Coping with task demand in aging using neural compensation and neural reserve triggers primarily intra-hemispheric-based neurofunctional reorganization

Jennyfer Ansado [a,b,c,*], Oury Monchi [b,d], Nourane Ennabil [a,b], Johnathan Deslauriers [b], Thomas Jubault [b], Sylvane Faure [c], Yves Joanette [a,b]

[a] *Faculty of Medicine, Université de Montréal, Montreal, Quebec, Canada*
[b] *Centre de Recherche, Institut Universitaire de Gériatrie de Montréal, Montreal, Quebec, Canada*
[c] *Department of Psychology, Université Nice-Sophia Antipolis, France*
[d] *Department of Radiology, Université de Montréal, Montreal, Quebec, Canada*

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ABSTRACT

It has been proposed that cognitive reserve is supported by two neural mechanisms: neural compensation and neural reserve. The purpose of this study was to test how these neural mechanisms are solicited in aging in the context of visual selective attention processing and whether they are inter- or intra-hemispheric. Younger and older participants were scanned using fMRI during a visual letter-matching task with two attentional load levels. The results show that in the low-load condition, the older participants activated frontal superior gyri bilaterally; these regions were not activated in the younger participants, in accordance with the compensation mechanism and the Posterior-Anterior Shift in Aging (PASA) phenomenon. However, when task demand increased, the older participants recruited the same regions (parietal) as the younger ones, showing the involvement of a similar neural reserve mechanism. This result suggests that successful cognitive aging relies on the concurrent use of both neural compensation and neural reserve in high-demand tasks, calling on the frontoparietal network. In addition, the finding of intra-hemispheric-based neurofunctional reorganization with a PASA phenomenon for all attentional load levels suggests that the PASA phenomenon is a function more of compensation than of reserve.

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1. Introduction

The notion of cognitive reserve was introduced to explain successful cognitive aging despite age-related neural changes. Two distinct mechanisms are suspected to underlie cognitive reserve: neural reserve and neural compensation (for a review, see Stern, 2009). Neural reserve refers to brain networks or brain capacity that allow people to cope with increased task demands; it can differ in its expression as a function of its efficiency or capacity. Any condition that affects brain function, including normal aging, can have an impact on network efficiency or capacity. Neural compensation, on the other hand, is based on the existence of presumed alternative networks or sets of brain areas that would compensate for the loss of cognitive efficiency associated with age-related decline. The purpose of the current study was to explore the ability of these neural mechanisms to engage in visual selective attention processing in aging and specify the pattern of reorganization – inter-hemispheric or intra-hemispheric – involved in these mechanisms, using a letter-matching task that varies the amount of perceptual load.

Because of its limited computational resources, the human brain must process information selectively. It is impossible to process all available stimuli simultaneously; when numerous stimuli are present at the same time, one can attend to only one or a subset of them, at the expense of the remaining items. Visual selective attention improves our perception and performance by biasing sensory input at the early stages of processing (Itti et al., 1998). Early investigations of the control of visual selective attention emphasized the role of the posterior parietal cortex, but a far more complex neural architecture is now assumed to play a role. The consensus (for a review, see Yantis, 2008) is that subregions of the posterior parietal cortex (part of the intraparietal sulcus and the superior parietal lobule [BA 7]) and of the prefrontal cortex (the frontal eye field [FEF: between BA 4, 6 and 8] and the supplementary eye field [SEF: upper part of the paracentral sulcus; into the mesial area 6]), as well as the superior colliculus (for voluntary eye movements), make distinct contributions. As Driver and Frackowiak (2001) summarized the situation, control, which is instantiated mainly by this

* Corresponding author at: Centre de Recherche, Institut Universitaire de Gériatrie de Montréal, 4565 Queen-Mary Road, Montreal, Quebec, Canada H3W 1W5. Tel.: +1 514 340 3540x4021; fax: +1 514 340 3548.

E-mail address: jennyfer.ansado@umontreal.ca (J. Ansado).

frontoparietal network, allows one to generate preparatory states that specify the current target for selective attention and modulate cortical activity in the posterior sensory regions so one can favor certain stimuli over others; the FEF, the superior parietal lobule and the intraparietal sulcus are the main sources of attentional control signals, while the middle and ventral temporal cortex and visual cortex V1–V4 (primary [BA 17] and extrastriate [BA 18 and 19] visual areas) are the targets of these modulatory signals.

In normal aging, Maylor and Lavie (1998) reported that older adults show a greater adverse effect as a result of an incompatible distracter than younger ones even at the lowest attentional loads. This result signals a decline in attentional filtering, together with the possibility of adaptive flexibility. Indeed, endogenous attention in complex perceptual situations, coordinating and controlling the performance of multiple tasks, and holding task-relevant information online while filtering out task-irrelevant information can all be compromised. But older adults can use alternative or additional strategies and/or neural networks to cope with task demands and optimize performance. Madden (2007) maintains that some aspects of top-down guidance are still operative and may play a larger role in older adults' performance to compensate for the decline in bottom-up visual sensory processes and in executive processing related to task control. Cognitive performance in healthy aging can be conceived of as resulting from both age-related neurocognitive decline and age-related compensatory mechanisms (for reviews, see Park and Reuter-Lorenz, 2009; Salthouse, 2009). A number of studies have offered evidence suggesting that neural reorganization is necessary to cope with the significant changes in the brain's anatomy and physiology in aging. Thus, functional neuroimaging has shown that elderly individuals who have maintained a given cognitive ability are characterized by more bilateral patterns of activation, a phenomenon Cabeza (2002) refers to as Hemispheric Asymmetry Reduction in Older Adults (HAROLD).

At the same time, other studies have indicated that the preservation of certain other cognitive abilities was associated with some intra-hemispheric reorganization of the patterns of activation, frequently from the occipitotemporal to the frontal cortex, a phenomenon Dennis and Cabeza (2008) referred to as the Posterior-Anterior Shift in Aging (PASA). This second phenomenon was first reported by Grady et al. (1994) in a positron emission tomography study of faces and locations. With both materials, older adults showed weaker activity than younger adults in occipitotemporal regions but greater activity in anterior regions, including the prefrontal cortex (PFC). Several explanations have been advanced to explain these patterns of activation. On one hand, they might express the age-related reductions in occipital activity attributed to deficits in sensory processing, along with age-related increases in PFC activity to compensate for these deficits (Cabeza, 2004; Grady et al., 1994, 2005; Madden et al., 1997; Reuter-Lorenz et al., 2000; Cappell et al., 2010).

Typically, the PASA phenomenon is associated with an absence of significant differences in accuracy between younger and older individuals and with longer response times for older individuals (Dennis and Cabeza, 2008). Indeed, several studies have linked greater PFC activity in older adults, in the form of bilateral recruitment, to better cognitive performance. Reuter-Lorenz et al. (2000) found that older adults who recruited bilateral PFC regions were faster in a working memory task, and Cabeza (2002) found bilateral PFC recruitment in high- but not in low-performing older adults (see also Daselaar et al., 2003; Rosen et al., 2002). Supporting the compensatory hypothesis, a negative correlation has been reported between PFC and occipital activations in aging (Cabeza et al., 2004b). A more recent study found that age-related increases in frontal activity were positively correlated with performance and negatively correlated with the age-related occipital decreases (Davis et al., 2008). On the other hand, many studies suggest that

these patterns reflect a phenomenon related to task complexity in older participants. In this view, the task is more complex for older than younger subjects, and the age-related pattern (i.e., HAROLD and PASA) is induced by an adaptation mechanism that allows people to cope with increasing complexity. This same network or set of regions is recruited in younger people at a higher level of complexity; in other words, it is solicited to different degrees according to age. Thus, these patterns result from an adaptation mechanism that is present throughout life and is flexibly deployed depending on the cognitive demands of the task (Ansado et al., 2009; Park and Reuter-Lorenz, 2009; Reuter-Lorenz et al., 1999).

Many studies have proposed that greater activation should be seen in older people than in younger ones for simple tasks, while greater activation should be seen in young subjects than in elderly people for complex tasks (for a review, see Reuter-Lorenz and Lustig, 2005). For example, the PASA phenomenon may indicate that the difficulty of a given task differs for young and older participants, such that an older participant dealing with an easy condition could experience a level of difficulty similar to a younger participant facing a more difficult condition. There is indeed abundant evidence (Schneider-Garces et al., 2010) that the same cognitive tasks tend to be more demanding for older than for younger adults (Braver et al., 2001; Grady et al., 1998; Logan et al., 2002; Paxton et al., 2008; Rypma and D'Esposito, 2000). If this is the case, the age-determined change in the level of complexity could account, at least partly, for the phenomena associated with successful cognitive aging (for a review, see Ansado et al., 2009). Reuter-Lorenz and Cappell (2008) referred to this tradeoff as the Compensation-Related Utilization of Neural Circuits Hypothesis (or CRUNCH), in which processing inefficiencies cause the aging brain to recruit more neural resources to achieve computational output equivalent to that of a younger brain. Mattay et al. (2006) reported a similar result using a verbal n-back task with variable working memory load. These frontal activations may therefore reflect the brain's response to increased task difficulty by recruiting "reserve" resources (Reuter-Lorenz and Cappell, 2008).

In his theoretical model of Cognitive Reserve, Stern (2003, 2009; Stern et al., 2005) encompasses all these explanations. Cognitive reserve is then defined as the ability to optimize performance and, based on the involvement of two mechanisms: neural reserve and neural compensation. Cognitive reserve depends on the ability to effectively recruit these brain mechanisms and is measured by the amount of task-related activation as a function of performance or task load. Thus, manipulating the level of cognitive demand, by parametrically varying the level of complexity of the task, should help to identify which of these two mechanisms – neural reserve and neural compensation – can be observed in older people.

The "*neural reserve*" hypothesis refers to the possibility that younger and older adults may use the same pre-existing network or set of brain areas to mediate task performance, albeit with different levels of efficiency and capacity. In this case, a network underlying task performance may differ in its expression as a function of its efficiency or capacity. While younger individuals may invoke this network when coping with increased task demands, it could also help an older person cope with aging. In this view, differences in patterns of activation between groups do not necessarily indicate that the two groups are using different brain networks to mediate task performance. The difference indicates that the older individuals need to recruit these networks because they are already dealing with increased cognitive demand. This difference is linked to the system's efficiency or capacity. At relatively low task demand, greater activation might be seen in older people than in young people. Conversely, at greater task demand, greater activation might be seen in the young subjects than in the older ones. The brain network has a greater capacity in the younger subjects than in the