

Massive Modularity and Brain Evolution

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Word Count: 5600

Abstract

Quartz (2002) argues that some recent findings about the evolution of the brain (Finlay & Darlington, 1995) are inconsistent with evolutionary psychologists' massive modularity hypothesis. In substance, Quartz contends that since the volume of the neocortex evolved in a concerted manner, natural selection did not act on neocortical systems independently of each other, which is a necessary condition for the massive modularity of our cognition to be true. I argue however that Quartz's argument fails to undermine the massive modularity hypothesis.

Massive Modularity and Brain Evolution

Introduction

Evolutionary psychologists often argue that if natural selection has shaped human cognitive architecture, human cognition is likely to be *massively modular*.¹ That is, as a first approximation, the mind is likely to consist of many systems, each having been designed by natural selection to fulfill a specific function. This proposal has encountered much resistance.² Arguments based on the nature of the brain are among the strongest objections against the massive modularity of human cognition.³ Most of these neurological objections have been rebutted—successfully, in my mind (Samuels, 1998b; Machery & Barrett, forthcoming).

In this article, I focus on a new neurological argument against the massive modularity of cognition. Steve Quartz has recently argued that an important finding about the evolution of the human brain—the allometric relation between the volume of many brain parts and the volume of the brain—is inconsistent with the massive modularity of human cognition (Quartz, 2002). If Quartz’s argument were sound, it would have major implications: Evolutionary psychologists would have to rethink one of their core tenets. In what follows, I argue however that Quartz’s argument fails to undermine the massive modularity hypothesis.

Here is how I will proceed. In the first section, I briefly elucidate the massive modularity hypothesis. In section 2, I spell out Quartz’s argument against this hypothesis. The last two sections rebut this argument. In the third section, I argue that the finding highlighted by Quartz does not show that the volume of the human neocortex did not

evolve in a mosaic manner. In the last section, I argue that even if the volume of the human neocortex did not evolve in a mosaic manner, this does not undermine the massive modularity hypothesis.

1 The Massive Modularity Hypothesis

1.1 Modules

The notion of modularity is used in many different ways in cognitive psychology and in neuropsychology. To prevent any confusion, it is useful to contrast the notion of module developed by Fodor in the *Modularity of Mind* (1983) and the notion endorsed by most evolutionary psychologists. Fodorian modules are those psychological systems that possess most of the following properties. A Fodorian module has a specific type of inputs, it produces shallow or non-conceptual outputs, it is fast, automatic, cognitively impenetrable, and informationally encapsulated, it is realized in a discrete brain area, it is innate and it has specific breakdowns. Fodor (1983) has argued that our senses, our motor systems as well as the systems underlying our linguistic faculty are modules, so defined.

Be it as it may, the notion of module that is used by evolutionary psychologists—the notion of Darwinian module—is substantially different from the notion of Fodorian module.⁴ What characterizes Darwinian modules is that they are designed to fulfill a specific function. That is, first, Darwinian modules are *adaptations*—the products of evolution by natural selection. Second, they fulfill a specific function: They evolved to *underlie a specific cognitive competence*. Third, being committed to some form of adaptationism, evolutionary psychologists often assume that modules are *well-designed* for fulfilling this function.

Some Darwinian modules might be fast and automatic, if being fast and automatic is a property of their evolved design. Other Darwinian modules might be cognitively impenetrable or informationally encapsulated, if they have been designed to fulfill their function in such a way. But, by contrast with Fodorian modules, Darwinian modules need not be fast, automatic, cognitively impenetrable, or informationally encapsulated.

Modules are neural systems. It is important to emphasize that the notion of Darwinian modularity does not entail that these systems are localized. Rather, Darwinian modules can be distributed. Since the neocortex is often believed to play an important role in cognition, many modules are likely to be, partially or entirely, neocortical systems. But, since it is also known that subcortical brain structures, such as the cerebellum, play an important role in some cognitive tasks, several modules might also involve subcortical areas.

There are very few examples of uncontroversial Darwinian modules. Famously, Tooby and Cosmides have argued for the existence of a cheater-detection module (Cosmides, 1989; Cosmides & Tooby, 1992). This hypothesized module is designed to fulfill a specific function—identifying cheaters, that is, individuals who have broken contracts and norms. Tooby and Cosmides argue that information about contracts and norms as well as information about potential cheaters are represented in a specific way. Moreover, this information feeds into a well-designed reasoning system that determines whether a given individual has broken a contract or a norm. This hypothesized cheater-detection module is supposed to be a distributed neural system. Neuropsychological evidence from brain lesions suggests that complete bilateral damage involving both the orbitofrontal cortex and the amygdala affects reasoning about social norm violations, but

not about prudential norm violations (Stone et al. 2002). Thus, the distributed neural network that involves these neural areas might be an essential component of the hypothesized cheater-detection module.¹

1.2 The Massive Modularity Hypothesis

The massive modularity hypothesis proposes that the human mind consists of many Darwinian modules. To put it differently, according to evolutionary psychologists, many human cognitive competences, such as choosing a mate, choosing one's diet, seeing, spatial orientation, face recognition, or syntactic parsing, are underwritten by dedicated Darwinian modules. For instance, it is often proposed that in humans, a cognitive system was specifically selected for recognizing faces.

Importantly, the massive modularity hypothesis is not committed to the claim that the human mind consists *only* of Darwinian modules (Tooby & Cosmides, 1992). Even though some evolutionary psychologists regard this possibility with skepticism, it is consistent with the massive modularity hypothesis that besides our modules, humans also have a cognitive system that can be put to use in many tasks, for instance a capacity to learn to solve new tasks. Moreover, evolutionary psychologists are adamant that many competences, such as reading, programming in C++, and piloting an airbus, are not underwritten by dedicated modules. There is no module whose evolved function is, say, to read, since, obviously, reading is a recent cultural invention. Rather, reading is underwritten by a collection of modules that evolved for other reasons.

2 Quartz's Argument from the Evolution of the Brain

¹ For another example, see Duchaine et al. 2001 on the fusiform face area.

Steven Quartz has recently argued that recent progresses in the study of the evolution of the human brain undermine the massive modularity hypothesis (Quartz, 2002). Quartz refers to an important finding—the allometric relation between brain parts and the whole brain. In this section, I examine this finding and I spell out Quartz’s argument.

2.1 Allometry and Evolution

The term “allometry” was introduced in 1936 by the evolutionary biologist Julian Huxley (Huxley & Teissier, 1936; Gayon, 2000). “Allometry” refers to the proportional relationship between the volume (or size, or weight, etc.) of an organ and the volume (or size, or weight, etc.) of the whole body, between the volume (or size, or weight, etc.) of the part of an organ and the volume (or size, or weight, etc.) of the whole organ, or between some physiological property and the volume (or weight, etc.) of the body. Allometric relations can be studied during development (ontogenetic allometry), across individuals (static allometry), across environments (plastic allometry), or across species (evolutionary allometry). In what follows, I focus on evolutionary allometry.

Allometric relations between the part of an organ and the whole organ (*mutatis mutandis*, for an organ or a physiological property and the body) are described by a power law:

$$1. \quad x = by^k$$

where x is the volume (size, etc.) of the part of the organ (or some other physiological property), y is the volume (size, etc.) of the organ, b and k are parameters. The parameter k is usually called “the constant differential growth-ratio.” Importantly, for a given part, k is *constant*, regardless of species, age, and environment. That is, if the volume of the part

of an organ is allometrically related to the volume of the whole organ, during evolution, the volume of the part is a function of the volume of the whole organ raised to a constant exponent.⁵

When the volumes of two organs are allometrically related, these organs cannot evolve independently of each other with respect to their volume.⁶ Particularly, if natural selection were to favor a change in volume of one of these two organs, this change would be accompanied by a related change in volume of the other organ. In such cases, evolution is said to be concerted (Striedter, 2005). By contrast, if the volume (or any other property) of an organ evolves independently of the volume of the other organs, its evolution is said to be mosaic. A simple example might cast some light on this point.

Across a large number of mammalian taxa, the metabolism rate (r), measured in kilocalorie per day, is an allometric function of the weight (w), measured in kilogram, of the organism:

$$2. \quad r = 73.3 w^{0.75}$$

In these taxa, any selection for an increased mass would have resulted in a non-selected increase in metabolism rate—and vice-versa. The body weight and the metabolism rate have a concerted evolution. Natural selection cannot favor a change in one of these two physiological variables without changing the other one.

2.2 Allometry and the Brain

Allometric relations are to be found at many levels of organic organization, from the dimensions of cells, to the blood circulation time, to the length of bones, to the weight of organs, to the volume of the brain. In what follows, I focus on allometric relations in the

brain. In an influential paper, the neuroscientists Barbara Finlay and Richard Darlington (1995) have argued that across many mammalian taxa, the volume of many brain parts is an allometric function of the volume of the whole brain.⁷ Using Stephan and colleagues' data set (Stephan, Frahm, & Baron, 1981), Finlay and Darlington (1995) mapped the logarithm of the volume of 11 adult brain parts, such as the cerebellum, the striatum, and, most important for present purposes, the neocortex, as a function of the logarithm of the volume of the brain across 131 species, including *homo sapiens*. Save for the accessory olfactory nucleus, these brain parts constitute the entire brain. Finlay and Darlington highlighted the diversity of the niches of these species as well as the range of brain sizes and body weights represented in their sample.⁸

They found that except for the main olfactory bulb, the logarithm of the volume of all the brain parts studied is a linear function of the logarithm of the volume of the brain, establishing thereby that the volume of these brain parts is a power function of the volume of the whole brain (Figure 1).

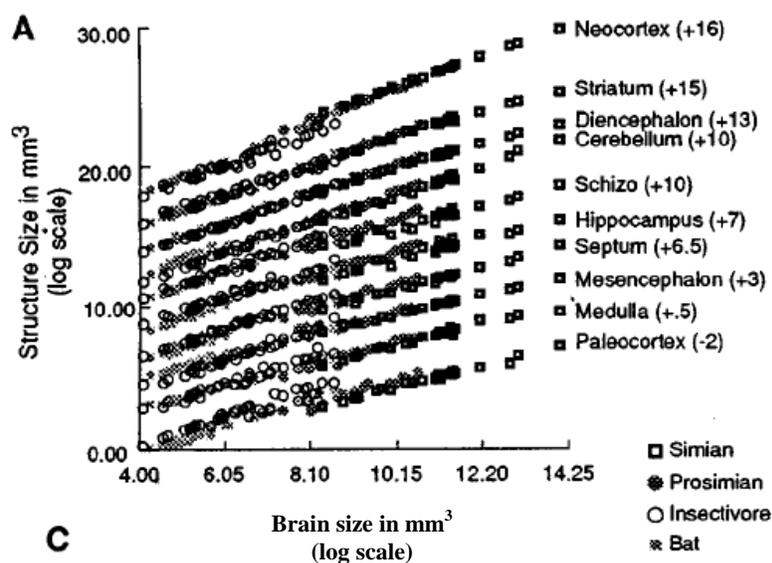


Figure 1: Allometric Relations between the Volume of the Brain and the Volume of Brain Parts
(from Finlay, Darlington, & Nicastro, 2001, 266)

Finlay and Darlington (1995) concluded that the volume of 10 of the 11 brain parts studied is an allometric function of the volume of the whole brain. They concluded that the evolution of the volume of brain parts has been concerted.⁹

2.3 Quartz's Argument

Steven Quartz (2002) has argued that Finlay and Darlington's finding was inconsistent with the massive modularity hypothesis. He writes (2002, 189):

“[D]espite a 10,000-fold range in neocortex size across mammals, the relative size of many brain structures is highly correlated. I review evidence indicating that that heterochronic changes in the duration of neurogenesis result in the coordinated pattern of brain size across a variety of mammalian species. These results, suggest that neural systems covary highly with one another as a consequence of the restricted range of permissible alterations that evolutionary psychology can act upon. This makes the massive modularity hypothesis of narrow evolutionary psychology untenable.”²

Quartz's rationale for this strong claim goes as follows. **(1)** He takes the massive modularity hypothesis to be committed to the thesis that each module has “a semi-independent evolutionary account” (2002, 190), that is, to use a more common terminology, to the thesis that modules evolved in a mosaic manner: The massive modularity is true only if it is possible for each module to have been under selective

² See also Quartz 1999, 49.

pressure independently of the other modules, at least to a large extent. This follows from the fact that each Darwinian module is supposed to have evolved to fulfill a specific function. (2) Since modules are assumed to be (maybe distributed) neural systems, particularly neocortical systems, the massive modularity hypothesis is true only if it is possible for neural systems in the neocortex to have been under selective pressure independently of one another, at least to a large extent. (3) Finlay and Darlington found that across mammalian taxa, the volume of brain parts, including the volume of the neocortex, is allometrically related to the volume of the whole brain. Quartz takes this finding to show that the necessary condition stated in (2) is not fulfilled.

Unfortunately, Quartz does not justify this last step in the argument as precisely as one might want. Why do (3) show that (2) is not fulfilled? Clark does not say. We need to reconstruct Clark's argument, by adding some implicit premises. But, as we shall see, doing so will bring to light the shortcomings of Quartz's argument. (4) The idea, it seems, is that if the volume of the brain parts considered by Finlay and Darlington, including the neocortex, is allometrically related to the volume of the whole brain, the volume of the main parts of the human brain, including the human neocortex, evolved in a concerted manner—not in a mosaic manner. (5) If the volume of the human neocortex did not evolve in a mosaic manner, then no system within the human neocortex evolved in a mosaic manner. These two premises, which remain implicit in Quartz (2002), are necessary for the argument to go through. (6) It follows from (1) to (5) that the massive modularity hypothesis is false.¹⁰

3. Mosaic Brain Evolution?

Quartz is rightly impressed by Finlay and Darlington's work. However, his rejection of the massive modularity hypothesis does not follow from their work—or so I contend in the remainder of the paper. In this section, I argue that Premise 4 ought to be rejected. Finlay and Darlington's finding does not show that the volume of the human neocortex did not evolve in a mosaic manner

3.1 What did Finlay and Darlington Really Show?

It is important not to misunderstand the significance of Finlay and colleagues' finding. They show that for a large range of mammals, the volume of the whole brain accounts for most of the variance in the volume of the brain parts under consideration, including the neocortex. The significance of this finding is that *during mammal evolution*, the increase in volume of the neocortex, did not result from a positive selection for a larger neocortex, independently of the volume of the other brain parts (*mutatis mutandis*, for the cerebellum, the striatum, etc.). But this is not tantamount to showing that during the evolution of a given species or a given taxon, the increase in volume of the neocortex has not evolved, to some extent, in a mosaic manner.

The reason is that some variance in the volume of the brain parts considered by Finlay and Darlington is not accounted for by the volume of the whole brain. Thus, for many brain volumes v , many species have a neocortex (but also a striatum, a cerebellum, etc.) whose volume diverges from the allometric expectation, based on v . Because for these species, the volume of the neocortex diverges from the allometric expectation, based on their brain volume, the volume of the neocortex has evolved in a mosaic manner

and might have been under selection, independently of the volume of the other brain parts.

An example might cast some light on this idea. Based on Krebs and colleagues' research on the volume of the hippocampus in birds that store food ("storerers") and birds that do not ("non-storerers") (Krebs, Sherry, Healy, Perry, & Vaccarino, 1989), Striedter has shown that the volume of the hippocampus, a brain structure involved in spatial memory, is allometrically related to the volume of the telencephalon (2005, 171-172). However, he found that for many species, the volume of the hippocampus diverges from allometric expectations by a factor of 2, showing that the volume of the hippocampus evolved to some extent in a mosaic manner. Importantly, storerers have a larger hippocampus than expected based on their brain volume, and non-storerers have a smaller hippocampus than expected based on their brain volume. Since across species, a large hippocampus correlates with a need for spatial memory, these divergences from allometric expectations suggest that the volume of the hippocampus has been under independent selection.

Similarly, because some variance in the volume of the neocortex is not accounted for by the brain volume, Finlay and Darlington's finding does not show that the volume of the neocortex in humans or in primates has not been under independent selection.

3.2 Evidence for Mosaic Evolution of the Neocortex

The point above raises two questions:

- Is there any evidence that the volume of the neocortex diverges from the allometric expectation in humans, or, at least, in primates?

- Is there any evidence that this divergence results from selection?

Answers to both questions are tentatively affirmative.¹¹

Barton and Harvey (2000) have reanalyzed the data set used in Finlay and Darlington (1995). Surprisingly, their analysis led to a very different conclusion. While recognizing the existence of some constraints on changes in brain volume, they concluded that these constraints do not prevent the mosaic evolution of the size of brain parts. They write (2000, 1057-1058):

“[T]he constraints are evidently insufficiently tight to prevent (...) evolutionary change in individual neural systems.”

Barton and Harvey’s analysis is not inconsistent with Finlay and Darlington’s (1995) analysis. Rather, while Finlay and Darlington focus on the fact that the brain volume accounts for most of the variance in the volume of the brain parts under consideration, Barton and Harvey focus on the unaccounted variance.

Particularly, Barton and Harvey plotted the volume of the neocortex against the volume of the non-cortical brain in a double logarithmic scale. Unsurprisingly, they found that the volume of the neocortex was an allometric function of the volume of the non-cortical brain (Figure 2).

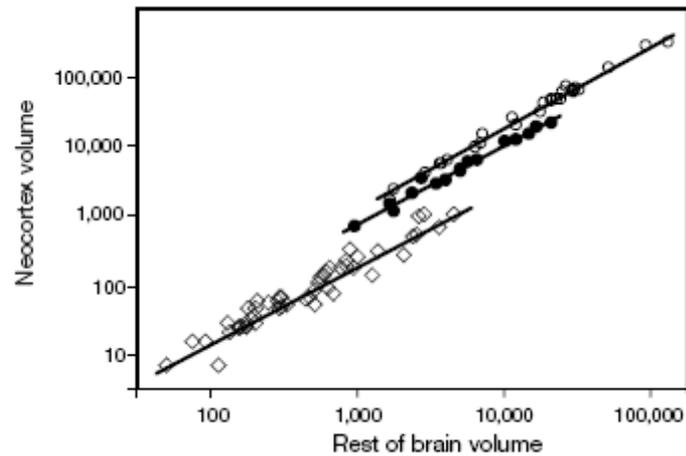


Figure 2: Allometric Relations between the Volume (mm^3) of the Non-Cortical Brain and the Volume of the Neocortex (open circles, haplorhines; closed circles, strepsirhines; diamonds, insectivores) From Baron & Harvey, 2000, 1055

However, they also found differences between the intercepts of the regression lines for the insectivore mammals and for the two primate taxa, i.e., the haplorhines, which include the tarsiers, the new-world monkeys, the old-world monkeys, and the apes, and the strepsirhines, which consist of the non-tarsier prosimians (Figure 2). These differences in intercepts mean that after having taken into account the allometric relationship between the neocortex and the whole brain, there remains a substantial difference (in fact, a fivefold difference) in the volume of the neocortex between the primates and the insectivores, as well as a smaller difference between the haplorhines and the strepsirhines.

The differences in neocortex volume between orders show that the increased volume of the neo-cortex in primates in general and in haplorhines in particular is not merely the result of its allometric relation with the volume of the whole brain. Rather,

besides the convergent evolution of the volume of the neocortex, which explains much of the increase in volume of neocortex during mammal evolution, the volume of the neocortex has also evolved in a mosaic manner in primates and, among primates, in haplorhines.

Finally, since cortical tissue is metabolically expensive (Aiello and Wheeler 1995), it is very plausible that this mosaic evolution resulted from positive selection for a larger neocortex.

3.3 An Objection

Quartz could reply that Barton and Harvey's analysis does not show that the *human* neocortex differs from the allometric expectation, based on the volume of the human brain and on the intercept for the haplorhines' regression line. Thus, evidence is lacking that the increase in volume of the human neocortex has evolved in a mosaic manner. But, if the increase in volume of the human neocortex has not evolved in a mosaic manner, then the human mind is not massively modular—or so the objection could go.

Such a reply would, however, cut both ways. It is true that Barton and Harvey's analysis does not tell whether the human brain diverges from the allometric expectation. But neither does Finlay and Darlington's analysis. Thus, Finlay and Darlington (1995) do not undermine the massive modularity hypothesis.

4. Massive Modularity Upheld

4.1 Evolution of the Neocortex vs. Evolution of its Volume

In this section, I argue that Premise 5 ought also to be rejected. To put it simply, the concerted evolution of the *volume* of the human neocortex neither entails nor suggests that *no other aspect* of the neocortex evolved in a mosaic manner.

Let's grant that the volume of the brain parts considered by Finlay and Darlington (1995), including the neocortex, evolved in a concerted manner. The main difficulty for Quartz's argument is that there is obviously more to the evolution of the neocortex than its change in volume.¹² In spite of the concerted evolution of the volume of the neocortex, distributed or localized neural systems within the neocortex might have been under selective pressure, to a large extent independently of each other and of the rest of the brain. Mosaic changes in various properties in these neocortical systems might have been selected for, such as their relative volume, their connections within each other, their internal structure, and so on.

Compare indeed the neocortex with the human body. The dimensions of many organs are allometrically related to the dimensions of the whole body. However, this neither entails nor suggests that these organs have not evolved in a mosaic manner with respect to aspects other than their dimensions. Particularly, the concerted evolution of the dimensions of a given organ in the human body is consistent with parts of this organ having been under selection independently of other parts of the same organ or of other organs. Consider the heart. The weight of the heart, in grams, is allometrically related to the weight of the body, in kilogram:

$$3. \quad w_H = 5.8 w_B^{0.98}$$

Thus, the weight of the heart and the weight of the body evolved in a concerted manner. But it would be preposterous to conclude that for this reason, no parts of the heart

evolved, in some respect or other, in a mosaic manner. The four valves in the heart are particularly well-designed for fulfilling their function, suggesting that at least to some extent, these valves have been the target of selection, independently of the other parts of the heart.

Similarly, *pace* Finlay and Darlington (1995) and Quartz (2002), the allometric relation between the volume of the neocortex and the volume of the rest of the brain is not inconsistent with the massive modularity hypothesis. Nor does it make the massive modularity hypothesis unlikely to be true.

4.2 Evidence for the Mosaic Evolution of some Neocortical Systems

Evidence suggests in fact that some neocortical systems have evolved to some extent in a mosaic manner. This shows that in general, cortical systems *could* evolve in a mosaic manner, consistent with the idea that in spite of the concerted evolution of the volume of the neocortex, selection acting on the neocortex might have favored a modular organization.

There is a large body of evidence for evolutionary changes in the neocortex during mammal evolution besides the evolution of its volume—including the addition of new cortical areas, the modification of connections, and the emergence of new cells (Striedter, 2005). For instance, primates have twice as much premotor areas than non-primates. Primates are the only mammals who possess a premotor area dedicated to the face and the mouth, with direct projections to the spinal cord (Striedter, 2005, 307). Striedter (2005) notes these evolutionary changes enable primates to increase their motor control, which was probably adaptive in the ecological niche of early primates, the “fine-

branch niche.” The issue with this body of evidence is that most of these evolutionary changes take place during the evolution of whole taxa, not during the evolution of single species. They distinguish primates from non-primate mammals, or, within primates, strepsirhines from catarrhines, and so on. An opponent of the massive modularity hypothesis might object that what is really needed to support the idea that neocortical systems could have evolved in a mosaic manner is evidence of mosaic evolutionary changes in the neocortex within the evolution of single species, preferably within the evolution of the human species. For, many modules assumed by evolutionary psychologists (but of course, not all) are supposed to be specific to a single species—namely the human species. So, the question is, Is there any evidence for the mosaic evolution of neocortical systems during the evolution of single species or at last, smaller taxa than primates or catarrhines?

The answer is affirmative. Finlay and Darlington’s work focuses on allometric relations between very coarse brain divisions (neocortex, cerebellum, striatum, etc.). The volume of the neocortical areas themselves has been left untouched. It is known, however, that the volume of many neocortical areas varies across mammals, depending on their functional importance for the species under consideration. For instance, the relative size of the somatosensory cortical areas is to a large extent predicted by their functional importance of the represented organs for the species under consideration. In the somatosensory cortex of pigs, the snout is highly represented compared to other mammals such as dogs (Striedter, 2005, 159). This suggests that the size of the area of the somatosensory cortex dedicated to the snout has been under selective pressure. The

evolution of the size of this area seems to have taken place independently of most other cortical systems.

There is also evidence that the internal structure of some cortical systems, particularly the visual system, has evolved, probably by natural selection, in a mosaic manner. Todd Preuss and colleagues have shown that there are many structural differences between, on the one hand, the visual system in humans and in apes and, on the other, the macaque visual system (e.g., Preuss, 2004). To take only one example, consider layer 4A in the macaque visual cortex. The macaque organization of this layer is widespread, though not universal, among new-world and old-world monkeys, suggesting that it was present in the ancestor of apes and humans. However, the organization of layer 4A is very different in humans and apes, showing that it has been extensively modified during ape and human evolution. It is likely that the evolution of layer 4A in hominoids' visual cortex has been independent of most (but probably not all) other neocortical areas. This example shows that a very specific property of a system of the neocortex has probably evolved in a mosaic manner. This is evidence that in spite of the concerted evolution of the volume of the neocortex, neocortical systems could evolve in a mosaic manner, which is consistent with the massive modularity hypothesis.

Conclusion

Relying extensively on Finlay and Darlington's findings, Quartz (2002) argues that the massive modularity hypothesis is false. Since the volume of the neocortex evolved in a concerted manner, he concludes that natural selection did not act on neocortical systems independently of each other, which is a necessary condition for the massive modularity

hypothesis to be true. Quartz's argument is however unsound. Finlay and Darlington's finding does not show that the volume of the human cortex did not evolve, at least to some extent, in a mosaic manner. Further, even if the volume of the human neocortex had evolved in a concerted manner, it would not follow that the neocortex and the neocortical systems did not evolve in a mosaic manner. Similarly, while the size of many organs in the human body is allometrically related to the size of the whole body, many properties of the parts of these organs have evolved to some extent in a mosaic manner. Evidence shows indeed that some neocortical systems evolved in precisely this way. Thus, *pace* Quartz, Finlay and Darlington's finding fails to undermine the massive modularity hypothesis.

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¹ See, e.g., Tooby & Cosmides, 1992; Sperber, 1994; Pinker, 1997; Carruthers, 2005; Barrett & Kurzban, forthcoming.

² See, e.g., Samuels, 1998a; Sterelny & Griffiths, 1999; Fodor, 2000.

³ See, e.g., Elman et al., 1996; Quartz & Sejnowski, 1997; Buller & Hardcastle, 2000; Bechtel, 2002; Buller, 2005, chap. 4; Kovas & Plomin, 2006.

⁴ Pinker, 1997; Samuels, 2000.

⁵ The term “allometric” (by contrast to “isometric”) is sometimes used only when the constant k differs from 1. I do not draw this distinction in this article.

⁶ *Mutatis mutandis*, for any other physiological property.

⁷ See also, e.g., Gould, 1975; Finlay et al., 2001.

⁸ The brain of mammals varies greatly in size, from less than a gram for some shrews to 1400 grams for homo sapiens.

⁹ Finlay and colleagues have also proposed a hypothesis about what type of developmental change during evolution underwrote the allometric changes in the volume of the brain parts under consideration. For the sake of space, I do not discuss this explanation.

¹⁰ Quartz’ argument against the massive modularity hypothesis dovetails nicely with the conclusion that was drawn by Finlay and Darlington themselves in their original paper (1995).

¹¹ See, particularly, Barton & Harvey, 2000; De Winter & Oznard, 2001; Striedter, 2005, chap. 5.

¹² For an overview, see Striedter, 2005.
