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Hemispheric asymmetry and aging: right hemisphere decline or asymmetry reduction

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Abstract

We review evidence for two models of hemispheric asymmetry and aging: the right hemi-aging model, which proposes that the right hemisphere shows greater age-related decline than the left hemisphere, and the hemispheric asymmetry reduction in old adults (HAROLD) model, which proposes that frontal activity during cognitive performance tends to be less lateralized in older than in younger adults. The right hemi-aging model is supported by behavioral studies in the domains of cognitive, affective, and sensorimotor processing, but the evidence has been mixed. In contrast, available evidence is generally consistent with the HAROLD model, which is supported primarily by functional neuroimaging evidence in the domains of episodic memory encoding and retrieval, semantic memory retrieval, working memory, perception, and inhibitory control. Age-related asymmetry reductions may reflect functional compensation or dedifferentiation, and the evidence, although scarce, tends to support the compensation hypothesis. The right hemi-aging and the HAROLD models are not incompatible. For example, the latter may apply to prefrontal regions and the former to other brain regions.

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It is well known that the brain hemispheres are anatomically and functionally asymmetric. Even though the molecular and genetic bases of this asymmetry are not well understood [1], its existence is supported by abundant converging evidence from *in vivo* and post-mortem neuroanatomy, neurochemistry, neuropsychology, neuroimaging, and behavioral research [2–4]. There is also evidence that these asymmetries are affected by conditions that alter the anatomical and functional integrity of the brain, such as brain damage and aging. In this article, we review evidence for two different models of hemispheric asymmetry and aging: the right hemi-aging model [5,6], which proposes that the right hemisphere shows greater age-related decline than the left hemisphere, and the hemispheric asymmetry reduction in old adults (HAROLD) model [7], which proposes that frontal activity during cognitive performance tends to be less lateralized in older than in younger adults.

1. Right hemi-aging model

The right hemi-aging hypothesis states that age-related cognitive declines affect functions attributed to the right hemisphere to a greater degree than those associated with the left hemisphere [5,6]. The validity of this hypothesis has been investigated in various functional domains. In this article we briefly review evidence from the areas of verbal/spatial, affective, and sensorimotor functions, which are lateralized in young adults and relevant for aging research.

1.1. Verbal/spatial

The first cognitive evidence for the right hemi-aging hypothesis comes from studies comparing the effect of aging on verbal and spatial tasks [8]. This asymmetry involving the type of information processed by the two hemispheres (verbal/spatial) is the clearest functional hemispheric asymmetry: the left hemisphere is more involved in the processing of verbal information, whereas the right hemisphere is more involved in the processing of

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pictorial/spatial information [9,10]. Using the Wechsler Adult Intelligence Scale (WAIS), Goldstein and Shelley [8] found that elderly participants were less impaired on the verbal component, which relies more heavily on the left hemisphere, than on the spatial component, which is more dependent on the right hemisphere. Consistent with these findings, Klisz [11] found that performance of elderly subjects resembled that of patients with right-hemisphere damage when tested with a neuropsychological battery intended to diagnose lateralized brain injury. Taken together, these findings suggest that functions attributed to the right hemisphere are more affected by aging. However, additional evidence has shown that, when test variables such as task complexity are controlled, elderly performance on verbal and spatial tasks does not differ significantly [12]. These findings do not support the idea that the right hemisphere processing capabilities are selectively affected by aging.

Evidence for the right hemi-aging hypothesis in other cognitive domains has also been inconclusive. Employing dichotic listening tasks to relate encoding, retention, and retrieval deficits in elderly to their learning performance, Clark and Knowles [13] observed age-related declines in both written and vocal recall, predominantly for material presented to the left ear. The authors attributed these results to a deficiency during encoding, probably due to an age-related decrease in left ear/right hemisphere processing capabilities. However, this effect was not replicated by later studies [14,15]. For example, a study by Schear and Nebes [15] intended to investigate the effect of aging on memory for spatial vs. verbal information, did not find any evidence of a greater decline with age in spatial compared to verbal memory. Similar results were reported in a recent study comparing visuospatial and verbal memory across the life span [16].

1.2. Affective domain

The right hemi-aging hypothesis has also been explored in the affective domain. The results of studies investigating hemispheric asymmetries in emotional processing are generally interpreted in the context of two more influential hypotheses: the right hemisphere hypothesis and the valence hypothesis. The right hemisphere hypothesis proposes that emotions are mainly processed in the right hemisphere independent of emotional valence [17], whereas the valence hypothesis proposes that pleasant emotions are mainly processed in the left hemisphere and unpleasant emotions are mainly processed in the right hemisphere [18]. To test the right hemi-aging hypothesis in the affective domain, McDowell et al. [19] compared accuracy and intensity measures of emotional and neutral facial recognition in both young and elderly participants and found that older subjects exhibited a deficit in the perception of unpleasant emotions when compared to young subjects. However, older subjects were as accurate as young subjects in identifying happy

faces. Interpreting these results in the context of the right hemisphere hypothesis of emotional processing, the authors have concluded that their findings only partially support the right hemi-aging hypothesis. However, if interpreted in the context of the valence hypothesis of emotional processing, these results fully support the right hemi-aging hypothesis. Nevertheless, the results of other studies investigating emotional faces do not support this hypothesis. For instance, a study investigating the effect of aging on processing of emotional facial expressions [20] found that the patterns of left-right asymmetries were comparable for younger and older participants.

1.3. Sensorimotor processing

Finally, the right hemi-aging hypothesis has also been investigated in lower-level processing (e.g. simpler sensory/perceptual and motor tasks) and again the evidence is not conclusive. Weller & Latimer-Sayer [21] used a sensory-motor task (i.e. pegboard) to investigate changes in manipulative skill as a function of age and found evidence supporting the right hemi-aging hypothesis; abilities associated with the right hemisphere were more affected by aging when compared with those associated with the left hemisphere. Additional studies [22] reported similar results. On the other hand, studies of perceptual asymmetries using visual-field presentations have not systematically reported evidence supporting the right hemi-aging hypothesis [14,20,23].

In summary, although there are findings supporting the notion that functions attributed to the right hemisphere are more affected by aging [8,11,13–15,19–29] the overall pattern of results is not clear [12,14,15,20,23,30–34]. One possible explanation for the inconsistent results is differences in methodology. For instance, studies reporting a larger right-ear advantage with age (left-lateralized hemisphere asymmetry) involved more complex tasks than those showing no difference in the magnitude of right-ear advantage or reduced asymmetry [24]. If we assume that the cerebral hemispheres cooperate to perform complex, but not simple tasks [35], it is more likely to observe a change in hemispheric asymmetry associated with more complex tasks. Another possible explanation of the inconsistent findings is that differential age-related decline applies only to some regions within the right hemisphere [36]. If this restricted right hemi-aging hypothesis is correct, a differential effect of aging on the right hemisphere could be found in some tasks but not others depending on the particular brain regions involved. Consistent with this idea, it has been suggested that tasks relying on posterior right hemisphere are more susceptible to age-related decline [36,37]. At any rate, regardless of whether these inconsistencies are related to the complexities of the tasks or the right hemisphere regions they engage, it is clear that further research on the right hemi-aging hypothesis is required.

2. Hemispheric asymmetry reduction in older adults (HAROLD)

As mentioned earlier, the HAROLD model states that, under similar conditions, prefrontal cortex (PFC) activity tends to be less lateralized in older adults than in younger adults. This model is supported by functional neuroimaging evidence in the domains of episodic memory encoding and retrieval, semantic memory retrieval, working memory, perception, and inhibitory control (Table 1). Moreover, evidence has also been obtained using other methods, such as electrophysiological [38] and behavioral [39] measures. Here we mention only a few examples of functional neuroimaging evidence in the domains of episodic memory and working memory.

2.1. Episodic memory

HAROLD was first noted in the episodic memory retrieval domain, probably because in this cognitive domain there was a strong expectation concerning the lateralization of PFC activity. During episodic retrieval, PFC activity tends to be right lateralized in young adults [40,41]. This, it is not surprising to find right lateralized PFC activity during a cued-recall task in young adults. Interestingly, in older adults, bilateral PFC activations were found during the same

task [42]. The finding of right-lateralized activity in young adults coupled with bilateral activity in older adults was replicated on a variety of episodic retrieval tasks, including word-stem cued recall [43], word recognition [44], and face recognition [45]. Thus, HAROLD during episodic retrieval has been demonstrated for both recall and recognition, and for both verbal and nonverbal materials. Moreover, HAROLD can be also found during episodic memory encoding [46–48]. For example, Logan and colleagues [47] found that during intentional learning of words, young adults showed more activity in left than in right PFC, whereas older adults showed similar levels of activity in both hemispheres. Furthermore, when subjects were provided with an explicit encoding strategy (concrete-abstract decision), the overall level of PFC activity in older adults increased to the level of young adults, but continued to show a bilateral pattern of activation. This finding suggests that HAROLD does not reflect the adoption of an alternative cognitive strategy, but rather reflects a change in neural architecture.

2.2. Working memory

In the working memory domain, there were also expectations concerning the lateralization of PFC activity; several studies have shown that PFC activity during verbal working memory tasks tended to be left lateralized whereas PFC activity during spatial tasks tended to be right lateralized [49]. Consistent with this pattern, Reuter-Lorenz et al. [50] found that in younger adults PFC activity during a delayed response task was significant in the left hemisphere for verbal stimuli but in the right hemisphere for spatial stimuli. In contrast, PFC activity was significant bilaterally for both types of stimuli in older adults. In addition, a recent study investigating the early effects of aging on working memory found evidence for HAROLD [51]. Using an N-back task, Dixit et al. [51] found greater neural activity in right PFC than in left PFC for younger adults, whereas middle-aged subjects exhibited bilateral activity. This effect suggests that the HAROLD pattern may develop before the age of 50. As shown in Table 1, age-related asymmetry reductions can be found when PFC activity is right lateralized in young adults, as in the case of episodic retrieval, as well as when PFC activity is left lateralized in young adults, as in the case of episodic encoding/semantic retrieval. The results in the working memory domain indicate that this is also true when the task is constant and that it is the nature of the information processed that affects the lateralization of PFC. In other words, the working memory data demonstrate that age-related asymmetry reductions may be found not only for process-related hemispheric asymmetries (e.g. episodic retrieval vs. semantic retrieval) but also for stimuli-related hemispheric asymmetries (e.g. verbal vs. spatial working memory).

While growing evidence continues to support the HAROLD model, the function of the reduction in

Table 1
PET/fMRI activity in left and right PFC in younger and older adults

Cognitive domain	Younger		Older	
	Left	Right	Left	Right
<i>Episodic retrieval</i>				
PET: word pair cued-recall [42]	-	++	+	+
PET: word stem cued-recall [43]	-	+	+	+
PET: word recognition [44]	-	+	++	++
PET: face recognition [45]	-	++	+	+
<i>Episodic encoding/semantic retrieval</i>				
fMRI: word-incidental [46]	++	+	+	+
fMRI: word-intentional [47]	++	+	+	+
fMRI: word-incidental [47]	++	+	++	++
fMRI: word-SME [48]	++	+	++	++
<i>Working memory</i>				
PET: Letter DR [50]	+	-	+	+
PET: Location DR [50]	-	+	+	+
PET: Number N-back: [51]	+	+++	++	++
<i>Perception</i>				
PET: face matching [71, Exp. 2]	-	+	++	++
PET: Face matching [72]	+	+++	++	++
<i>Inhibitory control</i>				
fMRI: No-GO trials [73]	-	+	+	+

Note: Plus signs indicate significant activity in the left or right PFC, and minus signs indicate nonsignificant activity. The number of pluses is an approximate index of the relative amount of activity in left and right PFC in each study, and it cannot be compared across studies. DR, delayed response task; SME, subsequent memory effect.

asymmetry is still under debate. One hypothesis is that bihemispheric recruitment in older adults plays a compensatory role in the aging brain [42]. This compensation account is consistent with evidence that bilateral activity in older adults is associated with enhanced cognitive performance [50] and that the particular brain regions showing age-related increases in activation are likely to enhance performance in the task being investigated. For example, there is evidence that left PFC can contribute to episodic retrieval performance. Although PFC activity during episodic retrieval is usually right lateralized, left PFC activations have also been found in many studies and seem to be associated with demanding retrieval tasks [52]. Since the same tasks tend to be more demanding for older than for younger adults, it is possible that older adults recruit left PFC in order to cope with increased retrieval demands. The compensation account is also consistent with evidence that recovery of function following unilateral brain damage is associated with the recruitment of the unaffected contralateral hemisphere [53,54].

However, there is an alternative view of age-related asymmetry reductions, the dedifferentiation account, which proposes that the reductions reflect age-related difficulty in engaging specialized neural mechanisms that were available during young adulthood [55]. It has been suggested that there is a gradual evolution from an amorphous general ability into a group of distinct cognitive processes during childhood development [56] and that during the aging process different functions once again begin to rely on similar executive or organizing resources [57,58]. In other words, a process of functional differentiation during childhood is reversed during aging by a process of functional dedifferentiation. This account is consistent with evidence that correlations among different cognitive measures, and between cognitive and sensory measures, tend to increase with age [58].

These two accounts of HAROLD were recently tested using PET [59]. Before scanning two groups of older adults were selected from a larger sample, one group that performed as well as a young group in a battery of memory tests (old-high group) and another group that performed significantly worse than the young group (old-low group). The two groups of older adults and the group of young adults were then scanned in a source memory task, which was shown to be associated with right PFC activity in young adults in a previous study [60]. The compensation hypothesis predicted bilateral PFC activity in old-high participants, whereas the dedifferentiation hypothesis predicted bilateral PFC in old-low participants. As illustrated by Fig. 1, the results supported the compensation hypothesis. Old-low participants showed no reduction in lateralization, whereas old-high participants showed a bilateral activation pattern. This finding was interpreted as suggesting that the old-low participants recruited similar PFC regions as young adults but used them inefficiently, whereas old-high participants compensated for age-related memory

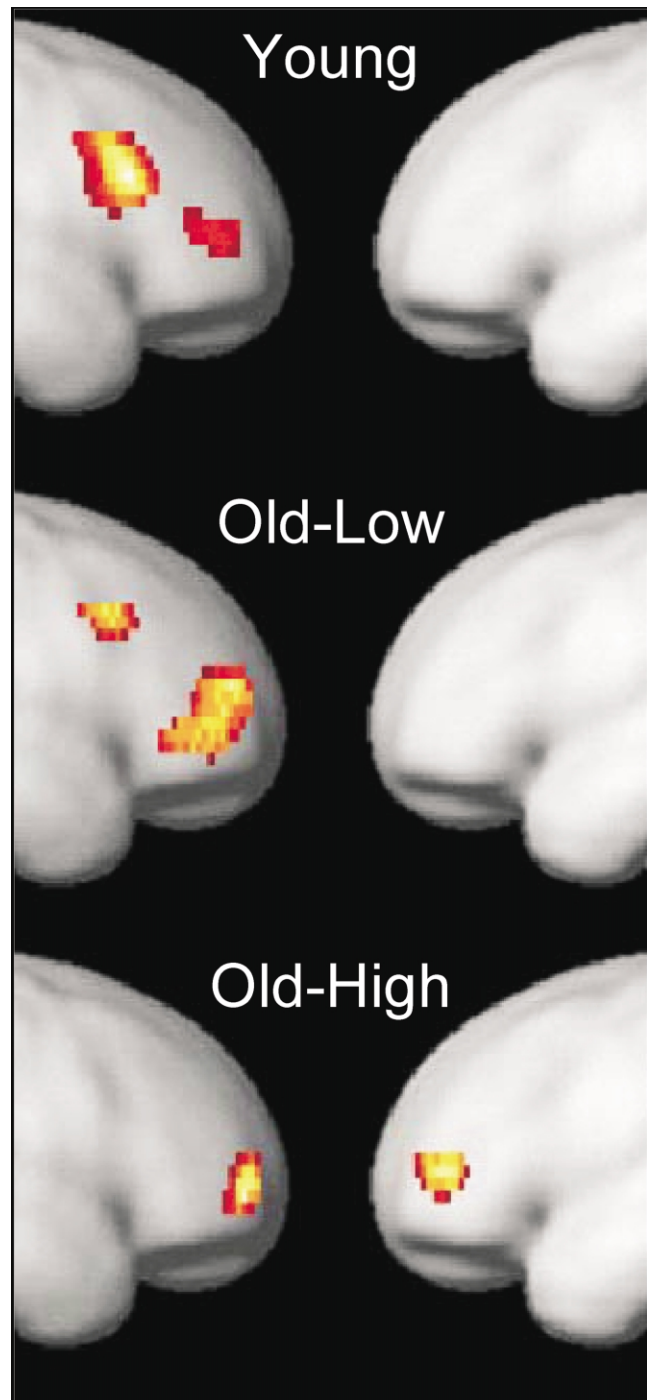


Fig. 1. PFC activity supporting the compensation account of HAROLD. In a source memory task, low performing participants (old-low) showed no reduction in lateralization, whereas high-performing participants (old-high) showed a bilateral activation pattern.

decline by reorganizing the episodic retrieval network. In contrast, the results in Fig. 1 are inconsistent with the dedifferentiation view, which predicts the asymmetry reduction, as other forms of age-related neurocognitive decline, should be more pronounced in low-performing than in high-performing older adults. It is important to note that

the term ‘dedifferentiation’ may also be used in a more neutral sense, as a description of more widespread activation pattern [61]. In that sense, the term dedifferentiation is not incompatible with the concept of dedifferentiation [7], and one may even talk about compensatory forms of dedifferentiation [61]. However, since the term dedifferentiation implies a deficit (i.e. de-differentiation denotes a lack or loss of differentiation) using it to merely mean ‘widespread activation pattern’ can be confusing.

Recently, Randy Buckner suggested an alternative explanation based upon previous research revealing age-related decreases in callosal volume [62,63]. If one assumes there is competition between the two hemispheres in young adults, an age-related decrease in lateralization could reflect an age-related reduction of interhemispheric inhibition due to callosal deterioration [64]. Yet, the notion that the two hemispheres compete with each other in young adults has not received strong empirical support [65]. On the contrary, there are strong suggestions that the two hemispheres collaborate during the performance of cognitive tasks, particularly when the tasks are more complex or difficult [35,66–68]. The issue of task difficulty is particularly important when comparing young and elderly groups, because what is difficult for elderly subjects may not be that difficult for young subjects. Consistent with the compensation view, an experiment investigating the effect of aging on performance of a task with three difficulty levels [39] suggests that older adults may indeed benefit from bi-hemispheric processing at levels of task complexity for which unilateral processing seems to be enough for young adults.

In summary, evidence for HAROLD continues to mount within the functional neuroimaging literature, across such domains as perception, episodic, semantic, and working memory. However, it is necessary to address a caveat of the HAROLD model. Evidence for HAROLD comes predominantly from neuroimaging studies. The functional imaging studies reviewed here do not take into account structural changes that have been shown to occur during the aging process [69]. Consequently, it is unclear whether differences in activation patterns reflect structural changes within the neural architecture, rather than alterations in recruitment patterns. Although the neuroimaging evidence of age-related structural changes is not clear with regard to the issue of hemispheric asymmetry, given that different brain areas show preferential patterns of age-related decline [70], it would be interesting to simultaneously investigate functional and structural aspects to see how changes in activation patterns relate to structural changes during aging.

3. Conclusion

The two models reviewed here provide different views of age-related changes in hemispheric asymmetry. The right hemi-aging model proposes that the right hemisphere shows

greater age-related decline than the left hemisphere [5,6], whereas the HAROLD model [7] proposes that frontal activity during cognitive performance tends to be less lateralized in older than in younger adults. Whereas empirical evidence relevant to the right hemi-aging model has been mixed, empirical evidence relevant to the HAROLD model has been largely consistent. Although no study has explicitly compared the two models, several of the functional neuroimaging studies reviewed earlier have investigated conditions in which the two models make opposite predictions. These conditions involve tasks in which PFC activity in young adults is left lateralized. Tasks in which PFC in young adults is right lateralized are not very useful for testing the models because in such conditions both models predict a more symmetric activation pattern in older adults (either due to an age-related reduction in right hemisphere function or to a reduction in hemispheric asymmetry). In contrast, when PFC activity is left lateralized in young adults, the two models make opposite predictions: the right hemi-aging model predicts an increased in hemispheric asymmetry, whereas HAROLD predicts reduced hemispheric asymmetry. The results of three functional neuroimaging studies of episodic encoding/semantic retrieval [46–48] support the latter prediction. At any rate, the two models are not necessarily mutually exclusive. Whereas the right hemi-aging hypothesis attempts to account for changes throughout the entire brain, HAROLD primarily accounts for changes in PFC. It may be that aging results in differing patterns of hemispheric asymmetry throughout the brain, with regions such as the occipital and temporal lobes exhibiting a pattern more indicative of the right hemi-aging hypothesis, while PFC shows a reduction in asymmetry. Therefore, it would be important to compare the effects of aging on the lateralization of brain activity both inside and outside PFC.

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