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Unity and diversity of executive functions: Individual differences as a window on cognitive structure

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ABSTRACT

Executive functions (EFs) are high-level cognitive processes, often associated with the frontal lobes, that control lower level processes in the service of goal-directed behavior. They include abilities such as response inhibition, interference control, working memory updating, and set shifting. EFs show a general pattern of shared but distinct functions, a pattern described as "unity and diversity". We review studies of EF unity and diversity at the behavioral and genetic levels, focusing on studies of normal individual differences and what they reveal about the functional organization of these cognitive abilities. In particular, we review evidence that across multiple ages and populations, commonly studied EFs (a) are robustly correlated but separable when measured with latent variables; (b) are not the same as general intelligence or *g*; (c) are highly heritable at the latent level and seemingly also highly polygenic; and (d) activate both common and specific neural areas and can be linked to individual differences in neural activation, volume, and connectivity. We highlight how considering individual differences at the behavioral and neural levels can add considerable insight to the investigation of the functional organization of the brain, and conclude with some key points about individual differences to consider when interpreting neuropsychological patterns of dissociation.

Inhibition
→ interference control

1. Introduction

Executive functions (EFs) are high-level cognitive processes that, through their influence on lower-level processes, enable individuals to regulate their thoughts and actions during goal-directed behavior. The term EFs has been used to describe a number of abilities (Banich, 2009; Diamond, 2013; Jurado & Rosselli, 2007), such as stopping prepotent or automatic responses, resisting distraction or interference from irrelevant information in the environment or memory, switching between task sets, aspects of working memory processes (such as maintenance, manipulation, and updating), dual tasking, planning, monitoring, and verbal and design fluency.

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In the context of questions about the functional organization of cognitive abilities, EFs have been particularly perplexing. They are typically considered to be domain-general and to implicate a frontal-parietal network (Niendam et al., 2012) that is recruited across diverse tasks (Fedorenko, Duncan, & Kanwisher, 2013). Yet despite this apparently common neural substrate, performance on EF tasks is remarkably fractionated: Individual EF tasks typically show low intercorrelations (Miyake et al., 2000). Although such correlational dissociations are not the same as the kind of dissociations used as evidence in neuropsychological studies of brain lesions (e.g., Shallice, 1988), they can be interpreted as indicating separable functions (Duncan, Johnson, Swales, & Freer, 1997; Miyake et al., 2000; Teuber, 1972).

In this article, we review evidence for EF unity and diversity at the behavioral and genetic levels, focusing on studies of normal individual differences. On the basis of this review, we also discuss what individual differences reveal about the functional organization of these cognitive abilities, and what implications they may have for interpreting neuropsychological evidence of dissociations.

2. Patterns suggesting unity and diversity

2.1. Neuropsychological studies

EFs are often associated with the prefrontal cortex (PFC), because studies of patients with frontal lesions suggest that such damage leads to problems with goal-directed behavior (Luria, 1966; Stuss, 2011), particularly in novel tasks that require controlled processing (Rabbitt, 1997). Although it is clear that such behavior involves the interaction of frontal and other cortical and subcortical areas (e.g., Miller & Cohen, 2001; Royall, 2002; Stoet & Snyder, 2009), the PFC is thought to play an important role in coordinating activity across diverse areas.

It is apparent from neuropsychological work that there are a large variety of impairments arising from frontal lesions. Single-case dissociations and low correlations across EF tasks in patient groups support proposals that executive control might be a collection of processes rather than an entirely unitary function (Duncan et al., 1997; Godefroy, Cabaret, Petit-Chenal, Pruvo, & Rousseaux, 1999; Shallice & Burgess, 1996; Stuss & Alexander, 2007; Teuber, 1972). For example, Stuss and Alexander (2007) have argued that EFs can be dissociated into energization, task setting, and monitoring processes.

At the same time, there are some similarities that have led researchers to champion the view that such impairments share something in common. For example, Teuber (1972) used the term "unity and diversity" to describe frontal lobe functions:

> We thus return to our old contention that there is some unity in the diversity of frontal-lobe symptoms, because all of the superficially different symptoms have some family resemblance. Depending on species and localization of lesion, the behavioral pathology after frontal-lobe damage is differently expressed, but across those differences, there are more general features, and these can be traced to our central theme: that the prefrontal cortex, in all of its presumed functions, is neither sensory nor motor, but supports those processes that convey information in the central nervous system in a direction opposite to the classical one: not from input to output but conversely, by corollary discharges that modulate sensory systems in anticipation of future change (Teuber, 1972, p. 645).

This commonality has since been proposed to reflect associations among elements in working memory (Kimberg & Farah, 1993), an interaction of working memory and inhibition (Roberts & Pennington, 1996), goal selection (Duncan, Emslie, Williams, Johnson, & Freer, 1996), and behavioral inhibition (Barkley, 1997). Duncan has also proposed that this common component is closely related to general fluid intelligence (Duncan, 2010; Duncan et al., 1996), which implicates a fronto-cingulo-parietal network similar to one that has been implicated in neuroimaging studies of EF tasks (Niendam et al., 2012).

2.2. Studies of normal individual differences

Like neuropsychological studies, studies of normal individual differences have also yielded patterns suggesting unity and diversity. Although tasks often show significant correlations with large samples, the sizes of those correlations suggest some separability (e.g., Lehto, 1996; Robbins et al., 1998). However, low correlations could arise for a number of reasons, not just diversity of EFs (Miyake, Emerson, & Friedman, 2000). In particular, as noted by several researchers, EF tasks might not correlate well because of low reliability, different strategy use, and task impurity (Burgess, 1997; Shallice & Burgess, 1996; Stuss & Alexander, 2000). Task impurity especially seems to be an unavoidable quality of EF tasks: By definition, EFs involve controlling lower-level processes, so any EF task must include nonexecutive processes that could influence performance in addition to the EF of interest.

One method for removing the influence of unreliability and task impurity is latent variable analysis. Latent variables can be defined in a variety of ways (Bollen, 2002), but for the present purposes, their important characteristic is that they capture only common variance across multiple measures; this common variance cannot include random measurement error, and will not include non-EF variance to the extent that tasks are selected to have different lower-level processes (so task choice is important). Using this approach, we (Miyake et al., 2000) examined the relations among three of the most commonly discussed EFs at the level of latent variables: prepotent response inhibition (Inhibition), working memory updating (Updating), and task-set shifting (Shifting). Specifically, we selected three tasks to tap each construct, attempting to minimize the degree to which those three tasks required similar lower-level processes (e.g., for inhibition, we used tasks that required stopping eye movements [antisaccade], well-practiced manual word categorization responses [stop-signal], and word reading [Stroop]).

Although we found the typical pattern of low zero-order correlations across the nine EF tasks we used ($rs = -.05$ to .34), we also found that the tasks clustered according to the three EFs they targeted, and the correlations of the latent

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variable EFs were much higher (*rs* = .42 to .63) than the individual task correlations (Miyake et al., 2000). Importantly, neither a one-factor model (assuming no separability of the three EFs), nor a three-uncorrelated-factors model (assuming total independence of the three EFs), fit the data as well as the three-correlated-factors model. Moreover, the latent variable correlations among the three EFs could not be constrained to 1.0 or zero without worsening model fit, indicating that these three EFs were not all tapping the same construct (i.e., showed diversity), but did have something in common (i.e., showed unity).[1] This pattern mirrored that seen in earlier studies examining zero-order correlations, but represented a significant advance because it provided a view of EF structure when the influences of unreliability and task impurity were reduced.

Unity and diversity of EFs has been replicated numerous times in independent samples, including young adults (e.g., Fournier-Vicente, Larigauderie, & Gaonac'h, 2008; Ito et al., 2015), older adults (e.g., Fisk & Sharp, 2004; Hedden & Yoon, 2006; Hull, Martin, Beier, Lane, & Hamilton, 2008; Vaughan & Giovanello, 2010), clinical populations (e.g., Willcutt et al., 2001), and children and adolescents (e.g., Brydges, Fox, Reid, & Anderson, 2014; Duan, Wang, & Shi, 2010; Friedman et al., 2006; Huizinga, Dolan, & van der Molen, 2006; Lee, Bull, & Ho, 2013; Lehto, Juujarvi, Kooistra, & Pulkkinen, 2010; Miller, Giesbrecht, Müller, McInerney, & Kerns, 2012; Rose, Feldman, & Jankowski, 2012; Usai, Viterbori, Traverso, & De Franchis, 2013). Many of these studies have examined the same three EFs examined by Miyake et al. (2000), though not always with the same tasks. Most studies find that EF tasks cluster into separable but correlated factors, though the specific factor structures differ across studies. For example, although some results suggest more unity at young ages (Brydges et al., 2014; Wiebe et al., 2011), all the studies we reviewed found evidence that shifting was separable from updating or working memory in older children and adults. When inconsistencies arise, they tend to involve the inhibition factor: For example, Klauer, Schmitz, Teige-Mocigemba, and Voss (2010) found that inhibition and updating were not separable, and a few studies (Hull et al., 2008; van der Sluis, de Jong, & van der Leij, 2007) have failed to find an inhibition factor, primarily because the inhibition tasks in these studies did not correlate sufficiently strongly with one another to extract a latent variable.

The three EFs examined by Miyake et al. (2000) were chosen because they were commonly discussed in the literature and represented an intermediate level of complexity with which to examine the question of unity and diversity. It is important to note, however, that the model should not be considered to be comprehensive (i.e., there are likely other EFs), nor should it be considered to be a hypothesis about elementary processes. When researchers have examined how other candidate EFs relate to one or more of these three (e.g., Fisk & Sharp, 2004; Fournier-Vicente et al., 2008; Friedman & Miyake, 2004), the result is usually that there is something common to these putative EF abilities, but there are also distinctions. For example, Fisk and Sharp (2004) factor analyzed EF tasks thought to measure inhibition, updating, shifting, and access to long-term memory (verbal fluency tasks). They found that the fluency tasks loaded on a fourth factor, and that this factor was the only one not to show age-related decline. Fournier-Vicente et al. (2008) found that verbal and spatial working memory were dissociable from each other, and from strategic retrieval, selective attention, and shifting, but they failed to find a coherent dual-task factor. Friedman and Miyake (2004) found that different processes all described as involving "inhibition" could be dissociated at the latent variable level: Although "response inhibition" and "resisting perceptual distractor interference" were not separable from each other, they were not significantly correlated with "resisting proactive interference". Taken together, these results support the general principle of unity and diversity of EFs, and suggest that there are likely dissociations within EFs (e.g., inhibition, working memory), as well as EFs (e.g., fluency, dual-task coordination) other than those examined by Miyake et al. (2000).

3. Unity/diversity framework for individual differences in EFs

3.1. *Bifactor model*

In confirmatory factor analyses, the relations among EF latent variables are typically examined by estimating multiple correlated factors (e.g., Inhibiting, Updating, and Shifting in Fig. 1A). In such correlated-factors models, unity and diversity is reflected in the magnitudes of the correlations: Factor correlations larger than zero suggest some unity, and correlations smaller than 1.0 (or factors that cannot be collapsed) suggest some diversity.

In the Friedman et al. (2008) study, we estimated an alternative parameterization that moves unity and diversity out of the correlations and into the latent variables. In this bifactor model (shown in Fig. 1B), unity is captured by a Common EF latent variable that predicts all tasks, and diversity is captured by the Updating-Specific and Shifting-Specific factors that are formed from the remaining correlations among the updating and shifting tasks, respectively, once the correlations due to the Common EF factor are removed (for this reason, they are orthogonal to the common factor and each other).

In multiple independent datasets (e.g., Friedman et al., 2008; Ito et al., 2015), we were not able to extract an Inhibiting-Specific factor, because the Common EF factor explained all the correlations among the inhibiting tasks (Miyake & Friedman, 2012). Although this result is sometimes interpreted as evidence that the Common EF factor is

[1] To examine hypotheses about the separability of latent variables in confirmatory factor analysis, one typically tests whether collapsing two factors into a single factor, or setting a parameter to a particular value (e.g., a correlation to 1.0 or zero), results in a significant decrement in model fit. Collapsing two factors into one factor will be equivalent to testing that their correlation is 1.0 when there are only two factors in the model, but will involve more degrees of freedom when there are three or more factors in the model (the extra degrees of freedom come from the assumption that the two factors that are hypothesized to be the same have the same covariances with the other factors in the model). Miyake et al., 2000 tested whether factors were separable by testing whether their correlations could be constrained to 1.0, but did not report the multiple-degree-of-freedom tests for collapsing each pair of factors; subsequent studies reported both types of tests (e.g., Friedman et al., 2008).

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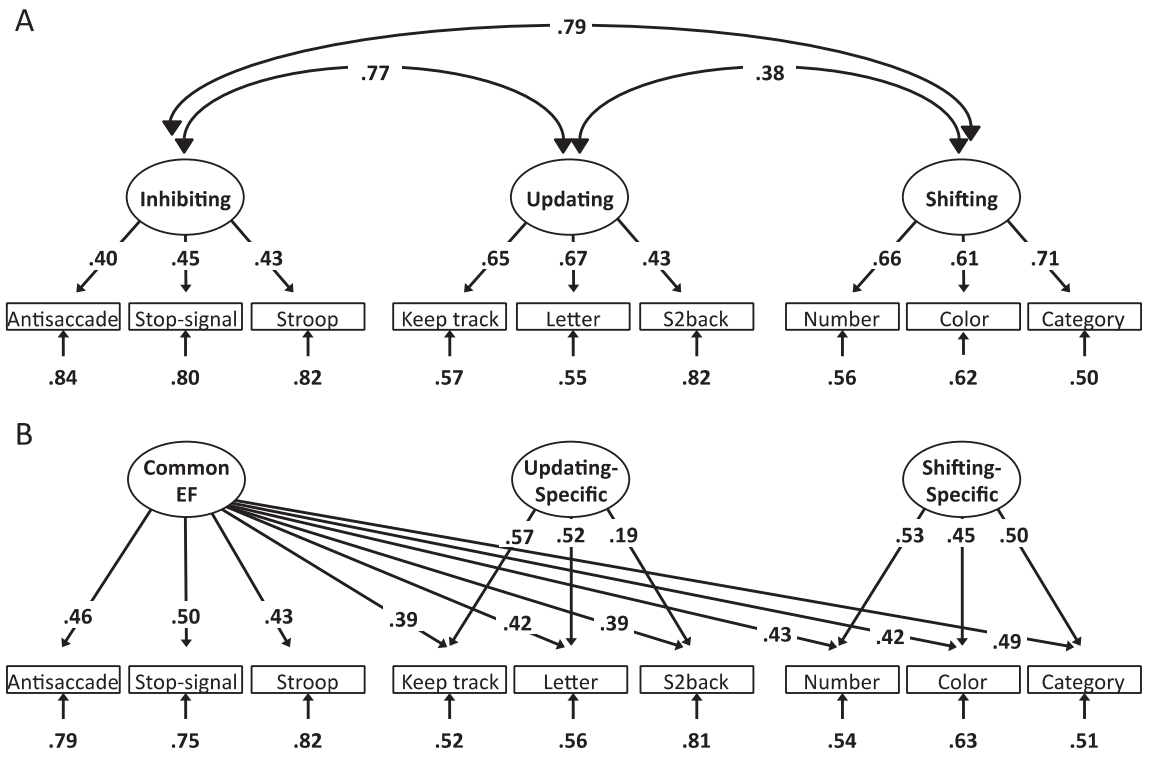

Fig. 1 – Latent variable models of executive functions (EFs). Inhibiting tasks require avoiding a dominant or prepotent response (eye movements, categorization, or word reading for antisaccade, stop-signal, and Stroop, respectively); Updating tasks require continuously updating the contents of working memory, adding new information and removing no-longer-relevant information (with category exemplars, letters, or spatial locations for keep track, letter memory, and spatial 2-back, respectively), and Shifting tasks require switching between two subtasks according to a cue that appears before each trial (between categorizing numbers as odd/even or letters as consonant/vowels, shapes as red/green or circle/triangle, or words as living/nonliving or big/small for the number–letter, color–shape, and category-switch tasks, respectively); see Friedman et al. (2008) for more details. In the correlated factors parameterization (panel A), three latent variables (represented with ellipses) each predict separate tasks (represented with rectangles). The numbers on the single-headed arrows are standardized factor loadings, and the numbers on the curved double-headed arrows are correlations between the latent variables. All of the correlations are significantly larger than zero (indicating unity), but none of the factors can be collapsed without significantly harming model fit (indicating diversity). In the bifactor parameterization (panel B), unity is captured with a common factor that predicts all nine tasks, and diversity is captured by orthogonal factors that capture remaining correlations among the updating and shifting tasks, respectively, once the Common EF variance is removed. Parameters taken from Friedman et al. (2011); all $p < .05$. Letter = letter memory; S2back = spatial 2-back; Number = number–Letter; Color = Color–shape; Category = category-switch.

inhibition (e.g., Valian, 2015), or that inhibition is the most central of all EFs (e.g., Hall & Fong, 2015), it has also been interpreted as evidence that there is nothing special about inhibition (e.g., Banich & Depue, 2015; Munakata et al., 2011), which is more consistent with our current view. We will discuss these interpretations more in section 5.1.1.

This bifactor model (Fig. 1B) provides a similar fit to the data as the correlated factors model (Fig. 1A), but has the advantage that it allows for more direct examination of how other individual differences are related to the unity and diversity components. For example, if a measure is related to multiple correlated EFs, then that pattern could reflect a relation just with the common factor, or relations with both the common and specific components. One could conduct a multiple regression (in a structural equation model) in which all three correlated factors predict the measure (as was done by Miyake et al., 2000), but in such a model, the common factor may be lost because each path quantifies the relation with that EF, controlling for the other EFs; moreover, multicollinearity can lead to large standard errors. The bifactor model allows for direct estimates of the relationships with both the common and specific components.

3.2. *Further insights into unity and diversity based on third-variable correlations*

Further evidence for EF unity and diversity comes from patterns of relations of EFs to other individual differences, such as other cognitive abilities and behavior. As reviewed by Snyder, Miyake, and Hankin (2015), EFs have been implicated in a number of clinical disorders, including schizophrenia, major depressive, bipolar, obsessive compulsive, attention-

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deficit/hyperactivity, and substance use disorders. Meta-analyses indicate that multiple EFs seem to be impaired in most of these disorders, suggesting that the unity component may be associated with psychopathology. However, it is not clear whether diversity components may also be implicated. Snyder (2013) found that meta-analytic effect sizes for depression-related EF impairments were significantly larger for inhibition than verbal working memory or shifting, but Snyder, Kaiser, Warren, & Heller (2015)found that obsessive-compulsive disorder impairments were largest for working memory updating, though the standard errors were large due to few studies examining updating. Although such meta-analytic data focusing on each EF are valuable, it is difficult to predict whether such patterns would translate to significant associations with specific EF components in a study with the unity/diversity model.

Comparing results using the correlated factors and bifactor models shown in Fig. 1 in a nonclinical population sample has yielded some important insights. First, although the correlated factors model sometimes suggests differential relationships, this pattern can be consistent with a relation to the Common EF factor, because Inhibiting is isomorphic with this common factor, whereas Updating and Shifting are less related to it (Friedman et al., 2008). For example, Young et al. (2009) found that behavioral disinhibition, a liability towards externalizing behavior, was more strongly related to Inhibiting than Updating or Shifting, and Friedman et al. (2007) found a similar result with teacher-rated attention problems. When reanalyzed with the bifactor model, these patterns translated into associations with the Common EF factor (Herd et al., 2014; Miyake & Friedman, 2012).

Second, third-variable correlations with the bifactor model often reveal a trade-off between the Common EF and the Shifting-Specific factors, such that behaviors that are associated with worse Common EF are associated with better Shifting-Specific abilities. For example, Friedman, Miyake, Robinson, and Hewitt (2011), using the correlated factors model shown in Fig. 1A, found that toddlers with higher self-restraint had better age 17 Inhibiting and Updating abilities, but not different Shifting abilities, compared to toddlers with lower self-restraint. Yet using the bifactor model in Fig. 1B, toddlers with better self-restraint showed better Common EF ability, no difference in Updating-Specific ability, and significantly worse Shifting-Specific ability. Because the overall Shifting factor is a combination of Common EF and Shifting-Specific, opposing relations tend to cancel out, looking like a null relationship with overall Shifting ability. In other words, correlations with Shifting are lower than one would expect given the relationship of Shifting with the other EFs, suggesting that something unique to Shifting is suppressing the correlations (see Herd et al., 2014; for more examples).

As discussed in more detail in section 5.1.2, we have proposed that this pattern reflects a stability-flexibility tradeoff (Goschke, 2000; Herd et al., 2014; Miyake & Friedman, 2012). Interestingly, similar tradeoffs have recently been shown at the level of individual tasks and without multiple regression. For example, Blackwell, Chatham, Wiseheart, and Munakata (2014) found that children who were better at switching in a card-sorting task were worse at response inhibition. Similarly, Mittal, Griskevicius, Simpson, Sung, and Young (2015) found that adults who had grown up in stressful environments showed worse response inhibition but better task switching in uncertain contexts, compared to adults raised in less stressful environments.

3.2.1. *Relations to intelligence*

One question that often arises is whether the Common EF factor is just recapitulating Spearman's *g* (or general intelligence), especially its fluid aspects, as suggested by research showing that there is a close relationship between EF tasks and fluid intelligence (Duncan et al., 1996; Salthouse, 2005). When we directly examined this issue by predicting fluid and crystallized intelligence latent variables[2] with the correlated Inhibiting, Updating, and Shifting variables (as in Fig. 1A), we found that all three EFs were related to some extent to both intelligence factors (Friedman et al., 2006). However, when we controlled for their intercorrelations with structural equation modeling, only Updating was significantly related to intelligence, suggesting that the correlations of Inhibiting and Shifting with intelligence were due to their overlapping variances with Updating (i.e., Common EF variance).

In later studies including more data from the same sample (Friedman et al., 2008), we examined the relations between the EFs in the bifactor unity/diversity parameterization (as in Fig. 1B) and full-scale intelligence scores (Wechsler, 1997). At the phenotypic level, intelligence was about equally related to the Common EF ($r = .51$) and Updating-Specific ($r = .49$) factors, and also showed a significant negative correlation with the Shifting-Specific factor ($r = -.24$; Friedman et al., 2011); results were similar at the genetic level and using a latent *g*-factor based on 11 intelligence subtests (Friedman et al., 2008). These results suggest that the Common EF factor is not *g*, and in fact only shares about 25% of its variance with *g*. Moreover, *g* is also related to unique variance in Updating. A similar analysis with a psychometric perceptual speed latent variable also suggested that the Common EF factor was separable from speed (Friedman et al., 2008).

The Common EF factor also predicts behavior even when controlling for intelligence. For example, we found that toddlers' self-restraint predicted the variance in age 17 Common EF that was independent of intelligence, but did not predict the variance in intelligence that was independent of EFs (Friedman et al., 2011). We found a similar pattern in the relations between teacher-rated attention problems and EFs: The common variance in attention problems from ages 7–14 years correlated with the variance in age 17 Inhibiting that was independent of intelligence (Friedman et al., 2007). Taken together, these findings suggest that Common EF measures something beyond *g*, and moreover, that extra something is importantly related to real-world behavior.

[2] The fluid intelligence factor included Raven's Progressive Matrices Test (Raven, 1960) and the Block Design subtest of the Wechsler Adult Intelligence Scale (Wechsler, 1997). The crystallized intelligence factor included a multiple choice vocabulary test (DeFries, Plomin, Vandenberg, & Kuse, 1981), and the Information subtest of the Wechsler Adult Intelligence Scale.

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4. Genetic influences on EFs

To what extent do individual differences in these EFs reflect genetic and/or environmental influences? Two main behavioral genetic approaches can be used to answer this question: family studies (such as twin studies) that examine the extent to which individuals who are more similar genetically are also more similar in terms of EF abilities; and molecular genetic studies that correlate specific genotypes with performance, usually across unrelated individuals. We review studies using each of these approaches in the following subsections.

4.1. *Twin studies*

Twin studies partition the total phenotypic variance of a trait into three components: additive genetic (A; genetic influences that additively combine to influence variation, indicated when monozygotic twins correlate more strongly than dizygotic twins), common environment (C; environmental influences that lead twins to correlate, regardless of zygosity, such as socioeconomic status), and nonshared environmental (E; environmental influences that lead twins to not correlate, such as different peer groups). These variance components provide estimates of the extent to which each kind of influence is reflected in the individual differences at the aggregate level (i.e., how heritable a trait is, but not which specific genes influence it).

Moreover, multivariate ACE models can be used to ascertain whether correlations across tasks or constructs are due to the same or correlated genes, environments, or both. Such studies have been useful in the realm of cognitive abilities for understanding to what extent the genetic/environmental structures differ from the phenotypic structure. For example, when it comes to the relations among specific cognitive abilities (verbal, spatial, speed, and memory), genetic influences occur mostly on the *g*-factor, and it is primarily environmental influences that distinguish different abilities from each other (Petrill, 1997), a result that Petrill interpreted as reflecting "molarity" of genetic influences and "modularity" of environmental influences.

4.1.1. *Genetic influences on both unity and diversity of EFs*

If the unity and diversity of EFs is similar to that for specific cognitive abilities, we might expect to see the same pattern: i.e., that unity is primarily genetic, and diversity is primarily environmental. However, substantial genetic influences on the diversity components would further distinguish EFs from other cognitive abilities and suggest that different sets of genes contribute to the various EFs. This pattern is exactly what we found in first twin study of latent EF variables (Friedman et al., 2008), which examined a sample of 17-year-old twins.

Fig. 2 depicts an updated version of the results of that study (using the full sample reported by Friedman et al., 2011). Specifically, the Common EF factor was highly heritable (96%), but so were the Updating-Specific (100%) and Shifting-Specific (79%) factors; the latter was the only EF with significant environmental variance (E = 21%). This pattern suggested that both the unity and diversity of EFs are primarily genetic in origin. We have also recently found (Friedman et al., 2016) that the same genetic influences are operating across a 6-year span, leading to high stability in individual differences (age 17 to 23 phenotypic correlations of .86, 1.0, and .91 for Common EF, Updating-Specific, and Shifting-Specific, respectively).

Similar results have been reported by Engelhardt, Briley, Mann, Harden, and Tucker-Drob (2015) in a twin study of 8–15 year-olds. They found that a hierarchical common factor (predicting Inhibition, Switching, Working Memory, and Updating latent variables) was 100% heritable, and that there were significant additional genetic influences on the Switching latent variable.[3] Though they did not estimate the heritability of a latent variable, Lee et al. (2012) examined the genetic and environmental structure of individual tasks tapping working memory, fluency, inhibition, and flexibility in a sample of older (>65 years) twins. They also found that all the shared variance across tasks was genetic, and that there were significant unique genetic influences on the fluency and inhibition tasks but not on a flexibility task.

Taken together, these results from separate studies examining multiple ages suggest that individual differences in EFs are highly heritable (at the latent variable level),[4] and, unlike studies on specific cognitive abilities, also show not only unity but also diversity at genetic levels of analysis. Such results suggest that, at least with respect to the EFs examined in these studies, the processes that distinguish EFs from one another are linked to different sets of genes.

4.1.2. *Interpreting heritability*

Whenever discussing the high heritability of EFs, we feel compelled to emphasize that high heritability does not imply immutability, because many researchers misinterpret our findings this way. For example, Müller, Baker, and Yeung (2013) criticized the behavioral genetic approach to understanding individual differences in EF, arguing that evidence for experience-dependent effects on EFs (such as stress and training) "challenge the claim that EF is almost entirely genetic" (p. 39). Similarly, some researchers have argued that EFs that show environmental influences should be the most likely target for training studies. For example, Braver, Cole, and

[3] In the Englehardt et al. (2015) study, the Inhibition latent variable did not load at 1.0 on the common factor, though it also did not show significant residual genetic or environmental variance. This result may seem inconsistent with no evidence for the Inhibition-Specific factor in our studies (e.g., Friedman et al., 2008). However, they included both Working Memory and Updating factors in their model, which, because of their high correlation ($r = .91$ after partialling out age), tended to dominate the common factor (loadings of .93 and .97, respectively). Thus, their common factor may be more like the overall Updating factor in Friedman et al. (2008).

[4] The heritabilities of the EF latent variables were strikingly high compared to some previous studies that reported heritability at the level of individual tasks (e.g., Ando, Ono, & Wright, 2001; Polderman et al., 2006). This difference occurs because heritabilities calculated at the level of latent variables quantify the genetic influences on the variance common to multiple tasks; each task had significant environmental influences (and sometimes genetic influences) in addition to those for the latent variables, as illustrated in Fig. 2.

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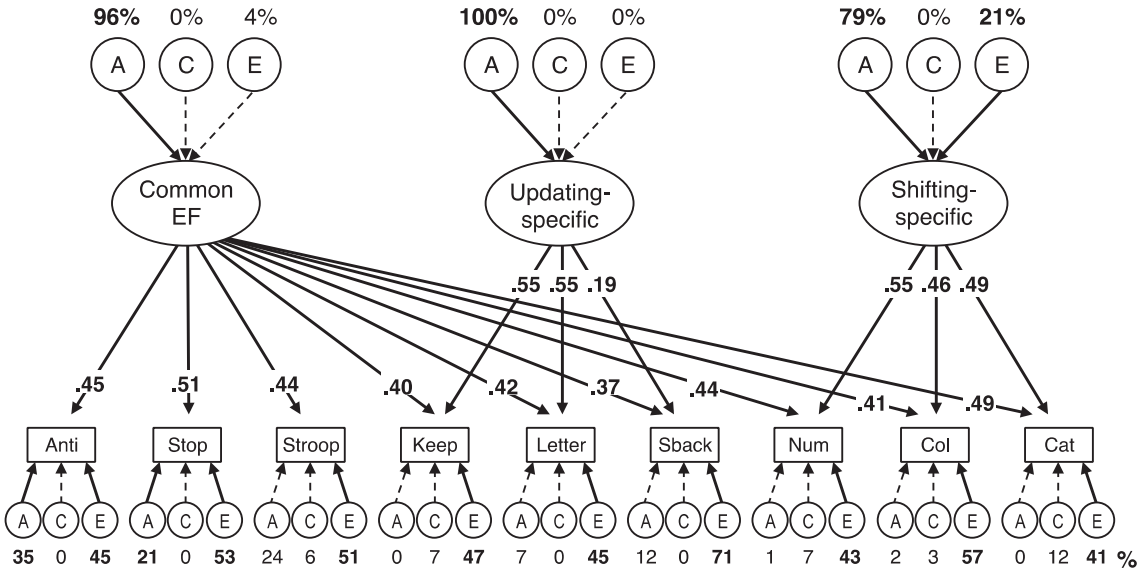

Fig. 2 – Twin model estimates for the bifactor unity/diversity model (parameters taken from Friedman et al., 2011). Each latent variable variance is decomposed into additive genetic (A), shared environmental (C), and nonshared environmental (E) variances (percentages at top of figure), as are the residual variances for each task (i.e., variances not explained by the EF factors; percentages at bottom of figure). Numbers on arrows are standardized factor loadings. Boldface type and solid lines indicate $p < .05$. Anti = antisaccade, Stop = stop-signal, Keep = keep track; Letter = letter memory, Sback = spatial 2-back, Num = number–letter, Col = color–shape, Cat = category-switch.

Yarkoni (2010) described the Friedman et al. (2008) findings as follows: "Intriguing evidence that a latent executive function variable comprising measures of inhibition, working memory updating and task-set shifting had 99% of variance explained by a genetic contribution. Note that WM capacity was not included in their statistical model, leaving open the possibility that it can be strongly influenced by practice (as suggested by others)" (p. 249). These interpretations reflect common misunderstandings of genetic influences as indicating that a trait is predetermined and unchangeable. But high heritability is not inconsistent with the possibility of environmental effects for several reasons.

First, heritability is an estimate of the proportion of variance accounted for by genetic differences in the population being studied at a particular age, during a particular period in history, and under particular environmental conditions; changes to the population or environmental surroundings can lead to changes in heritability. For example, the heritability of general cognitive ability changes with age (e.g., Briley & Tucker-Drob, 2013; Plomin & Deary, 2014), and some reports suggest that heritability is higher in samples with higher socioeconomic status (Tucker-Drob, Briley, & Harden, 2013; Turkheimer, Haley, Waldron, D'Onofrio, & Gottesman, 2003). Because heritability reflects the proportion of total variance due to genes, changing the environment can actually lead to higher heritability if it reduces environmental variance. For example, the consequence of maximizing nutrition for all students should be increased heritability for school performance, because environmental individual differences related to nutrition would be greatly reduced.

Second, heritability is not about means, but, rather, about individual variability around the means. Given an environmental intervention that influences most members of the population (e.g., better nutrition across generations), the entire distribution could shift upwards (i.e., higher means), but the change may preserve a similar rank order among individuals.

Third, it is likely that environmental influences that affect EFs are correlated with genetic influences (e.g., individuals with good EFs seek out activities that further develop these EFs); twin models may include such gene-environment correlations in the A estimate (Plomin, DeFries, & Loehlin, 1977). Such correlations can also lead to genetic amplification, whereby genetic variance increases across development because initially moderate genetic differences lead children to select certain environments, which then magnify those differences (Briley & Tucker-Drob, 2013; Plomin & Deary, 2014; Tucker-Drob et al., 2013).

As this discussion indicates, heritability should not be interpreted as an index of the extent to which EFs are amenable to environmental interventions. In particular, high heritability of EFs should not be used as a basis for pessimism about the potential for environmental interventions and training.

4.2. *Molecular genetic studies*

These findings about the heritability and genetic structure of EFs suggest that we may eventually be able to link individual differences in these EF components to particular genetic polymorphisms. Doing so could provide considerable insight not just into the mechanisms of cognitive control, but also into the genetic liabilities for related disorders. As discussed earlier, EF deficits are seen in almost all forms of psychopathology (Snyder, Miyake, et al., 2015). These associations have led some to propose EFs as endophenotypes for

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psychopathology. An endophenotype is a phenotype that is more directly related to the disorder because it lies on the pathway between genes and disease; it is thought to "represent simpler clues to genetic underpinnings than the disease syndrome itself" (Gottesman & Gould, 2003, p. 636). EFs do satisfy many endophenotype criteria (e.g., Doyle et al., 2005; Gau & Shang, 2010), so it is hoped that they might yield bigger effects sizes than psychiatric phenotypes (Flint & Munafò, 2007), and that discovered genetic influences might illuminate genetic influences on psychopathology.

4.2.1. *Candidate gene studies*

Unfortunately, the progress in identifying genes associated with EFs has been disappointing so far. Early studies focused on a handful of candidate genes, investigated in relatively small samples, with the expectation that genetic effect sizes would be large. Variants in genes for neurotransmitter systems such as dopamine were particularly popular (for a review, see Barnes, Dean, Nandam, O'Connell, & Bellgrove, 2011). For example, the COMT val$^{108/158}$met polymorphism, which is thought to influence levels of tonic dopamine in the PFC (Meyer-Lindenberg et al., 2005), has been included in hundreds of studies of cognitive and psychopathology phenotypes. Yet despite strong theoretical reasons for examining these genes, many effects were inconsistent (e.g., Barnett, Scoriels, & Munafò, 2008; Chabris, Lee, Cesarini, Benjamin, & Laibson, 2015; Hirschhorn, Lohmueller, Byrne, & Hirschhorn, 2002).

At the same time, early genome-wide analysis studies (GWAS) of various complex traits reported few significant hits across the entire genome, even for highly heritable and relatively straightforward to measure traits like height; together these few hits accounted for only a small percentage of the genetic variance estimated from family studies (Manolio et al., 2009). Although numerous explanations have been advanced for this "missing heritability" (Manolio et al., 2009), it appears that a good deal of the missing genetic variance is not missing at all; rather it reflects the sum of thousands of genetic variants, each of which only accounts for a fraction of a percent of the total variance (e.g., Chabris et al., 2015).

The realization that most complex traits are highly polygenic (i.e., influenced by many genes), with any one variant typically showing a 1.1 odds ratio or R^2 of approximately .0007 (Dick et al., 2015), has led to much skepticism of candidate gene results, including candidate gene-environment interactions (Dick et al., 2015; Duncan & Keller, 2011). The sample sizes used for such studies mean that they are often underpowered (Duncan & Keller, 2011), so reported effects are likely to be false positives (Button et al., 2013). For example, a meta-analysis of the COMT polymorphism on Wisconsin Card Sorting Test performance (Barnett, Jones, Robbins, & Müller, 2007) included studies that had sample sizes ranging from 22 to 402 individuals for particular groups (the sample sizes for particular genotypes within those groups were as low as 3 individuals).

Moreover, most replicated variants found in GWAS are not those that were hypothesized as candidate genes (Dick et al., 2015). This finding raises the possibility that it is extremely difficult to accurately predict which genes may be important; thus focusing on only a handful of variants in insufficiently understood biological pathways may not be as useful as more theoretically neutral GWAS (Manolio et al., 2009).

4.2.2. *Genome-wide association studies*

The sample sizes needed for GWAS are only achievable through meta-analyses combining data across a large number of studies. Although the idea that EFs are endophenotypes raises the hope that they might be genetically simpler and hence yield larger effect sizes, a meta-analysis indicated that proposed endophenotypes, including EFs, actually do not show larger effect sizes than psychiatric phenotypes (Flint & Munafò, 2007). The largest GWAS meta-analysis of EF tasks to date (Ibrahim-Verbaas et al., 2015) did not yield a single genome-wide significant hit for any individual EF task (trail making test form B, semantic and phonemic fluency, and Stroop interference), despite sample sizes of 17,027 to 28,243 for these individual measures. This result suggests that individual differences in EFs, like other complex traits, are highly polygenic (reflect the contribution of many thousands of genes), and that even larger sample sizes will be needed to identify individual genetic variants.

The prospect of such an effort is daunting, but the existing genetic literature on psychiatric disorders and general cognitive ability suggest that it will be fruitful. For example, a recent GWAS of general cognitive ability in approximately 54,000 middle-aged and older adults yielded 13 significant associations (Davies et al., 2015). Consortia have also been formed for GWAS of neuroimaging phenotypes, with significant associations found for measures of brain volume (Thompson et al., 2014).

5. Proposed mechanisms

5.1. *What processes do the unity and diversity components reflect?*

The unity/diversity model is primarily descriptive, quantifying how well-studied tasks cluster. However, the patterns emerging from analyses with these models, combined with the literature on EFs and frontal lobe functioning more generally, can provide some clues as to what these factors may be measuring.

5.1.1. *Hypothesized functions for the Common EF factor*

An important finding that provides some insights into the underlying mechanisms for Common EF is the absence of an inhibition-specific factor. One possible interpretation of this result is that the Common EF factor is inhibition (e.g., Valian, 2015). Proponents of this view often note that many EF tasks require some sort of inhibition (e.g., suppressing responses, distraction, memory representations; c.f., Zacks & Hasher, 1994). If these sorts of inhibition are the same as the response inhibition tapped by the Inhibiting factor in the unity/diversity model, then the fact that Inhibiting is isomorphic with the Common EF factor would make sense. However, this conceptualization of inhibition may be overly broad, lumping together processes that are conceptually and empirically separable (Friedman & Miyake, 2004; Hedden & Yoon, 2006; Nigg, 2000). Moreover, some researchers have argued that the idea of top-down inhibition (i.e., frontal areas suppress activity of other areas or even particular representations) is not only unnecessary to explain "inhibitory" phenomena (Hampshire & Sharp, 2015;

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MacLeod, Dodd, Sheard, Wilson, & Bibi, 2003), but also overgeneralizes a real neural mechanism (local lateral inhibition) in a way that is not biologically plausible (Munakata et al., 2011). Rather, phenomena taken to reflect top-down inhibition can be explained with top-down activation of correct responses that compete with incorrect responses through local lateral inhibition.

According to this view, areas of the frontal lobes that are consistently implicated in inhibition (particularly the right inferior frontal gyrus; Aron, Robbins, & Poldrack, 2014) may be performing more goal-related processing, such as monitoring for goal-relevant information (Chatham et al., 2012; Hampshire, Chamberlain, Monti, Duncan, & Owen, 2010), and inhibition of irrelevant stimuli, memoranda, responses, etc., emerges from competition (Banich & Depue, 2015; Egner & Hirsch, 2005; Hampshire & Sharp, 2015; Munakata et al., 2011). A key individual difference factor would then be the quality, and effective use, of goal representations that bias these competitive dynamics.

For this reason, we have suggested that the Common EF factor reflects individual differences in the ability to maintain and manage goals, and use those goals to bias ongoing processing (Friedman et al., 2008; Gustavson, Miyake, Hewitt, & Friedman, 2015; Miyake & Friedman, 2012), a proposal consistent with many existing theories of EF and frontal lobe functioning (e.g., Courtney, 2004; Desimone & Duncan, 1995; Miller & Cohen, 2001; Roberts & Pennington, 1996). This goal maintenance and implementation is a general requirement of all EF tasks, and may be particularly important for inhibition tasks, in which the main requirement is avoiding strong prepotent responses or conflicting information; thus, this mechanism could explain why all tasks load on the Common EF factor, but the inhibition tasks do not load on an additional factor.

One misconception about this proposal is that Common EF is just about simple maintenance of goals, making it virtually indistinguishable from short-term memory. In our view, goal representation and implementation are about much more. First, the ability to use goals to bias ongoing processing may be an individual differences factor that is at least somewhat separable from the active maintenance of the goals themselves (e.g., related to neural structural and functional connectivity; Herd et al., 2014). Second, a number of other processes likely contribute to forming and implementing goals, such as identifying good goals in the first place, and then using environmental cues to achieve them. For example, success in the stop-signal task requires translating an arbitrary cue (e.g., an auditory tone) into a goal to stop, and then continuously monitoring the environment for the presence of that cue (e.g., Chatham et al., 2012). Indeed, Chevalier (2015) recently suggested that goal identification and cue processing are overlooked components in the development of EF; moreover, he proposed that because these processes are general to multiple EFs, "they may help clarify what 'common' executive abilities are" (p. 366). We have also found that Common EF is genetically linked to measures of self-reported goal management/retrieval failures (Gustavson et al., 2015), suggesting that Common EF is not just about maintenance of goals, but could also be about retrieving and implementing the right goals at the right time.

5.1.2. *Hypothesized mechanisms for the Shifting-Specific factor*

A repeated finding that provides some insights into what individual differences the Shifting-Specific factor may be capturing is that it often shows patterns of correlations with other measures that are seemingly opposite to those of Common EF, as reviewed in section 3.2. In our studies, the tasks loading on this factor are all task-switching paradigms in which participants must rapidly shift between two subtasks according to random cues (e.g., categorizing the shape *vs* color of stimuli); performance is measured with local switch costs (i.e., switch–repeat response times within mixed blocks). Thus, these tasks require selecting and applying the correct task set (explaining the loadings on the Common EF factor), but also rapidly replacing task sets or goals. We have posited that perhaps the speed of this goal replacement is an individual difference related to Shifting-Specific variance (Miyake & Friedman, 2012).

There also is likely a tradeoff with aspects of Common EF, such that stronger goals take longer to replace. That is, given equivalent goal representations across individuals, some individuals take longer to replace those goals with new goals than others; and given equivalent clearing rates, more active goals take longer to replace than less active ones. Thus, individuals who have weak goal representations (e.g., individuals with attention-deficit disorder) may show poor performance across a range of EF tasks, but actually show smaller switch costs than would be expected given their Common EF scores; in the unity/diversity model, this pattern would manifest in a negative association between attention problems and Common EF, but a positive relationship with the Shifting-Specific factor.

Recently, Herd et al. (2014) showed that manipulations of these proposed Common EF and Shifting-Specific mechanisms in a biologically based neural network model could produce Common EF and Shifting-Specific effects, as well as a trade-off in the model's performance of a response inhibition task (Stroop) and a shifting task (color–shape). The general model architecture, based on the prefrontal-cortex-basal-ganglia working memory model (PBWM; Frank, Loughry, & O'Reilly, 2001), is shown in Fig. 3. Specifically, lowering the model's connection strength between PFC and posterior cortex (intended to decrease the strength of top-down biasing) worsened performance on both tasks (i.e., increased Stroop interference and switch costs), consistent with a Common EF effect. In contrast, lowering the model's signal-to-noise ratio in the PFC layer (intended to decrease the strength of active goal maintenance) had opposite effects on the inhibition and switching tasks (i.e., increased Stroop interference but decreased switch costs), consistent with a stability/flexibility tradeoff. Increasing the extent to which the model cleared PFC representations when new representations were gated by the basal ganglia (thought to be related to the strength of GABAergic inhibition, which is triggered by a wave of excitatory activity when a thalamocortical circuit is activated) decreased switch costs but had no effect on Stroop interference, consistent with a Shifting-Specific effect.

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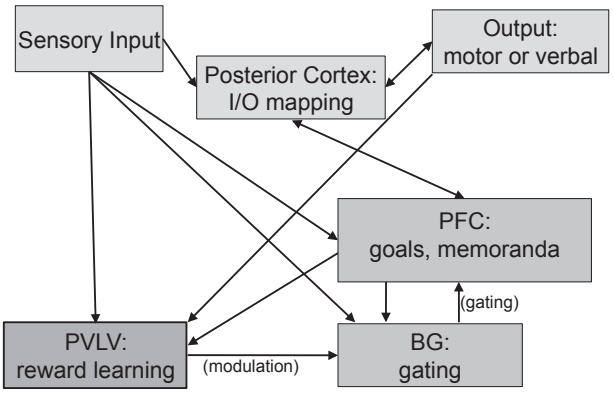

Fig. 3 – General structure and connectivity of the prefrontal cortex (PFC) basal ganglia (BG) computational model used to simulate executive function (EF) tasks in Herd et al. (2014). Each box represents a layer or set of layers, and arrows indicate connectivity. Layer properties and connectivity incorporate extensive physiological data (Frank et al., 2001). The BG learn whether incoming information (in the sensory input layer) should be gated into the PFC, based on dopaminergic signals representing learned reward values associated with those inputs generated by the primary value–learned value (PVLV) system. If information is deemed relevant, active maintenance currents within PFC are turned on to enable that information's representation to persist in the absence of input. That information can then be used to bias ongoing processing and select response mappings (learned by the posterior cortex). I/O = input/output.

These results demonstrated that these proposed mechanisms could produce some of the unity and diversity of these EFs seen in individual differences studies. Interestingly, they also demonstrated that diversity could emerge within a unified architecture: The Shifting-Specific effect arose not because different neural areas were involved in the shifting task, compared to the response inhibition task, but because the shifting task was sensitive to different parameters within those same areas. This pattern raises the possibility that the Shifting-Specific factor may not be easily identifiable in imaging or lesion studies that focus on spatial dissociations.

5.1.3. *Hypothesized mechanisms for the Updating-Specific factor*

Our hypotheses regarding the nature of the Updating-Specific mechanisms are less developed. As the name implies, updating tasks require constantly replacing information in working memory, but an important aspect of these tasks is that this updating occurs only for some information, while other information must be maintained (in contrast to shifting tasks, in which goals are constantly updated, but only one goal is relevant at a time). For this reason, Updating-Specific variance may be related to the precision of the updating process, thought to be controlled by the basal ganglia (e.g., Frank et al., 2001). It is also possible that memory-specific factors, like retrieval from episodic memory, contribute to Updating-Specific variance.

5.2. *Relations to other theoretical proposals and frameworks*

Of course, the unity/diversity framework is not the only model of (individual differences in) EFs. Indeed, the proposed mechanisms discussed in the previous section draw on much existing research and theory. Although other frameworks may carve up EFs differently, we see many similarities between their proposed mechanisms of individual differences and those of the unity/diversity framework, particularly with respect to the Common EF factor.

5.2.1. *Multiple demand system*

Our use of the term "unity and diversity" was influenced in large part by the work of Duncan et al. (1997), who noted that despite their low intercorrelations, the common element among EF tasks was closely related to the phenomenon of goal neglect and to *g*. Specifically, Duncan et al. (1996) has argued that a key function of the frontal lobes is "shaping of behavior by activation of action requirements or goals specified at multiple levels of abstraction" (p. 293). That is, tasks that load highly on *g* tend to be complex tasks that require developing and carrying out multiple goals and subgoals in appropriate sequence; i.e., breaking down complex problems into manageable chunks. Duncan (2010) has proposed that this sequential mental programming is key to understanding what he calls the "multiple demand" system, a set of frontal and parietal brain regions that activates during diverse cognitive tasks, and that is associated with general fluid intelligence.

In many ways, our proposal that Common EF ability reflects goal maintenance and top-down bias is highly consistent with Duncan's emphasis on goal neglect as a common element for EF tasks in both frontal lobe patients and intact individuals. Where our frameworks diverge, however, is in our emphasis on the presence of specific factors in addition to the common factor, and in how these factors are linked to *g*. As discussed in section 3.2.1, we have found that, indeed, Common EF is related to intelligence (both fluid and crystallized; Friedman et al., 2006), but intelligence is also substantially related to the Updating-Specific factor (Friedman et al., 2008, 2011). In fact, the combination of Common EF and Updating-Specific (i.e., the overall Updating factor in the correlated factors model in Fig. 1A) correlates .70 with full-scale IQ (Friedman et al., 2008). Thus, the link between goal neglect and intelligence is perfectly consistent with our finding that Common EF correlates with intelligence, but it does not mean that Common EF equals intelligence. Without using multiple tasks tapping several EFs to separate working memory/updating tasks into Common EF and Updating-Specific components, it is difficult to tell whether the variance shared by goal neglect and *g* reflects just Common EF, or a combination of Common EF and Updating-Specific.

5.2.2. *Executive (or controlled) attention*

The framework proposed by Engle, Kane, and colleagues (e.g., Engle, Kane, & Tuholski, 1999; Kane & Engle, 2003) has similar origins as the unity/diversity model (i.e., models of working

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memory; Baddeley & Hitch, 1974). They argued that complex working memory span tasks, which require interleaved processing and storage (like the reading span task; Daneman & Carpenter, 1980), explain performance on measures of fluid intelligence better than simple storage measures because, in part, they require "controlled attention": "WM capacity, the construct measured by WM span tasks, reflects the general capability to maintain information, such as task goals, in a highly active state" (Kane, Bleckley, Conway, & Engle, 2001, p. 170). They went on to discuss the importance of controlled attention in conditions of interference and strong prepotent responses, arguing that inhibition might occur by boosting activation for goal representations. Consistent with this idea, they found in several studies that working memory span tasks predict abilities related to inhibition and interference control (Kane & Engle, 2003; Kane et al., 2001; Rosen & Engle, 1998).

In addition to goal maintenance, the executive attention framework also posits that competition resolution may be an important determinant of individual differences (Kane & Engle, 2003). That is, goal maintenance may be important in some contexts that do not reinforce the goal (e.g., infrequent incongruent trials in the Stroop task), but even with active goals, poorer interference resolution leads to poorer performance. They suggested that both goal maintenance and interference resolution are interdependent processes that are both related to individual differences in working memory capacity.

Though complex span tasks' structure is somewhat different than the tasks used to assess the updating construct, working memory capacity (measured with complex span tasks) and updating (measured with working memory updating tasks) are closely related constructs at the level of individual differences (Schmiedek, Hildebrandt, Lövdén, Wilhelm, & Lindenberger, 2009). Thus, the observation of overlapping variance across working memory tasks and other EF tasks that tap inhibition and interference control (Kane et al., 2001) is consistent with the observation of shared variance across Inhibiting and Updating constructs in the unity/diversity model. Indeed, we propose essentially the same mechanism to explain this common variance: active goal maintenance and top-down bias. Our discussion differs mainly in that we see top-down bias as capturing the potentially separable conflict resolution mechanism that Kane and Engle (2003) discuss (i.e., bias may be particularly important in the context of high interference).

5.2.3. *Proactive control*

The conceptualization of Common EF also shares many similarities with the notion of proactive control in the dual mechanisms framework (Braver, 2012; Braver, Gray, & Burgess, 2007): "The proactive control mode can be conceptualized as a form of 'early selection' in which goal-relevant information is actively maintained in a sustained manner, before the occurrence of cognitively demanding events, to optimally bias attention, perception and action systems in a goal-driven manner" (Braver, 2012, p. 106). Although this framework focuses on the temporal dynamics of cognitive control (with proactive control recruited in anticipation of the need for control, reactive control recruited as a corrective mechanism, and the balance between them dependent to some extent on context), Braver (2012) also notes that there may be stable individual differences in the tendency to adopt a proactive mode based on cognitive abilities: " … cognitive individual differences such as working memory capacity and fluid intelligence should impact the utilization of proactive control, potentially because they reflect the ease or efficacy of active goal maintenance in working memory" (p. 109). Thus, Common EF may be related to stable biases in the balance between proactive and reactive control across tasks.

5.2.4. *Processes of the supervisory attentional system*

Our proposal about the unity component in the unity/diversity framework is compatible with the conceptualizations of the multiple demand system, controlled attention, and proactive control, but what of the diversity components? Although other frameworks have fractionated EFs, the proposed components are quite different than ours, in part because they focus on different levels of analysis.

One framework that explicitly adopts diversity is that of the supervisory attention system (originally proposed by Norman & Shallice, 1986). Shallice and Burgess (1996) argued that, "even if it is appropriate to view the supervisory system as a single system, it is not correct to view it as carrying out only a single type of process. Indeed, the evidence points to the existence of a variety of processes carried out by different subsystems but operating together to have a globally integrated function" (p. 1405). They discussed eight processes involved in strategy generation, implementation, and monitoring, and argued for separability for some of these processes on the basis of dissociations and imaging studies.

Stuss and Alexander (2007), also using the supervisory attentional system as a starting point, arrived at a somewhat different fractionation. Drawing on work with frontal lobe patients, they argued for three independent supervisory functions of the frontal lobes that work together in goal-directed behavior: energization (initiating and sustaining responses, which they did not consider executive per se), task setting (setting a stimulus–response relationship and contention scheduling), and monitoring (checking performance and adjusting behavior when necessary). They localized these functions to dorsomedial, left dorsolateral, and right dorsolateral areas of frontal cortex, respectively (Stuss, 2011). Interestingly, Stuss and Alexander's (2007) framework did not have any special role for inhibition: "Apparent inhibitory processes can be explained by our triad of frontal processes" (p. 910). Their mapping of inhibitory processes to a combination of energization, task setting, and monitoring suggests that these three functions may not map onto the three components in the unity/diversity model; rather, they may be a fractionation of our Common EF factor (which is isomorphic with response inhibition; Miyake & Friedman, 2012).

Energization is perhaps the most similar to the active maintenance of goals and top-down bias that we proposed as a mechanism for Common EF in section 5.1.1. Stuss and Alexander (2007) explained the need for energization, which they likened to phasic attention and cognitive effort, as follows: "[I]n the absence of external triggers or motivational conditions to optimize responding, lower level perceptual or motor schemata would have to be energized or re-energized

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when activation becomes low, as would be required, for example, for detecting occasional stimuli or performing occasional motor acts" (p. 904). Energization has also been used as an explanation for a common deficits across multiple tasks (specifically, verbal and nonverbal fluency tasks) observed in individuals with superior medial frontal lesions (Robinson, Shallice, Bozzali, & Cipolotti, 2012).

However, task setting and monitoring may also map onto the Common EF factor. Though setting a stimulus–response relationship (task setting) should be quite important for shifting tasks, especially the types of cued tasks we use, it may also be important for inhibition tasks (e.g., in antisaccade, look left if the cue appears on the right, or in stop-signal, do not respond when the signal occurs), and updating tasks (e.g., in 2-back, a target is the same as the stimulus two trials ago). Performance checking (monitoring) is also important for avoiding errors in most EF tasks. In this sense, the Common EF factor may itself be fractionated into separable components that are closely intertwined during task performance. That is, because the tasks used in the unity/diversity framework are at a medium level of complexity, they may all involve a combination of potentially separable abilities, which together drive the correlations among tasks. More fine-grained tasks may be needed to begin to see heterogeneity in these functions at the level of lesions or individual differences (Stuss & Alexander, 2000).

6. Neural substrates

6.1. EF-related activation

The last two decades have witnessed an explosion of neuroimaging studies of EFs in healthy populations that have further informed unity and diversity models of EFs. On the one hand, a consistent set of frontal and parietal regions dubbed the "multiple demand system" (Duncan, 2010; including areas around the inferior frontal sulcus, insula/frontal operculum, pre-supplementary motor area and dorsal anterior cingulate, and intraparietal sulcus) are implicated across diverse complex tasks (Duncan & Owen, 2000; Fedorenko et al., 2013). Individual studies and meta-analyses that incorporate one or more domains of EF support the conclusion that this multiple-demand system is generally active across different tasks, including tasks thought to tap inhibiting, updating, or shifting abilities (Collette et al., 2005; Derrfuss, Brass, & Yves von Cramon, 2004; Nee et al., 2013; Niendam et al., 2012; Sylvester et al., 2003). On the other hand, these same studies indicate that there are also distinct areas associated with particular EFs (see also meta-analyses of particular EFs: Kim, Cilles, Johnson, & Gold, 2011; Nee, Wager, & Jonides, 2007; Owen, McMillan, Laird, & Bullmore, 2005; Rottschy et al., 2012; Wager & Smith, 2004; Wager, Jonides, & Reading, 2004).

The wealth of neuropsychological and neuroimaging studies have led to a number of perspectives (not mutually exclusive) on the functional organization of the PFC. Some researchers have focused on ascribing a particular process to an area or areas or interest (e.g., Aron et al., 2014; Banich, 2009; Botvinick, Cohen, & Carter, 2004; Muhle-Karbe et al., 2016; Stuss & Alexander, 2007). Others have taken a broader view, positing a rostral-caudal organization or hierarchy according to complexity or abstraction, a dorsal/ventral distinction by type of information, and a medial/lateral distinction related to emotional and motivational content (Badre & D'Esposito, 2009; Christoff & Gabrieli, 2000; Courtney, 2004; Fuster, 2001; Koechlin & Summerfield, 2007; Nee et al., 2013; O'Reilly, 2010; Petrides, 2005; Smith & Jonides, 1999). Still others have emphasized distinct functional networks associated with particular processes or temporal aspects of cognitive control (Corbetta & Shulman, 2002; Dosenbach, Fair, Cohen, Schlaggar, & Petersen, 2008; Hampshire, Highfield, Parkin, & Owen, 2012; Power et al., 2011; Seeley et al., 2007). Although these theories have different flavors in terms of their emphasis on common *vs* specific functions and in how they cut across the range of EF tasks that have been examined, taken together, they underscore the notion of unity and diversity. Yet they also underscore that diversity may be interpreted in a number of ways.

6.2. Individual differences

Most neuroimaging studies focus on what areas are active during EF tasks, or more specifically, what areas are significantly more active in the EF-demanding condition when subtracting a baseline condition that attempts to control for non-EF demands. Such contrasts reveal which brain areas reliably activate across subjects during task performance, but they do not necessarily reveal which neural areas predict individual differences in performance.

6.2.1. Individual differences in task-related activation

A common strategy for examining neural correlates of individual differences is to focus on areas that are active at the group level. Often this strategy is successful, and the results add to our understanding of these areas' functions. For example, observations that higher activation in some areas, such as anterior cingulate, insula, and left ventrolateral PFC (Nee, Jonides, & Berman, 2007; Wager, Sylvester, et al., 2005), predicts worse performance has been interpreted to indicate that activity in those areas may not reflect control per se, but may track interference (Wager, Sylvester, et al., 2005), or selection demands (Nee, Jonides, et al., 2007), though other explanations for this pattern (e.g., neural efficiency) are also prevalent (Yarkoni & Braver, 2010).

Finding different patterns of correlations across active areas can also be informative. For example, Wager, Jonides, Smith, and Nichols (2005) found that areas that predicted individual differences in response time switch costs in one or more types of attention switching tasks were also active at the group level for the switch *vs* repeat contrasts. Because the correlations showed different directionalities (higher switch costs were associated with larger switch-related activation in dorsolateral and medial PFC and intraparietal sulcus, but lower activity in the ventromedial PFC), they concluded that the functions of dorsal and ventral regions in task switching are dissociable. Specifically, they suggested that the higher activation in dorsal areas associated with higher switch costs may reflect inefficient goal representation, and the higher ventral activation associated with lower switch costs may reflect better control.

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However, this approach of focusing on areas significant at the group level may also miss areas of importance for individual differences. On the one hand, it is not necessarily the case that such areas that are active on average play a role in individual differences. For example, Wager, Sylvester, et al. (2005) found that three tasks requiring response inhibition (a spatial Stroop task, go/no-go, and a flanker task) activated a common network of regions including anterior insula, anterior PFC, right dorsolateral PFC and premotor cortex, caudate/putamen, anterior cingulate, and parietal cortex. However, only activity in the anterior insula correlated with performance of all three tasks (though some areas predicted performance in one or two tasks).

On the other hand, there may be areas that are not significant at the group level but do predict individual differences, because areas with higher variability across subjects may not reach significance at the group level. Yarkoni and Braver (2010) pointed out that integrating group-level and individual differences effects can inform theories about the function of the areas involved, with areas that are active at the group level reflecting processes that are necessary for performing a task, and areas related to individual differences most likely reflecting processes that can be differentially recruited to boost performance (such as effort or strategy). This difference in characterization of processes can help resolve the seemingly paradoxical observations that most complex tasks activate a similar network of regions (Duncan & Owen, 2000), yet EFs show unity and diversity: " … the fact that the 'task-positive' frontoparietal network is activated during virtually all tasks involving cognitive effort likely indicates that an intact frontoparietal network is necessary to maintain a minimal level of goal-directed attention; however, this network may play little or no role in supporting many of the task-specific processes that distinguish one effortful cognitive task from another" (Yarkoni & Braver, 2010, pp. 92–93).

6.2.2. *Differences in structure and functional connectivity*

Relating individual differences in structural measures to performance outside the scanner may provide insights into the unity and diversity of EFs. Such studies also have the advantage that they can use multiple assessments to increase reliability and minimize task-specific influences, and examine more stable individual differences (Braver et al., 2010).

Smolker, Depue, Reineberg, Orr, and Banich (2014) correlated Common EF, Updating-Specific, and Shifting-Specific abilities, derived from three tasks performed outside the scanner in a separate session, with *anatomical MRI* measures. They found that better scores on the three EF components were related to reduced gray matter volume and cortical folding in different areas of PFC (ventromedial, dorsolateral, and ventrolateral to Common EF, Updating-Specific, and Shifting-Specific, respectively), and Common EF and Shifting-Specific abilities were additionally related to higher fractional anisotropy in tracts that connected their respective PFC regions with posterior and subcortical areas (see also Tamnes et al., 2010, for an analysis of cortical thickness in relation to inhibition, updating, and shifting tasks in younger subjects).

Using the same out-of-scanner measures in relation to fMRI *resting state networks*, Reineberg, Andrews-Hanna, Depue, Friedman, and Banich (2015) found that higher Common EF was related to stronger coupling of a right frontoparietal network with the cerebellum and expansion of a dorsal attention network to include frontopolar and cerebellar regions. In contrast, higher Shifting-Specific abilities were associated with expansion of a somatomotor/ventral attention network to include the left angular gyrus.

Given that these two studies examined very different measures (structural *vs* functional resting-state) in relation to individual differences, it is not surprising that they arrived at different potential localizations for the EF factors. It is possible that the structural and functional correlates of individual differences do not converge on the same areas or networks. What these studies do reveal, however, is that individual differences in structure and functional connectivity have important implications for performance of different EF tasks. They also add complexity to the interpretation of activation differences: If individuals with higher EF have expanded networks evident even when they are not performing a challenging task, then how should these differences be considered when interpreting average activation and individual differences in activation during EF tasks?

As reviewed here, many studies have examined what brain areas are involved in particular EF tasks and even across multiple EF tasks (section 6.1), and how individual differences in activation, structure, and functional connectivity relate to performance (section 6.2). However, there does not seem to be a strong consensus with respect to localization of the multiple EFs examined in the unity/diversity framework and whether the areas that are active during a task are the same ones implicated in individual differences in performance on that task (or across similar tasks). What is missing from the literature is information about how individual differences in activation across multiple tasks (tapping Inhibiting, Updating, and Shifting) relate to performance on the Common EF, Updating-Specific, and Shifting-Specific factors. That is, are there some regions or networks that individuals with high Common EF activate more or less across these diverse tasks, and are there regions or networks whose activation during updating and shifting tasks distinguish individual differences in the diversity components? We are currently running a study that will hopefully answer these questions by combining in-scanner inhibiting, updating, and shifting tasks with out-of-scanner EF latent variables.

6.3. *Lesion studies*

We began by noting that the notion of unity and diversity originally arose in the context of neuropsychological studies of frontal lobe lesions. Whereas neuroimaging studies reveal areas active during a task, lesion studies can provide information as to which areas are necessary for task performance (*vs* just correlated). To what extent do such neuropsychological studies and studies of normal individual differences agree on the cognitive structure of EFs?

Duncan et al.'s (1997) earlier use of the term "unity and diversity" (following Teuber's, 1972, review) was based on a correlational study of multiple EF tasks (Wisconsin Card Sorting Test, verbal fluency, verbal learning, and a spatial puzzle) in 90 head-injured patients. They found generally

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low correlations among these tasks, and no evidence for separability of the EF measures from other tests thought to be relatively insensitive to frontal lesions. They also did not find that the locations of damage (assessed with computerized tomography) related systematically to deficits in particular tasks. Importantly, in a follow-up study, a subset of 24 of these patients returned to complete additional tests and measures of fluid intelligence. Though Duncan et al. found a similar pattern in the correlations of the EF tests and their relations to focal lesions, they did find that an aggregate of the EF tasks correlated well with measures of fluid intelligence and goal neglect (rs = .59 and .72, respectively), and all performance measures were more related to a measure of global atrophy than to specific localizations of lesions. This pattern supported their assertion that to the extent that there is some unity in EFs, it seems to be related to goal neglect (as discussed in section 5.2.1). Beyond that, they did not observe any structure to the diversity of EFs.

In contrast, Stuss and Alexander (2007) did find structure in the diversity aspect of EFs. Specifically, they dissociated three supervisory processes based on lesion studies. As discussed in section 5.2.4, the energization (superior medial) process has a straightforward mapping to the Common EF factor, but the task setting (left dorsolateral), and monitoring (right dorsolateral) processes do not map onto the Updating-Specific and Shifting-Specific factors; rather, they may also contribute to the Common EF factor. However, of the tasks examined by Stuss and Alexander (2007), none would be classified as clearly tapping Updating or Shifting, with the possible exception of the Wisconsin Card Sorting Test (other tests included Stoop, verbal fluency, the California Verbal Learning Test, a feature integration test, and the Rotman-Baycrest Battery to Investigate Attention). Thus, although this framework suggests some fractionation of Common EF, it does not necessarily rule out additional EF components.

Tsuchida and Fellows (2013) specifically examined whether lesions in different areas of PFC would differentially impair inhibiting (Stroop color-word), updating (spatial search), and shifting (letter/number naming) tasks. They found that both inhibition and shifting were sensitive to lesions in the same left ventrolateral PFC area, whereas spatial updating was not (performance on the spatial updating task was generally impaired in the lesion group, but was not significantly associated with any particular region). With respect to the Shifting-Specific factor, it is interesting that they did not find a dissociation for the shifting and inhibition tasks; recall that the Herd et al. (2014) simulation discussed in section 5.1.2 suggested that a dissociation between Common EF and Shifting-Specific variance could occur not because the tasks relied on different neural areas, but because they were sensitive to different parameters within the same neural substrates. The finding that the updating measure was impaired by lesions in different locations than those that impaired the inhibition and shifting tasks is somewhat inconsistent with the unity/diversity framework, because we might expect all measures to be impaired by some lesions if they load on a common factor. However, they note that this dissociation could have been due to the spatial nature of the updating task; in a prior study with a letter n-back task (Tsuchida & Fellows, 2009), they found that updating was related to left lateral and medial PFC lesions. These results thus provide some evidence that left ventrolateral PFC may be related to the Common EF factor, but few clues as to what areas may be unique to the diversity factors.

Overall, it seems that the results of these lesion studies are in partial agreement with the unity/diversity framework. Specifically, they indicate that some frontal lesions result in broad impairments across multiple EFs, consistent with the Common EF factor, and there are also dissociations across tasks, consistent with diversity. However, the processes that dissociate in these lesion studies are not clearly the same as those that dissociate in studies of normal individual differences. We have focused on these particular lesion studies because they have most thoroughly investigated questions of EF dissociations with multiple lesion locations and multiple tasks. Yet, as noted, the tasks used do not always tap the diversity factors as we have measured them in the unity/diversity framework, so a clear test of convergence is difficult. Another important characteristic of these studies is that, with the exception of Duncan et al. (1997), they examined only frontal lesions. Thus, they would find little evidence for diversity if Updating-Specific and Shifting-Specific processes depend more on non-frontal regions. Indeed, we have suggested that Updating-Specific variance might relate to the precision of gating information into working memory, controlled by the basal ganglia (Miyake & Friedman, 2012).

7. Conclusion

We have highlighted how considering individual differences at the behavioral, genetic, and neural levels can add considerable insight to the investigation of the functional organization of the brain. At the same time, it can also add considerable complication, as our review of the neuroimaging (section 6.2) and lesion studies (section 6.3) has suggested. We conclude by summarizing some key points about individual differences to consider when interpreting evidence for neuropsychological dissociation:

1. EF abilities show large individual differences. Premorbid individual differences in performance are important to consider in interpreting the impact of lesions (Shallice, 1988): A patient may perform worse than nonpatients on a number of tasks, but some of those differences may have nothing to do with the lesion.
2. EF abilities show unity and diversity (section 2, especially 2.2). The extent to which tasks tap different EF components in normal individuals may help interpret patterns in patients. It is also important to note that the unity and diversity framework we have reviewed here exists at an intermediate level of complexity. Inhibiting, Updating, and Shifting likely combine in the service of more complex EFs like planning, but they also can likely be themselves broken down into more basic functions. Different levels of analysis could lead to different dissociations (sections 5.1.1 and 5.2.4). Thus, when assessing patients, tasks at a finer level of

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analysis may be necessary to narrow down what processes may be impaired.
3. Even within the same construct, individual EF tasks show low correlations due to task impurity (section 2.2). Thus, multiple measures of the same construct are necessary to obtain purer measures of the underlying EF.
4. EFs are not the same as intelligence, and some EF components differentially relate to intelligence (section 3.2.1). Thus, controlling for premorbid intelligence may be more effective for some EFs than others.
5. EFs are highly heritable at the latent level (section 4.1), but also appear to be highly polygenic (section 4.2). Thus, the use of individual candidate genes with small samples (e.g., fewer than 10,000 participants based on a typical R^2 ~.0007; Dick et al., 2015) is probably more likely to result in a false positive than a true finding.
6. The neural areas that predict individual differences in EFs may not be the same as those that are active at the group level (section 6.2). Dissociations between group-level and correlational effects may inform which areas are necessary *vs* beneficial for performance.
7. Lesion studies also show unity and diversity of EFs, though to date the structure suggested by these lesion studies does not easily map onto that found in studies of normal individual differences (section 6.3).

With respect to the question raised by this special issue –– whether a single brain model is sufficient, given recent discoveries of individual differences in connectivity –– it is important to point out that most models of individual differences do assume a single model, but allow variations in some of its parameters. For example, the unity/diversity model assumes that all people have the same EF processes, which are supported by multiple brain regions (Fig. 3). However, individuals have different levels or profiles of abilities, leading to the observed pattern of correlations. Those differences arise due to different "model parameters," such as higher signal to noise in the PFC, or stronger connections between the PFC and posterior regions in Fig. 3 (section 5.1.2). Thus, rather than being a challenge to a single brain model, individual differences (in performance, brain activation, connectivity, volume, etc.) serve as a window through which to view the underlying functional organization of executive control.

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