A systematic review of the complex organization of human cognitive domains and their heritability

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Abstract

Background: Models of cognition propose a hierarchical structure for human cognitive processes, in which the sequences of human action are organized into parts or subunits of analysis that can be grouped into progressively more complex, inclusive higher-order functions. This organizational structure from partial to whole may be reflected in the neural representations that underlie human behaviour, and in its genetic underpinnings. The objective of the present study was to explore a putative hierarchical organization of the genetic influences underlying cognitive domains. **Method:** Thirty four studies of the heritability of cognition on population-based samples were reviewed, which included measures of intelligence, verbal and performance abilities, memory, working memory and processing speed. **Results:** Specific cognitive domains showed diverse proportions of genetic underpinnings such that higher-order cognitive functions present high heritability estimates, whereas lower-order functions respond to small/moderate heritability estimates. **Conclusions:** Based on current understanding of the developmental processes of the neurobiological substrates of human cognition, the genetic contributions to cognitive abilities seem to be organized in line with the ontogenic maturation of the brain. We discuss the large genetic control of the combinatory capacity of basic cognitive functions, and its interaction with environmental influences.

Keywords: Cognition, heritability, organization, hierarchy.

Resumen

Una revisión sistemática de la organización compleja de los dominios cognitivos humanos y su heredabilidad. **Antecedentes:** se ha propuesto que la estructura de la cognición humana respondería a un sistema jerárquico, donde las secuencias propias a una acción se organizarían desde sub-unidades de análisis hasta funciones de nivel superior relativamente complejas. Esta estructura organizacional estaría reflejada en las representaciones neurales que subyacen al comportamiento humano, así como también en sus sustratos genéticos. El objetivo del presente estudio fue explorar la posible organización jerárquica de las influencias genéticas subyacentes a los dominios cognitivos humanos. **Método:** se revisaron treinta y cuatro estudios de la heredabilidad de la cognición en muestras de la población general, que incluyeron medidas de inteligencia, habilidades verbales y manipulativas, memoria, memoria de trabajo y velocidad de procesamiento. **Resultados:** diversos dominios cognitivos mostraron distintas proporciones de influencias genéticas, con las mayores estimaciones de heredabilidad halladas para las funciones cognitivas de nivel superior y las menores estimaciones para las funciones de orden medio o inferior. **Conclusiones:** tomando como referencia los conocimientos actuales acerca del neurodesarrollo humano, las contribuciones genéticas de las habilidades cognitivas parecen organizarse paralelamente al crecimiento ontogénico del cerebro. Se discuten estos resultados en relación a la interacción entre el control genético de las funciones cognitivas y sus influencias ambientales.

Palabras clave: cognición, heredabilidad, organización, jerarquía.

With the advances in technology and the emergence of new statistical approaches, the last decades have witnessed outstanding scientific progress in the study of the neurobiological bases of psychological phenomena (Soderlund et al., 2006). At the molecular level, genes involved in neurotransmitters have been specifically associated with cognitive performance, and are presumed to present a regulatory activity that builds and maintains brain functioning and mind processing necessary to adapt to a changing physical and social environment (Carlier & Roubertoux, 2010).

These findings integrate to a vast research focused on the environmental influences of human cognition, while gene-environment interaction studies are showing that the nature versus nurture debate on the possible causal processes of cognitive domains may be futile (Rutter, 2007). Furthermore, and contrary to what was once assumed, ongoing research on neurogenetics shows that gene expression is not uniform across the cerebral cortex, and that the proportion of genetic determination and environmental effects regulating specific cognitive domains varies greatly (Ramus, 2006).

Psychological models of cognition propose a hierarchical structure for human cognitive processes (Carroll, 1997). This hierarchical structure organizes the sequences of human action

into parts or subunits of analysis, with the subunits being simpler elements, or of lower order, that can be grouped into progressively more complex, inclusive higher-order functions (Botvinick, 2008). In addition, the organizational structure from partial to whole in human action might be reflected in the neural representations that underlie it. For example, the prefrontal cortex has been associated with cognitive control or the ability to guide behaviour in accordance with objectives, plans and broad conceptual knowledge (Duncan, 2001). This ability seems to be organized in such a way that the rostral regions of the frontal cortex are associated with demands for control and representations that are progressively more abstract, and that it is maintained by a hierarchical organization reflected in the functioning of the brain (Badre, Hoffman, Cooney, & D'Esposito, 2009).

Such hierarchical organization according to which more complex functions require a number of subunits to process and analyse cognitive information has been proposed to reflect the genetic contributions underling these highly complex networks (Deary, Penke, & Johnson, 2010). Accordingly, the contributions of these genetic components on neurocognition may become larger as the complexity of the tasks increases from lower-order to higher-order cognitive functions (Beaujean, 2005). However, there is still not reported review systematically addressing this topic, although there seems to be a large body of information on the heritability estimates of cognitive functions.

In the present study, we explored a putative hierarchical organization of the genetic influences underlying human cognitive domains. We addressed the relative contribution of genetic and environmental factors on the variability of higher-, middle- and lower-order domains of human cognition by systematically reviewing previously published reports on the heritability of these cognitive functions. Estimations of heritability quantify the effects of genetic components on a specific trait. Assuming that genes and environment can explain the entirety of the observed (phenotypic) variability between individuals in a population, the influence of environmental factors is broadly calculated as the proportion of the variance not explained by genetic components (i.e., 1-heritability) (Plomin, DeFries, McClearn, & McGuffin, 2008).

Methods

A Pubmed search for reports on the heritability of human cognition published until October 2010 was undertaken to identify empirical studies that explored the relative proportion of genetic and environmental influences on normal cognitive variability. Various keywords and truncated terms (indicated with an asterisk) related to higher- and lower-order cognition were used, including: Cognit*, neurocog*, intel*, IQ, memory, attent*, executive function, prefrontal function, working memory, processing speed, reaction time. These terms were combined with heritab*. The searches were limited to peer-reviewed reports published in English.

A total of 285 hits were returned. Studies focused on any type of pathological process were excluded from the analysis, as did articles that dealt with exceptionally high or low cognitive performance compared to the expected normal variation in general population. Among the 85 articles that resulted from these criteria, 7 were reviews, 13 were author's comments, and 25 focused on either variables that did not concern the objective of our study (such as temperament), or studied specific genes and polymorphisms. Finally, 6 studies were excluded based

on methodological characteristics such as genetically isolated samples (1 study), very small sample sizes (1 study), and reliability of the measures (4 studies). A total of 34 studies reported clear cross-sectional data of heritability estimates in human cognitive domains of interest and were further analyzed.

In order to classify higher-, middle- and lower-order functions, we used as a reference models that have been previously put forward for human cognitive structure and functioning (Botvinick, 2008; Carroll, 1997). In keeping with this background, in the present review we use the term "lower-order" functions for those cognitive processes that are considered to be the constituent subunits of middle-order functions, which in turn are grouped into progressively more complex or "higher-order" cognitive processes.

Results

Out of the 34 empirical studies included, 9 were based on subjects between the ages of 2 and 13, while 4 reported the heritability estimates of samples ranging from 65 to 98 years old. As has been recently proposed by longitudinal studies, heritability seems to vary considerably according to age groups until prepubescent childhood, and later in older adults (Davis, Haworth, & Plomin, 2009; Finkel, Pedersen, Plomin, & McClearn, 1998; Polderman et al., 2006). Therefore, we based our review only on reports that included subjects above the age of 13, and below 66 years old. The studies, organized by the cognitive domains of interest, are reported in Table 1. Nevertheless, the available information on other age groups might broaden the understanding of these processes, and thus we included these data as complementary information among the results.

The models of cognitive organization used in the revised publications include within the broad construct of intelligence a series of functions that are also considered complex, such as memory or executive control. In the following sections we consider the nature of the genetic and environmental influences on the specific components of these constructs. Several studies assessed more than one cognitive domain; we included all the measures examined in each report among our results.

General intellectual ability

The range of heritability for measures of general intelligence varied from moderate values (66% of explained variance) in a sample of 22000 subjects (Haworth et al., 2009) to the highest estimate of 87% reported in a study that included samples from different countries (Wright et al., 2001).

As mentioned before, the range of heritability for measures of general intelligence across age groups is broad. The lowest values for intelligence (23% of explained variance) were reported in samples of twins aged between 2 and 5 years (Bartels, Rietveld, Van Baal, & Boomsma, 2002; Spinath, Ronadl, Harlaar, Price, & Plomin, 2003), followed by estimates of 62% in subjects between 7 and 10 years (Davis et al., 2009). This tendency over the early years of life continues into adolescence, as studies that include subjects between 9 to 17 years of age show a significant increase in the genetic component of intelligence: starting at 41% at age 9, increasing to 55% during prepubescent stage, and finally reaching 66% in adolescence. Results for adults over 65 tend to be more uniform, with reported values in the range of 53 to 68% (Giubilei et al., 2008; McClearn et al., 1997; Read et al., 2006).

Table 1
Cognitive domains and tests used for their assessment in reviewed studies based on adult samples

Cognitive domain	Study	Sample size	Age range	Tests used for assessment	h2 (%)
General intellectual ability	Haworth *et al*. (2009)	22000	14-34	Standarized g Scores	66
	Luciano, Smith *et al*. (2001)	780	15-18	MAB Total IQ Score	70
	Luciano, Wright *et al*. (2001)	780	15-18	MAB Total IQ Score	81
	Rijsdijk *et al*. (2002)	388	15-18	WAIS Total IQ Score	82
	Wright *et al*. (2001)	2129	15-70	*Netherlands:* WAIS Total IQ Score	87
			15-19	*Australia:* MAB Total IQ Score	85
	Finkel[…] McClearn (1995)	794	27-64	WAIS - age 27 to 49	81
				WAIS - age 50 to 64	81
	Plomin *et al*. (1994)	446	mean 64.1 (SD= 7.5)	Standarized g Scores	82
General performance ability	Alarcón *et al*. (1998)	977	12 onwards	Standardized Performance Scale Score	35
	Luciano *et al*. (2001b)	780	15-18	MAB Performance IQ Score	43
	Rijsdijk *et al*. (2002)	388	15-18	WAIS Performance IQ Score	68
	Luciano *et al*. (2005)	2010	15-65	MAB/WAIS Performance IQ Score	83
	Posthuma *et al*. (2001)	688	15-70	WAIS Performance IQ Score	69
	Posthuma *et al*. (2003)	135	mean 29.2 (SD= 7.3)	WAIS Performance IQ Score	68
Sub-components of performance ability	Finkel[…] McClearn(1995)	794	27-85	Block Design	
				age 27 to 49 American Sample	24
				age 50 to 64 American Sample	24
				age 27 to 49 Swedish Sample	51
				age 50 to 64 Swedish Sample	51
	Plomin *et al*. (1994)	446	mean 64.1 (SD= 7.5)	Blocks	52
				Card Rotations	48
				Figure Logic	37
	Rijsdijk *et al*. (2002)	388 subjects	15-18	Block design	31
				Picture Completion	8
General verbal ability	Alarcón *et al*. (1998)	977	12 onwards	Standardized General Verbal Score	26
	Luciano, Wright *et al*. (2001)	780	15-18	MAB Verbal IQ Score	55
	Rijsdijk *et al*. (2002)	388	15-18	WAIS Verbal IQ Score	84
	Luciano *et al*. (2005)	2010	15-65	MAB/WAIS Verbal IQ Score	77
	Posthuma *et al*. (2001)	688	15-70	WAIS Verbal IQ Score	85
	Posthuma *et al*. (2003)	135	mean 29.2 (SD= 7.3)	WAIS Verbal IQ Score	84
Sub-components of verbal ability	Finkel[…] McClearn (1995)	794	27-85	Information	
				age 27 to 49 American Sample	39
				age 50 to 64 American Sample	39
				age 27 to 49 Swedish Sample	33
				age 50 to 64 Swedish Sample	33
	Plomin *et al*. (1994)	446	mean 64.1 (SD= 7.5)	Information	65
				Synonyms	60
				Analogies	60
	Rijsdijk *et al*. (2002)	388	15-18	Similarities	40
				Vocabulary	52
				Information	44
				Arithmetics	53
General memory ability	Finkel[…] McGue (1995)	838	27-88	Standardized General Memory Score	
				age 27 to 49 American Sample	55
				age 50 to 64 American Sample	57
				age 27 to 49 Swedish Sample	43
				age 50 to 64 Swedish Sample	63

Cognitive domain	Study	Sample size	Age range	Tests used for assessment	h2 (%)
Sub-components of memory ability	Finkel[…] McGue(1995)	838	27-88	Logical memory immediate	
				age 27 to 49	47
				age 50 to 64	56
				Visual reproduction	
				age 27 to 49	49
				age 50 to 64	63
				Thurstone's Picture Memory	
				age 27 to 49	39
				age 50 to 64	50
				Names and Faces	
				age 27 to 49	39
				age 50 to 64	40
	Plomin *et al*. (1994)	446	mean 64.1 (SD= 7.5)	Names and Faces	42
				Thurstone Test	36
General speed of processing ability	Finkel[…] McClearn (1995)	794	27-85	*Digit symbol (WAIS)*	
				age 27 to 49 American Sample	24
				age 50 to 46 American Sample	24
				age 27 to 49 Swedish Sample	41
				age 50 to 64 Swedish Sample	41
	Plomin *et al*. (1994)	446	mean 64.1 (SD= 7.5)	Digit Symbol	68
				Figure Identification	50
	Posthuma *et al*. (2003)	135	mean 29.2 (SD= 7.3)	Digit Symbol	63
	Wright *et al*. (2001)	2129	15-19	8-choice reaction time	64
	Luciano, Wright *et al*. (2001)	780	15-18	8-choice reaction time	70
Sub-components of speed of processing ability	Posthuma *et al*. (2001)	688	15-70	Inspection time	46
	Wright *et al*. (2001)	2129	18-70	*Netherlands:* inspection time	40
			14-19	*Australia:* inspection time	36
	Luciano *et al*. (2005)	2010	15-65	Inspection time	57
	Luciano, Smith *et al*. (2001)	780	15-18	Inspection time - 2-choice reaction time	52
				Inspection time - 4-choice reaction time	59
	Neubauer *et al*. (2000)	600	18-70	Sternberg Task Reaction time - 3 digit	45
				Sternberg Task Reaction time - 5 digit	47
				Sternberg Task Reaction time - slope	11
				Sternberg Task Reaction time - intercept	23
				Reaction time - Physical Identity	0
				Reaction time - Name Identity	61
				Reaction time - Total Retrieval	22
				Common Reaction Time Factor	52
General working memory executive control ability	Finkel[…] McGue (1995)	838	27-88	Digit span	
				age 27 to 49 American Sample	59
				age 50 to 64 American Sample	66
				age 27 to 49 Swedish Sample	27
				age 50 to 64 Swedish Sample	54
	Finkel[…] McClearn (1995)	794	27-85	Digit span	
				age 27 to 49 American Sample	39
				age 50 to 64 American Sample	39
				age 27 to 49 Swedish Sample	33
				age 50 to 64 Swedish Sample	33
	Karlsgodt *et al*. (2010)	467	19-85	Letter-number Span	44

Table 1 (continue)
Cognitive domains and tests used for their assessment in reviewed studies based on adult samples

Cognitive domain	Study	Sample size	Age range	Tests used for assessment	h2 (%)
	Plomin *et al.* (1994)	446	mean 64.1 (SD= 7.5)	Digit Span	49
	Posthuma *et al.* (2003)	135	mean 29.2 (SD= 7.34)	WAIS Working Memory Subscale	65
	Rijsdijk *et al.* (2002)	388	15-18	Digit Span	30
	Anokhin *et al.* (2003)	168	17-28	WCST Total Nº Errors	43
				WCST Trials to Complete 1st Category	31
				WCST Perseverative Responses	46
				WCST Perseverative Errors	44
	Kremen, Jacobsen *et al.* (2007)	693	41-58	WCST	0
	Taylor (2007)	218	18-83	WCST	0
				Stroop Interference	38
Sub-components of working memory ability	Karlsgodt *et al.* (2010)	467	19-85	Spatial-Delayed Response	15
				Forward Digit Span	54
				Backward Digit Span	47
	Kremen, Jacobsen *et al.* (2007)	690	41-58	Digit Span Forward	19
	Luciano, Wright *et al.* (2001)	780	15-18	Delayed Response Task	48
	Wright *et al.* (2001)	2129	15-19	Delayed Response Task	46
	Taylor (2007)	218	18-83	Stroop Word Score	50
				Stroop Color Score	53

WAIS: Wechsler Adult Intelligence Scale, MAB: Multidimensional Aptitude Battery, WCST: Wisconsin Card Sorting Test

Performance ability

The construct of general intellectual ability can be decomposed into middle-order constitutive subunits, such as performance intelligence. The lowest estimates reported for this domain were 35% in a family-based study (Alarcón, Plomin, Fulker, Corley, & DeFries, 1998) and 43% in a twin-based study (Luciano, Smith et al., 2001). The highest estimates reached 83% of the total variance explained (Luciano et al., 2005).

When the analysis focused on lower-order components of this general performance ability, heritability values diminish to between 8 and around 50%. The lowest value corresponded to the measure of Picture Completion (Rijsdijk, Vernon, & Boomsma, 2002). The highest estimates were for the test Block Design (Finkel, Pedersen, McGue, & McClearn, 1995; Plomin, Pedersen, Lichtenstein, & McClearn, 1994).

A similar trend of results was found for older adults aged over 65 years: values ranged from 32 to 51% of the variance in general performance ability explained by genetic influences (McClearn et al., 1997; Read et al., 2006).

Verbal ability

A second middle-order constitutive subunit that was identified among studies was the verbal aspect of intelligence. The lowest estimate reported for the general verbal ability was 26% (Alarcón et al., 1998). Following this value, the range of heritability was moderate to high: 55 to 85% (Luciano, Smith et al., 2001; Posthuma, de Geus, & Boomsma, 2001).

When the analysis focused on functions that are hierarchically simpler, heritability values diminished to between 33 and 65% for verbal subtests, specifically for the Information test (Finkel, Pedersen, McGue, & McClearn, 1995; Plomin et al., 1994; Rijsdijk et al., 2002).

These subcomponents of the higher-order global function of intelligence have also been studied in subjects over the age of 65, where verbal ability gave a heritability of between 38 and 55% (McClearn et al., 1997; Read et al., 2006).

Memory

A theory that is generally shared among specialists is that memory could also be modelled by its own hierarchical organization; there would be a higher-order, general memory ability, composed of more or less specific skills. Based on this idea, multifactorial studies of adults aged between 27 and 64 examined the heritability of memory as a construct made up of specific short-term memory functions, verbal memory and visual memory (Finkel, Pedersen, & McGue, 1995). The hypothesis of a hierarchical organization of memory was not supported by the results, since the average of the results for the specific tests showed a variation of between 40 and 56%, while the general construct of memory (of higher order) was found to have an average heritability of 54%.

Within this context, conservative results for moderate heritability estimates along memory measures have also been found by studies on different age groups. In children aged between 6 and 13 years, the proportion of the variance explained by genetics for memory was 32-56% (Thapar, Petrill, & Thompson, 1994). These last results were repeated in a more recent study, with values for heritability in tasks of visual learning of 45%, and tasks of directed learning of 37% (Luo, Thompson, & Detterman, 2003).

When adults over 64 years of age are considered, different studies also converge on similar results. Performance of long-term episodic memory responds partially to genetic variability, with a

heritability of 34-54% (Giubilei et al., 2008; Read et al., 2006). Performance of general memory ability in subjects over 80, has given heritability estimates of 43-52% (McClearn et al., 1997; McGue & Christensen, 2001).

Speed of information processing

The estimates of the general construct of this cognitive ability showed heritability between 24 to70% (Finkel, Pedersen, McGue, McClearn, 1995; Luciano, Smith et al., 2001; Plomin et al., 1994; Posthuma et al., 2003; Posthuma, Mulder, Boomsma, & de Geus, 2002; Wright et al., 2001). By contrast, the heritability of the sub-components of this domain varied from as low as 11% (although in one study there was no evidence for heritability in the reaction time of a physical identity test (Neubauer, Spinath, Riemann, Angleitner, & Borkenau, 2000) to 61% (Luciano et al., 2005; Luciano, Smith et al., 2001; Neubauer et al., 2000; Posthuma et al., 2001; Wright et al., 2001).

Just as for the construct of intelligence, younger groups seem to present lower values for the influence of genetics on processing speed. In subjects aged between 6 and 12, heritability values for reaction and inspection times were between 20 and 53% (Luo et al., 2003), while in groups of adolescents the estimates were between 60 and64% (Luciano, Wright et al., 2001; Rijsdijk, Vernon, & Boomsma, 1998; Wright et al., 2001). At the other end of the age range, in a population of people over 80 the estimate of heritability showed stable results and presented a value of 62% (McClearn et al., 1997), although one Swedish sample of individuals over the age of 65 showed lower influence of genetic factors on this particular domain (Finkel, Pedersen, McGue, & McClearn, 1995).

Working memory

The concept of working memory consists of a multi-component system that is responsible for the active maintenance and manipulation of information (Baddeley, 2003). One of the paradigmatic tests for measuring this cognitive function is the Wisconsin Card Sorting Task (WCST) (Heaton, Chelune, Talley, Kay, & Curtiss, 1993), which evaluates cognitive flexibility and ability to change sets. However, the heritability of performance in this test is the object of much controversy, given that some studies of adult populations find no evidence for genetic influences (Kremen, Eisen, Tsuang, & Lyons, 2007; Taylor, 2007), while other studies have reported a moderate heritability of around 45% (Anokhin, Heath, & Ralano, 2003). These contradictory findings might be explained by sex specificity, as suggested by the longitudinal development of the genetic component of the variance in performance in the WCST between 12 and 14 years of age (Anokhin, Golosheykin, Grant, & Heath, 2010).

Meanwhile, tasks of attention control and interference resistance have been reported to have moderate values of heritability, varying from 38 to 53% (Taylor, 2007). The highest estimates for the executive control component of working memory corresponded to the measure of Digit Span (66%) (Finkel, Pedersen, & McGue, 1995) and the Working Memory Subscale of the Wechsler Adult Intelligence Scale (65%) (Posthuma et al., 2003). A lower value of 56% was reported in a sample of subjects between 15 and 18 years of age (Rijsdijk et al., 2002), and of 43% in adults between 27 and 49 years (Finkel, Pedersen, & McGue, 1995). Of note, the digit span test is commonly used to evaluate working memory, as

this task involves mental double tracking in which operations of memory and reversibility must be performed simultaneously.

There are several studies that focus on the subsystems that constitute working memory. These studies report more moderate values for the visuo-spatial sketchpad: 46% (Wright et al., 2001) and 19% (Kremen, Jacobsen et al., 2007). Even if it may be controversial due to the lack of clear evidence to support it, some authors postulate that working memory could be characterized by being, in part at least, a modality-specific system. In this way, a spatial working memory should be identifiable and could be differentiated from a verbal working memory. Although a study of young subjects aged between 14 and 29 provided evidence in favour of this, the proportion of the variance explained by genetic factors in each type of working memory did not seem to vary consistently (43-48% for verbal working memory, and 45-49% for spatial working memory) (Ando, Ono, & Wright, 2001).

These last subcomponents of executive control have also been studied in a sample of 12-year-old twins, with reported heritabilities between 70 and 75% (Stins, van Baal, Polderman, Verhulst, & Boomsma, 2004). The authors attribute these high heritability values to a general executive control factor, while the efficiency of the system that grapples with the answer to the problem resulted in a moderate heritability: 49 and 36% in measures of Digit Span (Kuntsi et al., 2006).

The general executive control factor has also been studied in subjects over 65 (Swan & Carmelli, 2002). This domain resulted in a high heritability of 62 to 79%, while for the rest of the subcomponents evaluated (verbal fluency, attention control, resistance to interference), the heritability varied within moderate values: 34 to 50% (Giubilei et al., 2008).

Discussion

All of the cognitive domains covered in our review showed some degree of heritability, which supports the importance of genetic influences in determining individual differences in human cognitive abilities. Interestingly, specific cognitive domains responded to diverse proportions of genetic underpinnings. High heritability estimates were found for the General Intellectual Ability, followed by General Performance and Verbal Abilities, and middle-order Speed of Processing, Working Memory and Memory. Low heritability estimates were found for the subcomponents, or lower-order domains.

This variability may respond to a hierarchical organization of the genetic architecture of human cognition. Intelligence is a highly complex construct, which involves a variety of functions such as the capacity to understand verbal meaning, spatial skills, and abstract reasoning. The neurobiological underpinnings of intelligence have been associated with total brain size, white matter volume, and a sophisticated network of cerebral regions including dorsolateral prefrontal cortex (DLPFC), parietal lobe, anterior cingulated cortex and specific regions in the temporal and occipital lobe (Jung & Haier, 2007). Of interest, the neurobiological basis of verbal aspects of intelligence have been reported to include the same regions as global intelligence, though the left hemisphere has been found to be particularly involved in these processes (Deary et al., 2010). Performance aspects of intelligence seem to be somewhat more dependent on brain functioning that possibly includes the frontal lobe, prefrontal and parietal cortex, although findings in this respect are not conclusive.

Executive control refers to cognitive inhibition and flexibility, which has been associated at the neuro-anatomical level with prefrontal rostral activation areas of the cortex that are part of the more inclusive working memory domain (Karlsgodt et al., 2010). Our results highlight that working memory seems to respond in the same way as intelligence to a hierarchical organization, in which the lower-order components present a lower proportion of genetic effects in their interindividual variability. However, the heritability of working memory, taken as an overall measure, does not reach such high levels as general intelligence. In this way, working memory might be considered a subcomponent of global intellectual performance, and therefore a possible source of individual differences. Being a complex domain, it seems possible to speculate that executive control and general intelligence might share similar genetic structures.

Our results for speed of information processing follow a similar trend of results. It is noteworthy that this cognitive domain has been shown to make a substantial genetic contribution to the learning and general cognitive abilities (Luo et al., 2003), and that individual differences in speed of information processing may underlie the interindividual variability in IQ measurements. Tests used to assess this domain require a cluster of functions highly correlated with intelligence, such as response speed and visual-motor coordination (Lezak, 2004), and some authors posit that this domain is a fundamental predictor of cognitive changes due to cerebral development and aging (Head, Rodrigue, Kennedy, & Raz, 2008). These results are supported by the association between speed of processing and axonal myelinisation of the central nervous system (Posthuma et al., 2001), and by the finding of shared genetic components in the correlation between processing speed and general cognitive ability (Finkel & Pedersen, 2000). However, the moderate value for heritability indicates that environmental factors play a fundamental role in this domain in all the age ranges.

The results for memory seem to contrast with other cognitive functions in two main aspects: (a) estimates show only moderate heritability, and (b) the heritability of the more general component of memory was similar to that found for the subcomponents; being the more complex functions as heritable as the lower-order ones. These results suggest characteristics of genetic structure that are different from those found in other cognitive functions, supporting stable genetic and environmental contributions to memory performance. Interestingly, the temporal brain regions that support the functioning of this cognitive domain seem to develop independently from the frontal areas of executive control (Shaw et al., 2008), suggesting that memory can be differentiated from intelligence in its basic structure. The first can be essentially conceptualized as a relational code, resulting from divergence of connectivity into multiple networks, that may form analytical and discriminant neural networks associated by experience. In contrast, intelligence more likely results from both convergence and divergence of connectivity into large networks (i.e., integration and distribution of information along separate channels) (Fuster, 2003).

Further evidence for a hierarchical organization of cognition comes from recent studies of the ontogenic development of the human brain. According to these studies, the primary motor and sensorial areas of the brain are completely formed first, followed by superior and inferior parietal areas that involve spatial orientation, development of language and attention. The frontal and occipital poles, involved in the senses of smell and taste, and the primary visual cortex, also mature early (Gogtay et al., 2004).

Once the neurobiological bases of these cognitive abilities is established, the process continues with the maturation of areas of the frontal lobe involved in executive functions, higher attentional processes, and motor control. The temporal cortex, which constitutes a heteromodal association region and is involved in the integration of processes of memory, audiovisual association and recognition of objects, continues its maturation process even after other association areas whose functions are articulated within the temporal cortex have finished their developmental process (Raznahan et al., 2011).

These findings indicate a relatively long ontogenic period required for the developmental maturation of higher-order cognitive functions when compared to those of lower order. It is possible that the found heritability estimates of complex cognitive domains reflect the summed genetic influences of the other simpler, yet constitutional, cognitive subcomponents, leading to an increase in the heritability of the tasks with their corresponding loading on general intelligence (Karlsgodt et al., 2010). In this way, the multi-component structure of intelligence would respond to a polygenic substrate in which the constituent subunits have lower estimates of heritability than the more general construct. It is possible that cognitive associations at higher cortical levels, and thus the acquisition of new knowledge, can be understood as a self-adjustment of weights in self-organized associative networks (Kohonen, 1977, 1984).

A further, not exclusive, explanation for these findings point in the direction of a large genetic control of the combinatory capacity of basic cognitive functions, which seems to be to some extent shared by cognitive systems (Marcus, 2006). Unlike other cognitive functions, intellectual capacity cannot be limited to one region of the brain or to a specific neural network. Furthermore, the differences found in the heritability of intelligence throughout the lifespan probably reflect a global dynamic functioning that involves other cognitive domains, brain systems, and the influence of the environment. Given that the functional connections among single brain areas respond to a dynamic organization that develop during ontogenic learning (Luria, 1966, 1973), such combinatory capacity is probably facilitated by experience from environment-dependent processes. The impact of society on cognitive processes has been largely addressed by studies on the development of language (Kotik-Friedgut, 2006). This process, that involves both physical maturation and cultural modelling, provides the psychological functions of adults its final appearance. In this way, the mutual dependency between cognitive domains and cultural settings might enhance the development of intellectual performance, allowing subjects to recognize and confront the complexity of the human world.

Our results are not without limitations. The articles showed a large variability in terms of the cognitive domains chosen for analyses as well as the tests selected for assessment, which made the data unsuitable for meta-analyses. In line with this, the revised literature lacked information on the genetic contribution specific to each cognitive domain (i.e., genetic variance not shared with other cognitive traits), preventing a more definite conclusion about the putative organization we propose. Nevertheless, the present review provides systematic evidence for a renewed perspective to understand the etiological underpinnings of psychological processes. Rapid and consistent progress of scientific development has promoted substantial results supporting that cognitive abilities are, to a large extent, genetically determined (Nilsson, Van Broeckhoven, & Adolfsson, 2001). However, it is not without the

influence of environment that these neurobiological underpinnings of human cognitive traits may reach their current appearance and phenotypic variability. Although further evidence on the specific nonshared genetic contribution to each cognitive domain is yet required, the genetic contributions to cognitive abilities seem to be organized in line with these neurobiological substrates: as ontogenic maturation of functions determines a progressively more complex organization, heritability becomes consequently larger in higher-order domains.

Acknowledgments

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(γ)= complementary articles (subjects under the age of 12, or over 65).

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