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Research Article

Neurobiological mechanisms for nonverbal IQ tests: implications for instruction of nonverbal children with autism

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Abstract

Traditionally, the neurological correlates of IQ test questions are characterized qualitatively in terms of 'control of attention' and 'working memory.' In this report we attempt to characterize each IQ test question quantitatively by two factors: a) the number of disparate objects that have to be imagined in concert in order to solve the problem and, b) the amount of recruited posterior cortex territory. With such a classification, an IQ test can be understood on a neuronal level and a subject's IQ score could be interpreted in terms of specific neurological mechanisms available to the subject.

Here we present the results of an analysis of the three most popular nonverbal IQ tests: Test of Nonverbal Intelligence (TONI-4), Standard Raven's Progressive Matrices, and Wechsler Intelligence Scale for Children (WISC-V). Our analysis shows that approximately half of all questions (52±0.02%) are limited to mental computations involving only a single object; these easier questions are found towards the beginning of each test. More difficult questions located towards the end of each test rely on mental synthesis of *several* disparate objects and the number of objects involved in computations gradually increases with question difficulty. These more challenging questions require the organization of wider

posterior cortex networks by the lateral prefrontal cortex (PFC). This conclusion is in line with neuroimaging studies showing that activation level of the lateral PFC and the posterior cortex positively correlates with task difficulty. This analysis has direct implications for brain pathophysiology and, specifically, for therapeutic interventions for children with language impairment, most notably for children with Autism Spectrum Disorder (ASD) and other developmental disorders.

Keywords

differential neuroscience; human intelligence; psychometric tests

Highlights

- Three popular nonverbal IQ tests were quantitatively analyzed by a panel of neuroscientists

- Each question was assigned a score based on the cortical area required for a solution

- This classification yields clear insights into the neurology of intelligence

- Implications for instruction of nonverbal children with autism are discussed

Abbreviations

NOB score = number of objects score

PCT score = posterior cortex territory score

Introduction

Throughout history humans have been searching for a way to define and measure human intelligence. In the 20th century, differential psychology settled on IQ tests as its leading benchmark. At the present time, despite many criticisms and their undisputable shortcomings, IQ tests remain the basis of efforts to quantify and qualify human intelligence (Deary et al. 2010; Neisser et al. 1996). Many clinical papers mention subjects' IQ score and randomized clinical trials of psychological medications often match the test and control groups by their IQ score (e.g., Ref. Dawson et al. 2010). Historically, the first IQ tests presented questions verbally, but during World War I the U.S. Army had to evaluate recruits who were illiterate or had a limited English proficiency (McCallum et al. 2001). Thus, nonverbal tests were developed as a means to measure general cognition without the confounding element of language. Over time, nonverbal tests became increasingly popular and have been extensively used by many organizations and professions including military, private and public schools and clinicians which use them to evaluate and assign recruits, for student selection and placement, to assign additional educational help and to make decisions on treatment eligibility.

Despite the fundamental role of nonverbal IQ tests in modern psychology, there has been little attempt to dissect IQ tests in terms of the underlying neurobiological mechanisms necessary to solve specific questions, beyond using general terms such as “control of attention” and “working memory” (Deary et al. 2010; Gray et al. 2003; Kane and Engle 2002; Prabhakaran et al. 1997; Waltz et al. 1999). Neuroimaging studies ubiquitously implicate the lateral prefrontal cortex (PFC) as a leading player in all cognitive activities essential for *novel* challenges presented by an IQ test (Buchsbaum et al. 2005; Duncan and Owen 2000). It is also clear that the lateral PFC is not working alone, but is relying on the sensory information encoded in the posterior cortex (occipital, temporal, and parietal lobes) (Fuster 2008; Ghatan et al. 1995; Gray et al. 2003; Haier et al. 1988; Houdé and Tzourio-Mazoyer 2003; Kroger et al. 2002; Newman et al. 2003; Prabhakaran et al. 1997). Furthermore, a number of studies have shown that the activation level of these cortical areas exhibits a correlation with the level of task difficulty (Braver et al. 1997; Klingberg et al. 1997; Lee et al. 2006). In this report, we attempt to correlate a variety of IQ test items to the specific neurological mechanisms which they require, i.e. dynamic rearrangements imposed by the lateral PFC on objects encoded in the posterior cortex. We aim to relate a subject’s IQ score to the underlying neurobiological processes and for that purpose we utilize nonverbal IQ tests since they describe the questions visually and thus avoid a significant layer of neurobiological complexity added by the verbal domain. For our analysis, we selected three widely used IQ tests: Test of Nonverbal Intelligence (TONI-4), Standard Raven's Progressive Matrices, and Wechsler Intelligence Scale for Children (WISC-V).

Material and methods

1. Non-verbal IQ tests evaluated

1.1 Test of Nonverbal Intelligence (TONI-4)

The Test of Nonverbal Intelligence (TONI) was developed by Linda Brown, Rita J Sherbenou and Susan K Johnsen (Brown et al. 1997, Brown et al. 1982, Brown et al. 1990) and quickly gained popularity due to its short administration time. There are two versions of TONI-4 (Form A and B) which allows a subject to retake the test with minimal practice effect. The test consists of 60 multiple choice questions which gradually become more demanding. In each test question, the subject is asked to identify the missing element that completes a pattern. Many patterns are presented in the form of a 2x2, 3x3 or 6x1 matrix. The IQ score is assigned based on the number of correct answers and the subject’s age.

1.2 Standard Raven's Progressive Matrices

Raven's Progressive Matrices were originally developed by John C. Raven in 1936 (Raven 1936, Raven 1998). The simple nonverbal test has quickly found widespread practical application and is broadly accepted as an essential test of fluid reasoning (Alderton and Larson 1990; Anastasi 1988). The Standard Progressive Matrices test is made of 60 multiple choice questions organized into five sets (A to E) of 12 questions each. Questions within each set are becoming increasingly difficult; each consecutive set of questions is on average more difficult than the previous set. In each question, the subject is asked to identify the missing element that completes a pattern. Questions are presented in the form of a 2×2, or 3×3matrix. The IQ score is assigned based on the number of correct answers and the subject’s age.

1.3 Wechsler Intelligence Scale for Children (WISC-V)

The Wechsler Intelligence Scale for Children (WISC) was developed by David Wechsler for children between the ages of 6 and 16 (Wechsler 1949). We limited our investigation to the three non-verbal parts of the test: Matrix Reasoning (34 questions), Visual Puzzles (31 questions), and Figure Weights (36 questions). From these primary measures, WISC-V derives a Fluid Reasoning Index, comparable to an IQ score generated by TONI-4 and Raven's Progressive Matrices.

2. Assessment of IQ test questions

A panel of three independent neuroscientists classified all questions in the three tests according to the minimal neurobiological requirements for the correct answer. Specifically, panel members analyzed all questions in TONI-4, Standard Raven's Progressive Matrices, and WISC-V determining (1) The minimum number of disparate objects that have to be purposefully imagined together in order to solve the problem (number of objects = NOB score), and (2) The type of object modification required by the question (see details below). Members of the panel analyzed each question independently of each other and then discussed questions one by one to reach a unanimous opinion.

(2.1) Establishment of the type of object modification:

For any object in the mind’s eye, we can voluntarily change its color, size, position in space or rotation. The mechanisms of these processes involve PFC-controlled modification of the object’s representation in the posterior cortex. As related to the posterior cortex neuronal territory, such mechanisms can be classified into three classes: 1) those that involve coordination of activity in both the posterior and ventral visual cortices, Fig. 1 (the greatest amount of posterior cortex territory); 2) those that involve modification of activity in only the ventral visual cortex; and 3) those that do not involve any object modification (least amount of territory). E.g., object comparison does not involve modification of any object; modifying the color or size of an object recalled in memory is limited to the ventral visual cortex (Gabay et al. 2016); finally, modifications in an object’s location in space or rotation involve coordination of activity in both the ventral and posterior visual cortices (Cohen et al. 1996;

Goodale and Milner 1992; Lee et al. 2006; Schendan and Stern 2007; Zacks 2008). Accordingly, the three types of questions were assigned the posterior cortex territory score (PCT score) ranging from zero to two, with zero corresponding to least posterior cortex territory and two corresponding to greatest amount of posterior cortex territory.

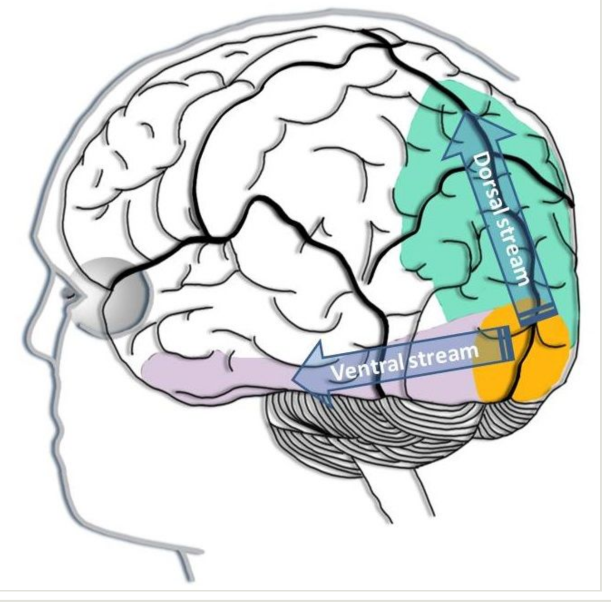

Figure 1.

Visual information processing in the cortex. From the primary visual cortex (V1, shown in yellow), the visual information is passed in two streams. The neurons along the ventral stream also known as the ventral visual cortex (shown in purple) are primarily concerned with what the object is. The ventral visual stream runs into the inferior temporal lobe. The neurons along the dorsal stream also known the dorsal visual cortex (shown in green) are primarily concerned with where the object is. The dorsal visual stream runs into the parietal lobe.

3. Examples of typical IQ questions

3.1 Find the same object

A task commonly found in IQ tests requires the subject to find a matching object. In a verbal setting, the subject may be asked to “find the ball” or shown a ball and asked to “find the same object” with a variety of physical objects (or pictures) to choose from. A similar type of question can be extended to the nonverbal setting using a matrix scheme, a staple of nonverbal IQ tests. For example, Fig. 2a shows a typical 2x2 matrix commonly found in IQ tests such as the TONI-4, with six answer choices displayed below the problem. In a typical IQ-testing environment, the subject receives minimal verbal instructions and is expected to 1) extract the rule from the top row, 2) apply that rule to the bottom row, and 3) point to the solution.

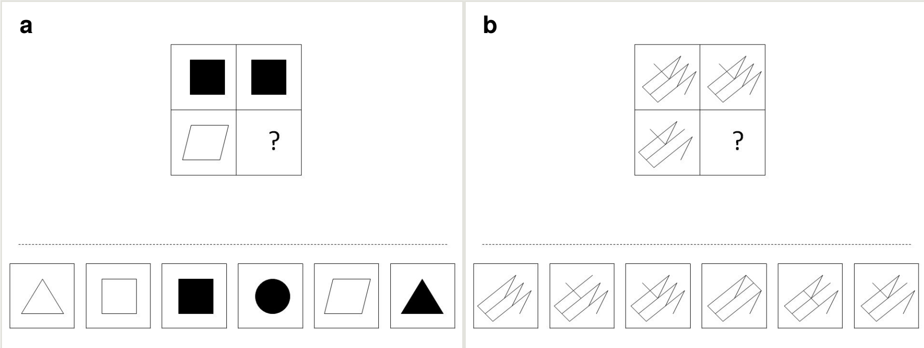

Figure 2.

Examples of “Find the same object” questions.

a: A typical 2x2 matrix commonly used in an IQ test, with six answer choices displayed below the problem. The top row of the matrix indicates the rule: “the object in the right column is the same as the object in the left column.” Applying this rule to the bottom row, we arrive at the correct answer: the white rhombus.

b: A more complicated object, where the top row of the matrix indicates the rule: “the object in the right column is the same as the object in the left column” (the 6th square). The “Find the same object” questions were assigned the NOB score of one and the PCT score of zero. Note: since all three IQ tests investigated in this report are copyrighted, the examples presented are not actual items from a test but are representative of a typical question.

Fig. 2b shows a more complicated object that, unlike the white rhombus in Fig. 2a, is difficult to describe verbally. Despite this complexity as well as the similarity of the decoy answers, this problem nevertheless falls under the “find the same object” category and requires the subject to apply the same rule: “the object in the right column is the same as the object in the left column,” leading the subject to chose the correct solution displayed in the 6^{th} cell.

Despite the clear differences in difficulty between the two examples in Fig. 2a and Fig. 2b, “find the same object” questions are, neurologically speaking, quite similar. They are both based of one’s ability to compare the internal representation of the target object with all the possible solution objects. Since this type of question does not require any mental combination of disparate objects, it is assigned the NOB score of one. Furthermore, since this type of question does not require any modification of the object, it corresponds to the PCT score of zero (i.e. requiring the least amount of the posterior cortex territory).

3.2 Integration of modifiers in a single object

Another task commonly found in IQ tests requires the subject to integrate a noun and an adjective. In a verbal version of the *integration of modifiers* task, a subject may be asked to point to the picture with a {yellow/red} + {circle/triangle/square} placed among several decoy images thus forcing the integration of color and noun. Similarly, to integrate size and noun one may be asked to point to a {big/little} + {circle/triangle/square}. In a nonverbal equivalent of the “integration of modifiers” task, adjectives can be presented in rows and nouns in columns (or vice versa). For example, in Fig. 3a, the rows indicate a color (black, gray and white) while the columns indicate a noun (square, circle and triangle). To find the shape that belongs in the empty cell, the subject must integrate the adjective (in this case, the color white) with the noun (in this case, the triangle). Similarly, Fig. 3b requires the integration of size and shape and Fig. 3c requires the integration of number and shape. Because of its very nature, a nonverbal test presents the subject with the additional challenge of extracting the rule by observing the top and middle rows.

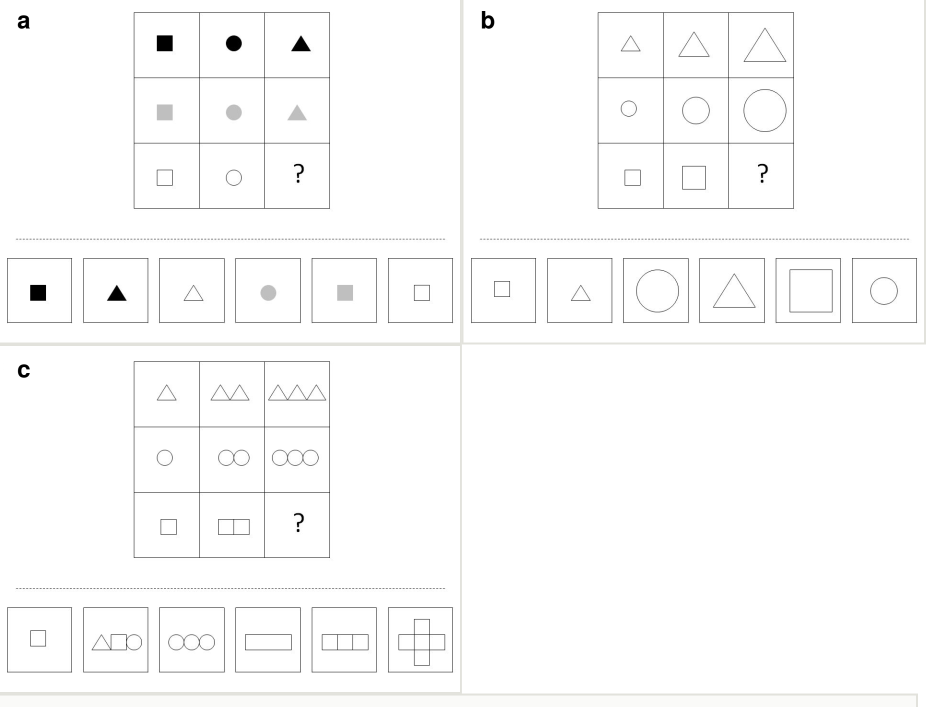

Figure 3.

Examples of “Integration of modifiers” questions.

a: Integration of color modifier. The top two rows of the matrix indicate the rule: “the object in the right column is the result of combining color indicated in the row and the object indicated in the column” (solution: the white triangle in the tird cell).
b: Integration of size modifier. The top two rows of the matrix indicate the rule: “the object in the right column is the result of combining size indicated in the column and the object indicated in the row” (solution: the square in the fifth cell).
c: Integration of number modifier. The top two rows of the matrix indicate the rule: “the object in the right column is the result of combining number indicated in the column and the object indicated in the row” (solution: the three squares in the fifth cell). Since integration of modifiers involves modification of neurons encoding a single object, this type of questions was assigned the NOB score of one. Integration of size and color modifier questions were assigned a PCT score of one since modification is limited to the ventral visual cortex (Gabay et al. 2016). Integration of number modifier questions were assigned a score of two since the numerical information is represented by regions of the posterior parietal lobes (Dehaene et al. 2004, Nieder and Dehaene 2009).

Neurologically, the integration of modifiers involves the modification of neurons encoding a *single* object and therefore has the NOB score of one. In terms of the PCT, questions that modify size and/or color were assigned a score of one (modification is limited to the ventral visual cortex, Ref. Gabay et al. 2016) while those that modify the number of objects were assigned a score of two based on the reports that numerical information is represented by regions of the posterior parietal lobes (Dehaene et al. 2004; Nieder and Dehaene 2009).

3.3 Mental rotation and modification of a single object's location in space

A number of IQ test questions require mental rotation or other modification of an object's location in space, Fig. 4. These processes involve the PFC-coordinated activity in *both* the ventral and the posterior visual cortices (Cohen et al. 1996; Harris et al. 2000; Schendan and Stern 2007), and are therefore assigned the PCT score of two. However, these tasks are still limited to a single object and, consequently, assigned the NOB score of one.

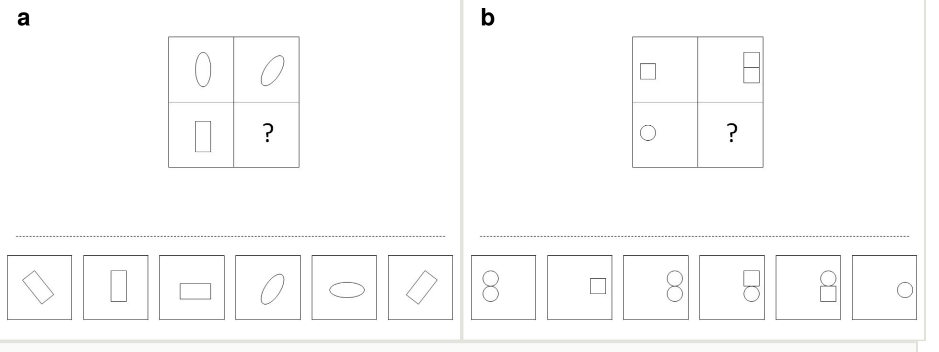

Figure 4.

Typical questions testing subject's ability to mentally rotate an object or/and modify object's location in space. These questions likely involve PFC-directed coordination of *both* the ventral and the posterior visual cortices. Accordingly, they are assigned the PCT score of two and NOB score of one.

a: mental rotation

b: modification of object's location in space

3.4 Mental synthesis of several objects

More advanced questions found within nonverbal IQ tests require a subject to superimpose several objects. The score in these questions is defined as the number of disparate objects that have to be imagined together. Fig. 5a shows a typical mental synthesis question from an IQ test that requires the combination of two objects (NOB score of two).

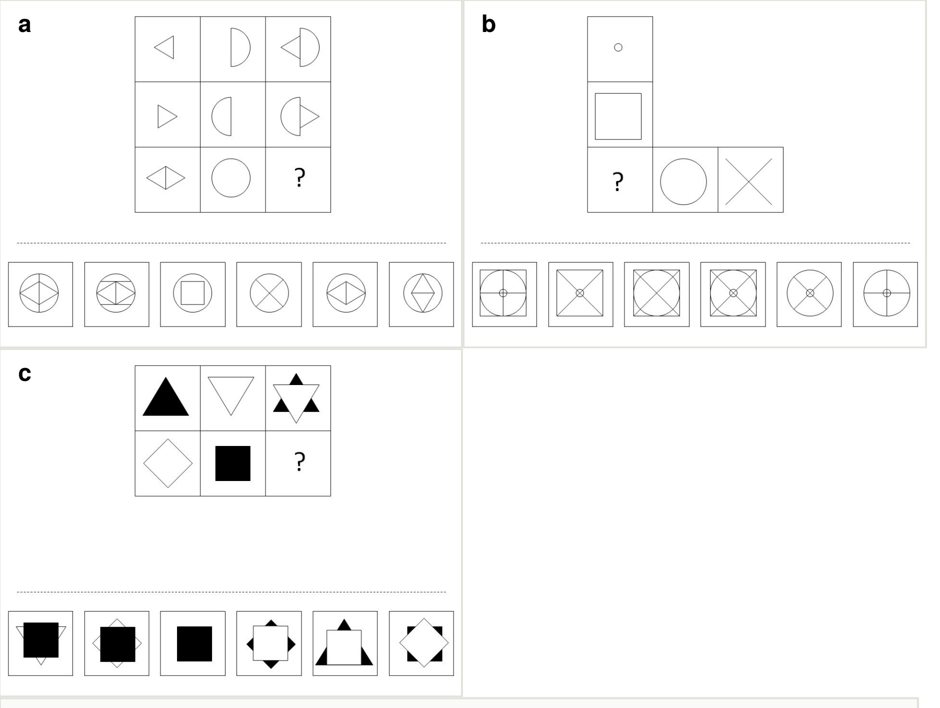

Figure 5.

Typical questions involving mental synthesis of several objects.

a: requires the combination of two objects. The top two rows of the matrix indicate the rule: "the object in the right column is the result of the combination of the two objects shown in the left and middle row" (the solution in the 5th square).
b: shows a question that relies on the mental synthesis of four objects.
c: shows a question in which mental synthesis of two objects has to be conducted according to the following rule specified in the top row: "the object in the middle column goes on top of the object in the left column" (the solution in the second square).

More difficult mental synthesis questions increase the number of objects that must be combined and impose more complex rules of combination. Fig. 5b shows a question that relies on the mental synthesis of four objects. The subject is again expected to mentally combine the objects and then compare the result of their mental synthesis with the six possible solutions. Fig. 5c shows a question in which two objects have to be combined according to the rule that the object in the middle column goes on top of the object in the left column.

Since the exact number of objects is not always easily assertained, all test items that require mental synthesis of three or more objects received an NOB score of "3+"and, since all mental synthesis questions require spatial manipulation, they received the PCT score of two.

4. Special cases

4.1 Amodal completion

The classification of some IQ test questions was not readily obvious upon initial examination. Consider the easy questions in the Standard Raven's Progressive Matrices, Fig. 6. While these questions could be solved by relying on mental synthesis, the objective was to identify the *minimal* neurobiological requirements for the correct answer. The simplest neurobiological mechanism sufficient to answer these questions is amodal completion (Gerbino and Salmaso 1987; Weigelt et al. 2007), sometimes referred to as gestalt formation (De Weert et al. 2005), which is the process of automatic completion of an occluded object. The lateral PFC is not essential in the process of amodal completion (Kanizsa 1985; Weigelt et al. 2007). Accordingly, the amodal completion questions were assigned the same score as “Find the same object”: the NOB score of one and the PCT score of zero.

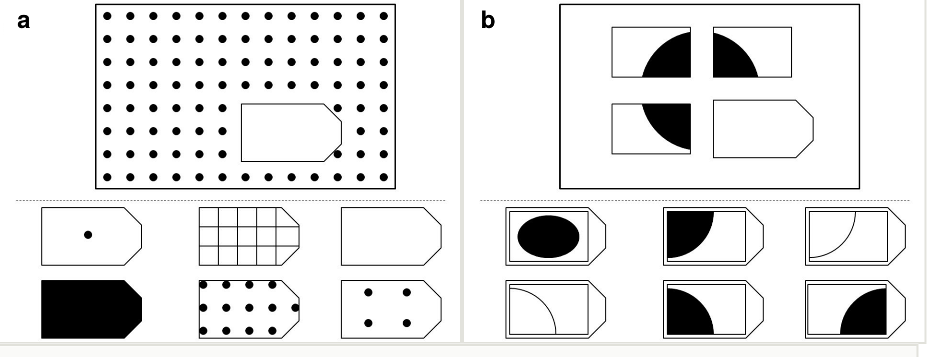

Figure 6.

Two examples of easy questions in the Standard Raven's Progressive Matrices. The simplest neurobiological mechanism sufficient to answer those questions is the mechanism of amodal completion. The amodal completion questions were assigned the NOB score of one and the PCT score of zero.

5. Relating neurobiological mechanisms to their associated IQ score

Once the NOB and PCT scores for each question were assessed, we calculated the IQ score equivalent for each neurological mechanism. For example, to calculate an IQ score associated with the “Find the same object” mechanism (NOB score = 1, PCT score = 0, Table 1), we assumed that all questions that were classified as “Find the same object” were answered correctly and all questions that had a greater PCT score or a greater NOB score were answered incorrectly. The sum of all the questions answered correctly (the raw score) was then converted to an IQ score using a conversion table provided by the publishers of TONI-4 and WISC-V tests.

Table 1.

The hierarchical classification of IQ test question by the NOB score and the PCT score.

Neurological mechanism	**Number of objects score**	**Posterior cortex territory score**
Find the same object	**1**	**0**
Amodal completion	**1**	**0**
Integration of color and size modifiers in a single object	**1**	**1**
Integration of number modifier in a single object	**1**	**2**
Mental rotation and modification of a single object's location in space	**1**	**2**
Mental synthesis of two objects	**2**	**2**
Mental synthesis of three or more objects	**3**+	**2**

The Raven manual does not provide an IQ score but rather percentile norms (Raven J et al. 2000, Table SPM13) that can then be converted to an IQ score using a psychometric conversion table (see Ref. Psychometric conversion table 2011). An additional difficulty with the Raven manual was the lack of norms for low performers. The lowest percentile norms provided in the Raven manual for 18 to 22 year old subjects is 33 correct answers, which corresponds to 3% of the population and an IQ score of 72. For fewer correct answers, we used an extrapolation technique: the percentile norms provided in the Table SPM13 (Raven J et al. 2000) for 18 to 22 year old subjects were plotted on a graph against the number of correct answers and an exponent was fitted to the lower end of the graph from 33 to 44 correct answers resulting in the following equation: $y=0.0591e^{0.1252x}$ (equation 1), where is the number of correct answers and is the percentile.

Results

Classification of IQ tests

Each question in the Test of Nonverbal Intelligence (TONI-4), Standard Raven's Progressive Matrices, and the Wechsler Intelligence Scale for Children (WISC-V), were analyzed according to the paradigm described in Methods. Table 2 lists the mental processes for each question in Form A of TONI-4. Note that both the NOB score and the PCT score increase steadily from easier questions found at the beginning of the test to the more difficult questions found towards the end (Fig. 7).

Table 2.

Panel classification for TONI-4, Form A. Note: since all IQ tests investigated in this report are copyrighted, we cannot reproduce the original questions. The stylistic representation of typical questions for each category are shown in the methods section. Here we report question numbers for each test, so that a reader in possession of the test may be able to refer to the original test question.

Question #	Number of objects score	Posterior cortex territory score	The simplest process that could be used to both deduce the rule and solve the question
1	1	0	Find the same object
2	1	0	Find the same object
3	1	0	Find the same object
4	1	0	Find the same object
5	1	0	Find the same object
6	1	0	Find the same object
7	1	0	Find the same object
8	1	0	Find the same object
9	1	0	Find the same object
10	1	0	Find the same object
11	1	0	Find the same object
12	1	0	Find the same object
13	1	0	Find the same object
14	1	0	Find the same object
15	1	0	Find the same object
16	1	0	Find the same object
17	1	0	Find the same object
18	1	2	Integration of number modifier
19	1	0	Find the same object
20	1	0	Find the same object
21	1	1	Integration of color modifier
22	1	0	Find the same object
23	1	2	Integration of number modifier
24	2	2	Mental synthesis of two objects
25	1	2	Mental rotation
26	1	2	Mental rotation
27	1	0	Find the same object
28	2	2	Mental synthesis of two objects
29	3+	2	Mental synthesis of three+ objects as well as generalizing and categorizing

30	2	2	Mental synthesis of two objects
31	1	0	Find the same object
32	2	2	Mental synthesis of two objects
33	2	2	Mental synthesis of two objects
34	2	2	Mental synthesis of two objects as well as generalizing and categorizing
35	1	0	Find the same object
36	3+	2	Mental synthesis of three+ objects
37	2	2	Mental synthesis of two objects as well as generalizing and categorizing
38	2	2	Mental synthesis of two objects
39	3+	2	Mental synthesis of three+ objects
40	1	2	Mental rotation
41	2	2	Mental synthesis of two objects
42	2	2	Mental synthesis of two objects as well as generalizing and categorizing
43	2	2	Mental synthesis of two objects
44	3+	2	Mental synthesis of three+ objects
45	2	2	Mental synthesis of two objects
46	2	2	Mental synthesis of two objects
47	2	2	Mental synthesis of two objects as well as generalizing and categorizing
48	3+	2	Mental synthesis of three+ objects
49	3+	2	Mental synthesis of three+ objects as well as generalizing and categorizing
50	1	2	Mental rotation
51	2	2	Mental synthesis of two objects as well as generalizing and categorizing
52	3+	2	Mental synthesis of three+ objects
53	3+	2	Mental synthesis of three+ objects
54	3+	2	Mental synthesis of three+ objects
55	3+	2	Mental synthesis of three+ objects
56	1	2	Mental rotation
57	2	2	Mental synthesis of two objects
58	3+	2	Mental synthesis of three+ objects
59	3+	2	Mental synthesis of three+ objects
60	3+	2	Mental synthesis of three+ objects

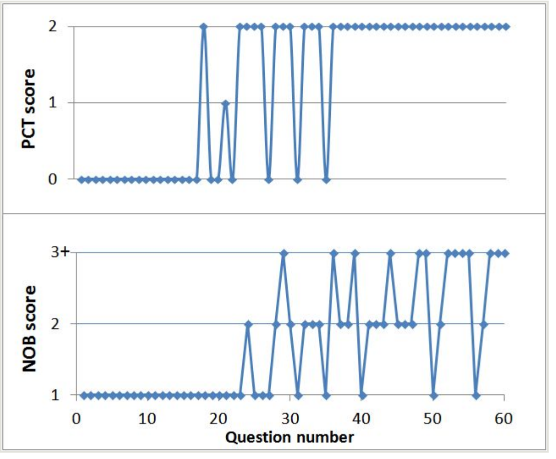

Figure 7.

Graphical representation of neurobiological requirements for TONI-4, Form A. The minimal number of objects involved in mental calculations (the NOB score, bottom) and the minimal amount of posterior cortex territory required (the PCT score, top) as a function of question number.

Table 3 similarly lists the processes for Form B of TONI-4. Again, both the NOB score and the PCT score increase from easier questions found at the beginning of the test to the more difficult questions found towards the end (Fig. 8).

Table 3.

Panel classification for TONI-4, Form B.

Question #	Number of objects score	Posterior cortex territory score	The simplest process that could be used to both deduce the rule and solve the question
1	1	0	Find the same object
2	1	0	Find the same object
3	1	0	Find the same object
4	1	0	Find the same object
5	1	0	Find the same object
6	1	0	Find the same object
7	1	0	Find the same object
8	1	0	Find the same object
9	1	0	Find the same object
10	1	0	Find the same object
11	1	0	Find the same object
12	1	0	Find the same object
13	1	0	Find the same object

14	1	0	Find the same object
15	1	1	Integration of size modifier
16	1	0	Find the same object
17	1	1	Integration of size and color modifiers
18	1	0	Find the same object
19	1	0	Find the same object
20	1	0	Find the same object
21	1	0	Find the same object
22	2	2	Mental synthesis of two objects
23	2	2	Mental synthesis of two objects
24	2	2	Mental synthesis of two objects
25	2	2	Mental synthesis of two objects as well as generalizing and categorizing
26	2	2	Mental synthesis of two objects
27	2	2	Mental synthesis of two objects
28	1	1	Integration of color modifier
29	1	2	Mental rotation
30	2	2	Mental synthesis of two objects
31	2	2	Mental synthesis of two objects
32	2	2	Mental synthesis of two objects
33	2	2	Mental synthesis of two objects as well as generalizing and categorizing
34	1	0	Find the same object
35	2	2	Mental synthesis of two objects
36	2	2	Mental synthesis of two objects
37	2	2	Mental synthesis of two objects
38	1	0	Find the same object
39	2	2	Mental synthesis of two objects
40	1	0	Find the same object
41	2	2	Mental synthesis of two objects as well as generalizing and categorizing
42	2	2	Mental synthesis of two objects as well as generalizing and categorizing
43	1	2	Mental rotation
44	2	2	Mental synthesis of two objects as well as generalizing and categorizing
45	1	2	Mental rotation
46	3+	2	Mental synthesis of three+ objects
47	2	2	Mental synthesis of two objects

48	2	2	Mental synthesis of two objects
49	2	2	Mental synthesis of two objects as well as generalizing and categorizing
50	2	2	Mental synthesis of two objects
51	2	2	Mental synthesis of two objects
52	2	2	Mental synthesis of two objects as well as generalizing and categorizing
53	3+	2	Mental synthesis of three+ objects
54	2	2	Mental synthesis of two objects
55	1	2	Mental rotation
56	3+	2	Mental synthesis of three+ objects
57	3+	2	Mental synthesis of three+ objects
58	2	2	Mental synthesis of two objects
59	2	2	Mental synthesis of two objects as well as generalizing and categorizing
60	3+	2	Mental synthesis of three+ objects

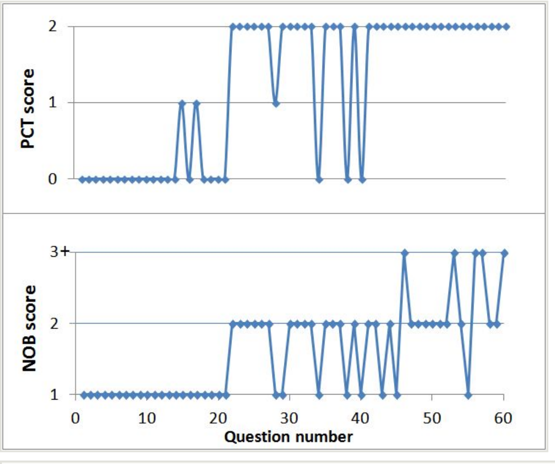

Figure 8.

Graphical representation of neurobiological requirements for TONI-4, Form B. The NOB score (bottom) and the PCT score (top) as a function of question number.

The analysis of the Standard Raven's Progressive Matrices is shown in Table 4 and Fig. 9. The sixty questions of this test are not designed to linearly increase in difficulty, but are organized into five sets (A to E) of twelve questions which become increasingly more difficult. Furthermore, each consecutive set of questions is on average more difficult than the previous set. According to the 1979 standardization (Raven J et al. 2000, Table SPM2), the expected score composition for a subject who answers 30 out of 60 questions correctly is 10, 7, 6, 5, and 2 correct answers in sections A through E, respectively.

Table 4.

Panel assignment of mental processes for Standard Raven's Progressive Matrices.

Set	Question #	Number of objects score	Posterior cortex territory score	The simplest process that could be used to both deduce the rule and solve the question
A	1	1	0	Amodal completion
A	2	1	0	Amodal completion
A	3	1	0	Amodal completion
A	4	1	0	Amodal completion
A	5	1	0	Amodal completion
A	6	1	0	Amodal completion
A	7	1	0	Amodal completion
A	8	1	0	Amodal completion
A	9	1	0	Amodal completion
A	10	1	0	Amodal completion
A	11	1	0	Amodal completion
A	12	1	0	Amodal completion
B	1	1	0	Find the same object
B	2	1	0	Find the same object
B	3	1	0	Find the same object
B	4	1	0	Amodal completion
B	5	1	0	Amodal completion
B	6	1	1	Integration of color modifier
B	7	1	1	Integration of color modifier
B	8	1	1	Integration of color modifier
B	9	1	1	Integration of color modifier
B	10	2	2	Mental synthesis of two objects
B	11	2	2	Mental synthesis of two objects
B	12	2	2	Mental synthesis of two objects
C	1	1	0	Find the same object
C	2	1	1	Integration of size modifier
C	3	1	2	Integration of number modifier
C	4	1	2	Integration of number modifier
C	5	1	2	Integration of number modifier
C	6	2	2	Mental synthesis of two objects
C	7	1	2	Modification of an object’s location in space
C	8	2	2	Mental synthesis of two objects
C	9	1	2	Modification of an object’s location in space

C	10	2	2	Mental synthesis of two objects
C	11	2	2	Mental synthesis of two objects
C	12	2	2	Mental synthesis of two objects
D	1	1	0	Find the same object
D	2	1	0	Find the same object
D	3	1	0	Find the same object
D	4	2	2	Mental synthesis of two objects
D	5	2	2	Mental synthesis of two objects
D	6	2	2	Mental synthesis of two objects
D	7	2	2	Mental synthesis of two objects
D	8	1	1	Integration of color modifier
D	9	2	2	Mental synthesis of two objects
D	10	2	2	Mental synthesis of two objects
D	11	2	2	Mental synthesis of two objects
D	12	2	2	Mental synthesis of two objects
E	1	2	2	Mental synthesis of two objects
E	2	2	2	Mental synthesis of two objects
E	3	2	2	Mental synthesis of two objects
E	4	2	2	Mental synthesis of two objects
E	5	3+	2	Mental synthesis of three+ objects
E	6	3+	2	Mental synthesis of three+ objects
E	7	3+	2	Mental synthesis of three+ objects
E	8	3+	2	Mental synthesis of three+ objects
E	9	3+	2	Mental synthesis of three+ objects
E	10	3+	2	Mental synthesis of three+ objects
E	11	3+	2	Mental synthesis of three+ objects
E	12	3+	2	Mental synthesis of three+ objects

The three non-verbal parts of WISC-V are presented in Tables 5, 6, 7. Questions in each part are designed to gradually increase in difficulty. Table 5 and Fig. 10 show analysis of the Matrix Reasoning section (34 questions). Table 6 and Fig. 11 show analysis of the Matrix Reasoning section (34 questions). Table 7 and Fig. 12 shows analysis of the Visual Puzzles section (31 questions). and show analysis of the Figure Weights section (36 questions).

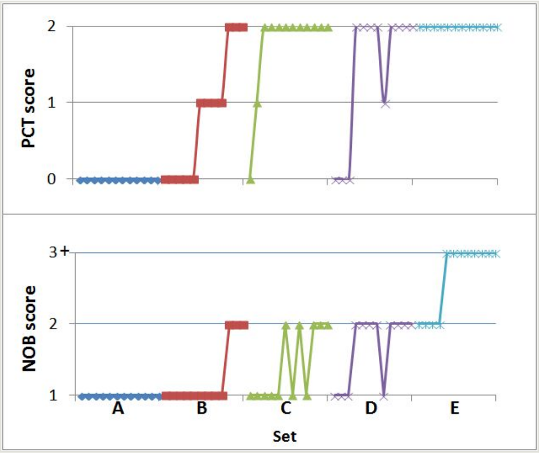

Figure 9.

Graphical representation of neurobiological requirements for Standard Raven's Progressive Matrices questions. The NOB score (bottom) and the PCT score (top) as a function of question number. The five sets of 12 questions are shown with different markers.

Table 5.

Panel assignment of mental processes for WISC-V, Matrix Reasoning.

Question #	Number of objects score	Posterior cortex territory score	The simplest process that could be used to both deduce the rule and solve the question
1	1	0	Find the same object
2	1	0	Find the same object
3	1	0	Find the same object
4	1	0	Find the same object
5	1	0	Find the same object
6	1	0	Find the same object
7	1	0	Find the same object
8	1	0	Find the same object
9	1	0	Find the same object
10	1	0	Find the same object
11	1	2	Mental rotation
12	1	2	Mental rotation
13	1	1	Integration of size modifier
14	1	2	Integration of number modifier
15	1	1	Integration of size modifier
16	1	1	Integration of color modifier
17	2	2	Mental synthesis of two objects

18	2	2	Mental synthesis of two objects
19	2	2	Mental synthesis of two objects
20	2	2	Mental synthesis of two objects
21	1	2	Modification of an object's location in space
22	2	2	Mental synthesis of two objects
23	2	2	Mental synthesis of two objects
24	1	2	Mental rotation
25	3+	2	Mental synthesis of three+ objects
26	2	2	Mental synthesis of two objects
27	3+	2	Mental synthesis of three+ objects
28	3+	2	Mental synthesis of three+ objects
29	3+	2	Mental synthesis of three+ objects
30	3+	2	Mental synthesis of three+ objects
31	3+	2	Mental synthesis of three+ objects
32	2	2	Mental synthesis of two objects
33	3+	2	Mental synthesis of three+ objects
34	2	2	Mental synthesis of two objects

Table 6.

Panel assignment of mental processes for WISC-V, Visual Puzzles.

Question #	Number of objects	Posterior cortex territory score	The simplest process that could be used to both deduce the rule and solve the question
1	1	0	Find the same object - the three parts of the rectangle break up in a bottom-up process; each individual part can then be found among the answers, essentially reducing this question to "Find the same object" task conducted three times.
2	1	1	Find the same object - the three parts of the rectangle break up in a bottom-up process; each individual part can then be found among the answers, essentially reducing this question to "Find the same object" task conducted three times. One of the rectangles requires modification of size.
3	1	0	Find the same object - the three parts of the rectangle break up in a bottom-up process; each individual part can then be found among the answers, essentially reducing this question to "Find the same object" task conducted three times.
4	1	0	Find the same object - the three parts of the rectangle break up in a bottom-up process; each individual part can then be found among the answers, essentially reducing this question to "Find the same object" task conducted three times.

5	1	0	Find the same object - the three parts of the rectangle break up in a bottom-up process; each individual part can then be found among the answers, essentially reducing this question to "Find the same object" task conducted three times.
6	3+	2	Mental synthesis of three+ objects
7	1	0	Find the same object - the three parts of the rectangle break up in a bottom-up process; each individual part can then be found among the answers, essentially reducing this question to "Find the same object" task conducted three times.
8	1	0	Find the same object - the three parts of the rectangle break up in a bottom-up process; each individual part can then be found among the answers, essentially reducing this question to "Find the same object" task conducted three times.
9	3+	2	Mental synthesis of three+ objects
10	1	0	Find the same object - the three parts of the rectangle break up in a bottom-up process; each individual part can then be found among the answers (NB: even though all the correct answers are rotated 45 degrees, they are the only possible correct answers)
11	1	0	Find the same object - the three parts of the figure break up in a bottom-up process; each individual part can then be found among the answers.
12	3+	2	Mental synthesis of three+ objects - the bottom-up amodal completion process in this case is actually deceiving a subject into selecting an incorrect answer. The correct answer requires mental synthesis.
13	3+	2	Mental synthesis of three+ objects
14	3+	2	Mental synthesis of three+ objects
15	3+	2	Mental synthesis of three+ objects
16	1	0	Find the same object - the three parts of the figure break up in a bottom-up process; each individual part can then be found among the answers.
17	3+	2	Mental synthesis of three+ objects
18	3+	2	Mental synthesis of three+ objects
19	3+	2	Mental synthesis of three+ objects
20	3+	2	Mental synthesis of three+ objects
21	3+	2	Mental synthesis of three+ objects
22	3+	2	Mental synthesis of three+ objects
23	3+	2	Mental synthesis of three+ objects
24	3+	2	Mental synthesis of three+ objects
25	3+	2	Mental synthesis of three+ objects
26	3+	2	Mental synthesis of three+ objects
27	3+	2	Mental synthesis of three+ objects
28	3+	2	Mental synthesis of three+ objects
29	3+	2	Mental synthesis of three+ objects
30	3+	2	Mental synthesis of three+ objects
31	3+	2	Mental synthesis of three+ objects

Table 7.

Panel assignment of mental processes for WISC-V, Figure Weights.

Question #	Number of objects score	Posterior cortex territory score	The simplest process that could be used to both deduce the rule and solve the question
1	1	0	Find the same object
2	1	0	Find the same object
3	1	0	Find the same object
4	1	0	Find the same object
5	1	0	Find the same object
6	1	0	Find the same object
7	1	0	Find the same object
8	1	0	Find the same object
9	1	0	Find the same object
10	1	0	Find the same object
11	1	0	Find the same object
12	1	0	Find the same object
13	1	0	Find the same object
14	1	0	Find the same object
15	1	0	Find the same object
16	1	0	Only one possible answer
17	1	0	Only one possible answer
18	1	2	Integration of number modifier
19	1	2	Integration of number modifier
20	1	2	Integration of number modifier
21	1	2	Integration of number modifier
22	1	0	Find the same object
23	1	2	Integration of number modifier
24	1	2	Integration of number modifier
25	1	2	Integration of number modifier
26	2	2	Mental synthesis of two objects
27	2	2	Mental synthesis of two objects
28	2	2	Mental synthesis of two objects
29	3+	2	Mental synthesis of three+ objects
30	3+	2	Mental synthesis of three+ objects
31	3+	2	Mental synthesis of three+ objects
32	3+	2	Mental synthesis of three+ objects
33	3+	2	Mental synthesis of three+ objects

34	3+	2	Mental synthesis of three+ objects
35	3+	2	Mental synthesis of three+ objects
36	3+	2	Mental synthesis of three+ objects

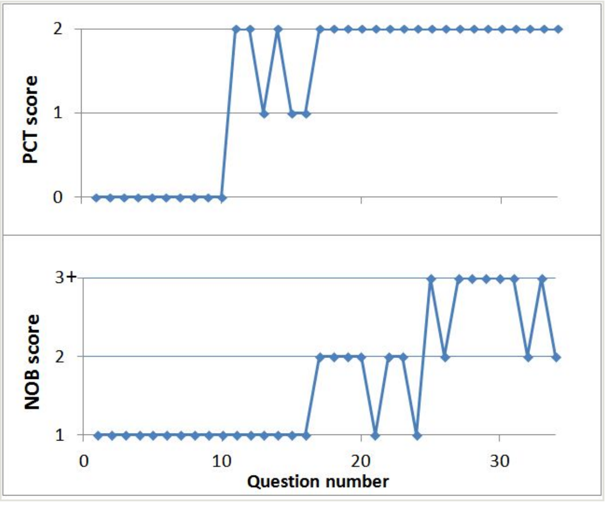

Figure 10.

Graphical representation of neurobiological requirements for WISC-V, Matrix Reasoning. The NOB score (bottom) and the PCT score (top) as a function of question number.

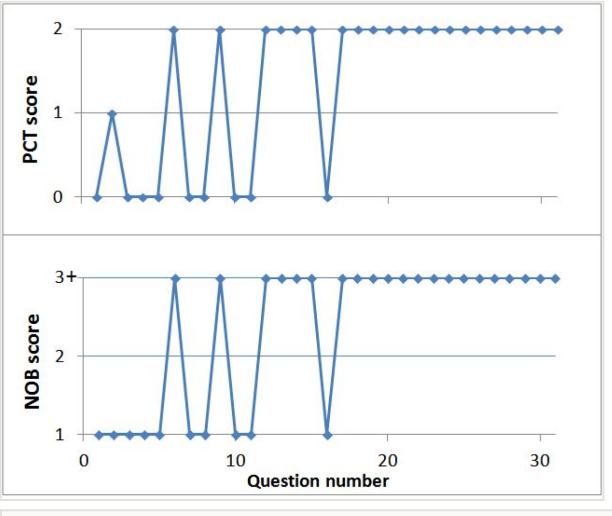

Figure 11.

Graphical representation of neurobiological requirements for WISC-V, Visual Puzzles. The NOB score (bottom) and the PCT score (top) as a function of question number.

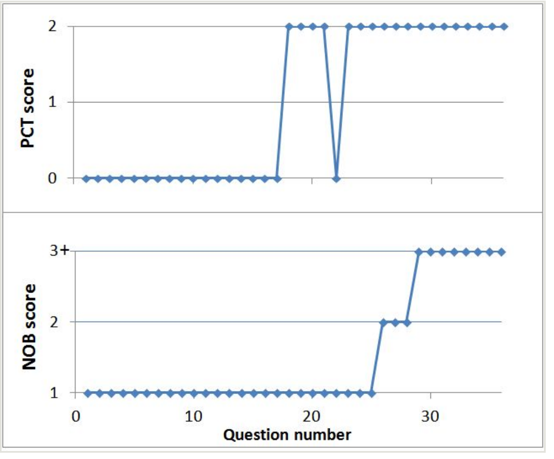

Figure 12.

Graphical representation of neurobiological requirements for questions WISC-V, Figure Weights. The NOB score (bottom) and the PCT score (top) as a function of question number.

Our analysis indicates a slow and consistent increase in both the NOB and PTC scores within each IQ test, Figures 7 through 12. The questions at the start of each test typically require working with only a single object (NOB score of one, 52±0.02% of all test questions). In the first half of each test, there is a consistent increase of PTC score from zero, at the start, to two, towards the middle. In the second half of each test, we only find questions with the PTC score of two; the NOB score increases to 3+ towards the end of each test.

Neurobiological mechanisms and their associated IQ score

To calculate the IQ score equivalent for each neurobiological mechanism (Table 8), we assumed that all questions classified by that mechanism were answered correctly and all the more difficult questions were answered incorrectly. The sum of all questions answered correctly (raw score) was then converted into an IQ score using a conversion table provided by the publishers of the tests. Since IQ tests are scored differently for different age brackets, we decided to use the scores corresponding to the 19 to 30 age bracket for TONI-4, the 18 to 22 age bracket for Raven's Matrices and the 16-year-old bracket for WISC-V (which is the oldest age bracket for this test).

Table 8.

The analyzed nonverbal IQ tests and the respective IQ score threshold for each identified neurological mechanism. The corresponding raw score is indicated in square brackets.

Subjects can solve questions requiring:	TONI-4, A: IQ score	TONI-4, B: IQ score	Raven's Progressive Matrices: IQ score	WISC-V, Fluid Reasoning index	Average ± Standard deviation

NOB score = 1 and PCT score = 0 -"Find the same object"-"Amodal completion"	80 [20]	80 [19]	65 [26]	72	74±7
NOB score =1 and PCT score ≤ 1 -"Find the same object" "Integration of size/color modifier"	81 [21]	82 [21]	68 [31]	79	78±7
NOB score =1 and PCT score ≤ 2 -"Find the same object" -"Integration of size/color modifier" -"Integration of number modifier" -"Mental rotation and modification of object's location in space" -Subjects *cannot* solve any "Mental synthesis" questions.	86 [26]	82 [21]	76 [35]	100	86±10

The TONI-4 test is halted once a subject fails to answer three questions. A subject incapable of solving anything more difficult than the "find the same object" tasks (PCT score = 0) would be stopped after failing to correctly answer the first three questions that require a PCT score>0: questions 18, 21, and 23 for Form A (Table 2); questions 15, 17, and 22 for Form B (Table 3). Assuming that this subject made no other errors, s/he would have correctly answered a total of 20 questions (Form A) or 19 questions (Form B), which corresponds to an IQ score of 80 for both tests (Table 8). Note that the Forms A and B of TONI-4 use different tables for converting the raw score to an IQ score.

Similarly, we can calculate an expected IQ score for a subject who can only solve the "find the same object" or "integration of size/color modifier" questions that require a PCT score of zero or one. Such a subject would be expected to fail the first three questions that require a PCT score >1: questions 18, 23, and 24 (Form A) and 22, 23, 24 (Form B). This subject would correctly answer 21 questions (in both Forms A and B), which corresponds to an IQ score of 81 (Form A) or 82 (Form B).

The first three questions involving mental synthesis of multiple objects in TONI-4 are 24, 28, and 29 (Form A) and 22, 23, 24 (Form B). Accordingly, a subject who can solve all single object questions (NOB score = 1) but none of the mental synthesis questions is expected to correctly answer questions 1-23, and 25-27 (Form A) or the first 21 questions (Form B). Accordingly, the mental synthesis threshold for the TONI-4 is an IQ score of 86 (Form A) or 82 (Form B). Note that, for Form B, the first three questions that have a PCT score = 2 are all mental synthesis questions, which is why this threshold is the same as the one above (Table 8).

A subject taking the Standard Raven's Progressive Matrices is given an opportunity to examine all 60 questions regardless of how many questions are answered incorrectly. The analysis of the test shows that a subject only capable of answering “find the same object” questions (NOB score=1; PCT score=0), is expected to correctly answer 12, 5, 1, 3, and 0 questions in sections A through E respectively (Table 4), resulting in a total of 21 correct answers. A subject unable to solve the more difficult items and therefore answering randomly would be expected to pick up an additional 5 correct answers from among the remaining 39 questions, which have either six answer choices (sections A, B) or eight answer choices (sections C-E). Using equation 1, the raw score of 26 results in a percentile of 1.5 and a corresponding IQ score of 65.

A subject who solves all “find the same object” and “integration of modifiers” questions, but not more difficult questions (NOB score=1; PCT score≤1) is expected to correctly answer 12, 9, 2, 4, and 0 questions in sections A through E respectively, resulting in a total of 27 correct answers. A subject picking at random for the remaining 33 questions would be expected to pick up an additional 4 correct answers. Using equation 1, the raw score of 31 corresponds to a percentile of 2 and an IQ score of 68.

A subject who can solve all single object questions but none of the “mental synthesis” of multiple objects questions (NOB score=1; PCT score ≤2) is expected to correctly answer 12, 9, 7, 4, and 0 questions in sections A through E respectively, resulting in a total of 32 correct answers, with an additional 3 correct answers picked up at random from amongst the remaining 28. The raw score of 35 corresponds to a percentile of 5 and an IQ score of 76.

Like the TONI-4, the WISC-V is halted after three consecutive incorrect responses. Accordingly, a subject who can only answer the “find the same object” questions is expected to correctly answer 10 questions in the Matrix Reasoning subtest (Table 5), 8 questions in Visual Puzzles (Table 6), and 17 questions in Figure Weights (Table 7), resulting in a Fluid Reasoning Index of 72.

A subject who can answer the “find the same object” and “integration of modifiers” questions is expected to correctly answer 13 questions in the Matrix Reasoning subtest, 9 questions in Visual Puzzles, and 17 questions in Figure Weights, resulting in a Fluid Reasoning Index of 79.

Finally, a subject who can solve all single object questions but none of the “mental synthesis of multiple objects” questions is expected to correctly answer 16 questions in the Matrix Reasoning subtest, 9 questions in Visual Puzzles, and 25 questions in Figure Weights, resulting in the Fluid Reasoning Index of 100.

Discussion

In this report we set out to relate IQ test questions to specific neurological mechanisms. We have analyzed the three most common non-verbal IQ tests and classified all questions in those tests according to their minimal neurobiological requirements.

Traditionally, the neurological requirements of IQ test questions are characterized qualitatively in terms of control of attention and working memory. In this report we attempt to characterize the neurological mechanism of each IQ test question quantitatively along two axes: the amount of physical territory within the posterior cortex recruited for a particular task and the number of disparate objects that have to be imagined together to solve the problem. The posterior cortex territory was characterized by a score ranging from zero to two. The high score of two was assigned to rotation and spatial modification of objects that likely involved both the dorsal and the ventral visual cortices (Goodale and Milner 1992, Lee et al. 2006); the score of one was assigned to color and size modification that likely only involved the ventral visual cortex (Gabay et al. 2016); and the score of zero was assigned to questions that involved no modifications of the object.

In all IQ tests, questions gradually increase in difficulty from the beginning of the test to the end, which provides a measure of difficulty that can be related to neurological mechanisms. In all analyzed IQ tests we detected the following pattern of questions from easy to more difficult:

1. Find the same object: no modification of any object / Amodal Completion
2. Integration of modifiers: modification of color or size or number of a single object
3. Mental rotation and modification of a single object's location in space
4. Mental synthesis of two objects
5. Mental synthesis of three or more objects

Note that approximately half of all questions (52±0.02%) are limited to mental computations involving only a single object (the top three categories in the list above), and are found towards the beginning of each test. More difficult questions located towards the end of each test rely on mental synthesis of *several* objects. Moreover, the number of objects involved in mental synthesis gradually increases with question difficulty. We conclude that as questions become increasingly more difficult, the lateral PFC is being called to organize a more widespread network of the posterior cortex. This conclusion is in line with neuroimaging studies showing that activation level of both the lateral PFC and the posterior cortex positively correlate with task difficulty (Braver et al. 1997; Klingberg et al. 1997; Lee et al. 2006). Furthermore, this analysis is in line with observations in patients with PFC damage who are often unable to correctly answer questions that require integration of modifiers, mental rotation and modification of an object's location in space, as well as mental synthesis of several objects. In their 1999 paper, "A system for relational reasoning in human prefrontal cortex," Waltz et. al. give an example (Ref. Waltz et al. 1999, Figure 2C) of a test question that PFC damaged individuals were unable to solve. Using our classification system, this question involves "integration of color modifier in a single object," though the authors refer to it using a variety of terms such as "integration of multiple relations," "relational integration," "two-relation problems (Level 2 complexity)" and "transitive inferences," showing a lack of consistent, neurologically related terminology for IQ test questions.

All of this leads us to propose that the relationship between the IQ score and the underlying functioning of the central nervous system is intimately connected to the control of the PFC over objects encoded in the brain.

Neuronal ensembles as units of perception

At the heart of every nonverbal IQ test item is a subject's ability to manipulate objects. The scientific consensus is that objects are encoded in the cerebral cortex by a network of neurons known as a neuronal ensemble (Hebb 1949). When one perceives any object, the neurons of that object's neuronal ensemble activate into synchronous resonant activity (Quiroga et al. 2008). The neuronal ensemble binding mechanism, based on the Hebbian principle "neurons that fire together, wire together," came to be known as the binding-by-synchrony hypothesis (Singer 2007, Singer and Gray 1995).

While the term "neuronal ensemble" is often used in a broad sense to refer to any population of neurons involved in a particular neural computation, in this discussion we will use the term more narrowly to mean a stable group of neurons which are connected by enhanced synapses and which encode specific objects. This connection between neuronal ensembles and physical objects must be further explained. Our visual world consists of meaningful, unified, and stable objects that move coherently as one piece. Objects, therefore, constitute the functional units of perception (Vallortigara 2004). Over time, neurons synchronously activated by visual observation of an object, get wired together by enhanced synapses and form a resonant system that tends to activate as a single unit resulting in perception of that object. Thus, neuronal ensembles are internal equivalents of objects: while the latter are physical or external units of perception, the former are the internal units of perception; each object that has been seen and remembered by a subject is encoded by a neuronal ensemble.

The neurons of an ensemble are distributed throughout the posterior cortex (occipital, temporal, and parietal lobes). Most neurons encoding a stationary object are located within the ventral visual cortex (also known as the "what" stream) (Goodale and Milner 1992, Fig. 1). These thousands of neurons encode the various characteristics of each object, such as shape, color, texture, etc. (Quiroga et al. 2009; Waydo et al. 2006). The majority of neurons encoding one's favorite cup are located in the primary visual area (V1). A smaller number of more specific neurons are located in the extrastriate areas such as V2 and V4, and an even smaller number of the most specific neurons are located in the temporal lobe. Most humans can use their PFC to purposefully change elements of a neuronal ensemble enabling an alteration of an object's color, size, rotation, or position in space within the "mind's eye."

The role of the PFC

The PFC consists of two functionally distinct divisions. The ventromedial PFC is predominantly involved in emotional and social functions such as the control of impulse, mood, and empathy (Striedter 2004). The lateral PFC is predominantly, but not exclusively, involved in "time integrating and organizing functions, such as control of working memory and imagination" (Fuster 2008). The lateral PFC is evolutionarily related to the motor cortex and there are a number of pertinent parallels between the two (Fuster 2008; Striedter 2004). Just as the primary motor cortex can recruit motor units of voluntary muscles, the lateral PFC is able to activate neuronal ensembles in the posterior cortex. If motor units are homologous to neuronal ensembles and the lateral PFC is homologous to the motor cortex, then movement of muscles is homologous to "movement" of thoughts. The underlying mechanisms behind this "movement" of thoughts are the primary focus of the following discussion.

Lateral PFC-driven synchronization of neurons as the likely mechanism of internal computations

We have previously hypothesized that the mechanism behind the mental synthesis of independent objects involves the lateral PFC acting in the temporal domain to *synchronize* the neuronal ensembles which encode those objects (Vyshedskiy 2014, Vyshedskiy and Dunn 2015b). Once these neuronal ensembles are time-shifted by the lateral PFC to fire *in-phase* with one another, they are consciously experienced as a unified object or scene and could therefore be examined as a cohesive unit in the mind's eye. In the present analysis, we address mental synthesis as well as the simpler neurological process of modifier integration, whereby the lateral PFC modifies the activity of neurons in a single neuronal ensemble resulting in changes of an object's perceived color or size. We hypothesize that integration of modifiers also involves the lateral PFC acting in the temporal domain to *synchronize* the color encoding neurons in the visual area V4 with the object's neuronal ensemble in the ventral visual cortex. Once these neurons in V4 are time-shifted by the lateral PFC to fire *in-phase* with the object's neuronal ensemble, the object is consciously experienced in the new color. Lateral PFC-driven synchronization of neurons in the posterior cortex is likely a general mechanism necessary to achieve any *internally-driven novel* sensory experience.

From an IQ score to underlying neurology

The three neurological thresholds in the present analysis of IQ tests are 1) integration of modifiers, 2) mental rotation and modification of an object's location in space, and 3) mental synthesis of several objects. In this analysis we assume that the difficulty of extracting the rule does not change between different IQ questions. The limitations of this assumption are discussed in the "limitations" section.

1. The "Integration of modifiers" threshold. Our analysis indicates that the average IQ score for a person at the peak performance age who answers just below the "integration of modifiers" threshold is 74±7. Consulting a psychometric conversion table (Ref. Psychometric conversion table 2011), we find that 4% of the population have a non-verbal IQ score at or below this threshold. Assuming the subject's test performance is reflective of their best abilities, we can speculate on the underlying neurological organization. Since this person has answered most "find the same object" questions, the lateral PFC is capable of extracting instructions, holding a neuronal ensemble in working memory, and comparing it to the answer choices. However, the lateral PFC is unable to impel any novel features (such as new color or size) onto this existing neuronal ensemble following the instructions. According to the model described above, the lateral PFC is unable to synchronize color neurons in the cortical area V4 with the rest of the object's neuronal ensemble in the ventral visual cortex. In the verbal domain, a subject scoring below the threshold for "integration of modifiers" tasks is expected to succeed in finding a familiar noun, or color, or size, but is expected to fail to integrate a *new* color onto the familiar object. Accordingly, they may fail to correctly identify a {big/little} + {red/green/blue} + {circle/triangle/square} hidden among distracter pictures. This ability to integrate multiple modifiers is highly developed in typical children before the age of 5 (Halford 1984), but it is known to be a common challenge for children with autism (Lovaas et al. 1971). Persons with low-functioning autism spectrum disorder (ASD) often focus on only one cue at a time while ignoring other cues, a characteristic known as "stimulus overselectivity," or "tunnel vision, " or "lack of responsivity to multiple cues" (Lovaas et al. 1979; Schreibman 1988), which results in an impaired ability to integrate multiple cues and affects virtually every area of person's functioning (Ploog 2010).

What is the pathophysiology in an individual unable to perform "integration of modifiers" tasks? The underlying pathophysiology may include a general inability of the lateral PFC to phase-shift neurons or a lack of synchronous connections between the PFC and the neurons in the posterior cortex. Such synchronous connections have been observed between multiple brain areas that depend on precise timing for communication despite varying path lengths. In the cat retina, axons from peripheral regions have a greater conduction velocity than axons from neurons at the center of the retina to assure the simultaneous arrival of impulses in the brain (Fregnac et al. 1987). Experiments in rats show that myelination is the primary factor producing uniform conduction time (to within 1ms) in connections between the inferior olive nucleus in the brainstem and the cerebellar cortex, despite wide variation in axon length (Lang and Rosenbluth 2003; Sugihara et al. 1993). In cats, isochronous activation of groups of cells distributed in distant cortical locations has been shown in the visual cortex (Gray et al. 1989) and even between the two hemispheres of the brain (Engel et al. 1991). In the cerebral cortex, the layer V pyramidal neurons in the ventral temporal lobe innervate various subcortical regions. It was also shown in rats that isochronous action potential delivery to target regions located in the ipsilateral hemisphere is based on the differential conduction velocity in each fiber branch (Chomiak et al. 2008), which appears to be best explained by differential myelination changing the conduction velocity of the individual axons (Kimura and Itami 2009). The synchronous connections achieved by differential myelination were also observed in cats between the amygdala and the perirhinal cortex (Pelletier and Paré 2002) and in mice between the thalamus and the somatosensory cortex (Salami et al. 2003). Synchronous connections have also been hypothesized to be essential in humans for the lateral PFC's ability to synchronize posterior cortex neurons located at various physical distance from the PFC (Vyshedskiy 2014).

2. The "Mental rotation and modification of object's location in space" threshold. According to our analysis, the average IQ score of a person who falls just below the threshold for mental rotation and modification of object's location in space is 78±7. Consulting a psychometric conversion table (Ref. Psychometric conversion table 2011), we find that 7% of the population tested with non-verbal IQ tests scored below this threshold. A person answering below this threshold would answer all or most "find the same object" and "integration of modifiers" questions, i.e. would be able to integrate novel color and size onto a variety of neuronal ensembles. According to the model described above, the lateral PFC of such an individual would be capable of achieving synchronicity between different neurons in the ventral visual cortex (encoding the object, as well as a multitude of colors and sizes), but not between the neurons in the ventral visual cortex and the neurons in the parietal lobe, encoding an object's spatial characteristics. The subject's PFC can apply a novel color or size onto the object's neuronal ensemble in the ventral visual cortex, but cannot mentally rotate or modify an object's location in space, which would require the lateral PFC to synchronize neurons in the ventral visual cortex and in the posterior visual cortex. Thus, this cognitive disability cannot be explained by a general inability of the lateral PFC to phase-shift neurons or a lack of synchronous connections between the PFC and the neurons in the ventral visual cortex (since a subject answering below this threshold succeeded in answering all or most "integration of modifiers" questions). Rather, the pathophysiology may involve a lack of synchronous connections between the PFC and the neurons in the posterior visual cortex.

The fact that the synchronization of neurons in the posterior visual cortex is more challenging than the synchronization of neurons in the ventral visual cortex alone should not be surprising. After all, the ventral visual cortex contains the majority of neurons forming the object's neuronal ensemble. The neurons encoding the color and size are located in close physical proximity to the neurons encoding the object itself inside the ventral visual cortex. Consequently, mental integration of a novel color or size with an object requires synchronization of neurons located physically closer and should therefore be easier than synchronization of neurons between the ventral and the posterior visual cortices, located physically at different poles of the posterior cortex (Fig. 1).

An inability to mentally rotate or modify an object's location in space can be observed in some individuals with low-functioning ASD (for review, see Ref. Boucher et al. 2008, Table 14.1), linguistic isolates who were not exposed to syntactic language before the end of the critical period (Emmorey et al. 1993; Martin 2009; Martin et al. 2013; Pyers et al. 2010), and patients with damage to their lateral PFC or frontoparietal connections (Ditunno and Mann 1990; Gläscher et al. 2009; Heremans et al. 2012; Kosslyn et al. 1985).

3. The "Mental synthesis of multiple objects" threshold. Finally, the IQ score threshold for mental synthesis of two objects as calculated in our analysis is 86±10. Consulting a psychometric conversion table (Ref. Psychometric conversion table 2011), we find that 18% of the population tested with non-verbal IQ tests scored below this threshold. According to the model described above, the lateral PFC in a subject performing just below the mental synthesis threshold is able to synchronize neurons within a single neuronal ensemble to achieve integration of size, color, and spatial modifiers, but is unable to synchronize the firing of independent neuronal ensembles. It is likely that mental synthesis of independent objects requires fine temporal top-down control over many more neurons than integration of modifiers within a single object. As a result, mental synthesis of independent objects likely depends on an even finer tuning of frontoposterior connections as well as better voluntary control of the lateral PFC.

A person with a mental synthesis disability would be expected to fail in a number of language-based tests: s/he would likely be unable to understand spatial prepositions, flexible syntax, and verb tenses since these complex linguistic constructs require being able to imagine a novel situation. For example, the verbal request “to put a green box {inside/behind/on top of} the blue box” requires an initial mental simulation of the scene, only after which is it possible to correctly arrange the physical objects. An inability to produce a novel mental image of the green box {inside/behind/on top of} the blue box would lead to the use of trial-and-error (resulting, more often than not, in an incorrect arrangement). Such an individual would likely be unable to understand flexible syntax (i.e., to distinguish between the phrase “my friend chased a dog” and the phrase “a dog chased my friend”) and, furthermore, would not be able to follow instructions to draw a novel object such as *a five-headed horse*, as this process relies on mental synthesis of a never-before-seen image in the mind’s eye.

Crucially, the mental synthesis disability does not derive from a lack of semantic understanding, since the subject is tested in a *non-verbal* setting. Rather, the disability derives from a general inability of the lateral PFC to construct novel images in the mind’s eye.

A child who is not able to understand spatial prepositions and complex syntax would be commonly described as having “receptive language acquisition delay” (Baldassari et al. 2009). The data presented above show that this description is highly ambiguous. The differential diagnosis of “receptive language delay” must at the very least differentiate between the inability to associate words with objects (primarily the function of the posterior cortex) and the inability of the lateral PFC to consciously and purposefully modify these objects to construct novel images in the mind’s eye. Furthermore, language acquisition therapy in children with developmental delays may benefit from both: verbal exercises for expansion of vocabulary and grammar as well as mental synthesis exercises directed for development of synchronous frontoposterior connections.

High IQ performers

Our analysis indicates that highly difficult questions found towards the end of each IQ test primarily rely on mental synthesis of three or more neuronal ensembles. Accordingly, better performance at the high difficulty range indicates a greater ability of the lateral PFC to reorganize and time-shift neuronal ensembles in the posterior cortex. In addition, such superior performance also likely relies on finely-synchronous connections between the lateral PFC and the neuronal ensembles in the posterior cortex located at significantly different physical distances from the PFC.

Implications for children with autism

As mentioned above, the lateral PFC control over the posterior cortex is typically impaired in individuals with low-functioning autism, leading to what is commonly described as "stimulus overselectivity", or "tunnel vision" (Lovaas et al. 1979, Lovaas et al. 1971, Schreibman 1988; Ploog 2010). Improving mental integration has been shown to reduce stimulus overselectivity, which in turn leads to vast improvements in general learning (Burke and Cerniglia 1990). Currently, training a child to overcome stimulus overselectivity by developing responsivity to multiple cues is provided by language therapists who structure the natural environment in such a way that a child must use his/her lateral PFC to integrate multiple cues. In a typical verbal approach a therapist would start with tasks with one cue ("give me the crayon"), practice until a child becomes proficient and then move to more demanding tasks with two cues ("give me a red crayon"). Once the child is proficient in two cues, the therapist would move on to three cues ("give me a long, red crayon") and then four ("give me a long, red crayon from under the table"). Unfortunately, this approach fails with approximately 30-40% of children with ASD (Fombonne 2003), leaving them with a significant life-long impairment in the ability to integrate new modifiers, intentionally imagine novel scenarios and to mentally solve even the simplest of problems. These individuals, commonly referred to having low-functioning ASD, typically exhibit full-scale IQ below 70 (Beglinger and Smith 2001; Boucher et al. 2008) and perform below the score of 85 in non-verbal IQ tests (see Ref. Boucher et al. 2008, Table 14.1, Performance Quotient).

There may be several reasons for the failure of conventional language therapy in teaching mental integration. The first setback is that it requires a verbal command which makes it inaccessible to those children who have difficulty processing audio stream. The second setback of the conventional approach is that the verbal nature of the commands creates large steps between successively more demanding tasks, resulting in a steep learning curve. If a child cannot make the leap between recognizing a crayon to imagining a *novel* red crayon, then the child would be unable to make progress.

The neurological analysis of the mechanisms of mental integration suggests an additional opportunity for educating non-verbal children. Integration of modifiers, mental rotation, modification of an object's location in space, and mental synthesis of multiple objects, all rely on the synchronous connections between the lateral PFC and neurons in the posterior cortex. In neurotypical children these synchronous frontoposterior connections are acquired in an experience-dependent manner primarily through the use of syntactic language (Vyshedskiy 2014); the lack of syntactic language usage being the main culprit in non-verbal children. We hypothesized that it is possible to train the synchronous frontoposterior connections by visuospatial exercises and that such training shall result in improvement within the language domain (Vyshedskiy and Dunn 2015a). To test this hypothesis, we have developed and are currently testing a methodology based exclusively on visual puzzles, called Mental Imagery Therapy for Autism (MITA), which provides non-verbal exercises designed to facilitate the development of *synchronous frontoposterior connections* (Vyshedskiy and Dunn 2015a). MITA is currently being tested in several clinical trials.

Limitations

This study is limited in its analysis by its focus on the posterior cortex. The dynamic rearrangements of neurons inside the frontal lobe were not discussed in this report because very little is known about the frontal cortex mechanisms (De Pisapia et al. 2007; Miller 2000). Accordingly, we did not analyze changes in difficulty that result from the subject having to extract the governing rule implicit in a problem (such as “make the circle larger” or “combine these shapes”). In other words, we assume that the subject understands the imbedded instructions and an incorrect answer is a result of an inability to apply those instructions. This would be a serious problem if our report focused on the more difficult questions found at the end of each test, where extracting the rule becomes the primary challenge, but is not a major limitation for this report since the easier questions for which we discuss neurological mechanisms rely on relatively simple and comparable rules.

Furthermore, we have only considered the top-down processes used in answering IQ test questions, i.e. processes driven by the PFC, but not spontaneous bottom-up processes. Some studies have demonstrated that spontaneous bottom-up insight could result in even better outcomes than top-down reasoning (Salvi et al. 2016). The neurological mechanisms of spontaneous insight are likely very different from those of top-down PFC-driven approach. The visual perception of an insight solution may also involve *synchronization* of independent neuronal ensembles, however such synchronization is likely to be a spontaneous process. In such a process the role of the PFC may not be to phase-shift the neurons, but to select and prime the neuronal ensembles with categories relevant to a problem thus increasing their probability to fire and synchronize spontaneously with other primed ensembles.

Another limitation was that the analysis was based in large part on the subjective judgment of the panelists. The panelists reported challenges in identifying the *minimal* neurobiological requirements for the correct answer for two main reasons: 1) there were often multiple ways to arrive at the correct answer and 2) their own ability to perform mental synthesis routinely obscured other methods of solving a problem. The panelists reported that they had to apply extra effort in order to “simulate” the mind of a subject with mental synthesis disability to try to solve questions without relying on mental synthesis.

Panelists also noted that some test questions could be simplified or solved by the process of elimination of impossible answers. To reduce ambiguity, panelists were instructed to avoid this approach entirely. However, actual subjects taking the test who employ this approach would have likely answered more questions correctly and therefore received a higher IQ score. Accordingly, the IQ score threshold determined by the panel may underestimate the actual IQ score thresholds for each neurological disability.

Despite these limitations, we think that the panelists were able to grasp the gist of neurological mechanisms tested by non-verbal IQ tests and to correlate subject’s IQ score to specific neurological mechanism disability. We hope this analysis will be useful for both designers of future IQ tests and designers of educational materials for people with intellectual disabilities.

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