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When less is more and when more is more: The mediating roles of capacity and speed in brain-behavior efficiency

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ABSTRACT

An enduring enterprise of experimental psychology has been to account for individual differences in human performance. Recent advances in neuroimaging have permitted testing of hypotheses regarding the neural bases of individual differences but this burgeoning literature has been characterized by inconsistent results. We argue that careful design and analysis of neuroimaging studies is required to separate individual differences in processing capacity from individual differences in processing speed to account for these differences in the literature. We utilized task designs which permitted separation of processing capacity influences on brain-behavior relationships from those related to processing speed. In one set of studies, participants performed verbal delayed-recognition tasks during blocked and event-related fMRI scanning. The results indicated that those participants with greater working memory (WM) capacity showed greater prefrontal cortical activity, strategically capitalized on the additional processing time available in the delay period, and evinced faster WM-retrieval rates than low-capacity participants. In another study, participants performed a digit-symbol substitution task (DSST) designed to minimize WM storage capacity requirements and maximize processing speed requirements during fMRI scanning. In some prefrontal cortical (PFC) brain regions, participants with faster processing speed showed less PFC activity than slower performers while in other PFC and parietal regions they showed greater activity. Regional-causality analysis indicated that PFC exerted more influence over other brain regions for slower than for faster individuals. These results support a model of neural efficiency in which individuals differ in the extent of direct processing links between neural nodes. One benefit of direct processing links may be a surplus of resources that maximize available capacity permitting fast and accurate performance.

1. Introduction

One aim of cognitive neuroscience has been to identify those aspects of neurophysiology that underlie the consistent individual differences in performance that have long been observed in experimental psychology. Spearman's (1904) observation that some individuals consistently perform better than others across a broad range of tasks has spawned generations of research investigating the hypothesis that a limited set of resources govern cognitive performance. (Spearman, 1904; Kahneman, 1973; Norman & Bobrow, 1975; Vernon, 1983; Baddeley, 1986; Just & Carpenter, 1992).

The proposal that processing speed is one such resource is based on the notion that individuals differ in the efficiency with which fundamental cognitive operations are performed. Cognitive efficiency theories suggest that when these operations can be performed quickly, resource allocation can be minimized and performance maximized. Efficiency theorists have long hypothesized that correlations between reaction time (RT) and intelligence measures reflected individual differences in "neural efficiency" which permitted some individuals to overcome WM

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capacity limits (via chunking or other data reduction processes) more than others (e.g., Jensen, 1982, 1998; Vernon, 1983). The advent of modern neuroimaging techniques has made it possible to test such hypotheses by permitting more direct observation of brain-behavior relationships than was possible in the past.

2. Neuroimaging evidence for neural efficiency

Neuroimaging studies in healthy adults support efficiency explanations of individual differences. Results using electroencephalography (EEG) have shown differences in amplitude and coherence measures that correspond to participants' performance (e.g., Gevins & Smith, 2000; Reiterer, Berger, Hemmelmann, & Rappelsberger, 2005; Grabner, Stern, & Neubauer, 2003). In one study for instance, Gevins and Smith (2000) required high ability and low-ability (as measured by WAIS-R performance) participants to perform an n-back working memory task during EEG recording. The important result was that high-ability participants showed less prefrontal, and more parietal activity than their low-ability counterparts. Other EEG studies have measured "event-related desynchronizations" (ERDs) between alpha and theta frequencies that are interpreted as an index of mental effort (Nunez, Wingeier & Silberstein, 2001). In EEG literature, an ERD is said to occur when the amplitude of one frequency increases while the amplitude of another decreases. These studies have observed reduced ERD in higher, as compared to lower performing individuals (e.g., Grabner et al., 2003).

Results from PET and fMRI studies also show reduced activation in faster than in slower individuals (e.g., Haier et al., 1988, Haier, Siegel, Tang, & Abel, & Buchsbaum, 1992; Kosslyn, Thompson, Kim, Rauch, & Alpert, 1996; Larson, Haier, LaCasse, & Hazen, 1995; Rypma & D'Esposito, 1999; Rypma, Berger, & D'Esposito, 2002; Rypma, Berger, Genova, Rebbechi, & D'Esposito, 2005). In one study for instance, Haier et al. (1992) had 8 participants perform a spatial reasoning task, Raven Progressive Matrices. Next, they recorded participants' glucose metabolic rate (GMR; measured by PET) during performance of a complex visual manipulation task ("tetris") both before and after extensive practice. In addition to observing GMR reduction after learning, they observed that the extent of GMR reduction was correlated with participants' scores on the Raven Progressive Matrices. Similarly, Kosslyn et al. (1996) have observed neural activity reductions for faster, compared to slower participants on a mental imagery task. Consistent with these results, Rypma and D'Esposito (1999) observed a significant correlation between participants' memory search rates and PFC activity. These results suggest a specific model of neural efficiency in which the integrity of structural connections between task-critical brain regions is reflected in PET and fMRI activation. Specifically, they suggest that more direct connections between task-critical brain regions may correspond to decreases in task-related neural activity and improvements in performance (cf. Vernon, 1983; Cerella, 1991; Rypma & D'Esposito, 1999, 2000; Rypma et al., 2006).

Behavioral and neuroimaging studies have yielded results that lend support to an efficiency explanation of individual differences in performance in a broad range of populations. Systematic relationships between juvenile and adult RTs across different cognitive tasks (e.g., Keating & Bobbitt, 1978; Kail, 1986, 1988; Kail & Salthouse, 1994) support the notion of a global processing-speed ability governing developmental performance improvements. Such changes have been associated with PFC development (Gomez-Perez, Ostrosky-Solis, & Prospero-Garcia, 2003), neural activity differences in PFC between children and adults as measured by fMRI (Bunge, Dudukovic, Thomason, Vaidya, & Gabrieli, 2002), and development of PFC white matter as measured by diffusion tensor imaging (Liston et al., 2006).

Systematic RT correlations between younger and older adults have led to the proposal of a global processing speed factor that governs adult-aging performance changes (e.g., Salthouse, 1996b; Cerella, 1991; Hale, Myerson, & Wagstaff, 1987). As in child development, age-related processing speed changes have been associated with age-related PFC changes. Such changes appear especially pronounced relative to other regions (e.g., Kemper, 2002; Raz et al., 1997; Raz, Williamson, Gunning-Dixon, Head, & Acker, 2000; Haug & Eggers, 1991) possibly due to decrements in white-matter (e.g., Peters, 2002; Peters & Sethares, 2004; Madden et al., 2004; Ross, Hansel, Orbelo, & Monnot, 2005). Age-related changes in relationships between neural activity and performance implicate PFC in age-related declines in processing efficiency (e.g., Rypma, Prabhakaran, Desmond, Glover, & Gabrieli, 1999; Rypma & D'Esposito, 2000; Reuter-Lorenz et al., 2000; Cabeza, 2002; Stebbins et al., 2002; Rypma et al., 2005) and in age-related disease processes (e.g., West, 1996; Medina et al., 2006; Sawamoto, Honda, Hanakawa, Fukuyama, & Shibasaki, 2002; Small, Kemper, & Lyons, 2000).

Attenuation of WM performance differences between schizophrenic patients and controls when processing-speed, as measured by DSST, was statistically controlled implicate processing-speed as an important factor in disease-related performance changes (Brebion, Amador, Smith, & Gorman, 1998; Brebion et al., 2000, Brebion, Bressan, David, & Pilowsky, in press; Jogems-Kosterman, Zitman, Van Hoof, & Hulstijn, 2001; Hartman, Steketee, Silva, Lanning, & McCann, 2003). Schizophrenics show greater performance decreases, but greater PFC activation increases, relative to controls during WM performance (Callicott et al., 2000). Changes in activation-performance relations have also been observed when healthy control participants are compared to those with multiple sclerosis, a condition with known white-matter impairment, suggesting that the integrity of white matter may mediate individual differences in processing-speed (Genova, Hillary, Wylie, Rypma, & DeLuca, in press; Lange et al., 2005; Archibald & Fisk, 2000; Vernon, 1983).

3. Efficiency explanations of individual differences: Divergent results

Despite the suggestive data and explanatory power of the neural efficiency hypothesis, neuroimaging findings have not consistently replicated across studies. For instance, some studies have shown between-subject performance differences in which greater task-dependent activation was observed in higher than in lower performing individuals (e.g., Newman, Carpenter, Varma, & Just, 2003; Larson et al., 1995; Gray, Chabris, & Braver, 2003). Mixed results in ERD measurements have been observed as well. For instance, unlike the Grabner