

How the Brain Creates Unity and Diversity of Executive Functions

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Abstract

Different executive functions, such as response inhibition, working memory updating, and mental set shifting, are correlated but separable. The focus of this chapter is the neural substrates of this “unity and diversity,” with particular reference to the “multiple demand” (MD) system, a set of well-localized frontal, parietal, and posterior temporal brain regions that are active in tasks with diverse cognitive demands. After evidence for unity and diversity in behavioral studies is reviewed, the anatomy and function of the MD system is described and its potential mapping to unity and diversity discussed. Unity is evident in strong patterns of activation in core MD regions across tasks with different demands. Diversity is evident in differential activation of adjacent, more domain-specific regions, with strongest activation sometimes at the boundary between the MD core and these adjacent regions, suggesting communication between the two. It is suggested that the MD core serves to combine information from many brain regions and networks, integrating the diverse contents of an attended cognitive operation. Overlaps of the MD system and executive function unity with general cognitive ability are discussed, as are difficulties in integrating studies focusing on group-mean contrasts with individual-differences results. Understanding how behavior arises from the brain will involve understanding how information is represented, communicated, and transformed within and between brain networks, with the MD system likely contributing a core, integrative role.

Introduction

The terms executive functions and cognitive control generally refer to the cognitive processes used to regulate thoughts and action in the course of goal-directed behavior (Friedman and Miyake 2017; Friedman and Robbins 2022). Although these processes involve a large network of frontal,

parietal, and other regions, they are often called “frontal lobe” functions due to their notable impairment after frontal lobe damage. Commonly examined executive functions include, but are not limited to, response inhibition, interference control, working memory updating, and mental set shifting. The relationships among these functions have been described by several researchers with the phrase “unity and diversity” (Duncan et al. 1997; Miyake et al. 2000; Teuber 1972): Executive functions are correlated with one another (show some unity), but those correlations are often only moderate, indicating that particular executive functions have unique variance (diversity). Here we discuss the neural substrates of this unity and diversity, with particular reference to the “multiple demand” (MD) system, a set of well-localized brain regions that are active in tasks with diverse cognitive demands (Duncan 2010).

Unity and Diversity of Executive Functions

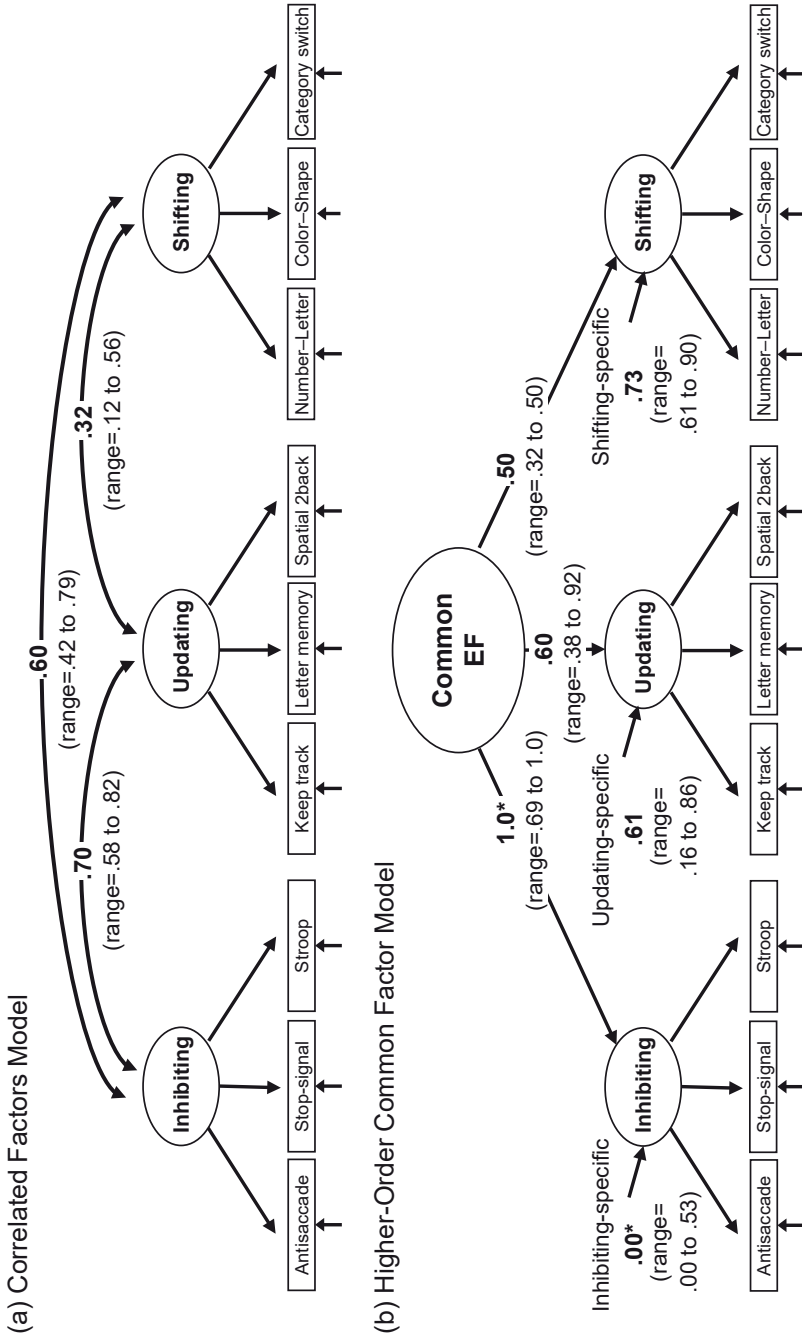
Teuber (1972) first used the term “unity and diversity” to capture a “bewildering variety” (p. 637) of behaviors observed after frontal lobe damage, which shared elements of “compulsiveness” or “abnormally stimulus-bound behavior” (p. 640). Duncan et al. (1997) echoed this “unity and diversity” phrase in their study of deficits after frontal lobe injuries, noting that despite low correlations among scores on so-called frontal lobe tests, these tests shared a common element of goal neglect and association with general fluid ability. Later, Miyake et al. (2000) invoked this “unity and diversity” phrase once again to describe the pattern of correlations among executive functions and so-called frontal lobe tasks in neurologically intact young adults: Using confirmatory factor analysis, they found evidence for separable factors of response inhibition (Inhibiting), working memory updating (Updating), and mental set shifting (Shifting) tasks (i.e., diversity), yet there were also moderate correlations between these factors (i.e., unity), as shown in Figure 9.1a. This figure also shows the range of correlations observed across subsequent studies (reviewed by Friedman and Robbins 2022).

Although the model examined by Miyake et al. (2000) is sometimes called the “three-factor model” of executive functions by others, the focus on these three functions was purely practical (only so many latent factors can be assessed in one study) and was not intended to imply that these three functions are the only executive functions that exist or are necessarily “core” executive functions (Friedman and Miyake 2017; Miyake et al. 2000). Indeed, Miyake et al. (2000:90) noted that “although our choice of the three target functions in this study seemed a reasonable one, it is certainly not exhaustive and there are other important relatively basic functions that need to be added to the current list.” Subsequent research has examined how other

executive functions (e.g., dual tasking, verbal fluency, verbal and spatial working memory capacity, interference control) relate to these three functions (for further discussion, see Friedman and Miyake 2017). In addition, Miyake et al. discussed the possibility that there might be more complex functions (e.g., planning, problem solving) which draw on these three functions, as well as the possibility that these three functions might “be decomposed into more basic component processes” (Miyake et al. 2000:90), such as the monitoring, energizing, inhibiting, and adjustment of contention scheduling processes proposed by Stuss et al. (1995). Nevertheless, as the most widely studied executive functions, the three examined by Miyake et al. (2000) are a useful set with which to consider the key question of whether executive functioning is a unitary construct.

In Figure 9.1a, unity and diversity live in the correlations between the factors, specifically in the magnitudes of these correlations (the fact that they are greater than zero, but less than one). Alternative model parameterizations can be used to capture unity and diversity with latent factors. The statistically equivalent hierarchical model shown in Figure 9.1b illustrates that these correlations can be described with a higher-order “Common Executive Function (EF)” factor, which does not explain all the variance in updating or shifting abilities. Hence, in this model, unity is captured by the Common EF factor, and diversity is evident in the residual variances for the Updating and Shifting factors. The lack of significant residual variance for Inhibiting in several independent samples using similar batteries of EF tasks indicates that the Common EF factor captures all of the covariance among the response inhibition/interference control tasks (Friedman and Miyake 2017). It is important to note that this lack of Inhibiting-specific variance does not mean that there is no Inhibiting factor, just that individual differences in the Inhibiting factor are closely related to what is shared across many EFs.

More recently, Miyake and colleagues have used an alternative “bifactor” or “nested factor” model to capture EF unity and diversity in latent factors, rather than in their intercorrelations (Friedman and Miyake 2017). As shown in Figure 9.1c, the bifactor model has a Common EF factor that predicts all executive tasks directly, and orthogonal Updating-specific and Shifting-specific factors that capture remaining correlations among the updating and shifting tasks after the variance captured by the common factor is removed. Although the models shown in Figure 9.1 look a bit different, they all capture the data well; rather than being pitted against each other, they should be considered as complementary ways of carving up the variance among EF tasks. For example, Friedman et al. (2008) adopted the bifactor model because it enabled them to examine how other variables (such as speed and intelligence) relate to the EF unity and diversity factors directly, whereas the correlations of these other variables with the correlated factors shown in Figure 9.1a could reflect



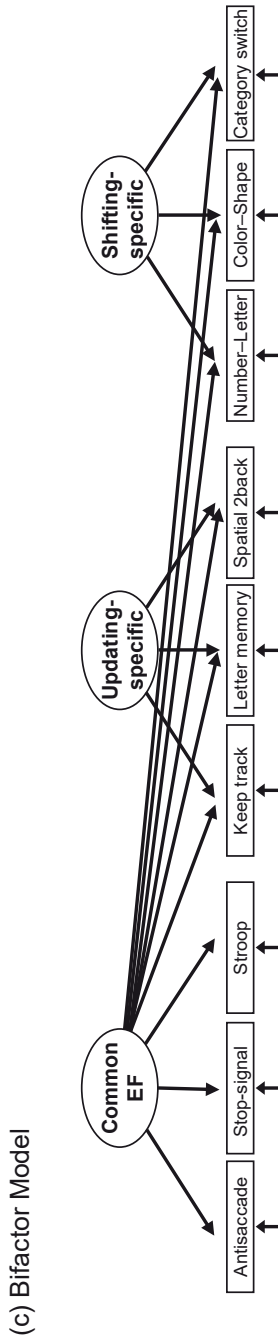


Figure 9.1 Latent variable models of three executive functions (EFs). Latent variables are depicted with ovals, whereas the nine observed tasks that define them are depicted with rectangles. Single-headed arrows indicate factor loadings and double-headed arrows indicate correlations (numbers shown are average correlation estimates from six studies using a similar battery, $N_s = 137-786$). (a) In the correlated factors model, unity is represented by the fact that the correlations among the factors are greater than zero, and diversity is represented by the fact that the correlations are less than one. (b) In the higher-order common factor model, unity is captured by a higher-order Common EF factor that predicts the lower-order Inhibiting, Updating, and Shifting factors; diversity is captured by the significant Updating and Shifting residual (specific) variances. (c) In the bifactor model, unity is captured with a Common EF factor that directly predicts all nine tasks; diversity is captured by orthogonal Updating- and Shifting-specific factors, which capture remaining variance in the Updating and Shifting tasks, respectively, once Common EF variance is removed.

correlations with unity variance, diversity variance, or a combination of both unity and diversity variance.¹

This general pattern of unity and diversity has been observed in numerous studies of individuals at different ages (Friedman and Miyake 2017), although specific patterns (e.g., which functions have been examined and how strongly they correlate) vary from study to study (Karr et al. 2018). This general unity and diversity pattern has also been observed at different levels of analysis (e.g., at genetic and environmental levels). For example, twin studies suggest that unity and diversity are due to common and specific genetic and sometimes environmental influences on different EFs (Engelhardt et al. 2015; Freis et al. 2022; Friedman et al. 2016, 2020; Gustavson et al. 2018, 2022). That is, the Common EF factor shows both genetic and environmental influences that are shared by all the executive function tasks examined in these studies, but there also appear to be different sets of genetic and environmental influences (i.e., reflecting different genes and environments than those that influence Common EF) that only affect the Updating- and Shifting-specific factors. Taken together, a wealth of evidence suggests that EFs can be distinguished but also share something in common, prompting the search for cognitive mechanisms and neural correlates that underlie this pattern.

With respect to cognitive mechanisms, the Common EF component is hypothesized to capture the ability to form, actively maintain, and use goals to bias ongoing processing (Friedman and Miyake 2017), consistent with classic models of cognitive control and frontal lobe function (Duncan 1986; Luria 1966a; Miller and Cohen 2001; Norman and Shallice 1986). In laboratory experiments, goals are set by experimental instructions. In the real world, candidates for goals must be derived by working forward from the current state (including stimulus input), suggesting goals that are currently achievable, and working backward from active overarching goals to suggest subgoals that are desirable. Candidates must then be weighted by some measure of importance, allowing one to be selected (Duncan 1990). This broad characterization of Common EF shares many similarities with other models of executive function/cognitive control (for a review, see Friedman and Miyake 2017). The mechanisms underlying diversity are less investigated. The variance specific to the Updating factor might reflect processes related to working memory gating,

¹ For example, Friedman et al. (2008) reported that intelligence correlated .53, .70, and .19 with the Inhibiting, Updating, and Shifting factors shown in Figure 9.1a, but it is not clear from those correlations to what extent intelligence correlated with the Common EF factor and whether the nominally higher correlation with Updating could be attributed to a correlation between intelligence and the variance unique to updating abilities. Those questions are answered in the same dataset by examining the correlations of intelligence with the bifactor parameterization shown in Figure 9.1c, which were .50 ($p < .001$), .47 ($p < .001$), and $-.17$ ($p > .05$) with the Common EF, Updating-specific, and Shifting-specific factors, respectively. These correlations reveal that intelligence showed a higher correlation with the Updating factor in Figure 9.1a because it was correlated approximately equally with both the Common EF and the Updating-specific variance in Updating.

perhaps enabled by updating signals from the basal ganglia to the prefrontal cortex (Chatham et al. 2011), as well as item maintenance and potentially episodic retrieval (Friedman and Miyake 2017). These mechanisms include processes that are more general to working memory, as opposed to specifically related to the updating process. Although the Updating factor is so named because it is based on tasks that all involve continuous updating (e.g., the *n*-back task), the dependent measures do not subtract conditions that require working memory but no updating. Therefore, this factor necessarily reflects individual differences in working memory capacity as well as updating. Indeed, individual differences as measured by this Updating factor are closely related to those tapped by a working memory capacity factor based on complex span tasks (Schmiedek et al. 2009). Finally, according to one model, the variance specific to the Shifting factor may relate to differences in persistence of no-longer-relevant goal representations, which could be linked to multiple sources including local GABAergic inhibition within cortical regions (Herd et al. 2014).

Although EF unity and diversity at the behavioral level was discovered in conjunction with neuropsychological studies of brain damage, its neural substrates have remained unclear—or, rather, the substrates of diversity remain unclear. With respect to unity, brain imaging studies robustly show that different EF tasks recruit a similar network of frontal, parietal, and sometimes posterior temporal areas (Collette et al. 2005; Fedorenko et al. 2013; Niendam et al. 2012). This network has been dubbed the MD system due to its response during a wide variety of demanding cognitive tasks (Duncan 2010).

The Multiple Demand System: Anatomy and Function

This common pattern of brain activity associated with diverse cognitive demands has been known since the early days of brain imaging (Duncan 2006; Duncan and Owen 2000). A state-of-the-art version of this MD pattern is shown in Figure 9.2a, on inflated views of lateral and medial cortical surfaces (left) as well as on a cortical flatmap (right). To obtain this version, Assem et al. (2020) used data from 449 participants in the Human Connectome Project (HCP), averaging activations across three different demands (working memory, reasoning, arithmetic processing). The MD pattern consists of nine distinct patches in each hemisphere, widely distributed across lateral frontal (regions 1–4), insular (5), dorsomedial frontal (6), lateral and medial parietal (7, 8) and posterior temporal (9) cortex. Dividing these nine patches at a finer scale, using the cortical parcellation of Glasser et al. (2016a), Assem et al. (2020) identified a set of 27 individual MD regions, defined by the conjunction of significant activation for all three contrasts. Core MD regions, defined by the strongest common activity, are individually shown and labeled in Figure 9.2b (bright green), with additional MD regions (“penumbra”) in darker green. At the higher resolution afforded by HCP methods (Glasser et al. 2016b), the MD

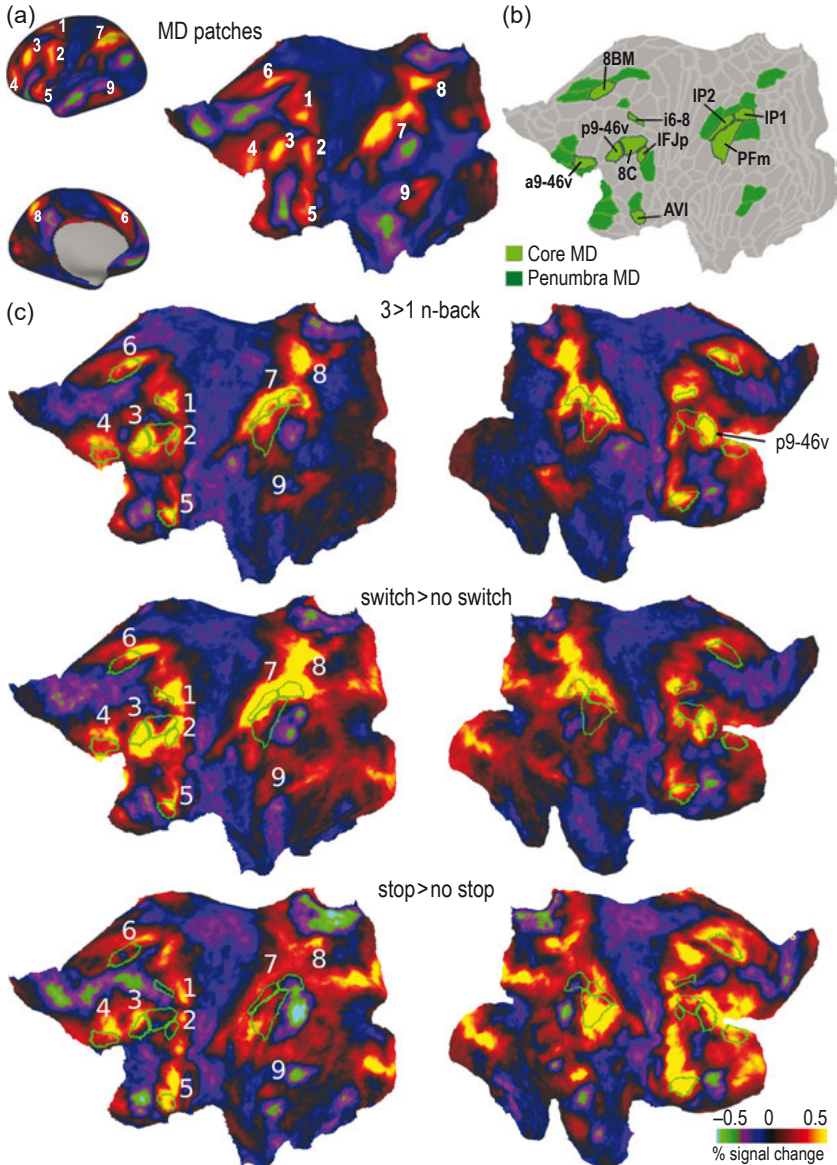


Figure 9.2 Multiple demand (MD) pattern. (a) MD regions from Assem et al. (2020) shown on inflated brain (left) and cortical flatmap (right). MD activity was largely symmetrical in the two hemispheres; just left hemisphere data are shown. Numbers indicate the nine individual MD patches identified in each hemisphere. (b) Fine-scale MD parcels from the Glasser et al. (2016a) parcellation. Bright green indicates the core; dark green, the penumbra. (c) Activations for three executive contrasts in Assem et al. (2024). Results for each contrast are shown on cortical flatmaps, with core MD regions from Assem et al. (2020) marked in green.

system identified here strongly resembles previous versions (e.g., Fedorenko et al. 2013; Niendam et al. 2012). Noteworthy is the tight definition of each patch: On the lateral frontal surface, for example, MD patches are immediately adjacent to patches with quite different functional properties, such as involvement in language (Fedorenko et al. 2013) or preferential response to visual versus auditory stimuli (Assem et al. 2022).

The suggestion of “unity” in these findings is obvious, but what of the “diversity” of EFs? Figure 9.2c shows results from a recent follow-up study (Assem et al. 2024), again using HCP methods on a new group of 37 participants. To examine the unity-diversity framework, the study used three contrasts: one for updating (3- vs. 1-back working memory), one for switching (blocks with or without cued task switches), and one for inhibition (blocks with or without stop signals). Figure 9.2c shows results for each contrast, again on cortical flatmaps, with core MD regions from Assem et al. (2020) marked in green.

On one hand, results show unity, with much the same nine MD patches visible in each contrast and each hemisphere. In individual participants, many individual surface vertices showed significant activation for all three contrasts. On the other hand, there is diversity, with the detailed pattern of activity for each contrast different from the other two. With the high-quality data obtained using HCP methods, many of these differences were significant. At the coarse level, for example, switch activations were stronger in the left hemisphere than the right (see also Crone et al. 2006; Tsumura et al. 2021), whereas stop activations were stronger on the right (see, e.g., Apšvalka et al. 2022; Aron and Poldrack 2006).

Many differences can also be seen at a much finer level; for example, in core region p9-46v, activation was most dorsal for stop, firmly within this region for *n*-back, and spreading more ventral for switch, whereas around the core MD regions of lateral parietal cortex, activation was most anterior/ventral for stop, especially visible in the right hemisphere, intermediate for *n*-back, and most posterior/dorsal for switch. In part, these shifts relate to additional networks preferentially involved in each contrast. To make this point, Assem et al. (2024) used networks defined by Ji et al. (2019) using HCP resting-state data. Of the 27 MD regions from Assem et al. (2020), the ten core MD regions all belonged to the Ji et al. (2019) frontoparietal control network, while penumbra regions were distributed between frontoparietal control and several other networks. In their EF data, Assem et al. (2024) found differences between the three contrasts in several of the original penumbra regions, plus others in their associated networks. Stop, for example, preferentially activated the cingulo-opercular network, and even in core MD regions, activations shifted somewhat in the direction of adjacent cingulo-opercular regions. Switch preferentially activated the dorsal attention network, and even in core MD regions, activations were somewhat shifted in the direction of adjacent dorsal attention regions. Such shifts were unique for each contrast, different from a simple expansion

or contraction of the activated region. Often activation was strongest at the border of core MD and adjacent regions. A reasonable interpretation is that each type of executive control involves activation at the point of communication between core MD and adjacent networks, including those contributing to MD penumbra.

Core MD regions have strong functional connectivity with each other (Assem et al. 2020), and multivoxel pattern analysis shows extensive MD coding of task stimuli, rules, and responses (Woolgar et al. 2016). Widespread coding of task-relevant content is also well known in potential macaque homologues of human MD regions, including regions of lateral frontal and inferior parietal cortex (Goodwin et al. 2012; Miller and Cohen 2001). These properties suggest a potential function for the MD system with its multiple, strongly interacting parts. For any cognitive operation, multiple components (e.g., stimuli, rules, responses, context) must be integrated into a computational structure that reflects their required roles and relationships and allows the operation to be executed. A simple example would be integrating the parts of an attended object, and the actions directed toward it, but a similar integration is required for components of any cognitive operation. With parts widely distributed through the cortex, strongly interconnected with one another, the core MD system is well placed to take in and integrate representations of many kinds and flexibly feed out the results for selective cognitive control. Duncan et al. (2020) call this process “attentional integration,” suggesting that the combined elements of a current cognitive operation correspond to the momentary contents of “attention.”

This proposal fits well with the unity-diversity findings outlined above. As local communication is strong in the cortex, different kinds of cognitive content will enter the core MD system through different routes, perhaps reflected in coactivation of other adjacent networks, including penumbra regions, and strong activation at borders. Wherever information enters the core MD system, however, strong functional connectivity allows information to be widely distributed throughout this system, in turn giving local access to many potential outputs. On this view, core MD regions play a central role in integrating the components of any cognitive operation, explaining activation in tasks of many different kinds and bringing an element of unity to cognitive control. Regions of the network differ, however, in the information to which they have the most immediate local access, perhaps reflected in the relative functional preferences shown by different MD regions (Figure 9.2c) (Assem et al. 2020). As core MD regions exchange information so freely, clear functional dissociations will be hard to discern in the slow fMRI signal. At the same time, this interaction of core MD regions with different, more domain-specific regions brings an element of diversity to different executive tasks.

In Figure 9.2c, unity and diversity are illustrated with three canonical executive tasks from the unity-diversity framework, but on the above interpretation, the MD core brings together the diverse components of any task.

Are there a relatively small number of separate patterns of MD recruitment, reflecting a relatively restricted set of core EFs, or is every task likely to have its own, unique pattern of activity? With the high resolution of HCP methods, we are now in a position to examine exact patterns of MD activity for tasks of many different kinds, dependent on different combinations of cortical networks and regions.

Common EF Versus Spearman's *g*

The issue of whether there is a restricted number of separate patterns of MD recruitment, reflecting a core number of EFs, raises another question: Is there a restricted set of functions that we might call “executive,” or does any task require its specific content to be drawn together, giving it an element of all integration reflected in its unique pattern of MD recruitment? While the Common EF factor is defined from a test battery including just inhibition, updating, and shifting tasks, there is some similarity to the concept of general intelligence or Spearman's *g*. In any broad cognitive test battery, correlations tend to be universally positive. To explain this result, Spearman proposed that some *g* factor contributes to success in all kinds of mental activities. If this explanation is correct, a measurement of *g* can be obtained as the first principal component extracted from the task battery, explaining the largest amount of shared variance between all the tasks it contains. This similarity naturally raises the question of whether Common EF is just a recapitulation of *g*; that is, a common element that contributes to success in all manner of tasks, including but not restricted to those commonly called “executive,” and perhaps closely linked to the attentional integration functions of the MD system.

Certainly, the common element extracted for a typical executive battery (Common EF) is not identical to the *g* extracted from a typical IQ test battery. For example, Friedman et al. (2011) examined how the models shown in Figure 9.1 related to full-scale intelligence scores based on eleven subtests of the Weschler Adult Intelligence Scale III; Friedman et al. (2008) found similar results when examining a latent *g* factor for the eleven IQ subtests using an earlier subset of the same dataset. Using the bifactor parameterization shown in Figure 9.1c, IQ correlated .51, .49, and $-.24$ with the Common EF, Updating-, and Shifting-specific factors, respectively (Friedman et al. 2011). These correlations could not be constrained to 1, suggesting separability of IQ and Common EF. Moreover, the genetic correlations of IQ with the Common EF ($r_G = .57$) and Updating-specific ($r_G = .56$) factors were also only moderate, indicating that IQ and Common EF share some overlapping genetic influences; they are, however, not equivalent even at the genetic level (see also Gustavson et al. 2022).

Similar results have been obtained in other twin studies using different EF batteries and different aged samples. In a sample of middle-aged male twins,

Gustavson et al. (2018) found that a Common EF factor based on neuropsychological tests genetically correlated ($r_G = .59$) with the Armed Forces Qualifying Test, a measure of g , as did a Working Memory-specific factor ($r_G = .24$). Interestingly, studies of younger twin samples have found higher genetic correlations between Common EF factors and IQ or g (Engelhardt et al. 2016; Freis et al. 2022), raising the possibility that the association between Common EF and g may be stronger at younger ages; there is also some evidence that executive functions show more unity at younger ages (e.g., Brydges et al. 2012).

Neuroimaging studies also suggest a stronger association of IQ with updating ability compared to inhibition and shifting abilities. Specifically, a recent meta-analytic analysis of fMRI and PET data (Santarnecchi et al. 2021) suggested that an activation map for fluid intelligence overlapped 80% with a map of activation for updating tasks, but only 34% and 17% with maps for inhibition and shifting tasks, respectively.

Further evidence for this genetic separability of IQ and Common EF comes from a recent genome-wide association study of a Common EF factor estimated in the middle-aged UK Biobank sample (Hatoum et al. 2023). Common EF and IQ were genetically separable ($r_G = .74$); moreover, the two constructs showed discriminant validity in their associations with other measures, with Common EF more strongly associated genetically with psychopathology factors compared to and controlling for IQ, but IQ more strongly associated genetically with educational attainment compared to and controlling for Common EF.

Several scenarios would be consistent with the observation that IQ is correlated with Common EF but not perfectly so, and that Common EF and IQ sometimes show different patterns of associations with outcomes like psychopathology and educational attainment. A common interpretation of a less than perfect correlation between two factors is that each factor captures some unique variance: In this case, it may be that Common EF and IQ both capture the same cognitive function(s), but that each also captures some cognitive function(s) that the other does not. A less than perfect correlation between two factors can also arise when one factor captures some unique variance in addition to the variance captured by the second factor, but the second factor does not capture anything unique from the first factor. Thus, it might be that Common EF captures something extra that is not captured by g , or that g captures something extra that is not captured by Common EF. The latter possibility is consistent with the findings that measures of IQ are related to both the Common EF and Updating-specific factors. That is, g seems to capture both Common EF and Updating-specific ability and may capture other abilities as well.²

² Friedman et al. (2008) found that the correlation ($r = .70$) of WAIS IQ with the full Updating factor (which does not separate Updating-specific variance from Common EF variance) was significantly lower than 1, suggesting that individual differences in IQ are not fully explained by working memory Updating.

Results might also depend on the task batteries that have been used to extract Common EF and *g* factors. In general, a common factor extracted from any set of tasks, explaining the most shared variance between them, varies from quite specific to quite general, depending on the breadth of the task battery. If the battery contains only verbal working memory tasks, for instance, then its first principal component will reflect specific strengths in verbal working memory. If batteries are very broad, their first principal component corresponds to a measure of *g*, and with enough breadth, the content of the individual battery ceases to affect the result. Thus, future studies could target this question with broader EF task batteries. What would happen if, in addition to inhibition, updating and shifting, an executive test battery was extended to include a wide range of other, putatively “executive” functions? If the first principal component resembled the Common EF extracted for just inhibition, updating, and shifting, this would be strong evidence that executive functions are indeed a natural kind, with a shared element not also common to non-executive tasks. If instead this first principal component resembled any other measure of *g*, the implication would be that EFs share little that is not also shared by any kind of task. In this case, the Common EF extracted from a more restricted executive battery would in part reflect the specific content of the particular executive tasks employed.

We also note that the universal positive correlations that underlie *g* may not be entirely explained by a single common element, such as a common cognitive or brain function, shared by all tests. One alternative is the idea of mutualism: Through development, acquisition of one cognitive strength (e.g., reading) promotes development of others, producing a pattern of universal positive correlations but no real *g* or shared brain function (Kievit et al. 2017). Another possibility is that positive correlations reflect process overlap, with many different overlaps underlying different correlations (Kovacs and Conway 2016). It may be that the cognitive process(es) captured by a Common EF factor or an Updating/Working Memory factor—as opposed to those captured by a broader *g* factor—are most closely related to a specific aspect of cognitive/brain function.

Returning to neural substrates, there is evidence relating both Common EF and Spearman’s *g* to the MD system. In line with the results in Figure 9.2, meta-analyses of fMRI studies examining inhibition, updating, and shifting tasks all produce similar findings, with a strong MD pattern (e.g., Niendam et al. 2012). The same is true of fMRI studies that employ standard problem-solving tests, often termed tests of fluid intelligence, and widely used to measure *g* (Mitchell et al. 2023). In addition, some evidence shows that after brain damage, fluid intelligence deficits are predicted by volume of damage to the MD system (Barbey et al. 2012; Woolgar et al. 2010; but see Cipolotti et al. 2023). Given the strong relationship of IQ to EF, this neural overlap is not surprising. However, this overlap does not necessarily suggest that *g* and Common EF are equivalent; we still do not know whether the Common EF

factor measures something more constrained than a broader *g* contributing to a wider range of tasks.

In the above studies, it is striking that *g* is often more related to Updating than to Inhibition and Shifting. Outside research specifically aimed at EFs, the tests with the highest *g* loadings tend to be complex reasoning tasks, such as Raven's Progressive Matrices, as well as measures of vocabulary. Duncan et al. (2020) argued that problem-solving tests, such as matrices, put an especially strong load on attentional integration and the MD system. Typically, such tasks are solved in a series of component steps, each requiring a new set of fragments to be assembled into the right cognitive operation. Attentional integration might also be important for building crystallized knowledge like vocabulary (e.g., to learn the meanings of unfamiliar words based on context). At the same time, a long history of research has linked performance on these tasks to individual differences in working memory, particularly the "central executive" or "controlled attention" component of working memory (e.g., Carpenter et al. 1990; Engle et al. 1999; Kyllonen and Christal 1990). There is much overlap between the concepts of attentional integration and working memory, particularly those aspects of working memory that go beyond simple storage capacity. Specifically, working memory tasks that require individuals to process and/or mentally manipulate information (e.g., to rearrange a list of items in order of size), in addition to remembering items, show stronger relationships with intelligence and reasoning tasks compared to tasks that only require individuals to remember a list of items (e.g., Engle et al 1999). Similarly, in line with the proposal of Friedman and Miyake (2017), there is much in common between the idea of attentional integration and the ability to form, maintain, and use a current goal. These overlapping concepts of Common EF, executive working memory, and attentional integration provide some explanation for the shared variance tapped by *g*, but the data suggest that they do not fully explain *g*. As we indicated above, *g* is likely to reflect sources of shared variance across tasks additional to any one shared cognitive function or brain system. While the attentional integration functions of the MD system may be linked to both Common EF and *g*, there is quite likely no simple one-to-one correspondence.

Linking Cognition to Brain: Methods and Levels

Our characterization of EFs here has relied on two quite different methodological approaches. Evidence for behavioral unity and diversity of EFs was based on analyses of individual differences in performance, whereas evidence for the MD system was based on analyses of group-mean activations for imaging tasks. We have attempted to link these two lines of research yet acknowledge that there is no necessary correspondence between brain regions or functions and factors derived from individual-differences studies. For example, individual differences could be heavily influenced by genetic or developmental factors that are common to several or even all brain regions, leading to

behavioral correlations with no link to specific cognitive functions or brain regions. Alternatively, as noted above, correlations in individual-differences data could reflect factors, such as mutualism, not captured in imaging data.

In general, different methods and levels of analysis produce different links of behavior to brain, making it challenging to integrate across these levels. In particular, studies that focus on which brain areas are active during EF tasks versus those looking for brain areas associated with individual differences in performance yield different results. For example, in a large fMRI study ($N=546$) with a design similar to that used by Assem et al. (2024), Reineberg et al. (2022) evaluated how individual differences in Common EF scores (based on six EF tasks) were associated with brain activity in three tasks selected to tap response inhibition, working memory updating, and mental set shifting. At the group-mean level, all three tasks robustly activated the MD system. However, individual differences in Common EF were not uniformly related to the degree of MD activation in each task, nor even to the degree of activation in the same areas outside the MD system across tasks. Only when the constraint that Common EF be related in the same direction (e.g., to greater activation) across the three tasks was discarded were there significant areas of conjunction, which included the bilateral middle frontal gyrus, medial superior frontal gyrus, left angular/superior parietal cortex, and cerebellum. Some of these areas are similar to some MD regions identified by Assem et al. (2024) but Reineberg et al. (2022) noted that these areas were also all at the anatomical borders between major functional networks. They concluded that their results were inconsistent with simple models in which EF performance is associated with higher or lower MD activation across tasks. They suggested, however, that the results could be consistent with a model in which performance is related to the activation of task-specific targets of executive control. Reineberg et al. (2022) also found some evidence that individual differences in Common EF were related to task-based connectivity of lateral PFC to these task-specific targets, which they interpreted as reflecting prefrontal biasing toward task-relevant information; however, these connectivity results were considered “preliminary” as they did not survive whole-brain correction for multiple testing.

Results such as these suggest that the brain regions that show mean activation differences in executively demanding conditions, compared to less demanding conditions across participants, do not necessarily predict individual differences in performance. Several factors might contribute to this null finding. Individual differences could be related to activation of different task-specific areas that are the targets of control. For example, in the Stroop task, individuals who show higher activation in brain regions associated with color representations, when the task is to ignore words and name the colors in which they are printed, might perform better on the task than those who show lower activation of these regions. Such activations may not simply be related to the activation levels of the control regions across individuals. In addition,

even if a cognitive activity depends on some specific brain system X, it is far from clear whether individuals with stronger function should show more or less activity in X. One plausible scenario is that in each individual, the link of activity to demand follows an inverted U, initially increasing as demand goes up, then declining once the task appears impossible (Mattay et al. 2006). For relatively low demand, activation of X may be stronger in the low-ability individual, reflecting a greater struggle to satisfy task demands. For higher demands, activation is already declining for the low-ability individual, whereas for the higher-ability person, this downturn has yet to be reached. Such explanations could also account for small effect sizes in brain associations more generally (Marek et al. 2022), although many other factors could also explain small effect sizes (e.g., low reliability of measures and brain activation, and distributed associations across networks rather than specific associations with particular regions).

Similarly, the view of a “multiple demand” system will vary depending on the level of analysis. At the level of univariate fMRI, even in single participants, there is strong evidence for similar MD activity across many cognitive demands. A region of univariate activity, however, is made up of many millions of neurons, and it cannot be that each neuron responds similarly to all these demands. Neurons contribute to information processing to the extent that they respond differently to different things. Correspondingly, in any one individual, higher-resolution methods (e.g., multivoxel pattern analysis) reveal that MD regions carry information about many kinds of task content, such as discriminating a task’s stimuli, rules, and responses; exact patterns of neural recruitment differ for different task events (Woolgar et al. 2016). The same, of course, follows from single neuron recordings in potential monkey homologues of MD regions, with neurons showing a very large number of different, idiosyncratic patterns of selective activity (Miller and Cohen 2001). A “multiple demand” region of cortex in fMRI suggests a body of neurons that are differentiated and have the flexibility to carry information of many different kinds in different task contexts (Rigotti et al. 2010), integrating the components of each individual cognitive operation.

Conclusions and Future Directions: Beyond Classical Functional Localization

In this chapter, we have reviewed evidence for unity and diversity of EFs at a behavioral level in an attempt to understand how unity and diversity emerges from neural activity during various tasks. Two key take-home points are as follows: First, EFs show unity and diversity at the level of individual differences in task performance. This unity and diversity is most clearly seen with latent variable models of multiple executive functions, which show that multiple executive function factors are correlated (show unity, captured with a Common

EF factor) but are also separable (show diversity, captured with factors such as Updating-specific and Shifting-specific factors). Second, when people complete different EF tasks and cognitive tasks more generally, they activate a similar network of frontal, parietal, and posterior temporal regions (the MD system). We characterized the spatial distribution of MD activation across EF tasks and discussed differences in patterns across tasks, which might relate to the observed diversity of EFs. We also discussed a potential cognitive mechanism for the MD system, attentional integration, which could explain why this network is active across diverse cognitive tasks.

In addition to these key messages, we discussed two related questions. First, we outlined our view on whether the Common EF factor recapitulates the *g* factor or IQ, a question that has preoccupied the literature for decades. Though future analyses of different batteries of executive function tasks may be useful to consider, the current literature suggests that the Common EF factor is not equivalent to IQ. Importantly, IQ is related to individual differences in working memory capacity and updating, over and above the Common EF factor. These patterns suggest that the *g* factor/IQ may capture more cognitive processes than the Common EF factor captures. Second, we pointed out the difficulty with integrating across different methods or levels of analysis, particularly findings related to population-level effects (i.e., everyone activates the MD system during cognitively demanding tasks) as well as those related to individual differences (i.e., individuals who perform better on demanding tasks may not necessarily consistently activate the MD system more strongly or weakly than individuals who do not perform as well). We cautioned that there may be no simple mapping between brain regions or functions and factors derived from individual-differences studies and provided potential reasons for discrepancies across methods. Although we do not have an answer on how best to integrate across methods and levels, such integration is needed to produce a comprehensive view of EFs and their associated brain networks.

For more than a century, ideas of how brain function may relate to behavior have been limited by the methods available. Animal and human lesion studies as well as many early results from human brain imaging invite a link between coarse regions of the brain, perhaps “dorsolateral frontal cortex,” and some specific aspect of cognition or behavior. In this context, the “unity” element of unity and diversity has sat uneasily, in tension with the enterprise of linking specific brain regions to specific cognitive operations. We now know substantial limits to this conceptualization of the problem. Brain functions must be understood not in terms of the coarse regions that might be studied through lesions, but in terms of distributed, strongly interacting cortical and subcortical networks. We need to understand how information is represented, communicated, and transformed within and between such networks, with the MD system likely contributing a core, integrative role. Closely adjacent cortical regions can belong to different networks, with quite different patterns of

resting-state activity and functional activation. As demonstrated in Figure 9.2, functional specializations can reflect extremely fine-scale gradients of activation and between-network communication. Accordingly, the enterprise of linking brain to behavior is not a search for simple regional mappings. Instead, perhaps not surprisingly, it is a matter of asking how whole-system function is assembled from the detailed dynamics of many interacting parts.