Age effects on sensorimotor predictions: What drives increased tactile suppression during reaching?

Lena Klever

Experimental Psychology, Justus Liebig University Giessen, Germany
Center for Mind, Brain, and Behavior (CMBB), University of Marburg and Justus Liebig University Giessen, Germany ✉

Dimitris Voudouris

Experimental Psychology, Justus Liebig University Giessen, Germany

Katja Fiehler

Experimental Psychology, Justus Liebig University Giessen, Germany
Center for Mind, Brain, and Behavior (CMBB), University of Marburg and Justus Liebig University Giessen, Germany

Jutta Billino

Experimental Psychology, Justus Liebig University Giessen, Germany
Center for Mind, Brain, and Behavior (CMBB), University of Marburg and Justus Liebig University Giessen, Germany

Tactile suppression refers to the phenomenon that tactile signals are attenuated during movement planning and execution when presented on a moving limb compared to rest. It is usually explained in the context of the forward model of movement control that predicts the sensory consequences of an action. Recent research suggests that aging increases reliance on sensorimotor predictions resulting in stronger somatosensory suppression. However, the mechanisms contributing to this age effect remain to be clarified. We measured age-related differences in tactile suppression during reaching and investigated the modulation by cognitive processes. A total of 23 younger (18–27 years) and 26 older (59–78 years) adults participated in our study. We found robust suppression of tactile signals when executing reaching movements. Age group differences corroborated stronger suppression in old age. Cognitive task demands during reaching, although overall boosting suppression effects, did not modulate the age effect. Across age groups, stronger suppression was associated with lower individual executive capacities. There was no evidence that baseline sensitivity had a prominent impact on the magnitude of suppression. We conclude that aging alters the weighting of sensory signals and sensorimotor predictions during movement control. Our findings suggest that individual differences in tactile suppression are critically driven by executive functions.

Introduction

Developmental changes across the adult life span provide a critical source of functional differences between individuals. Although the demographic shift toward older populations in many societies has provided a strong impetus to investigate decline and stability of functional resources during aging, our understanding of behavioral age effects so far is mostly limited to defined domains and falls short of sufficiently considering the complexity of aging processes (see, e.g., Cabeza, Nyberg, & Park, 2005; van den Bos & Eppinger, 2016). Age-related changes are well documented for sensory capacities, motor performance, and in particular cognition (for reviews, see Owsley, 2011; Park & Reuter-Lorenz, 2009; Seidler et al., 2010). However, interactions between age effects on percep-

tion, action, and cognition are often neglected. Only recently endeavors to understand those functional links and how they shape age-specific capacities have begun to increase (Maes, Gooijers, Orban de Xivry, Swinnen, & Boisgontier, 2017; Monge & Madden, 2016).

Sensorimotor suppression can be considered as a well-suited opportunity to investigate complex mechanisms of functional aging. It involves efficient interactions between motor, sensory, and predictive processes. The phenomenon is based on dynamic gating of sensory information during movement preparation and execution. The crucial link between motor actions and perception of sensory stimulations is provided by the forward model of motor control (Shadmehr & Krakauer, 2008; Wolpert, Diedrichsen, & Flanagan, 2011; Wolpert & Flanagan, 2001). The model proposes that movement control relies on internal representations of motor commands and predicted sensory consequences of the corresponding movement. Performance is stabilized by a continuous comparison between sensory information from the environment and predicted movement consequences. In this framework, efficient regulation of performance can be achieved by enhancement and suppression of sensory signals that are relevant and irrelevant for movement control, respectively.

Tactile suppression, in particular, refers to the attenuation of tactile signals during movement planning and execution when presented on a moving limb compared to rest (for review, see Juravle, Binsted, & Spence, 2017). Originally, tactile suppression was primarily considered as a cancellation of specific afferences that are predicted based on the efference copy of the motor commands (e.g., Bays, Flanagan, & Wolpert, 2006; but see Chapman & Beauchamp, 2006). For instance, self-applied forces (Bays, Wolpert, & Flanagan, 2005; Shergill, Bays, Frith, & Wolpert, 2003) or self-tickling sensations (Blakemore, Frith, & Wolpert, 1999; Blakemore, Wolpert, & Frith, 1998) are perceived less intensely than when triggered externally. However, there has been cumulating evidence that not only self-generated, but also externally generated tactile signals are suppressed when applied to a moving limb (e.g., Buckingham, Carey, Colino, de Grosbois, & Binsted, 2010; Fraser & Fiehler, 2018; Voss, Ingram, Wolpert, & Haggard, 2008). Thus, tactile suppression during movements is not limited to afferences predicted from specific efference copies of motor commands, but can emerge from general predictions of sensory movement consequences, e.g., tactile signals from the moving limb. Accordingly, reduced neuronal activity in secondary somatosensory areas related to tactile signals has been observed for self-generated (Blakemore et al., 1998; Shergill et al., 2013) as well as for externally triggered stimulations (Jackson, Parkinson, Pears, & Nam,

2011; Parkinson et al., 2011) during movement. Therefore, it has been suggested that tactile suppression reflects a general gating mechanism fueled by the forward model. Sensory information irrelevant for movement execution is attenuated and thereby putatively capacities for optimizing voluntary movements are freed (Brown, Adams, Parees, Edwards, & Friston, 2013; Gertz, Voudouris, & Fiehler, 2017; Haggard & Whitford, 2004). Consistently, a lack of suppression or even enhancement has been observed when tactile information is relevant to action performance (Colino, Buckingham, Cheng, van Donkelaar, & Binsted, 2014; Juravle, Colino, Meleqi, Binsted, & Farnè, 2018; Voudouris & Fiehler, 2017a, 2017b).

Given pronounced sensory and motor changes during aging, functional effects on somatosensory suppression can be expected. Integration of sensory and motor signals might be challenged by increased somatosensory noise (e.g., Decorps, Saumet, Sommer, Sigaudo-Roussel, & Fromy, 2014), greater movement variability (e.g., Contreras-Vidal, Teulings, & Stelmach, 1998; Darling, Cooke, & Brown, 1989), or general movement slowing (e.g., Buckles, 1993). However, behavioral evidence is sparse. Age effects on somatosensory suppression have been considered only recently in a study by Wolpe et al. (2016). They measured the perception of forces applied to the index finger in a well-established matching task (see Bays et al., 2005; Shergill et al., 2003). Forces were generally felt less intensely when they were self-produced than when they were externally produced. Data supported that this effect increased with age, providing first evidence for stronger tactile suppression in older adults. Stronger suppression argues for a greater reliance on predictive signals while weighting sensory input less. This altered balance might be attributed to the basic principles of Bayesian integration (Körding & Wolpert, 2004) and could represent an adaptive mechanism during aging. Accumulating experience across the life span makes predictive signals more reliable, but sensory signals become increasingly noisy. Thus, the weighting of sensorimotor predictions is amplified, which contributes to a greater attenuation of the sensory action consequences.

Although age-related reliability changes in sensory and predictive signals provide a plausible account for increased somatosensory suppression, also cognitive processes are likely to play a critical role that has not been considered so far. Cognitive resources are subject to massive decline during aging (Hasher & Zacks, 1988; Park & Reuter-Lorenz, 2009; West, 1996), and numerous studies have provided evidence for close interactions between age effects on cognition and sensorimotor control, respectively. Older adults have been consistently found to show higher dual task costs when they have to share attentional resources between

a motor task and secondary cognitive demands (Doumas, Rapp, & Krampe, 2009; Huxhold, Li, Schmiedek, & Lindenberger, 2006; Lee, Wishart, & Murdoch, 2002; Lövdén, Schaefer, Pohlmeyer, & Lindenberger, 2008; Overvliet, Wagemans, & Krampe, 2013). Age-related changes in motor learning processes have been linked to memory resources (Anguera, Reuter-Lorenz, Willingham, & Seidler, 2010; Trewartha, Garcia, Wolpert, & Flanagan, 2014) and also to executive functions (Heuer & Hegele, 2014; Heuer, Hegele, & Sülzenbrück, 2011; Huang, Gegenfurtner, Schütz, & Billino, 2017; Huang, Hegele, & Billino, 2018). These findings suggest that cognitive resources represent a major modulator of sensorimotor control in old age. Thus, it is to be clarified how cognitive processes contribute to increased somatosensory suppression in older adults. There is indeed evidence that auditory (Cao & Gross, 2015) as well as tactile (van Hulle, Juravle, Spence, Crombez, & van Damme, 2013) suppression can be modulated by attentional mechanisms in younger adults, suggesting a critical functional role in predictive processes (compare also Brown et al., 2013).

We aimed to investigate whether cognitive processes contribute to increased tactile suppression during aging. We assessed the attenuation of tactile perception during reaching movements compared to rest, using a paradigm that has yielded reliable suppression effects in younger adults (Buckingham et al., 2010; Fraser & Fiehler, 2018; Gertz, Fiehler, & Voudouris, 2018; Gertz et al., 2017). It has been consistently shown that externally generated, unpredictable tactile signals are attenuated when applied to the reaching limb. Being irrelevant for movement execution, they are assumed to be suppressed due to general predictions of sensory movement consequences. In addition, these suppression effects are specifically bound to the reaching limb and are not explained by secondary demands involved in the reaching movement (cf. Gertz et al., 2018). We manipulated cognitive task demands during reaching by introducing an additional memory task. In addition, we assessed individual executive resources in our participants. Cognitive decline during aging is most pronounced for executive functions (Hasher & Zacks, 1988; West, 1996), and they might crucially modulate the balancing of sensorimotor signals. We expected to corroborate stronger tactile suppression effects in older adults indicating an increased reliance on sensorimotor predictions. We further hypothesized that age effects are modulated by cognitive task demands and individual executive resources. More specifically, higher cognitive task demands as well as limited individual availability of cognitive resources might contribute to increased suppression.

Methods

Participants

A total number of 49 participants, of which 23 were younger adults (11 females), ranging in age from 18 to 27 years ($M = 22.6$, $SD = 2.6$), and 26 older adults (13 females), ranging in age from 59 to 78 years ($M = 69.3$, $SD = 5.2$) took part in this study. Participants had normal or corrected-to-normal vision. Handedness was assessed with the Edinburgh Handedness Inventory (Oldfield, 1971), yielding ambidexterity in three participants, i.e., laterality indexes 18, 10, and zero, respectively, and right-handedness in all other participants, i.e., laterality indexes ≥ 50. Using a detailed interview protocol, we further screened out any history of ophthalmologic, neurologic, or psychiatric disorders as well as medications presumed to interfere with visuomotor capacities. In addition, all participants were screened for mild cognitive impairment using a cutoff score of ≥ 26 on the Montreal Cognitive Assessment scale (Nasreddine et al., 2005). Participants received financial compensation or course credits. Methods and procedures agreed with the Declaration of Helsinki (World Medical Association, 2013) and were approved by the local ethics committee of the Faculty of Psychology and Sports Science, Justus Liebig University Giessen. Informed consent was obtained by all participants, and protection of data privacy was provided.

Assessment of executive functions

Individual executive capacities were characterized by performance in three established measures known to be highly sensitive to aging (compare with Park & Reuter-Lorenz, 2009). The Victoria Stroop Test (VST) uses different colored naming tasks to provide a measure of inhibitory control (Strauss, Sherman, & Spreen, 2006; Stroop, 1935). We ran a computerized version of this test included in the Psychology Experiment Building Language (PEBL) Test Battery (Mueller & Piper, 2014). In particular, the response latency when naming the color of ink of written color words giving an incongruent color indicates the difficulty of inhibiting a dominant response, classically called Stroop interference. The Trail Making Test, specifically part B (TMT-B), captures cognitive flexibility and task-switching ability (Kortte, Horner, & Windham, 2002; Reitan & Wolfson, 1985). The task requires continuous switching between the numerical system and the alphabetical system. The Digit Symbol Substitution Test (DSST), a subtask of the Wechsler Adult Intelligence Scale (Wechsler, 2008), taps working memory and set
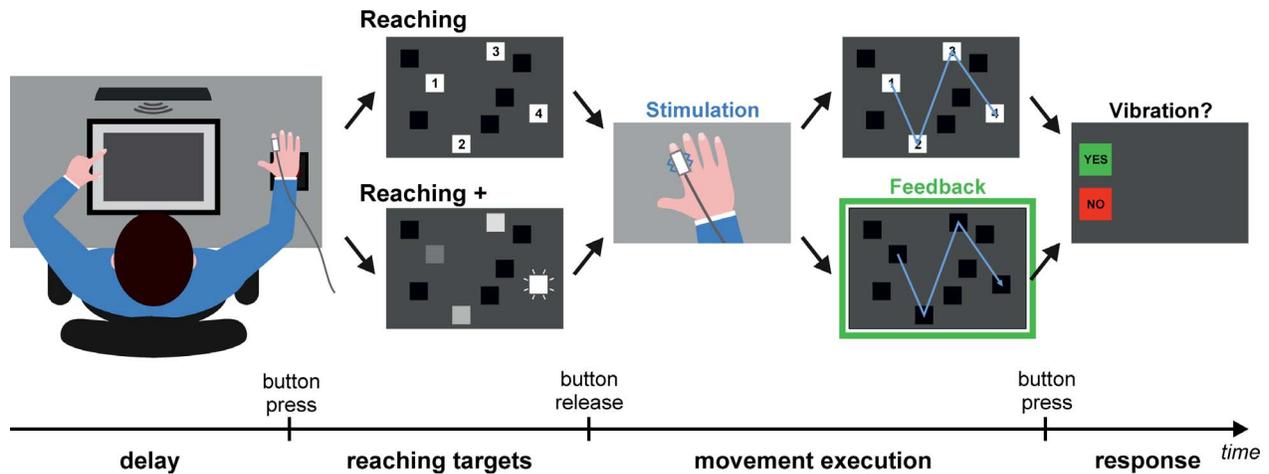
Figure 1. Schematic top view of the setup and trial procedure. Participants sat in front of a table, which was equipped with a touchscreen, a start button, and a speaker. In the baseline condition (not shown in detail), participants performed the detection task while the stimulated right hand was at rest. In the reaching condition, four out of the nine black squares turned white simultaneously and permanently. A fixed order was given by consecutive numbers. In the reaching plus memory condition, four squares turned white after one another, each for 1,000 ms, and participants had to remember their temporal order. In both reaching conditions, tactile stimulation was applied with a variable onset after release of the start button. After finishing the reaching movement in the reaching plus memory condition, participants were provided with performance feedback (green/red frame). At the end of each trial, participants indicated whether they had felt a vibration or not via the respective response squares.

shifting. A series of symbols has to be correctly coded within a time limit.

Experimental setup and stimuli

Figure 1 illustrates the setup and summarizes the procedure of the experimental task. Participants sat in front of a 21-in. ELO touchscreen (ELO TouchSystems ET2125C, resolution of $1,280 \times 960$ pixel, refresh rate of 100 Hz) at a distance of approximately 25 cm. The touchscreen was horizontally placed and tilted by 15° toward the participants in order to allow for comfortable viewing of and reaching toward the display. A custom-made input device was positioned 16 cm to the right of the touchscreen's center. It was composed of a start button embedded in a hand-rest cup so that it could be handled comfortably by the heel of the right hand.

Targets for reaching movements were provided on the touchscreen using an arrangement of nine black squares (2.5×2.5 cm each) on a gray background. The spatial arrangement corresponded to the outline of the Corsi Block Tapping Task (Berch, Krikorian, & Huha, 1998) that is typically used to assess spatial working memory (see Figure 1).

Vibrotactile stimulation was applied by a custom-made tactile stimulator (Engineering Acoustics Inc., Casselberry, FL) that was attached to the dorsal part of participants' right index finger. Position of the stimulator was chosen not to interfere with touching the

screen when reaching with the finger. Stimuli were presented for 35 ms and at a frequency of 100 Hz. In order to mask any auditory cues emerging from the tactile stimulators, we presented white noise via an external loudspeaker hidden behind the touchscreen.

The presentation of tactile stimuli and reaching targets was controlled by MATLAB (MathWorks, Natick, MA) using the Psychophysics Toolbox (Brainard, 1997; Kleiner, 2010).

Procedure

Our experimental procedure started with a short introduction to our setup in order to allow all participants to get acquainted with our equipment. This introduction included the demonstration of vibrotactile stimulations as well as the use of the touchscreen as input device. We particularly took care that those older adults who reported to have only minor experience with technical devices felt comfortable with our setup.

Tactile detection was then measured under three different conditions, i.e., baseline, reaching, and reaching plus memory (see Figure 1). We investigated perceptual performance based on psychometric functions that were determined from a *Yes–No* detection task. This method of single stimuli is known to be well accepted by participants naïve to psychophysical measurements and allows efficient threshold estimations from a limited number of trials (Jäkel & Wichmann, 2006; Leek, Dubno, He, & Ahlstrom, 2000;

Yeshurun, Carrasco, & Maloney, 2008). However, because psychometric functions derived from *Yes–No* tasks are prone to response biases, careful consideration of individual decision criteria is indicated during data analysis. Participants performed a tactile detection task in which signal intensity was varied by 12 constant levels defined by peak-to-peak displacements. Because age-related differences in tactile sensitivity are well documented (A. K. Goble, Collins, & Cholewiak, 1996), we chose for each adult group an appropriate intensity range that was supposed to comprise just detectable to reliably detectable intensities. Intensities, defined as peak-to-peak displacements, ranged from 0.007 mm to 0.085 mm for younger adults and from 0.009 mm to 0.169 mm for older adults. Each of the 12 intensity levels was presented eight times, giving overall 96 stimulation trials. In addition, we included 24 catch trials without tactile stimulation in order to impose uncertainty about the presence of a stimulus. For each condition, we, thus, presented a total of 120 trials.

All participants first performed the detection task under the baseline condition in which the stimulated right hand was at rest. Participants were informed that a tactile stimulation would be present or absent in each trial, but the proportion of trials with and without stimulation was not specified. The start of each trial was indicated by a black circle displayed on a gray background for 700 ms. After the circle was extinguished, a tactile stimulation followed in the respective trials. In order to prevent participants anticipating the moment of stimulation, onset varied between 10 ms and 100 ms in steps of 10 ms. This range of delays was assumed to be sufficient to introduce reliable ambiguity about the timing of the tactile stimulus because it matches documented duration discrimination thresholds (Grondin, 2010; Rammsayer, 1990). There is no evidence for pronounced age effects on temporal discrimination (Rammsayer, Lima, & Vogel, 1993). In addition, catch trials contributed to further ambiguity about the stimulus onset. Onsets were randomized and balanced across trials. Two vertically arranged squares, a green one labeled "yes" and a red one labeled "no," appeared on the left side of the display 700 ms after the disappearance of the black start circle. Participants responded whether they felt a stimulation or not by touching the respective square with their left index finger. The vertical arrangement of the two response squares was randomized across participants but was kept constant for each individual participant. After the response, no feedback was given, and the next trial started.

The baseline condition was followed by the reaching condition and reaching plus memory condition. The order of these two conditions was randomized across participants. The procedure of the tactile detection task in both reaching conditions was equivalent to the baseline condition but was embedded in reaching tasks. Required reaching movements were comparable across both reaching conditions. They comprised a sequence of taps on four target squares and the sequence was defined completely before movement onset. Each trial started with the participants pressing the start button with the heel of the right hand. After a delay of 2,000 ms, the targets for the reaching movements were presented.

In the reaching condition, four out of the nine black squares turned white simultaneously and permanently. A fixed order was given by consecutive numbers. Participants had to touch the white squares in their ascending order with the right index finger to which the stimulator was attached. Reaching movements were instructed to be executed immediately after onset of the white squares and as naturally as possible. The onset of the tactile stimulations was locked to the release of the start button so that detection performance was measured during movement execution. Timing of the tactile stimulations was subject to the delay jitter described above. Ambiguity about stimulus onset was important in order to prevent strategic changes in movement execution, e.g., slowing at the moment of stimulation. When the reaching movement was completed, participants returned the right hand to the start button. The response squares were then displayed, and participants indicated whether they had noticed a tactile stimulation and the next trial started.

In the reaching plus memory condition, four out of the nine black squares turned white after one another, each for 1,000 ms. Participants were instructed to remember the sequence of squares. After the last square turned back to black, they had to touch the remembered squares in the correct order with their right index finger. Again, reaching movements were instructed to be executed immediately after extinction of the last white square and as naturally as possible. The onset of the tactile stimulations was locked to the release of the start button so that detection performance was measured during movement execution. Timing of the tactile stimulations was again subject to the given delay jitter in order to keep the stimulus onset sufficiently ambiguous. When the hand returned to the start button, feedback on the memory performance was provided for 200 ms. If the sequence of squares was touched in the correct order, a green frame was displayed around the arrangement of black squares, otherwise a red frame was given. Afterward, participants indicated whether they had noticed a tactile stimulation and the next trial started.

Executive functions were assessed after completion of the tactile detection tasks in the three different conditions. In addition to the executive tests, we determined the maximal block span of each participant using the respective subtest of the Wechsler Memory

Scale (Härting et al., 2000). We chose a constant block sequence length of four blocks in the reaching plus memory condition in order to keep the task procedure comparable across participants. The block span measure allowed the evaluation of individual memory task demands. Overall, the procedure took about 60–90 min so that the duration was still appropriate for the older participants.

Data analysis

Tactile detection performance under the three experimental conditions was analyzed by fitting cumulative Gaussian functions to the detection rates for the different intensity levels. We used the psignifit 4 toolbox in MATLAB, which provides an accurate Bayesian estimation of psychometric functions and has been shown to be robust to overdispersion in measured data. In particular, the toolbox has been evaluated for data from *Yes–No* paradigms as used in our procedure, and extensive numerical simulations support accuracy of derived estimates (Schütt, Harmeling, Macke, & Wichmann, 2016). From the fitted psychometric functions, we determined 50% detection thresholds. Due to inconsistent detection data, psychometric functions could not be fitted for six participants in the reaching plus memory condition (two younger and four older adults). For all other functions, goodness of fit was evaluated by comparing the measure of deviance with the critical chi-square value for 13 comparisons, $\chi^2_{13, 95\%} = 22.36$ (Wichmann & Hill, 2001). Deviance is defined as the log-likelihood ratio between the saturated model, i.e., no residual error between empirical data and model predictions, and the best-fitting model. Smaller deviance values indicate better fits. Out of all 141 estimated functions, 99.29% met this criterion. In order to consider possible response biases that could impose a critical confound when interpreting psychometric estimates, we analyzed the lower asymptotes, γ, of the psychometric functions. The lower asymptotes indicate individual decision criteria, i.e., participants' inclination to report the presence of a stimulus. We particularly aimed to clarify whether response biases systematically varied across the different measurement conditions and, thus, could contribute to threshold differences. Running a mixed ANOVA with the within-subject factor *measurement condition* (baseline, reaching, reaching +) and the between-subject factor *age group* (younger adults vs. older adults), we found no evidence for a critical confound. The lower asymptotes were affected neither by *measurement condition, F*(2, 82) = 1.76, $p = 0.179$, $\eta_p^2 = 0.04$, nor by an interaction between *measurement condition* and *age group, F*(2, 82) = 1.11, $p = 0.334$, $\eta_p^2 = 0.03$. We indeed determined a significant main effect of *age group, F*(1, 41) = 4.59, $p =$

0.038, $\eta_p^2 = 0.10$, indicating higher guess rates in older adults. Although this might contribute to an overall underestimation of detection thresholds in older adults and, thus, an underestimation of the age effect on detection thresholds (compare with Morgan, Dillenburger, Raphael, & Solomon, 2012), tactile suppression effects can be considered as undistorted because they were evaluated within individual participants.

Tactile suppression effects were assessed by subtracting each participant's baseline detection threshold from their thresholds determined in the reaching condition and the reaching plus memory condition, respectively (compare, e.g., Gertz et al., 2017; Voudouris & Fiehler, 2017a). The resulting difference values represent the strength of tactile suppression. Positive values indicate suppression during movement execution. Note that, due to the missing detection thresholds for the abovementioned six participants in the reaching plus memory condition, we calculated tactile suppression effects only for 43 participants in this particular condition.

For the reaching and the reaching plus memory conditions, we collected reaction times and movement times. For the former condition, reaction time was defined as the time between the onset of the numbered squares and the release of the start button. For the latter condition, it was defined as the time difference between the extinction of the last white square and the release of the start button. Movement time was given by the difference between the release of the start button and the first screen contact. For statistical analyses, time measures were averaged across trials for each participant.

Accuracy of reaching movements was assessed by the proportion of correctly reproduced reaching sequences. Accuracy in the reaching plus memory condition provides a measure of individual task demand. Please note that, in the reaching condition, accuracy was expected to deviate only minimally from 100% as participants just had to follow the order of the four numbers correctly. However, the touch sequence was sometimes not registered appropriately because participants touched the screen too weakly or in an unfavorable angle. Thus, accuracy in the reaching condition can be considered as a technically determined upper limit.

Basic age effects on tactile perception were explored by contrasting detection thresholds in younger and older adults using separate *t* tests for each measurement condition, i.e., baseline, reaching, and reaching plus memory conditions. Tactile suppression effects were analyzed using a mixed ANOVA with the within-subject factor *reaching condition* (reaching vs. reaching +) and the between-subject factor *age group* (younger adults vs. older adults). The link between cognitive measures and tactile suppression was explored by linear

regression analyses. In order to back up our results against violations of assumptions underlying these parametric statistical methods, we complemented our analyses by bootstrapping methods (Efron & Tibshirani, 1993). For group comparisons and regression analyses, we computed 95% percentile confidence intervals using 2,000 bootstrap samples. Given evidence from extensive simulations studies, we assumed relative robustness of ANOVAs (Berkovits, Hancock, & Nevitt, 2000; Wilcox, 2012). A significance level of $\alpha = 0.05$ was applied for all statistical analyses. If not stated otherwise, descriptive values are given as means $\pm$ SEMs.

Results

In order to explore basic perceptual performance in both age groups, we first contrasted tactile detection thresholds in younger and older adults. Figure 2 illustrates the thresholds we derived for each age group in the three different measurement conditions. We observed robust age effects on tactile perception. Older adults consistently showed higher detection thresholds than younger adults in the baseline condition, 0.040 ± 0.004 mm versus 0.014 ± 0.002 mm, $t(47) = 5.91$, $p < 0.001$, $d = 1.73$, 95% CI [0.017, 0.034]; the reaching condition, 0.075 ± 0.008 mm versus 0.026 ± 0.006 mm, $t(47) = 4.84$, $p < 0.001$, $d = 1.40$, 95% CI [0.027, 0.067]; and the reaching plus memory condition, 0.090 ± 0.011 mm versus 0.032 ± 0.006 mm, $t(41) = 4.69$, $p < 0.001$, $d = 1.44$, 95% CI [0.035, 0.082]. In all conditions, older adults needed approximately three times higher intensity levels than younger adults for detecting the tactile stimulation on their right index finger. Cohen's d values indicate pronounced age effects on tactile perception. Please note that these effects might indeed be subject to an underestimation because the lower asymptotes of psychometric functions suggested that older adults were more inclined to report the presence of a stimulus, possibly reducing the age effect (compare with the section *Data analysis*).

Tactile suppression effects during reaching were quantified using threshold difference measures. Baseline thresholds were subtracted from thresholds in the reaching and the reaching plus memory condition, respectively. Figure 3A provides exemplary psychometric functions for the three measurement conditions derived for a typical younger and a typical older participant. Functions for both reaching conditions are shifted to the right on the stimulus intensity axis, indicating higher detection thresholds. Suppression effects in each age group are summarized in Figure 3B.

In the reaching condition, we were not able to observe tactile suppression consistently. We determined
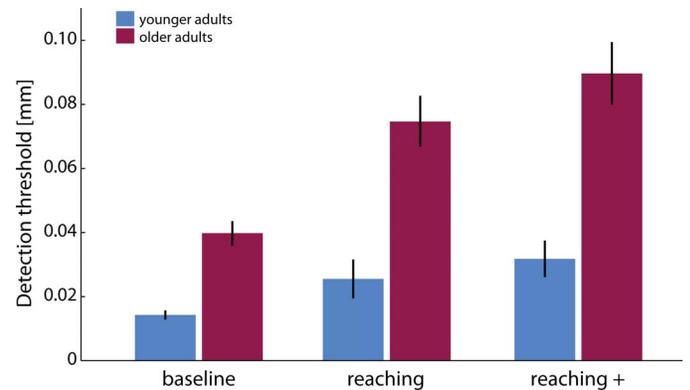

Figure 2. Detection thresholds in younger and older adults for all three conditions, i.e., baseline, reaching, and reaching plus memory condition. Stimulus intensity is defined as peak-to-peak displacement in millimeters. Error bars indicate ± 1 *SEM*.
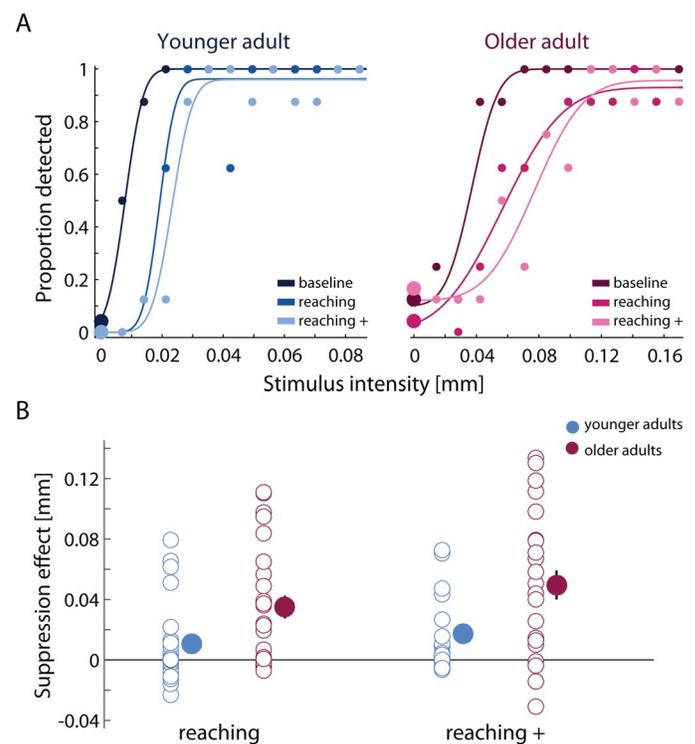

Figure 3. Tactile suppression effects in younger and older adults. (A) Psychometric functions in the three conditions, i.e., baseline, reaching, and reaching plus memory, for an exemplary younger and an exemplary older adult; stimulus intensity is defined as peak-to-peak displacement in millimeters; please note that the scale of stimulus intensity on the *x*-axis varies between age groups; data points for each intensity level are based on eight trials each except for the zero-intensity level that comprised 24 catch trials without tactile stimulation. (B) Tactile suppression effects given by the detection threshold differences between the baseline condition and the respective reaching condition; open symbols illustrate individual data, filled symbols average data in each age group; error bars indicate ± 1 *SEM*.

suppression effects >0 in 47.83% of the younger and 71.43% of the older adults. On average, younger adults showed tactile suppression of 0.011 ± 0.006 mm, but this effect failed to differ significantly from zero, $t(22) = 1.83$, $p = 0.081$, $d = 0.38$, 95% CI [−0.001, 0.020]. In contrast, older adults showed an average suppression effect of 0.035 ± 0.008 mm, yielding a significant difference from zero, $t(25) = 4.64$, $p < 0.001$, $d = 0.91$, 95% CI [0.017, 0.046]. In the reaching plus memory condition, the majority of participants in both age groups showed tactile suppression, i.e., 73.08% and 77.27% in younger and older participants, respectively. On the group level, suppression effects were pronounced and differed significantly from zero for younger adults, 0.018 ± 0.006 mm, $t(22) = 3.00$, $p = 0.007$, $d = 0.65$, 95% CI [−0.067, 0.030], and for older adults, 0.050 ± 0.011 mm, $t(25) = 4.64$, $p < 0.001$, $d = 1.01$, 95% CI [0.030, 0.070].

We were particularly interested in determining whether tactile suppression effects vary systematically between age groups and between reaching conditions that involve differential task demands. To this end, we ran a 2 × 2 mixed ANOVA on the suppression effects with the between-subject factor *age group* and the within-subject factor *condition*. The analysis yielded significant main effects for *age group*, $F(1, 41) = 7.98$, $p = 0.007$, $\eta_p^2 = 0.16$, and *condition*, $F(1, 41) = 7.53$, $p = 0.009$, $\eta_p^2 = 0.16$. There was no significant interaction effect between *age group* and *condition*, $F(1, 41) = 0.97$, $p = 0.330$, $\eta_p^2 = 0.02$, so that main effects could be interpreted directly. In both reaching conditions, older adults consistently showed larger tactile suppression effects in comparison to younger adults. In addition, independent of age group, suppression effects were more pronounced when task demands were enhanced by memory load, i.e., suppression was more pronounced in the reaching plus memory condition than in the reaching condition.

We scrutinized the described main effects by exploring their link to individual perceptual capacities and individual task demands. First, we considered the possibility that the age-related increase in tactile suppression was driven by the overall higher detection thresholds in older adults. We used baseline detection thresholds as a reference for tactile perception and found no evidence for a significant correlation with the magnitude of suppression during reaching, neither in the reaching condition, $r(49) = 0.17$, $p = 0.245$, 95% CI [−0.04, 0.37], nor in the reaching plus memory condition, $r(43) = 0.16$, $p = 0.319$, 95% CI [−0.10, 0.45]. Note that, because baseline thresholds enter these analyses twice, i.e., with a positive sign for perceptual capacity and with a negative sign for suppression effects, a systematic negative bias is inherent to these correlations. Thus, we indeed cannot rule out an impact of perceptual capacities on the magnitude of suppres-

sion effects. However, given the observed weak positive correlations that did not significantly deviate from zero, it appears rather unlikely that individual threshold differences are the main driving factor for the variability in suppression effects.

In addition, we aimed to clarify how task demands might modulate tactile suppression. In the reaching plus memory condition, the task required memory resources. The extent of task demands consequently depended on individually available resources. More pronounced suppression effects in older adults in comparison to younger adults could be triggered by age-related differences in memory capacities and, thus, differences in task demands. Indeed, our two age groups varied substantially in their memory capacities, and it can be plausibly assumed that task demands in the reaching plus memory condition were more challenging for older adults. We determined significant age-related differences in the maximal block span measure we obtained for each participant, $t(47) = −5.87$, $p < 0.001$, $d = −1.67$, 95% CI [−1.69, −0.82]. Older adults reached, on average, a maximal memory span of 5.0 ± 0.1 blocks, and younger adults accomplished a sequence of 6.3 ± 0.2 blocks. Congruently, older adults showed lower accuracy in our block span task in the reaching plus memory condition than younger adults, 76.89 ± 3.29% versus 91.51 ± 1.42%, $t(41) = −4.02$, $p < 0.001$, $d = −1.24$, 95% CI [−22.17, −8.02]. Please note that, in the reaching condition, when accuracy was supposed to exclusively rely on putative difficulties in touchscreen handling, older and younger adults showed comparable accuracy rates, 89.52 ± 2.23% versus 91.45 ± 1.65%, $t(47) = −0.68$, $p = 0.500$, $d = −0.20$, 95% CI [−8.45, 3.67]. However, the extent of individual demands was not significantly linked to suppression effects. Correlations between maximal block span measures as well as accuracy and suppression effects did not reach significance, $r(43) = −0.27$, $p = 0.075$, 95% CI [−0.51, 0.01], and $r(43) = −0.12$, $p = 0.464$, 95% CI [−0.47, 0.18], respectively.

Because different strategies in accomplishing the additional memory task might obscure effects of individual task demands, we investigated time measures of the reaching movements that could indicate systematic differences between age groups. Reaction times and movement times in each reaching condition are illustrated in Figure 4.

We submitted both time measures to 2 × 2 mixed ANOVAs with the between-subject factor *age group* and the within-subject factor *condition*. Analyses yielded significant main effects of *age group* for reaction time $F(1, 41) = 34.69$, $p < 0.001$, $\eta_p^2 = 0.46$, and for movement time $F(1, 41) = 28.74$, $p < 0.001$, $\eta_p^2 = 0.41$. These main effects consistently support typical age-related slowing in our sample. In addition, timing of reaching movements was modulated by *condition*.
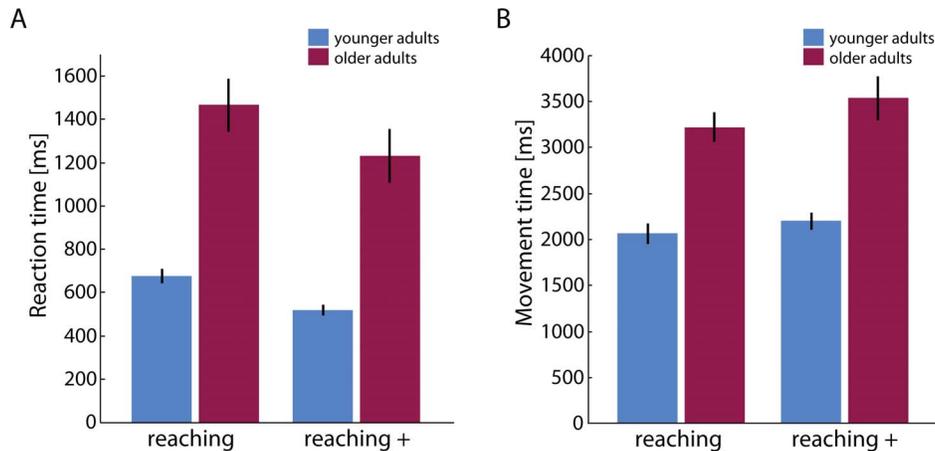
Figure 4. Time measures in the reaching condition and the reaching plus memory condition for younger and older adults. (A) Average reaction times. (B) Average movement times. Error bars indicate ±1 *SEM*.

Reaction times tended to be shorter in the reaching plus memory condition, $F(1, 41) = 3.74$, $p = 0.060$, $\eta_p^2 = 0.08$, whereas movement times were significantly slower $F(1, 41) = 5.82$, $p = 0.020$, $\eta_p^2 = 0.12$. This pattern most likely emerges from the specific procedure in each condition. In the reaching condition, the start of the reaching movement is preceded by locating the first reaching target on the display. Movement execution then is directly guided by the visible target numbers. In contrast, in the reaching plus memory condition, the start of the reaching movement can be already prepared during successive presentation of the targets. Movement execution is slowed by repeated decisions on where to reach next. Most importantly, we found no evidence for interactions effects between *age group* and *condition* on time measures: for reaction time: $F(1, 41) = 0.33$, $p = 0.567$, $\eta_p^2 = 0.01$; for movement time: $F(1, 41) = 1.83$, $p = 0.183$, $\eta_p^2 = 0.04$. Thus, participants in both age groups can be assumed to have applied similar strategies to accomplish the reaching tasks.

Finally, we investigated whether individual executive capacities contribute to differences in tactile suppression. We assessed individual executive functions with established measures, i.e., the VST, the TMT-B, and the DSST. Age groups differed significantly in all measures, all ps < 0.001. We aimed to test whether suppression effects can be predicted by executive functions. We found consistent correlations between our measures and tactile suppression in both reaching conditions across all participants, indicating that more pronounced suppression effects were linked to lower performance in the executive tests. All correlations, except for the correlation between the VST and the suppression effect in the reaching plus memory condition, $r(43) = 0.18$, $p = 0.261$, 95% CI [–0.17, 0.53], reached significance, rs ranging between 0.31 and 0.49, ps ≤ 0.031. Because all tests tap the same functional domain, intercorrelations accordingly were high, rs >

0.59, ps < 0.001. For a simple linear regression analysis, we chose the TMT-B, capturing primarily cognitive flexibility because it was most robustly linked to suppression in the reaching, $r(49) = 0.40$, $p = 0.005$, 95% CI [0.14, 0.62], as well as in the reaching plus memory condition, $r(43) = 0.49$, $p = 0.001$, 95% CI [0.15, 0.73]. Figure 5 illustrates the correlations for both conditions. Higher time measures in the TMT-B indicate lower cognitive flexibility. Depiction of group membership for each data point suggests that the reported correlations are not merely driven by group differences but can actually be observed across the whole sample. Please note that our data supports a specific link between executive functions and tactile suppression because neither tactile thresholds in the baseline condition nor overall speed in the reaching tasks, both measures highly age-sensitive, correlated with suppression effects.

Using performance in the TMT-B as predictor explained 16% and 24% of the variance in the tactile suppression effect in the reaching condition, $F(1, 48) = 8.74$, $p = 0.005$, $R^2 = 0.16$, and the reaching plus memory condition, $F(1, 42) = 12.82$, $p = 0.001$, $R^2 = 0.24$, respectively. Overall, the regression analysis supported that executive resources critically contribute to individual differences in the magnitude of tactile suppression during reaching, independent of task demands.

Discussion

This study was concerned with age effects on tactile suppression and the specific contributions of cognitive processes. Recent evidence indicates stronger suppression in older adults, putatively due to an increased reliance on sensorimotor predictions (Wolpe et al.,
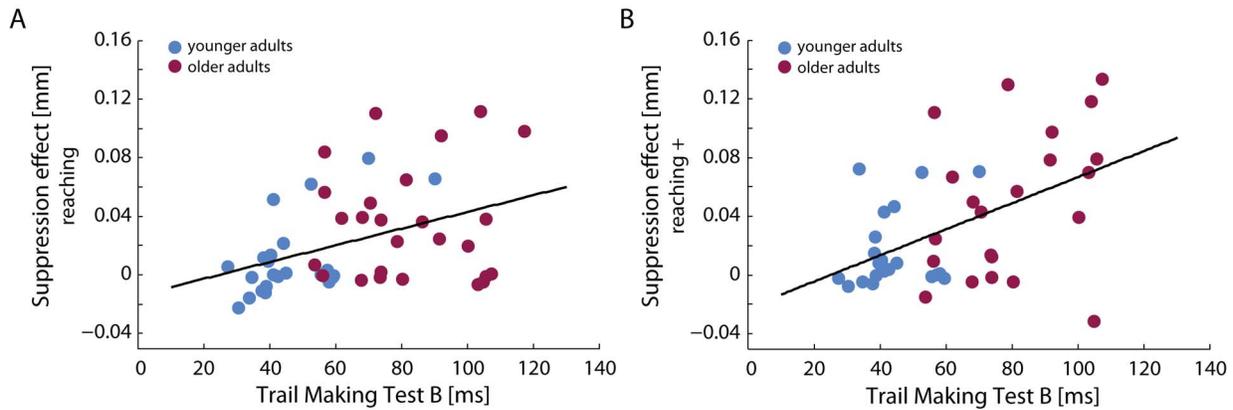
Figure 5. Correlations across all participants, i.e., younger and older adults, between cognitive flexibility as measured by the TMT-B and tactile suppression effects as given by detection threshold differences. (A) Data in the reaching condition. (B) Data in the reaching plus memory condition.

2016). We investigated tactile suppression during reaching in an established paradigm that is known to reliably induce an attenuation of tactile signals on the moving limb (Fraser & Fiehler, 2018; Gertz et al., 2018; Gertz et al., 2017; Voudouris & Fiehler, 2017a). Furthermore, we explored how the magnitude of suppression was modulated by cognitive task demands and individual executive resources, respectively. Task demands were manipulated by introducing a secondary memory task linked to the primary reaching task. Comparison between tactile suppression in conditions with and without additional memory load allowed us to evaluate the impact of cognitive task demands. Moreover, we tested whether tactile suppression is associated with available individual executive resources.

Our main aim was to examine whether the reliance on sensorimotor predictions reduces tactile sensitivity and whether this effect is modulated by age. We succeeded in triggering tactile suppression during reaching in both younger and older adults. The magnitude of suppression in young adults was overall consistent with findings from previous studies that used a comparable paradigm (Fraser & Fiehler, 2018; Gertz et al., 2018; but see Gertz et al., 2017) but, indeed, just failed to reach significance in the reaching condition without additional memory load. We speculate that our adaptation of the reaching task might have induced an attenuation of suppression effects. While typically only single reach targets have been used, we presented a sequence of reach targets. Thus, in our task, movement execution can be supposed to overlap with movement planning. This might result in attenuated suppression in comparison to straight execution because sensory attenuation has been found to be less pronounced during movement planning (Voss et al., 2008). Most importantly, our results support stronger tactile suppression with increasing age. On average, older adults

showed approximately more than three times stronger suppression than younger adults. This finding extends recent evidence for an age-related increase of somatosensory suppression in a force-matching task (Wolpe et al., 2016), confirming that the age effect is reliable across paradigms.

Because we derived tactile suppression effects by subtracting baseline thresholds from thresholds during reaching, a possible confound with secondary attentional demands inherent to the movement task has to be considered. Whereas in the baseline condition, attention can be exclusively focused on a possible tactile stimulation, in the reaching condition, also movement execution requires attention. Divided attention per se might contribute to an attenuation of sensory signals. However, it appears rather unlikely that suppression effects are primarily driven by attentional demands. There is converging evidence that suppression effects observed in our paradigm are not explained by general attentional differences. Gertz et al. (2018) showed that a secondary visual discrimination task does not modulate suppression effects. Furthermore, suppression effects occur on the hand involved in the reaching movement but not on the static hand (e.g., Voss et al., 2008; Voudouris & Fiehler, 2017a, 2017b). Similarly, it has been reported that tactile suppression occurs even when the movement is just planned but not executed (e.g., Buckingham et al., 2010; Voss et al., 2008), indicating that suppression effects are not exclusively bound to specific attentional demands. These findings, overall, suggest that observed suppression effects predominantly originate from planning and execution of the movement itself.

Somatosensory suppression has been discussed in the context of a forward model predicting the sensory consequences of movements (Shadmehr & Krakauer, 2008; Wolpert et al., 2011; Wolpert & Flanagan, 2001). Indeed, it has been previously claimed that this internal

model of motor control is prone to age-related decline. This claim is supported by several findings showing that sensorimotor adaptation is reduced in old age (Bock, 2005; Buch, Young, & Contreras-Vidal, 2003; Heuer & Hegele, 2008; Seidler, 2006). Because adaptation substantially relies on the evaluation of prediction errors, age effects have been interpreted as indicating a vulnerability of the forward model. In addition, the cerebellum, which is considered as a critical neural substrate of the forward model (Shadmehr & Krakauer, 2008), is subject to massive structural changes during aging (Raz et al., 2005; Sowell et al., 2003; Walhovd et al., 2011). Several studies have linked cerebellar decline to age-related changes in internal models (Bernard & Seidler, 2014; Boisgontier, 2015; Boisgontier & Nougier, 2013; Seidler, 2006). We propose that increased tactile suppression qualifies the general notion of age-related decline in the forward model.

Consistent with the study by Wolpe et al. (2016), our results support an increased reliance on sensorimotor predictions. Given that proprioceptive signals during movements become increasingly noisy with age (D. J. Goble, Coxon, Wenderoth, van Impe, & Swinnen, 2009), the altered balance of signals might indicate a beneficial adaptive mechanism that agrees with Bayesian integration principles (Körding & Wolpert, 2004). Increased weighting of sensorimotor predictions and reduced weighting of sensory signals, for example, could stabilize the sense of agency in old age, i.e., the experience to control one's own actions and their consequences (David, Newen, & Vogeley, 2008). It critically relies on the evaluation of congruency between predicted action consequences and actual sensory outcome. Increased sensory noise putatively could compromise the reliability of this evaluation so that reduced weighting of these afferent signals might be favorable. We conclude that aging is linked to a shift in weighting of sensory signals and sensorimotor predictions during movement control, respectively, suggesting preserved recalibration of the forward model across the adult life span (compare also Vandevoorde & Orban de Xivry, 2018). However, please note that our results did not indicate that tactile suppression directly scales with tactile sensitivity, i.e., no pronounced positive correlations between baseline tactile detection thresholds and the magnitude of suppression effects were observed. Thus, although differential signal noise can be discussed as a plausible account for shifted weighting of predictions and sensory signals, additional functional mechanisms need to be considered.

A prominent functional age difference concerns processing speed. General slowing and, in particular, slowing of movements are well documented (Buckles, 1993; Salthouse, 1996). Congruently, we observed typical age-related slowing of reaction and movement times in our reaching tasks. Slowing, however, is unlikely to explain the observed age effects on tactile suppression as tactile suppression has been shown to be generally stronger with faster movements (Cybulska-Klosowicz, Meftah, Raby, Lemieux, & Chapman, 2011; Gertz et al., 2017; but see Fraser & Fiehler, 2018). Thus, if movement speed modulated tactile suppression, we might have rather underestimated the age differences. However, we speculate that such modulation might be calibrated to the individual range of movement speed. Therefore, we propose that age-related slowing does not bias our results. Moreover, time measures might be considered as indicative for task demands because previous evidence suggests that movement initiation is faster in easier tasks (Hesse, de Grave, Franz, Brenner, & Smeets, 2008). Due to the overall differences in processing speed, a comparison between our conditions only seems feasible within each age group. Indeed, for both groups, reaction times were consistently shorter in the reaching plus memory condition, seemingly in conflict with the intended boost in task demands. We, though, suggest that the link between movement initiation and task demands does not apply to our specific paradigm. Time measures in both reaching conditions cannot be directly compared because the differential contributions of reaction and movement times to overall reaching time vary systematically due to the different task procedures. The extended preparation phase in the reaching condition systematically speeds up reaction times, whereas repeated decisions based on memory enhance movement times. In contrast, in the reaching condition movement initiation takes longer, but execution directly guided by visual cues is faster. This pattern did not differ between age groups. Hence, we conclude that our main findings are not qualified by differential time measures in both age groups.

Our second main aim of this study was to scrutinize the contribution of cognitive processes to age effects on tactile suppression. We manipulated cognitive demands during reaching by introducing an additional memory task. This load substantially boosted the magnitude of tactile suppression across both age groups. We propose that the additional task increased the weighting of predictive signals by withdrawing processing resources from sensory input. Our results add to previous evidence that tactile suppression is reduced when attention is directed to the stimulus location (van Hulle et al., 2013). Notably, age effects were not modulated by the additional cognitive load. This finding appears in conflict with the well-documented increase in dual task costs in older adults (Huxhold et al., 2006; Li & Lindenberger, 2002; Lindenberger, Marsiske, & Baltes, 2000). It appears rather unlikely that the absence of more pronounced dual task costs was due to insuffi-

cient task demands. Accuracy rates as well as individual maximal span measures suggested that the additional memory task was challenging for the older adults. We speculate that enhanced task demands overall magnify tactile suppression effects, but they do not specifically drive the age-related increase in suppression. If tactile suppression was merely a function of task demands, then age effects should have been more pronounced when the load was enhanced. A similar pattern has been reported for the impact of aging and memory resources on motor adaptation (Trewartha et al., 2014). While memory resources can be linked to performance in motor learning tasks, age effects are independent of the age-related memory decline. Thus, forward model function seems to be overall modulated by memory load, but aging specifically alters the balance between predictive and sensory signals.

The most pronounced age-related changes in cognition concern executive functions (Hasher & Zacks, 1988; West, 1996). Indeed, they might be crucial for the efficient balancing of predictive and sensory signals in the forward model. Some core resources include cognitive flexibility, task-switching abilities, allocation and shifting of attention, and inhibitory capacities. Our findings provide evidence for a strong link between executive resources, in particular, cognitive flexibility and task-switching ability, and the magnitude of tactile suppression. Lower performance in executive tasks was associated with more pronounced suppression across both age groups. Limited executive resources might contribute to an over-reliance on predictive signals. Given the pronounced age-related decline in executive functions, we suggest that they qualify as a plausible candidate resource that drives age effects on tactile suppression.

Neural changes during aging have been extensively studied, and it can be speculated how they relate to increased somatosensory suppression. Although the functional correlates of suppression are not completely understood, some key regions have been identified. They comprise subcortical regions, in particular, the cerebellum (Blakemore et al., 1998; Shadmehr & Krakauer, 2008; Synofzik, Lindner, & Thier, 2008) as well as cortical regions, including somatosensory areas of the parietal lobe (Parkinson et al., 2011; Shergill et al., 2013; Wolpert, Goodbody, & Husain, 1998), the supplementary motor area, the medial frontal cortex, and the prefrontal cortex (Haggard & Whitford, 2004). Aging is associated with widespread structural brain changes; however, volume loss is most pronounced in frontal areas (Raz et al., 2005; Sowell et al., 2003). These areas not only represent the main neural correlates of executive functions (Aron, 2008; Rushworth, Hadland, Paus, & Sipila, 2002), but also are a prominent part of the functional network for somatosensory suppression. In addition to regional gray matter changes, forward model function might be most critically challenged by connectivity changes during aging (Gunning-Dixon, Brickman, Cheng, & Alexopoulos, 2009; McWhinney, Tremblay, Chevalier, Lim, & Newman, 2016; Sala-Llonch, Bartrés-Faz, & Junqué, 2015; Sullivan & Pfefferbaum, 2006). Age-related decrease in connectivity shows a posterior–anterior gradient with the prefrontal white matter being particularly vulnerable to age-related functional decline. Indeed, Wolpe et al. (2016) provided evidence that the age-related increase in somatosensory suppression is associated with reduced connectivity in frontostriatal circuits. In addition, frontostriatal connectivity is crucially modulated by dopaminergic transmission (Jahanshahi et al., 2010), which is subject to age-specific decline (Kaasinen, 2000; Rinne, Lönnberg, & Marjamäki, 1990). These age-related changes in the dopamine system have not only been associated with impaired motor function, but also with cognitive deficits, specifically with declined executive functions, which are grounded in frontal brain regions (Bäckman et al., 2000; Klostermann, Braskie, Landau, O'Neil, & Jagust, 2012; Volkow et al., 1998). In summary, evidence suggests that age-related differences in tactile suppression are linked to frontal connectivity changes and that dopamine plays a major role in regulating the integration of sensorimotor predictions and sensory signals (compare also Wolpe et al., 2018).

Conclusions

Our findings provide evidence for age-related changes in forward model function and expand our understanding of individual differences in movement control. We corroborated stronger tactile suppression in older adults, indicating an increased reliance on sensorimotor predictions that can be observed across different perceptual paradigms. We were particularly interested in how cognitive processes, which are known to deteriorate during aging, modulate suppression effects. Although dual task demands overall triggered an increase in tactile suppression, they did not significantly contribute to the observed age effect. Thus, secondary cognitive task demands increase the weighting of predictive signals putatively by withdrawing processing resources from sensory input but do not specifically drive age-related changes. In contrast, we determined a strong association of suppression effects with individual executive functions so that they qualify for driving age differences in tactile suppression. Our findings highlight the role of executive functions for weighting predictive and sensory information during movement control (compare also Chang, Shibata, Andersen, Sasaki, & Watanabe, 2014;

Monge & Madden, 2016) and elaborate complex interactions between cognition and action. We conclude that the fine tuning of forward model function is subject to significant age effects that are linked to declining executive resources (compare with Vandevoorde & Orban de Xivry, 2018). It remains to be clarified whether increased reliance on predictions provides a beneficial adaptive mechanism, i.e., compensation for declining sensory capacities, or can also be detrimental to behavioral control because over-reliance on predictions might hamper plasticity.

Keywords: healthy aging, individual differences, sensory attenuation, movement control, executive functions

Acknowledgments

Commercial relationships: none.
Corresponding author: Lena Klever.
Email: Lena.Klever@psychol.uni-giessen.de.
Address: Experimental Psychology, Justus Liebig University Giessen, Germany.

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