In normal ageing, structural and functional changes in the brain lead to an altered processing of sensory stimuli and to changes in cognitive functions. The link between changes in sensory processing and cognition is not well understood, but physical fitness is suggested to be beneficial for both. We recorded event-related potentials to somatosensory and auditory stimuli in a passive change detection paradigm from 81 older and 38 young women and investigated their associations with cognitive performance. In older adults also associations to physical fitness were studied. The somatosensory mismatch response was attenuated in older adults and it associated with executive functions. Somatosensory P3a did not show group differences, but in older adults, it associated with physical fitness. Auditory N1 and P2 responses to repetitive stimuli were larger in amplitude in older than in young adults. There were no group differences in the auditory mismatch negativity, but it associated with working memory capacity in young but not in older adults. Our results indicate that in ageing, changes in stimulus encoding and deviance detection are observable in electrophysiological responses to task-irrelevant somatosensory and auditory stimuli, and the higher somatosensory response amplitudes are associated with better executive functions and physical fitness.
Somatosensory change detection paradigms and their associations with ageing are less studied than their auditory counterparts. Only one study has applied the somatosensory mismatch response (sMMR) to investigate age-related changes in older adults. In the study, it was found that the sMMR to electrical pulses applied to different fingers was altered in a group of healthy older adults compared to young adults\(^ \text{28} \). The sMMR was evident in young adults in early and late latency ranges (180–220 ms and 250–290 ms after stimulus onset, respectively), while the early sMMR was absent and the late sMMR was attenuated in older adults. In addition to MMN, other ERP components elicited in the passive oddball condition—N1, P2, and P3a—are shown to be sensitive to ageing\(^ \text{27, 29} \). Auditory N1 reflects automatic stimulus encoding and is elicited in the auditory cortex approximately 100 ms after tone onset\(^ \text{10} \). A recent study reported increased N1 responses to repetitive standard stimuli in older compared to young adults, reflecting an age-related decrease in sensory inhibition\(^ \text{31} \). P2, which is mostly studied in the auditory modality and typically peaks at around 150–250 ms post-stimulus, is involved in stimulus classification and the processing of task-irrelevant stimuli\(^ \text{32, 33} \). The effects of ageing on P2 are inconclusive. Notably, the only study reporting age-related decrease of P2 amplitude to frequency changes\(^ \text{34} \) used a passive oddball condition, where stimuli are outside of the attention of the participant. The studies reporting the opposite effects\(^ \text{35, 36} \) or no effects related to ageing\(^ \text{37, 38} \) used active oddball tasks, where the stimuli are attended to. In a passive oddball condition, P3a peaks at approximately 250–500 ms and usually has a fronto-central scalp topography. This reflects the automatic re-orienting of attention that follows the pre-attentive auditory cortex approximately 100 ms after tone onset\(^ \text{30} \). A recent study reported increased N1 responses to repetitive standard stimuli in older compared to young adults, reflecting an age-related decrease in sensory inhibition\(^ \text{31} \).

| Mean amplitude (µV) ± SD | Mean difference | Age group main effect | Age group effect with stimulus intensities as covariates |
|--------------------------|----------------|----------------------|--------------------------------------------------------|
|                          | Young          | Older                | F (df, error df) | p           | η\(^2\)  | F (df, error df) | p           | η\(^2\)  |
| P50                      |                |                      |                |             |         |                |             |         |
| std                      | 0.58 ± 0.45    | 0.83 ± 0.60          | 0.23 [0.10]    | 4.57 (1,117) | 0.035*  | 0.38 (1,115)   | 0.638       |<0.001  |
| dev                      | 0.82 ± 0.51    | 1.24 ± 0.75          | 0.42 [0.12]    | 9.55 (1,117) | 0.002** | 0.075         | 0.30 (1,115) | 0.592   |<0.003  |
| N80                      |                |                      |                |             |         |                |             |         |
| std                      | 0.06 ± 0.41    | 0.42 ± 0.48          | 0.37 [0.08]    | 16.77 (1,117) |<0.001*** | 0.125 (1,115) | 0.074       | 0.028   |
| dev                      | 0.30 ± 0.70    | 0.62 ± 0.61          | 0.32 [0.13]    | 6.56 (1,117) | 0.012*  | 0.053         | 0.88 (1,115) | 0.350   |<0.008  |

Table 1. Results of ANCOVA of early somatosensory ERP components in response to deviant and standard stimuli in younger and older adult groups. Stimulus intensities for little finger and forefinger were used as covariates. SEM, standard error of mean; SD, standard deviation; df, degrees of freedom; η\(^2\), partial eta squared; p, statistical significance; \*p < 0.05; \**p < 0.01; \***p < 0.001.

| Age group Main effect | Stimulus type Main effect | Stimulus type \(×\) Age group Interaction |
|----------------------|--------------------------|--------------------------------------|
| F (df, error df)    | p                        | η\(^2\)                                    |
| sMMR                 | 2.73 (1,117)             |<0.001***                                  |
| p3a                  | 0.32 (1,117)             | 0.025                                    |
| N1                   | 16.52 (1,117)            |<0.001***                                  |
| aMMN                 | 1.93 (1,117)             | 0.124                                    |
| P2                   | 1.72 (1,117)             | 0.015                                    |
| F (df, error df)    | p                        | η\(^2\)                                    |
| sMMR                 | 24.57 (1,117)            |<0.001***                                  |
| p3a                  | 83.40 (1,117)            |<0.001***                                  |
| N1                   | 324.09 (1,117)           |<0.001***                                  |
| aMMN                 | 127.35 (1,117)           |<0.001***                                  |
| P2                   | 44.20 (1,117)            |<0.001***                                  |
| F (df, error df)    | p                        | η\(^2\)                                    |
| sMMR                 | 5.24 (1,117)             | 0.024*                                    |
| p3a                  | 0.12 (1,117)             | 0.730                                    |
| N1                   | 10.63 (1,117)            | 0.001***                                  |
| aMMN                 | 0.37 (1,117)             | 0.541                                    |
| P2                   | 11.65 (1,117)            | 0.001***                                  |

Table 2. Results of the two-way repeated measures MANOVA of later somatosensory and auditory ERP components in response to deviant and standard stimuli in younger and older adult groups. Df, degrees of freedom; η\(^2\), partial eta squared; p, statistical significance; \*p < 0.05; \**p < 0.01; \***p < 0.001.

Results

Early somatosensory ERP components. P50 and N80 peak amplitudes were analysed due to apparent differences in grand-average waveforms between the age groups (Fig. 1). The mean amplitude of P50 and
N80 were larger in older participants than in young participants for both standard and deviant stimuli (Table 1, Fig. 1a). Within both age groups, the amplitudes of P50 and N80 were larger for deviants than for standards. The age differences on P50 and N80 were not significant after controlling for the stimulus intensities, indicating that the group differences are due to higher stimulus intensities in older adults than in young adults (Table 1). The

Figure 1. (A) Grand-averaged ERPs to somatosensory standard and deviant stimuli for young and older adults and (B) the differential waveforms (standard minus deviant) for young and older adults. Waveforms represent averages of the electrode pools applied in the analyses. The grey area shows the latency range of 153–193 ms for sMMR and of 258–358 for sP3a, from where the averaged amplitude values were extracted to analyse each ERP component. (C) The scalp voltage distributions of responses to standard (std) and deviant (dev) stimuli and differential responses (diff) (deviants minus standards). The topographic maps are shown as average voltages from 153–193 ms for sMMR and from 258–358 for sP3a. Note, due to keeping the scaling equal throughout, the lateralisation of differential response in older adults is no longer observable in the scalp topography of sMMR.
Table 3. Mean amplitude values and standard deviations and results of the independent samples t-tests (two-tailed, bootstrapped with 1000 iterations) comparing the response amplitudes between the groups of young and older adults in the later somatosensory and auditory ERP components in response to standard and deviant stimuli. SEM, standard error of mean; SD, standard deviation; CI, confidence interval; d, Cohen’s d; df, degrees of freedom; p, statistical significance; *p < 0.05; **p < 0.01; ***p < 0.001.

| Component | Young Mean ± SD | Older Mean ± SD | Mean [SEM] | 95% CI | t (df) | p | d |
|-----------|----------------|----------------|------------|--------|--------|---|---|
| sMMR std  | 0.26 ± 0.40    | 0.26 ± 0.35    | <0.01 [0.07]| -0.14  | to 0.15| 0.01 (117)| 0.992 | 0.02 |
|           | dev            | 0.70 ± 0.74    | 0.42 ± 0.63| 0.28    | [0.14]| 0.01 to 0.56| 2.16 (117)| 0.043* | 0.40 |
| aN1 std   | 0.62 ± 0.74    | -0.16 ± 0.70   | 0.78 [0.15]| 0.48    | to 1.08| 5.54 (117)| 0.001***| 1.02 |
|           | dev            | -1.36 ± 0.85   | 0.25 [0.15]| -0.06   | to 0.53| 1.57 (117)| 0.105 | 0.30 |
| aP2 std   | -0.18 ± 0.45   | 0.18 ± 0.39    | 0.36 [0.08]| 0.19    | to 0.52| 4.48 (117)| 0.001***| 0.83 |
|           | dev            | 0.43 ± 0.56    | 0.16 [0.15]| -0.12   | to 0.47| 1.27 (117)| 0.298 | 0.23 |

Later somatosensory and auditory ERP components. Topographic maps for somatosensory responses (Fig. 1) show a positive polarity sMMR and sP3a similar to those reported earlier in the somatosensory modality. sMMR topography illustrated contralaterally localised positivity for standard and deviant stimuli in both age groups although lower amplitude in the older group. In the group of young adults, both sMMR and sP3a to deviant stimuli elicited activity at fronto-central electrode sites, while in the older adults the activation was prominent only in central electrode sites.

Topographic maps for the auditory responses show typical aN1 and aP2 responses with most of the activity in the frontal electrode sites (Fig. 2). There were no clearly observable differences in auditory grand-averaged topographies between the groups other than those caused by an amplitude difference in the standard response (Fig. 2).

A two-way repeated measures multivariate analysis of variance (MANOVA) revealed the main effect of age group for amplitude values in the sMMR time window (mean for young adults, 0.48 μV; mean for older adults, 0.36 μV; amplitude values averaged for the standard and deviant stimuli) and aN1 time window (mean for young adults, 0.25 μV; mean for older adults, -0.76 μV; amplitude values averaged for the standard and deviant stimuli) (Table 2, Figs 1 and 2). For all components—sMMR, sP3a, aN1, aMMN, and aP2u—the main effect of stimulus type was found, indicating that the amplitudes to the deviant stimuli were larger than those to the standard stimuli for all components (Table 3, Figs 1 and 2). An interaction effect of stimulus type × age group was found for sMMR, aN1, and aP2 (Table 2, Figs 1 and 2). The following independent samples t-tests (two-tailed, bootstrap statistics) showed that the deviant responses in the sMMR analysis window were attenuated and that the standard responses for aN1 and aP2 were enlarged in older adults compared to young adults (Table 3). The interaction effect of stimulus type × age group for sMMR remained significant after controlling for stimulus intensity (p = 0.019); similarly, the interaction effect for aP2 was significant when controlling for hearing threshold (p = 0.005), but hearing threshold as a covariate decreased the p value of the interaction effect of stimulus type × age group for aN1 (p = 0.055).

Relationships between ERPs, cognitive test scores, and physical fitness measures. Table 4 illustrates the significant correlations within 95% and 99% confidence intervals (CIs). In older adults, the most robust positive correlations (within 99% CI) were found between sMMR and executive functions and between sP3a and walk test performance. These correlations in older adults remain significant (p < 0.05, 99% CI does not include zero) after controlling for age but not for education. Within the young adult group, a robust positive correlation was found between the aMMN and working memory, which remained significant after controlling for age and education (Table 4). In older adults, aMMN correlated neither with any of the cognitive measures nor with physical fitness measures.

The walk test performance had a robust negative correlation with total body fat percentage in older adults (two-tailed Pearson’s r = −0.523, n = 79, p < 0.001, 99% CIs = −0.732 to −0.267) and body mass index (BMI) (r = −0.462, p < 0.001, 99% CIs = −0.683 to −0.199) and positively correlated with the self-reported weekly physical activity hours (Spearman’s rho = 0.481, n = 74, p < 0.001, 99% CIs = 0.220–0.687).
Discussion

We measured the ERPs to auditory frequency and somatosensory location changes in an ignore condition in young and older adults. The somatosensory P50, N80, and sMMR and the auditory aN1 and aP2 differed in amplitude between the groups. As expected, within the older group, higher sMMR amplitude showed a robust association with better executive functions, and higher sP3 amplitude was associated with longer walking distance (CI 99%, Table 4). There were also correlations between the auditory brain responses and tapping speed and explicit memory within the older group, but these associations were less robust (CI 95%, Table 4).

Somatosensory MMR was observed as a shift toward positive polarity at 153–193 ms in both age groups, which is in line with prior findings. The differential response was larger in the young group than in the older group due to a larger deviant stimulus response amplitude in the young group, as was found in our earlier study.

Figure 2. (A) Grand-averaged ERPs to auditory standard and deviant stimuli for young and older adults and (B) the differential waveforms (standard minus deviant) for young and older adults. Waveforms represent averages of the electrode pools applied in the analyses. The grey area shows the latency range of 88–138 ms for aN1, of 139–189 ms for aMMN, and of 208–280 ms for aP2, from where the averaged amplitude values were extracted to analyse each ERP component. (C) The scalp voltage distributions of responses to standard (std) and deviant (dev) stimuli and differential responses (diff) (deviant minus standard). The topography maps are shown as average voltages from 88–138 ms for aN1, 139–189 ms for aMMN, and 208–280 ms for aP2.
Table 4. Correlations between cognitive and physical measures and ERPs. Variables that show correlation at least in one of the groups within 95% CI are listed; those showing significant correlation within 99% CI are marked with *. Age and/or education (edu) in parentheses refers to significant partial correlations after controlling for the mentioned variable. r, Pearson's correlation coefficient (bootstrap statistics with 1000 iterations); p, significance (one-tailed); CI, confidence interval; ns, non–significant; —, not measured within the young adult group.

| Test                                | Older adults                  | Young adults                  |
|-------------------------------------|-------------------------------|------------------------------|
|                                     | Variable                      | r, p                         | 99% CI                        | 95% CI                        | r, p                         | 99% CI                        | 95% CI                        |
|                                     | sMMR (age)                    | 0.259*                       | 0.004                         | 0.001 to 0.594                | 0.035 to 0.524               | ns                           | ns                           | ns                           |
|                                     | sP3a                           | 0.359                        | 0.017                         | —0.62 to 0.517                | 0.003 to 0.468               | ns                           | ns                           | ns                           |
|                                     | Six-minute walk distance (age, edu) | 0.203 | 0.036 | —0.076 to 0.443 | 0.011 to 0.395 | — | ns | ns | ns |
|                                     | Error susceptibility PC       | —0.276                       | 0.007                         | —0.491 to 0.021               | —0.465 to —0.055             | ns                           | ns                           | ns                           |
|                                     | Explicit memory PC            | —                            | —                             | —                              | —                             | ns                           | ns                           | ns                           |
|                                     | Working memory PC             | —                            | —                             | —                              | —                             | ns                           | ns                           | ns                           |
|                                     | sMMR (edu, age)               | —                            | —                             | —                              | —                             | ns                           | ns                           | ns                           |
|                                     | sP3a                           | 0.354                        | 0.012                         | —0.25 to 0.508                | 0.025 to 0.439               | ns                           | ns                           | ns                           |
|                                     | Six-minute walk distance      | —                            | —                             | —                              | —                             | ns                           | ns                           | ns                           |
|                                     | Tapping speed – dominant hand | sP3a                         | 0.272                        | 0.008                         | —0.099 to 0.533               | 0.034 to 0.478               | ns                           | ns                           | ns                           |
|                                     |                                 | sMMR                         | 0.215                        | 0.028                         | —0.064 to 0.463               | 0.017 to 0.393               | ns                           | ns                           | ns                           |
|                                     |                                 | aMMN                         | —0.229                       | 0.021                         | —0.477 to 0.033               | —0.417 to —0.032             | 0.417                         | 0.005                         | —0.026 to 0.715               | 0.116 to 0.658               |
|                                     | Tapping speed – non-dominant hand | sP3a                         | 0.298                        | 0.004                         | —0.019 to 0.600               | 0.067 to 0.520               | ns                           | ns                           | ns                           |
|                                     | sN1 (age)                     | —0.252                       | 0.013                         | —0.481 to 0.009               | —0.436 to —0.058             | ns                           | ns                           | ns                           |
|                                     | sMMN                           | ns                           | ns                            | ns                             | ns                           | ns                           | ns                           | ns                           |

probably indicating attenuated deviance detection in older adults. Since the deviance detection the mismatch response reflects is suggested to be a cortical process, the changes in the sMMR can be expected to be related to the function of the somatosensory cortex. For sP3a, no group differences were found, and the deviant vs. standard differential response was significant in both groups. The pattern of results in the somatosensory modality showing attenuated sMMR, but no changes in amplitude of sP3 suggest that change detection, but not the following automatic shift of attention, is affected in ageing. It is notable, however, that the response latency of sP3a seems to be delayed in the older adults compared to young adults, but the data did not allow a valid statistical analysis to investigate this difference since there were no clear peak for sP3a for each individual, and mean amplitude values were thus applied in the analysis.

In addition to longer latency components, the amplitudes of the early somatosensory P50 and N80 were also larger in the older group than in the young group. This was mainly explained by higher sensory thresholds and thus higher stimulus intensities in older than younger participants. The result cannot be directly compared with the previous results where stimulus conditions (oddball vs. paired-pulse condition) and stimulus properties have been different between the studies. When comparing the ageing-related findings between the two modalities it is notable that the somatosensory change detection, as indexed by the mismatch response, was altered in older adults while there was no such indication in the auditory modality. The somatosensory mismatch response thus seems to be more sensitive in indicating the ageing-related sensory decline than its auditory counterpart. On the other hand, in the auditory modality, ageing-related alterations were observed in response amplitudes of the N1 and P2 components that reflect stimulus encoding. For these components, increased amplitudes in older compared to young adults were found, reflecting that N1 and P2 are indicative of the altered cortical suppression in older adults. There was no evidence on age-related changes in the functioning of the attention shift mechanism towards stimulus changes.
The auditory stimuli elicited no clear P3a, and therefore ageing-related effects on P3a could not be studied.

Somatosensory, but not auditory, ERP amplitudes correlated robustly (99% CI) with cognitive performance (larger sMMR was associated with better executive functions) and physical fitness (larger sP3a was associated with longer walking distance) in older adults. A less substantial positive correlation was found between executive functions and walking distance. Thus far, no studies have investigated the relationships between ERPs elicited by somatosensory oddball stimuli and both cognition and physical fitness. However, a recent study demonstrated that sMMR is a sensitive indicator of long-term physical activity in young adults. The study compared the brain responses to somatosensory oddball stimuli and both cognition and physical fitness. However, a recent study demonstrated that sMMR is a sensitive indicator of long-term physical activity in young adults. The study compared the brain responses to somatosensory oddball stimuli and both cognition and physical fitness. However, a recent study demonstrated that sMMR is a sensitive indicator of long-term physical activity in young adults. The study compared the brain responses to somatosensory oddball stimuli and both cognition and physical fitness.

The auditory stimuli elicited no clear P3a, and therefore ageing-related effects on P3a could not be studied.

Somatosensory, but not auditory, ERP amplitudes correlated robustly (99% CI) with cognitive performance (larger sMMR was associated with better executive functions) and physical fitness (larger sP3a was associated with longer walking distance) in older adults. A less substantial positive correlation was found between executive functions and walking distance. Thus far, no studies have investigated the relationships between ERPs elicited by somatosensory oddball stimuli and both cognition and physical fitness. However, a recent study demonstrated that sMMR is a sensitive indicator of long-term physical activity in young adults. The study compared the brain activity of male twin pairs with discordant physical activity. The more active twin, who also had higher aerobic capacity and lower body fat percentage, produced a lower peak amplitude sMMR. The authors interpreted that active young adults showed better gating of deviant sensory stimuli. In the current study within the older adult group, however, better performance in the walk test was associated with higher sP3a and sMMR amplitude, but there was no correlation with ERPs that more directly reflect sensory gating, namely P50 and N80. Direct comparison of Tarkka et al. with the current data is also hampered by the different methodology to analyse sMMR. Furthermore, P50 and N80 were not analysed in their data and thus the results concerning these components remain open.

Previous aMMN studies with older participants, which employed duration changes as stimuli, reported a correlation between the aMMN amplitude and executive functions and working memory. In our data, aMMN to frequency deviations showed no correlations to cognitive tests in older adults. However, within the young adult group, the aMMN amplitude correlated robustly (99% CI) with working memory performance, possibly indicating that a well-functioning auditory sensory memory supports working memory. Since the age groups differed in working memory but not in aMMN, it suggests that decline in working memory functions may precede alterations of the auditory sensory memory in ageing. However, it is possible that the short ISI applied here was not the most optimal in revealing possible ageing-related alterations in the sensory memory. Additionally, aMMN showed some association (95% CI) with psychomotor speed (finger tapping test) in both age groups, although the results are inconclusive due to opposite direction correlations between the age groups.

Better performance in the walk test was associated with cognitive functions requiring executive control in older adults. This finding is congruent with the findings of a meta-analysis, which showed that higher physical fitness is associated with better executive functions in older adults. Better performance in the six-minute walk...
test was associated with a lower body fat percentage, lower BMI, and higher self-reported physical activity levels, indicating that the six-minute walk test was a suitable objective measure of sub-maximal exercise in older adults.55

There are some limitations to the present study. A part of the sample of older females was initially recruited for a physical exercise intervention study, which may mean these participants were on average more active than other participants of their age. However, this was balanced by recruiting about the same number of physically passive older females. Obviously, the results of the present study apply to women only. It is also worth noting that the age range in the older group (18 years) is wider than that within the young group (10 years) although most of the results remain stable after controlling the analyses for age (see Table 4). One limitation is that the somatosensory stimulus intensities were adjusted individually, but the auditory stimulus intensities were constant between the participants. Individual adjustment of the somatosensory stimulus intensities is important because it is difficult to find a fixed intensity that is not painful for someone and still discriminable for all participants. Since the ERPs were measured to frequency and location changes, not to intensity changes, it might not be critical that the intensities of the auditory stimuli were of individually adjusted. Importantly, most of the results remained the same when controlling the analyses of the somatosensory brain responses for stimulus intensities and of auditory brain responses for hearing thresholds.

Due to the lack of participants’ individual MRI data and suitable head models for the two relatively distant age groups, our data do not allow source analysis to compare the neural generators of the analysed brain responses between the age groups. In the grand average level, the topographies of the electrical fields of the two groups were relatively similar. Future studies should investigate whether the sources of the responses between the age groups are different.

In conclusion, ageing affects the preattentive processing of somatosensory and auditory stimuli. The sMMR indicated attenuated change detection in older adults. The long latency somatosensory brain responses were also associated with executive functions (sMMR) and physical fitness (sP3a). In the auditory modality, brain responses showed an altered encoding of sensory information in older adults, as reflected by larger standard stimulus sN1 and aP2a responses in older than young adults. Together these results suggest that ageing-related cognitive decline is observable both in cortical sensory responses and in behaviour and that physical fitness can help preserve executive functions during ageing.

### Methods

**Participants.** Experiments were carried out in spring 2013 and summer 2014 at the University of Jyväskylä. Data were collected from 131 (41 young and 90 older) healthy females. The data of three young and nine older participants were excluded from further analyses due to contaminated electroencephalography (EEG) data or due to a lack of behavioural data or fitness assessment, resulting in the analysis of a total of 38 young and 81 older women. The ages of the young and older participants ranged from 20–30 (mean ± SD, 23.6 ± 2.8) years and 63–81 (68.1 ± 4.4) years, respectively. In terms of educational background, the percentage of young and older adults, respectively, who had completed elementary school only was 1 and 11%; 34 and 46% had completed secondary school only; 26 and 46% had completed lower tertiary school or bachelor’s degrees only; and 37 and 31% had completed master’s degrees or higher academic degree. All participants were right-handed and lacked any history of neurological illnesses or brain operations. The older participants were recruited from the University of the Third Age in Jyväskylä and the Society of the Retired in Jyväskylä as well as through an announcement in the local newspaper. Participants for the 2013 data collection were recruited for a larger study investigating the effectiveness of a 10-week physical exercise intervention. Here, we reported the results of their baseline measurements. For the 2014 data collection, participants who do not exercise regularly or at all were recruited for a single-day measurement. Young adult participants were recruited from the mailing lists of the University of Jyväskylä’s students’ association. Ethical approval for the study was obtained from the ethical committee of the Central Finland Health Care District. Written informed consent was collected from all participants, and all were given either a movie ticket or coffee package as compensation for their efforts. The experiments were undertaken in accordance with the Declaration of Helsinki.

| Sensory threshold and intensity | Young mean ± SD | Older mean ± SD | Mean difference (95% CI) | p   | d   |
|-------------------------------|----------------|----------------|--------------------------|-----|-----|
| Somatosensory                 |                |                |                          |     |     |
| Forefinger threshold (mA)     | 15.8 ± 2.8     | 24.2 ± 6.7     | 8.4 (6.7 to 10.1)        | 0.001 | 1.38 |
| Little finger threshold (mA)  | 15.5 ± 3.3     | 22.9 ± 6.1     | 7.7 (6.2 to 9.2)         | 0.001 | 1.33 |
| Forefinger intensity (mA)     | 31.3 ± 6.0     | 48.3 ± 13.5    | 17.4 (13.5 to 20.3)      | 0.001 | 1.37 |
| Little finger intensity (mA)  | 30.4 ± 5.2     | 45.2 ± 11.7    | 14.9 (11.6 to 17.6)      | 0.001 | 1.38 |
| Auditory                      |                |                |                          |     |     |
| Hearing threshold right ear 1000Hz (dB) | 3.3 ± 0.2 | 15.9 ± 12.2 | 12.6 (9.7 to 16.4) | 0.001 | 1.24 |
| Hearing threshold right ear 500 Hz (dB) | 8.2 ± 3.5 | 21.4 ± 13.3 | 13.2 (10.3 to 16.8) | 0.001 | 1.44 |
| Hearing threshold left ear 1000Hz (dB) | 5.1 ± 1.3 | 13.1 ± 11.8 | 8.0 (6.5 to 14.0) | 0.001 | 0.90 |
| Hearing threshold left ear 500Hz (dB) | 12.9 ± 6.7 | 23.4 ± 13.4 | 10.5 (7.3 to 14.6) | 0.001 | 0.90 |

Table 6. Sensory thresholds and stimulus intensities. The differences between age groups were tested with independent samples t-tests (two-tailed, bootstrap statistics). SD, standard deviation; CI, confidence interval; p, statistical significance; d, Cohen’s d.
**Cognitive tests.** Participants’ cognitive performance was assessed with cognitive tests selected to encompass domains sensitive to cognitive ageing, including executive functions, perceptual speed, and verbal memory (see Supplementary Table S1). Tests were administered by a psychologist or a trained research assistant during a 60-minute session. The characteristics, including cognitive test scores, of the sample are summarised in Table 5.

**Assessment of physical fitness.** Three measures were used to assess physical fitness among the older adults: BMI, total body fat percentage, and a six-minute walk test\(^6\). Only BMI was calculated for the young adults. Participants completed all the measures during one day within two weeks of the behavioural tests and EEG experiments. BMI was calculated according to the following formula: $\text{BMI} = \frac{\text{mass (kg)}}{\text{height (m)}^2}$. Total body fat percentage was measured using dual-energy X-ray absorptiometry (DXA) (Delphi QDR series, Hologic, Bedford, MA, USA) to estimate boneless and muscleless body tissue. Participants were instructed to avoid eating just before the DXA measurement. During the scan, participants lay still on the device for approximately 10 minutes. After the DXA, the participants took part in a six-minute walk test on a 200-metre indoor track, where they were instructed to walk as far as they could for six minutes, and their heart rate was monitored after every minute. The self-reported physical activity was assessed by a five-scale question of weekly hours of medium-intensity (inducing perspiration) activity, as follows: <1, 1–2, 2–3, 3–4, and >5 hours.

**Stimuli and procedure.** During the EEG recording, the participant was seated in a chair in an electrically shielded, dimly lit room and monitored via a video camera. The participants were instructed to avoid all additional body movement, facial expressions, talking, and excessive head movement; to not pay any attention to any stimuli; and to be engaged in the silent movie that was played on a screen at a distance of about 1.5 metres. In both auditory and somatosensory experiments, a run of 1000 stimuli of two types varying in either location (somatosensory) or frequency (auditory) was delivered with a randomly varying stimulus onset asynchrony (SOA) of 400, 450, or 500 ms. The relatively short SOA was selected based on our earlier findings showing ageing-related changes in the amplitude of the sMMR with ISI of 500 ms\(^2\) providing thus a solid basis for the cross-modal investigation. In an oddball condition, ‘standard’ stimuli were frequently presented at a probability of 86%, and rare ‘deviant’ stimuli were presented at a probability of 14%. The somatosensory stimuli were always presented first followed by the auditory stimuli.

Somatosensory stimulation was generated with a constant current stimulator (Digitimer Ltd, model DS7A, Welwyn Garden City, UK). Electrical pulses of 200 µs were delivered via flexible metal ring electrodes moistened with conductive jelly (Technomed Europe Ltd, Maastricht, Netherlands) to the left forefinger and little finger; stimulating the cathode above the proximal phalanx and the anode above the distal phalanx. A piece of gauze was placed on the finger between the electrodes to prevent conductivity between the two electrodes in the same finger. Both fingers, forefinger and little finger, were applied standard and deviant stimuli in all participants with a counterbalanced order across the participants. Stimulus intensities were adjusted independently for each participant, and for both stimulated fingers, by double the intensity of the subjective sensory threshold. The subjective thresholds were determined by stimulating the individual fingers and asking the participants to verbally report when they sensed the stimulation. The stimulation began with very low intensities, continued with higher intensities step by step (in steps of 0.1 mA), and eventually went over the somatosensitivity threshold. The procedure was repeated three times and applied separately for both stimulated fingers. Overall, the stimulus intensities for both forefinger and little finger were greater in the older adults than in the young participants (Table 6), similar to our earlier study\(^7\) and in line with earlier findings\(^2\).

The auditory stimuli were sinusoidal sounds 50 ms in duration with a 10-ms onset and offset time, presented from a loudspeaker placed 90 cm above the participant, at an intensity of 75 dB (sound pressure level [SPL]) and at a frequency of either 1000 Hz or 750 Hz. Both frequencies were applied as standard and deviant stimuli in all participants in a counterbalanced order across the participants. Individual hearing thresholds for 500 and 1000 Hz separately for both ears were tested prior to the experiment with an audiometer (Medrill SA-51, Medrill Ltd, Debrecen, Hungary) by starting from very low intensities, going stepwise (5 dB) over the hearing threshold and lowering the intensity again well below the hearing threshold reported by the participant. This procedure was repeated three times and the lowest threshold was recorded. The hearing threshold level was generally higher among the older group than in the young group (Table 6).

**Electroencephalography.** The EEG was recorded using a high-impedance amplifier and the 128-channel EGI Sensor Net (Electrical Geodesics Inc., Hydrogel GSN 128, 1.0). Impedances were kept below 80 kΩ throughout the experiment. The sampling rate was 1000 Hz, and data were filtered online from 0.1 to 400 Hz. During the recording, the vertex electrode (Cz) was used as the reference electrode.

**EEG data processing.** Brain Vision Analyzer 2.0 software was used to analyse the data (Brain Products Gmbh). Eye blinks were removed using the Gratton & Coles method\(^8\), and channels with excessive noise and insufficient skin contact were interpolated using a spherical spline model. Offline, an average reference was applied. The electrode signals were filtered with a low cut-off of 0.1 Hz and a high cut-off of 20 Hz, both with 24 dB/octave roll-off. In addition, a 50-Hz notch filter was applied. Then, extensively large amplitude values, outside −100 to 100 µV from peak to peak, in the EEG data were rejected, and low activity periods (<0.5 µV of change within a 100-ms range) were removed. The average number of included trials (with responses to deviant and preceding standard stimuli) in the auditory experiment were 134 (min. 83, max. 150) for the older and 134 (min. 110, max. 150) for the young adults and for the somatosensory experiment 132 (min. 83, max. 150) for the older and 134 (min. 106, max. 150) for the young adults. Stimulus-locked time windows of 600 ms, from 200 ms...
prior to stimulus onset to 400 ms after the stimulus onset, were extracted. A pre-stimulus onset time of 200 ms was determined as a baseline.

Although previous studies have not shown age group differences in the somatosensory oddball condition for the early components (P50, N80)\(^6\), a visual inspection of the current data indicated potential group differences for P50 and N80. Accordingly, the maximum peak amplitudes at the C4 electrode\(^1\) and its latency were extracted from time windows of 30–80 ms (P50) and 40–110 ms (N80) after stimulus onset.

To select the regions of interests (time windows and electrode sites) for each of the later ERP components (sMMR, sP3a, aN1, aMMN, and aP2), permutation tests\(^59\) (4000 permutations) were performed as implemented in BESA Statistics 1.0 software (BESA GmbH) starting with all 128 electrode locations. This process was used to compare the average responses of standard and deviant stimuli in the group of young adults, which was considered a reference group for the older adult group. The time windows were defined by first finding the time point with the highest t-value for each component and then using this time point as the centre of the time window. A 40-ms time window was applied for sMMR, a 50-ms window was applied for aN1 and aMMN, a 72-ms window was applied for aP2, and a 100-ms window was applied for sP3a (see Supplementary Figure S2). The width of the time window was set taking into account the latency of the differential response based on a visual inspection of the grand-averaged waveforms. The applied time windows were 153–193 ms after stimulus onset for sMMR, 258–358 ms for sP3a, 88–138 ms for aN1, 139–189 ms for aMMN, and 208–280 ms for aP2. The applied time windows based on permutation tests fitted well to the latencies of the differential responses as charged by visually observing the grand average waveforms.

The electrodes for the analysis were selected by first finding the electrode with the highest t-value in the middle of the each selected time window and then defining the surrounding electrodes (see Supplementary Figure S2). The activity of the electrodes within the region of interest was averaged.

The regions of interests were defined based on the data of the young adults, and the same time windows and electrode locations were used in the analysis for the older participants, since there were no substantial differences between the groups.

**Statistical analysis.** To compare differences in the peak amplitude and latency of somatosensory P50 and N80 between the age groups, univariate analysis of variances (ANOVA) was applied.

Due to higher sensory thresholds and thus higher stimulus intensities in the older than in the young adults, univariate analysis of covariates (ANCOVA), was also applied using stimulus intensities to forefinger and little finger as covariates. For the other ERP components, repeated measures MANOVA was used to assess differences in response amplitudes to stimulus types (standard, deviant) between the age groups separately for each response (sMMR, sP3a, aN1, aMMN, and aP2). Stimulus type (standard vs. deviant) was applied in the analysis order to investigate whether possible group differences are associated specifically to one or both of the stimulus types (see also Fig. 8 in\(^60\)). The mean amplitude values from the component-specific electrode pools were applied in the analysis (see Supplementary Figure S2). For these latter components, response latencies were not analysed because it was not always possible to find clear peaks for each individual and both stimulus types. The same analyses were also run with age and education as covariates.

Whenever a stimulus type × age group interaction was found, differential ERPs (deviant minus standard responses) were calculated separately for the young and older participants, and independent samples t-tests (two-tailed, bootstrap statistics with 1000 iterations) were performed to compare the standard and deviant responses between the groups. Effect size estimates are described as partial eta squared (\(\eta^2\)) for MANOVA and Cohen's \(d\) for t-tests.

A principal component analysis (PCA) was applied to reduce the dimensionality of the cognitive test scores within the whole sample. Following an exploratory analysis, an oblimin with Kaiser normalisation rotated PCA resulted in four components (eigenvalue > 1.0), including the scores from 14 cognitive tests (communalities > 0.600, \(r^2 = 69.4\%\)), which are listed in Table 1. The principal components (PCs) were labelled executive function, error susceptibility, explicit memory, and working memory (see Supplementary Table S3).

One-tailed Pearson's correlation coefficients and partial correlations with age and education as covariates were computed within the age groups to examine the relationships between the ERPs (deviant - standard differential response), the PC scores from the cognitive test scores, and physical fitness measures. Bootstrap statistics were performed with 1000 iterations and CIs of 99% and 95%. The threshold for statistical significance was \(p < 0.05\).

**Data availability.** The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

**References**

1. Raz, N. et al. Regional brain changes in aging healthy adults: General trends, individual differences and modifiers. Cereb. Cortex 15, 1676–1689 (2005).
2. Hedden, T. & Gabrieli, J. D. E. Insights into the ageing mind: a view from cognitive neuroscience. Nat. Rev. Neurosci. 5, 87–96 (2004).
3. Reuter-Lorenz, Pa & Park, D. C. Human Neuroscience and the Aging Mind: A New Look at Old Problems. Journals Gerontol. Ser. B-Psychological Sci. Soc. Sci. 65, 405–415 (2010).
4. Grady, C. The cognitive neuroscience of ageing. Nat. Rev. Neurosci. 13, 491–505 (2012).
5. Rossini, P. M., Rossi, S., Babiloni, C. & Polich, J. Clinical neurophysiology of aging brain: From normal aging to neurodegeneration. Prog. Neurobiol. 83, 375–400 (2007).
6. Näätänen, R. et al. The mismatch negativity: An index of cognitive decline in neuropsychiatric and neurological diseases and in ageing. Brain 134, 3432–3450 (2011).
7. Näätänen, R. et al. The mismatch negativity (MMN) – A unique window to disturbed central auditory processing in ageing and different clinical conditions. Clin. Neurophysiol. 123, 424–458 (2012).
8. Näätänen, R., Astikainen, P., Ruusuvirta, T. & Huotilainen, M. Automatic auditory intelligence: An expression of the sensory-cognitive core of cognitive processes. *Brain Res. Rev.* 64, 123–136 (2010).

9. Näätänen, R. & Alho, K. Mismatch negativity — a unique measure of sensory processing in audition. *Int. J. Neurosci.* 80, 317–337 (1995).

10. Näätänen, R., Gaillard, A. W. K. & Mäntykoski, S. Early selective-attention effect on evoked potential reinterpreted. *Acta Psychol. (Amst)*. 42, 313–329 (1978).

11. Kekoni, J. et al. Rate effect and mismatch responses in the somatosensory system: ERP-recordings in humans. *Biol. Psychol.* 46, 125–142 (1997).

12. Akinsuoka, K. et al. Mismatch responses related to temporal discrimination of somatosensory stimulation. *Clin. Neurophysiol.* 116, 1930–1937 (2005).

13. Shinozaki, N., Yabe, H., Sutoh, T., Hiruma, T. & Kaneko, S. Somatosensory automatic responses to deviant stimuli. *Cogn. Brain Res.* 7, 165–171 (1998).

14. Spackman, L. A., Towell, A. & Boyd, S. G. Somatosensory discrimination: An intracranial event-related potential study of children with refractory epilepsy. *Brain Res.* 1310, 68–76 (2010).

15. Astikainen, P., Lilja, T., & Ruusuvirta, T. Visual mismatch negativity for changes in orientation – A sensory memory-dependent response. *Eur. J. Neurosci.* 28, 2319–2324 (2008).

16. Kimura, M., Schröger, E., Czigler, I. & Ohira, H. Human visual system automatically encodes sequential regularities of discrete events. *J. Cogn. Neurosci.* 22, 1124–1139 (2010).

17. Pause, B. M. & Krauel, K. Chemosensory event-related potentials (CSERP) as a key to the psychology of odors. *Int. J. Psychophysiol.* 36, 105–122 (2000).

18. Cheng, C. H., Hsu, W. Y. & Lin, Y. Y. Effects of physiological aging on mismatch negativity: A meta-analysis. *Int. J. Psychophysiol.* 90, 165–171 (2013).

19. Gaeta, H., Friedman, D., Ritter, W. & Cheng, J. An event-related potential study of age-related changes in sensitivity to stimulus deviance. *Neurobiol. Aging* 19, 447–459 (1998).

20. Alain, C. & Woods, D. L. Age-related changes in processing auditory stimuli during visual attention: Evidence for deficits in inhibitory control and sensory memory. *Psychol. Aging* 14, 513–519 (1999).

21. Cooper, R. J., Todd, J., McGill, K. & Michie, P. T. Auditory sensory memory and the aging brain: A mismatch negativity study. *Neurobiol. Aging* 27, 752–762 (2006).

22. Kiang, M., Braff, D. L., Sprock, J. & Light, G. A The relationship between preattentive sensory processing deficits and age in schizophrenia patients. *Clin. Neurophysiol.* 120, 1949–1957 (2009).

23. Kisley, M., Dauval, D. B., Engleman, L. L., Guinther, P. M. & Davis, H. P. Age-related change in neural processing of time-dependent stimulus features. *Cogn. Brain Res.* 25, 913–925 (2005).

24. Foster, S. M. et al. Cognitive function predicts neural activity associated with pre-attentive temporal processing. *Neuropsychologia* 51, 211–219 (2013).

25. Ruzzoli, M., Pirulli, C., Brignani, D., Maioli, C. & Muntiussi, C. Sensory memory during physiological aging indexed by mismatch negativity (MMN). *Neurobiol. Aging* 33, 625.e21–625.e30 (2012).

26. Strömmer, I. M., Tarkka, I. M. & Astikainen, P. Somatosensory mismatch response in young and elderly adults. *Front. Aging Neurosci.* 6, 1–9 (2014).

27. Crowley, K. E. & Colrain, I. M. A review of the evidence for P2 being an independent component process: Age, sleep and modality. *Psychophysiology* 41, 732–744 (2004).

28. Friedmann, D., Cycowicz, Y. M. & Gaeta, H. The novelty P3: An event-related brain potential (ERP) sign of the brain’s evaluation of novelty. *Neurosci. Biobehav. Rev.* 25, 355–373 (2001).

29. Tome, D., Barbosa, E., Nowak, K. & Marques-Texeira, J. The development of the N1 and N2 components in auditory oddball paradigms: a systematic review with narrative analysis and suggested normative values. *J. Neural Transm.* 122, 375–391 (2015).

30. Näätänen, R. The role of attention in auditory information processing as revealed by event-related potentials and other brain measures of cognitive function. *Behav. Brain Sci.* 13, 201–233 (1990).

31. Stothart, G. & Karanina, N. Auditory perception in the aging brain: The role of inhibition and facilitation in early processing. *Neurobiol. Aging* 47, 23–34 (2016).

32. Novak, G., Ritter, W. & Vaughan, H. G. Mismatch Detection and the Latency of Temporal Judgments. *Psychophysiology* 29, 398–411 (1992).

33. García-Larrea, L., Łukaszewicz, A. C. & Mauguière, F. Revisiting the oddball paradigm. Non-target vs neutral stimuli and the evaluation of ERP attentional effects. *Neuropsychologia* 30, 723–741 (1992).

34. Czigler, I., Csibra, G. & Csontos, A. Age and inter-stimulus interval effects on event-related potentials to frequent and infrequent auditory stimuli. *Biol. Psychol.* 33, 195–206 (1992).

35. Amenedo, E. & Díaz, E. Aging-related changes in processing of non-target and target stimuli during an auditory oddball task. *Biol. Psychol.* 48, 235–267 (1998).

36. Ford, J. M. & Pfeiferbaum, A. Event-related potentials and eyeblink responses in automatic and controlled processing: effects of age. *Electroencephalogr. Clin. Neurophysiol.* 78, 361–377 (1991).

37. Barrett, G., Neshige, R. & Shibasaki, H. Human auditory and somatosensory event-related potentials: effects of response condition and age. *Electroencephalogr. Clin. Neurophysiol.* 66, 409–419 (1987).

38. Iragui, V. J., Kutras, M., Michiner, M. R. & Hillyard, S. A. Effects of aging on event-related brain potentials and reaction times in an auditory oddball task. *Psychophysiology* 30, 10–22 (1993).

39. Knight, R. T. Ageing decreases auditory event-related potentials to unexpected stimuli in humans. *Neurobiol. Aging* 8, 109–113 (1987).

40. Gaal, Z. A., Coshaw, R. & Molnar, M. Age-dependent changes of auditory evoked potentials – Effect of task difficulty. *Biol. Psychol.* 76, 196–208 (2007).

41. Gaeta, H., Friedman, D., Ritter, W. & Cheng, J. An event-related potential evaluation of involuntary attentional shifts in young and older adults. *Psychol. Aging* 16, 55–68 (2001).

42. Colcombe, S. & Kramer, A. F. Fitness effects on the cognitive function of older adults: A meta-analytic study. *Psychol. Sci. a J. Am. Psychol. Soc./APS* 14, 123–130 (2003).

43. McDowell, K., Kerick, S. E., Santa Maria, D. L. & Hatfield, B. D. Aging, physical activity, and cognitive processing: An examination of P300. *Neurobiol. Aging* 24, 597–606 (2003).

44. Chang, Y.-K., Huang, C.-J., Chen, K.-F. & Hung, T.-M. Physical activity and working memory in healthy older adults: An ERP study. *Psychophysiology* 50, 1174–1182 (2013).

45. Höfting, K. & Röder, B. Beneficial effects of physical exercise on neuropsychology and cognition. *Neurosci. Biobehav. Rev.* 37, 2243–2257 (2013).

46. Davenport, M. H., Hogan, D. B., Eskes, G., Longman, R. S. & Poulin, M. J. Cerebrovascular reserve: The link between fitness and cognitive function? *Exerc. Sport Sci. Rev.* 40, 153–158 (2012).

47. Duzel, E., van Praag, H. & Sendtner, M. Can physical exercise in old age improve memory and hippocampal function? *Brain* 662–673 (2016).
48. Lenz, M. et al. Increased Excitability of Somatosensory Cortex in Aged Humans is Associated with Impaired Tactile Acuity. *J. Neurosci.* **32**, 1811–1816 (2012).

49. Cheng, C. H. & Lin, Y. Y. Aging-related decline in somatosensory inhibition of the human cerebral cortex. *Exp. Brain Res.* **226**, 145–152 (2013).

50. Bolton, D. E. & Staines, W. R. Age-related loss in attention-based modulation of tactile stimuli at early stages of somatosensory processing. *Neuropsychologia* **50**, 1502–1513 (2012).

51. Gaeta, H., Friedman, D., Ritter, W. & Hunt, G. Age-related changes in neural trace generation of rule-based auditory features. *Neurobiol. Aging* **23**, 443–455 (2002).

52. Pekkonen, E. et al. Aging Effects on Auditory Processing: An Event-Related Potential Study. *Exp. Aging Res.* **22**, 171–184 (1996).

53. Pekkonen, E., Jousmäki, V., Partanen, J. & Karhu, J. Mismatch negativity area and age-related auditory memory. *Electroencephalography and Clinical Neurophysiology* **87**, 321–3 (1993).

54. Tarkka, I. M. et al. Long-term physical activity modulates brain processing of somatosensory stimuli: Evidence from young male twins. *Biol. Psychol.* **117**, 1–7 (2016).

55. Du, H., Newton, P. J., Salamonson, Y., Carrieri-Kohlman, V. L. & Davidson, P. M. A review of the six-minute walk test: Its implication as a self-administered assessment tool. *Eur. J. Cardiovasc. Nurs.* **8**, 2–8 (2009).

56. Crapo, R. O. et al. ATS statement: Guidelines for the six-minute walk test. *Am. J. Respir. Crit. Care Med.* **166**, 111–117 (2002).

57. Kemp, I., Despréz, O., Pechayl, T. & Dufour, A. Age-related decrease in sensitivity to electrical stimulation is unrelated to skin conductance: An evoked potentials study. *Clin. Neurophysiol.* **125**, 602–607 (2014).

58. Gratton, G., Coles, M. & Donchin, E. A new method for off-line removal of ocular artifact Electroencephalography and clinical Neurophysiology. *Electroencephalography and Clinical Neurophysiology* **55**, 468–482 (1983).

59. Maris, E. & Oostenveld, R. Nonparametric statistical testing of EEG- and MEG-data. *J. Neurosci. Methods* **164**, 177–190 (2007).

60. Kremlaczek, J. et al. Visual mismatch negativity (vMMN): A review and meta-analysis of studies in psychiatric and neurological disorders. *Cortex* **80**, 76–112 (2015).

Acknowledgements

The authors thank Emmi Pentikäinen, Kaisa Pentikäinen, Anniina Kuusela, Mirjami Margaritis, and Laura Nuutinen for their help in the data collection and Petri Kinnunen and Lauri Viljanto for technical assistance. The study was supported by the Jenny and Antti Wihuri Foundation and The University of Jyväskylä Graduate School for Doctoral Studies.

Author Contributions

J.M.S., P.A., and I.M.T. designed the experiment. J.M.S., V.K., T.W., S.J., S.K., and N.P. recorded and analysed the data. The interpretation of the data was performed by P.A., J.M.S., and I.M.T. The manuscript text was prepared by J.M.S. and P.A. J.S. prepared all the figures and tables. All authors reviewed the manuscript, and all the authors approved the final version of the manuscript to be published.

Additional Information

Supplementary information accompanies this paper at https://doi.org/10.1038/s41598-017-14139-9.

Competing Interests: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher’s note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. The images or other third party material in this article are included in the article’s Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article’s Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit http://creativecommons.org/licenses/by/4.0/.

© The Author(s) 2017