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Images of the Cognitive Brain Across Age and Culture

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1. Introduction

While structural and functional characteristics of the brain are largely similar across individuals, there is also evidence that much neural heterogeneity, both structural and functional, is present between different groups of people. For example, some individuals have greater regional brain volumes and thicknesses than others, and neural activity in response to the same stimuli varies across different individuals as well. Moreover, neural structure and function are temporally dynamic, showing changes across the human lifespan. Understanding how such neural heterogeneity arises between different individuals over the human lifespan is important for uncovering factors that influence developmental trajectories from adulthood to advanced age. In this article, we consider two general sources that contribute to neural heterogeneity over the adult lifespan - age-related biological changes and culture-related differences in external experience.

Over the human lifespan, biological processes related to brain structural integrity and neurobiological function change from adulthood to advanced aging (Goh, 2011; Goh & Park, 2009a; Park & Goh, 2009; Park & Reuter-Lorenz, 2009). In brief, aging has been associated with shrinkage of gray matter volume and thickness, reductions in white matter integrity, reductions in neurogenesis, and dysregulation of neuromodulatory mechanisms such as neurotransmitter action and synaptic communication. These age-related neurobiological changes have been associated with age-related changes in cognitive processing that is generally characterized by lower performance in tests of cognitive flexibility, fidelity, and speed in older adults compared to younger adults. Functionally, aging is associated with a decrease in the selectivity of brain responses to different types of stimuli as well as an increase in engagement of frontal regions. Importantly, it has been suggested that because age-related neurobiological changes tend to level off individual differences, neural differences between older adult individuals may be reduced compared to younger adult individuals (Baltes & Lindenberger, 1997; Park & Gutchess, 2002; Park et al., 1999; Park et al., 2004; Park & Gutchess, 2006). Thus, along with lower cognitive behavioral performance, aging may also be associated with greater, albeit compromised, similarity in brain structure and function across individuals.

Over the lifespan as well, individuals undergo different life experiences such as culturally different social and cognitive environments that emphasize dissociable ways of processing information (Nisbett, 2003; Nisbett & Masuda, 2003; Nisbett et al., 2001). For example,

Western culture has been associated with an emphasis on independence and individualism as important societal values. In addition, studies have shown that these values may bias Westerners towards a more analytic cognitive processing style, reflected as greater attention to objects and the features associated with an object. In contrast, East Asian culture tends to emphasize societal interdependence and collectivism, which are reflected in a bias towards a more holistic style of cognitive processing, involving greater attention to contextual relationships between different objects. Importantly, neuroimaging studies have shown that there are neural differences between Western and East Asian samples that are associated with these culture-related differences in individualistic-collectivistic values and analytic-holistic cognitive processing biases, respectively (Goh & Park, 2009b; Han & Northoff, 2008; Park & Huang, 2010). These neuroimaging findings suggest that culture-related differences in external experience may result in dissociable neural structural and functional development over the lifespan.

A key question that arises when considering the influences of age and culture on the brain is how they interact with each other over the human lifespan (Park & Gutchess, 2002; Park et al., 1999; Park & Gutchess, 2006). Three possible cases arise with respect to this interaction between age and culture. First, culture-related neural differences across individuals may accentuate with increasing age. With increasing age, and assuming that individuals remain in the same cultural environment, individuals gain greater experience in their cultural environment. Such prolonged cultural exposure may result in more engrained psychological biases and also increasingly divergent expression of neural structural and functional development between different cultural groups. Second, culture-related neural differences, once attained, may remain at the same level throughout the lifespan. This case may arise because external cultural factors reach an asymptotic level of influence on neurocognitive processing, such that further experience does not increase the biases. This cap on the influence of external experience may be necessary to maintain a homeostatic level of neural processing important for adaptive function in the environment. For example, it would be detrimental for Westerners to become so completely attentive to objects and lose all attention to contextual information (and vice versa for East Asians) the more experience they accrue in their analytic processing style. In addition, the maintenance of cultural neural differences over the lifespan may also arise because neurobiological effects of age in reducing individual neural differences dampen the diverging effects of cultural experiences. Third, culture-related neural differences may be reduced with increasing age. It is possible that age-related neurobiological changes impact all individuals to such a degree that differences in brain structure and function across older individuals is diminished relative to younger adults. Overall, these first two cases of age by culture interactions (or lack thereof) suggest that the neurobiological effects of age do not completely diminish individual differences in brain structure and function that arise from external experience, at least those associated with cultural influences. In contrast, the third case of an attenuation of culture-related neural differences with aging would suggest that the neurobiological effects of age exert a stronger influence on brain structure and function than external experiences related to culture.

To characterize how age and culture influence brain structure and function, this article reviews recent neuroimaging studies from both these fields, and considers the evidence for the above three cases of interaction between age and culture. In the following section, we provide an overview of neuroimaging findings pertaining to cognitive aging. We show that, due to changes in neurobiological structure and function, aging is generally associated with a reduction in the distinctiveness of neurocognitive representations as well as increases in

the neural effort involved in cognitive processing perhaps to compensate for the age-related declines. Next, we provide an overview of findings pertaining to cultural differences in cognition. We cover the evidence for cultural differences in behavior and functional brain responses related to perceptual processing and attention that are consistent with an analytic-holistic dichotomy in processing styles between Westerners and East Asians. We then consider some findings in children and older adults that relate to the development of cultural biases over the lifespan. These studies are few, but they provide an initial platform for understanding how neurobiological changes with aging and culture-related external experiences interact in the brain. Finally, we evaluate some important methodological issues that limit the extent to which current data can be interpreted and applied to other samples. Overall, the findings reviewed below will show that culture-related behavioral and neural differences are quite evident and seem to be present from a very young age during childhood. Moreover, these culture-related neural differences appear to be present even in older adulthood. Thus, the evidence suggests that aging does not disproportionately diminish the influence of experience on neural processing in the brain, at least for those sensitive to culture-related experiences.

2. Age-related functional imaging findings

There is a wealth of literature that documents age-related changes in fundamental cognitive processes across the lifespan (Park et al., 2002). The speed at which information is processed (Salthouse, 1996), the capacity of working memory (Park et al., 1996; Park et al., 2002), the ability to selectively attend to relevant information (Hasher & Zacks, 1988), and the efficiency of sentence processing (Wlotko et al., 2010) - all of these behavioral measurements of cognitive functions show age-related declines in many older adults (Figure 1). At the same time, studies have shown age-related reductions in gray matter regional brain volumes and thickness (Fjell et al., 2009; Raz et al., 2005; Raz & Rodrigue, 2006; Salat et al.,

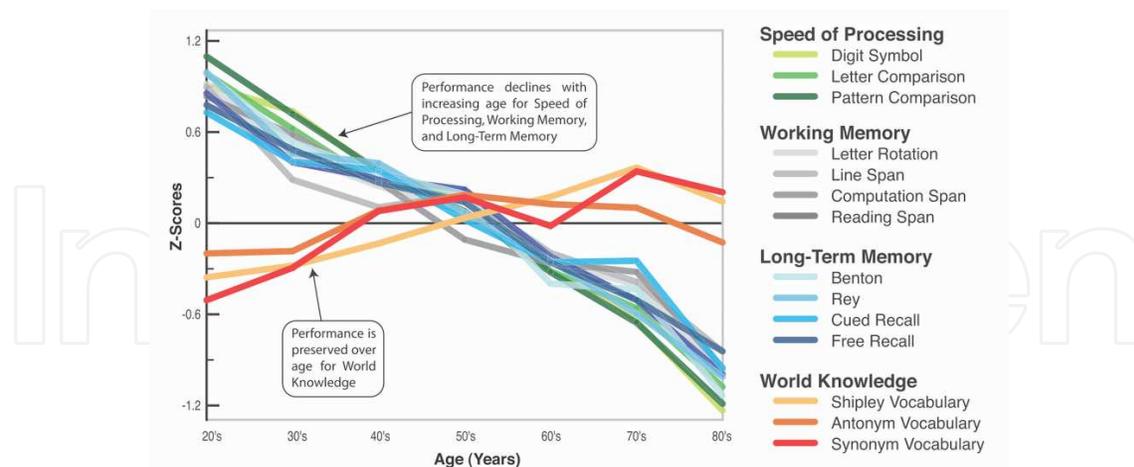


Fig. 1. Age-related cognitive changes in fluid and crystallized abilities in normal aging. Cross-sectional aging data show gradual age-related declines on the cognitive mechanisms of speed processing, working memory and long-term memory, beginning in young adulthood. But verbal-crystallized knowledge is protected from age differences. Copyright © 2002 by the American Psychological Association. Adapted with permission from Park et al. (2002). Models of visuospatial and verbal memory across the adult life span. *Psychology and Aging*, 17(2), 299-320.

2004), reductions in white matter integrity (Davis et al., 2009; Head et al., 2004; Kennedy & Raz, 2009a, 2009b), slower rates of neurogenesis and proliferation of new neuron (Kempermann & Gage, 1999; Kempermann et al., 2002; Kempermann et al., 1998), and dysregulation of neurotransmitter and synaptic action (Burke & Barnes, 2006; Burke & Barnes, 2010; Kaasinen et al., 2000; Li & Sikström, 2002), that may be underlying bases for cognitive declines observed in older adults (Goh, 2011; Goh & Park, 2009a; Greenwood, 2007; Park & Goh, 2009; Park & Reuter-Lorenz, 2009; Reuter-Lorenz & Park, 2010). However, despite such universal age-related declines in neurobiology and cognition, cognitive aging studies using functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) have revealed a more mixed picture. These studies, which we now review, show that the functional brain ages in a dynamic way, declining in some respects but maintaining the ability to engage adaptive neural functions even in advanced age (Dennis & Cabeza, 2008; Park & Reuter-Lorenz, 2009).

2.1 Reduced distinctiveness of cognitive representations

Studies have shown that young adults have a high degree of functional specialization in the ventral visual cortex for different categories of visual stimuli (for review, see Grill-Spector & Malach, 2004; Grill-Spector et al., 2008; Spiridon & Kanwisher, 2002). Briefly, the ventral visual cortex is a broad region encompassing the infero-medio-temporal and occipital regions that are specialized for processing the identity of objects—the “what” pathway (Mishkin et al., 1983), with many structures within this region characterized by a high specificity of neural responses. These functionally distinct subregions that respond selectively to categories of visual input include (1) the “fusiform face area (FFA)” within the fusiform gyrus that is specialized to process faces but not other categories of stimuli (Kanwisher et al., 1997), (2) the “parahippocampal place area (PPA)” in the parahippocampal gyrus that is specialized to selectively respond to outdoor scenes, places, and houses (Epstein & Kanwisher, 1998), (3) the lateral occipital complex (LOC) that is specialized to recognize objects (Grill-Spector et al., 1998; Malach et al., 1995), and (4) the left visual word form area (VWFA) located in the fusiform gyrus that is specialized for letters and words (Polk et al., 2002). Note that these visual categories elicit responses across a network of ventral visual regions (Haxby et al., 2001; Haxby et al., 2000), but these specialized regions respond most preferentially to these respective categories.

It has been shown that, relative to young adults, there is a reduced distinctiveness of cognitive representations (i.e., dedifferentiation) in perceptual function with age. Baltes & Lindenberger (1997) and Lindenberger & Baltes (1994) examined a large lifespan sample and reported that measures of visual and auditory perception explained most of the age-related variance on measures of high-level cognition such as memory and reasoning. This suggests that whereas younger adults have a high degree of specificity across different cognitive domains, a dedifferentiation of different cognitive functions occurs with age. In addition, some studies have shown that older adults are less able than younger adults to behaviorally distinguish between stimuli that are close in perceptual resemblance (Bartlett & Leslie, 1986; Betts et al., 2007; Goh et al., 2010a; Stark et al., 2010). It has been suggested that such age-related reduction in distinctiveness of cognitive representations is due to a decrease in neural specificity and a broadening of neural tuning curves such that a given region that responds selectively in young adults will respond to a wider array of inputs in older adults (Goh et al., 2010a; Leventhal et al., 2003; Park & Reuter-Lorenz, 2009; Schmolesky et al., 2000; Wang et al., 2005; Yu et al., 2006).

Indeed, Park et al. (2004) presented pictures of faces, houses, pseudowords, chairs and scrambled controls to both older and young adults and acquired functional brain data as the participants passively viewed the stimuli. The results showed markedly less neural specificity for these categories in the aging brain in the fusiform face area (FFA) and parahippocampal place area (PPA), amongst others. Whereas the FFA showed greater response to faces and less activation to other categories (i.e., places, chairs and words) in young adults, the FFA in older adults responded to faces but also with considerable activation to other categories, reflecting an age-related reduction in selective neural responses to these different visual categories. Voss et al. (2008) replicated this neural pattern of reduced selectivity of neural responses to different visual categories in older compared to younger adults, indicating the robustness of this finding across different samples of older adults.

In initial work on exploring age-related differences in functional specialization of ventral visual cortex, Goh et al. (2004) used fMRI adaptation to isolate brain regions that were involved in processing objects from those involved in processing scenes in younger adults. The fMRI adaptation paradigm allows for the evaluation of neural selectivity and specialization based on the phenomenon that neural response to repeated stimuli is typically reduced (Grill-Spector & Malach, 2001; Henson, 2003). In Goh et al., (2004), research participants passively viewed quartets of pictures that consisted of central objects embedded within background scenes (Figure 2). The objects and scenes of the picture quartets were selectively changed allowing for the identification of distinct brain regions in young adults that were clearly sensitive to object repetition only (object-processing regions in the LOC), or background scene repetition only (scene-processing regions). In subsequent studies, Goh and colleagues applied the same experiment on older adults and compared age-related differences in functional specialization of the ventral visual cortex for objects and scenes, albeit in an East Asian sample (Chee et al., 2006; Goh et al., 2007). They found a decreased specificity in older adults for object recognition within the lateral occipital cortex, suggesting that age-related reduction in distinctiveness of cognitive representation is present even in a culturally different sample of older adults.

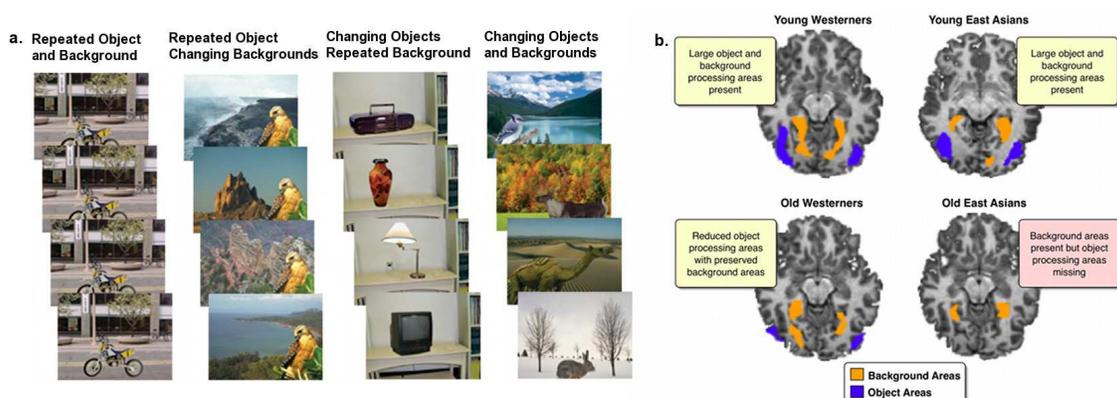


Fig. 2. Ventral visual brain regions selectively sensitive to object and background scene repetition in young and older, Westerners and East Asians, adapted from Goh et al. (2007), *Age and culture modulate object processing and object-scene binding in the ventral visual area*, *Cognitive, Affective & Behavioral Neuroscience*, 7(1), 44-52, copyright © 2007, with permission from Psychonomic Society Publications. a) Sample of picture quartet stimuli with selectively repeated objects and backgrounds used in that fMRI adaptation study. b) Young adults show clear object-related processing in lateral occipital regions and background-related processing in parahippocampal regions. Object processing regions are reduced in older adults with older East Asians showing disproportionately greater reduction.

Goh et al. (2010a) further demonstrated that age-related cognitive dedifferentiation is associated with reduced neural selectivity for within-category stimuli (i.e., different types of faces) as well. In this fMRI adaptation study, young and older adults were instructed to make same-different judgments to serially presented face-pairs that were Identical, Moderate (40 % difference) in similarity through morphing, or completely Different. They found that older adults showed adaptation in the fusiform face area (FFA) during the identical as well as the moderate conditions relative to the different condition (Figure 3). In contrast, young adults showed adaptation during the identical condition, but minimal adaptation to the moderate condition relative to the different condition. In addition, greater adaptation in the FFA was associated with poorer ability to discriminate faces. These findings provided clear evidence for reduced fidelity of neural representation of faces with age that was associated with poorer behavioral perceptual performance.

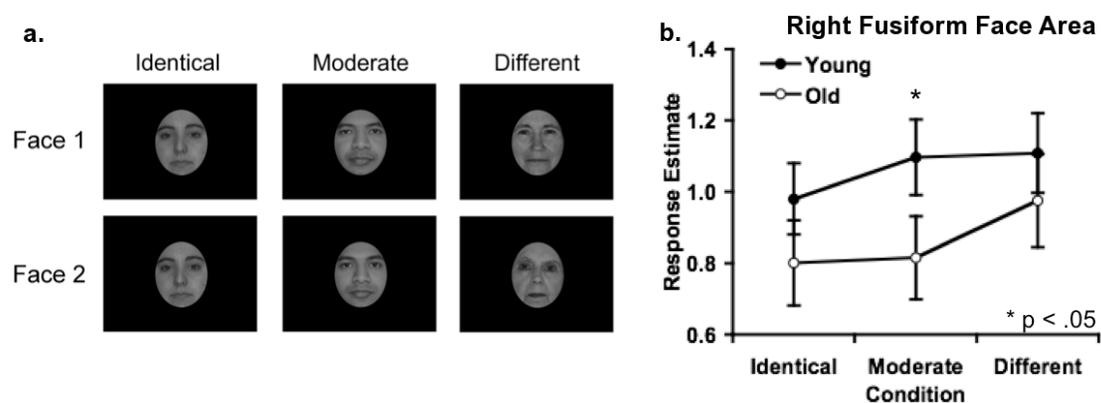


Fig. 3. Functional responses to Identical, Moderate (40% morph difference), and Different face-pairs in young and older adults, adapted from Goh et al. (2010a), Reduced neural selectivity increases fMRI adaptation with age during face discrimination, *NeuroImage*, 51(1), 336-344, copyright © 2010, with permission from Elsevier. a) Sample face-pair stimuli used in the fMRI adaptation experiment. b) Functional responses in the right fusiform face area show that younger adults treated moderately different face-pairs like they were completely different, whereas older adults treated moderately different face-pairs like they were identical.

In a different approach involving multi-voxel pattern analysis (MVPA), Carp et al. (2010) compared age differences in the distinctiveness of distributed patterns of neural activation evoked by different categories of visual images. They found that neural activation patterns within the ventral visual cortex were less distinctive among older adults, congruent with neural dedifferentiation with aging. In addition, they also showed such age-related neural dedifferentiation extend beyond the ventral visual cortex, with older adults showing decreased distinctiveness in early visual cortex, inferior parietal cortex, and prefrontal regions. Moreover, using MVPA as well, J. Park et al. (2010) investigated how well these age-related differences in neural specificity could explain individual differences in cognitive performance. They found that neural specificity significantly predicted performance on a range of fluid processing behavioral tasks (e.g., dot-comparison, digit-symbol) in older adults (~ 30% of the variance in a composite measure of fluid processing ability).

Taken together, the evidence from these different neuroimaging studies consistently demonstrate a reduced neural distinctiveness of cognitive representations with age in ventral visual cortex. Given such age-related dedifferentiation of the ventral visual cortex, which links age-related changes in behavior with brain changes, we now consider a more mixed pattern of functional responses in older adults in cognitive aging studies on the frontal regions.

2.2 Increased neural effort involved in cognitive processing

Although some studies have reported an under-recruitment of brain activity with age (e.g., Logan et al., 2002), different patterns of age-related neural over-recruitment, especially in the prefrontal cortex, have been consistently reported across several cognitive domains (Dennis & Cabeza, 2008; Grady, 2008; Park & Reuter-Lorenz, 2009; Reuter-Lorenz & Cappell, 2008). These neural patterns are such that older adults appear to (1) exhibit increased activity in similar regions engaged by young adults, (2) reveal additional activation in regions that are not activated in young adults, and (3) elicit greater bilateral activity than the more unilateral activity observed in their young counterparts (Cabeza et al., 2002; Cabeza et al., 2004; Daselaar et al., 2003; Jimura & Braver, 2010; Morcom et al., 2003) when performing equivalently or only slightly poorer relative to young adults. Prefrontal over-recruitment is so common across such a wide range of tasks that some authors have suggested that it is a general characteristic of age-related neural change (Cabeza et al., 2004; Davis et al., 2008).

A dominant observation of age-related over-recruitment is the bilateral activation of homologous prefrontal regions in older adults on tasks where their younger counterparts show unilateral activation pattern. Specifically, whereas young adults typically engage left lateralized frontal activity for tasks that involve verbal working memory, semantic processing, and recognition memory, older adults tend to show preserved left frontal activity with additional contralateral recruitment in the homologous site of the right hemisphere that is not observed in young adults (Figure 4; Cabeza et al., 1997; de Chastelaine et al., 2011; Daselaar et al., 2003; Duverne et al., 2009; Leshikar et al., 2010; Madden et al., 1999; Reuter-Lorenz et al., 2000; Schneider-Garces et al., 2010). Similarly, older adults engage both right and left prefrontal activity during tasks in which younger adults engage only right lateralized prefrontal activity, such as in tasks associated with face processing, spatial working memory, non-verbal spatial judgment, and episodic recall (Cabeza et al., 1997; Grady et al., 1995; D. Park et al., 2010; Reuter-Lorenz et al., 2000). This additional contralateral prefrontal recruitment that results in the pattern of greater bilateral activation in older adults has been described as Hemispheric Asymmetry Reduction in OLDER adults (HAROLD; Cabeza, 2002).

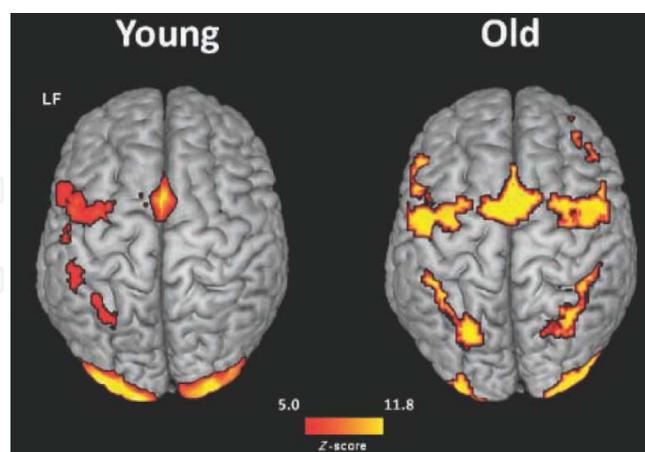


Fig. 4. Age-related over-recruitment of neural activation in verbal working memory. young adults engage unilateral frontal activity for tasks that involve verbal working memory, whereas older adults reveal preserved left frontal activity with additional contralateral recruitment in the homologous site of the right hemisphere. Adapted from Schneider-Garces et al. (2010), Span, CRUNCH, and beyond: working memory capacity and the aging brain, *Journal of Cognitive Neuroscience*, 22(4), 655-669, copyright © 2010, with permission from MIT Press.

Age-related over-recruitment of frontal regions is often interpreted as being compensatory and involved in the improvement or maintenance of performance in the face of age-related neurodegeneration (Cabeza, 2002; Davis et al., 2008; Heuninckx et al., 2008; Vallesi et al., 2011). For example, Rossi et al. (2004) reported direct evidence for the compensatory role of age-related over-recruitment in prefrontal regions by conducting a repetitive Transcranial Magnetic Stimulation (rTMS). rTMS is a technique which transiently disrupts neural function by applying repetitive magnetic stimulation to a specific area of the brain, creating a temporally artificial brain lesion. Rossi et al. (2004) showed that younger adults' memory retrieval accuracy was more affected when the rTMS was applied to the left prefrontal cortex but less affected when rTMS was applied to the right prefrontal region. In contrast, older adults' retrieval accuracy was equally affected, whether rTMS was applied to the left or right prefrontal regions, suggesting bilateral prefrontal activation has a causal link to behavioral performance in older adults. A compensatory account of age-related over-recruitment was also supported in Morcom et al. (2003) who showed that greater frontal bilaterality in older adults compared to young predicted better performance when successfully encoding subsequently remembered items.

Some studies have reported impaired behavioral performance associated with additional contralateral prefrontal recruitment, suggesting that prefrontal over-recruitment may not always be compensatory. For example, de Chastelaine et al. (2011) found that older adults' memory performance positively correlated with neural over-recruitment in the left prefrontal cortex, a region also engaged by young adults. However, the correlation was negative with respect to additional recruitment in the right prefrontal cortex of older adults, a region that was not observed in young adults, suggesting that over-recruitment in the right frontal regions in older individuals does not always contribute to memory performance (see also Duverne et al., 2009). Resolving whether age-related over-recruitment is associated with compensatory or declining function, would require studies that more effectively measure and equate differences in cognitive ability and performance across young and older adults, as well as better define what compensation means. Nevertheless, a broad number of studies are at least in agreement that there is consistent age-related over-recruitment that is generally associated with better cognitive outcomes.

In addition to being beneficial for behavioral performance, evidence also suggests that increased neural effort observed in prefrontal cortex may reflect a compensatory response to deteriorating neural systems in more posterior sites of the brain, including the medial temporal lobe (Cabeza et al., 2004; Gutchess et al., 2005; Park et al., 2003), and occipital cortex (Cabeza et al., 2004; Davis et al., 2008; Goh et al., 2010a). Park & Gutchess (2005) systematically reviewed neural activations associated with long-term memory and noted that decreased hippocampal and parahippocampal activation in medial temporal lobes are coupled with the increased frontal activation in older adults. Indeed, Gutchess et al. (2005) showed that during an incidental memory encoding task, older adults had lower activation than young adults in the left and right parahippocampus and greater activation than young adults in the middle frontal cortex. Goh et al. (2010a) also showed that increased frontal engagement was also associated lower neural selectivity in the ventral visual regions. Moreover, Cabeza et al. (2004) reported that older adults showed increased bilateral prefrontal activation and decreased occipital function compared to their young counterparts across various cognitive tasks, indicating a Posterior Anterior Shift in Aging (PASA) functional activity (Davis et al., 2008). These results suggest a neurocognitive compensatory role of prefrontal regions for age-related neural deterioration in posterior brain regions.

With this review on the pattern of age-related reductions in neural distinctiveness in cognitive representations and increases in frontal engagement, we now turn to consider the evidence for the second source of influence on brain structure and function – cultural experience.

3. Culture-related findings

In a comprehensive review of sociopolitical and historical progressions, Nisbett (2003) proposed that the value system of one's cultural environment exerts an influence on self-perceptions and even cognitive processing. That is, social and physical pressures in the cultural environment encourage certain modes of behavior and thinking and suppress others. Over time, these cultural pressures become internalized and act as a bias with which individuals process subsequent social and physical situations as well. In this article, we focus on differences between Westerners and East Asians, as there have been more studies that directly compared these two culture groups. It has been shown that whereas Western culture places more emphasis on independence and individualism, East Asian culture values interdependence and collectivism (Hofstede, 1980, 2001; Kitayama et al., 1997; Nisbett, 2003; Nisbett & Masuda, 2003; Nisbett et al., 2001; Oyserman et al., 2002; Triandis et al., 1988; Triandis, 1995). Nisbett (2003) argues that Westerners embedded in a culture of individualism tend to adopt an analytic style of cognitive processing. This style of processing can be characterized as a bias to treat stimuli items in the environment as individual and distinctive objects composed on a set of features. Likewise, East Asians are embedded in a culture of collectivism that is associated with a holistic style of cognitive processing, which is reflected as a bias to regard items in the environment as related to one another, and more tightly bound to the context.

This section considers the evidence for the existence of these culture-related differences in analytic and holistic processing styles between Westerners and East Asians and their neural correlates. While many of these studies have been previously reviewed (Goh & Park, 2009b; Han & Northoff, 2008; Nisbett & Masuda, 2003; Nisbett & Miyamoto, 2005; Nisbett et al., 2001), we highlight important and novel aspects of these findings here as they pertain to the overall question on the interaction between age and culture. As will be seen, many of these studies show culture-related differences in the way Westerners and East Asians perceive and attend to items in the visual environment. Critically, both behavioral and neuroimaging studies report findings that are remarkably consistent with the analytic and holistic biases in Westerners and East Asians, respectively.

3.1 Cultural differences in perception and attention: Behavioral foundations

3.1.1 Face stimuli

In a study that used visual aesthetics as an approach to characterizing object-context perception in Westerners and East Asians, Masuda et al. (2008a) evaluated differences in the content of portrait photographs taken by American and Japanese participants. They found that American participants took portrait photographs in which the face, the object of the portrait, occupied a larger ratio of the frame than the background. In contrast, photographs taken by Japanese participants consisted of a much larger portion of the background relative to the face. Thus, Japanese may have considered the background context as more important to the portrait than Americans did. In another study on the degree to which Americans and Japanese incorporate contextual social information, Masuda et al. (2008b) asked participants

to judge the emotion of a facial expression that was presented amidst other emotional facial expressions that were either congruent or conflicting with the target expression. The results of that study suggested that Japanese were more likely to modulate their judgment of the target face emotion based on the other faces whereas Americans were less sensitive to contextual face emotions in their behavioral responses.

Eye movements to face stimuli also show distinctions between Westerners and East Asians. In Masuda et al. (2008b) study above, eye-movements of participants were also measured as they judged the emotional content of a target face amidst other faces in the background. They found that Japanese devoted less time fixating on the target face than Americans, and thus, Japanese were looking more at the contextual faces than the Americans as well. Blais et al. (2008) recorded eye movements as Westerners and East Asians viewed single face stimuli across several different types of tasks to examine which components of the face participants tended to look at. It was found that, across all tasks, Westerners tended to fixate on the eyes and mouth of the faces whereas East Asians focused on central regions of the face, around the nose. Westerners may have attended to facial features that contain distinguishing information about the face, consistent with an analytic style of face processing. In contrast, East Asians may have treated faces more holistically and thus de-emphasized the distinctiveness of facial features. Taken together, these findings reflect the bias for a more analytic style in Westerners and a more holistic style in East Asians when processing aesthetics and social information involving face stimuli.

3.1.2 Objects and backgrounds

Culture-related differences in analytic-holistic processing is supported by evidence that shows that Westerners have a greater affinity for visuo-spatial judgments involving absolute quantities whereas East Asians are better at relative comparisons. In the Frame Line Test, participants are presented with a test stimulus consisting of a line embedded within a square box frame. The test stimulus is then removed and replaced with probe, which was an empty square frame that was either smaller or larger in size relative to the test square. During the absolute judgment task, participants were instructed to draw a line in the probe square that was of the same length as the original test line, regardless of the size of the square. During the relative judgments task, however, participants were to draw a line that was of the same length relative to the size of the square frame. Kitayama et al. (2003) found that Americans were more accurate for the absolute line drawing and Japanese were more accurate for the relative line drawing. Thus, Westerners may have attended more to the features of the line (length), in accordance with an analytic style of processing, whereas East Asians integrated the line and square frame as a whole, in accordance with a holistic processing style.

Differences between Westerners and East Asians have also been found in the sensitivity to changing visual elements of complex scenes. Change blindness refers to the phenomenon whereby participants take some time to detect relatively salient changes in rapidly alternating scenes (Simons & Ambinder, 2005; Simons & Levin, 1997). Boduroglu et al. (2009) found that East Asians were better at detecting color changes in the stimuli periphery than Westerners, but East Asians also showed poorer performance than Westerners when the color changes occurred in the central regions of the screen. Using the change blindness paradigm as well, Masuda & Nisbett (2006) presented Americans and Japanese with rapidly alternating pictures of scenes with objects. They found that whereas Americans were faster at detecting changes occurring in the central object, they were slower with background changes.

In contrast, Japanese were equally fast for changes occurring in both objects and backgrounds. Moreover, Americans detected more object changes whereas Japanese detected more background changes. Thus, the more analytic style of processing in Westerners was reflected as greater sensitivity to central object changes, and the more holistic processing style in East Asians manifested as greater sensitivity to the peripheral background.

Again, evidence from eye-tracking studies provides compelling evidence that Westerners and East Asians are attending in different ways to the same scene stimuli. Chua et al. (2005) recorded eye-movements while American and Chinese participants looked at naturalistic pictures that depicted a central object presented against a contextual background scene. Compared to American participants, Chinese participants made more fixations to the background and had slower onsets of the first fixation to central objects. In addition, Chinese participants generally showed a greater proportion of background relative to object fixations throughout the time course of the stimulus viewing, whereas Westerners had greater proportions of object fixations over the time course with very brief periods of increased proportions of background fixations. Goh et al. (2009c) further evaluated whether these cultural differences in eye-movements were robust to visual stimuli that captured participants' attention against their own cultural preferences, using an experimental design adapted from Goh et al. (2007). It was found that, as expected, Westerners were more sensitive to object changes than East Asians, and East Asians alternated more between the objects and backgrounds. Moreover, these cultural differences in eye-movements were relatively robust to the attention capturing manipulation of changing objects and backgrounds. Critically, Westerners' eye-movements were characterized by fewer fixations with longer dwell times whereas East Asians had fewer but shorter fixations that covered a greater area of the visual stimuli (Figure 5).

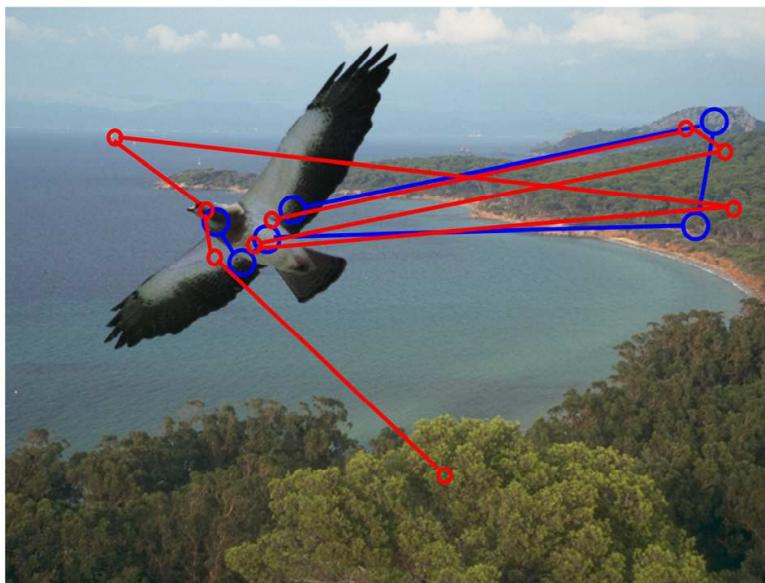


Fig. 5. A schematic of eye-movements during scene viewing in Westerners (blue) and East Asians (red). Circles represent fixations and size of circles represent fixation dwell times, with larger circles indicating longer times adapted from Goh et al. (2009c).

Some eye-tracking studies did not find cultural difference in eye-movements when Westerners and East Asians viewed scenes (Caldara et al., 2010; Mielliet et al., 2010; Rayner

et al., 2009). For example, Rayner et al. (2009) found that when visual scenes depicted a bizarre or impossible circumstance (e.g. a boy with an extra leg), there were no differences in the way Westerners and East Asians fixated on the scene. It is possible that in such cases, basic universal attentional processes take precedence over cultural differences in visual attention. It is also certainly possible that these results reflect how cultural biases are amenable to change since Westerners are capable of focusing on scenes and East Asians are capable of focusing on objects (see studies on cultural priming; Chiao et al., 2010; Miyamoto et al., 2006).

Overall, these findings show that there are culture-related differences in perception and attention between Westerners and East Asians. These differences are such that Westerners have a more analytic processing style, focusing on object features, and East Asians have a more holistic processing style, focusing on contextual information. With this in mind, we now consider the neural correlates of these visual processing behavioral patterns.

3.2 Cultural differences in perception and attention: Functional brain studies

3.2.1 Face, object, and scene processing in the ventral visual cortex

As mentioned previously, one of the most consistent observations related to visual processing in the brain is that specific regions within the ventral visual cortex show heightened sensitivity to specific categories of visual stimuli. It should also be noted that greater attention to the stimulus tends to increase the selectivity of the ventral visual region involved in processing that stimulus (Murray & Wojciulik, 2004; Yi et al., 2006). The following studies show that there are culture-related differences in the way the selective regions of the ventral visual cortex respond to faces, objects, and scenes in Westerners and East Asians, and that the analytic-holistic dichotomy operates in visual perception and attentional neural processes as well.

In a simple blocked-design fMRI experiment, Goh et al. (2010b) presented Americans (Westerners) and Singaporeans (East Asians) with face and house stimuli and compared the selectivity of their fusiform regions for faces relative to houses, and lingual regions for houses relative to faces. It was found that Americans showed greater face selectivity than Singaporeans in the left fusiform region, and face selectivity in the right fusiform regions was equivalent in both groups (Figure 6). Right fusiform engagement has been associated with more holistic processing of face stimuli as a whole; however, left fusiform activity has been associated with more analytic face processing of specific facial features (Rossion et al., 2000). Thus, the finding that Americans engaged greater left fusiform responses than Singaporeans to faces, and the findings on cultural differences in behavioral and eye-movement responses to faces reviewed above, provide a compelling basis for a greater bias to attend to facial features in Westerners than East Asians, consistent with a more analytic face processing style in Westerners. In addition, Goh et al. (2010c) found that Singaporeans showed some evidence for greater house selectivity than Americans in bilateral lingual regions. Taken together with the behavioral findings again, this suggests that Singaporeans were attending more than Americans to the contextual environment, consistent with a more holistic processing style for scenes in East Asians.

With respect to objects and scenes, fMRI studies have also found that Westerners engage more object-related processing in the ventral visual regions compared to East Asians. In Gutchess et al. (2006), Westerners and East Asians performed an incidental encoding task on stimuli consisting of objects and scenes. Whereas they did not find any group differences in

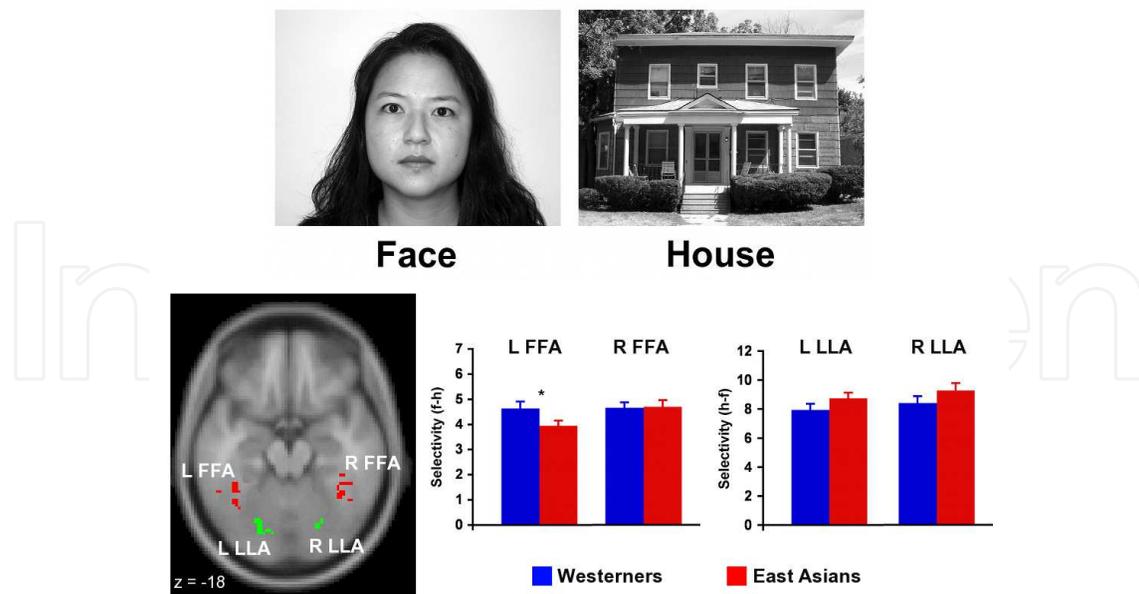


Fig. 6. Neural selectivity to face and house stimuli in the fusiform face areas (FFA) and lingual landmark areas (LLA) of Westerners and East Asians, adapted from Goh et al. (2010b), Culture differences in neural processing of faces and houses in the ventral visual cortex, *Social Cognitive and Affective Neuroscience*, 5(2-3), 227-235, with permission from Oxford University Press. Sample stimuli used in the blocked-design fMRI experiment are on top. The bottom left panel illustrates peak voxel locations of the FFA and LLA from a sample of individual participants. The bottom right panel shows greater selectivity for faces (f-h) in the left FFA in Westerners compared to East Asians (* $p < .05$), and marginally greater selectivity for houses (h-f) in bilateral LLA in East Asians compared to Westerners.

background-related processing regions, Westerners showed greater recruitment of object processing regions than East Asians in the middle temporal, supramarginal, and parietal regions. In Goh et al.'s (2007) fMRI adaptation study mentioned in the section on aging, brain imaging data from both Westerners and East Asians were also acquired to investigate cultural differences in ventral visual responses to objects and background scenes (see Figure 2). They found that although there were no group differences in scene processing regions, East Asians showed less object-related responses in the lateral occipital regions compared to Westerners. Interestingly, this culture-related difference in object processing was more evident in older adults than in younger adults, implying an age dependency, which is further discussed below.

Apart from cultural differences in the processing of objects and scenes as separate items, studies have also found evidence for cultural differences in sensitivity to the relationship between objects and scenes in the stimuli. Jenkins et al. (2010) used a similar fMRI adaptation experiment as in Goh et al. (2007), and presented participants pictures with selectively repeated objects and scenes. Critically in that study, some of the object-scene pairings were congruent (e.g. a plane in the sky) whereas some objects were incongruent with the scenes (e.g. an elephant in a kitchen), but not impossible. They found that whereas Westerners were relatively insensitive to object-scene congruity, East Asians showed greater responses to incongruent relative to congruent pairings, suggesting that they attended more to objects when the pairing with the scene was incongruent (see Goto et al., 2010, for a

similar study using event-related potentials). Taken together, these findings are consistent with the analytic-holistic dichotomy, and suggest that Westerners treat each visual element in a picture more as separate objects, whereas East Asians regard the picture elements as more tightly bound together into the whole context.

3.2.2 Visual attention processing

Using the Frame Line Test from Kitayama et al. (2003), Hedden et al. (2008) acquired fMRI data as Westerners and East Asians made absolute and relative line judgments in the scanner. They found that Westerners showed greater brain responses during relative compared to absolute line judgments in frontal and parietal regions, brain areas typically associated with attentional processing. In contrast, East Asians showed greater brain responses during absolute compared to relative judgments in the same regions (Figure 7). These findings suggest that participants required greater effort when engaging non-preferred visual processing styles, which is associated with cultural differences in attention-related responses in fronto-parietal regions. Importantly, the finding that Westerners required greater effort for relative judgments and East Asians for absolute judgments is again consistent with the analytic-holistic dichotomy in these two groups.

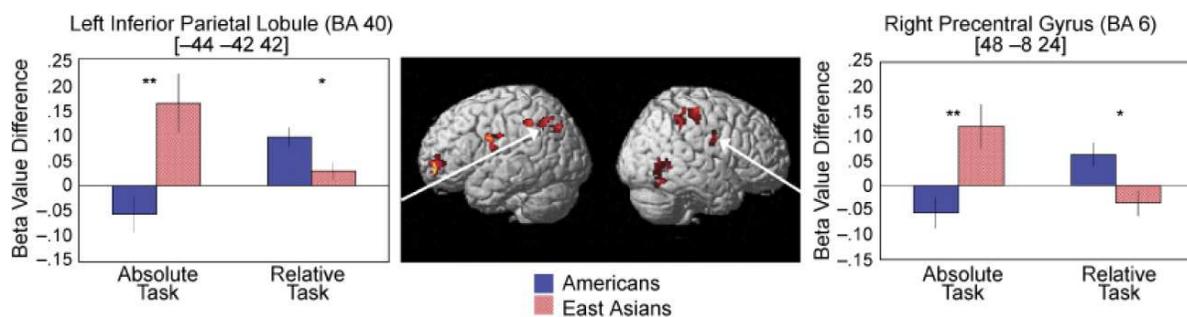


Fig. 7. Functional brain responses during the Frame Line Test in Americans and East Asians, adapted from Hedden et al. (2008), Cultural influences on neural substrates of attentional control, *Psychological Science*, 19(1), 53-81, copyright © 2008, with permission from Sage Publications. Americans showed greater responses in fronto-parietal regions during the relative compared to the absolute task. East Asians showed greater responses during the absolute compared to the relative task.

In a yet unpublished study, Goh et al. (submitted) acquired fMRI data as Westerners and East Asians made judgments on the distance between a dot and a horizontal line, relative to the length of a vertical line. In that study, while accuracy was equivalent in both groups, East Asians responded significantly faster than Westerners, suggesting that the task was easier for East Asians and harder for Westerners. In line with this interpretation, during task performance, Westerners showed greater activation of the frontal and parietal regions compared to East Asians. Importantly, they also found that Westerners showed greater suppression of responses compared to East Asians in the default-network regions that included the medial frontal and supramarginal regions. Suppression of these default-network regions has been linked to a greater need to attend to external stimuli (Anticevic et al., 2010; Benjamin et al., 2010; Greicius et al., 2003; Hayden et al., 2010; Mayer et al., 2010; Raichle et al., 2001). Thus, Westerners may have required greater attention than East Asians to perform the relative spatial judgment task, and correspondingly suppressed default-network activity more in the process.

In Goh et al. (2007), it was also suggested that the lack of object-processing responses in the lateral occipital regions in older adult East Asians was related to a reduction in attentional resources. Interestingly, Chee et al. (2006) investigated this by repeating the fMRI adaptation experiment on the same older East Asians but with the instruction to attend to the object while ignoring the scenes. Under those circumstances, the older East Asians showed a reinstatement of object-related processing in the lateral occipital region, suggesting that the lack of responses in the initial study was indeed due to attentional mechanisms. This finding suggests that under reduced attentional resources, the older East Asians maintained their focus on the background scenes but devoted less attention to objects, in line with a bias for holistic processing in East Asians.

Thus, culture-related functional brain differences are observed in perceptual regions as well as in regions involved in attention. It is possible that such chronic differential functional engagement may result in structural brain differences. And, while there are fewer studies on cultural differences in brain structure, there have been several studies on how different external experiences and expertise do bear on regional brain size and integrity.

3.3 Culture, experience, and brain structure

At present, only four studies have directly compared brain structural differences between Westerners and East Asians. Zilles et al. (2001) only examine gross brain size and shape differences and found that Japanese brains were shorter and wider, i.e. more circular in shape, compared to European brains, which were more elongated or oval. Green et al. (2007) and Kochunov et al. (2003) examined structural differences related to differences in the usage of the Chinese and English language. These latter two studies generally found that Chinese-speaking East Asians have more brain tissue than English-speaking Westerners in the left inferior frontal, middle temporal, and right superior temporal regions. The fourth study by Chee et al. (2011) examined a much larger sample of structural brain images of Americans and Singaporeans, which is critical since there is a large amount of variability in structural MRI data. Using various data analysis methods, including cortical thickness

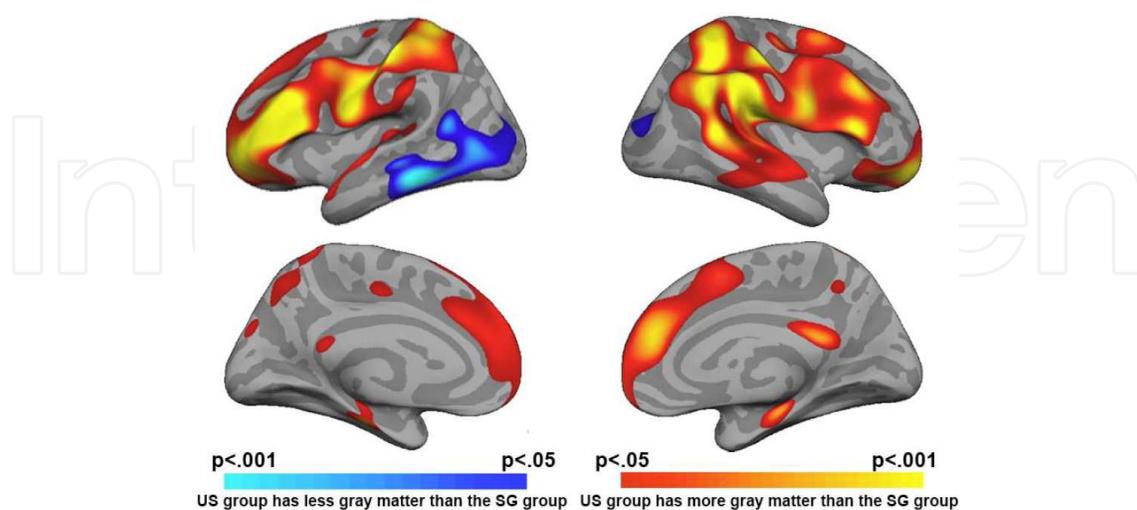


Fig. 8. Cortical thickness differences between Americans (US) and Singaporeans (SG). Adapted from Chee et al. (2011), Brain structure in young and old East Asians and Westerners: comparisons of structural volume and cortical thickness, *Journal of Cognitive Neuroscience*, 23(5), 1065-1079, copyright © 2011, with permission from MIT Press.

measures, voxel-based morphometry and pattern classification approaches, they found that Americans had thicker cortical gray matter than Singaporean in frontal, parietal, and temporal polymodal association areas, whereas Singaporeans had thicker left inferior temporal regions (Figure 8).

While more studies are required to relate these culture group differences in cortical thickness, it is clear from other non-culture studies that external experiences do have a modulatory influence on brain structure. For example, Maguire et al. (2000) showed London taxi-cab drivers have larger hippocampal volumes than control participants possibly due to their expertise in navigating around the city streets. This finding was consistent with the important role that hippocampus has in spatial navigation as well as memory (Cohen et al., 1999). In addition, Draganski et al. (2004) showed that novices who acquired juggling skills longitudinally developed more gray matter in the middle temporal gyrus and intra-parietal sulcus, regions important for visuo-spatial coordination. It is therefore no surprise that cultural differences in functional engagement of specific brain regions would also result in the regional differences in brain structure described above, and future studies will establish more mechanistic links between cultural experience and brain structure.

4. Cultural differences across age

Having established that there are culture-related differences in brain structure and function, we now evaluate how these brain differences interact with the neural changes associated with aging described above. Studies that integrate age and culture are sparse at present. Nevertheless, the few studies that do consider this aspect of neural structure and function over the lifespan provides some initial guidance as to the nature of culture-related neural differences in older adulthood.

It is useful to first consider when culture-related neural differences start in the course of the human lifespan. As yet, we are not aware of any neuroimaging studies that have directly examined culture-related brain differences in children or adolescents. A few developmental studies, however, provide some clues as to when cultural experience may begin to have an influence on neurocognitive processes. For example, a linguistic study involving Western and East Asian infants developing in different language environments (English vs. Japanese) show language-specific perceptual biases as early as 7 months (Yoshida et al., 2010). In addition, Wang & Leichtman (2000) examined narratives of 6-year-old children and found that compared to Western children, East Asian children described stories and memories with a greater emphasis on social relationships and contextual information, characteristic of a collectivistic culture. Wang (2008) also examined autobiographical memory in Western and East Asian children as young as 3 years old. It was found that Western children tended to recall memories with greater specificity whereas East Asian children recalled memories in a more general manner, consisting of less specific details. In an fMRI study, Golarai et al. (2007) managed to examine the selectivity of the ventral visual cortex of young children, albeit just in a sample of Westerners. They showed that by 7 years of age, children had developed selective responses for faces in the FFA and scenes in the PPA to the level observed in mature adults. This imaging finding and the behavioral comparisons above suggest that the culture-related neural differences observed in young adults at approximately 20-30 years of age may begin in quite early in childhood.

With respect to culture-related differences in older adults, only one published functional neuroimaging study thus far has directly examined the interaction between age and culture.

As mentioned, Goh et al. (2007) used the fMRI adaptation paradigm to investigate ventral visual selectivity for objects and scenes in young and older, Westerners and East Asians (Figure 2). The main finding in that study was that older East Asians (aged 65 and above) showed reduced object-related processing compared to the other three groups. This finding was interpreted as an accentuation of the bias for contextual processing in older East Asians due to a reduction in attentional resources with age. In addition, Chee et al.'s (2011) structural brain study also compared young and older, Westerners and East Asians. It was found in that study that whereas the cultural differences in cortical thickness seen in younger adults was not present in older adults as a whole group, cultural differences emerged when older adults were split into high and low cognitive performance. This result suggests that in older adult individuals who show greater susceptibility to neurobiological decline with aging and thus poorer cognition, culture-related experiential influences on the brain become diminished with age. However, in older adults who remain relatively cognitively intact, cultural differences in brain structure are maintained throughout the lifespan.

Distinct from the more global effect of aging on the brain, the effect of cultural experience on the brain seems more localized and specific. That is, whereas aging is associated with a general decline in brain structure and function, culture and other experiential factors modulate neural structure and activity only in regions that are involved in a given cognitive process (e.g. the FFA for processing faces). While more studies are required to evaluate the extent and robustness of these effects, it appears that neurobiological declines associated with aging do not completely overwhelm the influence of experiential factors, at least those related to culture. Thus, the effect of culture-related experiences is likely to have an enduring impact on neural structure and function from adulthood to advanced age.

5. Methodological issues

Interpreting age-related differences in cognitive performance between age groups has proven to be a unique challenge, and exploring the effects of age and culture compounds these difficulties. Here we evaluate some important methodological issues that may limit the extent to which current data can be interpreted and applied to other samples, and suggest recommendations for future studies.

5.1 Cohort, age, and culture considerations

At all times, it should be noted that there is much heterogeneity in the cultural makeup of Westerners and East Asians and the attribution of cultural characteristics is always at the group level. In addition, while culture is defined in terms of value systems, many studies operationalize culture based on geopolitical boundaries, i.e. countries and nationalities. For example, Westerners are predominantly Americans and East Asians are typically Japanese, Chinese, or other Chinese Asian individuals (e.g., Hong Kong Chinese, Singaporean Chinese, Taiwanese Chinese, etc.). Moreover, people within these different cultural affiliations demonstrate varying degrees of individualism and collectivism. For example, Oyserman et al. (2002) documented that native Japanese are not necessarily more collectivistic relative to Caucasian Americans, and cultural differences in individualism and collectivism are not static over time between groups (Oyserman & S. W. S. Lee, 2008). Moreover, in an fMRI study involving native Japanese and Americans, Chiao et al. (2009) reported that neural activity within the ventral medial frontal regions predicted how individualistic or collectivistic a

person is across cultures, regardless of the participants' cultural affiliation. These findings suggest that although some aspects of cultural groups remain stable across time, neural representations of self in Americans and East Asians are not inherently different, but instead reflect different cultural values that are endorsed by the individual.

Given the cost of conducting imaging studies and relatively low reliability of physiological signals, it is also particularly difficult to acquire neuroimaging data from participant samples that are saturated with culture- and/or age-specific experience, yet equated on other factors such as education, cohort-specific experiences and other demographics (Manly, 2008; Park et al., 1999; Whitfield & Morgan, 2008). Thus far, a variety of approaches to explore group differences across several neuroimaging studies have been utilized to deal with these sampling issues. The majority of cross-cultural studies involve East Asian and Western participants studying at the same institution (usually undergraduate/graduate students) as well as neuroimaging data from one MRI scanner (Gutchess et al., 2006; Hedden et al., 2008; Jenkins et al., 2010). However, there are two limitations to such an approach. First, immigrant participants from another culture (e.g., Chinese students in the United States) may already have had some biasing experiences in the host culture, even if they have not been exposed to the new environment for that long. This potentially results in an underestimation of cultural differences in behavioral performance and neural activation. Second, immigrant participants are often a select group of individuals (e.g. international students) who have been qualified to study or work overseas according to their conspicuous achievement, leading to a more high-performing, homogenous sample compared to native individuals. In such cases, conclusions of cultural variation may in fact be associated with sample differences in cognitive capabilities. To reduce these sampling biases described above, it is necessary to select samples based on equivalent levels of education, similar demographics and matched cognitive abilities between groups (Park & Huang, 2010).

Cohort-related effects within a cultural group may also influence the individual's value system, self-perceptions, cognitive processing, and even neural processing, over and above the cultural environment. For instance, in China, only older adults lived through the Cultural Revolution (~1970s), which had tremendous impact on their lifestyle and thinking, whereas younger adults in China had no such experience. A similarly situation applies to the Great Depression (~1930s) for young and older adults in America, and on a worldwide level, World War II. The effects of such socio-historical events on neuropsychological differences between age and culture groups are substantial and should be considered when recruiting participants in future studies.

The careful development of hypotheses and clear predictions of differentiated patterns of activation in older and young adults across cultures is also critical (Park et al., 1999; Park & Gutchess, 2006). Because of the distal nature of culture-related effects on the brain, combined with effects of education, diet, genetics and many other variables (Chee et al., 2011), it is difficult to simply theorize and test that differences observed in neural activation are directly linked to cultural experiences and behavioral practices. As an example, both well-established knowledge from the analytic-holistic framework (Nisbett & Masuda, 2003; Nisbett et al., 2001) and empirical findings from cross-cultural eye-movement studies (Chua et al., 2005) were used to guide Goh et al. (2007) and Goh et al.'s (2010) studies on neural correlates of age and culture in ventral visual processing. Using the existing knowledge base that prescribed specific expectations about the data facilitated the interpretation of the complex patterns of neuroimaging findings from different age and cultural groups in those studies.

5.2 Measurement and instrument comparability

Prior to cross-group comparisons in studies on cognitive neuroscience of aging and culture, it is first important to evaluate whether the experiment stimuli are equally familiar to both age and culture groups. Stimuli that are less familiar or evoke specific types of processing in one group during scanning would confound patterns of neural activation due to the stimuli familiarity differences rather than cognitive processes. Indeed, studies have found culture- and age-related variations in norms associated with how individuals from these groups name pictures of everyday objects (Yoon, et al., 2004a) and categorize words (Yoon et al., 2004b). Hedden et al. (2002) also found that Chinese had better performance than Americans in numerical cognitive tests such as digit comparison (a measure of speed of processing) and backward digit span (a measure of working memory). They suggested that such group differences could be due to differences in the number system and representation in the Chinese and English languages, rather than actual cognitive differences in speed or working memory. Thus, future studies should be aware of such differences in the stimuli used to ensure comparability of cognitive processing across cultural and age groups.

In studies that involved data from two different MRI scanner machines from different sites, it is possible that differences in the blood oxygen level dependent (BOLD) signal between cultural groups could occur as a result of differing properties between hardware rather than actual neural differences between cultures (Park, 2008; Park & Gutchess, 2002). Cases in point are Goh et al. (2007) and Goh et al. (2010), who acquired imaging data from Singapore and the United States, with both sites having identical imaging hardware and software.

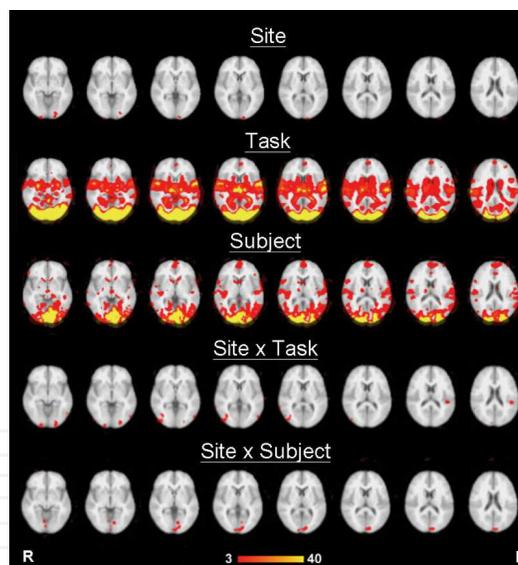


Fig. 9. Between-site comparison of functional MRI signal from Singapore and the United States equipped with identical imaging hardware and software. The same participants performed the same tasks at two magnet sites over several sessions. The statistical brain maps of a three-way Analysis of variance (ANOVA) are shown with the main effects and interactions of site, subject, and task, colored with increasing red intensities ($P < 0.001$ uncorrected). There were extensive regions showing significant main effects and interactions of subject and task, but the effects associated with magnet site were negligible. Adapted from Sutton et al. (2008), Investigation and validation of intersite fMRI studies using the same imaging hardware, *Journal of Magnetic Resonance Imaging*, 28(1), 21-28, copyright © 2008, with permission from John Wiley and Sons..

Prior to conducting these studies, the authors examined functional imaging data with a visual and motor task from four participants who were repeatedly imaged in both machines in Singapore and the United States (Sutton et al., 2008). They found that there was minimal variance in BOLD as a function of site, between-subject differences accounted for 10 times more variance than site of data collection, and task differences (motor versus visual) also accounted for a significant proportion of the variance (Figure 9). Phantom scans were also routinely acquired before testing participants in order to evaluate signal noise and stability of the two scanners as further checks that the two magnets were similarly calibrated. Given the careful evaluation of BOLD signal properties of the two different magnets, the results suggest that obtaining neuroimaging data from two geographically different sites with the identical systems used in those studies was feasible and had sufficient reliability.

6. Conclusion

In this review, we have covered imaging findings related to neurocognitive changes associated with aging and culture, and some findings pertaining to their interaction. Studies on neurocognitive aging show a general reduction in the distinctiveness of neural responses to different stimuli in the posterior brain regions that may be related to neurobiological declines. In the midst of such neurobiological declines, there is also consistent evidence showing increases in frontal responses that may be part of a compensatory response, in particular for the declines associated with posterior brain regions. In contrast to the more global effect of aging, studies on cultural differences in values, perception and attention have also shown specific and more localized differences in neural function that are consistently associated with the analytic-holistic dichotomy in Westerners and East Asians respectively. Specifically, Westerners show functional brain responses that reflect their bias for analytic processing styles that is associated with increased responses in object-processing regions probably related to greater attention to object features. In contrast, East Asians show brain responses that reflect a more holistic processing style associated with attention to contextual information in regions like the lingual landmark area. Some differences in brain structure have also been observed in these cultural groups, although a clear mechanism between cultural experience and brain structure has yet to be established. A few studies have shown that the impact of culture-related experiences on neural structure and function may be acquired at a very young age, and importantly, endures through to advanced aging with even some cases of accentuation.

In sum, the findings covered in this review suggest that there is a reliable and consistent effect of cultural experiences on neural structure and function. While more studies are required to strengthen the findings, initial studies have shown also that at least some of these culture-related effects present in young adults are maintained even in the face of neurobiological changes associated with aging. Importantly, these findings also suggest that neurobiological aging does not always lead to neurocognitive decline in a uniform manner, and that external experiences can modulate and perhaps alleviate some of the neural effects of aging in the brain.

7. Acknowledgement

We thank Dr. Wayne Chan and Dr. May Baydoun for their helpful comments. This research was supported in part by the Intramural Research Program of the NIH, National Institute on Aging, USA.

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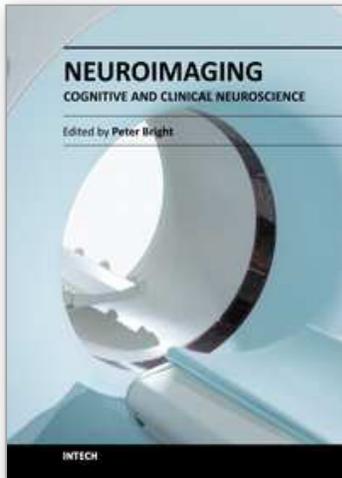
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Neuroimaging - Cognitive and Clinical Neuroscience

Edited by Prof. Peter Bright

ISBN 978-953-51-0606-7

Hard cover, 462 pages

Publisher InTech

Published online 16, May, 2012

Published in print edition May, 2012

The rate of technological progress is encouraging increasingly sophisticated lines of enquiry in cognitive neuroscience and shows no sign of slowing down in the foreseeable future. Nevertheless, it is unlikely that even the strongest advocates of the cognitive neuroscience approach would maintain that advances in cognitive theory have kept in step with methods-based developments. There are several candidate reasons for the failure of neuroimaging studies to convincingly resolve many of the most important theoretical debates in the literature. For example, a significant proportion of published functional magnetic resonance imaging (fMRI) studies are not well grounded in cognitive theory, and this represents a step away from the traditional approach in experimental psychology of methodically and systematically building on (or chipping away at) existing theoretical models using tried and tested methods. Unless the experimental study design is set up within a clearly defined theoretical framework, any inferences that are drawn are unlikely to be accepted as anything other than speculative. A second, more fundamental issue is whether neuroimaging data alone can address how cognitive functions operate (far more interesting to the cognitive scientist than establishing the neuroanatomical coordinates of a given function - the where question).

How to reference

In order to correctly reference this scholarly work, feel free to copy and paste the following:

Joshua Goh and Chih-Mao Huang (2012). Images of the Cognitive Brain Across Age and Culture, Neuroimaging - Cognitive and Clinical Neuroscience, Prof. Peter Bright (Ed.), ISBN: 978-953-51-0606-7, InTech, Available from: <http://www.intechopen.com/books/neuroimaging-cognitive-and-clinical-neuroscience/imaging-the-brain-across-culture-and-age>

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