



Relationship between Number of Muscles, Behavioral Repertoire Size, and Encephalization in Mammals

MARK A. CHANGIZI*

Department of Psychological and Brain Sciences, Duke University, Durham, NC 27708-0086, U.S.A.

(Received on 30 October 2001, Accepted in revised form on 1 July 2002)

Behavior for mammals is built out of multiple muscles acting in a coordinated fashion. *Prima facie*, there are three principal ways to increase an animal's behavioral repertoire size. The first is to, for each new behavior type, create a set of new muscle types (e.g. triceps, sartorius, etc.) with new functions specifically devoted to the implementation of that behavior type. If this were the case, then although each behavior is built out of many muscles, behavior is not built in a combinatorial fashion out of muscles. The second is similar to the first in that new behavior types are implemented via new muscle types, but, instead, muscles are used in a combinatorial fashion, so that it is the combination of the new muscle type with existing muscle types that makes the new behavior type possible. This is analogous to the addition of new words in a language. The third way behavioral complexity may be scaled up is to increase the complexity of behavioral expressions themselves (rather than increasing the number of muscles types), namely by having more muscles involved in an average behavior. This is analogous to uttering longer sentences in a language. My main task in this paper is to examine which of these ways underlies the increase of behavioral complexity among mammals. Behavioral repertoire sizes from the ethology literature were accumulated for mammals from two dozen species across eight orders, and the number of muscle types was estimated from atlases of anatomy across eight mammalian orders. The manner in which behavioral complexity actually increases among mammals appears to favor the second possibility mentioned above: greater behavioral complexity is achieved primarily by increasing the number of muscle types, and by using muscles in a combinatorial fashion. The theoretical framework I describe allows us to interpret the manner in which the number of muscle types scales with behavioral repertoire size, and I conclude that the number of degrees of freedom in the construction of behavioral expressions is on the order of three, which is probably due to neurobiological limitations in forming behaviors. The ontogeny of behavior in rat is also discussed within this framework. Finally, I show that there is a strong positive relationship between behavioral repertoire size and encephalization among mammals.

© 2003 Elsevier Science Ltd. All rights reserved.

Introduction

If one mammal possesses more behavior types than another mammal, then what can we say, if anything, about the number of functionally distinct kinds of muscle (e.g. biceps) in each mammal? That is, in what manner do mammals

*Correspondence address: Sloan-Swartz Center for Theoretical Neurobiology, California Institute of Technology, Pasadena, CA 91125, USA. Tel.: +1 919 660 5641; fax: +1 919 660 5726.

E-mail address: changizi@changizi.com (M. A. Changizi), <http://www.changizi.com>

scale up their number of muscle types as a function of behavioral repertoire size? Do animals with more behavior types possess novel muscle types, or do they, instead, have a greater number of muscles involved in the average behavior? In this paper, I describe a theoretical framework (first introduced in Changizi, 2001b; see also Changizi, 2001c, Changizi *et al.*, 2001, and Changizi, in press) allowing us to interpret the manner in which the number of muscle types scales with the number of behavior types, whatever that manner may be. I then present data on how the number of muscle types actually scales with behavioral repertoire size, and interpret the result in light of the theoretical framework. As we will see, the empirical scaling relationship suggests that the number of muscle types increases as a function of behavioral repertoire size, that muscles are used in a language-like manner to implement behaviors, and that diverse mammals have similar combinatorial power in the construction of behaviors.

Theoretical Framework

There is a long history of treating behavior as if it is a language, where muscles act as words, or components, and combine to make behavioral sentences, or expressions (e.g. Fentress & Stilwell, 1973; Slater, 1973; Dawkins & Dawkins, 1976; Douglas & Tweed, 1979; Rodger & Rosebrugh, 1979; Gallistel, 1980; Lefebvre, 1981; Fentress, 1983; Schleidt *et al.*, 1984; Berkinblit *et al.*, 1986; Greenfield, 1991; Allott, 1992; Bizzi & Mussa-Ivaldi, 1998). With this in mind, if there are C muscle types, and they may combine into behaviors of length L (i.e. behaviors consisting of L muscles), then there are a total of $E = C(E)^{L(E)}$ possible behavior types. For example, if A and B are the only muscle types—i.e. $C = 2$ —and $L = 4$, then there are $2^4 = 16$ possible behavior types, namely AAAA, AAAB, AABA, AABB, etc. This is not sufficiently general, however, for two reasons. First, only some constant fraction α of these expression types will generally be allowable, or grammatical, where α depends on the class of animal studied. For example, perhaps only the first eight of the above 16 strings of A's and B's are grammatical, in which case $\alpha = 1/2$. More

generally, then, the relationship is $E \sim C(E)^{L(E)}$. Second, the exponent $L(E)$ assumes that all $L(E)$ degrees of freedom in building behaviors is utilized, when, generally, only some fixed fraction β of the $L(E)$ degrees of freedom may be available (due to interdependencies between muscles). Let $d(E) = \beta L(E)$ be the actual number of degrees of freedom used, and call it the *combinatorial degree*. For example, suppose that the grammatical rules require that an A always be adjacent to a B, and vice versa. Effectively, the components are now just “AB” and “BA,” and that leaves only two, not four, degrees of freedom in the construction of expressions of length 4; the possible behavioral expression types are now just ABAB, ABBA, BAAB, and BABA (assuming $\alpha = 1$), and there are only $2^2 = 4$ possible expression types. The combinatorial degree is a measure of the “effective length” of an average behavior, or “how combinatorial” behaviors are, or the number of degrees of freedom in the average behavior. The combinatorial degree can range as low as 1 to as high as L . When the combinatorial degree is 1, it means that there is effectively just one muscle per behavior, and there is no combinatorial power. Higher combinatorial degrees mean more combinatorial power, or longer effective length. The relationship between number of behavior types, number of muscle types, and combinatorial degree is, then

$$E \sim C(E)^{d(E)}. \quad (1)$$

In light of this equation, I will consider several possible ways in which behavioral repertoire size E may be scaled up.

Before doing so, however, it is important to introduce an intermediate variable that I will use in the analysis. My empirical analysis of muscle and behavior scaling will involve determining how each scales as a function of encephalization P (i.e. brain size after correcting for body size), and thereby computing how they scale relative to one another. This is justified because behavioral repertoire size E is, as we will see, highly correlated with encephalization P . There are two other reasons to plot C and E vs. P (rather than plotting C directly against E). The first is that, as we will see, there are only five

mammalian orders where I was able to obtain *both* muscle counts and ethobehavior type counts. Since encephalization is easy to acquire, all the mammalian order data from Table 1 may thereby be used. The second advantage of plotting C and E vs. P is that, as we will see, the range of P is greater than that for E , and scaling relationships are more accurately determined when the x -axis range is greater. Because of this, in introducing the possible scaling relationships below, I give examples of how the number of muscle types C and behavior types E are predicted to scale, relative to one another, against encephalization P .

Possibility I is that each new behavior type requires the addition of a set of new muscle types specialized purely for the implementation of the new behavior type. In this possibility, $E \sim C$, and thus the combinatorial degree $d = 1$. If this possibility were true, then it would not be the case that muscles are used in a combinatorial fashion to build behaviors, despite there being many muscles involved in any given behavior. Mammalian behavior would not be language-like after all. This is akin to bird vocalization, where the number of syllable types scales nearly proportionally with the number of song types (Changizi, 2001b); bird syllables do not appear to act like words (in the combinatorial sense), despite the fact that there are multiple syllables per song. For this possibility, both C and E thus are predicted to scale in the same manner as a function of encephalization, and this is shown in Fig. 1, where the log-log curve for C vs. P is parallel to the log-log curve for E vs. P . [This was a special case of possibility (a) in Changizi, 2001b.]

Possibility II is that new behavior types are accommodated by keeping the combinatorial degree d constant and > 1 , and by increasing the number of muscle types C . In this possibility, E and C are related by a power law; i.e. $E \sim C^d$, where d is constant and is > 1 . If this possibility were true, then we could conclude that muscles act combinatorially to implement behaviors (this is because $d > 1$), and thus that behavior is language-like. This is akin to the manner in which the number of word and sentence types have historically scaled in the English language, where the combinatorial degree appears to be

roughly 5 (Changizi, 2001b). For this possibility, we expect C to scale up disproportionately more slowly than E as a function of encephalization P , and this is shown in Fig. 1, where both C and E are straight lines in a log-log plot against P , but the log-log slope of C vs. P is lower (namely d times lower) than that for E vs. P . Note that the number of muscle types scales up much less quickly than in Possibility I, and thus fewer muscle types tend to be required in order to obtain E behavior types. This is one *a priori* advantage to Possibility II over Possibility I, since muscles are costly to the extent that they add to body mass generally, that there must be more genetic material coding for the new muscle type, and that there must be new brain tissue handling the new muscle type. However, this possibility comes with the cost that there must exist a relatively sophisticated (relative to Possibility I) grammar governing how muscles are combined to make behaviors. [This was possibility (a) in Changizi, 2001b.]

Possibility III is that, in order to obtain new behavior types, new muscle types are added *and* behavioral expressions themselves become more complex, having more muscles involved in them. In this possibility, C increases more slowly than as a power law as a function of E , such as $E \sim e^C$ (i.e. $C \sim \log E$) and it follows that $d \sim (\log E) / \log(\log E)$ (see Changizi, 2001b). Because the combinatorial degree is greater than 1 (but not invariant), if this possibility were the case, behavior would, as in Possibility II, be language-like. The development of words and sentences (and of phonemes and morphemes) in children appears to follow this possibility, because as children grow, their combinatorial degree increases (Changizi, 2001b). If this possibility were true, we would expect that, as in Possibility II, C should scale disproportionately more slowly than E as a function of encephalization P , but the log-log slope of C vs. P should continually decrease compared to that of E vs. P . Namely, at each value of P in the log-log plot, we expect the instantaneous slope of C vs. P to be d times less than that of E vs. P , where recall that now d is slowly increasing. This is shown in Fig. 1, where the curve begins with a slope similar to that for Possibility II, and slowly decreases as P increases. This has similar advantages and costs

TABLE 1

Estimates for number of ethobehavior types, index of encephalization, and number of muscle types for a number of mammalian orders

Order and species latin name	Species common name	No. of Behavior types	Behavior citation	Index of enceph. types	No. of Muscle	Muscle citation
Artiodactyla		27.0		0.0297	203	Raghavan (1964)
<i>Alces alces</i>	North Am. Moose	22	Geist (1963)	0.0342		
<i>Cephalophus monticola</i>	Duikers	32	Dubost	0.0252		
Carnivora		71.5		0.0862	322	Evans (1993)
<i>Felis catus</i>	Cat	69	Fagen & Goldman (1977)	0.0888		
<i>Mustela nigripes</i>	Black-footed ferret	74	Miller (1988)	0.0837		
Cetacea		123.0		0.1721		
<i>Tursiops truncatus</i>	Bottlenose dolphin	123	Muller <i>et al.</i> (1988)	0.1721		
Chiroptera		93.0		0.0679		
<i>Pteropus livingstonii</i>	Fruit bat	93	Courts (1996)	0.0679		
Didelphimorphia				0.0185	159	Ellsworth (1976)
Insectivora		54.0		0.0490		
<i>Blarina brevicauda</i>	Short-tailed shrew	54	Martin (1980)	0.0490		
Lagomorpha		30.0		0.0345	214	Popesko <i>et al.</i> (1990)
<i>Leporidae</i> (family)	White rabbit	30	Gunn & Morton (1995)	0.0345		
Perissodactyla				0.0388	245	Pasquini <i>et al.</i> (1983)
Primates		106.6		0.1789	316	Williams <i>et al.</i> (1989)
<i>Cercopithecus neglectus</i>	De Brazza monkey	44	Oswald & Lockard (1980)	0.1454		
<i>Nycticebus coucang</i>	Malaysian slow loris	80	Ehrlich & Musicant (1977)	0.1231		
<i>Galago crassicaudatus</i>	Great Galagos	97	Ehrlich (1977)	0.0977		
<i>Calithrix jacchus</i>	Common marmoset	101	Stevenson & Poole (1976)	0.1445		
<i>Homo sapiens</i>	Human child	111	Hutt & Hutt (1971)	0.3502		
<i>Papio cynocephalus</i>	Baboon	129	Coehlo & Bramblett (1981)	0.1793		
<i>Macaca nemestrina</i>	Macaque monkey	184	Kaufman & Rosenblum (1966)	0.2116		
Proboscidea				0.0731	184	Mariappa (1986)
Rodentia		38.0		0.0555	218	Greene (1935)
<i>Meriones unguicul.</i>	Mongolian gerbil	24	Roper & Polioudakis (1977)	0.0569		
<i>Peromyscus manicul.</i>	Deer mouse	29	Eisenberg (1962)	0.0569		
<i>Dolichotis patagon</i>	Mara	30	Ganslosser & Wehnelt (1977)	0.0394		
<i>Rattus norvegicus</i>	White rat	33	Draper (1967)	0.0337		
<i>Spermophilus beecheyi</i>	Ground squirrel	34	Owings <i>et al.</i> (1977)	0.0803		
<i>Rattus rattus</i>	Albino lab rat	43	Bolles & Woods (1964)	0.0337		
<i>Marmota monax</i>	Woodchuck	43	Ferron & Ouellet (1991)	0.0803		
<i>Castor canadensis</i>	Beaver	51	Patenaude (1984)	0.0383		
<i>Sciuridae</i> (four species)	Squirrel	55	Ferron (1981)	0.0803		

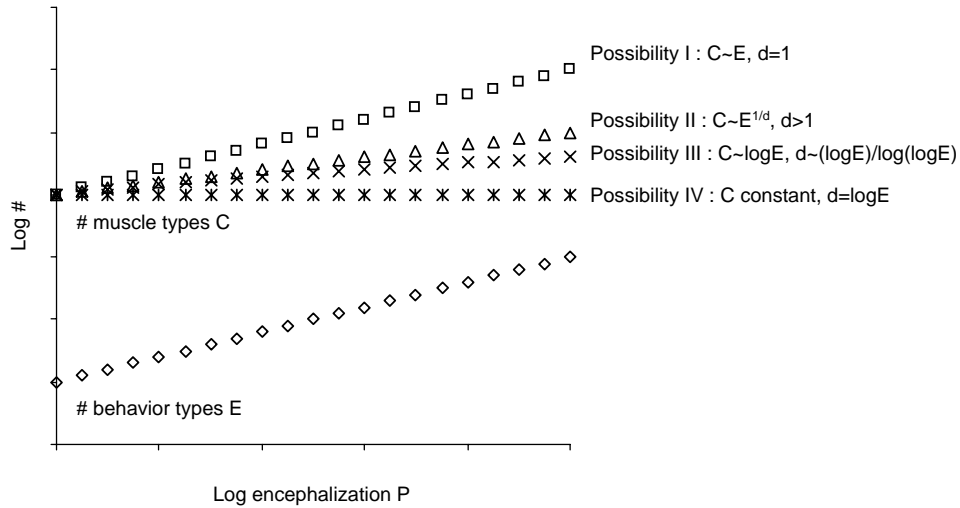


FIG. 1. Illustration of the four possible relationships between the number of muscle types C , the number of behavior types E , and encephalization P , as discussed in the text. The y -intercepts of the plot are not important to the illustration, other than to physically separate the C and E plots for viewing.

to Possibility II, except that by slowly increasing the combinatorial degree, the rate at which new muscle types must be created is even lower. [This was possibility (c) in Changizi, 2001b].

Finally, Possibility IV is that new behavior types are built *not* by the addition of any new muscle types, but purely by increasing the combinatorial degree d , in which case it must be the case that $d \sim \log E$. As in the previous two possibilities, because the combinatorial degree $d > 1$, this possibility would mean that muscles are used in a combinatorial fashion to build behaviors, and that mammalian behavior is language-like. If this possibility were true, we would expect that the number of muscle types C does not increase as a function of encephalization P , and this is shown in Fig. 1. This has the advantage that no increase in the number of muscle types need ever occur, but comes with the cost that the behavioral expressions themselves become progressively more and more complex. This possibility would mean that a fixed number of muscle types serve as a “universal behavioral language” from which any behavior may be built. [This was possibility (b) in Changizi, 2001b].

Ethobehaviors

There are multiple hierarchical levels at which behavior may be considered. At the lowest hierarchical level are muscle contractions, which

combine to instantiate simple behaviors, which, in turn, combine to make more complex behaviors, and so on. I am interested in behaviors for which it is natural to treat muscle contractions as the components, and it is thus relatively simple behaviors on which I will concentrate. The measure of the number of behaviors of an animal that I use is the *number of behaviors in a published ethogram*. Ethograms are catalogs of all the behaviors observed by the ethologist authors; I will refer to behaviors listed in ethograms as *ethobehavior types*. They are typically simple, whole-animal behaviors, such as jumping, scratching ears, burrowing, and sitting (see Appendix B for examples for rat). Ethobehaviors have the advantage that they are nearly always relatively low-level behaviors, serving themselves as components with which more complex, and higher level, behaviors are constructed; therefore, they are plausibly hierarchically just above the level of muscle contractions. (It is not important to the theoretical framework whether the two levels are really adjacent). For example, ethograms for primates tend to have on the order of 100 ethobehavior types, yet, intuitively, the number of “highest level behavior types” for primates would seem to be orders of magnitude higher than this. The 100 or so ethobehavior types for a primate cannot possibly represent its entire behavioral repertoire, and this is presumably because

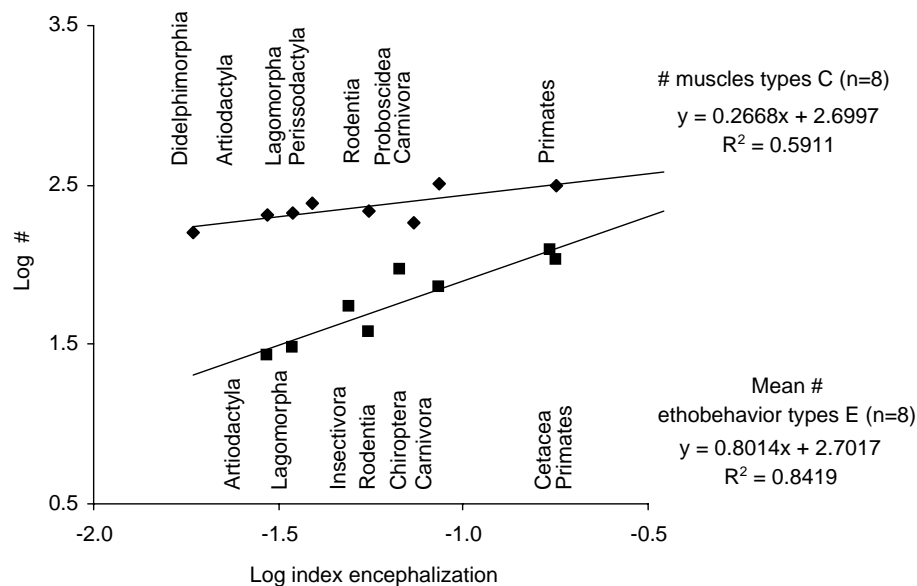


FIG. 2. Top: Logarithm (base 10) of the number of muscle types vs. the logarithm of the index of encephalization for eight mammalian orders. Bottom: Logarithm (base 10) of the mean number of ethobehavior types vs. the logarithm of the index of encephalization for eight mammalian orders.

ethobehaviors, being simple, act as components in the fabrication of higher level behaviors. Ethograms have another advantage, a tremendous practical one, that there is a long history within ethology of published ethograms, and we may access this literature for data.

There are, however, difficulties with the use of ethograms to measure behavioral repertoire size. The first is that there are no fixed, universal, standards for how ethograms are to be recorded (e.g. Schleidt *et al.*, 1984; Drummond, 1985). What counts as an ethobehavior type depends to a significant extent on the intuitions of the observer. While there can be little doubt that there is wide variability in the standards underlying delineating and counting ethobehavior types, ethogram size is nevertheless probably a useful and informative measure. Ethologists are members of an academic community and have familiarity with many ethograms from other authors. They are therefore likely to be implicitly following certain community standards they have learned, albeit rough and vague. [Note that the authors of ethograms may not be able to rigorously characterize the rules by which they count behavior types—i.e. their rules may be vague—but this does not mean ethograms are without foundation. After all, we all have

difficulty in precisely defining what we mean by the word “heap” (a vague word), but there is nevertheless tremendous agreement on the objects that are heaps and those that are not (Changizi, 1999).] Another difficulty with ethograms is that even if there were no variability among researchers in how they count ethobehavior types, what reason do we have to believe that they are counting behavior types at the “correct” resolution? For our purposes—since we are interested in how the number of muscle types *scales* with the number of behavior types—all that we require is a measure for behavioral repertoire size that is *proportional* to the actual number of behaviors. It seems plausible that if there is a tendency to overcount (or undercount) by a certain factor, then this tendency will not itself depend on the ethogram size. It would follow that overcounting (or undercounting) will not affect the utility of using ethogram size as a proportional measure of the number of behaviors. A final worry about ethograms is that perhaps ethologists record a greater number of ethobehavior types when the animal is phylogenetically close to humans. As a test for this, consider the plot in Fig. 2—to be discussed later—of the number of ethobehavior types *E* as a function of encephalization *P*, where it is

well described by the relationship $E \sim P^{0.80}$ ($R^2 = 0.842$, $n = 8$). Removing primates from the plot results in the relationship $E \sim P^{0.89}$ ($R^2 = 0.829$, $n = 7$), or substantially unchanged. (In fact, removing primates somewhat increases the exponent, which is a direction opposite to what one might expect by the present worry).

Results

I surveyed the animal behavior and ethology literature for ethograms. Many ethograms attempt to catalog just, say, mating behaviors or agonistic behaviors; I only accepted ethograms attempting to catalog all the behaviors of the animal. Ethobehavioral repertoire sizes were thereby obtained for 24 mammalian species across eight orders, and are shown in Table 1. Ethobehavioral repertoire sizes for the eight mammalian orders are estimated by averaging the values for each species within the order in Table 1. (See Changizi, in press, for ethobehavioral repertoire sizes for over two dozen non-mammals).

I obtained estimates of the number of muscle types for species within eight mammalian orders by counting up the total number of muscle types listed in atlases of anatomy for species within the order. Counts are of the number of functionally distinct kinds of muscle, such as triceps, sartorius, etc. In my analysis, I use the maximum muscle type count within an order as my estimate of the number of muscle types for that order because lower muscle type counts are due to a lack of detail in the atlas, and thus the maximum estimate is an appropriate one for an order. These maximum values and citations are shown in Table 1; the other values and citations are given in Appendix A.

Finally, I acquired from Hrdlicka (1907), Bonin (1937), Crile & Quiring (1940), and Hofman (1982a, b) estimates of body and brain mass for each species in Table 1, and computed the index of encephalization P as brain mass B (in grams) divided by body mass M (in grams) to the power of $3/4$; i.e. $P = B/M^{3/4}$. [This is appropriate since brain mass B scales as body mass M to the power of about $3/4$ (Allman, 1999; Changizi, 2001a)]. These values are shown

in Table 1, and for each order the average is computed.

Figure 2 shows how the number of muscle types C and the number of ethobehavior types E scale up as a function of index of encephalization P . One can immediately see that the number of ethobehavior types is, as in Fig. 1, highly correlated with encephalization ($R^2 = 0.842$, $n = 8$, $t = 5.81$, $p < 0.01$). [See Cole (1985), for a similar kind of plot but for ants]. In particular, the relationship is well described by a power law, with $E \sim P^{0.8}$ (95% confidence interval for exponent is ± 0.39), although the correlation under a logarithmic assumption ($E \sim \log P$) is practically identical. In light of the four possibilities discussed earlier, we can see that (i) the number of muscle types C certainly appears to increase as a function of encephalization P (namely with correlation $R^2 = 0.591$, $n = 8$, $t = 2.94$, $p < 0.05$) with a log-log slope of 0.267 (95% confidence interval of ± 0.22), and (ii) scales up disproportionately more slowly than E , which implicates Possibilities II or III (compare Fig. 1 to Fig. 2). The data are over too meager a range—especially the muscle type counts—to distinguish between these two possibilities. However, recall that for each of these possibilities, the combinatorial degree either does not change at all (Possibility II) or changes very slowly as a function of E (Possibility III). If the range for E is relatively small, as it is in our data (E ranges over less than one order of magnitude), the combinatorial degree will not much change—and, indeed, there is no evidence of a striking fall in the slope of the C vs. P plot relative to the E vs. P plot—and a single overall estimate provides a profitable summary. We can compute this by noting from Fig. 2 that $C \sim P^{0.267}$ and $E \sim P^{0.8}$, and thus $E \sim C^3$. That is, the combinatorial degree is on the order of about three. Note that a log-log plot of C directly against E , not shown, conforms well to the power law $E \sim C^{2.73}$ ($n = 5$, $R^2 = 0.914$, $p < 0.05$), but, again, cannot be statistically distinguished from $E \sim e^C$.

Discussion

Recall that the central equation from the theoretical framework is eqn (1), which stated that $E \sim C(E)^{d(E)}$, where C is the number of

muscle types, d the combinatorial degree, and E the number of behavior types. Equation (1) allowed four empirical possibilities that were discussed earlier. The results in Fig. 2 suggest that either Possibility II or Possibility III applies to mammalian behavior. Possibility II was that the number of muscle types C increases and the combinatorial degree d is invariant and greater than 1; this led to the power law relationship $E \sim C^d$ (with constant $d > 1$). Possibility III differed only in that the combinatorial degree is not invariant, but, instead, slowly increases as a function of E [namely $d \sim (\log E) / \log(\log E)$]; this led to the relationship $E \sim e^C$. What may we conclude from the fact that mammalian behavior appears to conform to either Possibility II or Possibility III?

In both Possibilities II and III, the number of muscle types C increases as a function of the number of ethobehavior types. Increasing the number of muscle types is not an *a priori* necessity, for it is possible that some fixed set of muscle types could serve as a universal language from which any behavior may be built (this was Possibility IV), analogous to the manner in which any computation (“Turing-machine behavior”) may be carried out by a Turing machine with a fixed number of primitive operations (“basic behaviors”). Mammalian behavior does not, then, use a universal language strategy.

Furthermore, the combinatorial degree d is greater than one in Possibilities II and III (unlike in Possibility I). A combinatorial degree greater than 1 means that muscles are acting in a combinatorial, or language-like, manner in the construction of ethobehaviors. It is important to recognize that this is not a trivial conclusion. One cannot conclude that behavior is language-like merely by noting that any given behavior has multiple muscles involved. Only by knowing how the number of component (muscle) types scales against the number of expression (behavior) types can one conclude that the components really act combinatorially as words. [Knowledge of the grammatical rules themselves would, of course, suffice, since from them the scaling relationship could be determined; see Changizi (2001c) for more discussion of this].

Because the results in this paper are insufficient to help us distinguish between Possibilities II and III, we cannot distinguish between an invariant combinatorial degree and a slowly increasing combinatorial degree. However, in either case, we have been able to measure its order of magnitude, and it is on the order of 3. If Possibility III holds, then perhaps the combinatorial degree begins a little below this and rises somewhat above it. What does a combinatorial degree of around 3 mean for mammalian behavior? As discussed earlier, the combinatorial degree is the number of degrees of freedom in an expression, or the effective length of an expression. A mammalian ethobehavioral expression may have dozens of muscles involved in it, yet the combinatorial degree is only on the order of 3. This is because of the highly stereotyped and mutually dependent muscle contraction activity; what appears to be an immensely complex tangle of coordinated muscle contractions is, intuitively, no more complex than if each behavior were built out of just 3 muscles, and every combination (up to a constant proportion) of 3 muscles was grammatical. This is akin to the English language where sentences tend to have 10–20 words, yet the combinatorial degree is only about 5; or bird vocalization where bird songs have about three syllables per song on average, yet the combinatorial degree appears to be nearly 1 (Changizi, 2001b, c). Just as the combinatorial degree of 5 for English is probably due to neurobiological limits of working memory (Miller, 1956), the combinatorial degree of around 3 for mammalian behavior may similarly be due to neurobiological limits in the formation of ethobehaviors from muscle contractions (a “motor working memory” limit). Because the combinatorial degree of about 3 for mammalian behavior is obtained by effectively averaging across many mammalian orders, it is possible (if Possibility III holds) that the combinatorial degree for human behavior is nearer to 5, i.e. nearer to the combinatorial degree for human language.

With the theoretical framework, I have thus far been able to illuminate *what* appears to be happening as the number of ethobehavior types increases. I have not, however, provided an explanation for *why* Possibility II or Possibility

III holds, nor why the exponent is on the order of 3. (Even if the combinatorial degree is due to some kind “motor working memory” limit, we may still wish to know why mammals have *this* limit). And I do not have an explanation for this at present. Any such explanation would have to say why natural selection would favor these possibilities over the other possibilities, and also why the combinatorial degree is roughly what it is. (Speculations on the advantages and disadvantages were mentioned when I introduced the possibilities).

The combinatorial degree of about 3 for mammalian behavior was obtained via a phylogenetic analysis, but it is also possible to assess how the number of muscle-level behavior types scales with the number of ethobehavior types in ontogeny. I observed the behavior of a litter of ten Sprague–Dawley rat pups (housed in a cage with their mother) for their first 20 days; they were videotaped for 1 hr a day, and observations made by watching the video tape. Two hierarchical levels of behavior were measured: muscle-level behaviors, and ethobehaviors. The latter concerns whole-body behaviors such as grooming and jumping, as recorded in ethograms; in all, 42 such behavior types were observed over the 20 days. The former is intended to measure the number of low-level, or muscle-level, behavior types (just as the number of muscle types across mammals is a measure of the number of muscle-level behavior types). This was done by concentrating on the behavior types displayed by the observable joints of the rat pups; that is, the individuals under observation for this low level were not pups, but pup parts. Some example low-level behavior types are body-twist, head-left-right, and lick; in all, 29 low-level behaviors were observed over the 20 days. The muscle-level behavior types and ethobehavior types are listed in Appendix B, along with the age at which the behavior was first observed in any pup. (I expect that my estimates scale roughly in proportion to the true counts, but I do not expect that my counts reflect the actual magnitudes of the repertoire sizes, especially for the low-level components where I suspect severe undercounting). The number of muscle-level behavior types C and number of ethobehavior types E are plotted against brain

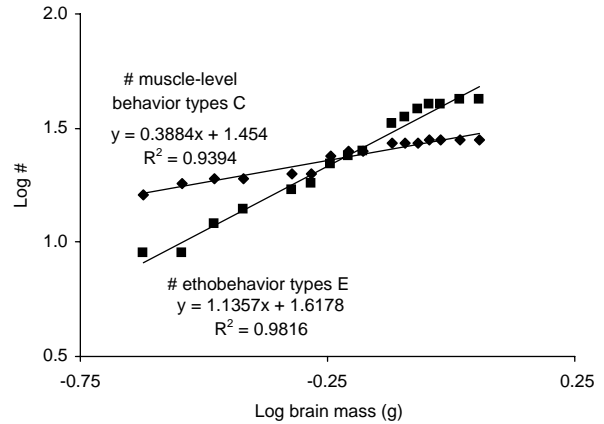


FIG. 3. Top: Logarithm (base 10) of the number of muscle-level behavior types vs. the logarithm of brain mass (g) for the first 20 days of rat development. Bottom: Logarithm (base 10) of the number of ethobehavior types vs. the logarithm of brain mass (g) for the first 20 days of rat development.

size (taken from Markus & Petit, 1987) in Fig. 3. One can immediately see a great deal of similarity to the phylogeny plot in Fig. 2: C grows as E increases, and does so disproportionately slowly compared to E . This means that, again, either Possibility II or Possibility III applies; and as was the case for phylogeny we cannot distinguish between them due to the limited data range. Computing a single approximate combinatorial degree for the ontogeny of behavior in rat gives $d \approx 2.84$ (i.e. $d = 1.1357/0.3995$), or again roughly 3. Unlike in phylogeny where I have no *a priori* reason to favor one of the Possibilities II or III, for ontogeny there is an *a priori* expectation that, since the pup’s brain is developing, the combinatorial degree may increase somewhat with age, eventually settling down to its adult value (e.g. as is the case for the ontogeny of language in Changizi, 2001b, c).

Conclusion

I have shown that there exists a relationship between number of muscle types and number of behavior types (as measured by ethograms) among mammals. In particular, the number of muscle types C increases as a function of behavioral repertoire size E , it does so disproportionately slowly, and is approximately described by the power law $E \sim C^3$, where this

exponent of 3 may be invariant, or instead may be increasing slowly as a function of E . From this empirical finding, it was possible to conclude that (i) there is no universal behavioral language employed (i.e. the number of muscles increases with behavioral repertoire size), (ii) mammalian behavior appears to be language-like in the sense that muscle contractions are used in a combinatorial fashion to build behaviors (i.e. the combinatorial degree $d > 1$), and (iii) although there may be tens of muscles involved in each behavior, the number of degrees of freedom in building behaviors from muscle contractions appears to be quite small, namely on the order of 3 (i.e. $d \approx 3$, although no conclusion can be made as to whether d is invariant). Evidence was presented suggesting that these conclusions appear to hold for ontogeny (of rat) as well as phylogeny. Also, although not the central thesis of this paper, it is notable that behavioral repertoire size appears to be significantly correlated with encephalization, which is intuitively expected, but, as far as I know, has never been verified in mammals.

I wish to thank W. G. Hall for useful discussion on these ideas.

REFERENCES

- ADAMS, D. R. (1986). *Canine Anatomy*. Ames: The Iowa State University Press.
- AGUR, A. M. R. & LEE, M. J. (1991). *Grant's Atlas of Anatomy*. Baltimore: Williams and Wilkins.
- ALLMAN, J. M. (1999). *Evolving Brains*. New York: Scientific American Library.
- ALLOTT, R. (1992). The motor theory of language: origin and function. In: *Language Origin: A Multidisciplinary Approach*. (Wind, J., Bichakjian, B. H., Nocentini, A. & Chiarelli, B. eds) pp. 123–157. Dordrecht: Kluwer.
- ANSON, B. J. (1966). *Morris' Human Anatomy*. New York: McGraw-Hill.
- ASHDOWN, R. R. & DONE, S. (1984). *Color Atlas of Veterinary Anatomy: the Ruminants*. Baltimore: University Park Press.
- BAST, T. H., CHRISTENSEN, K., CUMMINS, H., GEIST, F. D., HARTMAN, C. G., HINES, M., HOWELL, A. B., HUBER, E., KUNTZ, A., LEONARD, S. L., LINEBACK, P., MARSHALL, J. A., MILLER, G. S. Jr., MILLER, R. A., SCHULTZ, A. H., STEWART, T. D., STRAUS, W. L. Jr., SULLIVAN, W. E. & WISLOCKI, G. B. (1933). *The Anatomy of the Rhesus Monkey*. Baltimore: Williams and Wilkins.
- BERKINBLIT, M. B., FELDMAN, A. G. & FUKSON, O. I. (1986). Adaptability of innate motor patterns and motor control mechanisms. *Behav. Brain Sci.* **9**, 585–638.
- BIZZI, E. & MUSSA-IVALDI, F. A. (1998). Neural basis of motor control and its cognitive implications. *Trends Cogn. Sci.* **2**, 97–102.
- BOLLES, R. C. & WOODS, P. J. (1964). The ontogeny of behaviour in the albino rat. *Anim. Behav.* **12**, 427–441.
- BOLWIG, N. (1959). A study of the behaviour of the Chacma baboon, *Papio ursinus*. *Behaviour* **14**, 136–163.
- BONIN, G. VON (1937). Brain-weight and body-weight of mammals. *J. Gen. Psychol.* **16**, 379–389.
- BOYD, J. S., PATERSON, C. & MAY, A. H. (1991). *Clinical Anatomy of the Dog and Cat*. St. Louis: Mosby.
- BRADLEY, O. C. & GRAHAME, T. (1959). *Topographical Anatomy of the Dog*. New York: Macmillan.
- BUDRAS, K.-D. & SACK, W. O. (1994). *Anatomy of the Horse: An Illustrated Text*. London: Mosby-Wolfe.
- BUSAM, J. F. (1937). *A Laboratory Guide on the Anatomy of the Rabbit*. Boston: Spaulding-Moss.
- CHANGIZI, M. A. (1999). Vagueness, rationality and undecidability: a theory of why there is vagueness. *Synthese* **120**, 345–374.
- CHANGIZI, M. A. (2001a). Principles underlying mammalian neocortical scaling. *Biol. Cybern.* **84**, 207–215.
- CHANGIZI, M. A. (2001b). Universal scaling laws for hierarchical complexity in languages, organisms, behaviors and other combinatorial systems. *J. theor. Biol.* **211**, 277–295.
- CHANGIZI, M. A. (2001c). Universal laws for hierarchical systems. *Comments theor. Biol.* **6**, 25–75.
- CHANGIZI, M. A. *The Brain from 25,000 Feet: High Level Explorations of Brain Complexity, Perception, Induction and Vagueness*. Dordrecht: Kluwer Academic, in press.
- CHANGIZI, M. A., McDANNALD, M. A. & WIDDERS, D. (2001). Scaling of differentiation in networks: Nervous systems, organisms, ant colonies, ecosystems, businesses, universities, cities, electronic circuits, and Legos. *J. theor. Biol.*, in press.
- CHIN, E. JR. (1957). The rabbit. An illustrated anatomical guide. Master's Thesis, College of the Pacific.
- COELHO, A. M. JR. & BRAMBLETT, C. A. (1981). Interobserver agreement on a molecular ethogram of the genus *Papio*. *Anim. Behav.* **29**, 443–448.
- COLE, B. J. (1985). Size and behavior in ants: constraints on complexity. *Proc. Natl Acad. Sci. U.S.A.* **82**, 8548–8551.
- COOPER, G. & SCHILLER, A. L. (1975). *Anatomy of the Guinea Pig*. Cambridge: Harvard University.
- COURTS, S. E. (1996). An ethogram of captive Livingstone's Fruit bats *Pteropus livingstonii* in a new enclosure at Jersey Wildlife Preservation Trust. *Dodo J. Wildl. Preserv. Trusts* **32**, 15–37.
- CRAIGIE, E. H. (1966). *A Laboratory Guide to the Anatomy of the Rabbit*. Toronto: University of Toronto Press.
- CRILE, G. & QUIRING, D. P. (1940). A record of the body weight and certain organ and gland weights of 3690 animals. *Ohio J. Sci.* **40**, 219–259.
- DAWKINS, R. & DAWKINS, M. (1976). Hierarchical organization and postural facilitation: rules for grooming in flies. *Anim. Behav.* **24**, 739–755.
- DOUGLAS, J. M. & TWEED, R. L. (1979). Analysing the patterning of a sequence of discrete behavioural events. *Anim. Behav.* **27**, 1236–1252.
- DRAPER, W. A. (1967). A behavioural study of the home-cage activity of the white rat. *Behaviour* **28**, 280–306.
- DRUMMOND, H. (1985). Towards a standard ethogram: do ethologists really want one? *J. Comp. Ethol.* **68**, 338–339.

- DUBOST, PAR, G. (1983). Le comportement de *Cephalophus monticola* Thunberg et *C. dorsalis* Gray, et la place des céphalophes au sein des ruminants. *Mammalia* **47**, 141–177.
- EHRlich, A. (1977). Social and individual behaviors in captive Greater Galagos. *Behaviour* **63**, 192–214.
- EHRlich, A. & MUSICANT, A. (1977). Social and individual behaviors in captive Slow Lorises. *Behaviour* **60**, 195–220.
- EISENBERG, J. F. (1962). Studies on the behavior of *Peromyscus maniculatus gambelii* and *Peromyscus californicus parasiticus*. *Behaviour* **29**, 177–207.
- ELLSWORTH, A. F. (1976). *The North American Opossum: An Anatomical Atlas*. Huntington: Robert E. Krieger Publishing.
- EVANS, H. E. (1993). *Miller's Anatomy of the Dog*. Philadelphia: W. B. Saunders.
- FAGEN, R. M. & GOLDMAN, R. N. (1977). Behavioural catalogue analysis methods. *Anim. Behav.* **25**, 261–274.
- FENTRESS, J. C. (1983). Ethological models of hierarchy and patterning of species–species behavior. In: *Handbook of Behavioral Neurobiology* (Satinoff, E. & Teitelbaum, P., eds), pp. 185–234. New York: Plenum Press.
- FENTRESS, J. C. & STILWELL, F. P. (1973). Grammar of a movement sequence in inbred mice. *Nature* **244**, 52–53.
- FERRON, J. (1981). Comparative ontogeny of behaviour in four species of squirrels (Sciuridae). *J. Comp. Ethol.* **55**, 193–216.
- FERRON, J. & OUELLET, J.-P. (1991). Physical and behavioral postnatal development of woodchucks (*Marmota monax*). *Can. J. Zool.* **69**, 1040–1047.
- GALLISTEL, C. R. (1980). *The Organization of Action: A New Synthesis*. Hillsdale: Lawrence Erlbaum Associates.
- GANSLOSSER, U. & WEHNELT, S. (1997). Juvenile development as part of the extraordinary social system of the Mara *Dolichotis patagonum* (Rodentia: Caviidae). *Mammalia* **61**, 3–15.
- GEIST, V. (1963). On the behaviour of the North American moose (*Alces alces andersoni* Peterson 1950) in British Columbia. *Behaviour* **20**, 377–416.
- GREENE, E. C. (1935). *Anatomy of the Rat*. Philadelphia: The American Philosophical Society.
- GREENFIELD, P. M. (1991). Language, tools and brain: the ontogeny and phylogeny of hierarchically organized sequential behavior. *Behav. Brain Sci.* **14**, 531–595.
- GUNN, D. & MORTON, D. B. (1995). Inventory of the behaviour of New Zealand White rabbits in laboratory cages. *Appl. Anim. Behav. Sci.* **45**, 277–292.
- HEBEL, R. & STROMBERG, M. W. (1976). *Anatomy of the Laboratory Rat*. Baltimore: Williams and Wilkins.
- HOFMAN, M. A. (1982a). Encephalization in mammals in relation to the size of the cerebral cortex. *Brain Behav. Evol.* **20**, 84–96.
- HOFMAN, M. A. (1982b). A two-component theory of encephalization in mammals. *J. theor. Biol.* **99**, 571–584.
- HOWELL, A. B. (1926). *Anatomy of the Wood Rat*. Baltimore: Williams and Wilkins.
- HRDLICKA, A. (1907). Brain weight in vertebrates. In: *Smithsonian Miscellaneous Collections*, pp. 89–112. Washington, D.C.: Smithsonian.
- HUDSON, L. C. & HAMILTON, W. P. (1993). *Atlas of Feline Anatomy for Veterinarians*. Philadelphia: W. B. Saunders.
- HUTT, S. J. & HUTT, C. (1971). *Direct Observation and Measurement of Behaviour*. Springfield, IL: C. C. Thomas.
- KAUFMAN, J. C. & ROSENBLUM, L. A. (1966). A behavioral taxonomy for *Macaca nemestrina* and *Macaca radiata*: based on longitudinal observation of family groups in the laboratory. *Primates* **7**, 205–258.
- LEFEBVRE, L. (1981). Grooming in crickets: timing and hierarchical organization. *Anim. Behav.* **29**, 973–984.
- MARIAPPA, D. (1986). *Anatomy and Histology of the Indian Elephant*. Oak Park, Michigan: Indira Publishing House.
- MARKUS, E. J. & PETIT, T. L. (1987). Neocortical synaptogenesis, aging, and behavior: lifespan development in the motor–sensory system of the rat. *Exp. Neurol.* **96**, 262–278.
- MARTIN, I. G. (1980). An ethogram of captive *Blarina brevicauda*. *Am. Midl. Naturalist* **104**, 290–294.
- McLAUGHLIN, C. A. & CHIASSON, R. B. (1990). *Laboratory Anatomy of the Rabbit*. Dubuque: Wm. C. Brown Publishers.
- McCLURE, R. C., DALLMAN, M. J. & GARRETT, P. D. (1973). *Cat Anatomy: An Atlas, Text and Dissection Guide*. Philadelphia: Lea & Febiger.
- MILLER, B. J. (1988). Conservation and behavior of the endangered Black-footed ferret (*Mustela nigripes*) with a comparative analysis of reproductive behavior between the Black-footed ferret and the congeneric domestic ferret (*Mustela putorius furo*). Dissertation, University of Wyoming, DAI, 50, no. 03B: 08309.
- MILLER, G. A. (1956). The magical number seven, plus or minus two: some limits on our capacity for processing information. *Psychol. Rev.* **63**, 81–97.
- MÜLLER, M., BOUTIÈRE, H., WEAVER, A. C. F. & CANDELON, N. (1998). Ethogram of the bottlenose dolphin, with special reference to solitary and sociable dolphins. *Vie Milieu* **48**, 89–104.
- NETTER, F. H. (1997). *Atlas of Human Anatomy*. New Jersey: East Hanover.
- OSWALD, M. & LOCKARD, J. S. (1980). Ethogram of the De Brazza's Guenon (*Cercopithecus neglectus*) in captivity. *Appl. Anim. Ethol.* **6**, 285–296.
- OWINGS, D. H., BORCHERT, M. & VIRGINIA, R. (1977). The behaviour of California Ground squirrels. *Anim. Behav.* **25**, 221–230.
- PASQUINI, C., REDDY, V. K. & RATZLAFF, M. H. (1983). *Atlas of Equine Anatomy*. Sudz: Eureka.
- PATENAUDE, F. (1984). The ontogeny of behavior of free-living beavers (*Castor canadensis*). *J. Comp. Ethol.* **66**, 33–44.
- POPESKO, P., RAJTOVÁ, V. & HORÁK, J. (1990). *A Colour Atlas of the Anatomy of Small Laboratory Animals*. Bratislava: Wolfe Publishing.
- RAGHAVAN, D. (1964). *Anatomy of the Ox*. Calcutta: Indian Council of Agricultural Research.
- REIGHARD, J. & JENNINGS, H. S. (1929). *Anatomy of the Cat*. New York: Henry Holt and Company.
- RODGER, R. S. & ROSEBRUGH, R. D. (1979). Computing the grammar for sequences of behavioural acts. *Anim. Behav.* **27**, 737–749.
- ROHEN, J. W. & YOKOCHI, C. (1993). *Color Atlas of Anatomy*. New York: Igaku-Shoin.
- ROPER, T. J. & POLIOUDAKIS, E. (1977). The behaviour of Mongolian gerbils in a semi-natural environment, with special reference to ventral marking, dominance and sociability. *Behaviour* **61**, 207–237.
- SCHLEIDT, W. M., YAKALIS, G., DONNELLY, M. & MCGARRY, J. (1984). A proposal for a standard ethogram, exemplified by an ethogram of the

- blue-breasted quail (*Coturnix chinensis*). *J. Comp. Ethol.* **64**, 193–220.
- SCHLOSSBERG, L. & ZUIDEMA, G. D. (1997). *The Johns Hopkins Atlas of Human Functional Anatomy*. Baltimore: Johns Hopkins University Press.
- SINGH, H. & ROY, K. S. (1997). *Atlas of the Buffalo Anatomy*. Pusa, New Delhi: Indian Council of Agricultural Research.
- SISSON, S. & GROSSMAN, J. D. (1953). *The Anatomy of the Domestic Animals*. Philadelphia: W. B. Saunders.
- SLATER, P. J. B. (1973). Describing sequences of behavior. In: *Perspectives in Ethology* (Bateson, P. P. G. & Klopfer, P. H., eds.) pp. 131–153. New York: Plenum Press.
- STEVENSON, M. F. & POOLE, T. B. (1976). An ethogram of the Common Marmoset (*Calithrix jacchus jacchus*): general behavioural repertoire. *Anim. Behav.* **24**, 428–451.
- STONE, R. J. & STONE, J. A. (1990). *Atlas of the Skeletal Muscles*. Dubuque: Wm. C. Brown.
- WALKER, W. F. (1988). *Anatomy and Dissection of the Fetal Pig*. New York: W. H. Freeman.
- WAY, R. F. & LEE, D. G. (1965). *The Anatomy of the Horse*. Philadelphia: J. B. Lippincott.
- WILLIAMS, P. L., WARWICK, R., DYSON, M. & BANNISTER, L. H. (1989). *Gray's Anatomy*. New York: Churchill Livingstone.
- WINGERD, B. D. (1985). *Rabbit Dissection Manual*. Baltimore: The Johns Hopkins University Press.

APPENDIX A

Here I have listed all the muscle-type estimates for each mammalian order, only the maximum which was used in the analysis.

- Artiodactyla: 89 (Walker, 1988), 116 (Sisson & Grossman, 1953, ox), 138 (Sisson & Grossman, 1953, pig), 186 (Singh & Roy, 1997), 191 (Ashdown & Done, 1984), 203 (Raghavan, 1964).
- Carnivora: 160 (Sisson & Grossman, 1953), 169 (Bradley & Grahame, 1959), 197 (Reighard & Jennings, 1929), 204 (Boyd *et al.*, 1991, cat), 204 (Boyd *et al.*, 1991, dog), 208 (McClure *et al.*, 1973), 212 (Hudson & Hamilton, 1993), 229 (Adams, 1986), 322 (Evans, 1993).
- Didelphimorphia: 159 (Ellsworth, 1976).
- Lagomorpha: 67 (Busam, 1937), 85 (Chin, 1957), 112 (Wingerd, 1985), 126 (McLaughlin & Chiasson, 1990), 128 (Craigie, 1966), 214 (Popesko *et al.*, 1990).
- Perissodactyla: 146 (Sisson & Grossman, 1953), 172 (Way & Lee, 1965), 194 (Budras & Sack, 1994), 245 (Pasquini *et al.*, 1983).
- Primates: 160 (Schlossberg & Zuidema, 1997), 190 (Stone & Stone, 1990), 228 (Rohen

& Yokochi, 1993), 230 (Bast *et al.*, 1933), 255 (Anson, 1966), 267 (Agur & Lee, 1991), 278 (Netter, 1997), 316 (Williams *et al.*, 1989).

- Proboscidea: 184 (Mariappa, 1986).
- Rodentia: 104 (Popesko *et al.*, 1990, mouse), 113 (Popesko *et al.*, 1990, hamster), 134 (Popesko *et al.*, 1990, rat), 143 (Popesko *et al.*, 1990, guinea pig), 183 (Howell, 1926), 190 (Hebel & Stromberg, 1976), 206 (Cooper & Schiller, 1975), 218 (Greene, 1935).

APPENDIX B

Ethobehavior types recorded from rat pups during the first 20 days are here recorded, followed by the day of first appearance in at least one pup: back up, 8; bite cage, 14; bite sib, 15; break self from falling forward, 14; burrow into pile of pups, 1; clean face, 3; clean head, 12; climb wall, 8; dig chips with hands, 13; dig with hind feet, 18; eat chow or poop, 9; fight, 13; free self from pile or mother, 1; grasp bar, 18; grasp feet, 12; head search for nipple, 1; head shake, 4; jump, 15; lick body, 12; lick feet, 8; lick hands, 6; lick sib, 6; lie on back (to lick self), 12; manipulate object, 12; mouth floor, 3; push off pup, 8; righting, 1; run, 12; scratch body with hind leg, 4; scratch ears with front leg, 6; scratch ears with hind legs, 8; seeking nipple, 1; shoveling chips with head, 12; sit on haunches, 12; sleep, 1; sniff air, 10; stand, 14; suckle, 1; turn, 1; walk, 3; walk away from pile, 7; yawn, 1.

Muscle-level behavior types recorded from rat pups during the first 20 days are here recorded, followed by the day of first appearance in at least one pup: arm lateral push, 2; arm push at elbow, 1; arm push at shoulder, 1; arm push body back, 8; arm stretch, 1; body bend left-right, 1; body bend sit-up, 1; body stretch, 1; body twist, 1; chew, 12; eye open-close, 12; hand grasp, 9; hand to face, 3; head left-right, 1; head twist, 1; head up-down, 1; head rotate, 3; leg burst, 15; leg lateral push, 8; leg push at ankle, 1; leg push at knee, 1; leg stretch, 2; leg to body, 9; leg to face, 8; lick, 6; mouth open-close, 1; suck, 1; tail left-right, 1; tail up-down, 1.