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The stage of development of a species predicts the number of neurons

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ABSTRACT

Does the complexity of an organism's behavior predict the number of neurons in an organism's brain? In the model of hierarchical complexity, the behavioral stage of any organism can be assessed. These behaviors fall into discrete stages. The behavioral stage of development of an organism is defined by the highest order task that an organism has been observed performing. In this study, literature was reviewed to find animals where a neuron count had been taken, and to find behavioral studies to score for stage of development. Once those determinations were made, a power regression analysis addressed the question of whether the behavioral stage of development at which a species operating at predicts the number of neurons an organism has. The relationship between these two variables was $r(17) = 0.874$. These findings imply developing to the next higher stage requires an increase in the number of neurons a species has. The evolutionary benefit from a species evolving to have more neurons may be driven by reinforcement contingencies in the environmental niche that species occupies. If these reinforcement contingencies are one order of hierarchical complexity higher than the stage the species operates at, then the species must increase the number of neuronal connections; this increase reaches a maximum dictated by the number of neurons, so there is a time when the species must evolve more neurons. to perform the comparatively more hierarchically complex tasks required to attain new reinforcement. Therefore it is the attraction of higher stage reinforcers that drives neural development. This neurological correlation for behavioral complexity shows that there is a countable amount of processing power that limits the rate of stage change in a lifetime. The accuracy with which stage of development predicts the number of neurons cast behavioral development as a driving force in neuronal evolution.

KEYWORDS: model of hierarchical complexity, animal behavior, number of neurons, neural development, neuron count, neuron number, behavioral development

As has been shown in a number of studies, brain size differs widely in different species of mammals (see Herculano-Houzel, Collins, Wong & Kaas (2007) for a brief review). Herculano-Houzel and colleagues have also shown that brains of a variety of rodents and primates differ both in terms of their number of neurons and non-neuronal cells (Herculano-Houzel et al., 2007; Herculano-Houzel, Mota & Lent, 2006). These studies showed that the size of primate brains were linearly correlated to the numbers of neurons in those brains, with the size of the cells remaining constant. In rodents, brain size increased faster than the number of neurons. This was due to the finding that in larger rodent brains there was also an increase in neuron size. Their findings show that the number of neurons are better indicators of differences between species than is total surface area or volume of brains. At the same time, the ratio of neuronal cells to nonneuronal cells is constant across studied primates. Although the authors of these papers speculate that these differences in how brains are structured must be related to the increased cognitive abilities of primates as compared to rodents, there has thus far been little actual performance data that is explicitly related to this new measure of the number of neurons in the brains of different organisms.

Note that relating brain measurements such as the number of neurons to how different species perform on a variety of tasks is a difficult one, since many of the traditional measures have been developed and used with only a very limited range of species. For example, intelligence tests, developed on humans, cannot generally be used to assess animals. On the other hand, a great deal of the literature in the learning field uses extremely simple

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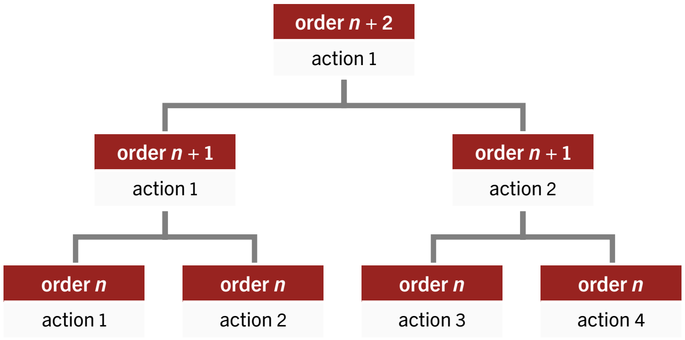

Figure 1. This figure demonstrates the coordination of same-order lower task actions by higher order task actions across two orders of complexity. Starting at the bottom of the figure, four tasks of order N are nonarbitrarily coordinated to form two tasks of order $N + 1$ and then two tasks at order $N + 1$ coordinated to form a task at order $N + 2$.

tasks that are appropriate for a variety of animal species but do not particularly tap into the higher levels of human performance. In our research group we have developed and have been working on a measure of performance that can be used across all species of animals, and is not tied to a particular type of task. This is called the *model of hierarchical complexity* (Commons & Pekker, 2008; Commons, et al. 2014).

The model of hierarchical complexity

The model of hierarchical complexity is a model of task complexity. It proposes that tasks can be ordered in terms of their hierarchical complexity using an equally-spaced unidimensional ordinal scale. It is used to predict the difficulty of behavioral tasks independent of domain and content. For a comprehensive review, see Commons, Gane-McCalla, Barker, & Li (2014).

Hierarchical complexity refers to the number of times that the coordinating actions must organize lower order actions. The hierarchical complexity of an action is determined by decomposing the action into the two or more simpler actions that make it up. This iterative process is done until the organization can only be carried out on a set of simple elements that are not built out of other actions. Actions at a higher order of hierarchical complexity can be described by several traits: *1)* They are defined in terms of actions at the next lower order of hierarchical complexity; *2)* organize and transform the lower-order actions; *3)* produce organizations of lower-order actions that are new and not arbitrary, and cannot be accomplished by those lower-order actions alone. Once these conditions have been met, the higher-order action coordinates the actions of the next lower order.

An example of the application of these axioms is shown in Figure 1. Using these axioms, it has been shown that tasks can be categorized into 17 orders of complexity (See Table 1). The order of hierarchical complexity is obtained by counting the number of hierarchical steps, with each step consisting of a coordination of lower order actions. An organism is said to be operating at a stage when it successfully completes a task at that order of hierarchical complexity (Commons, 2007).

Theory

This paper examines whether the stage of development an organism performs at predicts the number of neurons it has. The hypothesis of this paper is that neural development is an evolutionary means to obtaining higher rates of reinforcement. The mechanism is that successfully performing more hierarchically complex tasks, more reinforcement will be attained. With more reinforcement, the chances of survival should increase. The minimum number of actions required to perform a task at N order of hierarchical complexity = 2^N (Commons, Gane-McCalla, Barker, & Li, 2012), so that as task complexity rises as a power function so to should the amount processing power i.e. number of neurons.

It is important to start out by deriving a measure of stage that can be predicted. This starts with the following definition.

$$\text{Total amount of hierarchical complexity of a task} = 2^N_{OHC}.$$

This is based on Pascual-Leone's (1970) suggestion that to solve a problem at order N, there needs to be a working memory of 2^N. Due to the definitions of stage and of order given in Step 1, the stage number, N_{stage}, is the same as the number N_{OHC}, for the most hierarchically complex task solved

$$2^N_{OHC} = 2^N_{stage}.$$

Therefore, what we will be predicting is N_{stage} or performance. It is also predicted that because stage is 2 to a power, the function relating stage to the number of neurons will be a power function.

Table 1. order number and name

order	
number	name
0	computational
1	automatic
2	sensory or motor
3	circular sensory motor
4	sensory-motor
5	nominal
6	sentential
7	preoperational
8	primary
9	concrete
10	abstract
11	formal
12	systematic
13	metasystematic
14	paradigmatic
15	crossparadigmatic
16	meta-crossparadigmatic

Note. Adapted from "Correspondence between some life-span, stage" by Commons, M.L. & Tuladhar, C.T., 2014, *Behavioral Development Bulletin*, *19*(3), p.26.

The above table shows all known orders of hierarchical complexity and their corresponding numbers.

» METHOD

This paper investigates the relationship between the number of neurons and behavioral developmental stage attained in adults of a species. The number of neurons an animal had was obtained from published work. To assess stage, the highest order of hierarchical complexity of tasks completed by an adult of the species was assessed ($N = 19$). The order of hierarchical complexity of the task that each species has successfully completed was obtained from published work describing whichever task has been characteristically used with that species. This was done for eighteen different species for which adequate data on the tasks completed by that species or a highly similar species was available. The stage of an animal's performance on a task was defined as successful performance on that task of the same order. The stage data was found by scoring the tasks. The average numbers of neurons that has been measured in each species was found in published literature.

This paper predicts that the relationship between stage and number of neurons will be better expressed as a power function than as a linear function. This was tested using both linear regressions and non-linear regression, with stage of development as the independent variable and number of neurons as the dependent variable.

Animals species

Below is a list of species for which the investigator ascertained the neuron counts and had task descriptions. For each species or species group there had to be a published account of its behavior, which the investigators scored for stage of development. As can be seen, each species is placed within the stage that their behavior was scored at.

The weights of different species ascertained. When the sources for the weights in question yielded a range of weights, the mean of that range was used. When different weights for male and female members of the same species were found, the mean of those two number was used.

Automatic stage 1

At the automatic order 1, a single action that is an innate biological response to a single environmental stimulus. This stimulus is not paired with any other stimulus. Examples of the environmental stimulus could be a chemical emitted by possible food, or a physical stimulus such as light. The actions are "hard wired" into the organism. Examples include taxis, tropisms, phagocytosis and unconditionable reflexes. The organisms that perform these actions are single celled. While habituation and sensitization occur at this stage, they are not coordinated into classical conditioning (Commons & Giri, 2014). No organisms with brains have been found that operate with automatic stage 1 as their highest stage, therefore no stage 1 organisms were included in these analyses.

Sensory or motor stage 2

Respondent conditioning at order 2 of hierarchical complexity coordinates two stimulus response pairs from the lower automatic order 1. Two characteristics of this order are: ***a)*** two stimuli are paired either in a naturalistic environment or by an experimenter. In other words, an unconditioned stimulus that already elicits an unconditioned response is paired with another salient stimulus and, ***b)*** the organism's behavior does not directly cause the reinforcing stimuli in this situation as it does in operant conditioning. Reflexes that are conditioned are also order 2 behaviors.

Caenorhabditis elegans

stage:	*2*	**average weight:**	*(not found)*
neurons:	*302*[†]	**neurons per gram:**	*(not available)*

[†]*White et. al., 1986*

Caenorhabditis elegans, a kind of roundworm, has been classically conditioned in a laboratory environment (Rankin, 2000). No papers were found stating that this species has performed any tasks more hierarchically complex than being classically conditioned. Therefore the highest stage observed is stage 2, and this organisms' neuron count will be used.

Circular sensory-motor stage 3

Operant conditioning is an order 3 action. Operant conditioning is built out of the non-arbitrary coordination of three sensory or motor order 2 task actions or steps. These steps are step 1, "What to do"; step 2, "When to do it"; and step 3,"Why to do it" (Commons & Giri, in press). The three steps of respondent conditioning are from order 2 but are not coordinated until order 3.

Three very different cases of procedural respondent conditioning are used. The only commonality between the three respondent conditioning steps is the basic procedure. Those procedural steps are the "What to Do" (step 1), "When to Do" (step 2) and "Why to Do" (step 3). In step 1 of the respondent conditioning the *representation of behavior* takes on the elective properties of the s^{R+} making the *representation of behavior* salient. We leave the representation of behavior undefined. One might use common notions of it instead. In step 2, the now salient *representation of behavior* (*rb*) is paired with an environmental *s*. This makes the *s* elicit the representation of a behavior which requires the saliency of the *representation of a behavior*. In step 3, the environmental *s* is paired with the s^{R+} making the *s* more salient and valuable. When the environmental stimulus is more salient, the representation of a behavior rate relative to other *representation of a behavior*'s not associated with reinforcement increases.

Drosophila melanogaster (fruit flies)

stage:	*3*	**average weight:**	*~0.25 milligrams*[‡]
neurons:	*~100,000*[†]	**neurons per gram:**	*400,000,000*

[†]*Bharucha, 2009;* [‡]*Seiger, 1965*

Operant conditioning is the product of non-arbitrarily coordination of two or more classical conditioning contingencies (Commons & Giri, submitted). *Drosophila melanogaster* have been operantly conditioned in a laboratory environment (Brembs & Heisenberg, 2000), so they have performed an order 3 task. No order 4 tasks were found in a literature search. Therefore the highest stage observed is stage is 3.

Aplysia californica

stage:	*3*	**average weight:**	*(not found)*
neurons:	*20,000*[†]	**neurons per gram:**	*(not available)*

[†]*Retrieved November 9, 2014 from the Broad Institute website.*

Aplysia Californica have been operantly conditioned by pairing electric stimulating the anterior branch of the esophageal nerve (En2) with biting behavior (Baxter & Byrne 2006).

Apis mellifera (honey bee)

stage:	*3*	**average weight:**	*0.1 grams*[‡]
neurons:	*960,000*[†]	**neurons per gram:**	*9,600,000*

[†]*Menzel & Giurfa, 2001;* [‡]*Needham, 1995*

Erber, Pribbenow, Kisch, & Faensen (2000) trained honeybees (*Apis mellifera*) to move their antenna muscles to receive sugar water. This coordinates an arbitrary muscle motion with a reward. This simultaneously associatively conditions the bee to associate the touching of the stimuli objects with the reward of sugar water, in that non-arbitrary order. This pairs two order 2 behaviors into an order 3 task.

The only challenge to stage 3 being the ceiling of the stage that honeybees reach is the waggle dance (Von Frisch 2011). The waggle dance is a communicative act that begins when one bee returns to the hive after finding some food. This food source may be more than a kilometer away. This bee moves into the vicinity of other bees and moves its body in very particular ways. After this waggle dance is completed the bees who witnessed it navigate their way to the aforementioned food with few errors.

This behavior of following the directions from the waggle dance is a non-arbitrary sequence of operant (stage 3) behaviors, however these behaviors consist of simply following a sequence of motions over time. This paper argues that giving or following such a sequence is long chain of order 3 tasks, rather than an order 4 task. This argument is supported by the notion that the waggle dance may not be learned behavior. Ai and Hagio, (2013) found evidence that there is considerable specialization in bee anatomy that assists in the performance and response to this dance. In this case it would be an operant procedure requiring a tremendous amount of sequential coding. For the purposes of this paper, the waggle dance is a very horizontally complex order 3 task.

Rana esculenta (frog)

stage:	*3*	**average weight:**	*50 grams*[‡]
neurons:	*16,000,000*[†]	**neurons per gram:**	*320,000*

[†]Holmes, 1969; [‡]retrieved December 31, 2014, from http://a-z-animals.com/animals/common-frog/

Neveu, (2011) found that *Rana esculenta* could be trained to eat pellets, despite the fact that in the wild they only eat things that move. In this process the frogs are performing not only the order 2 task of learning to treat new substances as food, but also a whole new order 3 eating procedure.

Sensory-motor stage 4

At sensory-motor, order 4, organisms coordinate 2 or more circular sensory-motor subtask actions into a superordinate "concept." New and untrained instances of the concept are responded to correctly. These correct responses do not depend on simple stimulus generalization.

Rat

stage:	*4*	**average weight:**	*337 grams*[‡]
neurons:	*200,000,000*[†]	**neurons per gram:**	*592,592*

[†]Herculano-Houzel, 2005; [‡]retrieved December 31, 2014, from http://web.jhu.edu/animalcare/procedures/rat.html

The following is a description of order 4 behavior in rats. Rats were repeatedly presented with three scented stimuli. Two were always of identical scent, while the third was always different from the other two. The scents were different every trial. Reinforcement was received for selecting the third stimulus that was scented differently from the other two (Bailey & Thomas 1998). They had to discriminate what is termed oddity matching. This is an order 4 task, which coordinates multiple order 3 operant contingent behaviors. A literature search did not find any more hierarchically complex tasks than this performed by rats, therefore rat are operating at stage 4.

Mouse

stage:	*4*	**average weight:**	*26.5 grams*[‡]
neurons:	*71,000,000*[†]	**neurons per gram:**	*2,679,245*

[†]Herculano-Houzel, Mota, & Lent, 2006; [‡]retrieved December 31, 2014, from http://web.jhu.edu/animalcare/procedures/mouse.html

Watanabe (2013) demonstrated that mice can be conditioned to discriminate between the paintings of different artists. This process coordinates multiple order 3 (operant) cues to see the conceptual differences between paintings.

The example behaviors for rats were originally obtained from an unpublished paper by Miller, Commons, Commons-Miller, and Chen (2014).

The behavior of the following rodents was deemed to be similar enough to other rodents that the same is used for them:

Agouti

stage:	*4*	**average weight:**	*4200 grams*[‡]
neurons:	*857,000,000*[†]	**neurons per gram:**	*204,048*

[†]Herculano-Houzel, Mota, & Lent, 2006; [‡]Emmons, 1997

Capybara

stage:	*4*	**average weight:**	*50,500 grams*[‡]
neurons:	*1,600,000,000*[†]	**neurons per gram:**	*31,683*

[†]Herculano-Houzel, Mota, & Lent, 2006; [‡]Macdonald, 2006

Hamster

stage:	*4*	**average weight:**	*200 grams*[‡]
neurons:	*89,970,000*[†]	**neurons per gram:**	*449,850*

[†]Herculano-Houzel, Mota, & Lent, 2006; [‡]retrieved December 31, 2014, from http://hamsters-uk.org/content/view/70

Guinea pig

stage:	*4*	**average weight:**	*950 grams*
neurons:	*89,970,000*[†]	**neurons per gram:**	*252,232*

[†] *Herculano-Houzel, Mota, & Lent, 2006*

Nominal stage 5

Characteristics of order 5 include responding to words that represent concepts. They also follow sequences of word commands. A single word command is stage 4, sequences of them is stage 5.

A literature search was performed for dogs and cats, both are animals hypothesized to be performing at stage 5. No reliable data for the number of neurons in the whole brain was found.

Sentential stage 6

A characteristic of order 6 is following sequences of stage 5 representations of concepts. An example of this in humans is constructing sentences. This is the earliest form of grammar.

A literature search was performed for Crows, and African Grey parrots, both are animals previously informally scored to be performing at stage 5. No reliable data for the number of neurons in the whole brain was found for these animals. Some kinds of monkeys, however, can be scored at this stage.

Except when noted otherwise, weights for the primates in this section were retrieved from the University of Wisconsin Madison Primate Info Net.

Capuchin monkeys

stage:	*6*	**average weight:**	*3085 grams*
neurons:	*3,690,000,000*[†]	**neurons per gram:**	*1,196,110*

[†] *Herculano-Houzel, Collins, Wong, & Kaas, 2007*

Chen, Lakshminarayanan, and Santos (2005) performed a study where Capuchin monkeys were given tokens to trade for rewards. In this study, the Capuchin participants successfully exchanged tokens for different food rewards based of the preferences of the individual participant, and changed exchange rate of token for the different kinds of food rewards. The fact that the Capuchin monkeys changed their buying habits in response to changes in price shows that they can accurately respond multiple values for the same token. Using a token to represent a single concept is an order 6 task. Using the same token differently in different contexts coordinates multiple order 5 tasks into an order 6 task.

The behavior of the following small non-ape primates was deemed to be similar enough to squirrel monkeys that the same scoring could apply to these animals:

Squirrel monkey

stage:	*6*	**average weight:**	*861.5 grams*
neurons:	*3,246,430,000*[†]	**neurons per gram:**	*3,768,346*

[†] *Herculano-Houzel, Collins, Wong, & Kaas, 2007*

Tree shrew

stage:	*6*	**average weight:**	*190 grams*[‡]
neurons:	*261,400,000*[†]	**neurons per gram:**	*1,375,789*

[†] *Herculano-Houzel, Collins, Wong, & Kaas, 2007;* [‡] *Payne Francis, Phillips, 1985*

Marmoset

stage:	*6*	**average weight:**	*246 grams*
neurons:	*635,800,000*[†]	**neurons per gram:**	*2,584,553*

[†] *Herculano-Houzel, Collins, Wong, & Kaas, 2007*

Galago

stage:	*6*	**average weight:**	*1250 grams*[‡]
neurons:	*936,000,000*[†]	**neurons per gram:**	*748,800*

[†] *Herculano-Houzel, Collins, Wong, & Kaas, 2007*
[‡] *O'Mara, Gordon, Catlett, Terranova, & Schwartz, 2012*

Owl monkey

stage:	*6*	**average weight:**	*937.25 grams*
neurons:	*1,468,000,000*[†]	**neurons per gram:**	*1,566,284*

[†] *Herculano-Houzel, Collins, Wong, & Kaas, 2007*

Preoperational stage 7

Organisms form lists of organized sets of acts and make simple deductions that connect simple sequences of actions (without contradiction excluded). A human telling a story, for example, is like a sequence of sentences. One of the end results includes that organisms can count random events and objects placed in a row or presented in a sequence, combine numbers, and combine simple propositions.

Rhesus monkey

stage:	*7*	**average weight:**	*5300/7700 grams*[‡]
neurons:	*6,380,000,000*[†]	**neurons per gram:**	*981,538*

[†] *Herculano-Houzel, 2011;* [‡] *male/female*

Washburn and Rumbaugh (1991) trained Rhesus monkeys to select Arabic numerals associated with a number of food pellets. This task coordinates the order 6 sequence of numerals with the order 6 sequence of numbers of objects to create an order 7 action. A literature search yielded no order 8 tasks, so they are scored as operating at order 7.

Primary stage 8 and concrete stage 9

Logical deduction and empirical rules are applied in the primary order. In concrete order 8, simple logical deduction and time sequences are used to describe actual instances. The instances are actual because they occur in past or present time. They are composed of specific things, incidents events, actions, actors and places. Concrete order 8 actions are applied to a small number of specific instances.

Chimpanzees

stage:	*8*	**average weight:**	*44,000 grams*
neurons:	*26,040,000,000*†	**neurons per gram:**	*581,899*

† *estimated number of neurons based on brain weight and a model of primate data (Herculano-Houzel, 2009)*

Chimpanzees were not included in the analysis because the investigators did not find an empirical neuron count for them. The number of neurons given above is just an estimate.

Gomes and Boesch found that chimpanzees engage in a variety of trading behaviors including the exchange of meat, social support, and sex. The appraisal of value for a good or service is an order 7 task. To make a deal requires the non-arbitrary coordination of two or more such values, and it is therefore an order 8 task. No published evidence of order 9 behavior in chimpanzees has been found, so chimpanzees are scored to be operating at stage 8.

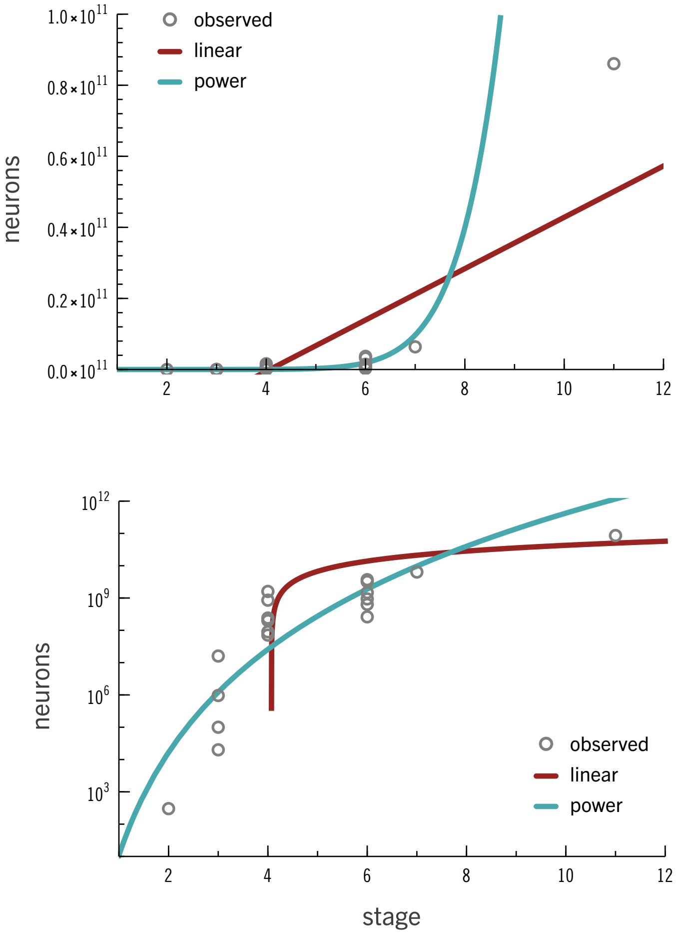

Figure 2. Both of these plots show the results of the regression of number of neurons on stage of development, though the bottom one is using log-transformed coordinates. Each circle represents a species. The *y*-axis shows the number of neurons and the *x*-axis shows the developmental stage of the species. The solid line shows a linear function, and the dotted line shows a power function.

Table 2. every animal in this analysis organized by number of neurons

species	stage	neurons	grams	neurons/grams
human	11	86,060,000,000	62,000	1,388,065
rhesus monkey	7	6,380,000,000	6,500	981,539
capuchin monkey	6	3,690,000,000	3,085	1,196,110
squirrel monkey	6	3,246,430,000	861.5	3,768,346
capybara	4	1,600,000,000	50,500	31,683
owl monkeys	6	1,468,000,000	937.25	1,566,284
galago	6	936,000,000	1,250	748,800
agouti	4	857,000,000	4,200	204,048
marmoset	6	635,800,000	246	2,584,553
tree shrew	6	261,400,000	190	1,375,789
guinea pig	4	239,620,000	950	252,232
rat	4	200,000,000	337.5	592,592
hamster	4	89,970,000	200	449,850
mouse	4	71,000,000	26.5	2,679,245
frog	3	16,000,000	50	320,000
honey bee	3	960,000	.1	9,600,000
fruitfly	3	100,000	0.00025	400,000,000
Aplysia californica	3	20,000	not found	—
C. elegans	2	302	not found	—

Abstract stage 10, formal stage 11, systematic stage 12

Humans

stage:	*10–12*	**average weight:**	*62,000 grams*†
neurons:	*86,060,000,000*	**neurons per gram:**	*1,388,065*

† *Walpole, Prieto-Merino, Edwards, Cleland, Stevens, & Roberts, 2012*

Human beings have a much wider range of developmental stages than any other animal. In Commons et al. (2005), at stage 10, humans coordinate a number of concrete instances of events, example, etc. to form variables. This allows for relative values that include such as stereotypes, ingroups and outgroups. Also emergent at this stage are variable quantities and qualities, as well as categorical assertions.

At formal stage 11, humans coordinate two variables into one-dimensional linear logic. Analytic examples of this include syllogistic logic, and univariate algebra. In univariate algebra, simple equations with one unknown (a variable) are solved. One gets a relationship between y, the dependent variable and x the independent variable.

At systematic stage 12 humans coordinate multiple stage 11 relationships among variables tasks. An example of this is solving systems of equations. (Commons et. al., 2005)

Not only are humans born at stage one, but stages 9-15 have only been observed in humans. Very few (less than 2%) of humans have been found to perform at stage 13 or above. Because of this special situation, the mean stage of stage 11 was used in the analysis (Commons, & Ross, 2008; Commons, Li, Richardson, Gane-McCalla, Barker, & Tuladhar, 2013).

The above table shows every animal in this analysis organized by number of neurons. From right to left is the name of the species, the highest stage the species was scored as operating at, the number of neurons the species has, the average weight of the species in grams, and the number of neurons the species has divided by their weight in grams.

» RESULTS

Regression of number of neurons and the stage of species

There were two groups of regressions performed. Each group used a different dependent variable: In the first group, the dependent variable was number of neurons; and in the second group the dependent variable was number of neurons per gram of body weight. For each group, first a traditional linear regression was used. And then second, a power function regression was used. This was because it was expect that a Power Function would fit much better because the number of actions required for a given stage was 2^N where N is the stage number.

Equations underlying regression

The following shows the equations underlying the regression analyses performed in this study. First, the linear regression equation is

$$y = \beta_0 + \beta_1 x, \tag{1}$$

where y is the number of neurons, x is the stage of performance of the animal, β_0 is the y-axis intercept constant in the linear case and the multiplicative constant in the power case, and β_1 is the slope constant in the linear case and the exponent in the power case.

With all values plugged in, the linear equation looks like:

$$y = 2.942 \times 10^{10} + 7.266 \times 10^9 x. \tag{2}$$

Second, the power regression equation is

$$y = \beta_0 x^{\beta_1}. \tag{3}$$

With all the values plugged in, the power equation looks like this

$$y = \beta_0 x^{\beta_1} = 7.266 \times 10^9 x^{-2.942\times10^{10}}. \tag{4}$$

Results of regression analyses

First, a linear regression was performed to examine the question of whether the average total number of neurons in a species predicts the highest stage of development observed in that species (See Figure 2). The results were $r(17) = 0.762$ ($R^2 = 0.580$, $p < 0.001$). This shows a strong relationship between number of neurons and the complexity of task observed in the animal.

As predicted, a power function predicted the number of neurons better, $r(17) = 0.874$ ($R^2 = 0.764$, $p < 0.001$) (See Figure 2). The animals with extremely high and low numbers of neurons are quite different from those in the middle

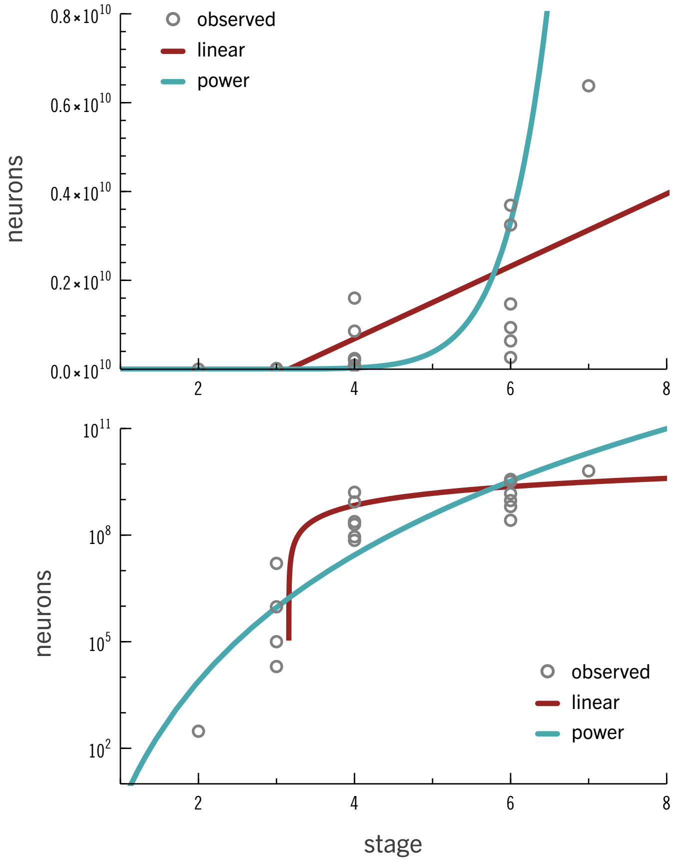

Figure 3. Both of these plots show the results of the regression of number of neurons on stage of development (not including humans), though the bottom one is using log-transformed coordinates. Each circle represents a species. The y-axis shows the number of neurons and the x-axis shows the developmental stage of the species. The solid line shows a linear function, and the dotted line shows a power function.

Regression of number of neurons on the stage of the species without humans

In order to investigate whether the extremely high stage of humans was distorting the regression, the investigators performed an additional regression that did not include humans. See Figure 2. The linear regression without humans resulted in a slightly higher $r(16) = 0.695$ and $R^2(16) = 0.483$ ($p < 0.001$). The power regression without humans resulted in a slightly higher $r(16) = 0.871$ and $R^2(16) = 0.759$ ($p < 0.001$). In summary removing humans from the regression analysis did not significantly change the results of the analysis. This figure demonstrates that there is a strong relationship between stage and neurons even when humans are not included in the analysis.

Regression of number of neurons divided by weight from the stage of the species

The next series of analyses examined the question of whether the stage of development of the species this paper discusses can be predicted by the number of neurons per gram of body weight. To test this hypothesis, stage of development of the organism divided by the weight of the organism was used to predict number of neurons. *Aplysia californica* and *Caenorhabditis elegans* were not included in this analysis, because their weight was not included. (See Figure 3).

The resulting $r(15) = 0.276$ ($R^2 = 0.077$, $p = 0.142$) was quite low. The power regression was worse $r(15) = 0.107$ ($R^2 = 0.012$, $p = 0.341$).

Stage did not predict the number of neurons to body weight ratio as well as it predicted the simple number of neurons. This may be seen by comparing the results to the other regression fits in this paper. These preliminary results support the hypothesis outlined by Herculano-Houzel (2011) that the total amount of neurons is more predictive of performance than brain size, or brain to body ratio.

Using stage of development to predict the number of neurons

The following shows how the equations underlying regression can be used to predict the number of neurons for an organism that is operating at a particular stage. As stated earlier in the results section the equation for linear regression is as follows. As stated earlier in this section, the linear prediction of how many neurons one expects to find for a stage of an animal is shown by

$$y = 2.942 \times 10^{10} + 7.266 \times 10^{9} x. \tag{5}$$

Next, it will be shown how to obtain the number of neurons from stage. As stated earlier in this section, the power equations is

$$y = \beta_0 x^{\beta_1}. \tag{6}$$

Within *ln* (natural log) form, this is

$$\begin{aligned} \ln(y) &= \ln(\beta_0) + \beta_1 x \\ y &= -2.942 \times 10^{10} + 7.266 \times 10^{9} x, \end{aligned} \tag{7}$$

where ln(y) is the natural log of the number of neurons and ln(stage) and ln(neurons) are the variables.

$$\begin{aligned} \beta_1 &= -2.942 \times 10^{10} \\ \beta_0 &= 7.266 \times 10^{9} \end{aligned}$$

With the estimates put into the equation z

$$\ln(y) = 2.153 + 11.806x. \tag{8}$$

As stated earlier in this section, put this in power function form this then becomes

$$y = \beta_0 x^{\beta_1} = 7.266 \times 10^{9} x^{-2.942 \times 10^{10}}. \tag{9}$$

Table 3. the values for the estimated parameters of equation (6) being used to predict the number of neurons an organism has

stage	β_1 slope = -2.942×10^{10}	β_0 constant = $7.266\times10^{9} x$	predicted neurons
1	−29,420,000,000	7,266,000,000	−22,154,000,000
7	−29,420,000,000	50,862,000,000	21,442,000,000
11	−29,420,000,000	79,926,000,000	50,506,000,000

Note. There cannot be a negative number of neurons which is what the constant β_0, implies.

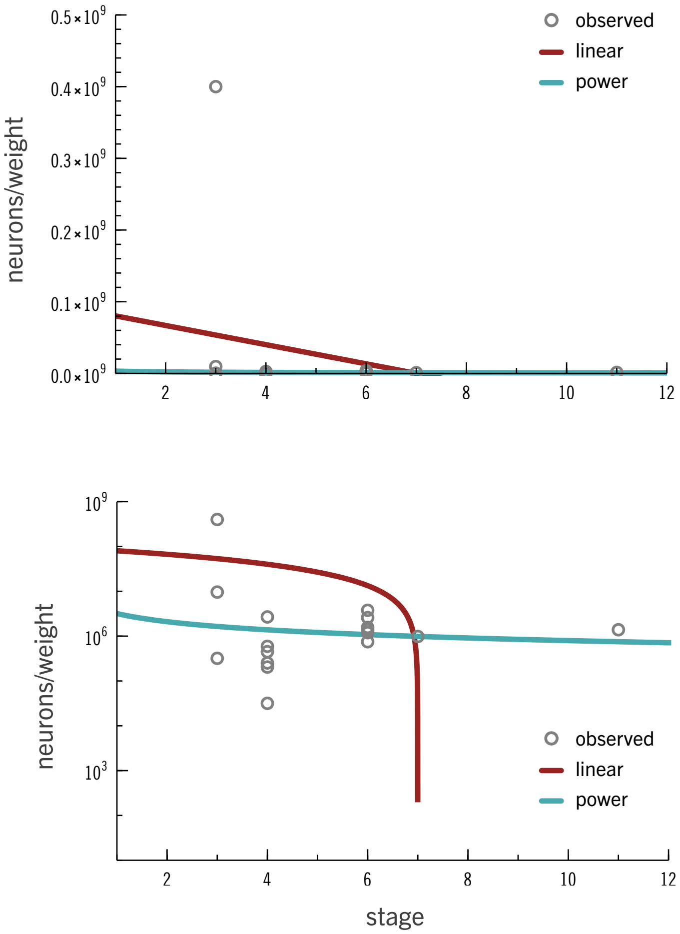

Figure 4. Both of these plots show the results of the regression of number of neurons divided by average weight on stage of development, though the bottom one is using log-transformed coordinates. Each circle represents a species. The *y*-axis shows the number of neurons and the *x*-axis shows the developmental stage of the species. The solid line shows a linear function, and the dotted line shows a power function.

Standard errors

The standard error of the parameters for the analysis that included all the species is given. Note that the standard error of the estimate of β_0 and β_1 are small compared to the size of the estimate and therefore the p values are significant.

The Standard Errors of $\beta_1(x) = 1.54\times10^9$, $p < 0.001$

The Standard Errors of $\beta_0 = 8.191\times10^9$, $p = 0.002$

Finally the standard error of the parameters in natural log form is given. Not that the standard error of the estimate of β_0 is very large and therefore the p value shows it is insignificant

The Standard Errors of $\beta_1 \ln(x) = 1.465$, $p < 0.001$

The Standard Errors of $\beta_0 = 21.274$, $p = 0.667$

» DISCUSSION

The most basic finding in this paper is that higher stage behavior requires more neurons. This means number of neurons in the brain limits development of an organism, because the number of neurons limits the number of synapses. The model of hierarchical complexity and the stage of the organism predict the number of neurons rather well.

No attempt is made to explain why there is variability in the number of neurons. A result of stage change is that it increases the chances of survival of an organism. This is because a higher stage organism can address more tasks. As the organisms on earth evolve to greater sophistication every aspect of every organism is subject to mutation. Sometimes brains mutate to have a greater number of neurons. If the organism or its offspring find a way to use these newer neurons to their evolutionary advantage, then the larger number of neurons succeeds and may eventually become the norm. Whereas if these neurons are never put to better use than a smaller amount of neurons then eventually the wasted cells will be selected against and the brain mutation will be lost. Therefore it is not enough to simply have more neurons to raise stage, but rather the organism that have found ways use incremental increases in neurons to find more advantageous behaviors throughout their evolutionary history.

Stage and energy rate density

Another central implication of this research relies on the finding that for most animals, neurons use roughly the same amount of energy per neuron. The amount of energy consumed per neuron across 6 species of rodent and primates varying in size from mice to humans varied by 40% (Herculano-Houzel, 2011). This shows the energetic consumption of the processing power of living organisms may be approximated by counting the number neurons. For a study of this scale data for more species may be required before calculations of energy rate density can be accurately performed. There has been considerable work in energetic complexity as energy rate density (Chaisson, 2012). This paper implies that the neuron could be used as a unit of hierarchical energetic complexity. That means that the stage of problem solving requires more energy as the stage increases. What is found is that the higher the stage, the more effective the animal is in obtaining total amount of energy. This rise in rate of reinforcement in turn increases energy consumption of the organism, and by this mechanism the organisms evolves to be more energetically complex, in term of control over energy in an organism's environment, and neuronal energy consumption.

Number of neurons and working memory

Next an explanation is given why stage change drives the number of neurons. Comparisons can be made between developmental stage and working memory. Developmental stage appears to be contingent on working memory. Working memory in this case is being used in the Pascual- Leone (1970) sense. In a simplified view of how hierarchical complexity and therefore stage interacts with number of neurons, we start with how order of hierarchical complexity is calculated. Higher order task actions are made from the non-arbitrary coordination of 2 or more lower order task actions. Therefore, the total number actions that need to be coordinated is 2^N, where N is the order of hierarchical complexity. Note that this is a count of actions irrespective of their order. There has to be enough "working memory" to correctly address a task, though this working memory is not directly comparable to computer memory. In order for an organism to coordinate lower order tasks into a task at the next higher stage the organism has to store and use the solutions from the lower stages long enough for the coordination to occur. Because of randomness and mutations in the variation in number of neurons there has to be enough neurons to make it possible to solve the next order problem. Working memory also includes the other requirement of the hierarchical organization. The higher order neural networks have to read the lower order neural networks.

Note that the analysis in this paper does not attend to the differences in brain structure between species. It looks only at the number of neurons. However, the results are strongly in support of the hypothesis that stage of development predicts the number of neurons in organisms. It was found that stage predicted number of neurons better than it predicted the neuron-weight ratio.

A power function proved to be more predictive/strongly correlated $r(17) = 0.860$ ($R^2 = 0.740$) than a linear model $r(16) = 0.839$ ($R^2 = 0.704$). The amount of neurons required to perform a task increases as a power function. This follows, as the number of task actions is $= 2^N$, which itself is a power function.

A more robust result could be attained by having more animals. Unfortunately, neuron counts have only begun just nine years ago (Herculano-Houzel, S. & Lent, R. 2005). Ideally, there would be at least two species for every stage and different taxonomic classes for each set of two (C. D. Barker, personal communication, December 30, 2014). For example, this analysis would benefit from having bird neuron counts, and the addition of species can further refine the model.

» CONCLUSION

Stage was used to predict number of neurons. A relatively large $r = 0.874$ was obtained. This high correlation may be interpreted as unidirectional with increase in stage leading to an increase in the number of neurons, and not the other way around. This is because higher order of hierarchical complexity tasks must exist in the environment in order for animals to obtain reinforcement for doing them. It is hypothesized that higher stage behavior afforded by neural development is an evolutionary *means* to obtaining higher rate of reinforcement. The mechanism is that successfully performing more hierarchically complex tasks, more reinforcement will be attained. With more reinforcement, the chances of survival should increase. ■

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