

# Age-related Shift in Neural Complexity Related to Task Performance and Physical Activity

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## Abstract

■ The human brain undergoes marked structural changes with age including cortical thinning and reduced connectivity because of the degradation of myelin. Although these changes can compromise cognitive function, the brain is able to functionally reorganize to compensate for some of this structural loss. However, there are interesting individual differences in outcome: When comparing individuals of similar age, those who engage in regular physical activity are less affected by the typical age-related decline in cognitive function. This study used multiscale entropy to reveal a shift in the way the brain processes information in older adults that is related to physi-

cal activity. Specifically, older adults who were more physically active engaged in more local neural information processing. Interestingly, this shift toward local information processing was also associated with improved executive function performance in older adults, suggesting that physical activity may help to improve aspects of cognitive function in older adults by biasing the neural system toward local information processing. In the face of age-related structural decline, the neural plasticity that is enhanced through physical activity may help older adults maintain cognitive health longer into their lifespan. ■

## INTRODUCTION

Evidence for neuroplasticity across the lifespan has opened the possibility that lifestyle factors can enhance cognitive function regardless of age. This tenet gave rise to the view that one's cognitive ability is best conceptualized as a range of potential that can be optimized; although this range is constrained by biological factors and declines with advancing age, older adults can maintain functional cognitive status for longer by engaging in critical lifestyle activities (Park & Reuter-Lorenz, 2009; Hertzog, Kramer, Wilson, & Lindenberger, 2008). Physical activity is a key factor that promotes cognitive function in older adults; however, the mechanisms through which physical activity changes the brain for better cognitive outcomes is not fully understood (Hillman, Erickson, & Kramer, 2008). This study reveals that physical activity may be associated with a change the way older brains process information.

With advancing age, the human brain undergoes marked structural changes including cortical thinning (Salat et al., 2004) and myelin degradation (Bartzokis, 2004). Although these structural changes disrupt connectivity and information processing, the brain is able to functionally reorganize to compensate for this structural loss. Interestingly, some older adults will perform similarly to younger adults but process the information through different underlying neural pathways (Davis, Dennis, Daselaar, Fleck, & Cabeza, 2008; Cabeza, Anderson, Locantore, & McIntosh, 2002).

For example, compared with younger adults engaged in the same working memory (WM) task, high-performing older adults who performed as well as young adults underrecruited parietal and temporal regions and overrecruited prefrontal regions, whereas low-performing older adults who performed worse than younger adults recruited the same brain regions as younger adults (Cabeza et al., 2004). Although these results do not exclude the possibility that high- versus low-performing older adults may be engaging in different strategy (Rypma, Berger, Genova, Rebbecki, & D'Esposito, 2005) nor does it negate the findings that high-performing older adults also engage youth-like pathways for some tasks (Nyberg, Lövdén, Riklund, Lindenberger, & Bäckman, 2012), the recruitment of different neural pathways by high-performing older adults compared with younger adults highlights the importance of functional adaptation in older adults for maintaining cognition.

Physical activity may be one way to promote neural plasticity and facilitate functional adaptation (Cotman & Berchtold, 2002). Indeed, older adults who are more physically active outperform their less active peers on tasks of executive functions (Clark, Vandermorris, & Heisz, in press; Smiley-Oyen, Lowry, Francois, Kohut, & Ekkekakis, 2008; Colcombe & Kramer, 2003); however, it is unclear how physical activity is supporting this aspect of cognition in advancing age. Although recent attempts to uncover potential mechanisms have focused on preserved youth-like neural structure and function in physically active older adults, these studies have been unable to convincingly

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link neural preservation in advancing age with the cognitive benefits associated with physical activity. For example, compared with their more sedentary peers, physically active older adults have less age-related white matter atrophy in areas of the prefrontal and temporal regions; however, these changes did not account for the exercise-related improvements in executive functions (Voss et al., 2012). Furthermore, resting state connectivity during a passive viewing task appears to be more youth-like in physically active older adults compared with more sedentary older adults; yet the link between this youth-like connectivity, physical activity, and executive functions was neither robust nor widespread (Voss, Erickson, et al., 2010; Voss, Prakash, et al., 2010). These results suggest that preserved youth-like brain structure and function may not be the key mechanism through which physical activity supports executive functions in advancing age. Instead, physical activity may be supporting executive functions in advancing age through the promotion of plasticity and functional adaptation.

Age-related improvements in executive functions by physical activity may be related to individual differences among older adults in their capacity for information processing. One can measure the information processing capacity of underlying functional networks by quantifying the regularity/irregularity of empirically recorded brain signals using measures of entropy (Mišić, Vakorin, Paus, & McIntosh, 2011; Stam, 2005). Simpler networks with fewer degrees of freedom produce more regular responses over time and have lower information processing capacity (Deco, Jirsa, & McIntosh, 2011; Mišić et al., 2011). In healthy young adults, brain signal entropy increases with learning (Heisz, Shedden, & McIntosh, 2012) and with the amount of cognitive information available for a particular stimulus (Heisz, Vakorin, Ross, Levine, & McIntosh, 2014; Heisz et al., 2012; Misić, Mills, Taylor, & McIntosh, 2010). Brain signal entropy is also correlated with more accurate and less variable behavior (McIntosh, Kovacevic, & Itier, 2008). In cases of brain damage, individuals with a moderate to severe traumatic brain injury (Raja, Kovačević, McIntosh, & Levine, 2012) or Alzheimer's disease (Park, Kim, Kim, Cichocki, & Kim, 2007) have significantly less brain signal entropy than healthy controls.

There are also interesting changes in the complexity of the brain's response across the lifespan, increasing early in life (Lippe, Kovacevic, & McIntosh, 2009; McIntosh et al., 2008) and decreasing to some extent as the brain ages (McIntosh et al., 2013; Garrett, Kovacevic, McIntosh, & Grady, 2011). However, the age-related decline in neural entropy is not uniform. Although some aspects of brain signal entropy decrease with age, other aspects of brain signal entropy increase with age: Compared with younger adults, older adults have less entropy at coarse timescales but more entropy at fine timescale (McIntosh et al., 2013). This change in the spatiotemporal dynamics of neural complexity maps onto a loss of cross-hemispheric functional connectivity (i.e., entropy at coarse timescales) and

a gain in local information processing (i.e., entropy at fine timescales; Vakorin, Lippé, & McIntosh, 2011), suggesting that there is a shift from distributed to local information processing with age. It remains unclear whether the age-related shift from distributed to local entropy is merely a consequence of aging or whether it reflects an adaptive neuroplasticity that supports cognitive function. It may be adaptive. The age-related loss of myelin disrupts long-range communication (Salat, 2011; Peters & Rosene, 2003). A system that is biased toward local information processing would rely less on distributed information processing and thus would maintain cognitive function in the face of white matter decline.

This study examined whether the age-related shift in brain signal complexity from distributed to local processing mediated the association between physical activity and cognition in older adults. To test this, we recorded EEG while younger and older participants performed a directed forgetting task involving executive control of the contents of WM (Zacks, Radvansky, & Hasher, 1996; Zacks & Hasher, 1988; Bjork, 1970). The complexity of the EEG recordings was estimated using multiscale entropy—an information-theoretic metric that quantifies the entropy of a signal over multiple timescales and relates that entropy to the information processing capacity of the system (Costa, Goldberger, & Peng, 2005). Consistent with previous reports (Hillman et al., 2006), we expected age-dependent differences in the association between physical activity and task performance (Heisz, Vandermorris, Wu, McIntosh, & Ryan, 2014), such that physical activity would be positively correlated with task performance for older adults (Clark et al., in press; Smiley-Oyen et al., 2008; Colcombe & Kramer, 2003) but not for younger adults. With respect to the brain signal complexity, we expected to see the typical age-related shift in entropy, with less entropy at coarse timescales and more entropy at fine timescale for older adults than younger adults. If this shift in brain signal entropy with age mediates the relation between physical activity and executive function in older adults, then this would point to a potential mechanism of plasticity through which physical activity supports executive function in aging.

## METHODS

### Participants

The 45 participants included in the study were healthy community-dwelling adults with English as their first language, normal or corrected-to-normal vision, and no reported memory, psychiatric, or learning problems. Benchmark measures of general cognitive status were assessed using the Montreal Cognitive Assessment (Nasreddine et al., 2005) and the American National Adult Reading Test (Blair & Spreen, 1989). Table 1 provides a description of the participants' characteristics. All procedures complied with the Canadian tricouncil policy on ethics and were approved by the Baycrest Research Ethics Board.

**Table 1.** Mean (and *SD*) Demographic Information for Younger and Older Adults

<i>Variable</i>	<i>Younger Adults (n = 24), M (SD)</i>	<i>Older Adults (n = 21), M (SD)</i>
Age (years)	21.8 ( $\pm 2.8$ )	71.7 ( $\pm 5.8$ )
Age range (years)	18–29	65–83
Sex (female/male)	12/12	12/9
Montreal Cognitive Assessment	26.8 ( $\pm 2.3$ )	25.8 ( $\pm 2.5$ )
American National Reading Test	30.0 ( $\pm 6.6$ )	38.8 ( $\pm 5.8$ )
Physical activity	26.3 ( $\pm 7.4$ )	15.9 ( $\pm 8.2$ )

Physical activity (max score = 48) reflects frequency of engagement in arbitrary units. See Methods, Task Procedures section for additional information regarding how this variable was computed. Physical activity did not correlate with either the Montreal Cognitive Assessment or the American National Adult Reading Test in older adults or younger adults (all *ps* > .05).

### Task Procedures

We used a list version of the directed forgetting paradigm to examine executive functions related to one's ability to forget irrelevant contents of WM (Zacks et al., 1996). Participants performed 144 trials. Stimuli consisted of unique randomly generated one-digit, two-digit, and three-digit numbers; the digit length was held constant within a trial but randomized evenly across the experimental session. Each trial was initiated by the participant and began with a white orienting-cross presented for 500 msec, which was followed by a study list of four unique numbers presented consecutively for 500 msec per number. The first two numbers were always red, and the last two numbers were always green (color order was counterbalanced across participants). The retention interval was denoted by a white orienting-cross, during which the participant was instructed to remember all the numbers. After 2500 msec, the orienting-cross changed color; this cued the participant to either continue remembering all the numbers (gray) or to remember only half the numbers (red or green, which matched the color of the to-be-remembered numbers) for the remaining 2000 msec of the retention interval. Note that this is the delay period of interest from which the EEG data were analyzed (see EEG Procedures). "Remember-all" and "remember-half" trials were randomized evenly across experimental session. A probe number was then presented, and the participant was to indicate whether the number was to be remembered or not by making a keyboard response. At 50% of the time, the probes were to-be-remembered numbers. For trials in which the participant was to remember only half the numbers, half of the "new" probes consisted of studied but to-be-forgotten numbers. Participants were instructed to be as accurate as possible. The cost of forgetting was computed as the mean proportion of correct rejections for the to-be-forgotten items minus the mean proportion of correct rejections for new items in the remember-half condition (Zacks et al., 1996).

After the experiment, participants completed the augmented Victoria Longitudinal Study Activity Questionnaire, rating their frequency of engagement in specific

lifestyle activities during the past 2 years, with individual item scores ranging from never (score = 0) to daily (score = 8; Jopp & Hertzog, 2010). Physical activity was computed as the sum of six exercise-related questions (max score = 48), including aerobics, resistance training, stretching, sport, and outdoor activities (Table 1). The scores derived from the augmented Victoria Longitudinal Study Activity Questionnaire demonstrate good reliability and validity evidence to support their use as measures of leisure activities in older individuals (Jopp & Hertzog, 2010). Furthermore, prior work has demonstrated that this measure of physical activity correlates with an objective measure of physical fitness (Clark et al., in press).

### EEG Procedures

#### *EEG Acquisition and Analysis*

The EEG analysis was conducted on remember-half trials during the delay period when only a fixation cross was present on the screen and the task required participants to manipulate the contents of their WM. The ActiveTwo Biosemi system was used to record continuous EEG activity from 64 Ag/AgCl scalp electrodes plus eight additional electrodes placed IO1/2, LO1/2, F9/10, and FT9/10. Two additional electrodes, common mode sense active electrode and driven right leg passive electrode were also used ([www.biosemi.com/faq/cms&drl.htm](http://www.biosemi.com/faq/cms&drl.htm)). The continuous signal was acquired with an open pass-band from DC to 150 Hz and digitized at 512 Hz. The continuous EEG signal was bandpass filtered between 0.1 and 55 Hz and re-referenced to a common average reference. Data were segmented into 2200 msec epochs with a 200-msec prestimulus baseline. Preliminary artifact removal was performed using independent component analysis (ICA) as implemented in EEGLAB software (Delorme & Makeig, 2004). Trials contaminated with excessive amplitudes were removed first. Then ICA decomposition was performed on the remaining concatenated trials, and ICA components carrying ocular and muscle artifacts were subtracted from the data.

## Multiscale Entropy

Sample entropy was used to quantify the entropy of the EEG time series ([www.physionet.org/physiotools/mse/](http://www.physionet.org/physiotools/mse/); Heisz & McIntosh, 2013; Costa et al., 2005):

$$S_E(m, r, N) = \ln \frac{\sum_{i=1}^{N-m} n_i^m}{\sum_{i=1}^{N-m} n_i^{m+1}} \quad (1)$$

where  $m$  is the pattern length,  $r$  is the similarity criterion, and  $n_i^m$  is the number of matches. Sample entropy quantifies the complexity of a time series by estimating the predictability of amplitude patterns across a time series of length  $N$ , where  $N$  is the length of the original EEG time series. The pattern length (i.e., embedding dimension)  $m$  was set to 2, which means that the entropy of the amplitude pattern of each time series was calculated by considering a sequence patterns for two versus three consecutive data points, respectively. The similarity criterion  $r$  was set to .5; this means that data points were considered to have indistinguishable amplitude values (i.e., to “match”) if the absolute amplitude difference between them was  $\leq 50\%$  of the time series standard deviation. The parameter value for  $m$  and  $r$  were set following the guidelines outlined by Richman and Moorman (2000) for time series with more than 100 data points (for a detailed procedure on selecting parameters, refer to Lake, Richman, Griffin, & Moorman, 2002).

For each participant, a source-specific estimate was obtained as a mean across single-trial entropy measures for timescales 1–20. Multiple coarse-grained time series were created from the original EEG time series by progressively down-sampling the poststimulus time series  $\{x_1, \dots, x_i, \dots, x_N\}$  per trial and per condition. For timescale  $\tau$ , the coarse-grained time series  $\{y^{(\tau)}\}$  is constructed by averaging data points within nonoverlapping windows of length  $\tau$ . Each element of a coarse-grained time series,  $j$ , is calculated according to Equation 1:

$$y_j^{(\tau)} = \frac{1}{\tau} \sum_{i=(j-1)\tau+1}^{j\tau} x_i, \quad 1 \leq j \leq \frac{N}{\tau} \quad (2)$$

## Statistical Analyses

The cost of forgetting was computed as the proportion of correct rejections for to-be-forgotten probes minus the proportion of correct rejections for new probes, separately for each WM load in the remember-half condition. Age differences in task performance were analyzed using a mixed design ANOVA with one between-subject variable of Participant age (younger, older) and one within-subject variable of WM load (low, moderate, high).

Age differences in physical activity were assessed by an independent samples  $t$  test contrasting physical activity for younger versus older adults.

To evaluate whether physical activity was related to better task performance, we conducted a one-tailed Pearson correlation, separately for younger and older adults and controlled for the age of the participant within each group.

Age differences in neural dynamics were analyzed using partial least squares (PLS; Lobaugh, West, & McIntosh, 2001) on sample entropy at 20 timescales for younger and older adults across low, moderate, and high WM loads. Singular value decomposition was used to project the mean-centered data matrix onto a set of orthogonal latent variables (LVs), with decreasing order of magnitude (analogous to PCA). Then, participants within each group were randomly split in half; the right and left singular vectors from the original singular value decomposition were projected onto each half of the data, and then the correlation between the projected left and right split-half patterns were taken as a measure of the robustness of the correspondence between the EEG data and the element loading on one hand and the group/condition membership and the condition loading on the other hand. Significance of the split-half correlations for both left and right singular vectors for each LV was estimated with permutations tests using 100 permutations.

The stability of the corresponding spatiotemporal distribution across subjects (i.e., element loading) by resampled subjects within conditions (100 bootstrap samples). The bootstrap ratio provides a measure of stability and is calculated by taking the ratio of the element loading and the standard error of the generated bootstrap distribution. The bootstrap ratio is approximately equivalent to a  $z$  score, whereby an absolute bootstrap ratio greater than 3 corresponds roughly to a 95% confidence interval. For a given LV, brain elements with positive bootstrap ratios supported the depicted contrast among conditions (e.g.,  $A > B > C$ ), whereas brain elements with negative bootstrap ratio supported the inverse of the contrast among conditions (e.g.,  $A < B < C$ ).

To evaluate the relations between neural dynamics, task performance, and physical activity, two entropy variables were extracted from the grand mean sample entropy (averaged across all electrodes): fine timescale entropy, which was computed as the area under the curve at fine timescales 1–10, and coarse timescale entropy, which was computed as the area under the curve at coarser timescales 15–20. The relationship between these two entropy variables was first examined using one-tailed Pearson correlations testing the hypothesis that an increase in entropy at a fine timescale was related to a decrease in entropy at a coarse timescale. Then a mediation analysis was used to determine whether the strength of the relationship between physical activity (predictor variable, X) and task performance (outcome variable, Y) was mediated by the neural dynamics at fine timescales (Mediator 1, M1) or coarse timescales (Mediator 2, M2). We tested three models: one with Mediators 1 and 2 entered in serial ( $X \rightarrow M1 \rightarrow M2 \rightarrow Y$ ) and two with the individual mediators assessed separately ( $X \rightarrow M1 \rightarrow Y$  and  $X \rightarrow M2 \rightarrow Y$ ). These

mediation analyses were conducted using the macro PROCESS for SPSS using Model 6 (Preacher & Hayes, 2004). Bootstrap sampling (1000 samples) was used to estimate the bias-corrected bootstrap 95% confidence intervals for the indirect of physical activity on task performance when controlling for entropy at fine and coarse timescales.

## RESULTS

### Age Differences in Task Performance

Table 2 presents mean cost of forgetting for younger and older adults. The ANOVA on the cost of forgetting revealed a main effect of WM load,  $F(2, 86) = 6.81, p < .01, \eta_p^2 = .14$ , indicating that the cost of forgetting increased with WM load. The main effect of Participant age was marginal but not statistically significant,  $F(1, 43) = 3.08, p = .086, \eta_p^2 = .07$ , suggesting a greater cost of forgetting in older adults than younger adults. The interaction between WM load and participant age was not significant,  $F(2, 86) = .43, ns$ .

### Age Differences in Physical Activity

Compared with younger adults, older adults reported being less physically active (Table 1). This observation was supported by the independent samples  $t$  test, comparing physical activity levels in younger adults versus older adults,  $t(43) = 4.50, p < .001$ , Cohen's  $d = 1.3$ .

### Relation between Task Performance and Physical Activity

A significant correlation between task performance and physical activity controlling for the age of the participants within each group was observed for older adults,  $r(18) = .50, p < .05$ , but not for younger adults,  $r(21) = .04, p = .43$ .

### Age Differences in Neural Dynamics

The first LV from the PLS analysis revealed age differences in sample entropy across multiple timescales ( $p < .001$ ; Figure 1A). Negative bootstrap ratios were reliable across fine timescales 1–10 (Figure 1B), indicating greater sample entropy for older adults than younger adults at fine timescales; the spatial distribution of this age effect was

stable across all electrodes. In contrast, positive bootstrap ratios were reliable across coarser timescales 15–20 (Figure 1B), indicating greater sample entropy for younger adults than older adults at coarser timescales; the spatial distribution of this age effect was stable at electrodes over frontal–central regions.

Figure 1C depicts the age by timescale interaction in the grand mean of sample entropy (averaged across electrodes and WM load), with greater sample entropy for older adults than younger adults at a fine timescale but not at a coarse timescale. To evaluate whether greater entropy at fine timescales was related to less entropy at coarse timescales, we extracted the grand mean for entropy at fine timescale (1–10) and coarse timescale (15–20) and examined the relationship between the two using a one-tailed Pearson correlation; this was done separately for younger and older adults. For older adults, the increases in entropy at fine timescales was related to the decrease in entropy at coarse timescales,  $r(19) = -.47, p < .05$ . In contrast, this relation was not observed for younger adults,  $r(22) = -.03, p = .45$ . Neither correlation was impacted by the age of the participants within each age group.

### Does the Shift in Entropy Mediate the Relation between Task Performance and Physical Activity in Older Adults?

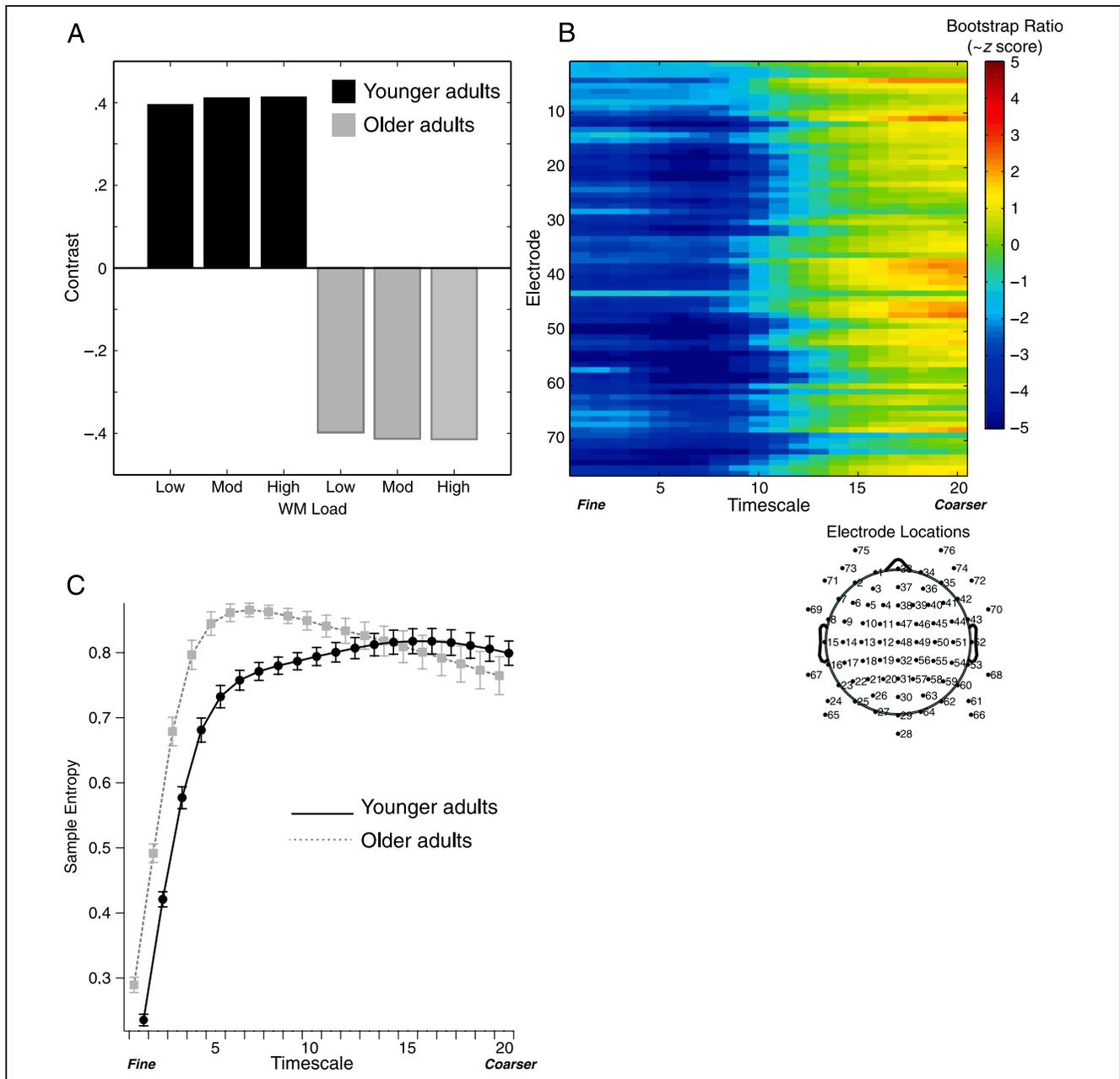
To determine whether the direct effect of physical activity on task performance in older adults was mediated by fine or coarse timescale entropy, we first ran Pearson correlations (one-tailed) for older adults controlling for age. Task performance and physical activity were positively related with entropy at fine timescales, whereas only task performance was negatively related to entropy at coarse timescales (Table 3). We then tested the direct effect of physical activity (X) on task performance (Y) and the indirect effect of physical activity (X) on task performance (Y) through fine timescale entropy (M1) and coarse timescale entropy (M2) in serial ( $X \rightarrow M1 \rightarrow M2 \rightarrow Y$ ). Both the direct effect (Beta = .57,  $p < .05$ ) and the indirect effect (Beta = .14; 95% CIs: .02 to .48) were significant, suggesting that physical activity increases fine scale entropy, which in turn decreases coarse scale entropy to affect task performance. There was no indirect effect through fine ( $X \rightarrow M1 \rightarrow Y$ , Beta =  $-.08$ ; 95% CIs [ $-.62, .09$ ]) or coarse ( $X \rightarrow M2 \rightarrow Y$ , Beta =  $-.13$ ; 95% CIs [ $-.46, .02$ ]) timescale entropy separately.

**Table 2.** Mean (and SE) Task Performance Indexed as the Cost of Forgetting (Lower Values Indicate Greater Cost) for Younger and Older Adults across Low, Moderate, and High WM Load

WM Load	Younger Adults	Older Adults
Low	-.05 ( $\pm .03$ )	-.09 ( $\pm .03$ )
Moderate	-.10 ( $\pm .04$ )	-.14 ( $\pm .04$ )
High	-.15 ( $\pm .05$ )	-.25 ( $\pm .05$ )

## DISCUSSION

Age impacts the way in which information is communicated across neural networks during a complex cognitive task. Compared with younger adults, older adults engaged in less distributed information processing and more local information processing. Prior studies have mapped this shift in complexity to a loss in long-range cross-hemisphere



**Figure 1.** Compared with younger adults, older adults had greater sample entropy at fine timescales but not at coarse timescales. (A) PLS results for LV1 that captured the condition contrast between younger versus older adults. (B) PLS results for LV1 depicting the spatiotemporal distribution across electrodes and timescales that expressed the condition contrast (i.e., age differences) in sample entropy. (C) Grand mean sample entropy across timescales 1–20 for younger and older adults collapsed across WM load. Error bars represent *SEM*.

**Table 3.** Pearson Correlations (One-tailed) for Older Adults Controlling for Age, Testing the Hypotheses that Task Performance and Physical Activity Will Be Positively Related with Entropy at Fine Timescales and Negatively Related to Entropy at Coarse Timescales

	Fine Timescale Entropy		Coarse Timescale Entropy	
	<i>r</i> (18)	<i>p</i>	<i>r</i> (18)	<i>p</i>
Task performance	.37	.05	-.44	.03
Physical activity	.51	.01	-.02	.46

communication and a gain in local processing (McIntosh et al., 2013). This study examined whether this age-related shift in information processing is adaptive or merely a deleterious consequence of aging. The results suggest it is adaptive: Higher-performing older adults showed a greater shift in information processing from distributed to local. Furthermore, older adults who reported being more physically active had better task performance and greater local information processing. These results suggest that physical activity may facilitate the shift toward local processing for better cognitive outcomes in aging.

Age-dependent differences in task performance and its relation to physical activity were observed. Overall, younger adults performed better than older adults on the task assessing executive functions. Furthermore, older adults' task performance was related to their physical activity level, whereas younger adults' task performance was not. These findings are consistent with prior research (Hillman et al., 2006) and suggest that the impact of physical activity on neural processes may differ for younger and older adults (Heisz et al., 2014).

In addition to the age-related effects, there were interesting individual differences among the older adults based on task performance and physical activity. Task performance in older adults was positively related to increased entropy at fine timescale and decreased entropy at coarse timescale entropy; these two indexes of entropy were negatively related to each other, indicating a shift in brain signal entropy with healthy aging. That is, higher-performing older adults had a greater shift toward local processing than lower-performing older adults suggesting that this shift in processing with aging is adaptive. The beneficial shift toward local information processing makes sense in the context of the aging brain. Although there are many age-related neural changes that have the potential to compromise executive functions, a key change is the loss of white matter integrity that disrupts long-range communication and distributed information processing (Salat, 2011; Peters & Rosene, 2003). Within the context of an aging brain, the reliance on distributed information processing may cause communication breakdown across widespread networks because of the loss of myelin; this, in turn, would compromise cognitive function. In contrast, a system that is biased toward more local information processing would be capable of effective function despite reduced myelin and connectivity. Interestingly, this pattern of results parallels prior fMRI studies showing that, compared with younger adults, lower-performing older adults have a similar activation pattern whereas higher-performing older adults recruit different brain regions for processing (Davis et al., 2008; Cabeza et al., 2002). Although these individual differences in brain signal entropy among older adults could reflect differences in strategy, the results suggest that the plasticity of functional network communication is an important factor for maintaining cognitive function in aging.

Physical activity in older adults was also associated with individual differences in brain signal complexity. Older adults who were more physically active had greater entropy at fine timescales and better task performance. The current results suggest that physical activity is not associated with youthful-like brain function in older adults; instead, physical activity may act as a catalyst for plasticity. This is consistent with evidence from animal models demonstrating that physical activity increases the fundamental components for neuroplasticity, including enhanced neurogenesis, synaptogenesis, angiogenesis, and neurotrophic factors, effectively priming the brain for change (Voss, Vivar, Kramer, & Van Praag, 2013; Van Praag, Kempermann, &

Gage, 1999). This may be especially critical in an aging brain where these components are normally low (Zitnik & Martin, 2002). For older adults, functional reorganization may be difficult to achieve without the promotion of neuroplasticity through external factors such as physical activity (Park & Reuter-Lorenz, 2009). Consequently, older individuals who lack the necessary supplements for plasticity will continue to process information as they did before age-related neural degeneration, even if that way has become suboptimal.

The association between physical activity and brain signal entropy in older adults was specific to local information processing and was not associated with the corresponding decrease in distributed processing that is seen with aging. Indeed, prior fMRI studies show local increases in the activation of frontal and parietal regions (Colcombe et al., 2004). Furthermore, although there is some evidence that aspects of structural and functional connectivity are elevated following physical activity intervention in older adults, the association between these connectivity changes and executive function is weak (Voss et al., 2012; Voss, Erickson, et al., 2010; Voss, Prakash, et al., 2010).

Taken together, the results point to a potential mechanism through which physical activity may improve executive function in older adults. A shift toward local information processing was associated with better executive functioning and higher physical activity in older adults. However, the increase in local information processing alone did not mediate the relation between physical activity and task performance. Instead, physical activity seemed to act as a catalyst—priming the plasticity by increasing local information processing, which in turn facilitated a decrease in distributed information processing to improve performance. Critically, this shift from distributed to local processing may allow older adults to maintain executive functions despite aging neural structures.

In conclusion, this study represents an important step in understanding the complex relationship between aging, neurophysiology, cognition, and lifestyle. The results demonstrate that the age-related shift in complexity toward local information processing and away from distributed information processing may be driven by physical activity and may result in better executive function in older adults. The findings point to a potential mechanism through which physical activity may change the aging brain to support aspects of cognition: Critically, the proposed mechanism does not preserve youthful-like brain function but rather facilitates functional reorganization of neural network processing to accommodate the infrastructure of an aging neural system.

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