predictions while we did not find any impairment in sensory function. Indeed, we could not find any age-related differences in either the slider condition or the position-matching task in our samples.

Previous studies show that sensory function and proprioceptive acuity decrease with aging (Dunn et al. 2015; Goble et al. 2009; Ranganathan et al. 2001). In the slider condition, participants only had to indicate the perceived force on a slider; there were no self-produced forces. This condition provides us with a proxy for proprioception. Our results from both experiments show that both young and elderly adults undershot the target forces. In experiment 1, this undershoot was larger for the young participants. Hence, elderly participants were more accurate, i.e. their produced forces were closer to target forces. However, in experiment 2, we did not observe such age-related difference. In contrast, young adults from the study of Wolpe et al. (2016) were on average less accurate than the older adults but, in contrast to our experiment, they overshot the target forces.

Both our experiments and that from Wolpe et al. used different level of target forces. In Wolpe et al., the older participants scaled their produced forces with target force less accurately than the younger participants did. In our study, we found that both age groups exhibited a larger undershoot with increasing levels of target force. However, we failed to find any evidence for an effect of age on the scaling of the produced force with the target force in the slider condition in both experiments. Walsh et al. (2011) report a similar finding in their finger force matching experiment that subjects overestimated smaller target forces than larger ones. Their matched forces were 2-3 N higher than the smaller target forces.

From our findings in the maximum hand deviations, the slider condition showed higher deviations on both matching and perception phases. We would tend to interpret this as a sign that, in the direct conditions, the ability to predict the sensory consequences of the movement helped the participants to anticipate the force that will be applied on their left arm. Such anticipation is more difficult in the slider condition as the mapping between the cursor motion from the right hand and the force applied on the left arm is less natural. We did not find large differences across age groups. If anything, older participants did better resist the predictable forces in the direct conditions during the matching phase.

In addition, across both studies, the effect size amounts to d=0.09 for the position matching task and d=-0.26 for the slider condition (with older people exhibiting a better performance than younger ones). While we cannot conclude that there is absolutely no age-related deterioration in proprioception in our samples, we did not find any evidence that an age-related difference in the slider condition could lead to larger sensory attenuation in older adults.

While age-related deficits in proprioception are taken for granted (Dunn et al. 2015; Goble et al. 2009; Ranganathan et al. 2001), recent studies failed to provide evidence for age-related deficits in proprioception (Vandevoorde et al., 2021, Kitchen et al.,2019, Kitchen et al., 2021). For instance, Djajadikarta et al., 2020 reported no effect of age on ankle proprioceptive performance in healthy adults. As highlighted by Han et al., 2020, future studies on the effect of age on proprioception should use multiple assessment methods to investigate different aspects of proprioception and the corresponding age-related deficits. Hence, it is imperative to consider the extent to which each proprioceptive task reflects proprioceptive function.

Overall, across the 130 participants, we did not find any evidence for age-related differences in proprioception as opposed to what was shown by previous studies (Dunn et al. 2015; Goble et al. 2009; Morrison and Newell 2012; Ranganathan et al. 2001). This could be attributed to the fact that our participants could have been more active than the general population from the same age (between 55-75 years) given that they were recruited through the Sport center of our university. Unfortunately, we do not have documented data supporting this.

In addition, our mean age in the elderly (mean=64 years) was lower than the mean age of elderly in previous studies (mean= 71 years, Goble et al, Doumas et al 2008). Future studies must quantitively look at this aspect in order to truly comprehend the effect of aging on sensory function.

Yet, while our older participants did not exhibit any impairment in proprioception, they did exhibit increased sensory attenuation. This begs the question whether the observed increase in sensory attenuation is due to poor sensory function as suggested by Wolpe et al. 2016. It rather seems to violate the idea that the increase in sensory attenuation is due to a shift in reliability-based balance between predictive and sensory signals. One possibility is that the average performance is similar but that the confidence in the sensory estimates is degraded with aging. Unfortunately, none of our proprioceptive tasks have enough repetitions (maximum 10) to measure standard deviation in a reliable way.

Sensory attenuation is higher in parallel condition than in the mirror

We used two different direct conditions where the force exerted by the right arm was directly felt on the left arm. In the mirror condition, the biceps of the right arm and the triceps of the left arm were simultaneously activated (non-homologous muscles). In contrast, in the parallel condition, both arms' biceps muscles (homologous muscles) were simultaneously activated. Our results show that sensory attenuation is higher when homologous muscles are activated.

Humans naturally couple limb movements and it is usually easier to move limbs in the same direction and contract homologous muscles (Huang and Ferris 2009; Meesen et al. 2006, Baldiserra et al., 1982). In addition, humans identify and perceive forces applied by the hand in terms of the motor activity required to resist or produce the force or a "sense of effort" rather than in terms of a perceived force magnitude (Toffin et al. 2003). In other words, force perception is controlled by the ease of resisting it rather than the actual force magnitude (Van Beek et al 2013). Given the more natural connections between homologous muscles, we postulate that the sense of effort required to contract homologous muscles was felt as lower in the parallel condition, which could explain the larger overshoot in this condition if one tries to match the effort perceived in the force perception phase.

In addition, we believe that the mirror condition might be less ecological than the parallel condition. In the parallel condition, the forces applied by both arms are in opposite direction, which is similar to our experience in everyday life activities when, for instance, carrying a box with two arms. In this case, pressing one side of the box with one arm creates a situation where the other arm has to resist that force. This fits to the experience of our participants in the parallel condition. In contrast, the mirror condition corresponds to a situation where one hand is on top of the other in order to push a box sideways. This is clearly a less ecological situation that happens less frequently. This difference in ecological validity could weaken the perceived causality between the force exerted by one hand and sensed on the other hand. Given the importance of causality and timing on sensory attenuation (Kilteni et al., 2019, Blakemore et al., 2000), this could explain why we observed less sensory attenuation in the mirror than in the parallel condition.

In contrast to previous studies (Wolpe et al., 2016), the force produced by the participants during the matching phase was lower than the target force, especially for higher target forces. This could be attributed to movement related gating, where tactile stimuli are felt less saliently during movement than in its absence (Williams and Chapman 2002). Previous studies did not report such observation. While we predominantly observed this phenomenon for the higher target forces, previous studies using the finger and arm (Logan et al., 2019) used lower target forces than we did. As a result and in contrast to previous studies, the force produced by the participants during the matching phase were not larger than the target forces (except at 4N). Yet, we observed overcompensation when comparing the forces produced during the direction condition to those produced during the slider condition. Future studies can investigate this by testing with a larger range of target forces.

In our study, the activation of the homologous muscles was coupled to a change in direction of the force in the left arm. While we are confident that it does not largely affect the amount of overcompensation, this could even become larger if the force direction was not changed. A future study could reproduce this result in the absence of change of force direction.

Limitations

While we have shown the effect of sensory attenuation on the arms, further investigation is required on the age-related differences between the mirror and parallel conditions. In the parallel condition, there was both an activation of homologous muscles and change in direction of movement. We believe that this change in direction did not play a big role in the result of the present study. Yet, a future study could correct this mistake and involve pushing the right arm in the rightward direction and the transmission in the rightward direction. Further studies on proprioception on the arm are required to explore the age-related differences or similarities deeper.

In addition, the understanding of the task instructions by the participants could have had an influence on the performance. We overcame this limitation in experiment 2 with clearer task instructions. Nevertheless, participants in both experiments reported that the task was difficult to follow, and future studies must be done with careful consideration to the development of detailed task instructions.

Moreover, the participants in our study was limited in number, and we divided them into two arbitrary age groups (N=35 for each of them in experiment 1 and N=30/group in experiment 2). Future studies are warranted to include a larger participant pool from a larger age range, such that it will also be possible to conduct correlation analyses between age and behavioral indices.

Conclusion

Our force-matching paradigm sheds a new light on the effect of aging on sensory attenuation and proprioception. First, we confirmed that sensory attenuation can be observed in the arms, similar to what has been found for the fingers (Logan et al. 2019; Shergill et al. 2003; Walsh et al. 2011; Wolpe et al. 2016) and that this is a phenomenon that goes beyond the fingers. Second, we replicated the finding that sensory attenuation is larger in adults over 55 years. The Bayesian perspective adopted by Wolpe et al. would let us interpret these results as indicative of a shift in the balance between sensory and predictive signals, which is in line with the hypothesis that internal model function is unaffected by aging (Heuer et al. 2011; Vandevoorde and Orban de Xivry 2019). Yet, in our sample, we did not detect any difference in proprioceptive function between our two age groups. This leads us to question the fact that the increased sensory attenuation with age is due to a deficit in proprioception.

Supplementary information

All supplementary information, raw data, processed data and scripts are available at http://www.doi.org/10.17605/OSF.IO/4TEB5.

Legends

Fig 1: Experimental blocks of the study. *Panel A: A target force that pushed the left arm to the +X direction was presented for 2 seconds (force perception phase), with a ramp-up and ramp-down of 1 second each. Participants were asked to counteract this force and judge the level. The force perception phase was followed by a second phase (force reproduction phase) where the participants were asked to reproduce the force that they perceived on their left hand. This phase differed across the three possible experimental conditions (panels B, C and D). In the slider condition (panel B), participants matched the target force by moving the right arm up or down on a slider. The position of the hand/slider was mapped to a certain level of force and transmitted to and felt on the left arm. There were also two direct Conditions: Mirror (panel C) and Parallel (panel D). In the mirror condition (panel C), participants matched the target force by applying a force to the right handle using the right arm. This was transmitted and felt on the left arm in the +X direction as shown by the arrows. In the parallel condition (panel D), participants matched the target force by applying a force to the right handle using the right arm. This was transmitted and felt on the left arm in the -X direction as shown by the arrows.*

Fig 2. Force profile of all participants across all three levels of force and three conditions for experiment 1. *The force profile is average of all trials across all participants. Each color corresponds to a different target force (4, 6 or 8 N) that was presented to the participant during the force perception phase. The X-axis represents the number of seconds since the start of the force perception period. The Y-axis shows the force measured by the force transducer of the left hand.*

Fig 3. Experiment 1: comparison of exerted forces and force errors of both age groups across the three conditions. *Each row corresponds to a different condition (top row: slider; middle row: mirror; bottom row: parallel). The average force exerted by the participants from the young (left column) and old group (middle column) is presented. The gray traces represented the average force for each individual participants. The red trace represents the group average. The blue trace corresponds to the target force. The X-axis shows the different force levels. Y-axis is the produced Forces (N). The third column present the average force errors (N=35/group) for both age groups and each force level. Black rectangle and error bars of 3C, 3F and 3I represent the mean and standard error respectively. Each dot is the average of all trials for each force level and for each participant.*

Fig 4. Results of the position matching task and slopes of slider compared with parameters of the position matching task. *The Absolute Error XY (top left panel) and Variability XY (top right panel) is shown for experiment 1. Each dot is the average across all trials and blue represents the young group and orange is the older group. The Absolute Error vs slopes of slider for experiment 1 (bottom left panel) and the variability vs slope of slider (bottom right panel) is shown. Each dot is an average across all trials, blue represents young and orange represents old.*

Fig 5. Normalized Overcompensation (experiment 1). The average normalized overcompensation is presented for each age group *(N=35/group) and each condition (panel A: mirror condition; panel B: parallel condition. Each dot is the average normalized overcompensation for each individual (collapsed across force levels). The black rectangle represents the average across all participants for each group separately. The error bar represents the standard error of the mean.*

Fig 6. Force profile of all participants across all three levels of force and three conditions for experiment 2. *The force profile is average of all trials across all participants. Each color corresponds to a different target force (4, 6 or 8 N) that was presented to the participant during the force perception phase. The X-axis represents the number of seconds since the start of the force perception period. The Y-axis shows the force measured by the force transducer of the left hand.*

Fig 7: Comparison of force error between age groups (experiment 2). *The average force errors (N=31 young, N=30 old) for both age groups and each force level for the slider condition (panel A) and mirror condition (panel B). Black rectangle and error bars represent the mean and standard error respectively. Each dot is the average across all trials for each force level and for each participant separately.*

Fig 8. Results of the position matching task and slopes of slider compared with parameters of the position matching task. *The Absolute Error XY (top left panel) and Variability XY (top right panel) is shown for experiment 2. Each dot is the average across all trials and blue represents the young group and orange is the older group. The Absolute Error vs slopes of slider for experiment 2 (bottom left panel) and the variability vs slope of slider (bottom right panel) is shown. Each dot is an average across all trials, blue represents young and orange represents old.*

Fig 9. Normalized Overcompensation (experiment 2). The average normalized overcompensation is presented for each age group *(N=31 young, N=30 old) in the mirror condition. Each dot represents the average normalized overcompensation for each individual (collapsed across force levels). The black rectangle represents the average across all participants for each group separately. The error bar represents the standard error of the mean.*

Fig 10. Maximum deviation of the left hand. *The maximum deviation of the left hand from the target for Experiment 1. Each dot is the average across all trials and force levels, and blue represents the young group and orange is the older group.*

Fig 11. Maximum deviation of the left hand. *The maximum deviation of the left hand from the target for Experiment 2. Each dot is the average across all trials and force levels, and blue represents the young group and orange is the older group.*

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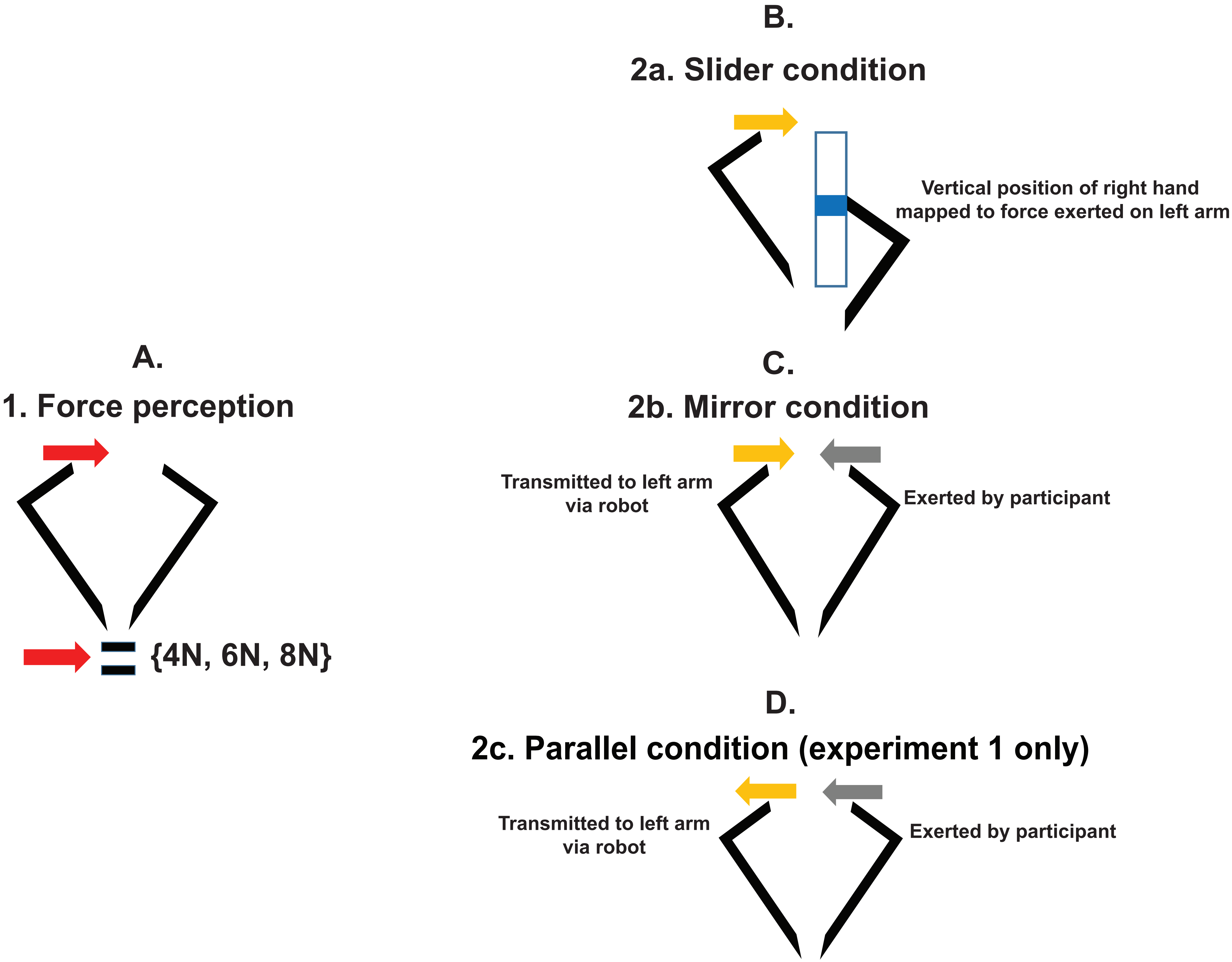
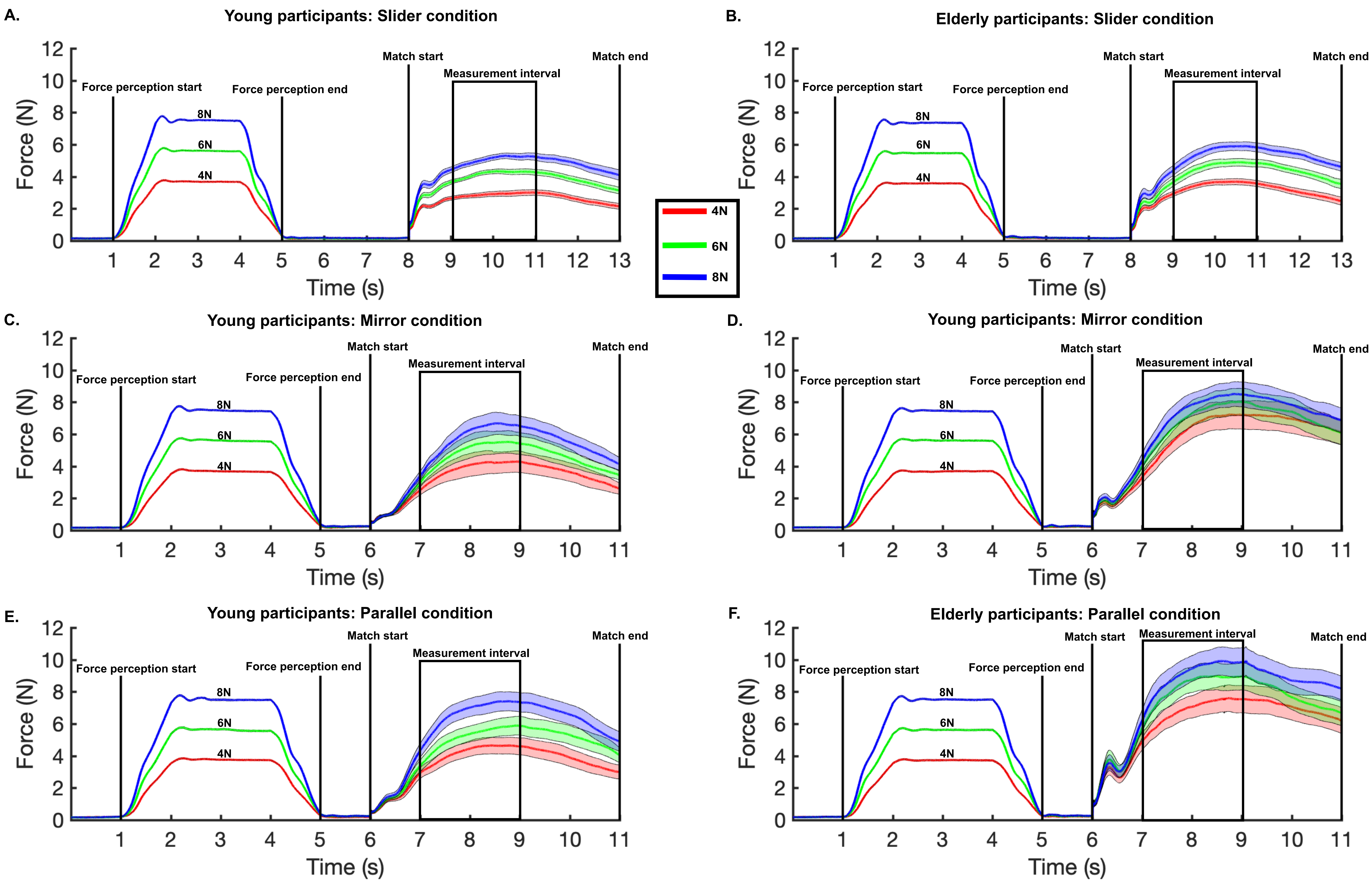
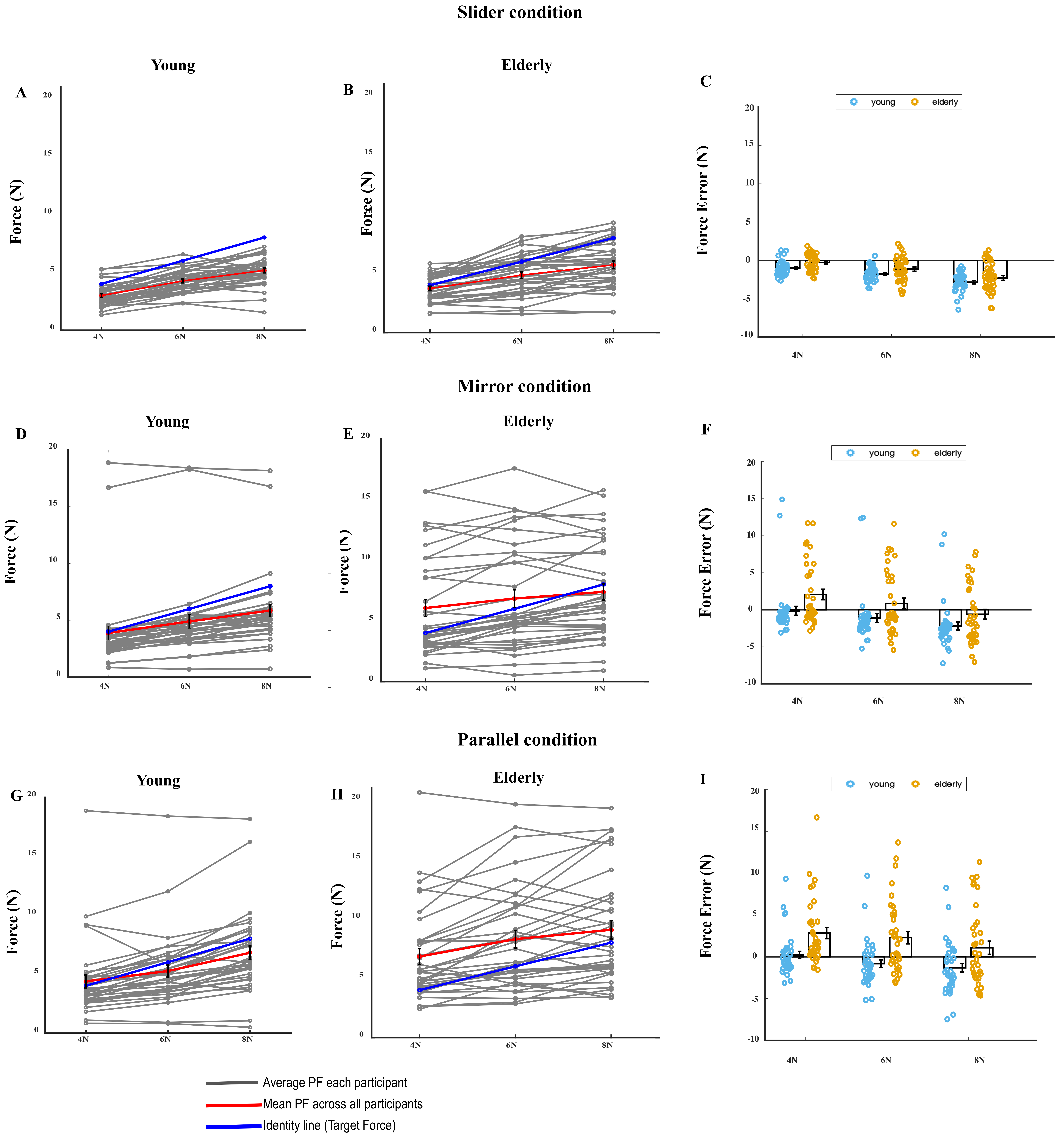

B.
2a. Slider condition
Vertical position of right hand
mapped to force exerted on left arm
A.
1. Force perception
{4N, 6N, 8N}
C.
2b. Mirror condition
Transmitted to left arm
via robot
Exerted by participant
D.
2c. Parallel condition (experiment 1 only)
Transmitted to left arm
via robot
Exerted by participant

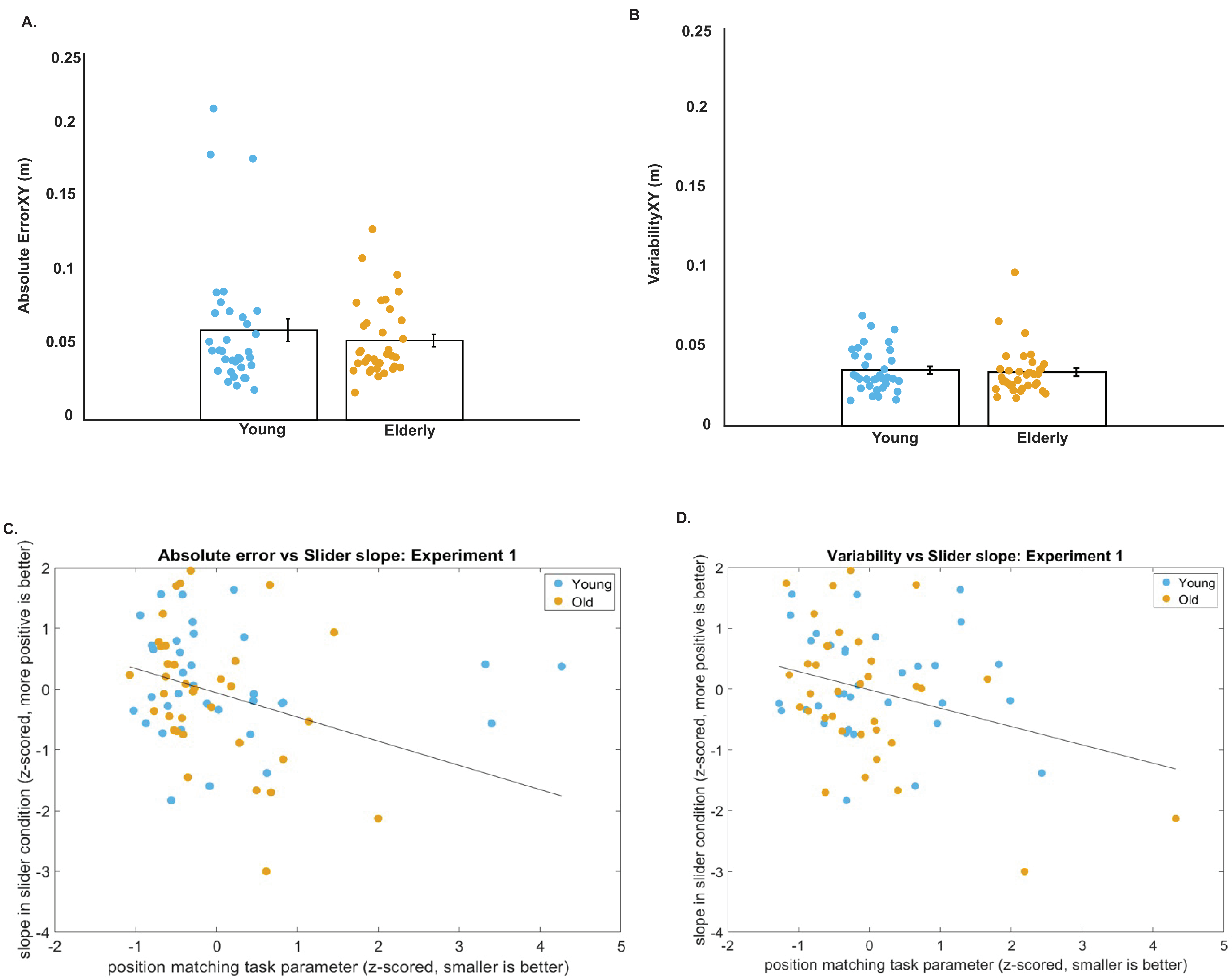


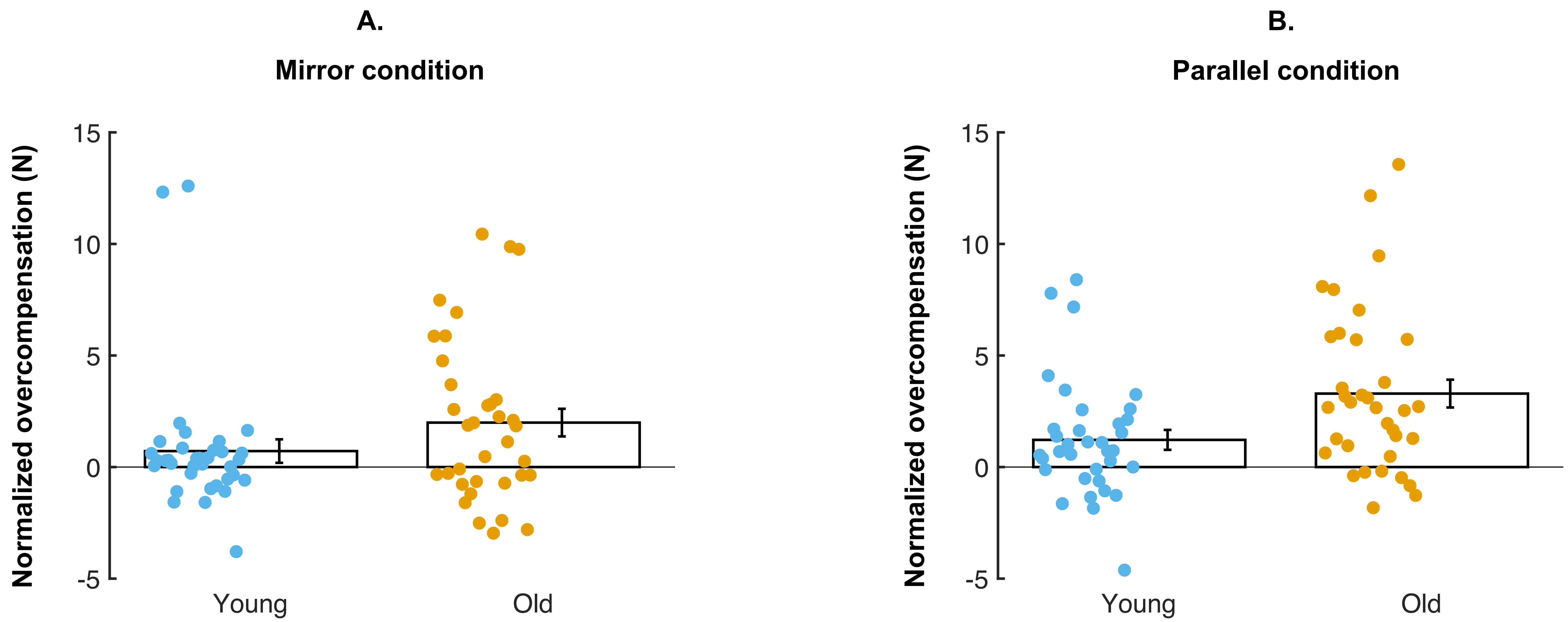
A.
Young participants: Slider condition
Force perception start
Force perception end
Match start
Measurement interval
Match end
8N
6N
4N
Force (N)
Time (s)
B.
Elderly participants: Slider condition
4N
6N
8N
C.
Young participants: Mirror condition
D.
Young participants: Mirror condition
E.
Young participants: Parallel condition
F.
Elderly participants: Parallel condition

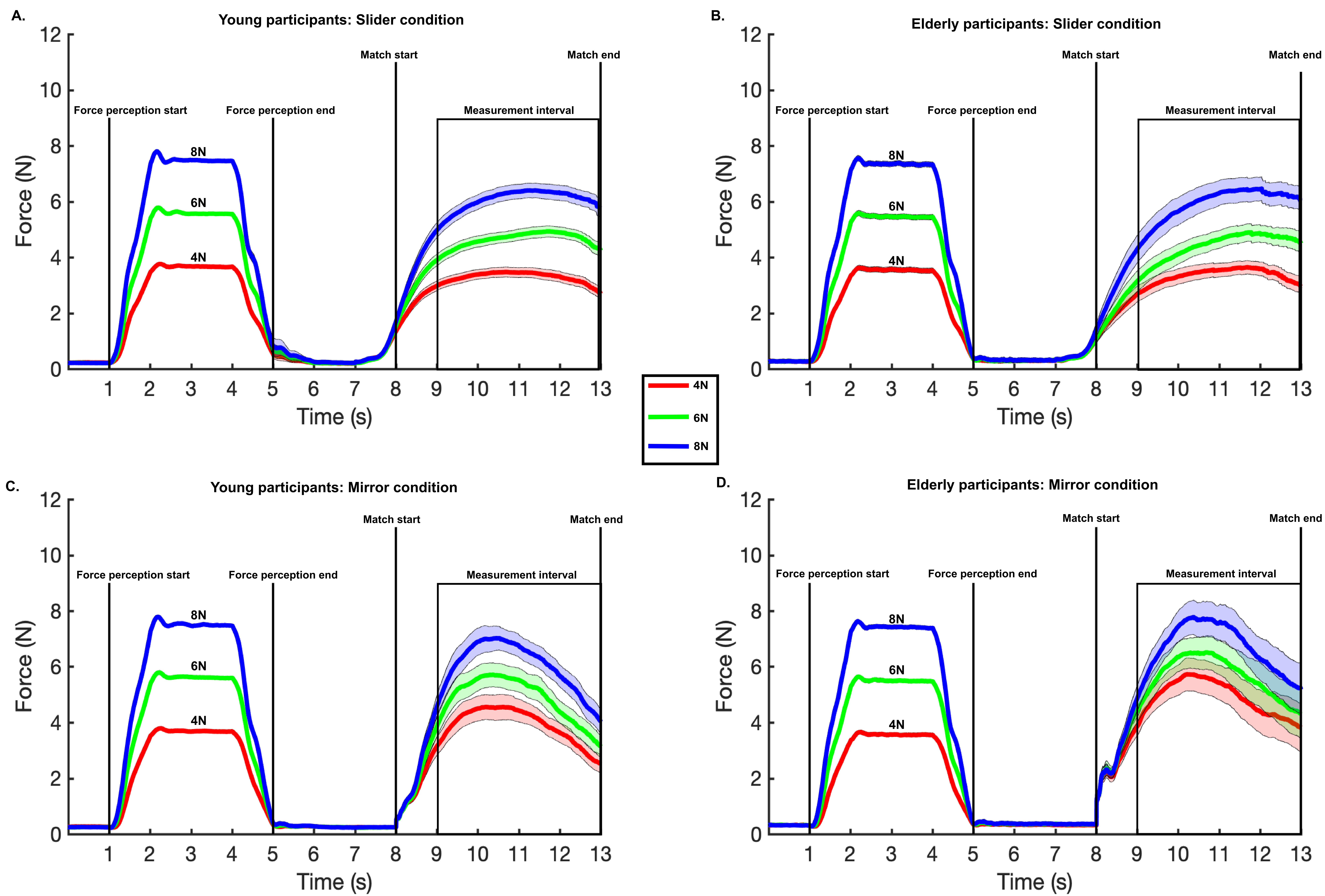


Slider condition
Young
Elderly
A
B
C
Force (N)
Force Error (N)
young
elderly
4N
6N
8N
Mirror condition
D
E
F
Parallel condition
G
H
I
Average PF each participant
Mean PF across all participants
Identity line (Target Force)

Fig 4.


A.
Absolute ErrorXY (m)
0.25
0.2
0.15
0.1
0.05
0
Young
Elderly
B
VariabilityXY (m)
0.25
0.2
0.15
0.1
0.05
0
Young
Elderly
C.
Absolute error vs Slider slope: Experiment 1
Young
Old
slope in slider condition (z-scored, more positive is better)
position matching task parameter (z-scored, smaller is better)
D.
Variability vs Slider slope: Experiment 1
Young
Old
slope in slider condition (z-scored, more positive is better)
position matching task parameter (z-scored, smaller is better)


A.
Mirror condition
B.
Parallel condition
Normalized overcompensation (N)
15
10
5
0
-5
Young
Old



A.
Young participants: Slider condition
B.
Elderly participants: Slider condition
C.
Young participants: Mirror condition
D.
Elderly participants: Mirror condition
Force perception start
Force perception end
Match start
Match end
Measurement interval
8N
6N
4N
Force (N)
Time (s)

Fig 7.

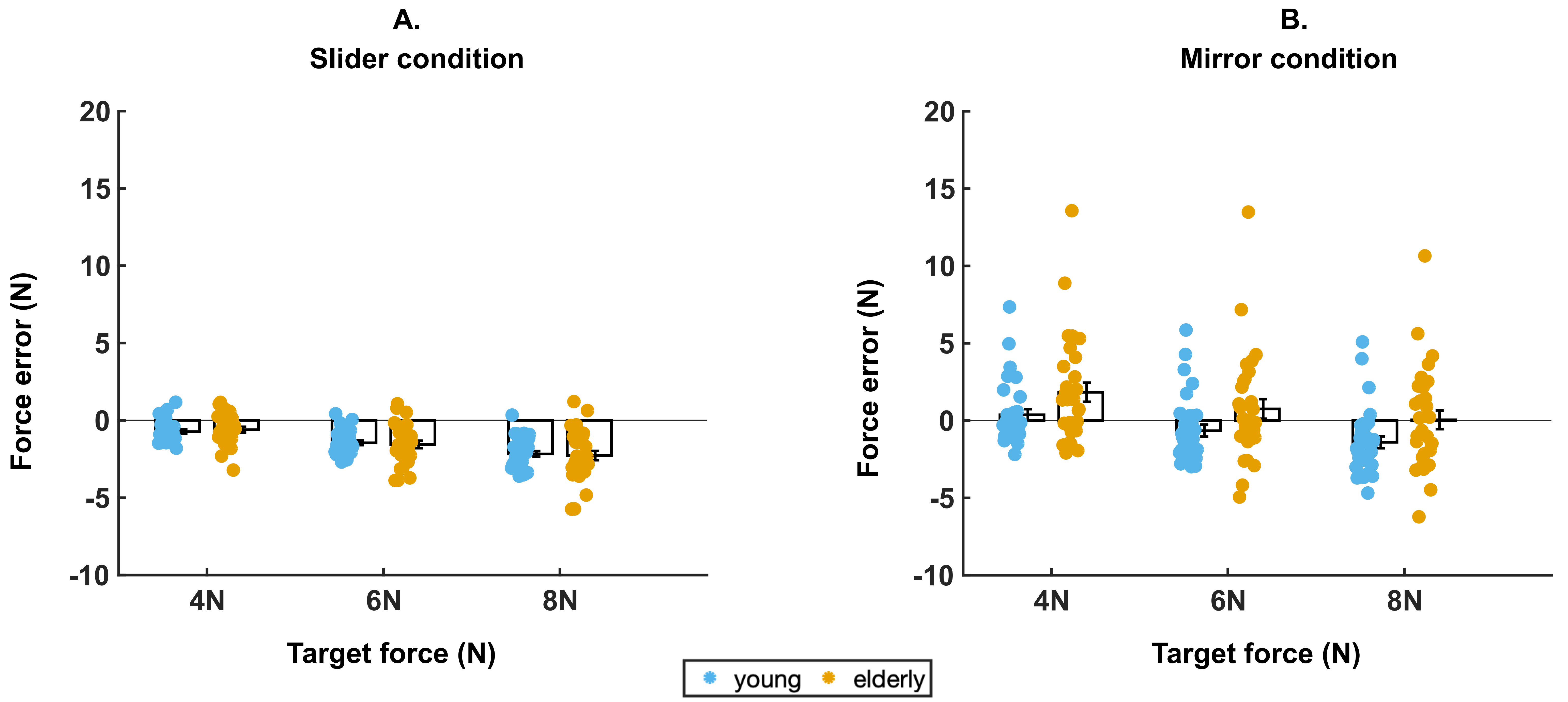

A.
Slider condition
B.
Mirror condition
Force error (N)
20
15
10
5
0
-5
-10
4N
6N
8N
Target force (N)
young
elderly

Fig 8

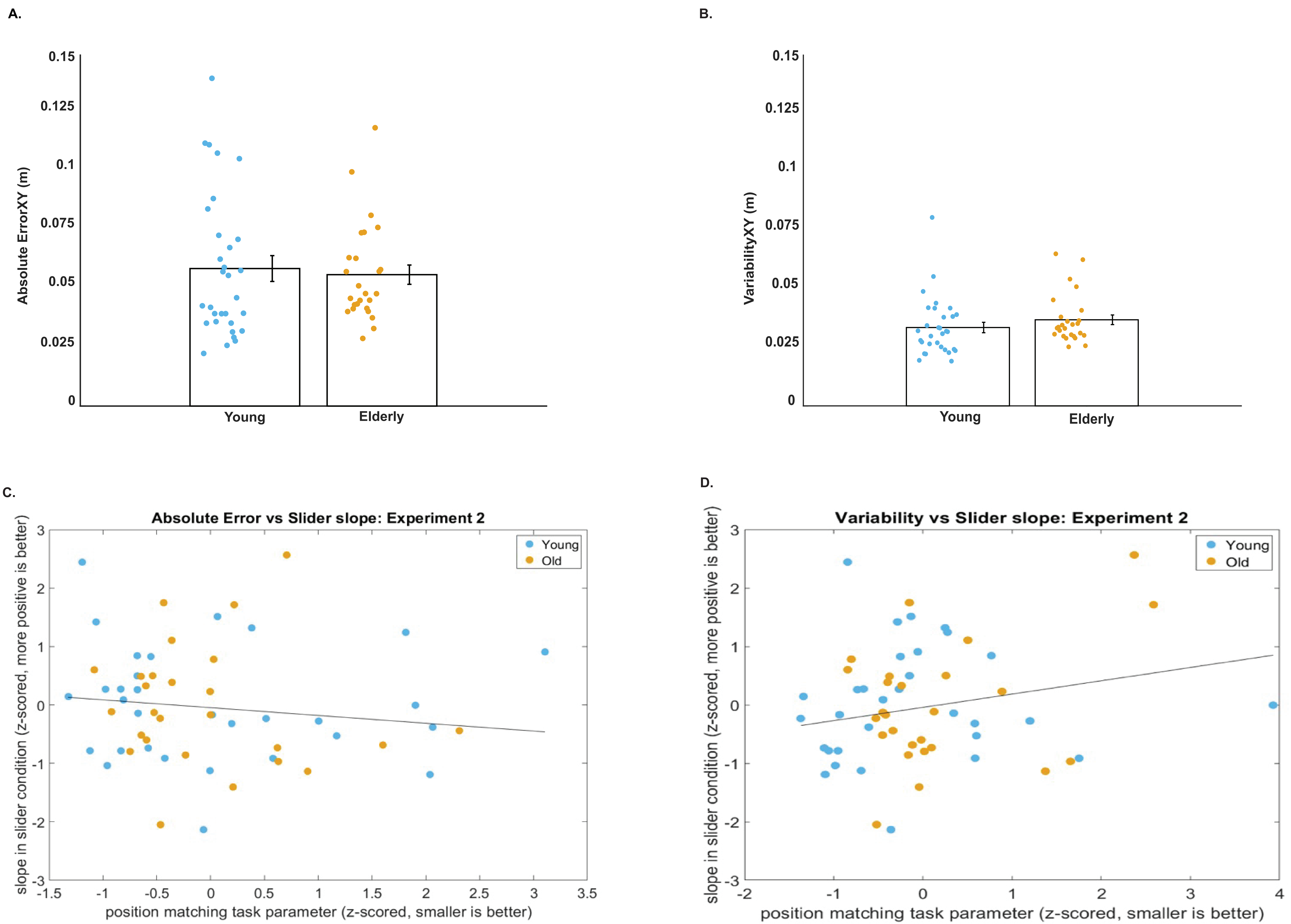

A.
B.
C.
D.
Absolute ErrorXY (m)
0.15
0.125
0.1
0.075
0.05
0.025
0
Young
Elderly
VariabilityXY (m)
0.15
0.125
0.1
0.075
0.05
0.025
0
Young
Elderly
Absolute Error vs Slider slope: Experiment 2
Young
Old
slope in slider condition (z-scored, more positive is better)
position matching task parameter (z-scored, smaller is better)
-1.5
-1
-0.5
0
0.5
1
1.5
2
2.5
3
3.5
3
2
1
0
-1
-2
-3
Variability vs Slider slope: Experiment 2
Young
Old
slope in slider condition (z-scored, more positive is better)
position matching task parameter (z-scored, smaller is better)
-2
-1
0
1
2
3
4
3
2
1
0
-1
-2
-3

Fig 9

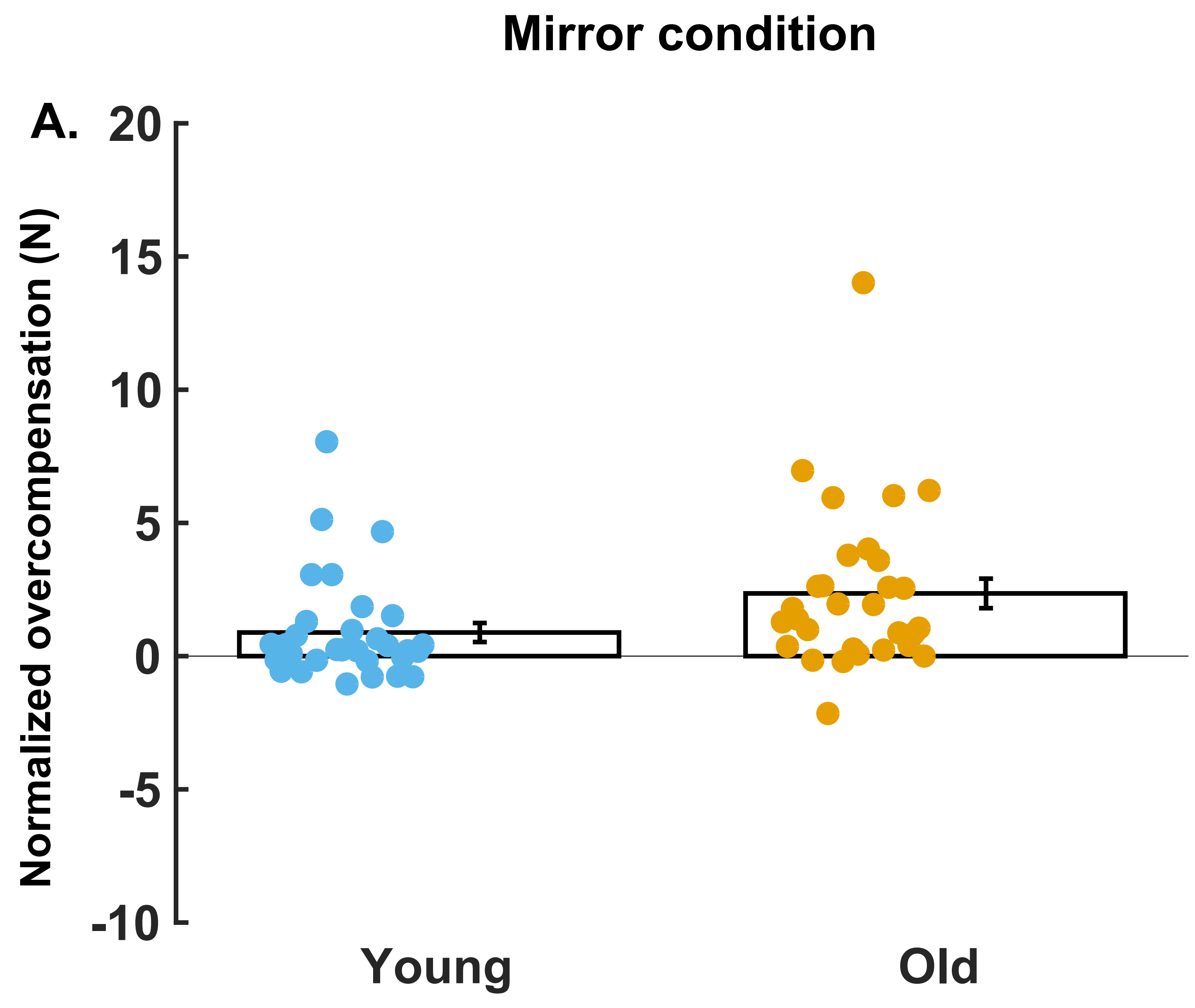

Mirror condition
A.
Normalized overcompensation (N)
20
15
10
5
0
-5
-10
Young
Old

Fig 10

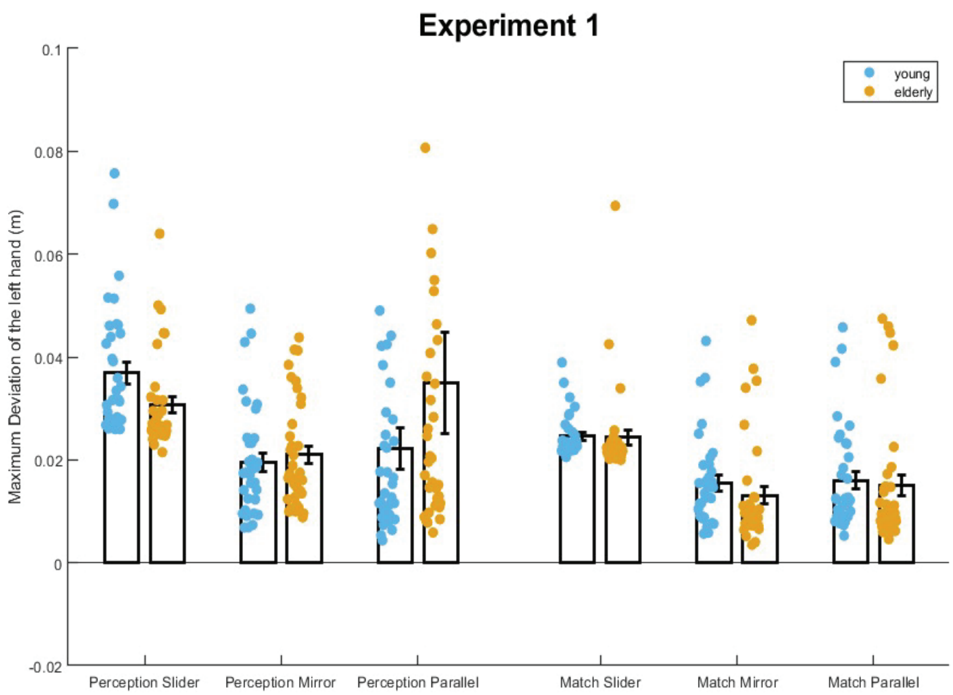
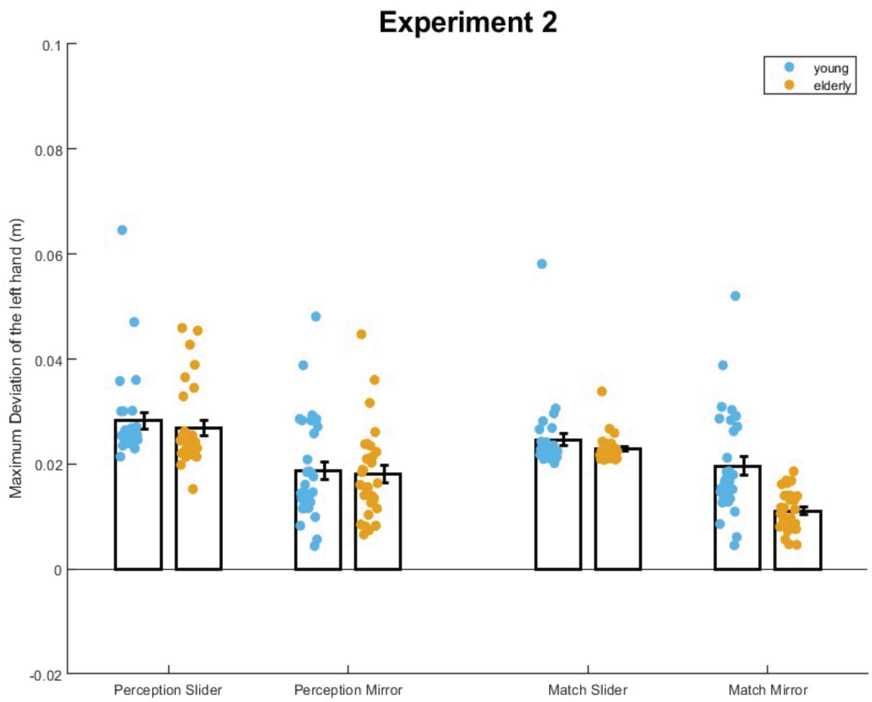

Experiment 1
young
elderly
Maximum Deviation of the left hand (m)
0.1
0.08
0.06
0.04
0.02
0
-0.02
Perception Slider
Perception Mirror
Perception Parallel
Match Slider
Match Mirror
Match Parallel

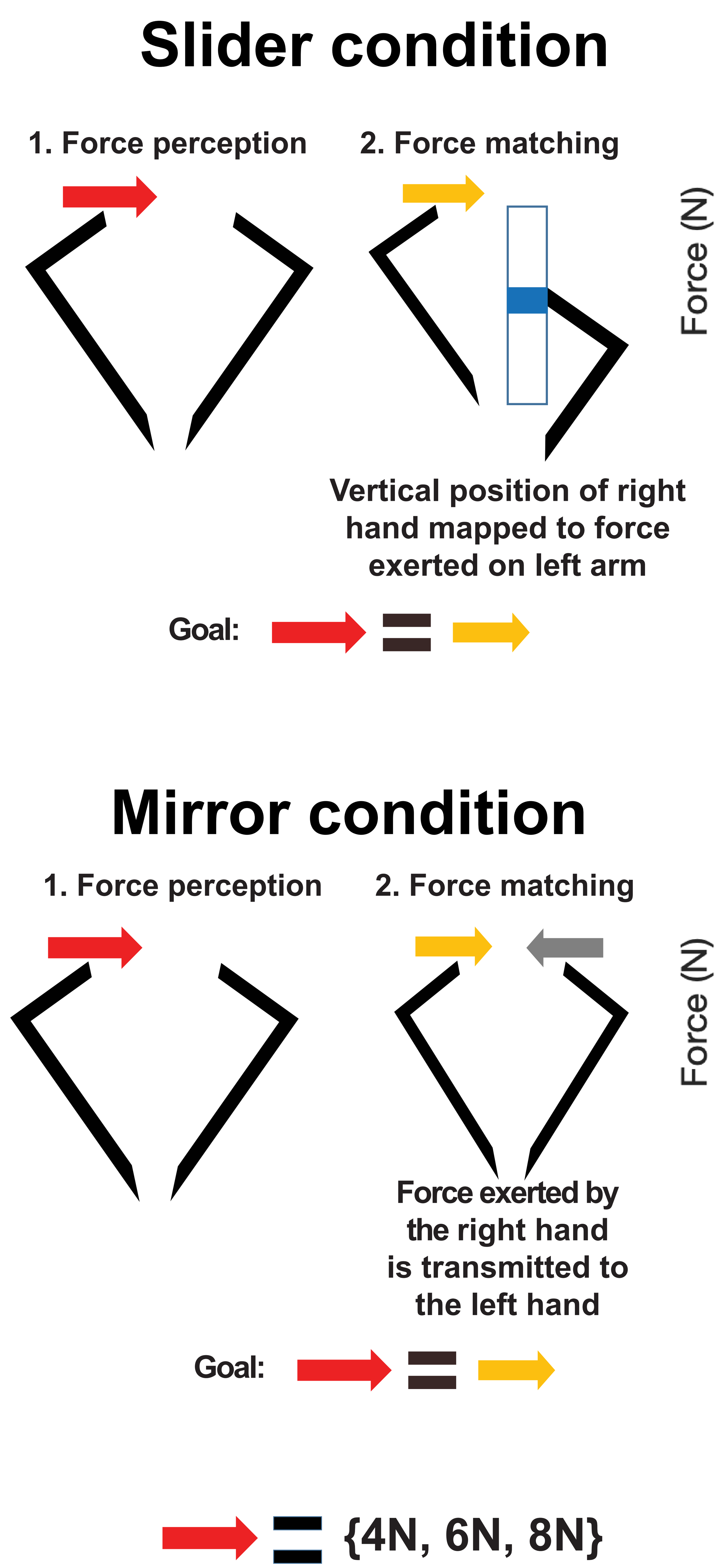
Fig 11

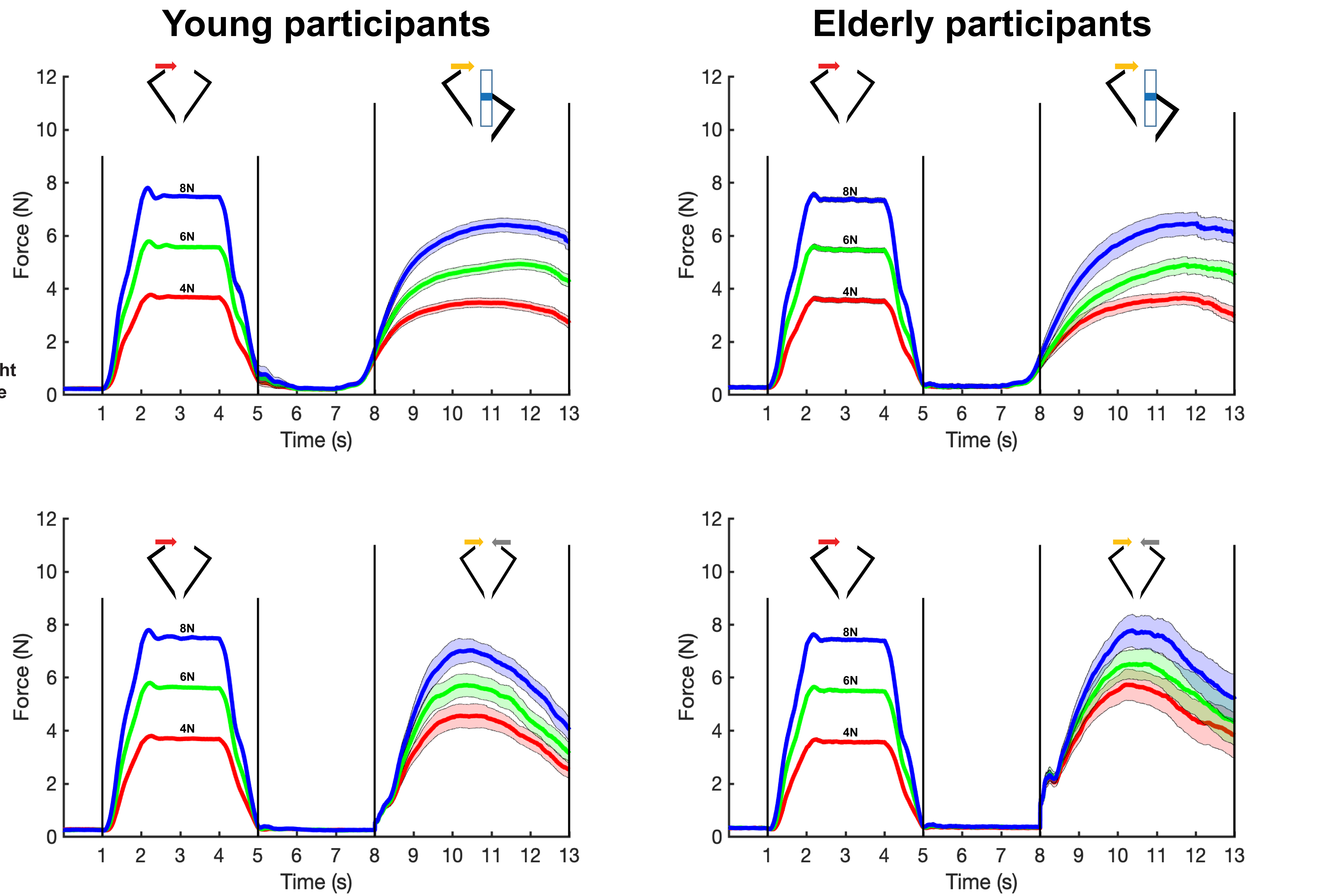


Experiment 2
young
elderly
Maximum Deviation of the left hand (m)
0.1
0.08
0.06
0.04
0.02
0
-0.02
Perception Slider
Perception Mirror
Match Slider
Match Mirror

Increased upper-limb sensory attenuation with age

Manasa Parthasharathy, Dante Mantini, Jean-Jacques Orban de Xivry





While both young and older adults overestimate a self-produced force, older adults overestimate it even more showing an increased sensory attenuation. While this is traditionally viewed as a consequence of decreased proprioception in older adults, proprioception appeared unimpaired in our older participants.