

Motor Learning and Movement Performance: Older versus Younger Adults

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ABSTRACT

Introduction: Motor skills play an important role during life span, and older adults need to learn or relearn these skills. The purpose of this study was to investigate how aging affects induction of improved movement performance by motor training.

Methods: Serial Reaction Time Test (SRTT) was used to assess movement performance during 8 blocks of motor training. Participants were tested in two separate dates, 48 hours apart. First session included 8 blocks of training (blocks 1-8) and second session comprised 2 blocks (blocks 9, 10).

Results: Analyses of data showed that reaction times in both online and offline learning were significantly shorter in older adults compared to younger adults ($P < 0.001$). Young adults demonstrated both online and offline learning ($P < 0.001$), but older adults only showed online learning ($P < 0.001$) without offline learning ($P = 0.24$).

Discussion: The result of the current study provides evidence that the healthy older adults are able to improve their performance with practice and learn motor skill successfully in the form of online learning.

1. Introduction

Population ageing is increasing rapidly in the current century. Worldwide, the number of people over 60 years is growing faster than other age groups. According to the most recent estimates in the world, the number of people aged over 60 years will double from 756 to 1400 million by 2030 (De Luca et al., 2011). To increase quality of life in this age group, various aspects of ageing should be studied carefully. Motor skills play an important role during life, and even older adults need to learn or relearn motor skills, as part of new task training dur-

ing daily activities or rehabilitation. Therefore, the learning during or following motor task performance for skill acquisition is an important issue for healthy living and during implementation of therapeutic approaches for rehabilitation of older adults (Hall et al., 2011).

Ageing is associated with brain changes that can limit its functional capacity (Lustig et al., 2009). Some studies indicated that ageing is accompanied with changes in sensory and motor system (Bock & Schneider, 2002), which may cause significant reduction in motor skill acquisition in older adults (Seidler, 2006; Voelcker-Rehage & Alberts, 2005; McDowd & Craik, 1988, Curran, 1997).

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There is no consensus in the literature over the capability of the brain in older adults for motor learning. Some studies have shown significant reduction in learning capacities in older adults (Harrington & Haaland, 1992; Feeney, Howard & Howard, 2002; Dennis, Howard, & Howard, 2003). While some other studies suggested considerable enhancement in learning capacities of this group for acquisition of new motor skills (Voelcker-Rehage, Godde, & Staudinger, 2011; Voelcker-Rehage & Willimczik, 2006; Pratt, Chasteen & Abrams, 1994; Durkin et al., 1995, Smith et al., 2005; Shea, Park & Braden, 2006; and Howard et al., 2008).

In this regard, functional Magnetic Resonance Imaging (fMRI) studies have shown that similar to younger adults, older adults can efficiently adapt with task demand and do perceptual and higher-order cognitive processing by using different strategies (Madden et al., 2010; Schulte et al., 2011). These strategies may be different for online performance improvement compared to retaining of this improvement after completion of training. Performance improvement includes temporary changes in motor behavior usually during a single session of training (online learning). However, if performance changes last longer than the training session, it is called motor learning (offline learning) (Shumway-cook & Woollacott, 2001). This study sheds light on the effects of motor training on online and offline learning in older adults compared to younger ones.

The purpose of this study was to investigate how aging affects induction of improved movement performance by motor training. In this regard, it was hypothesized that:

1. Older adults are able to achieve considerable performance improvement during the training session (online learning).
2. Older adults are able to achieve considerable performance improvement after completion of the training session (offline learning).
3. Younger adults learn better than older adults during both online and offline learning.

2. Methods

Thirty young adults (aged 18-35 y, 17 male, 13 female), and 30 older adults (aged 60-80 y, 7 male, 23 female) participated in this between groups controlled study. Participants had no history of neurological diseases or musculoskeletal disorders. Adults with severe perceptual and

memory problems evidenced by Mini Mental Status Examination (MMSE) scores of less than 21; having neurological disease, especially Parkinson and Alzheimer's, visual or auditory problems, upper extremity pathology and range of motion limitations were excluded from the study. All participants were right-handed, as determined by the Edinburgh Handedness Inventory (10 item version) (Light and Singh, 1987). They signed an informed consent form approved by the human participants' Ethics Committee at the University of Social Welfare and Rehabilitation Sciences before participating in the study.

2.1. Tools for measurement of motor learning

In this study, a software program known as Color Matching Test (CMT) that specially designed for motor learning analysis was used. In CMT program, a square is designed to be in the centre of screen, which can be changed to four different colors of yellow, red, green, and blue. For each color, a key is specified on the keyboard. Using CMT enabled the study to have SRTT (serial reaction time test), which is one of the most common methods for assessment of implicit learning (Nissen & Bullemer, 1987). SRTT has both motor and cognitive components and measures the temporal parameters of learning and considers time changes during task performance (Nissen & Bullemer, 1987).

The pattern of SRTT in this study had second-order structure. The designed program had 8 blocks and each block consisted of 10 trials. Each trial included 10 sequences. Each sequence possessed 8 colored-squares that their appearance pattern was ABCBDCAC. By pressing the specific key, the next different colored square would appear. However, the next square would not appear until the correct key was pressed. Before the test started, the general pattern of squares appearance and number of blocks were explained to the subject on a form of unconscious knowledge.

Thus, subjects should learn the sequences of SRTT implicitly. All participants attended two sessions of testing 48 hours apart. Participants were asked to sit in front of a computer monitor and press the relevant key as soon as they see each square in the monitor. There were 8 blocks in the first stage. The first two blocks had an ordered pattern; blocks 3 and 4 had a random pattern and again blocks 5 to 8 appeared with ordered pattern. The mean of each block time was recorded as the main variable by the software program. Two days later a retention test included two ordered blocks was applied to check out the stability of the first test performance improvement. The break time that planned in software program, was one

Table 1. Demographic data of the participants in young and older groups (Mean±SD).

Group	Variable	Mean	SD
Young adults	Age, y	29.23	3.5
	Gender (Male/Female)	7/23	-
	Education level (High/Low)	27/3	-
	MMSE Test	29.03	0.93
Older adults	Age, y	64.83	4.01
	Gender (Male/Female)	17/13	-
	Education level (High/Low)	18/12	-
	MMSE Test	27.33	1.37

MMSE: Mini Mental Status Examination

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minute between the training blocks. The aim of the second stage was to check whether the motor learning was real and stable or it was merely online learning and a temporary change due to the performance improvement. The data of participants who had recognized the order of sequences were omitted from data analysis.

2.2. Operational definitions

Online learning is the learning, which happens during training. In this study, reaction time difference between blocks 8 and 2 was considered as online learning. Any reduction in reaction time provides evidence for this type of learning. Unlike online learning, offline learning is defined as the learning, which happens after the completion of learning during the retention. In this study, the reaction time difference between measurements at blocks 10 and 8 was considered as offline learning. Again, any reduction in reaction time provides evidence for this type of learning.

3. Results

Demographic details for young and old groups are presented in Table 1. Regression analysis indicated no relationship between learning and degree of education (young group; $R_s: 0.198, P=0.249$ - older group; $R_s: 0.248, P=0.187$).

The results of a two-way mixed (split-plot) design (SPANOVA) are presented in Table 2. The between-subjects main effect of age was significant ($P<0.05$), which indicates differences in learning in younger group compared to older one. The within-subjects main effect of time was also significant, which indicates significant differences between degrees of learning during different time points (i.e. block 2, 8, and 10). Post hoc analysis using Bonferroni correction in young adults, indicates significant learning changes not only between blocks 2, pre-test, and 8, online learning follow-up, but also between blocks 2 and 10, retention follow-up, which characterize a combination of online and offline learning follow-up (Table 3). Moreover, analysis showed significant differences between the online learning at block 8 and a combination of online and offline learning at block 10. The post-hoc analysis for the elderly group revealed similar differences as younger adults except the difference between blocks 8 and 10, which was not significant ($P=0.242$) in this group (see Figure 1).

Finally, the interaction effect between age and time was significant ($P<0.05$). This effect indicates that the interpretation of the main effects should be considered cautiously. In this study, the significant interaction effect indicates that the observed difference in the learning between younger and older groups does not exist in all time points.

Table 2. Main and interaction effects of within and between subject variables.

	df	F	Sig.
Age (between-subject effects)	1	98.58	0.00
Time (within-subject effects)	2	57.16	0.00
Age*Time (interaction effects)	2	4.78	0.01

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Table 3: Post-hoc analysis using Bonferroni correction.

	Blocks time	Mean±SD	Pairwise comparison	t value	Sig.
Young adults	Block 2	87.98±24.83	Block 2& 8	8.50	0.00
	Block 8	62.04±15.39	Block 2& 10	12.23	0.00
	Block 10	52.31±17.20	Block 8& 10	3.48	0.002
Older adults	Block 2	164.64±63.15	Block 2& 8	5.18	0.00
	Block 8	113.11±16.09	Block 2& 10	5.09	0.00
	Block 10	110.17±19.5	Block 8& 10	1.19	0.24

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4. Discussion

The result of the present study indicates that online motor learning is more pronounced in older adults compared to younger ones. The result also shows that the offline component of learning is affected by ageing.

It was hypothesized that older adults could achieve considerable performance improvement during the training session (online learning). The result of the present study supports this hypothesis. This finding provides strong evidence for high capacity of implicit sequence online learning in older adults, which is consistent with the findings of Schult et al., 2011. They revealed that older adults could use different strategies, which are more effective than those of the younger adults for perceptual and higher-order cognitive processing. Some studies also observed that older adults have higher ability for retrieving, reorganizing and learning SRT task in using different compensatory strategies (Shea, Park, & Braden, 2006; Voelcker-Rehage & Willimczik, 2006; Voelcker-Rehage, Godde, & Staudinger, 2011) that are consistent with the finding in the present study.

Furthermore, a number of studies have shown that both young and older adults have comparable ability in implicit motor learning. They showed that older adults can efficiently adapt to environmental irregularities (Howard & Howard, 1992; Howard et al., 2008; Shea, Park, & Braden, 2006). On the other hand, Madden et al. (2010) study reported on age-related learning deficit. These conflicting results may be due to the difference in structure and complexity of the experimental tasks in these studies. The pattern of SRTT in this study had second-order structure with low level of complexity, while in Madden et al. study (2010), a fine motor skill with high degree of difficulty was used.

It was also hypothesized that older adults are able to achieve considerable performance improvement after

completion of the training session (offline learning). The result of the present study did not support this hypothesis. This is partly consistent with the findings of Spirdu-so, Smith and Choi (1993) that demonstrated a decrease in the performance improvement in older adults during retention in a nonlinear fashion. Bennett, Howard, and Howard (2007) and Smith et al. (2005) also showed that older adults need more training by analogy to younger adults, before showing a long term learning effect.

It seems that a single session of treatment is not enough for retention of the changes beyond the training session and multiple sessions of training is required for offline lasting of changes (Tunney et al., 2004). Long Term Potentiation (LTP) is the underlying mechanism for offline learning. During this process, the synaptic efficiency increases in certain brain structures. It may lead to chemical and structural changes underlying offline performance improvement (Hunt & Castillo, 2012). There are changes in levels of neurotransmitter receptors activation, oligodendrocytes activity, triggering Ca²⁺ influx, and release of Ca²⁺/calmodulin-dependent protein kinase II (Hunt & Castillo, 2012). All of these changes could be important for stabilizing synaptic contacts and functional plastic changes during offline learning (Yamazaki et al., 2014). Again, a single session of training may not be enough to trigger the above changes.

Some studies have indicated age-related LTP deficits during offline learning and reported alterations in gene expression such as c-fos, Arc, and de novo protein synthesis in older age group that are necessary for maintenance of late-phase LTP (Rosenzweig et al., 1997; Small et al., 2004; Small et al., 2002). Rosenzweig et al. had been observed that CA1 pyramidal cells (sub-regions of the hippocampus) got less depolarized in older rats during LTP. Another study demonstrated that granule cells of the dentate gyrus had a significantly smaller proportion of neurons that express Arc following spatial exploration in aged rats, while expression of Arc might be

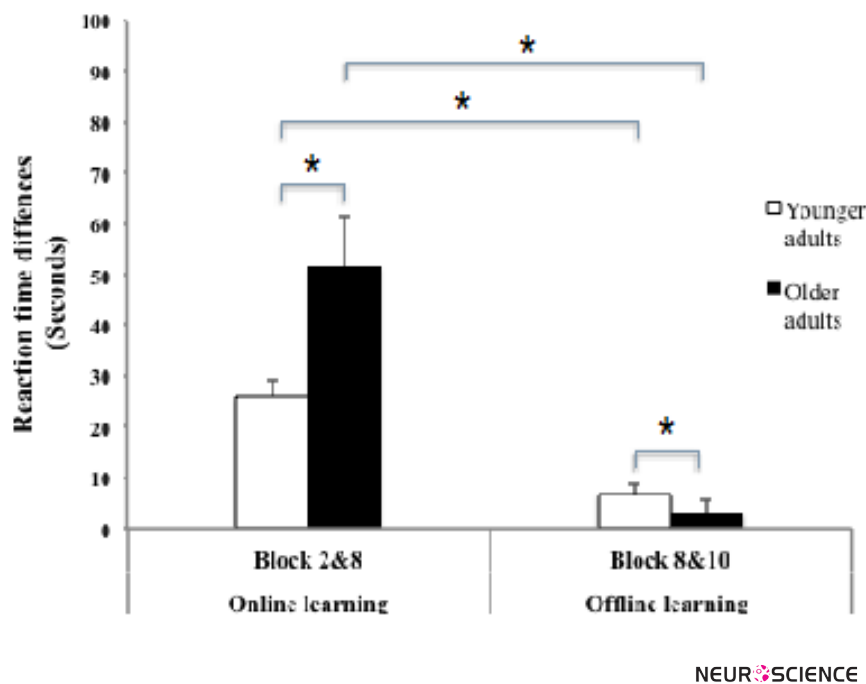


Figure 1. Reaction time differences among the blocks, * indicates significance difference.

important for plastic changes of synapses (Small et al., 2004). In addition, studies, which applied MRI methods in humans and monkeys, showed that the granule cells were particularly vulnerable to the effects of normal ageing (Small et al., 2004; Small et al., 2002). Therefore, although a similar number of pyramidal neurons express c-fos in different age groups, the individual cells from old animals transcribe less c-fos mRNA, which might lead to irregularity of other genes during LTP. All of these studies did not support the current hypothesis and indicated that functional and structural plastic changes would reduce in older adults during offline learning (Rosenzweig et al., 1997; Small et al., 2004; Small et al., 2002).

In this study, it was also hypothesized that younger adults learn better than the older adults during online and offline learning. The results support this hypothesis. In this study, younger adults showed a higher performance level in all blocks of training compared to older ones (however, older adults had a high improvement performance during online learning). Younger adults also showed significant performance improvement offline. Shea, Park, and Braden (2006) also indicated that there were no age-related differences in learning characteristics; however, younger adults performed significantly faster than older adults. The findings of Spirduso, Smith, and Choi (1993) are in line with the findings of the current study. They demonstrated that during online learn-

ing, older adults learn faster than younger adults, however, they could not maintain this learning effect offline. Chapman et al. (1999) had been reported that, although fast synaptic transmission and short-term plasticity were not reduced in aged transgenic mice, ageing would negatively affect LTP in regions of the hippocampus. Thus, reduction of synaptic efficiency and LTP may negatively affect offline learning in older adults (Watson et al., 2002). The changes in the ratio of long-term depression (LTD) and LTP induction during ageing may disrupt Ca^{2+} homeostasis of synapse with reduced intracellular Ca^{2+} concentration following neural activity and larger after hyperpolarizing potential observed in aged hippocampal neurons (Foster & Norris, 1997; Landfield, 1988). Consequently, young adults react to the external environmental changes appropriately and have a longer effect of performance improvement with offline learning than older adults.

One possible mechanism for better online learning of the older adults compared to younger ones is that older adults can use compensatory strategies by recruiting different brain areas and functional reorganization (Madden et al., 2010). This may enable older adults to learn better, based on the short-term plasticity during online learning. Hogan et al. (2011) compared the effects of encoding context and stimulus repetition in young and old adults. They showed that in comparison to older adults, younger adults had lower levels of frontal-temporal and

temporal-parietal coherence with higher levels of frontal-parietal coherence (Hogan et al., 2011). Likewise, Madden et al. showed that there are differences in functional connectivity of frontoparietal activation in older adults compared to younger ones (Madden et al., 2010). This difference is highlighted as healthy ageing is associated with functional reorganization of central nervous system to accommodate with functionally increasing task demands on perceptual and attention operations (Madden et al., 2010). The mentioned functional differences between younger and older adults may explain the differences in online learning between these two groups.

Changes in sensory and motor system might be one possible explanation for the slower performance in older adults (Bock & Schneider, 2002; Seidler, 2006; Voelcker-Rehage & Albers, 2005), while compensatory processes in cortical and sub-cortical functions may allow maintenance of the performance and online learning level (Hogan et al., 2011; Latash, 2008). Otherwise, age-related adaptive changes in CNS do not affect motor performance improvement in the form of online learning (Latash, 2008); however, aging affects LTP and synaptic plasticity or offline learning.

The findings in the current study must be interpreted in the context of several limitations. First, the data were obtained from a healthy population with no neurological conditions. Therefore, the results may not be necessarily generalized to people with different neurological conditions. Secondly, the number of males and females did not match and there were more females in younger age than older groups; females may respond differently to male participants and the findings in younger adults are more representative of females.

This study did not assess the cortical excitability changes during and following completion of the training sessions. For further studies, it is required to assess these changes to shed light on the underlying mechanisms of learning. There was also no attempt to compare gender effects; therefore, further studies are required to assess this factor on online and offline learning too. The length of the training session may also affect the online and offline learning. Thus, we suggest a study to characterize the length of a single session for production of both online and offline effects. We also recommend studies to compare the effects of explicit and implicit learning on online and offline performance in both younger and older adults. Further research is required to evaluate the effects of learning tasks with different levels of complexity on online and offline learning and performance improvement.

This study showed that offline component of learning was greatly affected by ageing. Although both younger and older adults had a high level of improvement during the training (online learning), younger adults showed significant improvement during retention (offline learning). Therefore, adults could learn practical and training skills; however, they could not maintain this learning effect. The result of the present study provided evidence that healthy older adults are able to improve their performance with practice and learn motor skill successfully in the form of online learning.

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References

- Bennett, I., Howard, J. H. Jr., & Howard, D. V. (2007). Age-related differences in implicit learning of subtle third-order sequential structure. *The Journal of Gerontology: Series B: Psychological Sciences and Social Sciences*, 62(2), 98-103.
- Bock, O., & Schneider, S. (2002). Sensorimotor adaptation in young and elderly humans. *Neuroscience & Biobehavioral Review*, 26(7), 761-7.
- Chapman, P. F., White, G. L., Jones, M. W., Cooper-Blacketer, D., Marshall, V. J., Irizarry, M., et al. (1999). Impaired synaptic plasticity and learning in aged amyloid precursor protein transgenic mice. *Nature Neuroscience*, 2(3), 271-6.
- Curran, T. (1997). Effect of aging on implicit sequence learning: accounting for sequence structure and explicit knowledge. *Psychological Research*, 60(1-2), 24-41.
- De Luca, D., Alessandro, E., Bonacci, S., & Giraldi, G. (2011). Aging populations: the health and quality of life of the elderly. *La Clinica Terapeutica*, 162(1), e13-8.
- Dennis, N. A., Howard, J. H. Jr., & Howard, D. V. (2003). Age deficits in learning sequences of spoken words. *Journal of Gerontology: series B: Psychological Sciences and Social Sciences*, 58(4), 224-227.
- Durkin, M., Prescott, L., Furchtgott, E., Cantor, J., & Powell, D. A. (1995). Performance but not acquisition of skill learning is severely impaired in the elderly. *Archives of Gerontology and Geriatrics*, 20(2), 167-183.
- Feeney, J. J., Howard, J. H. Jr., & Howard, D. V. (2002). Implicit learning of higher order sequences in middle age. *Psychology and Aging*, 17(2), 351-355.
- Foster, T. C., & Norris, C. M. (1997). Age-associated changes in Ca²⁺-dependent processes: relation to hippocampal synaptic plasticity. *Hippocampus*, 7(6), 602-612.

- Hall, C. D., Echt, K. V., Wolf, S. L., & Rogers, W. A. (2011). Cognitive and motor mechanisms underlying older adults' ability to divide attention while walking. *Physical Therapy, 91*(7), 1039-50. doi: 10.2522/ptj.20100114.
- Harrington, D. L., & Haaland, K. Y. (1992). Skill learning in the elderly: Diminished implicit and explicit memory for a motor sequence. *Psychology and Aging, 7*(3), 425-432.
- Hogan, M., Collins, P., Keane, M., Kilmartin, L., Kaiser, J., Kenney, J., et al. (2011). Electroencephalographic coherence, aging, and memory: distinct responses to background context and stimulus repetition in younger, older, and older declined groups. *Experimental Brain Research, 212*(2), 241-55. doi: 10.1007/s00221-011-2726-8.
- Howard, D. V., & Howard, J. H. Jr. (1992). Adult age differences in the rate of learning serial patterns: Evidence from direct and indirect tests. *Psychology and Aging, 7*(2), 232-241.
- Howard, D. V., Howard, J. H. Jr., Dennis, N. A., Lavine, S., & Valentino, K. (2008). Aging and implicit learning of an invariant association. *The Journals of Gerontology: Series B: Psychological Sciences and Social Sciences, 63*(2), 100-105.
- Hunt, D. L., & Castillo, P. E. (2012). Synaptic plasticity of NMDA receptors: mechanisms and functional implications. *Current Opinion in Neurobiology, 22*(3), 496-508. doi: 10.1016/j.conb.2012.01.007.
- Landfield, P. W. (1988). Hippocampal neurobiological mechanisms of age-related memory dysfunction. *Neurobiology of Aging, 9*(5-6), 571-579.
- Latash, M. L. (2008). *Neurophysiological Basis of Movement* (2nd Ed.). Urbana, IL: Human Kinetics.
- Light, L. L., & Singh, A. (1987). Implicit and explicit memory in young and older adults. *The Journal of Experimental Psychology-Learning Memory and Cognition, 13*(4), 531-41.
- Lustig, C., Shah, P., Seidler, R., & Reuter-Lorenz, P. A. (2009). Aging, Training, and the Brain: A Review and Future Directions. *Neuropsychology Review, 19*(4), 504-522. doi: 10.1007/s11065-009-9119-9.
- Madden, D. J., Costello, M. C., Dennis, N. A., Davis, S. W., Shepler, A. M., & Spaniol, J., et al. (2010). Adult age differences in functional connectivity during executive control. *Neuroimage, 52*(2), 643-57. doi: 10.1016/j.neuroimage.2010.04.249.
- McDowd, J. M., & Craik, F. I. (1988). Effects of aging and task difficulty on divided attention performance. *Journal of Experimental Psychology: Human Perception and Performance, 14*(2), 267-80.
- Nissen, M. J., & Bullemer, P. (1987). Attentional requirement of learning evidence from performance measures. *Cognitive Psychology, 19*(1), 1-32.
- Pratt, J., Chasteen, A. L., & Abrams, R. A. (1994). Rapid aimed limb movements: age differences and practice effects in component submovements. *Psychology and Aging, 9*(2), 325-334.
- Rosenzweig, E. S., Rao, G., McNaughton, B. L., & Barnes, C. A. (1997). Role of temporal summation in age-related long-term potentiation-induction deficits. *Hippocampus, 7*(5), 549-558.
- Schulte, T., Muller-Oehring, E. M., Chanraud, S., Rosenbloom, M. J., Pfefferbaum, A., & Sullivan, E. V. (2011). Age-related reorganization of functional networks for successful conflict resolution: A combined functional and structural MRI study. *Neurobiology of Aging, 32*(11), 2075-90. doi: 10.1016/j.neurobiolaging.2009.12.002.
- Seidler, R. D. (2006). Differential effects of age on sequence learning and sensorimotor adaptation. *Brain Research Bulletin, 70*(4-6), 337-346.
- Shea, C. H., Park, J., & Braden, H. (2006). Age-related effects in sequential motor learning. *Physical Therapy, 86*(4), 478-88.
- Shumway-Cook, A., & Woollacott, M. H. (2001). *Motor Control, Theory and Practice Application* (2nd Ed.). Philadelphia (PA): Lippincott Williams and Wilkins Publication.
- Small, S. A., Chawla, M. K., Buonocore, M., Rapp, P. R., & Barnes, C. A. (2004). Imaging correlates of brain function in monkeys and rats isolates a hippocampal subregion differentially vulnerable to aging. *Proceedings of the National Academy of Sciences of the United States of America, 101*(18), 7181-7186.
- Small, S. A., Tsai, W. Y., DeLaPaz, R., Mayeux, R., & Stern, Y. (2002). Imaging hippocampal function across the human life span: is memory decline normal or not? *Annals of Neurology, 51*(3), 290-295.
- Spiridus, W. W., Smith, K. L., & Choi, J. H. (1993). Age and practice effects on force control of the thumb and index finger in precision pinching and bilateral coordination. *Sensorimotor Impairment in the Elderly, NATO ASI Series, 75*, 393-412.
- Turney, N., Taylor, L. F., Gaddy, M., Rosenfeld, A., Pearce, N., & Tamanini, J., et al. (2004). Aging and motor learning of a functional motor task. *Physical & Occupational Therapy in Geriatrics, 21*(3), 1-16.
- Voelcker-Rehage, C., & Albers, J. L. (2005). Age-related changes in grasping force modulation. *Experimental Brain Research, 166*(1), 61-70.
- Voelcker-Rehage, C., Godde, B., & Staudinger, U. M. (2011). Cardiovascular and coordination training differentially improve cognitive performance and neural processing in older adults. *Frontiers in Human Neuroscience, 17*(5), 26. doi: 10.3389/fnhum.2011.00026.
- Voelcker-Rehage, C., & Willimczik, K. (2006). Motor plasticity in a juggling task in older adults—a developmental study. *Age and Ageing, 35*(4), 422-7.
- Watson, J. B., Khorasani, H., Persson, A., Huang, K. P., Huang, F. L., & O'Dell, T. J. (2002). Age-related deficits in long-term potentiation are insensitive to hydrogen peroxide: coincidence with enhanced autophosphorylation of Ca²⁺/calmodulin-dependent protein kinase II. *Journal of Neuroscience Research, 70*(3), 298-308.
- Yamazaki, Y., Fujiwara, H., Kaneko, K., Hozumi, Y., Xu, M., Ikenaka, K., et al. (2014). Short- and long-term functional plasticity of white matter induced by oligodendrocyte depolarization in the hippocampus. *Glia, 62*(8), 1299-312. doi: 10.1002/glia.22681.

