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Evidence that ageing yields improvements as well as declines across attention and executive functions

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Many but not all cognitive abilities decline during ageing. Some even improve due to lifelong experience. The critical capacities of attention and executive functions have been widely posited to decline. However, these capacities are composed of multiple components, so multifaceted ageing outcomes might be expected. Indeed, prior findings suggest that whereas certain attention/executive functions clearly decline, others do not, with hints that some might even improve. We tested ageing effects on the alerting, orienting and executive (inhibitory) networks posited by Posner and Petersen's influential theory of attention, in a cross-sectional study of a large sample (*N* = 702) of participants aged 58–98. Linear and nonlinear analyses revealed that whereas the efficiency of the alerting network decreased with age, orienting and executive inhibitory efficiency increased, at least until the mid-to-late 70s. Sensitivity analyses indicated that the patterns were robust. The results suggest variability in age-related changes across attention/executive functions, with some declining while others improve.

Life expectancy has risen substantially, increasing the importance of understanding age-related changes in cognition. Not surprisingly, ageing negatively affects many aspects of cognition, as demonstrated by a large body of work indicating that older adults show worse performance than younger adults in a variety of cognitive tasks. For example, older adults consistently display lower accuracy and/or slower performance in tasks measuring episodic memory[1–3], word recognition and retrieval[4,5], word learning[6,7], implicit learning of complex skills and sequences[8–10], and various visuo-spatial abilities[11,12]. Though some of these age differences may be due to age-related decreases in overall processing speed or other general factors[13–15], reductions in many cognitive functions are still detectable even when controlling for such variables[16–19] and thus seem to represent specific neurocognitive declines[1,20]. (For convenience, we use terms such as 'decline' and 'improvement' to refer to age-related differences in both longitudinal and cross-sectional studies, the latter of which constitute the vast majority of work on this topic; however, these terms should be treated with caution, since alternative explanations for age effects cannot be completely ruled out in cross-sectional studies[21,22]; see Discussion.)

The trajectories of age-related declines vary considerably, depending on the particular cognitive function in question. Some functions decrease robustly across the whole adult lifespan, while others show smaller age-related declines or show decreases that begin or become more pronounced later in life[3,22–28]. Such differentiation can even be detected within particular cognitive domains[1,29]. This variability raises the possibility that not all aspects of cognition decline. Indeed, evidence suggests that some functions may be fully preserved over the course of ageing, such as automatic processes of memory retrieval[30–32], aspects of lexical and grammatical processing in language comprehension[33–37], and skills that were well practised throughout life[38,39].

Furthermore, evidence suggests that some areas of cognition actually show improvements with increasing age. This has long been posited for 'crystallized' (knowledge-based) aspects of cognition[40–42], such as vocabulary, lexical–semantic knowledge, verbal comprehension and general information, which tend to exhibit age-related increases until quite late in life; these have traditionally been contrasted with 'fluid' (information processing) aspects of cognition[40–42], such as spatial visualization and processing speed, which often show age-related declines[24,26,43–49]. However, older adults have been found to outperform younger adults in other domains as well. These include 'wisdom'[50,51], theory of mind[52], emotional regulation[21,53–56], aspects of decision-making abilities[57–60], motivation related to one's job[61,62] and certain dimensions of personality such as agreeableness and conscientiousness[63]. Given that some of these domains seem to involve fluid (perhaps in addition to crystallized) aspects of cognition[64,65], this raises the possibility of multifaceted ageing outcomes in fluid processes, including not only decli nes[24,26,43–49] and age invariance (for example, automatic processes of memory retrieval[30–32]) but also improvements.

Going beyond which abilities show improvements, research has also begun to reveal the shapes of these trajectories—that is, when improvements may occur over the course of ageing. At least for crystallized cognition, and perhaps for aspects of fluid cognition, age-related improvements are often nonlinear, with increases tending to continue up to a certain point, often in one's 70s, after which age invariance or declines may set in[1,22,26,52,61,66,67]. Finally, the why of cognitive improvements is also beginning to be understood, though primarily for crystallized abilities thus far. In particular, age-related improvements seem to be largely explained by the lifetime accumulation of experience or practice, resulting in (neurobiologically based) increases in knowledge or perhaps in skill efficiency, which may outweigh any neurobiological declines[1,38,48,66,68–76].

We investigated the effect of age on attention and executive functions—the critical set of processes that allow us to focus on selective aspects of information in a goal-directed manner, while ignoring irrelevant information[77–79]. This set of functions is crucial

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for everyday life[80,81] and supports numerous higher-level cognitive capacities[82–86].

Theories of the neurocognition of ageing have widely posited age-related declines in attention and executive functions[87–96]. Moreover, these theories have generally assumed that such declines affect attention/executive functions quite broadly[87–93,95,96]. This view is consistent with broad declines in the neurobiological substrates of these functions[97–102]. However, reviews and meta-analyses of behavioural findings have suggested that age-related weakening of attention/executive functions is not universal. Rather, there seems to be large variability in age effects across tasks and functions, ranging from clear declines (for example, in working memory and dual-task paradigms) to age invariance (for example, in aspects of selective attention and inhibitory control)[26,29,79,103–113]. This variability is not surprising, given that different aspects of the broad capacities of attention and executive functions seem to constitute at least somewhat independent neurocognitive processes[78,114–117]. Moreover, even where age-related declines have been observed, including in various studies of inhibitory control, at least some of these effects can be attributed to general age-related slowing rather than to specific deficits of attention/executive functions[118,119]. There thus seems to be a mismatch between the theories as well as the neurobiological evidence on the one hand and at least some behavioural ageing patterns on the other.

Even more provocative than an absence of declines would be the existence of age-related improvements in specific aspects of attention or executive function. This is not as implausible as it might seem, given that age-related increases have been observed for a range of functions, including some that seem to involve fluid abilities. As far as we know, no reviews or meta-analyses have uncovered reliable age-related improvements in aspects of attention or executive function. It is possible, however, that reviews and meta-analyses have missed such improvements for various reasons. These reasons include not only experimental and analytical factors in the included studies (for example, categorical designs with younger and older adults preclude the examination of nonlinear ageing patterns; see below) but also the aggregation of studies with tasks probing different attention/executive functions that show different trajectories, such as declines and improvements that could cancel each other out. Examining the effect of age on clearly distinct theoretically motivated functions may therefore be useful.

Here we focus on the highly influential theory of attention proposed by Posner and Petersen, which posits that this broad capacity in fact comprises three 'networks'—namely, alerting, orienting and executive control[117,120]. The attentional network of alerting is characterized as a state of enhanced vigilance and preparedness to respond to incoming information, and it features both a phasic aspect (concerned with rapid changes of attention) and a tonic aspect (referring to more stable vigilance or arousal)[121]. The orienting network involves the selection of information from sensory inputs, which is achieved by shifting processing resources to a given location. Finally, the executive network consists of a set of top-down processes involved in inhibitory function—that is, in detecting conflict and inhibiting distracting or conflicting information.

The three attentional networks are at least partially independent. Such independence is supported by substantial behavioural and neurobiological evidence that associates each network with distinct processing mechanisms[117,120,122–125], neuroanatomical substrates[126–129], neuromodulators[130–133] and genetic polymorphisms[126,134]. Given that these attention/executive functions show neurocognitive differentiation, we suggest that they may also show distinct susceptibilities to ageing.

The most common paradigm used to examine the three attentional networks is the Attention Network Test (ANT)[122,135]. The ANT is a simple task that nonetheless simultaneously measures the efficiency of all three networks by combining a cued reaction time task[136] with a flanker task[137]. Importantly, the ANT shows moderate-to-high reliability[122], including in older adults[138–140]. Moreover, the task shows high construct and criterion validity[126,127,141], again including in older adults[138]. In the ANT, the target stimulus in every trial typically consists of a central arrow that points either left or right, with two flanker arrows on each side (Supplementary Fig. 1). These flanker arrows all point either in the same direction (congruent) or in the opposite direction (incongruent) as the central arrow. Participants are simply instructed to perform a flanker task—that is, to decide the direction of the central arrow (left or right) by pushing one of two buttons. Each target stimulus (the central arrow with its flankers) appears either above or below the centre of the screen. Three general types of warning cues are presented before the target: (1) no cue; (2) alerting cues such as central cues, which immediately precede the target, thus serving as a temporal signal for incoming information; and (c) orienting (spatial) cues, which are displayed above or below the centre of the screen, consistent with the location of the upcoming target, and thus convey spatial information relevant for the task. By comparing response times (RTs) to the target stimuli between the various conditions (the different types of cues and the different types of flankers), it is possible to estimate the efficiency of each attentional network (accuracy is generally near ceiling in these tasks and so is usually not analysed). Specifically, the efficiency of the alerting network is measured as the benefit (RT speed-up) of alerting cues relative to trials with no cues, the efficiency of the orienting network is measured as the benefit of orienting cues relative to alerting cues and the efficiency of the executive network is measured as the cost (RT slowdown) produced by incongruent flankers relative to congruent flankers—that is, the greater the interference caused by the flankers pointing in the opposite direction, the lower the efficiency of the executive network.

We are aware of 13 studies that have previously examined effects of ageing on the ANT; all were cross-sectional[140,142–153]. As expected, and not of primary interest here, these studies found general slowdowns with ageing in the task—that is, age-related increases in overall RTs across all conditions. Importantly, the studies also suggest that the three network efficiencies (defined by RT differences between conditions; see above) show somewhat different ageing trajectories. As can be seen in Table 1, decreases in efficiency with ageing have generally been observed for the alerting network, whether or not age-related declines in processing speed were controlled for (achieved in most studies by transforming RTs into proportions or *z*-scores relative to a participant's mean RT, or by treating participant mean RTs as a covariate). In contrast, no age-related changes in the efficiency of the orienting network have usually been reported, though sometimes efficiency increases have been found, especially when processing speed was not controlled for. The ageing trajectory of executive network efficiency has been less clear, with decreases or no changes reported when processing speed was not controlled for, but an apparent shift away from declines when processing speed was controlled for, with several studies even finding improvements.

Thus, despite the appearance of broadly different ageing trajectories for the three attentional networks, previous studies have demonstrated a fair bit of variability in this regard, even when processing speed was (or was not) controlled for. Such inconsistencies, which can obscure the true pattern of trajectories, may be due to various experimental and analytical factors, including the following. First, previous studies have had relatively small sample sizes: between 13 and 77 older adult participants (in addition to similar sample sizes of younger adults), except for two studies that focused on older adults, which tested 145 (ref. [149]) and 184 (ref. [140]) participants. Second, almost all studies employed categorical designs comparing younger and older adult groups rather than a continuous age design across the age range of interest (but see refs. [140,149]). Categorical (factorial) designs lead to information loss because the

Table 1 | Summary of results of prior studies examining effects of ageing on the ANT

Network	Age-related changes in efficiency	Summary of results
Alerting	Decrease: older adults benefit less from alerting cues	Nine studies reported efficiency decreases, generally regardless of whether processing speed was controlled for[142,145–148,150–153] or not[145–148,151,153].
	Age invariance: no effect of age on the benefit of alerting cues	Four studies reported no effects of age on alerting efficiency: three while controlling for processing speed[140,143,149] and two while not controlling for it[149,152].
	Increase: older adults benefit more from alerting cues	One study (with a small sample size) found age-related efficiency increases[144], both with and without controlling for processing speed.
Orienting	Decrease: older adults benefit less from spatial cues	One study found age-related decreases in orienting efficiency, with processing speed controlled for[142].
	Age invariance: no effect of age on the benefit of spatial cues	Eleven studies reported no effects of age on orienting efficiency, particularly when controlling for processing speed[140,144–153], though sometimes also when not controlling for it[144,146,149,153].
	Increase: older adults benefit more from spatial cues	Six studies reported efficiency increases, in one case when controlling for processing speed[143] but mainly when not controlling for it[145,147,148,151,152] (these five studies all reported age invariance when controlling for processing speed).
Executive	Decrease: older adults show more interference from incongruent flankers	Eight studies found age-related decreases in executive efficiency, sometimes when controlling for processing speed[140,149,153] but mainly when not controlling for it[145–147,149,151–153].
	Age invariance: no effect of age on interference from incongruent flankers	Seven studies reported no effects of age on executive efficiency, mainly when controlling for processing speed[143,145–148,151] but occasionally when not controlling for it[144,148].
	Increase: older adults show less interference from incongruent flankers	Four studies found age-related increases in executive efficiency, in all cases when controlling for processing speed[142,144,150,152].

All statements of efficiency decreases and increases refer to significant effects, as reported in the cited papers. Results from analyses that tested for but did not find significant age effects on network efficiency are classified as showing age invariance. Several studies reported results only with processing speed controlled for[140,142,143,150]. This must be taken into account in interpreting the pattern of findings described in the table, since in these cases the absence of reported effects without controlling for processing speed does not imply that a given pattern was more common when processing speed was controlled for.

variability in ages within each group cannot contribute to potential age effects[109,154]. Indeed, in such designs, any changes that occur within an age group cannot be detected; this can be especially problematic in ageing studies, since many cognitive changes seem to occur within middle to older adulthood[1,3,24,26,29]. Furthermore, categorical designs with two groups cannot examine nonlinear age effects, even though such nonlinearities are common in cognitive ageing (see above). Third, age effects (or the lack thereof) in previous ANT ageing studies may have been distorted by an absence of precise control of potentially confounding factors, such as the basic demographic variables of education and sex. Such variables can be correlated with age[109] and may play a role in the efficiency of the attentional networks[155–157]. Even when mean levels of education or sex ratios are matched groupwise (as in many previous studies), different distributions of these variables between the groups and different correlations with age can inflate both false positive and false negative errors[154].

The present study was designed to examine the effect of age on the efficiencies of the three attentional networks while addressing these issues. The ANT was given to a large sample of adults ranging in age from 58 to 98 years, in a cross-sectional continuous age design ($N = 702$ in our main analyses; see Extended Data Fig. 1 for demographic information). We focused on adults from late middle age to older adulthood to capture changes during the period when many cognitive changes occur. Our sample included participants at very old ages (higher than in most previous ANT studies), allowing us to examine ageing effects across a wide age range within older adulthood. The analyses were performed on RTs using mixed-effects regression. Our primary analyses examined the linear effect of age on the efficiency of each attentional network. We also examined nonlinear age effects on the efficiency of each network. We statistically controlled for both sex and education. We additionally controlled for processing speed to avoid confounding effects from general age-related processing slowdowns as well as speed decreases due to motor or perceptual declines in ageing[158] or to slowed responses from lower alertness[122]. Such processing speed differences were primarily addressed by log-transforming the RTs, yielding proportional effects while also reducing skewness and minimizing the influence of outliers. Finally, we performed a wide range of sensitivity analyses, including analyses further controlling for processing speed as well as not controlling for it at all.

On the basis of previous findings, we predicted age-related decreases in the efficiency of the alerting network, but no age-related differences or perhaps even increases in the efficiency of the orienting network. The expected ageing trajectory of executive efficiency was less clear, though we speculated that no differences or even increases might be possible. Indeed, a combination of age-related declines, invariance and improvements across and/or within the networks would not be inconsistent with the broader literature, given that all have been observed across as well as within cognitive domains, including in fluid aspects of cognition. (The predictions were not altered after data analysis or while writing or revising this paper.)

Results

Age and attentional network effects. Linear mixed-effects modelling revealed that age had a significant main effect on RTs (across all cue and flanker types), such that greater age was associated with overall slower responses on the task (regression coefficient (β), 0.0083; 95% confidence interval, (0.0068, 0.0098); $t = 10.70$; $P < 0.001$). (For the accuracy analyses, see Extended Data Fig. 2.) Each additional year of age was associated with a mean cost of 6.3 ms (in back-transformed RTs; because the analyses were conducted on log RTs, the cost per year in milliseconds was obtained by back-transforming the effect of age, over the entire age range). All three attentional network effects (the average effects from the whole sample of participants across the full age range) were significant: the alerting effect was 3.3 ms in back-transformed RTs ($\beta = 0.0048$ (0.0007, 0.0088), $t = 2.31$, $P = 0.021$), the orienting effect was 11 ms ($\beta = 0.0160$ (0.0120, 0.0201), $t = 7.79$, $P < 0.001$) and the executive effect was 47 ms ($\beta = 0.0680$ (0.0636, 0.0723), $t = 30.40$, $P < 0.001$). See Extended Data Fig. 3 for the complete model results, including

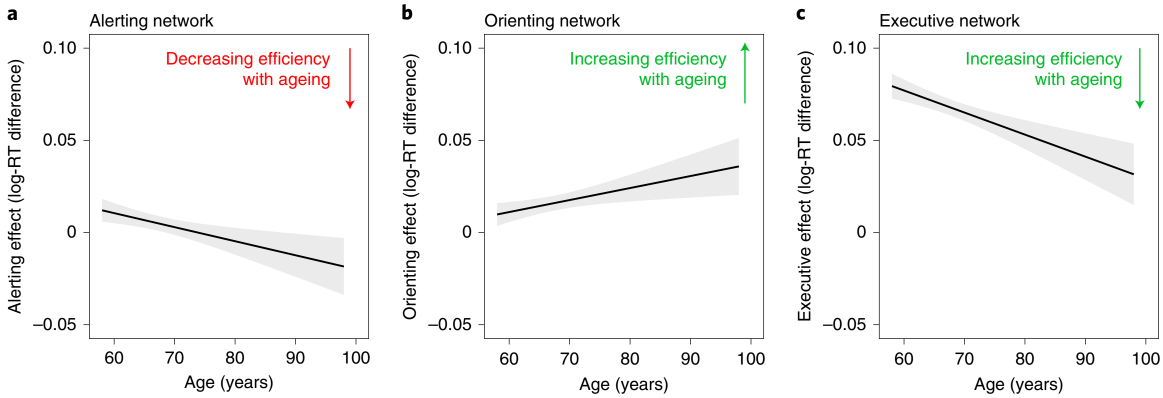

Fig. 1 | Linear effects of age on the efficiencies of the three attentional networks. **a**, Effect on the efficiency of the alerting network. **b**, Effect on the efficiency of the orienting network. **c**, Effect on the efficiency of the executive network. The shaded bands represent pointwise 95% confidence intervals. The regression lines and bands are shown from the minimum to the maximum age in our sample (ages 58–98). For each network, we followed up on the interaction between age and efficiency with analyses examining efficiency at different ages. For alerting (**a**), at the minimum age of 58 years, the benefit of a central cue was significant (8 ms benefit; $\beta=0.0121$ (0.0059, 0.0182), $t=3.82$, $P<0.001$), but by age 74 this effect was no longer positive ($\beta=-0.0001$ (−0.0053, 0.0050), $t=-0.05$, $P=0.957$). By the maximum age of 98 years, the central cue had a significant detrimental effect relative to no cue (16 ms cost; $\beta=-0.0184$ (−0.0339, −0.0030), $t=-2.34$, $P=0.019$). As there were only a few participants above age 90 (and thus the sparse data in this age range may not generalize to other samples), we additionally estimated the alerting effect at age 90; there was also a significant cost at this age ($\beta=-0.0123$ (−0.0240, −0.0006), $t=-2.06$, $P=0.039$). For orienting (**b**), although there was already a significant benefit from spatial cues at age 58 (6 ms; $\beta=0.0098$ (0.0036, 0.0160), $t=3.10$, $P=0.002$), this benefit was much larger by age 98 (32 ms; $\beta=0.0359$ (0.0204, 0.0513), $t=4.55$, $P<0.001$)—almost four times larger as indicated by the β values, which reflect differences in log-transformed RTs, and more than five times larger in back-transformed RTs (values in milliseconds). A similar orienting benefit was found at age 90 ($\beta=0.0306$ (0.0189, 0.0423), $t=5.13$, $P<0.001$) as at age 98. For the executive network (**c**), although the interference cost of incongruent flankers was present throughout the age range, it was much larger at age 58 (51 ms; $\beta=0.0794$ (0.0727, 0.0861), $t=23.14$, $P<0.001$) than at age 98 (28 ms; $\beta=0.0316$ (0.0149, 0.0483), $t=3.71$, $P<0.001$)—more than twice as large as revealed by the regression coefficients and almost twice as large in back-transformed RTs. A similar executive effect was obtained at age 90 ($\beta=0.0411$ (0.0285, 0.0538), $t=6.37$, $P<0.001$) as at age 98.

degrees of freedom, which are the same for all effects in the model. All reported P values here and elsewhere are two-tailed, with significance determined as $P<0.05$. Extended Data Fig. 4 shows the mean untransformed RTs for each condition (each cue and flanker type) in milliseconds, as well as the mean attentional network effects in milliseconds, presented in five-year age brackets.

Linear effects of age on each attentional network. Age interacted with all three attentional network effects—that is, with the efficiencies of the alerting, orienting and executive networks. Figure 1 displays these interactions as the effects of age on each of the three network effects, where each network effect is expressed as the contrast between the relevant cue or flanker types (see Extended Data Fig. 5 for an equivalent figure displaying the effects of age over scatter plots of the attentional effects for each of the 702 participants). These interactions can also be seen in Extended Data Fig. 6, which displays age effects separately for each of the cue and flanker conditions; although RTs in all conditions increased with age, these increases differed among the cue and flanker types, leading to the observed interactions between age and the three attentional network effects.

First, the alerting effect (that is, the response speed-up in trials with a central cue relative to trials with no cue) decreased with age ($\beta=-0.0008$ (−0.0013, −0.0003), $t=-3.05$, $P=0.002$)—that is, older participants showed less of a benefit from alerting cues than younger participants, suggesting that ageing was associated with decreasing efficiency of the alerting network (Fig. 1a). Second, the orienting effect (that is, the response speed-up in trials with a spatial cue relative to trials with a central cue) increased with age ($\beta=0.0007$ (0.0002, 0.0011), $t=2.61$, $P=0.009$)—that is, older participants benefited more from spatial cues than younger participants, suggesting increasing efficiency of the orienting network with ageing (Fig. 1b). Third, the executive effect (that is, the response slowdown in trials with incongruent flankers relative to trials with congruent flankers) also interacted with age ($\beta=-0.0012$ (−0.0017, −0.0007), $t=-4.42$, $P<0.001$). Specifically, the executive effect decreased with age, such that older participants showed less interference from incongruent flankers relative to congruent ones, suggesting that ageing was associated with increasing efficiency of the executive inhibitory network (Fig. 1c).

Linear effects of age: sensitivity analyses. The results were robust, in that the same pattern of significant age effects for the three network efficiencies was also obtained in a range of sensitivity analyses, each of which involved one type of change to the main analysis presented above. See Supplementary Table 1 for the results from all sensitivity analyses. First, the same pattern was found when participant mean log RT was included as a covariate[140,142] in addition to sex, education and trial position, to further control for age-related declines of processing speed. Note that in this analysis, processing speed declines are accounted for not only by employing log-transformed RTs as the dependent measure, but also by controlling for speed differences between participants, thereby further reducing the likelihood that age-related differences in processing speed from general, motor or perceptual slowdowns[158], or from slowdowns from other factors such as reduced alertness[122], could explain the observed patterns. Second, and conversely, we ran the original statistical model on raw (unlogged) RTs rather than log-transformed RTs as the dependent measure, and we again found the same pattern of results. This shows that the age effects on the three attentional networks were also detectable as linear effects on the millisecond scale. Thus, the pattern was found even when processing speed was not controlled for at all. Third, because correlations between predictors (see 'Participants' in Methods) can substantially change regression estimates and even

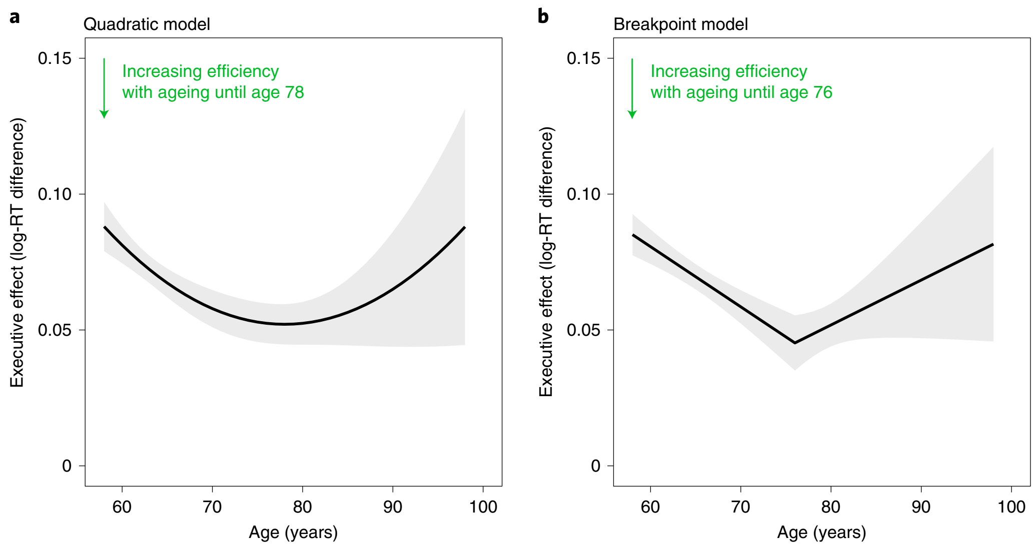

Fig. 2 | The nonlinear effect of age on the efficiency of the executive network. a, The model with a quadratic term for age. **b**, The breakpoint model with the optimal breakpoint—that is, at age 76. The shaded bands represent pointwise 95% confidence intervals. The regression lines and confidence interval bands are shown from the minimum to the maximum age in our sample (ages 58–98). See Extended Data Fig. 9 for an equivalent figure showing the executive effect for each of the 702 participants.

lead to sign reversals[159,160], we examined whether the observed age effects were also obtained when age was not adjusted for covariates, by refitting the original model without any covariates (that is, without sex, education and trial position). This model also yielded the same pattern of results. Fourth, age-related visual declines[161] could result in slowed or inaccurate perception of the stimuli, which might explain some of the observed patterns. For example, visual declines resulting in difficulties identifying the arrows could lead to reductions in congruent/incongruent RT differences, providing an alternative account for the observed age effect on the executive network. However, a model in which we also covaried out a measure of visual acuity (see 'Participants' in Methods) again produced the same pattern of significance, even though decreases in visual acuity negatively impacted RTs in the task ($\beta = -0.0454$ (-0.0906, -0.0001), $t = -1.98$, $P = 0.048$). Note also that the stimuli (cross, asterisk and arrows) were enlarged as compared with the original task[162] to minimize problems due to age-related declines in visual acuity, while the distance between the central point and the arrow positions above or below it was still maintained from the original task, to minimize difficulties from declines in peripheral vision or from any changes in participants' spatial attentional gradient[163] or 'useful field of view'[164]. Fifth, it might be argued that older participants showed less of an interference effect (an apparent increase in executive efficiency) because, being slower overall than younger participants, they were more likely to bump up against the trial timeout of 1,700 ms (particularly on the slower incongruent trials), thus yielding less of a difference between the congruent and incongruent conditions. However, as shown in Extended Data Fig. 7, very few of the RTs of even the older participants approached 1,700 ms for incongruent let alone congruent trials, arguing against such a timeout explanation. Furthermore, a sensitivity analysis restricted to responses below 1,600 ms as well as below 1,500 ms showed the same pattern as the main analysis, with age effects on executive function of the same magnitude. Sixth, although excluding double cues allowed for the analysis of all three attentional effects in the same statistical model[140,143,149,150] (see 'Data exclusions and analysis' in Methods), it resulted in information loss, specifically in the computation of the alerting and executive effects, both of which can be analysed with both central and double cues[122,145,146]. An alternative analysis of alerting and executive effects that included both the double and central cues again yielded the same pattern as the main analysis. Seventh, the same pattern of results remained when analysing a larger sample (734 participants) that additionally contained 32 'low-accuracy' participants, by employing a more lenient inclusion criterion of at least 50% task accuracy, rather than 75% (see 'Participants' in Methods). Eighth, and conversely, when we used a more stringent criterion of including only participants with at least 90% accuracy (643 participants), again the same pattern was obtained. Finally, the same results were also found when extremely old participants (that is, four participants aged 90–98) were excluded from the original model (since they may have constituted outliers).

Nonlinear effects of age on each attentional network. Given nonlinearities in other cognitive ageing effects[1,22,26,66,67], we also tested for nonlinearities in the effect of age on each of the three networks. First, we included a quadratic term for age (as an orthogonal polynomial), which interacted significantly with the executive effect ($\beta = 1.3482$ (0.3886, 2.3078), $t = 2.75$, $P = 0.006$). This interaction indicated that whereas the executive effect (response slowdown of incongruent relative to congruent flankers) was present throughout the age range, it first diminished (that is, efficiency increased) but then plateaued (with a maximum efficiency at age 78), after which there seemed to be a reversal, with decreasing efficiency from this point onwards (Fig. 2a). In contrast, the quadratic term for age did not interact significantly with either the alerting ($\beta = 0.4394$ (-0.4552, 1.3337), $t = 0.96$, $P = 0.336$) or orienting effects ($\beta = -0.3221$ (-1.2148, 0.5704), $t = -0.71$, $P = 0.480$). Note that the non-significance of these interactions should not be taken as evidence for the absence of nonlinearities in the effect of age on these two networks: even in a large sample, nonlinearities can remain undetected due to insufficient statistical power or because the particular nonlinearity that is tested (in this case, a quadratic effect) may not capture the shape of the underlying effect.

Indeed, despite their wide use, quadratic polynomials impose a particular functional form on the estimated effects. The observed quadratic effect thus might not indicate a true reversal for older participants but rather some other nonlinearity, such as a stable executive effect at older ages (consistent with the wide confidence interval

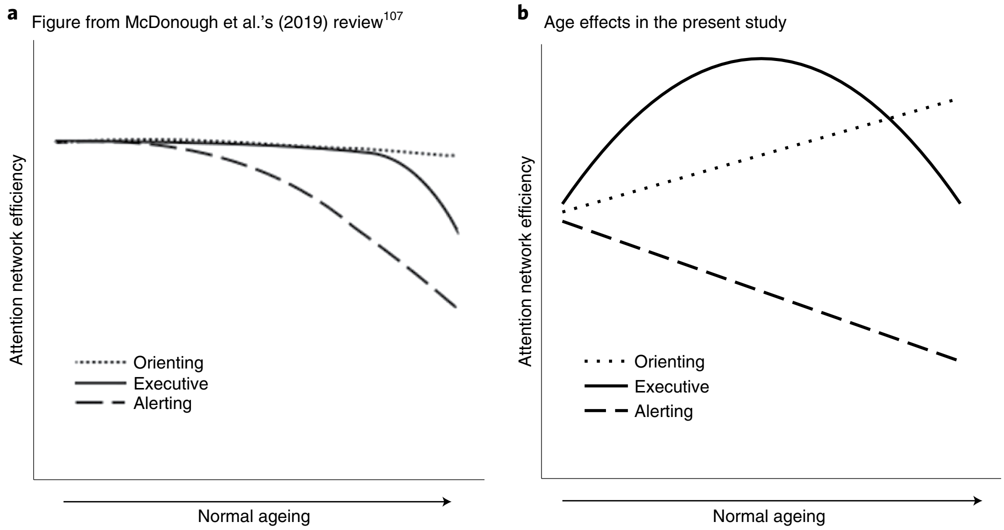

Fig. 3 | Comparison between a recent qualitative review of age effects on the three attentional networks and the findings from the present study. a, A graphical summary presented by McDonough et al., which examined effects of age on the three networks in the ANT and related tasks in prior studies. Image adapted with permission from ref. [107]. **b**, The findings obtained in the present study. The age effects in **b** are fitted values from the regression models presented in the Results: linear age effects for alerting and orienting, and a quadratic age effect for the executive network. To make the trajectories of the three networks more comparable, the executive effect was transformed from a cost metric to an efficiency metric (by multiplying the effect by −1); the three trajectories were made approximately equal at the origin (by subtracting the predicted effect at the minimum age from all predicted values, for each network); and the three trajectories were standardized (by dividing the predicted values by the standard deviation of by-participant effects, for each network). The graphical summary from the recent review is both similar to and critically different from our findings. On the one hand, the shapes of the three ageing trajectories in the summary show striking parallels to the pattern of our results, with strong declines for alerting but not for orienting or executive function. On the other hand, the summary emphasizes age-related stability rather than improvements for the orienting and executive networks, because significant age effects were not found in a number of prior studies of orienting[107] (which may have been partly due to low statistical power from small sample sizes) and because variability was found across studies for the executive network[107] (which may have been partly due to the use of linear rather than nonlinear analyses). Thus, while the recent review (as well as other reviews and theories[79,87–93,95,96,105,106,108]) indeed seems to have captured certain aspects of the effect of ageing on attention/executive functions, the results of the present study suggest updating this view to also include age-related improvements.

on the right side of Fig. 2a). We therefore also examined the nonlinearity with linear regression-with-breakpoints. This technique estimates two linear slopes joined at a 'breakpoint'[165,166]. Such breakpoint models allow various nonlinear shapes to be detected, including the reduction, elimination or reversal of an effect at a particular point. We employed a breakpoint discovery procedure to estimate the best location (age) of the breakpoint by fitting a set of regression models, each with a breakpoint at a different age, and selected the model with the best fit[165,167,168].

The discovery procedure (Extended Data Fig. 8) revealed that the optimal breakpoint model contained a breakpoint at age 76. The estimates of this model showed that the two linear slopes (that is, before versus after age 76) differed significantly from each other for the executive network ($\beta=0.0039$ (0.0014, 0.0063), $t=3.08$, $P=0.002$). Thus, consistent with the quadratic model, a nonlinear age effect was found for the executive network. In this model (Fig. 2b), the slope of the age effect from age 58 to 76 was significantly different from zero and indicated decreasing interference costs during this age range—that is, increasing executive efficiency ($\beta=-0.0022$ (−0.0030, −0.0014), $t=-5.20$, $P<0.001$). Follow-up analyses revealed that the interference produced by incongruent flankers relative to congruent flankers was much larger at the minimum age of 58 years (interference cost of incongruent flankers, 54 ms; $\beta=0.0851$ (0.0775, 0.0927), $t=21.95$, $P<0.001$) than at 76 years (33 ms; $\beta=0.0452$ (0.0351, 0.0554), $t=8.73$, $P<0.001$)—almost twice as large as revealed both by the regression coefficients and in back-transformed RTs. In contrast, the slope from ages 76 to 98 showed a numerical reversal of the effect (greater interference of the incongruent flankers with increasing age), though this was marginally significant ($\beta=0.0017$ (−0.0002, 0.0035), $t=1.72$, $P=0.086$). Unlike the executive network, the difference between the two linear slopes was not statistically significant for either the alerting ($\beta=0.0009$ (−0.0014, 0.0032), $t=0.76$, $P=0.445$) or orienting networks ($\beta=-0.0014$ (−0.0037, 0.0009), $t=-1.22$, $P=0.221$). Extended Data Fig. 9 displays the nonlinear effect of age on the efficiency of the executive network, from both the quadratic and breakpoint models, over scatter plots of the executive effects for each of the 702 participants.

Nonlinear effects of age: sensitivity analyses. The observed nonlinear breakpoint pattern was robust, in that the same results were obtained in the nine sensitivity analyses reported above for the linear analyses (see Supplementary Table 2 for the model results), namely: (1) with the mean log RT of each participant included as a covariate to further control for age-related processing slowdowns even beyond employing log-transformed RTs as the dependent measure; (2) with raw (unlogged) RTs as the dependent measure and thus not controlling for processing speed at all; (3) without any covariates; (4) when controlling for visual acuity; (5) with responses restricted to those below 1,600 ms as well as below 1,500 ms, to test for potential timeout effects; (6) when including both double and central cues in the analysis; (7) with a more lenient participant inclusion criterion, yielding a larger sample of participants; (8) with a more stringent participant inclusion criterion, yielding a smaller sample of participants; and (9) when excluding extremely old participants. All of these models yielded a significant difference between the age effect on executive efficiency from age 58 to 76 and the age effect from 76 to 98, but no such significant differences for the alerting and orienting networks.

Discussion

This study examined effects of ageing on the alerting, orienting and executive attentional networks posited by Posner and Petersen's theory of attention[117,120]. The efficiency of the networks was tested with the ANT—a behavioural task with high reliability and validity—in a large sample of middle-aged to older adults. Linear mixed-effects regression indicated that whereas the efficiency of the alerting network decreased with increasing age, the efficiency of both the orienting and executive networks increased. In other words, whereas older participants benefited less from the presence of a central cue relative to no cue (alerting effect), they benefited more from a cue that directed their attention to a particular location (orienting effect) and showed less interference from incongruent flankers (executive effect). Nonlinear mixed-effects modelling revealed that the effect of age on the executive network was in fact nonlinear: the increase in executive efficiency held until the mid-to-late 70s, but after that, the increase was eliminated and possibly reversed, with an apparent decrease in executive efficiency during older adulthood. (Note that since the ANT yields only behavioural measures, these findings should not be interpreted as direct reflections of age-related changes in the brain networks underlying the attentional processes.)

The linear and nonlinear age effects were robust and did not seem to be explained by a variety of alternative accounts. We have seen that these effects held across a wide range of sensitivity analyses. Moreover, further examination revealed that the age effects were probably not due to speed–accuracy trade-offs: unlike in the RT analyses, the accuracy analyses (Extended Data Fig. 2) revealed no significant age-related changes in efficiency for the alerting or orienting networks, and executive function actually showed significant efficiency increases, arguing against speed–accuracy trade-offs in all three networks. In fact, this accuracy result for the executive network underscores the robustness of the increases in executive efficiency, which were thus found in both speed and accuracy. The increases in orienting and executive efficiency also do not seem to be explained by sample selectivity at older ages—for example, survivor effects or the self-selection of fitter adults in old age[169–171]. First, whereas the efficiency of the orienting and executive networks indeed increased with age, alerting efficiency decreased in the same sample. Working memory abilities were also found to decrease with age in the same sample of participants, as reported in a recent study[109] (also see Extended Data Fig. 1). Finally, the nonlinear effect of age on executive function indicates that improvements occurred during earlier rather than later older adulthood, whereas selection biases should be stronger at later ages. The nonlinear effect of ageing on executive function also argues against the possibility that the increases in executive efficiency might actually be due to concomitant decreases in alertness[122], since alerting efficiency showed a linear decrease (with no evidence for a nonlinearity), which would predict a similar linear increase in executive efficiency. More generally, it is not clear how a variety of other alternative accounts (for example, age-related slowing or age-related changes in participants' visual abilities, spatial attentional gradient or useful field of view) could easily explain the different age-related trajectories of the three networks (and working memory), as well as the nonlinear effects obtained for executive function.

The fact that age-related efficiency decreases were not observed across all three networks is consistent with prior data, which suggest that ageing leads to declines in some but not other aspects of the wide domain of attention/executive functions. First, our results are broadly consistent with the pattern of clear declines observed for alerting efficiency but not for orienting or executive efficiency in previous ANT ageing studies (Table 1); see Fig. 3 for a comparison between a recent review of these studies and the findings presented here. Moreover, meta-analyses have suggested that attention/executive functions demonstrate different trajectories for different functions, including an absence of reliable declines in executive inhibitory tasks[110–113]. We emphasize that we are not suggesting that no executive functions show age-related declines, and indeed, meta-analyses and reviews reveal that other aspects of executive function decline robustly, including working memory[79,103,104,106,111–113]. In fact, as mentioned above, a recent study of the same sample of participants examined here found that working memory showed strong declines[109], underscoring that age-related decreases can be found in some but not other aspects of attention/executive function even in the same group of individuals. Thus, our findings, together with other data, argue against theories positing general age-related declines in attention and executive functions, including proposals such as that put forth by Hasher, Zacks and colleagues that ageing leads to broad deficits in inhibition[87–93,95,96].

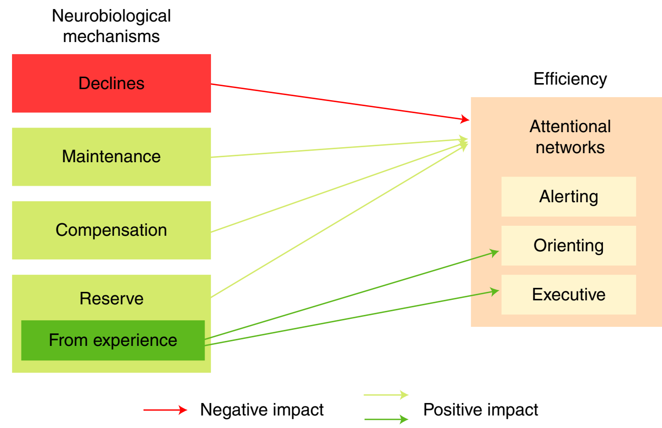

Fig. 4 | A neurocognitive account of age effects on the three attentional networks. We propose that the observed age-related efficiency changes in the three networks are explained by a combination of neurobiologically based mechanisms that have previously been implicated in other cognitive ageing trajectories[1,38]: declines, maintenance, compensation and reserve ("cumulative improvement…of neural resources"[38]), particularly from experience. First, the neurobiological substrates of all three networks show age-related declines, which probably differ in their trajectories[99–102,214–218]. Countering these declines, some age-related maintenance and compensation may occur across the networks[1,38,88,193]. This seems best studied for compensation, especially for the executive network[88,107], as well as more specifically for dopaminergic processes, which underlie executive function[219,220]. Crucially, the declines should also be countered by reserve-related gains in neural efficiency, in particular from lifelong experience and practice with the networks[43,48,66,69–72,75]. Depending on the degree of these gains and the extent of the neural declines (as well as the scope of any maintenance and compensation), this may not only mitigate performance decreases[38] but also lead to observable improvements[1,74,195]. We hypothesize that learning and thus experience-based gains are much more likely to occur in the orienting and executive than alerting networks. The orienting and executive networks involve skills of selective attention (that is, selectively attending to particular types of information, such as a spatial location or a particular object in space)[79], and as skills they can presumably improve with experience[221]. By contrast, alerting involves obtaining and maintaining an alert state and thus depends more on basic processes of vigilance and preparedness[117,120,131]. Evidence suggests that the inhibition of conflicting information, and more generally the efficiency of executive function, can benefit from practice and training, further supporting the hypothesis that age-related experience can lead to improvements in executive inhibitory function[221–223]. Additionally, a substantial if controversial literature suggests that individuals with more experience in certain aspects of executive function (including inhibitory control), such as bilinguals or musicians (versus monolinguals or non-musicians), may show broader improvements in such functions—especially in older adulthood, including in tasks such as the ANT[162,224–231].

Rather, the data support a view in which some but not other aspects of attention and executive functions decline[94,110,163]. Importantly, variability in age effects across attention/executive functions is also consistent with independent evidence indicating the neurocognitive separability of such functions, not only among the three attentional networks[117,122,123,127,134] but even to some extent among executive functions, including working memory and inhibitory control[78,114–116,172].

Our results suggest that aspects of attention/executive function are not just resistant to age-related declines but can even show improvements, which were observed for both orienting and executive inhibitory function. These improvements are not surprising. Age-related improvements have been found not only in various other domains (including some involving fluid intelligence)[21,40,42,43,52,53,60,66] but also crucially in orienting and executive efficiency in a number of prior ANT studies (Table 1). Indeed, these orienting and executive improvements were observed in a wide range of Western populations[143–145,147,148,150–152], suggesting that the present findings are not unique to people living in Taiwan, the population examined here ('Participants'). Furthermore, a number of previous studies using flanker tasks (which are incorporated in one form into the ANT) have found age-related improvements in the efficiency of the executive network[163,173–177]. Interestingly, a recent study examining age effects on multiple inhibition tasks reported that whereas tasks that tap into the inhibition of prepotent responses (such as stop-signal and Simon tasks) show performance declines with age, those that involve the inhibition of distractors (such as arrow flanker, letter flanker and number Stroop tasks) show improvements[163]. This generalizes our finding of age-related improvements in the executive network beyond the arrow flanker task (increasing the validity of the finding) and provides a possible framework for identifying which inhibitory functions improve and which decline. This fine-grained distinction, in which different ageing trajectories may be found for different inhibitory processes, is in fact consistent with empirical data and theoretical positions suggesting neurocognitive distinctions among different types of inhibition, including between the inhibition of distractors and prepotent responses[175,178–181]. More generally, such a finer-grained distinction agrees with the view espoused in this paper that different attention/executive (sub) processes may show different ageing trajectories, potentially even across different types of inhibition[110,111,113,175,182], and further counters unitary views of executive or inhibitory declines[87–93,95,96]. Note that, as with the ANT, not all studies using flanker[183–187] or number Stroop[188] tasks have reported age-related improvements (some have reported declines and others age invariance); we suggest that variability across ageing studies using these tasks may be due to some of the same experimental and analytical factors discussed in the Introduction.

Overall, our findings suggesting improvements in the orienting and executive networks have clear precedents in the literature, despite the emphasis on age-related declines of attention and executive functions in prior theoretical frameworks. Given these precedents, in addition to our relatively large sample size, the examination of age as a continuous variable (moreover within the period of likely changes, from middle age to older adulthood), the use of both linear and nonlinear analyses, the robustness of the effects and evidence against alternative accounts, our results do not seem likely to be false positives.

How important are the observed age-related improvements? The millisecond differences between middle-aged and older adults in orienting and executive efficiency were relatively small. Such small age effects are not surprising, given that the attentional effects over the full age range were also quite small—in fact, smaller than have generally been reported in older adults in previous ANT studies[140,143,145,146]. Indeed, this was not unexpected, since studies with larger sample sizes often yield smaller effect sizes that are probably closer to the true effects[189–192]. Nonetheless, the efficiency of the orienting network increased about four to five times over the age range in our sample (that is, from middle age to older adulthood), while the efficiency of the executive network increased about twofold from middle age to the mid-to-late 70s. In fact, this executive efficiency increase was large enough that even the subsequent apparent decline never led to worse predicted performance at very old ages than at the minimum age in our sample (Fig. 2). The relevance of the age-related improvements in executive efficiency is further underscored by the finding that executive improvements were observed for accuracy as well as RTs. Finally, given that orienting and perhaps especially executive function underlie many other—particularly higher-level—cognitive capacities, age-related improvements in these attention/executive functions probably have downstream effects on the wide range of cognitive abilities that use them, including spatial navigation, long-term memory encoding and retrieval, decision-making, reasoning, mathematical abilities and language processing[82–86]. The importance of the observed effects may therefore be substantial, perhaps especially for executive inhibitory function.

The multifaceted pattern of ageing observed across the networks (and working memory in the same sample) is probably explained by a combination of neurobiologically based mechanisms that have been invoked in the broader literature on ageing and cognition[1,20,38,48,66,69–75,88,193–195]: neural declines that are countered by maintenance (repair), compensation and experience-related gains, all of which may vary across the networks (Fig. 4). We suggest that orienting and executive function are especially susceptible to learning and thus to experience-based gains in neural efficiency (Fig. 4). An account invoking neural declines countered by experience-related gains can also explain the nonlinear effect of age found for the executive network: up to one's mid-to-late 70s, the impact of the declines may be outweighed by the benefits accrued from continual experience with the network; however, at older ages, the cumulative effect of the declines (perhaps together with an asymptotic learning effect) may yield detectable performance decreases. This account may also explain similar patterns of improvement till around one's 70s in other (crystallized and perhaps fluid) abilities[3,26,196]. Note that because different domains that yield improvements in ageing can show somewhat different trajectories, including the apparent absence of late declines[24,26,46,52,53], the lack of an observable late-age decline in orienting is not particularly unexpected. Future studies may reveal whether orienting in fact shows late or shallow declines that were not detectable here.

This study's limitations and findings suggest new lines of research. Studies should test the generalizability of the results to (1) other tasks, including additional tasks that involve the inhibition of distractors[163] as well as tasks probing other types of inhibition[163,175,178,179,181]; and (2) other populations, including samples with higher mean levels of education, more individuals at the oldest ages and younger adults—while still controlling for sex, education, processing speed, visual abilities and perhaps other variables. Studies should still use continuous age designs and investigate both linear and nonlinear effects of age. Testing the generalizability of our findings in longitudinal designs would be of particular interest, since age-related differences found in cross-sectional designs could also be due to other factors, and age effects in cognition can display different magnitudes in cross-sectional and longitudinal studies[22,196]. For discussions of comparisons between cross-sectional and longitudinal designs in ageing, see refs. [196–198].

Given our hypothesis that the orienting and executive improvements are largely explained by lifelong experience with these networks, future research should attempt to tease apart age and the amount (and perhaps quality) of this experience. Investigations that reveal the neural bases of the experience-based gains are particularly warranted. Indeed, underlying neurobiological gains could occur even if they do not lead to observable performance improvements, given the counteracting neurobiological declines[1,38]. Studies should also examine whether and to what extent the gains observed in orienting and executive function might share common mechanisms, including in aspects of (perhaps spatial-related) skills of selective attention. It may additionally be worthwhile to further probe whether orienting and executive improvements are found irrespective of whether processing speed is controlled for, as was observed here, or whether these improvements may be moderated by processing speed, as prior studies seem to suggest (Table 1). Understanding the nature of individual differences in age-related orienting and executive improvements, including the possibility of 'super-agers', also seems desirable. Critically, future research should investigate likely downstream effects of orienting and executive improvements on higher cognitive functions. These empirical contributions should lead to theoretical accounts of attention/executive functions in ageing that robustly integrate experiential, cognitive and neurobiological factors[25,71,199]. Finally, given the likely effect of experience on improvements in both orienting and executive function, our findings may open doors to translational research and practical benefits, perhaps beyond healthy ageing.

In sum, our findings suggest that whereas alerting efficiency shows age-related declines from middle age to older adulthood, both orienting and executive inhibitory efficiency improve during these years, apparently until quite old age for orienting and until one's mid-to-late 70s for executive function. This underscores the notion that, even though ageing is widely viewed as leading to cognitive declines, it in fact yields multifaceted outcomes, including a range of benefits[43,47,48,50,55,66,74,195]. Importantly, the evidence presented here demonstrates that these benefits are not limited to crystallized cognition but rather extend to fluid processes, in particular aspects of attention and executive function.

Methods

Participants. This study complied with all relevant ethical regulations and was approved by the Institutional Review Boards at Georgetown University, Princeton University and the Ministry of Health in Taiwan. Informed consent was obtained from all participants.

The study was part of the Social Environment and Biomarkers of Aging Study (SEBAS), conducted in Taiwan[200,201]. SEBAS was in turn part of the Taiwan Longitudinal Study of Aging, which examines a nationally representative sample of middle-aged and older adults in Taiwan[200,201]. During (only) the 2011 SEBAS collection wave, three computer-based cognitive tasks were included: a working memory task[109], a declarative memory task[73] and the ANT presented here. See Extended Data Fig. 1 for a summary of results from the working memory and declarative memory tasks. The computer-based tasks were given to all available consenting individuals in the health examination component of SEBAS, which excluded participants if they lived in an institution, were seriously ill or had some other health condition that precluded examination. The age range in the present study was determined by the age range of these participants in 2011 (refs. [109,200]).

The ANT was given to 948 participants, of whom 92 were excluded owing to participant identifier coding errors (3 participants), not performing the full task (18 participants) or a diagnosis of a neurological, psychiatric, learning, cognitive or other brain-related disorder (for more information, see ref. [109]), including dementia, brain atrophy/degeneration, stroke, intracranial haemorrhage, brain tumour, schizophrenia and epilepsy, among others (71 participants). An additional 154 participants were excluded because of low accuracy on the ANT (lower than 75%, following ref. [140]). Note that the same pattern of significance in the findings was obtained in a sensitivity analysis with a more stringent inclusion criterion of at least 90% accuracy (213 participants excluded rather than 154), as well as in another sensitivity analysis with a more lenient inclusion criterion of at least 50% accuracy (122 participants excluded); see Results. The exclusion of all participants who had diagnoses of brain-related disorders, as well as those who did not perform the full task or who had low accuracy, together with the sensitivity analyses showing that the same pattern of results was obtained with both more and less stringent accuracy inclusion criteria, suggests that the results represent healthy ageing and were not due to the inclusion of participants with cognitive impairment.

After these exclusions, statistical analyses were conducted on the data from the remaining 702 participants (mean age, 67.69 years; s.d., 8.30; range, 58–98; for the age distribution, see Extended Data Fig. 1). (Note that because there were few participants in their 90s, we also performed a sensitivity analysis with these individuals excluded; the same pattern of significance was obtained (Results)). The much larger sample size compared with previous ANT ageing studies increases statistical power, yields more precise estimates that are probably closer to true effects[189–192] and facilitates the detection of participant variability (for example, across ages) relative to trial noise[202,203]. To control for the possible confounding effects of education (mean years of education, 7.76; s.d., 4.52; range, 0–17+) and sex (323 female), both of which were associated with age (age–education correlation, with higher ages associated with lower education levels: $r=-0.33$ (-0.39, -0.26), $t(700)=-9.14$, $P<0.001$; males older than females, mean ages 68.39 versus 66.88: difference = 1.51 (0.28, 2.74), $t(700)=2.41$, $P=0.016$), these variables were included as covariates in the analyses[73,109]; the same pattern of results was obtained in a sensitivity analysis without these covariates included (Results). For the sensitivity analysis controlling for visual acuity, we obtained visual acuity measures (Snellen fraction) for 547 of our 702 participants, from the 2006 SEBAS collection wave, as such measures were not available in the 2011 wave. The validity of this measure was confirmed by its significant effect on RTs in the ANT (Results)—a finding that was not surprising, since participants were given the ANT only a few years after visual acuity was measured.

Materials and design. The ANT task was based on the version employed by Costa and collaborators[162]. In each of the 96 trials, the participants saw a 'target' row of five horizontally aligned images of arrows and had to indicate the direction of the central arrow, which faced either the same or the opposite direction as the four surrounding 'flanker' arrows (Supplementary Fig. 1). The target rows appeared either below or above the centre of the screen. In each trial, the target row was preceded by one of four different cue types: (1) no cue; (2) an asterisk in the centre of the screen (central cue); (3) an asterisk either above or below the centre of the screen (spatial cue), which was always consistent with the spatial location of the subsequent target row; and (4) two asterisks presented both above and below the central fixation point (double cue). Thus, there were 32 possible cue–target sequences (4 cue types × 2 target locations × 2 central arrow directions × 2 flanker arrow directions), each presented three times to each participant. Note that although Costa and collaborators[162] also included a neutral condition of dashes as flankers, this is often omitted from ANT tasks (as in the present study) or from analyses, including in studies of older adults[140,144,151], because responses to neutral and congruent flanker targets are highly correlated[122], and because this omission simplifies and shortens the task. The images were enlarged for all participants to minimize visual difficulties for the older population (see 'Linear effects of age: sensitivity analyses' in Results).

Procedure. Each trial began with a central fixation cross (400 ms), which was followed by one of the four types of cue (100 ms)[162]: the continuing fixation cross accompanied by one asterisk either above or below it (spatial cue; Supplementary Fig. 1); two asterisks both above and below the continuing cross (double cue); no asterisk—that is, just the continuing fixation cross (no cue); or a central asterisk in lieu of the fixation cross (central cue). The fixation cross was then shown alone for 400 ms, after which it was accompanied by the target row of arrows (until a response or the timeout of 1,700 ms; Supplementary Fig. 1). After an interstimulus interval of 400 ms (blank screen), the next trial began. The participants were instructed to report the direction of the central arrow as quickly and accurately as possible by pressing one of two buttons on a response box (SRBOX, Psychology Software Tools). The task was presented on a Windows XP laptop with E-Prime version 2.0. Both the participants and the experimenters were blind to the aims of the study, in particular the examination of age effects on the efficiency of each network.

Data exclusions and analysis. Before the analyses, trials with timeouts (1.08% of all trials), presses of inappropriate response box buttons (0.02%) and incorrect responses (1.62%) were excluded, since (following the ANT literature) our analyses focus on RTs of correct responses; for accuracy analyses, see Extended Data Fig. 2. Extremely fast responses (that is, below 100 ms) were discarded (0.009% of the remaining data) because they are likely to constitute 'short outliers'[204]. Responses to double cue trials were additionally excluded (following refs. [140,143,149,150]), owing to their redundancy with central cue trials[127,140]; this enabled the calculation of the alerting and orienting effects within a single statistical model by comparing no cue and spatial cue trials against the same baseline (central cue trials)[140]. A sensitivity analysis including both central and double cue trials yielded the same pattern of results (Results).

Analyses were conducted on the natural logarithms of RTs. The linear statistical models reported thus assume linear effects on the log scale and so correspond to proportional effects on the millisecond scale (for example, two distinct differences in milliseconds are treated similarly if they correspond to the same percentage differences). The log transformation is commonly applied to RT distributions because it provides several advantages relative to analyses of raw (untransformed) RTs: (1) it reduces the high skewness of RTs, normalizing the distribution of residuals and thus satisfying the assumptions of linear statistical models[205,206]; (2) it minimizes the influence of 'long outliers', which are common in button-pressing tasks[204]; and, perhaps most importantly, (3) it reduces the large differences that exist across items, conditions or individuals in their processing speed, a particular problem in studies of ageing[15,158,207]. Nevertheless, a sensitivity analysis was conducted on raw (untransformed) RTs; this yielded the same pattern of findings as the main analysis (Results).

The data were analysed with linear mixed-effects regression models in R, using lme4 package version 1.1-23[208]]. Fixed effects were cue type (no cue, central cue or spatial cue), flanker type (congruent or incongruent) and age (in years; continuous). The two-way interactions between these predictors were also included as predictors—namely, cue type × flanker type (which is standard in ANT analyses[122,140,146]) and the critical interactions of interest: age × cue type and age × flanker type, which allow estimating the effect of age on the three attentional networks (alerting, orienting and executive). Additionally, sex (male or female) and education (in years; continuous) were included as covariates (without interactions) to control for correlations between age and these variables. Trial position in the experiment was also included as a covariate without interactions to control for practice/fatigue effects and to reduce the autocorrelation of residuals[205]. A sensitivity analysis without any covariates yielded the same pattern of findings (Results). To avoid complexity, higher-level interactions were not included in the statistical model.

The predictors were coded to allow the assessment of the three attentional network effects and the main effect of age within a single statistical model. Specifically, we used 'sum contrasts' for the two-level factors—that is, for flanker (congruent = −0.5, incongruent = 0.5) and sex (female = −0.5, male = 0.5); we employed 'sliding difference contrasts' for the three-level factor cue (to estimate the alerting effect: central = −1/3, no cue = 2/3, spatial = −1/3; to estimate the orienting effect: central = 1/3, no cue = 1/3, spatial = −2/3)[209]; and we centred all continuous predictors at their respective means (age, education and trial position). With these regression contrasts included in the same model, it was possible to obtain estimates comparing central with no cue conditions (alerting), spatial with central cue conditions (orienting) and incongruent with congruent flanker conditions (executive)[209]. Each of these comparisons was estimated at the mean of all other predictors, while controlling for all covariates. Follow-up comparisons (for example, for specific conditions or at specific values of age) were obtained by dummy-coding predictors with different reference levels (that is, using 0, 1 contrasts) or by centring age at different values and then refitting the model.

The primary model, as well as all further models, included a random by-participant intercept. To further reduce the probability of committing false positive errors, a 'random slope' for flanker type by participant (which captures the variation of flanker effects across participants) was included in all models (except in cases of non-convergence; see the caption for Extended Data Fig. 2 and notes to Supplementary Tables 1 and 2), as it produced models with greater goodness of fit (lower Akaike information criterion) than the intercept-only models[210,211]. A random slope for cue type by participant was not included because models with this random structure did not converge. Item as a random effect was not included since all possible combinations of item types (cue types × target locations × central arrow directions × flanker arrow directions) are included in the study design, and thus items were not randomly sampled from a population. Assumptions of additivity and normality as well as homogeneity of variances were broadly satisfied in our models, as ascertained by visualizations of residuals[212,213].

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability
The anonymized data (with accompanying documentation) have been uploaded to the Open Science Framework. They can be found at https://osf.io/59er2/.

Code availability
Commented analysis scripts (in the R programming language) for all statistical models reported in this paper have been uploaded to the Open Science Framework. They can be found at https://osf.io/59er2/.

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References

1. Nyberg, L., Lövdén, M., Riklund, K., Lindenberger, U. & Bäckman, L. Memory aging and brain maintenance. *Trends Cogn. Sci.* **16**, 292–305 (2012).
2. Old, S. R. & Naveh-Benjamin, M. Differential effects of age on item and associative measures of memory: a meta-analysis. *Psychol. Aging* **23**, 104–118 (2008).
3. Rönnlund, M., Nyberg, L., Bäckman, L. & Nilsson, L.-G. Stability, growth, and decline in adult life span development of declarative memory: cross-sectional and longitudinal data from a population-based study. *Psychol. Aging* **20**, 3–18 (2005).
4. Ratcliff, R., Thapar, A., Gomez, P. & McKoon, G. A diffusion model analysis of the effects of aging in the lexical-decision task. *Psychol. Aging* **19**, 278–289 (2004).
5. Wierenga, C. E. et al. Age-related changes in word retrieval: role of bilateral frontal and subcortical networks. *Neurobiol. Aging* **29**, 436–451 (2008).
6. Greve, A., Cooper, E. & Henson, R. N. No evidence that 'fast-mapping' benefits novel learning in healthy older adults. *Neuropsychologia* **60**, 52–59 (2014).
7. Whiting, E., Chenery, H. J. & Copland, D. A. Effect of aging on learning new names and descriptions for objects. *Aging Neuropsychol. Cogn.* **18**, 594–619 (2011).
8. Howard, D. V. et al. Implicit sequence learning: effects of level of structure, adult age, and extended practice. *Psychol. Aging* **19**, 79–92 (2004).
9. Howard, J. H. & Howard, D. V. Aging mind and brain: is implicit learning spared in healthy aging?. *Front. Psychol.* **4**, 817 (2013).
10. Shea, C. H., Park, J.-H. & Braden, H. W. Age-related effects in sequential motor learning. *Phys. Ther.* **86**, 478–488 (2006).
11. Bo, J., Borza, V. & Seidler, R. D. Age-related declines in visuospatial working memory correlate with deficits in explicit motor sequence learning. *J. Neurophysiol.* **102**, 2744–2754 (2009).
12. Iachini, T., Iavarone, A., Senese, V., Ruotolo, F. & Ruggiero, G. Visuospatial memory in healthy elderly, AD and MCI: a review. *Curr. Aging Sci.* **2**, 43–59 (2009).
13. Monge, Z. A. & Madden, D. J. Linking cognitive and visual perceptual decline in healthy aging: the information degradation hypothesis. *Neurosci. Biobehav. Rev.* **69**, 166–173 (2016).
14. Naveh-Benjamin, M. & Kilb, A. Age-related differences in associative memory: the role of sensory decline. *Psychol. Aging* **29**, 672–683 (2014).
15. Salthouse, T. A. The processing-speed theory of adult age differences in cognition. *Psychol. Rev.* **103**, 403–428 (1996).
16. Jenkins, L., Myerson, J., Joerding, J. A. & Hale, S. Converging evidence that visuospatial cognition is more age-sensitive than verbal cognition. *Psychol. Aging* **15**, 157–175 (2000).
17. Lindenberger, U., Scherer, H. & Baltes, P. B. The strong connection between sensory and cognitive performance in old age: not due to sensory acuity reductions operating during cognitive assessment. *Psychol. Aging* **16**, 196–205 (2001).
18. Park, D. C. et al. Mediators of long-term memory performance across the life span. *Psychol. Aging* **11**, 621–637 (1996).
19. Verhaeghen, P. & Salthouse, T. A. Meta-analyses of age–cognition relations in adulthood: estimates of linear and nonlinear age effects and structural models. *Psychol. Bull.* **122**, 231–249 (1997).
20. Cabeza, R., Nyberg, L. & Park, D. C. *Cognitive Neuroscience of Aging: Linking Cognitive and Cerebral Aging* (Oxford Univ. Press, 2016).
21. Carstensen, L. L. et al. Emotional experience improves with age: evidence based on over 10 years of experience sampling. *Psychol. Aging* **26**, 21–33 (2011).
22. Schaie, K. W. & Willis, S. L. The Seattle Longitudinal Study of adult cognitive development. *ISSBD Bull.* **2010**(1), 24–29 (2010).
23. Anderson, N. D. & Craik, F. I. M. 50 years of cognitive aging theory. *J. Gerontol. B* **72**, 1–6 (2017).
24. Hartshorne, J. K. & Germine, L. T. When does cognitive functioning peak? The asynchronous rise and fall of different cognitive abilities across the life span. *Psychol. Sci.* **26**, 433–443 (2015).
25. Hedden, T. & Gabrieli, J. D. E. Insights into the ageing mind: a view from cognitive neuroscience. *Nat. Rev. Neurosci.* **5**, 87–96 (2004).
26. Park, D. C. et al. Models of visuospatial and verbal memory across the adult life span. *Psychol. Aging* **17**, 299–320 (2002).
27. Piolino, P., Desgranges, B., Benali, K. & Eustache, F. Episodic and semantic remote autobiographical memory in ageing. *Memory* **10**, 239–257 (2002).
28. Schaie, K. W. *Intellectual Development in Adulthood: The Seattle Longitudinal Study* (Cambridge Univ. Press, 1996).
29. Cansino, S. et al. The decline of verbal and visuospatial working memory across the adult life span. *Age (Dordr.)* **35**, 2283–2302 (2013).
30. Ikier, S., Yang, L. & Hasher, L. Implicit proactive interference, age, and automatic versus controlled retrieval strategies. *Psychol. Sci.* **19**, 456–461 (2008).
31. Jacoby, L. L. Ironic effects of repetition: measuring age-related differences in memory. *J. Exp. Psychol. Learn. Mem. Cogn.* **25**, 3–22 (1999).
32. Laver, G. D. Adult aging effects on semantic and episodic priming in word recognition. *Psychol. Aging* **24**, 28–39 (2009).
33. Campbell, K. L. et al. Robust resilience of the frontotemporal syntax system to aging. *J. Neurosci.* **36**, 5214–5227 (2016).
34. Cohen-Shikora, E. R. & Balota, D. A. Visual word recognition across the adult lifespan. *Psychol. Aging* **31**, 488–502 (2016).
35. Reifegerste, J., Elin, K. & Clahsen, H. Persistent differences between native speakers and late bilinguals: evidence from inflectional and derivational processing in older speakers. *Biling. Lang. Cogn.* **22**, 425–440 (2019).
36. Royle, P., Steinhauer, K., Dessureault, É., Herbay, A. C. & Brambati, S. M. Aging and language: maintenance of morphological representations in older adults. *Front. Commun.* **4**, 16 (2019).
37. Shafto, M. A. & Tyler, L. K. Language in the aging brain: the network dynamics of cognitive decline and preservation. *Science* **346**, 583–587 (2014).

38. Cabeza, R. et al. Maintenance, reserve and compensation: the cognitive neuroscience of healthy ageing. *Nat. Rev. Neurosci.* **19**, 701–710 (2018).
39. Horton, S., Baker, J. & Schorer, J. Expertise and aging: maintaining skills through the lifespan. *Eur. Rev. Aging Phys. Act.* **5**, 89–96 (2008).
40. Horn, J. L. in *Aging and Cognitive Processes* (eds Craik, F. I. M. & Trehub, S.) 237–278 (Plenum, 1982).
41. Horn, J. L. & Cattell, R. B. Age differences in fluid and crystallized intelligence. *Acta Psychol. (Amst.)* **26**, 107–129 (1967).
42. Li, S.-C. in *International Encyclopedia of the Social and Behavioral Sciences* (eds Smelser, N. J. & Baltes, P. B.) 310–317 (Elsevier, 2001).
43. Baltes, P. B. & Kliegl, R. in *Neurology* (eds. Poeck, K. et al.) 1–17 (Springer, 1986).
44. Ben-David, B. M., Erel, H., Goy, H. & Schneider, B. A. "Older is always better": age-related differences in vocabulary scores across 16 years. *Psychol. Aging* **30**, 856–862 (2015).
45. Cattell, R. B. *Abilities: Their Structure, Growth, and Action* (Houghton Mifflin, 1971).
46. Goral, M., Spiro, A., Albert, M. L., Obler, L. K. & Connor, L. T. Change in lexical retrieval skills in adulthood. *Ment. Lex.* **2**, 215–238 (2007).
47. Horn, J. L. & Donaldson, G. On the myth of intellectual decline in adulthood. *Am. Psychol.* **31**, 701–719 (1976).
48. Spreng, R. N. & Turner, G. R. The shifting architecture of cognition and brain function in older adulthood. *Perspect. Psychol. Sci.* **14**, 523–542 (2019).
49. Verhaeghen, P. Aging and vocabulary score: a meta-analysis. *Psychol. Aging* **18**, 332–339 (2003).
50. Baltes, P. B. & Smith, J. The fascination of wisdom: its nature, ontogeny, and function. *Perspect. Psychol. Sci.* **3**, 56–64 (2008).
51. Lim, K. T. K. & Yu, R. Aging and wisdom: age-related changes in economic and social decision making. *Front. Aging Neurosci.* **7**, 120 (2015).
52. Happé, F. G. E., Winner, E. & Brownell, H. The getting of wisdom: theory of mind in old age. *Dev. Psychol.* **34**, 358–362 (1998).
53. Burr, D. A., Castrellon, J. J., Zald, D. H. & Samanez-Larkin, G. R. Emotion dynamics across adulthood in everyday life: older adults are more emotionally stable and better at regulating desires. *Emotion* https://doi.org/10/gg3kg2 (2020).
54. Carstensen, L. L., Pasupathi, M., Mayr, U. & Nesselroade, J. R. Emotional experience in everyday life across the adult life span. *J. Pers. Soc. Psychol.* **79**, 644–655 (2000).
55. Carstensen, L. L., Fung, H. H. & Charles, S. T. Socioemotional selectivity theory and the regulation of emotion in the second half of life. *Motiv. Emot.* **27**, 103–123 (2003).
56. Urry, H. L. & Gross, J. J. Emotion regulation in older age. *Curr. Dir. Psychol. Sci.* **19**, 352–357 (2010).
57. Li, Y., Baldassi, M., Johnson, E. J. & Weber, E. U. Complementary cognitive capabilities, economic decision making, and aging. *Psychol. Aging* **28**, 595–613 (2013).
58. Mata, R., Schooler, L. J. & Rieskamp, J. The aging decision maker: cognitive aging and the adaptive selection of decision strategies. *Psychol. Aging* **22**, 796–810 (2007).
59. Strough, J., Schlosnagle, L. & DiDonato, L. Understanding decisions about sunk costs from older and younger adults' perspectives. *J. Gerontol. B* **66B**, 681–686 (2011).
60. Strough, J., Mehta, C. M., McFall, J. P. & Schuller, K. L. Are older adults less subject to the sunk-cost fallacy than younger adults? *Psychol. Sci.* **19**, 650–652 (2008).
61. Kanfer, R., Beier, M. E. & Ackerman, P. L. Goals and motivation related to work in later adulthood: an organizing framework. *Eur. J. Work Organ. Psychol.* **22**, 253–264 (2013).
62. Kooij, D. T. A. M., De Lange, A. H., Jansen, P. G. W., Kanfer, R. & Dikkers, J. S. E. Age and work-related motives: results of a meta-analysis. *J. Organ. Behav.* **32**, 197–225 (2011).
63. Donnellan, M. B. & Lucas, R. E. Age differences in the big five across the life span: evidence from two national samples. *Psychol. Aging* **23**, 558–566 (2008).
64. Ibanez, A. et al. Empathy, sex and fluid intelligence as predictors of theory of mind. *Pers. Individ. Differ.* **54**, 616–621 (2013).
65. Opitz, P. C., Lee, I. A., Gross, J. J. & Urry, H. L. Fluid cognitive ability is a resource for successful emotion regulation in older and younger adults. *Front. Psychol.* **5**, 609 (2014).
66. Kanfer, R. & Ackerman, P. L. Aging, adult development, and work motivation. *Acad. Manage. Rev.* **29**, 440–458 (2004).
67. Lövdén, M., Ghisletta, P. & Lindenberger, U. Cognition in the Berlin Aging Study (BASE): the first 10 years. *Aging Neuropsychol. Cogn.* **11**, 104–133 (2004).
68. Ng, T. W. H. & Feldman, D. C. The relationship of age to ten dimensions of job performance. *J. Appl. Psychol.* **93**, 392–423 (2008).
69. Ardelt, M. Wisdom as expert knowledge system: a critical review of a contemporary operationalization of an ancient concept. *Hum. Dev.* **47**, 257–285 (2004).
70. Buchler, N. E. G. & Reder, L. M. Modeling age-related memory deficits: a two-parameter solution. *Psychol. Aging* **22**, 104–121 (2007).
71. Ramscar, M., Hendrix, P., Shaoul, C., Milin, P. & Baayen, R. H. The myth of cognitive decline: non-linear dynamics of lifelong learning. *Top. Cogn. Sci.* **6**, 5–42 (2014).
72. Ramscar, M., Sun, C. C., Hendrix, P. & Baayen, R. H. The mismeasurement of mind: life-span changes in paired-associate-learning scores reflect the 'cost' of learning, not cognitive decline. *Psychol. Sci.* **28**, 1171–1179 (2017).
73. Reifegerste, J. et al. Early-life education may help bolster declarative memory in old age, especially for women. *Aging Neuropsychol. Cogn.* **28**, 218–252 (2021).
74. Stine-Morrow, E. A. L. The Dumbledore hypothesis of cognitive aging. *Curr. Dir. Psychol. Sci.* **16**, 295–299 (2007).
75. Umanath, S. & Marsh, E. J. Understanding how prior knowledge influences memory in older adults. *Perspect. Psychol. Sci.* **9**, 408–426 (2014).
76. Zaval, L., Li, Y., Johnson, E. J. & Weber, E. U. in *Aging and Decision Making* (eds Hess, T. M. et al.) 149–168 (Elsevier, 2015).
77. Fernandez-Duque, D. & Posner, M. I. Relating the mechanisms of orienting and alerting. *Neuropsychologia* **35**, 477–486 (1997).
78. Miyake, A. et al. The unity and diversity of executive functions and their contributions to complex 'frontal lobe' tasks: a latent variable analysis. *Cogn. Psychol.* **41**, 49–100 (2000).
79. Zanto, T. P. & Gazzaley, A. in *The Oxford Handbook of Attention* (eds Nobre, A. C. & Kastner, S.) 927–971 (Oxford Univ. Press, 2014).
80. Kinsella, G., Storey, E. & Crawford, J. R. in *Neurology and Clinical Neuroscience* (ed. Schapira, A. H. V.) 83–95 (Elsevier, 1998).
81. Vaughan, L. & Giovanello, K. Executive function in daily life: age-related influences of executive processes on instrumental activities of daily living. *Psychol. Aging* **25**, 343–355 (2010).
82. Del Missier, F., Mäntylä, T. & Bruine de Bruin, W. Executive functions in decision making: an individual differences approach. *Think. Reason.* **16**, 69–97 (2010).
83. García-Madruga, J. A., Gómez-Veiga, I. & Vila, J. Ó. Executive functions and the improvement of thinking abilities: the intervention in reading comprehension. *Front. Psychol.* **7**, 58 (2016).
84. Martin, R. & Allen, C. A disorder of executive function and its role in language processing. *Semin. Speech Lang.* **29**, 201–210 (2008).
85. Mazuka, R., Jincho, N. & Oishi, H. Development of executive control and language processing. *Lang. Linguist. Compass* **3**, 59–89 (2009).
86. Schiebener, J. et al. Among three different executive functions, general executive control ability is a key predictor of decision making under objective risk. *Front. Psychol.* **5**, 1386 (2014).
87. Braver, T. S. & Barch, D. M. A theory of cognitive control, aging cognition, and neuromodulation. *Neurosci. Biobehav. Rev.* **26**, 809–817 (2002).
88. Buckner, R. L. Memory and executive function in aging and AD. *Neuron* **44**, 195–208 (2004).
89. Fjell, A. M., Sneve, M. H., Grydeland, H., Storsve, A. B. & Walhovd, K. B. The disconnected brain and executive function decline in aging. *Cereb. Cortex* **27**, 2303–2317 (2016).
90. Hasher, L., Lustig, C. & Zacks, R. T. in *Variation in Working Memory* (eds Conway, A. R. A. et al.) 227–249 (Oxford Univ. Press, 2007).
91. Hasher, L. & Zacks, R. T. in *The Psychology of Learning and Motivation* (ed. Bower, G. H.) Vol. 22, 193–225 (Academic, 1988).
92. Hasher, L., Stoltzfus, E. R., Zacks, R. T. & Rypma, B. Age and inhibition. *J. Exp. Psychol. Learn. Mem. Cogn.* **17**, 163–169 (1991).
93. MacPherson, S. E., Phillips, L. H. & Della Sala, S. Age, executive function and social decision making: a dorsolateral prefrontal theory of cognitive aging. *Psychol. Aging* **17**, 598–609 (2002).
94. Posner, M. I., Rothbart, M. K. & Ghassemzadeh, H. Restoring attention networks. *Yale J. Biol. Med.* **92**, 139–143 (2019).
95. West, R. L. An application of prefrontal cortex function theory to cognitive aging. *Psychol. Bull.* **120**, 272–292 (1996).
96. West, R. L. In defense of the frontal lobe hypothesis of cognitive aging. *J. Int. Neuropsychol. Soc.* **6**, 727–729 (2000).
97. Goh, J. O., Beason-Held, L. L., An, Y., Kraut, M. A. & Resnick, S. M. Frontal function and executive processing in older adults: process and region specific age-related longitudinal functional changes. *NeuroImage* **69**, 43–50 (2013).
98. Kennedy, K. M. & Raz, N. Aging white matter and cognition: differential effects of regional variations in diffusion properties on memory, executive functions, and speed. *Neuropsychologia* **47**, 916–927 (2009).
99. Mather, M. & Harley, C. W. The locus coeruleus: essential for maintaining cognitive function and the aging brain. *Trends Cogn. Sci.* **20**, 214–226 (2016).
100. Pardo, J. V. et al. Where the brain grows old: decline in anterior cingulate and medial prefrontal function with normal aging. *NeuroImage* **35**, 1231–1237 (2007).
101. Raz, N., Ghisletta, P., Rodrigue, K. M., Kennedy, K. M. & Lindenberger, U. Trajectories of brain aging in middle-aged and older adults: regional and individual differences. *NeuroImage* **51**, 501–511 (2010).

102. Raz, N. & Rodrigue, K. M. Differential aging of the brain: patterns, cognitive correlates and modifiers. *Neurosci. Biobehav. Rev.* **30**, 730–748 (2006).
103. Bopp, K. L. & Verhaeghen, P. Aging and verbal memory span: a meta-analysis. *J. Gerontol. B.* **60**, P223–P233 (2005).
104. Bopp, K. L. & Verhaeghen, P. Aging and *n*-back performance: a meta-analysis. *J. Gerontol. B* https://doi.org/10/ggjwwt (2020)
105. Burke, D. M. & Osborne, G. in *Inhibition in Cognition* (eds Gorfein, D. S. & MacLeod, C. M.) 163–183 (American Psychological Association, 2007).
106. Glisky, E. L. in *Brain Aging: Models, Methods, and Mechanisms* (ed. Riddle, D. R.) Ch. 1 (Taylor & Francis, 2007).
107. McDonough, I. M., Wood, M. M. & Miller, W. S. A review on the trajectory of attentional mechanisms in aging and the Alzheimer's disease continuum through the Attention Network Test. *Yale J. Biol. Med.* **92**, 37–51 (2019).
108. McDowd, J. M. & Shaw, R. J. in *The Handbook of Aging and Cognition* (eds Craik, F. I. M. & Salthouse, T. A.) 221–292 (Lawrence Erlbaum, 2000).
109. Pliatsikas, C. et al. Working memory in older adults declines with age, but is modulated by sex and education. *Q. J. Exp. Psychol.* **72**, 1308–1327 (2019).
110. Rey-Mermet, A. & Gade, M. Inhibition in aging: what is preserved? What declines? A meta-analysis. *Psychon. Bull. Rev.* **25**, 1695–1716 (2018).
111. Verhaeghen, P. Aging and executive control: reports of a demise greatly exaggerated. *Curr. Dir. Psychol. Sci.* **20**, 174–180 (2011).
112. Verhaeghen, P. *The Elements of Cognitive Aging: Meta-analyses of Age-Related Differences in Processing Speed and Their Consequences* (Oxford Univ. Press, 2013).
113. Verhaeghen, P. & Cerella, J. Aging, executive control, and attention: a review of meta-analyses. *Neurosci. Biobehav. Rev.* **26**, 849–857 (2002).
114. Friedman, N. P. & Miyake, A. Unity and diversity of executive functions: individual differences as a window on cognitive structure. *Cortex* **86**, 186–204 (2017).
115. Karr, J. E. et al. The unity and diversity of executive functions: a systematic review and re-analysis of latent variable studies. *Psychol. Bull.* **144**, 1147–1185 (2018).
116. Miyake, A. & Friedman, N. P. The nature and organization of individual differences in executive functions: four general conclusions. *Curr. Dir. Psychol. Sci.* **21**, 8–14 (2012).
117. Petersen, S. E. & Posner, M. I. The attention system of the human brain: 20 years after. *Annu. Rev. Neurosci.* **35**, 73–89 (2012).
118. Salthouse, T. A. Is flanker-based inhibition related to age? Identifying specific influences of individual differences on neurocognitive variables. *Brain Cogn.* **73**, 51–61 (2010).
119. Uttl, B. & Graf, P. Color–Word Stroop test performance across the adult life span. *J. Clin. Exp. Neuropsychol.* **19**, 405–420 (1997).
120. Posner, M. I. & Petersen, S. E. The attention system of the human brain. *Annu. Rev. Neurosci.* **13**, 25–42 (1990).
121. Staub, B., Doignon-Camus, N., Després, O. & Bonnefond, A. Sustained attention in the elderly: what do we know and what does it tell us about cognitive aging? *Ageing Res. Rev.* **12**, 459–468 (2013).
122. Fan, J., McCandliss, B. D., Sommer, T., Raz, A. & Posner, M. I. Testing the efficiency and independence of attentional networks. *J. Cogn. Neurosci.* **14**, 340–347 (2002).
123. Fan, J. et al. Testing the behavioral interaction and integration of attentional networks. *Brain Cogn.* **70**, 209–220 (2009).
124. Posner, M. I., Sheese, B. E., Odludaş, Y. & Tang, Y. Analyzing and shaping human attentional networks. *Neural Netw.* **19**, 1422–1429 (2006).
125. Wang, H., Fan, J. & Johnson, T. R. A symbolic model of human attentional networks. *Cogn. Syst. Res.* **5**, 119–134 (2004).
126. Fan, J., Fossella, J., Sommer, T., Wu, Y. & Posner, M. I. Mapping the genetic variation of executive attention onto brain activity. *Proc. Natl Acad. Sci. USA* **100**, 7406–7411 (2003).
127. Fan, J., Mccandliss, B., Fossella, J., Flombaum, J. & Posner, M. I. The activation of attentional networks. *NeuroImage* **26**, 471–479 (2005).
128. Konrad, K., Neufang, S., Hanisch, C., Fink, G. R. & Herpertz-Dahlmann, B. Dysfunctional attentional networks in children with attention deficit/hyperactivity disorder: evidence from an event-related functional magnetic resonance imaging study. *Biol. Psychiatry* **59**, 643–651 (2006).
129. Niogi, S., Mukherjee, P., Ghajar, J. & McCandliss, B. D. Individual differences in distinct components of attention are linked to anatomical variations in distinct white matter tracts. *Front. Neuroanat.* https://doi.org/10/cghhr4 (2010).
130. Beane, M. & Marrocco, R. T. in *Cognitive Neuroscience of Attention* (ed. Posner, M. I.) 313–325 (Guilford, 2004).
131. Posner, M. I. & Rothbart, M. K. Research on attention networks as a model for the integration of psychological science. *Annu. Rev. Psychol.* **58**, 1–23 (2007).
132. Witte, E. A., Davidson, M. C. & Marrocco, R. T. Effects of altering brain cholinergic activity on covert orienting of attention: comparison of monkey and human performance. *Psychopharmacol. (Berl.)* **132**, 324–334 (1997).
133. Witte, E. A. & Marrocco, R. T. Alteration of brain noradrenergic activity in rhesus monkeys affects the alerting component of covert orienting. *Psychopharmacol. (Berl.)* **132**, 315–323 (1997).
134. Fossella, J. et al. Assessing the molecular genetics of attention networks. *BMC Neurosci.* **3**, 14 (2002).
135. Pozuelos, J. P., Paz-Alonso, P. M., Castillo, A., Fuentes, L. J. & Rueda, M. R. Development of attention networks and their interactions in childhood. *Dev. Psychol.* **50**, 2405–2415 (2014).
136. Posner, M. I. Orienting of attention. *Q. J. Exp. Psychol.* **32**, 3–25 (1980).
137. Eriksen, B. A. & Eriksen, C. W. Effects of noise letters upon the identification of a target letter in a nonsearch task. *Percept. Psychophys.* **16**, 143–149 (1974).
138. Ishigami, Y. et al. The Attention Network Test-Interaction (ANT-I): reliability and validity in healthy older adults. *Exp. Brain Res.* **234**, 815–827 (2016).
139. Ishigami, Y. & Klein, R. M. Repeated measurement of the components of attention of older adults using the two versions of the Attention Network Test: stability, isolability, robustness, and reliability. *Front. Aging Neurosci.* **3**, 17 (2011).
140. Mahoney, J. R., Verghese, J., Goldin, Y., Lipton, R. & Holtzer, R. Alerting, orienting, and executive attention in older adults. *J. Int. Neuropsychol. Soc.* **16**, 877–889 (2010).
141. MacLeod, J. W. et al. Appraising the ANT: psychometric and theoretical considerations of the Attention Network Test. *Neuropsychology* **24**, 637–651 (2010).
142. Dash, T., Berroir, P., Joanette, Y. & Ansaldo, A. I. Alerting, orienting, and executive control: the effect of bilingualism and age on the subcomponents of attention. *Front. Neurol.* **10**, 1122 (2019).
143. Deiber, M.-P., Ibañez, V., Missonnier, P., Rodriguez, C. & Giannakopoulos, P. Age-associated modulations of cerebral oscillatory patterns related to attention control. *NeuroImage* **82**, 531–546 (2013).
144. Fernandez-Duque, D. & Black, S. E. Attentional networks in normal aging and Alzheimer's disease. *Neuropsychology* **20**, 133–143 (2006).
145. Gamboz, N., Zamarian, S. & Cavallero, C. Age-related differences in the Attention Network Test (ANT). *Exp. Aging Res.* **36**, 287–305 (2010).
146. Jennings, J. M., Dagenbach, D., Engle, C. M. & Funke, L. J. Age-related changes and the Attention Network Task: an examination of alerting, orienting, and executive function. *Aging Neuropsychol. Cogn.* **14**, 353–369 (2007).
147. Kaufman, D. A. S., Sozda, C. N., Dotson, V. M. & Perlstein, W. M. An event-related potential investigation of the effects of age on alerting, orienting, and executive function. *Front. Aging Neurosci.* **8**, 99 (2016).
148. Knight, M. & Mather, M. Look out—it's your off-peak time of day! Time of day matters more for alerting than for orienting or executive attention. *Exp. Aging Res.* **39**, 305–321 (2013).
149. Lu, H., Fung, A. W. T., Chan, S. S. M. & Lam, L. C. W. Disturbance of attention network functions in Chinese healthy older adults: an intra-individual perspective. *Int. Psychogeriatr.* **28**, 291–301 (2016).
150. Westlye, L. T., Grydeland, H., Walhovd, K. B. & Fjell, A. M. Associations between regional cortical thickness and attentional networks as measured by the Attention Network Test. *Cereb. Cortex* **21**, 345–356 (2011).
151. Williams, R. S. et al. Age differences in the attention network test: evidence from behavior and event-related potentials. *Brain Cogn.* **102**, 65–79 (2016).
152. Young-Bernier, M., Tanguay, A. N., Tremblay, F. & Davidson, P. S. R. Age differences in reaction times and a neurophysiological marker of cholinergic activity. *Can. J. Aging* **34**, 471–480 (2015).
153. Zhou, S., Fan, J., Lee, T. M. C., Wang, C. & Wang, K. Age-related differences in attentional networks of alerting and executive control in young, middle-aged, and older Chinese adults. *Brain Cogn.* **75**, 205–210 (2011).
154. Baayen, R. H. A real experiment is a factorial experiment? *Ment. Lex.* **5**, 149–157 (2010).
155. Jacobsen, G. M., de Mello, C. M., Kochhann, R. & Fonseca, R. P. Executive functions in school-age children: influence of age, gender, school type and parental education. *Appl. Cogn. Psychol.* **31**, 404–413 (2017).
156. Kamkar, N. H. & Morton, J. B. CanDiD: a framework for linking executive function and education. *Front. Psychol.* **8**, 1187 (2017).
157. Liu, G., Hu, P., Fan, J. & Wang, K. Gender differences associated with orienting attentional networks in healthy subjects. *Chin. Med. J. (Engl.)* **126**, 2308–2312 (2013).
158. Faust, M. E., Balota, D. A., Spieler, D. H. & Ferraro, F. R. Individual differences in information-processing rate and amount: implications for group differences in response latency. *Psychol. Bull.* **125**, 777–799 (1999).
159. Friedman, L. & Wall, M. Graphical views of suppression and multicollinearity in multiple linear regression. *Am. Stat.* **59**, 127–136 (2005).
160. Wurm, L. H. & Fisicaro, S. A. What residualizing predictors in regression analyses does (and what it does not do). *J. Mem. Lang.* **72**, 37–48 (2014).
161. Gittings, N. S. & Fozard, J. L. Age related changes in visual acuity. *Exp. Gerontol.* **21**, 423–433 (1986).

162. Costa, A., Hernández, M. & Sebastián-Gallés, N. Bilingualism aids conflict resolution: evidence from the ANT task. *Cognition* **106**, 59–86 (2008).
163. Rey-Mermet, A., Gade, M. & Oberauer, K. Should we stop thinking about inhibition? Searching for individual and age differences in inhibition ability. *J. Exp. Psychol. Learn. Mem. Cogn.* **44**, 501–526 (2018).
164. Sekuler, A. B., Bennett, P. J. & Mamelak, M. Effects of aging on the useful field of view. *Exp. Aging Res.* **26**, 103–120 (2000).
165. Baayen, R. H. *Analyzing Linguistic Data: A Practical Introduction to Statistics Using R* (Cambridge Univ. Press, 2008).
166. Neter, J., Kutner, M., Nachtsheim, C. & Wasserman, W. *Applied Linear Statistical Models* (Irwin, 1996).
167. Bosch, S., Veríssimo, J. & Clahsen, H. Inflectional morphology in bilingual language processing: an age-of-acquisition study. *Lang. Acquis.* **26**, 339–360 (2019).
168. Veríssimo, J., Heyer, V., Jacob, G. & Clahsen, H. Selective effects of age of acquisition on morphological priming: evidence for a sensitive period. *Lang. Acquis.* **25**, 315–326 (2018).
169. Hassing, L., Wahlin, Å. & Bäckman, L. Minimal influence of age, education, and gender on episodic memory functioning in very old age: a population-based study of nonagenarians. *Arch. Gerontol. Geriatr.* **27**, 75–87 (1998).
170. Lindenberger, U., Singer, T. & Baltes, P. B. Longitudinal selectivity in aging populations: separating mortality-associated versus experimental components in the Berlin Aging Study (BASE). *J. Gerontol. B.* **57**, P474–P482 (2002).
171. Singer, T., Verhaeghen, P., Ghisletta, P., Lindenberger, U. & Baltes, P. B. The fate of cognition in very old age: six-year longitudinal findings in the Berlin Aging Study (BASE). *Psychol. Aging* **18**, 318–331 (2003).
172. Chen, Y. et al. Testing a cognitive control model of human intelligence. *Sci. Rep.* **9**, 2898 (2019).
173. Madden, D. J. & Gottlob, L. R. Adult age differences in strategic and dynamic components of focusing visual attention. *Aging Neuropsychol. Cogn.* **4**, 185–210 (1997).
174. Mathewson, K. J., Dywan, J. & Segalowitz, S. J. Brain bases of error-related ERPs as influenced by age and task. *Biol. Psychol.* **70**, 88–104 (2005).
175. Pettigrew, C. & Martin, R. C. Cognitive declines in healthy aging: evidence from multiple aspects of interference resolution. *Psychol. Aging* **29**, 187–204 (2014).
176. Sullivan, M. P. The functional interaction of visual-perceptual and response mechanisms during selective attention in young adults, young-old adults, and old-old adults. *Percept. Psychophys.* **61**, 810–825 (1999).
177. Wright, L. L. & Elias, J. W. Age differences in the effects of perceptual noise. *J. Gerontol.* **34**, 704–708 (1979).
178. Friedman, N. P. & Miyake, A. The relations among inhibition and interference control functions: a latent-variable analysis. *J. Exp. Psychol. Gen.* **133**, 101–135 (2004).
179. Nigg, J. T. On inhibition/disinhibition in developmental psychopathology: views from cognitive and personality psychology and a working inhibition taxonomy. *Psychol. Bull.* **126**, 220–246 (2000).
180. Rouder, J. N. & Haaf, J. M. A psychometrics of individual differences in experimental tasks. *Psychon. Bull. Rev.* **26**, 452–467 (2019).
181. Stahl, C. et al. Behavioral components of impulsivity. *J. Exp. Psychol. Gen.* **143**, 850–886 (2014).
182. Borella, E., Delaloye, C., Lecerf, T., Renaud, O. & de Ribaupierre, A. Do age differences between young and older adults in inhibitory tasks depend on the degree of activation of information? *Eur. J. Cogn. Psychol.* **21**, 445–472 (2009).
183. Hsieh, S., Liang, Y.-C. & Tsai, Y.-C. Do age-related changes contribute to the flanker effect? *Clin. Neurophysiol.* **123**, 960–972 (2012).
184. Kawai, N., Kubo-Kawai, N., Kubo, K., Terazawa, T. & Masataka, N. Distinct aging effects for two types of inhibition in older adults: a near-infrared spectroscopy study on the Simon task and the flanker task. *NeuroReport* **23**, 819–824 (2012).
185. Waszak, F., Li, S.-C. & Hommel, B. The development of attentional networks: cross-sectional findings from a life span sample. *Dev. Psychol.* **46**, 337–349 (2010).
186. Wild-Wall, N., Falkenstein, M. & Hohnsbein, J. Flanker interference in young and older participants as reflected in event-related potentials. *Brain Res.* **1211**, 72–84 (2008).
187. Zeef, E. J. & Kok, A. Age-related differences in the timing of stimulus and response processes during visual selective attention: performance and psychophysiological analyses. *Psychophysiology* **30**, 138–151 (1993).
188. Lambrechts, A., Karolis, V., Garcia, S., Obende, J. & Cappelletti, M. Age does not count: resilience of quantity processing in healthy ageing. *Front. Psychol.* **4**, 865 (2013).
189. Ioannidis, J. P. A. Issues in comparisons between meta-analyses and large trials. *JAMA* **279**, 1089 (1998).
190. Slavin, R. & Smith, D. The relationship between sample sizes and effect sizes in systematic reviews in education. *Educ. Eval. Policy Anal.* **31**, 500–506 (2009).
191. Sterne, J. A. C., Gavaghan, D. & Egger, M. Publication and related bias in meta-analysis. *J. Clin. Epidemiol.* **53**, 1119–1129 (2000).
192. Vadillo, M. A. Ego depletion may disappear by 2020. *Soc. Psychol.* **50**, 282–291 (2019).
193. Park, D. C. & McDonough, I. M. The dynamic aging mind: revelations from functional neuroimaging research. *Perspect. Psychol. Sci.* **8**, 62–67 (2013).
194. Reuter-Lorenz, P. A. & Cappell, K. A. Neurocognitive aging and the compensation hypothesis. *Curr. Dir. Psychol. Sci.* **17**, 177–182 (2008).
195. Staudinger, U. M., Cornelius, S. W. & Baltes, P. B. The aging of intelligence: potential and limits. *Ann. Am. Acad. Pol. Soc. Sci.* **503**, 43–59 (1989).
196. Salthouse, T. A. Selective review of cognitive aging. *J. Int. Neuropsychol. Soc.* **16**, 754–760 (2010).
197. Hoffman, L., Hofer, S. M. & Sliwinski, M. J. On the confounds among retest gains and age-cohort differences in the estimation of within-person change in longitudinal studies: a simulation study. *Psychol. Aging* **26**, 778–791 (2011).
198. Salthouse, T. A. All data collection and analysis methods have limitations: reply to Rabbitt (2011) and Raz and Lindenberger (2011). *Psychol. Bull.* **137**, 796–799 (2011).
199. Wulff, D. U., De Deyne, S., Jones, M. N., Mata, R. & The Aging Lexicon Consortium. New perspectives on the aging lexicon. *Trends Cogn. Sci.* https://doi.org/10/gf4x6z (2019).
200. Cornman, J. C. et al. Cohort profile: the Social Environment and Biomarkers of Aging Study (SEBAS) in Taiwan. *Int. J. Epidemiol.* **45**, 54–63 (2016).
201. Weinstein, M. et al. *Social Environment and Biomarkers of Aging Study (SEBAS) in Taiwan, 2000 and 2006* (Inter-university Consortium for Political and Social Research, 2014).
202. Haaf, J. M. & Rouder, J. N. Some do and some don't? Accounting for variability of individual difference structures. *Psychon. Bull. Rev.* **26**, 772–789 (2019).
203. Rouder, J. N., Kumar, A. & Haaf, J. M. Why most studies of individual differences with inhibition tasks are bound to fail. Preprint at https://doi.org/10.31234/osf.io/3cjr5 (2019).
204. Ratcliff, R. Methods for dealing with reaction time outliers. *Psychol. Bull.* **114**, 510–532 (1993).
205. Baayen, R. H. & Milin, P. Analyzing reaction times. *Int. J. Psychol. Res.* **3**, 12–28 (2010).
206. Kliegl, R., Masson, M. E. J. & Richter, E. M. A linear mixed model analysis of masked repetition priming. *Vis. Cogn.* **18**, 655–681 (2010).
207. Cerella, J., Poon, L. W. & Williams, D. M. in *Aging in the 1980s: Psychological Issues* (ed. Poon, L. W.) 332–340 (American Psychological Association, 1980).
208. Bates, D., Mächler, M., Bolker, B. & Walker, S. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48 (2015).
209. Schad, D. J., Vasishth, S., Hohenstein, S. & Kliegl, R. How to capitalize on a priori contrasts in linear (mixed) models: a tutorial. *J. Mem. Lang.* **110**, 104038 (2020).
210. Barr, D. J., Levy, R., Scheepers, C. & Tily, H. J. Random effects structure for confirmatory hypothesis testing: keep it maximal. *J. Mem. Lang.* **68**, 255–278 (2013).
211. Matuschek, H., Kliegl, R., Vasishth, S., Baayen, R. H. & Bates, D. Balancing type I error and power in linear mixed models. *J. Mem. Lang.* **94**, 305–315 (2017).
212. Fox, J. *Applied Regression Analysis and Generalized Linear Models* (SAGE, 2015).
213. Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. A. & Smith, G. M. *Mixed Effects Models and Extensions in Ecology with R* (Springer, 2009).
214. Bäckman, L., Nyberg, L., Lindenberger, U., Li, S.-C. & Farde, L. The correlative triad among aging, dopamine, and cognition: current status and future prospects. *Neurosci. Biobehav. Rev.* **30**, 791–807 (2006).
215. Mann, D. M. A. The locus coeruleus and its possible role in ageing and degenerative disease of the human central nervous system. *Mech. Ageing Dev.* **23**, 73–94 (1983).
216. Mather, M. in *The Cognitive Neurosciences* (eds Poeppel, D. et al.) 91–104 (MIT Press, 2019).
217. Schliebs, R. & Arendt, T. The cholinergic system in aging and neuronal degeneration. *Behav. Brain Res.* **221**, 555–563 (2011).
218. Walhovd, K. B. et al. Consistent neuroanatomical age-related volume differences across multiple samples. *Neurobiol. Aging* **32**, 916–932 (2011).
219. Braskie, M. N. et al. Relationship of striatal dopamine synthesis capacity to age and cognition. *J. Neurosci.* **28**, 14320–14328 (2008).
220. Karrer, T. M., Josef, A. K., Mata, R., Morris, E. D. & Samanez-Larkin, G. R. Reduced dopamine receptors and transporters but not synthesis capacity in normal aging adults: a meta-analysis. *Neurobiol. Aging* **57**, 36–46 (2017).
221. Kelley, T. A. & Yantis, S. Learning to attend: effects of practice on information selection. *J. Vis.* **9(7)**, 16 (2009).
222. Rueda, M. R., Rothbart, M. K., McCandliss, B. D., Saccomanno, L. & Posner, M. I. Training, maturation, and genetic influences on the development of executive attention. *Proc. Natl Acad. Sci. USA* **102**, 14931–14936 (2005).

223. Rueda, M. R., Checa, P. & Cómbita, L. M. Enhanced efficiency of the executive attention network after training in preschool children: immediate changes and effects after two months. *Dev. Cogn. Neurosci.* **2**, S192–S204 (2012).
224. Bialystok, E., Craik, F. I. M., Klein, R. & Viswanathan, M. Bilingualism, aging, and cognitive control: evidence from the Simon task. *Psychol. Aging* **19**, 290–303 (2004).
225. Bialystok, E., Martin, M. M. & Viswanathan, M. Bilingualism across the lifespan: the rise and fall of inhibitory control. *Int. J. Biling.* **9**, 103–119 (2005).
226. Bialystok, E., Craik, F. I. M. & Luk, G. Bilingualism: consequences for mind and brain. *Trends Cogn. Sci.* **16**, 240–250 (2012).
227. Costa, A., Hernández, M., Costa-Faidella, J. & Sebastián-Gallés, N. On the bilingual advantage in conflict processing: now you see it, now you don't. *Cognition* **113**, 135–149 (2009).
228. Hayakawa, S. & Marian, V. Consequences of multilingualism for neural architecture. *Behav. Brain Funct.* **15**, 6 (2019).
229. Pelham, S. D. & Abrams, L. Cognitive advantages and disadvantages in early and late bilinguals. *J. Exp. Psychol. Learn. Mem. Cogn.* **40**, 313–325 (2014).
230. Schroeder, S. R., Marian, V., Shook, A. & Bartolotti, J. Bilingualism and musicianship enhance cognitive control. *Neural Plast.* **2016**, 4058620 (2016).
231. Woumans, E., Ceuleers, E., Van der Linden, L., Szmalec, A. & Duyck, W. Verbal and nonverbal cognitive control in bilinguals and interpreters. *J. Exp. Psychol. Learn. Mem. Cogn.* **41**, 1579–1586 (2015).
232. Todd, M. et al. Apolipoprotein E, cognitive function, and cognitive decline among older Taiwanese adults. *PLoS ONE* **13**, e0206118 (2018).
233. Chung, Y., Rabe-Hesketh, S., Dorie, V., Gelman, A. & Liu, J. A nondegenerate penalized likelihood estimator for variance parameters in multilevel models. *Psychometrika* **78**, 685–709 (2013).
234. Baayen, R. H., Davidson, D. J. & Bates, D. M. Mixed-effects modeling with crossed random effects for subjects and items. *J. Mem. Lang.* **59**, 390–412 (2008).
235. Callejas, A., Lupiáñez, J. & Tudela, P. The three attentional networks: on their independence and interactions. *Brain Cogn.* **54**, 225–227 (2004).

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Author contributions

The study was conceived by M.T.U. and M.W. and designed by M.T.U., as part of the larger SEBAS project led by N.G. and M.W. J.V. performed the data preparation and analysis. J.V. and M.T.U. wrote the paper, with contributions from P.V. as well as N.G. and M.W. All authors read and approved the final manuscript.

Competing interests

The authors declare no competing interests.

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Age bracket	N (Females)	Education	Working memory	Declarative memory
55-59 (min. age 58)	87 (41)	9.69 (3.78)	2.32 (0.86)	1.03 (0.44)
60-64	263 (135)	9.11 (4.12)	2.14 (0.83)	0.94 (0.43)
65-69	109 (52)	7.17 (3.82)	1.98 (0.86)	0.84 (0.46)
70-74	88 (34)	6.28 (5.10)	1.63 (1.00)	0.67 (0.46)
75-79	67 (31)	4.93 (4.28)	1.23 (1.00)	0.56 (0.40)
80-84	60 (21)	6.33 (4.13)	1.10 (0.84)	0.48 (0.40)
85-89	24 (9)	5.71 (5.16)	0.93 (0.85)	0.38 (0.27)
90+	4 (0)	7.00 (8.25)	NA	0.29 (0.20)
Whole sample	702 (323)	7.76 (4.52)	1.81 (0.99)	0.79 (0.47)

Extended Data Fig. 1 | Demographic and cognitive information for participants, presented in 5-year age brackets. This table is for informational purposes only; we remind readers that all analyses were performed with age as a continuous variable. For each age bracket, the columns show first of all the sample size (total, with number of females in parentheses) and the mean (and SD) of years of education. Thus, these two columns display the age distributions of sex and education, the two variables covaried out in our analyses; for discussion of these distributions see refs. [73,109]. The subsequent columns display means (and SDs) of the previously published cognitive measures of working memory (*n*-back task; mean *d'* over 1-back and 2-back[109]) and declarative memory (recognition memory task; mean *d'* over real and novel objects[73]) for this sample. Note that the sample sizes in each 5-year age bracket are slightly different for the working memory scores (Supplementary Table 1 in ref. [109]) and the declarative memory scores (Table 1 in Ref. [73]) than for the data in the present paper (for example, due to slightly different subsets of participants having valid performance measures in the respective tasks). For a more general cognitive measure obtained in this sample, see Ref. [232]. N: number of participants; NA: not available; SD: standard deviation.

Fixed effect	*b*	95% CI	*z*	*p*
Intercept (grand mean)	5.0958	[4.9117, 5.2799]	54.25	<.001
Age (across all cue and flanker types)	-0.0382	[-0.0551, -0.0212]	-4.41	<.001
Alerting effect (no cue vs. central cue)	0.1430	[-0.0392, 0.3252]	1.54	.124
Orienting effect (central cue vs. spatial cue)	-0.1990	[-0.3838, -0.0141]	-2.11	.035
Executive effect (incong. vs. cong. flankers)	-0.6173	[-0.7739, -0.4606]	-7.73	<.001
Age X Alerting	-0.0142	[-0.0328, 0.0045]	-1.49	.136
Age X Orienting	0.0168	[-0.0020, 0.0356]	1.75	.080
Age X Executive	0.0165	[0.0008, 0.0323]	2.05	.040
Alerting X Executive	-0.0675	[-0.3865, 0.2515]	-0.42	.678
Orienting X Executive	0.0261	[-0.2958, 0.3480]	0.16	.874
Sex (males vs. females)	-0.2592	[-0.5331, 0.0147]	-1.86	.064
Education	0.1068	[0.0723, 0.1413]	6.07	<.001
Trial position	0.0023	[-0.0003, 0.0049]	1.71	.087

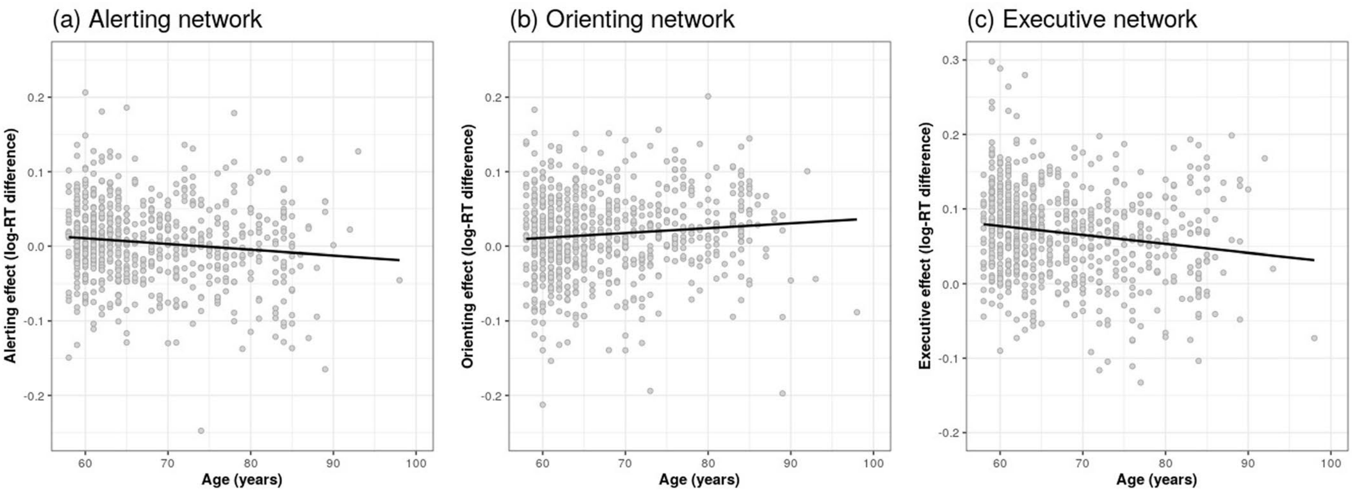
Extended Data Fig. 2 | Results from the mixed-effects logistic regression model on the accuracy of responses. We examined accuracy using generalized linear mixed-effects regression with a logit link function. We analysed correct/incorrect responses produced prior to the timeout period (number of data points: 49,980), for the same 702 participants as in the main analysis on RTs. The same fixed-effect predictors were included as in the main analysis. Models included a random by-participant intercept only, because models with random slopes did not converge. Model convergence was reached only by applying a weakly informative Bayesian prior on the effects[233] (priors on fixed effects were normal distributions with mean=0 and SD = 3 for the intercept, and mean=0 and SD = 0.4 for slopes). Effect sizes are reported as unstandardized estimates (*b*-values) in the logit scale with 95% confidence intervals, together with *z*-values; *p*-values are reported as two-tailed, with exact values to three digits. The significant interaction between age and the executive effect indicated that age was associated with increasing executive efficiency, parallel to the finding of increasing efficiency in the main analysis on RTs. Follow-up analyses indicated that there was an interference cost on accuracy for incongruent flankers at the minimum age of 58 years (back-transformed accuracy in percent correct for congruent, 99.70% vs. incongruent, 99.38%; $b = -0.7302$ [-0.9756, -0.4847], $z = -5.83$, $p < .001$), but no significant difference between incongruent and congruent flankers at the maximum age of 98 years (back-transformed accuracy for congruent, 98.10% vs. incongruent, 97.94%; $b = -0.0825$ [-0.4693, 0.3043], $z = -0.42$, $p = .676$). Likewise, there was no significant executive effect at age 90 ($b = -0.2127$ [-0.5150, 0.0897], $z = -1.38$, $p = .168$). The executive effect was almost nine times larger at the minimum than maximum age, as revealed by the regression coefficients in the logit scale (*b* values: 58 years: -0.7302 vs. 98 years: -0.0825), and twice as large in back-transformed accuracy (0.32% vs. 0.16%). Education effect: higher education was associated with higher accuracy (across all ages and all cues and flankers).

Fixed effect	*b*	95% CI	*t*	*p*
Intercept (grand mean)	6.5385	[6.5269, 6.5502]	1095.10	<.001
Age (across all cue and flanker types)	0.0083	[0.0068, 0.0098]	10.70	<.001
Alerting effect (no cue vs. central cue)	0.0048	[0.0007, 0.0088]	2.31	.021
Orienting effect (central cue vs. spatial cue)	0.0160	[0.0120, 0.0201]	7.79	<.001
Executive effect (incong. vs. cong. flankers)	0.0680	[0.0636, 0.0723]	30.40	<.001
Age X Alerting	-0.0008	[-0.0013, -0.0003]	-3.05	.002
Age X Orienting	0.0007	[0.0002, 0.0011]	2.61	.009
Age X Executive	-0.0012	[-0.0017, -0.0007]	-4.42	<.001
Alerting X Executive	-0.0158	[-0.0239, -0.0078]	-3.85	<.001
Orienting X Executive	0.0133	[0.0052, 0.0213]	3.23	.001
Sex (males vs. females)	-0.0154	[-0.0401, 0.0093]	-1.23	.220
Education	-0.0118	[-0.0146, -0.0089]	-8.09	<.001
Trial position	-0.0012	[-0.0012, -0.0011]	-38.11	<.001

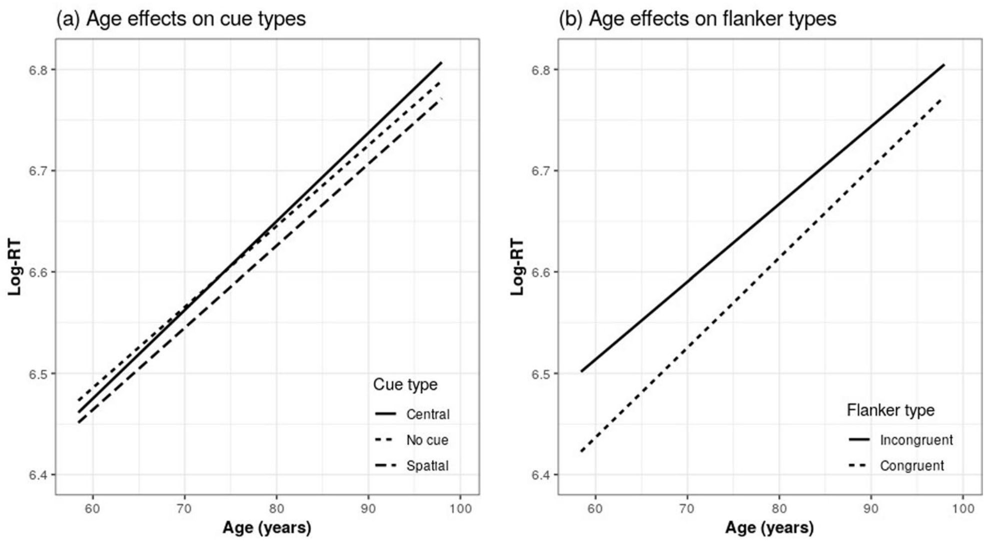
Extended Data Fig. 3 | Results from the linear mixed-effects regression model on log RTs. *P*-values were obtained from *t*-tests with 49,163 degrees of freedom, calculated as the number of data points (that is, 49,176) minus the number of fixed effect estimates (that is, 13)[234]. Here and elsewhere, effect sizes of linear mixed-effects models are reported as unstandardized estimates (*b*-values) with 95% confidence intervals, together with *t*-values; *p*-values are reported as two-tailed, with exact values to three digits. Education effect: higher education was associated with faster responses (across all ages and all cues and flankers). Trial effect: later trials were associated with faster responses. Follow-up analyses to the two network interactions (Alerting X Executive, Orienting X Executive) were performed. Note that both of these interactions, and the general patterns found in their follow-up analyses, are commonly reported for the ANT in both younger and older adults[122,138,140,144-146,152,235]. First, the alerting effect was significant in trials with congruent flankers ($b = 0.0127$ [0.0070, 0.0184], $t = 4.37$, $p < .001$), but not in trials with incongruent flankers ($b = -0.0032$ [-0.0089, 0.0026], $t = -1.08$, $p = .279$). Second, the orienting effect was larger in trials with incongruent flankers ($b = 0.0227$ [0.0169, 0.0284], $t = 7.76$, $p < .001$) than in those with congruent flankers ($b = 0.0094$ [0.0037, 0.0151], $t = 3.24$, $p = .001$), but was significant in both. We also followed up on both interactions by examining the executive effect in the different cue types involved in alerting and orienting. The executive effect was larger in trials with a central cue ($b = 0.0777$ [0.0713, 0.0841], $t = 23.79$, $p < .001$) than in trials with no cue ($b = 0.0618$ [0.0554, 0.0682], $t = 18.95$, $p < .001$) (Alerting X Executive). The executive effect was also larger in trials with a central cue (see just above) than in trials with a spatial cue ($b = 0.0644$ [0.0580, 0.0708], $t = 19.75$, $p < .001$) (Orienting X Executive). CI: confidence interval.

		Flanker type		Cue type			Attentional network effect		
Age bracket	N	Congruent	Incongruent	No cue	Central cue	Spatial cue	Alerting	Orienting	Executive
55-59 (min. age 58)	87	622 (159)	680 (180)	659 (171)	652 (170)	642 (175)	7	10	58
60-64	263	643 (168)	691 (176)	674 (173)	666 (173)	661 (176)	8	5	48
65-69	109	680 (183)	730 (197)	710 (194)	709 (192)	696 (188)	1	13	50
70-74	88	753 (220)	790 (232)	774 (225)	770 (227)	769 (230)	4	1	37
75-79	67	774 (223)	807 (225)	799 (231)	800 (222)	772 (221)	-1	28	33
80-84	60	795 (218)	836 (224)	823 (222)	824 (223)	799 (219)	-1	25	41
85-89	24	830 (238)	892 (248)	854 (235)	873 (250)	854 (249)	-19	19	62
90+	4	835 (268)	867 (203)	852 (197)	852 (259)	849 (253)	0	3	32
Whole sample	702	692 (201)	739 (208)	721 (205)	718 (206)	707 (206)	3	11	47

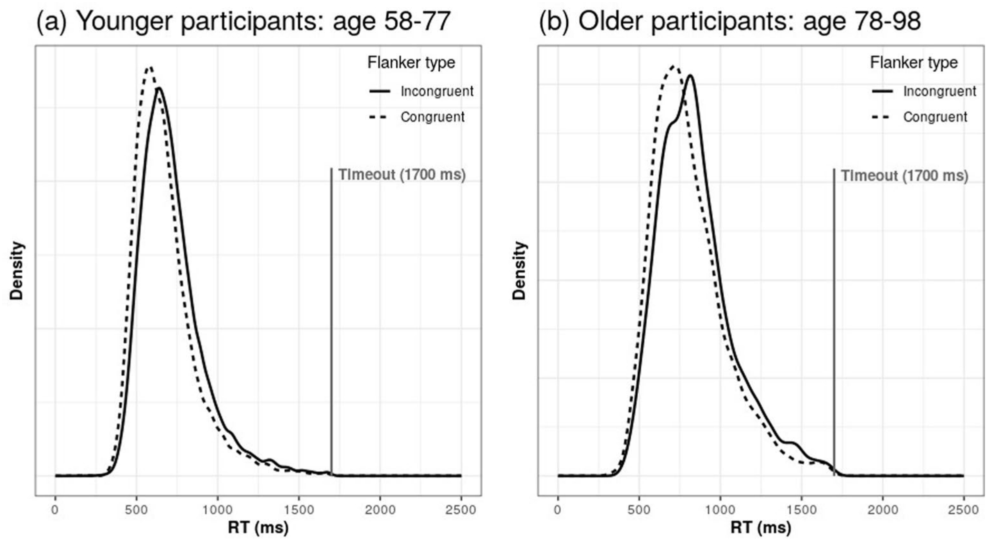
Extended Data Fig. 4 | Mean untransformed RTs for each condition, and mean attentional network effects, in milliseconds, presented in 5-year age brackets. This table displays mean untransformed RTs, by flanker and cue condition (with SDs in parentheses), together with mean attentional network effects (computed as differences between the mean untransformed RTs in each pair of relevant conditions for example, between the central and no cue conditions for alerting), in 5-year age brackets. This table is for informational purposes only; we remind readers that all analyses were performed on log-transformed RTs with age as a continuous variable. Congruent and incongruent flanker types are computed over all three cue types, and each cue type is computed over congruent and incongruent flankers. RTs: response times; N: number of participants; SDs: standard deviations.



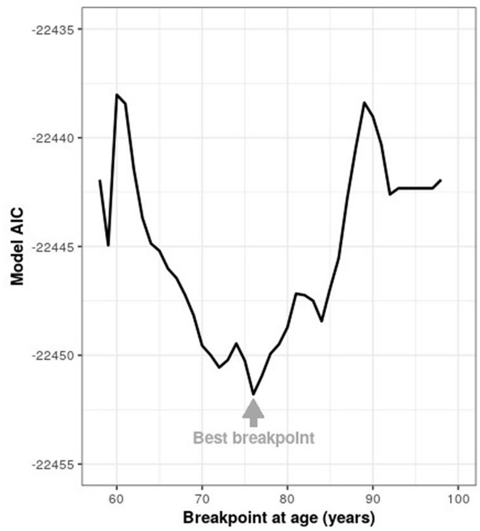
Extended Data Fig. 5 | Linear effects of age on the efficiencies of the three attentional networks, showing network effects for each of the 702 participants. The linear age effects are displayed for (**a**) the alerting network, (**b**) the orienting network, and (**c**) the executive network. For each network, each data point reflects the difference between mean log-transformed RTs in the two relevant conditions (for example, between no cue and central cue for alerting) for each participant. The y-axis ranges (maximum minus minimum) of the three panels are identical, while their numerical values differ; specifically, because the executive effect is larger than the other two attentional effects, the numerical values for the y-axis in panel (**c**) are shifted upwards.



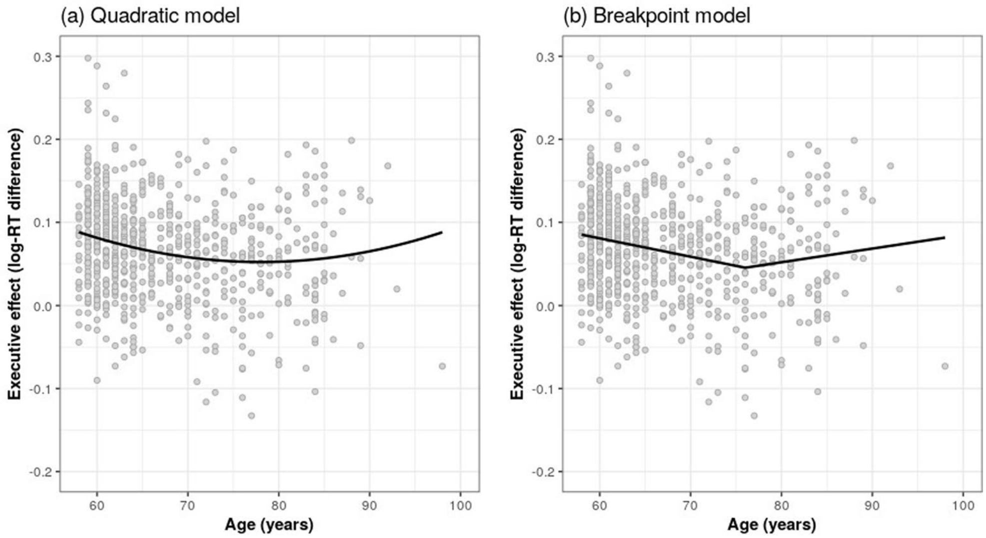
Extended Data Fig. 6 | Age effects on RTs shown separately for each of the cue and flanker conditions. Though age-related slowdowns were observed for all conditions, the RT increases differed among the relevant conditions, that is, among the cue or flanker types. These interactions yielded the observed age effects on efficiency for the three attentional networks. First (panel **a**), the RT increase with aging was greater for trials preceded by a central cue (solid line; $b = 0.0087$ [0.0072, 0.0103], $t = 11.12$, $p < .001$) than for those with no cue (line with short dashes; $b = 0.0080$ [0.0064, 0.0095], $t = 10.15$, $p < .001$), leading to the observed decrease of alerting efficiency with aging. (The reasons for the detrimental effect of the central cue relative to no cue at later ages remain to be determined; perhaps once the alerting benefit has decreased past a certain point, processing costs associated with the presentation of the cue become predominant.) Second (also in panel **a**), the RT increase with age was smaller for trials preceded by spatial cues (line with long dashes; $b = 0.0081$ [0.0065, 0.0096], $t = 10.29$, $p < .001$) than for those preceded by a central cue (see just above), yielding the reported increase in orienting efficiency with age (that is, older participants benefited particularly from spatial cues as compared to central cues). Third (panel **b**), the age-related RT increase in incongruent flanker trials (solid line; $b = 0.0077$ [0.0061, 0.0092], $t = 9.79$, $p < .001$) was smaller than for congruent trials (dashed line; $b = 0.0089$ [0.0073, 0.0104], $t = 11.29$, $p < .001$), leading to the observed increase in executive efficiency with aging.



Extended Data Fig. 7 | Density plots for the distributions of untransformed RTs of correct trials. The plots show these RTs (from the trials analysed in the main regression model) for incongruent flankers (solid lines) and congruent flankers (dashed lines), for younger participants (n = 592; panel **a**) and older participants (n = 110; panel **b**), split at the midpoint of the age range (age 78). As can be seen, very few responses for either the incongruent or congruent trials approached the timeout of 1,700ms for either group of participants, arguing against a 'timeout' alternative explanation for the age-related increase in efficiency of the executive network (see 'Linear effects of age: sensitivity analyses', in Results).



Extended Data Fig. 8 | Discovery of the optimal breakpoint model. This was achieved by comparing model goodness-of-fit (AIC) for regression-with-breakpoints models with breakpoints at successive ages. The AIC of the optimal model (with a breakpoint at age 76) is indicated with the gray arrow.



Extended Data Fig. 9 | The nonlinear effect of age on the efficiency of the executive network, showing the executive effect for each of the 702 participants. The nonlinear age effect is displayed for (**a**) the model with a quadratic term for age, and (**b**) the breakpoint model with the optimal breakpoint (age 76). Each data point reflects the difference between the mean log-RTs for incongruent and congruent flankers, for each participant.

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Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	E-Prime (version 2.0)
Data analysis	R (version 3.6.3), lme4 package (version 1.1-25), blme package (version 1.0-4). Our commented analysis code has been uploaded to Open Science Foundation, at https://osf.io/59er2/.

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Behavioural & social sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description

This was a quantitative experimental study, employing a cross-sectional continuous age design.

Research sample

This study was part of the Social Environment and Biomarkers of Aging Study (SEBAS), conducted in Taiwan. SEBAS was in turn part of the Taiwan Longitudinal Study of Aging, which examines a nationally representative sample of middle-aged and older adults in Taiwan. During (only) the 2011 SEBAS collection wave, the Attention Network Test (ANT) reported here was included. It was given to all available consenting participants of the health examination component of SEBAS. The main analyses reported here were based on data from 702 participants (323 female), with a mean age of 67.69 years, and mean years of education of 7.76.

Sampling strategy

As indicated above, we tested all available consenting participants from the health examination component of SEBAS in the 2011 collection wave. The sample size was considered to provide adequate statistical power, as it was far larger than previous ANT studies that have reported age effects.

Data collection

The task was presented on a Windows XP laptop with E-Prime Version 2.0. Participants responded on a response box (SRBOX, Psychology Software Tools). Participants were tested in the presence of a single experimenter. Both the participants and the experimenters were blind to the aims of the study, in particular the examination of age effects on the efficiency of each attentional network. Informed consent was obtained from all participants.

Timing

Participants were tested between October 24 2011 and May 6 2012.

Data exclusions

Subject and trial exclusions proceeded in four steps. First, the ANT was given to all available consenting individuals of the health examination component of SEBAS, which excluded respondents if they lived in an institution, were seriously ill, or had some other health conditions that precluded examination. This yielded a sample size of 948 participants. Second, of these participants 92 were excluded owing to: participant identifier coding errors (3 participants), not performing the full task (18 participants), or a diagnosis of a neurological, psychiatric, learning, cognitive, or other brain-related disorder (71 participants). Third, an additional 154 participants were excluded because of low accuracy on the ANT (lower than 75%). The same pattern of significance in the findings was obtained in a sensitivity analysis with a more stringent inclusion criterion of at least 90% accuracy (213 participants excluded, rather than 154), as well as in another sensitivity analysis with a more lenient inclusion criterion of at least 50% accuracy (122 participants excluded). Fourth, prior to analyses, trials with timeouts (1.08% of all trials), presses of inappropriate response box buttons (0.02%), and incorrect responses (1.62%) were excluded. Extremely fast responses (below 100ms) were discarded (0.009% of the remaining data) because they are likely to constitute 'short outliers'. Responses to double cue trials were additionally excluded, owing to their redundancy with central cue trials; this enabled the calculation of the alerting and orienting effects within a single statistical model by comparing no cue and spatial cue trials against the same baseline (central cue trials). A sensitivity analysis including both central and double cue trials yielded the same pattern of results.

Non-participation

18 of the 948 participants did not complete the task (see just above).

Randomization

Participants were not allocated into experimental groups.

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☒	☐	Eukaryotic cell lines
☒	☐	Palaeontology and archaeology
☒	☐	Animals and other organisms
☐	☒	Human research participants
☒	☐	Clinical data
☒	☐	Dual use research of concern

Methods

n/a	Involved in the study	
☒	☐	ChIP-seq
☒	☐	Flow cytometry
☒	☐	MRI-based neuroimaging

Human research participants

Policy information about studies involving human research participants

Population characteristics	See above for age, sex, and education population characteristics. In order to control for the possible confounding effects of sex and education, both of which were significantly associated with age, these variables were included as covariates in the main analysis; the same pattern of results was obtained in a sensitivity analysis without these covariates included.
Recruitment	We tested all available consenting participants from the health examination component of SEBAS in the 2011 collection wave; see above. The pattern of results does not appear to be explained by survivor effects or the self-selection of fitter adults in old age; see second paragraph of Discussion.
Ethics oversight	This study complied with all relevant ethical regulations, and was approved by the Institutional Review Boards at Georgetown University, Princeton University, and the Ministry of Health in Taiwan.

Note that full information on the approval of the study protocol must also be provided in the manuscript.