IS THE ANSWER REALLY BLOWING IN THE WIND? ASSESSING THE IMPACT OF CLIMACTIC VOLATILITY ON THE EVOLUTION OF THE MIND

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Abstract:

Evolutionary Psychology (EP) argues that our minds have been sculpted by recurrent selective pressures that our Pleistocene ancestors encountered over many thousands of generations. Conversely, critics of EP have made reference to the Variability Selection (VS) hypothesis in order to argue that climatic volatility has caused recent human evolution to be driven by erratic and generationally novel adaptive problems. These critics thus argue that we shouldn't expect the human mind to contain the constellations of functionally specialized mechanisms predicted by EP. Rather, we should expect natural selection to have favoured general-purpose mechanisms that would have given our ancestors the cognitive plasticity to respond to unpredictable and rapidly shifting ecological conditions. This thesis will seek to resolve this dispute in two ways. Firstly, the empirical robustness of the VS hypothesis will be queried. This will involve a paleoanthropologically informed investigation of whether there is satisfactory evidence that adaptive change correlates with periods of climactic volatility, both in relation to other species and human cognitive evolution in particular. Secondly, by appealing to cumulative cultural evolution and an enzymatic approach to modular information processing, I will examine whether critics of EP are correct to suppose that domain-specific mechanisms would have been implausible candidates for selection during periods of climactic volatility. Overall, it shall be my conclusion that the VS hypothesis is ultimately unconvincing, and that the empirical and conceptual results derived from the two modes of enquiry considered above vindicate the approach to our ancestral environment favoured by EP.

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1: Introduction:

According to Evolutionary Psychology (EP) our brain is a system of functionally-specialized mental adaptations (or 'modules') that were shaped by the recurrent adaptive problems our hunter-gatherer ancestors confronted during the Environment of Evolutionary Adaptedness (EEA).[1] Conversely, many critics of EP have made reference to paleoclimactic work by Richard Potts (1998 a, 1998 b) in order to argue that climatic volatility has caused recent human evolution to be driven by erratic adaptive problems. Consequently these critics (along with Potts) argue that we should *not* expect the human mind to contain functionally specialized mechanisms that are tethered to the regularities of a Pleistocene environment. Rather, we should expect natural selection to have favoured mechanisms that are either developmentally plastic or adapted to novelty (or some combination of both), since it is reasoned that such mechanisms would have given our ancestors the behavioural flexibility to adapt to ever shifting environmental conditions.

After providing a sufficient characterization of EP's treatment of the environment in which we acquired our species-typical adaptations (the EEA) and the way in which Richard Potts' Variability Selection (VS) hypothesis challenges this account, I shall provide an overview of empirical evidence which suggests that the evolution of multiple species has *not* been much affected by climactic volatility. Establishing this is of the utmost importance, since

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[1] Importantly, not all EPs embrace the massively modular approach to cognition endorsed by Tooby & Cosmides and cognitive anthropologists like Sperber (1994). EP – taken broadly – amounts to a field of research in psychology that attempt to understand properties of the mind in light of their possible evolution. For a useful discussion of how such an approach can depart from a massively modular brand of EP, see Buller (2005). For the remainder of this essay, I shall be examining the (dominant) modular form of EP that has its theoretical foundations in the writings of Tooby & Cosmides.

if there is a general evolutionary trend in which the emergence of adaptations correlates with periods of climactic volatility, it can strongly prime our expectations about hominine evolution also conforming to this pattern.

The next step in my argument will focus on the question of whether hominine cognitive evolution can be viewed as an exception to this pattern. In this respect, despite the fact that there is fossil evidence that hominine brain encephalization correlates strikingly with periods of climactic volatility during the Pleistocene, I shall attempt to establish that Potts underestimates the extent to which stable selective pressures in the social domain can exist despite external climactic disturbances. Indeed, I shall try to motivate the view that we can easily imagine how erratic climactic conditions can (paradoxically) exert strong stable selective pressures on the social environment. To empirically accentuate the credibility of this kind of approach, I shall argue that many social adaptations appear to be canalized, and that canalization is typically the result of stable selective environments.

Finally, both Potts and critics of EP assume that functionally specialized mechanisms (adapted to domain-specific Pleistocene problems) are less capable of generating behavioural flexibility than developmentally plastic mechanisms. Indeed, it is precisely this stance on cognition which precipitates their further claim that EP's modules could *not* have been plausible candidates for selection during periods of climactic volatility. Rather than focusing on the degree to which the EP modularity concept is compatible with developmental plasticity, I shall put the whole question of developmental plasticity aside, and (rhetorically) accept critics characterization of modules as genetically 'pre-specified' mechanisms that are ‘triggered’ into action (rather than shaped) by certain environmental inputs.[2] It shall be my claim that even if this rather uncharitable interpretation of the EP modularity concept is accepted, it can nonetheless absorb the problem of environmental novelty. More specifically, by appealing to cumulative cultural evolution and an enzymatic approach to modularity, I shall argue that a ‘massively modular’ mind does indeed have everything at its disposal to generate complex and flexible behaviour.

In my view, taken collectively, these objections provide compelling reasons for favouring EP’s account of the EEA rather than Potts’ – a conclusion I shall hopefully establish in the main body of this thesis.

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[2] Although it is not my intention to give a detailed synopsis of this issue, in my view even a cursory reading of the literature surrounding EP’s treatment of modularity and development will suffice to show that both Potts and critics are wrong to infer that EP modules are “innate” and not developmentally shaped by environmental factors (see esp. Tooby, Cosmide & Barrett, 2003).

2: Evolutionary Psychology and the EEA

EP holds the basic view that our ‘mental adaptations’ have been generated by recurrent selective pressures that Pleistocene hominines encountered over many thousands of generations in the EEA (Tooby & Cosmides, 1990).While considerations from evolutionary biology conjoined with arguments from cognitive science, artificial intelligence and developmental psychology motivate EP’s belief that modularity is a necessary structural feature of the mind[3] (Tooby & Cosmides, 1992, 2005), it is the EEA which gives EP the means to dress up the scaffolding of modularity with principled historical accounts about the specific adaptive problems our modules were designed to solve.

Furthermore, since such an account is premised upon our mind being *adapted* to a past environment, the EEA is one of the primary conceptual tools that distinguishes EP from sociobiology. In this respect, while sociobiology took behaviour itself to be adaptive and fitness maximizing (Griffiths, 2008; Symons, 1995), by being more cognitively minded and focusing on the *mechanisms* that are productive of behaviour,[4] EPs reason that natural selection cannot keep apace with the profound cultural and technological changes that have taken place in recent human history: consequently many of our modules are designed to mesh with an environment that no longer exists, a kind of ‘mismatch’ that gives rise to maladaptive behaviour. To illustrate this, EPs often mention how young urban children have a far greater fear of snakes than guns or cars (Buller, 2005) – an aversion which is patently maladaptive, since compared to being killed by a car or bullet, the chances of being taken out by an exotic

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[3] An important implication of this view is that – unlike certain evolutionary behavioural ecologists (Hawkes, 1990; Hrdy, 1999) – EPs think that the selective pressures responsible for human behaviour and development have operated at the level of genetically heritable (domain-specific) cognitive mechanisms.

[4] “To speak of natural selection as selecting for ‘behaviors’ is a convenient shorthand, but it is misleading usage. . . . Natural selection cannot select for behavior per se; it can only select for mechanisms that produce behavior” (Tooby & Cosmides, 1987).

predator in a modern industrial environment is virtually non-existent. If it is indeed true that this phobia does not owe its existence to a fear of ‘otherness’ or to gory TV specials on wild animals, and that it is innate to our psychology – and there is much evidence that this is the case (see DeLoache & LoBue, 2009) – such an example seems to nicely elucidate EP’s claim that our ‘stone-age’ mind can be thrown off kilter by present-day environments.

But, what, exactly, is the EEA? John Bowlby (1969) originally defined it as the “environment in which a species lived while its existing characteristics [...] were being evolved.” EP also views the EEA along these lines, but of course is most interested in the *human* EEA. Now, although EP’s agree that the human EEA can be bounded by a specific geological epoch during which our ancestors were hunter gatherers – the Pleistocene (roughly 2,588,000 to 11,700 years ago) – they are nonetheless adamant that the EEA is neither a particular place, habitat or time period. Rather, the EEA is a “statistical composite of the adaptation-relevant properties of the ancestral environments encountered by members of ancestral populations, weighted by their frequency and fitness consequences” (Tooby & Cosmides, 1990). EP’s work within the timeframe of the Pleistocene because they assume that it was long enough for virtually all human-specific adaptations to evolve and reach stabilization. They emphasize the ‘frequency’, or recurrence, of environmental properties because they assume only such generationally entrenched properties can have an average impact on a species’ fitness (and hence be targeted by natural selection). Finally, they highlight the ‘fitness consequences’ and ‘adaptation-relevant’ properties of the environment because EP’s conception of the EEA excludes any environmental properties that had no long term bearing upon human reproduction or survival.

All this is well and good, but how can EPs confidently know even the broad outlines of a vanished world that existed millions of years ago? Cosmides’ & Tooby’s (1989) flagship study of the cheat-detection module exemplifies one kind of multi-tiered approach to this problem. Noting that A) general evolutionary theory predicts that *any* cooperative system requiring reciprocation cannot tolerate cheaters (Axelrod, 1984; Triver, 1971) and that B) tit for tat social exchange is a cross-culturally universal human practice that is C) especially integral to hunter-gatherer societies and D) is rudimentarily present in primates, Cosmides & Tooby hypothesize that selection pressures for detecting cheats were part of the EEA. The reasons why these strands of evidence motivate Cosmides & Tooby's prediction is readably explainable. Firstly, classical evolutionary theory predicts that only certain kinds of evolutionary strategies can be stable (Maynard Smith, 1974) – thus if humans display an exchange system premised on reciprocal altruism, like all other species in existence, they *must* have evolved ways in which to detect and punish free riders (since blind reciprocity is not an evolutionary stable strategy). Secondly, the recurrence of a cultural trait across diverse and unrelated cultures is often taken to strongly suggest that a history of natural selection (rather than particular environmental or cultural contingencies) best explains the trait (see Sperber & Bloch, 2002). Thirdly, while present day hunter-gatherers are clearly not evolutionary throwbacks to Pleistocene hominines, they do offer the closest living approximation to an evolutionary ancient way of life that we've got – consequently traits prominently ingrained into a hunter gatherer way of life shed light on modes of behaviour that were most probably targeted for selection during the Pleistocene. Lastly, a descent with modification approach to Evolution (see Barrett, 2012; Nadal, Marcos *et al.*, 2009) – in which natural selection can be figuratively seen as a tinkerer (Jacobs, 1977) who hashes new adaptations out of pre-existent material – strongly indicates that if a species that is phylogenetically close to us (like chimpanzees) already possess adaptations for social exchange and the punishment of cheaters (see Brosnan & de Waal, 2003; Nichols & Mallon, 2006), there is good reason to suspect that selective pressures upon these adaptive traits would have continued into the human EEA.

Crucially, it must be stressed that EPs never suppose that this kind of theorizing scientifically confirms anything about the EEA. Rather, such theories are initially used to characterize the EEA in hypothetical terms. EPs then conduct experiments to determine if our psychology does indeed contain specialized mechanisms to solve a hypothesized EEA problem. It is the empirically verifiable existence of such a mechanism which confirms a particular fact about the EEA. Thus considered, a final significant fact about the EEA is revealed – as EP's primary hypothesis generator, the EEA is critical to EP's fundamental aspiration to become a credible scientific discipline.

Needless to say, the methods used by EP to reconstruct the EEA have proved particularly controversial. For instance, grave scepticism has been expressed about whether hunter-gatherer studies and primatolologcal data can tell us anything legitimate about our evolutionary ancestors (Buller, 2005; Headland & Reid, 1989). On these grounds alone, the EEA is, and remains, a controversial topic. However, since these criticisms has been largely addressed (successfully in my view) [see Machery & Barrett, 2005; Marlowe, 2002], in what follows I shall instead focus on a widespread complaint that has not received much – if any – attention from defenders of EP. This neglect is surprising, since, more than any other criticism, it attacks one of the most integral aspects of EP's understanding of the EEA.

3: The Variability Selection Hypothesis

In a series of influential papers (1998a, 1998b), the paleoanthropologist Richard Potts has sought to explain human evolution using the Variability Selection (VS) hypothesis. Cataloguing much empirical evidence[5] that a volatile and unpredictable climate reigned through much of the Pleistocene[6], and that it dramatically remodelled habitats in unpredictable bursts[7], Potts' theory stresses the *indeterminacy* of any selective regime during the Pleistocene. The VS hypothesis therefore puts forth the idea that natural selection favoured organisms with the adaptive flexibility to respond to high degrees of environmental variation and novelty. Crucially, though, Potts is careful to frame adaptive flexibility in a way that distinguishes it from phenotypic plasticity and the widening of genetic reaction norms. In this respect, while Potts is fully adamant that phenotypic plasticity offers one means to obtain adaptive flexibility, he carefully distinguishes it from VS on the grounds that VS produces mechanisms that are responsive to *novel* adaptive problems that are not anchored to any specific environment or range of environments previously experienced. In contrast, Potts cites mathematical modelling of phenotypic plasticity (Bull, 1987; Travis, 1994; Slatkin & Lande, 1976) which purportedly show that plasticity is favoured when "the environment varies between certain optimal values, each favoring an alternative phenotype" (Potts, 1998a). On this view, phenotypic plasticity is an adaptation to a selective environment in which variability can either make one phenotype or another phenotype optimal. However, due to its

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[5] This evidence is obtained through analyses of pollen samples and lake shrinkages, as well as through studies of isotopic traces and windblown continental dust found in deep sea cores. For a fascinating discussion on how and why this evidence is used to reconstruct ancient climates and habitats see Potts, 1998a, 1998b.

[6] The Pleistocene is commonly acknowledged to be a time of "massive climactic fluctuation" during which "periods of cold and warm climate occurred at irregular intervals and with varying durations" at an extent and the speed "quite remarkable" (Hofreiter & Stewart, 2009).To take just one example, there were "decade-scale oscillations between glacial and warm conditions" (Potts, 1998a).

[7] For instance "in Asia and eastern Europe, shifts between dense, moist forest and cold, dry steppe occurred repeatedly during the past 1 million years over large regions" (Potts, 1998a).

sensitivity to the wildness of Pleistocene climactic volatility, VS places far greater emphasis on environmental indeterminacy, painting a picture in which it is entirely likely that " no single combination of factors (for example, food abundance, competitors, predators, and parasites) that an organism experiences over several consecutive generations is replicated in distant generations" (Potts, 1998a). Since VS is premised on the idea that natural selection can be sensitive to such long term intergenerational environmental indeterminacy, it postulates the natural selection of mechanisms that are "decoupled from any specific set or range of environments", a phenomenon which "raises the possibility of novel response to adaptive problems" (Potts, 1998a).[8] Specifically, Potts defines VS mechanism as "specializations adapted to environmental novelty", and claims that such mechanisms are displayed in A) the locomotion structure in early australopithecines, B) brain encephalization in Pleistocene *Homo,* and C) the complex social mechanisms that emerged in certain late Pleistocene *Homo Sapiens* (1998a).

Naturally, this paints a picture of both the human EEA and cognitive evolution which radically bifurcates from the EP account previously considered. On Potts' view, since it is mistaken to understand the EEA in terms of recurrent adaptive problems, it is also mistaken to suppose that our brains are endowed with domain-specific cognitive devices to solve these (non-existent) problems. Rather, we should expect the brain to be adapted to environmental variability and novelty, since selection pressures corresponding to these problems dominated throughout the Pleistocene. In Potts' own words

> Within the perspective of variability selection, it is odd to think that human mental life is driven by task-specific devices designed solely to analyze and solve recurrent Pleistocene problems. While I agree with the idea of specific circuitry designed to handle adaptive problems, variability selection would have favored widespread plasticity within the circuitry and strong sensitivity to environmental input. The cognitive mechanisms unique to humans evidently emerged in a complex series of highly diverse selection regimes. These mechanisms thus include sensitive collectors and processors of environmental data; analytical devices that alter behavior in the light of complex

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[8] See Appendix (Diagram 1) for a concrete example of how such (a seemingly improbable) scenario operates.

> contextual information; mediators of novel response to adaptive problems; and calculators of temporal contingency. These mechanisms permit analysis of factors not immediately present or visible, and therefore require complex internal representation, including language.
>
> (Potts, 1998a)[9]

Given that VS is a serious paleoanthropological theory that explicitly rejects central tenants of EP, it is hardly surprising that Potts' thesis has spread like wildfire amongst critics of EP. Citing Potts' work on climactic instability, Woodward & Cowie (2004) argue that during the EEA there "would have been considerable selective pressure favoring the evolution of cognitive mechanisms allowing the rapid assimilation of new information and behavioral flexibility, rather than innately specified modules". Carrol (2006), in a similar vein, uses Potts to fuel his attack against EP's "static" approach to the EEA and its consequent emphasis upon a mind that is defined in terms of "innate cognitive architecture" and not adaptive flexibility.

Also referring to Potts' work, Chiappe & McDonald (2005) motivate their argument for the likely evolution of domain-general mechanisms by claiming that such mechanisms can best deal with environmental novelty, and that they are hence to be preferred to the domain-specific modules postulated by EP. And so on, with many others bolstering their arguments against the implausibility of the EP modularity concept by appealing to Potts' thesis (Quartz, 2003; Flinn et al., 2005; Sterelny, 2006). Implicit to most of these criticisms (as well as Potts' own critique) is the assumption that EP modules lack flexibility (either because they contain innate information or are domain-specific), and that therefore even the combined output of a wide array of domain-specific modules would have failed to contend with climactic volatility. Seen in this light, if its popularity is anything to go by, the VS hypothesis has inserted itself as

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[9] Given that Potts goes to such lengths to distinguish VS adaptive flexibility from phenotypic plasticity, it is strange that he describes human-specific VS mechanisms in terms of plasticity at this point. Rather than eliciting a contradiction, I take it that Potts implicitly assumes that VS mechanisms will of course display plasticity, but this plasticity – unlike phenotypic plasticity typically understood – will be specialized to deal with novelty and will have arisen due to a VS regime

one of the most serious criticisms against not only the EEA, but EP's whole approach to the mind. In what follows, I address the issue of how, and if, EP can resist its influential and rather telling challenge.

The reason for the fundamental clash between the way in which Potts and EP characterize the EEA is easy enough to identify – while EP argues that natural selection can only forge solutions to recurrent adaptive problems, VS is premised on the idea that natural selection can be responsive to non-recurrent adaptive problems. If EP is correct about natural selection, the fact that climactic volatility occurred during the Pleistocene wouldn't necessarily count against their view of the EEA or the mind. This is because, if natural selection is blind to wildly fluctuating environmental conditions, the EEA would have *had to* consist of the small subset of conditions that stably persisted through such variability – no matter how great an impact climactic volatility had upon human survival and reproduction. Conversely, if Potts' approach to natural selection is correct, it seems inexorable that a force able to speedily turn a forest into a tundra would have exerted a massive selective pressure upon the mind. Importantly, both stances towards natural selection rest on more than assumptions. While Potts has provided detailed modellings of how natural selection can track variability (see Appendix Diagram1 [taken from Potts 1998a] and Potts, 1996), EP's approach harmonizes with detailed theoretical work on natural selection and the aspects of the environment that can feasibly impinge upon an organism's fitness (see Abrams, 2014)

Seen in this light, there appear to be two principle ways in which to adjudicate upon whether the EP or VS account of the EEA is correct. Firstly, we can assess which theory has the best understanding of the adaptive problems natural selection can feasibly 'see' – a process which would involve a detailed meta-analysis of the complex mathematical underpinnings of the way in which the two theories model natural selection. Secondly, we may check the plausibility of the two theories claims in relation to their empirical implications and assumptions, especially regarding the nature of Pleistocene selection pressures and their effects. In what follows, I shall opt for the latter empirical mode of enquiry, as I feel that it offers a more direct and paleoanthropologically sensitized way to evaluate the question.

How, though, shall such an enquiry work? Firstly, we can investigate whether it is indeed true that evolutionary change does correlate with periods of climactic volatility (a straightforward testable implication of Potts' thesis). Secondly, we can ask whether it is feasible to suppose that a set of wildly fluctuating problems in one domain (e.g. the climactic environment) can generate or intensify a set of stable and recurrent selection pressures in another domain (e.g. the social environment), a phenomenon which could make the necessary connection that Potts draws between climactic volatility and VS deeply questionable. Since answering both these questions in a certain manner favours EP's approach to the EEA, deciding how they weigh in against Potts' theory will go some way to determining which account of the EEA is more plausible.

4: Evolutionary Change and Climactic Volatility

Is there satisfactory evidence that climactic volatility correlates with the emergence of VS adaptations in the Pleistocene? This is a rather coarse grained question and needs to be decomposed into two separate issues. Firstly, we may ask whether a statistically significant amount of Pleistocene species responded to climactic volatility by evolving adaptations. Secondly, we may enquire whether hominine brain enlargement correlates with climactic volatility during the Pleistocene. Here it is important to keep in mind that *even if* there is no compelling generalizable evidence for adaptations being triggered by climactic volatility during the Pleistocene, it could still be the case that there could be a strong causal link between hominine brain enlargement and periods of climactic variability. Indeed, there may even be good reasons for supposing that we should e*xpect* hominine cognitive evolution to be an exception to a general trend in which climate change does *not* correlate with adaptive change amongst other species. In this respect, sustaining the large working memory that flexible general-purpose cognition requires (see Chiappe & MacDonald [2005] for a detailed account of the relationship between working memory and domain-general cognition) calls for large quantities of brain tissue. Since brain tissues burn large amounts of calories, with the advent of fire (sometimes dated as far back as 790 ka. [see Goren et al., 2004]) Pleistocene hominines would have gained a crucial means to dramatically increase their calorie intake and thus their ability to support the evolution of the additional brain tissue required for flexible cognition (see Wrangham & Carmody [2010] for a discussion on the connection between fire and brain growth). Seen in this light, Pleistocene hominines would have perhaps been uniquely predisposed to evolve flexible/general purpose minds. Since Potts mainly applies the VS hypothesis to human evolution, this is perhaps the most important question to be settled.

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Did climactic volatility trigger the emergence of adaptations across Pleistocene species? Potts does not provide any *direct* answers to this question. He claims (in 1998a), for instance, that evidence for the VS hypothesis initially stemmed from studies establishing a correlation between periods of climate change and the *extinction* of certain mammalian species with habitat specific adaptations (Deino & Potts, 1990; Potts & Deino, 1995).While extinction does not yield any information about climate change producing VS adaptations, it does serve as a useful proxy for the claim that climactic volatility had a huge impact on species that were adaptively tethered to specific ecological niches. This, in turn, leads to the thought that there could have been considerable selection pressures for mechanisms that buffered species from ecological indeterminacy [i.e. VS adaptations] – an idea further bolstered by the fact that the species that went extinct in Potts' original studies were survived by closely related sister-species that possessed the adaptive flexibility to switch between different habitats and diets (see Appendix Diagram 2, taken from Potts, 1998a).

There is, moreover, reason to believe that Potts' findings are not idiosyncratic, and that they are compatible with a general evolutionary trend. In this respect, Vbra's 'turnover-pulse' hypothesis (1980, 1985, 1988) is premised on the idea that concentrations of speciation ('pulses') and extinction ('turnovers') occur during brief periods of time as a result of climate change. Since speciation obviously entails the evolution of many new adaptations, it thus strengthens the relationship between extinction, climate change and the emergence of adaptations to an even greater extent than Potts' original data. Evidence for the theory has primarily been culled from fossil records that purport to show a turnover-pulse event among African mammals 2.5 million years ago (Vbra, 1985).

However, Vbra's theory has been subject to much scrutiny. Examining one of the richest and best calibrated records of fossilized African Pliocene-Pleistocene mammals, Behrensmeyer et al. (1997) and Hill (1995) found that no significant turnover-pulse events occurred 2.5 million years ago. Furthermore, Vbra's hypothesis is not just contradicted early in the Pleistocene and in Africa. An analysis of an "exceptional" mammalian fossil record in North America has shown that neither speciation nor extinction correlate with glacial–interglacial transitions between 1,000,000 and 600,000 years ago (Barnosky et al., 2004). Finally, this trend appears to hold in geological epochs preceding the Pleistocene as well, as many have claimed extinction and speciation events do not match up with major climactic shifts in the Middle Eocene (Stucky, 1990, 1992; Alroy, 1998), Early Oligocene (Pothero & Heaton, 1996) or the Late Miocene (Prothero, 1999).

Seen in this light, Potts' original data linking climate change and extinction appears far more tenuous. While such a connection may have a legitimate basis in regard to the mammals in his own particular study, the general literature seems to bear out that there is no strong or necessary connection between extinction and climactic volatility. This, in turn, suggests that climate change is not as great a selective force as Potts makes it out to be, and that it needn't *necessarily* have driven recent human evolution. Of course, when it comes to decisively assessing the truth of the VS hypothesis there are obvious limitations to such an approach. Firstly, even if climactic volatility does not cause extinction, it could nonetheless exert a significant selective pressure on species. Secondly, even if speciation does not commonly occur during periods of climactic volatility, this obviously does not rule out the possibility of VS adaptations emerging at such points.

Fortunately, there are ways in which those concerns can (to a certain extent) be addressed. Examining well preserved fossils of insect fauna from the last Quaternary ice age (the past 2.4 Myr), Coope (2004) found that the fossils were morphologically identical with their living modern equivalents, even down to the "intimate intricacies of their male genetalia". This fact suggests that the insects evolved no new morphological adaptations during this period, despite the fact that it was a time of climactic oscillation in which ice-sheets retreated and advanced (Coope, 2004). This finding is especially significant given that insects are precisely adapted to their habitat and reproduce at a fast rate (thus giving natural selection ample opportunity to produce genetic change [Coope, 2004]). In addition, there is also reason to believe that Pleistocene mammals and birds were similarly unaffected by climate oscillation. Examining a wide variety of fossilized mammals and birds from the last glacial inter-glacial cycle (35000-9000 years ago), Prothero et al. (2012) found that despite an ecological shift from "warm interglacial scrub brush to snowy glacial pine forests", both the size and shape of the animals remained constant throughout the period.[10]

These findings suggest that climactic volatility didn't trigger adaptations or exert a large selective pressure on a wide array of species. Consequently, there does not seem to be any kind of generalizable correlation between climactic volatility and adaptive change. Once again, though, there are limitations to the data. For one thing, if many VS adaptations are

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[10] This leads to an obvious question: just how do species manage to adapt to climactic volatility? Coope's (2004) suggestion that insects adapted to Quaternary oscillations by changing their geographic range to track the location of acceptable conditions, provides one solution. Indeed, this same trend has been observed in the response of many species to climate change (Graham & Grimm, 1990; Walther *et al*., 2002; Root *et al*., 2003; Webb *et al*., 2004), and is consistent with evidence that suggests that many species during the Pleistocene migrated to northern and southern 'refugia' to escape glacial conditions (Hofreiter & Stewart, 2009).Humans appear to be no exception to this pattern. For instance, using inherited mitochondrial DNA to reconstruct ancient human migration routes, Forster (2004) concludes that " Ice Age conditions in the past 100 kyr have substantially determined times and routes for prehistoric humans settling the world [...] only movements in much more recent colonial and postcolonial times can compare with the Ice-Age movements of people 60–11 ka."

cognitive, they may simply leave too fine-grained a trace to fossilize.[11] This is an issue that will be directly addressed when we turn to Potts' main case study for VS – hominine evolution.

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[11] Still, the fact that morphological stasis often occurs during periods of climactic volatility, doesn't exactly sit at ease with the VS hypothesis either. This is especially the case since many of the mammalian VS adaptations originally put forth by Potts in regard to other species are morphological (see Potts 1998a).

5: Hominine Cognitive Evolution

The fastest and most dramatic increase in hominine brain size occurred between 600 00-10000 years ago (Aiello & Wheeler, 1995; Ruff et al., 1997), a time that correlates with “the largest [climate] oscillations known so far in environmental records in the past six million years” (Potts, 1998). Since it is uncontroversial that large brains (relative to body-mass) are demonstrative of intelligence (Falk, 1987; Holloway, 1968, 1996; Martin, 1983) brain encephalization reliably indexes that an organism’s intelligence has increased (and hence, presumably, indexes that an organism has acquired new cognitive adaptations). This immediately addresses the problem with the last data-set, in which it was inconclusive whether cognitive adaptations correlate with climate change. Moreover, as Potts himself notes, human cognitive adaptations have all the hallmarks of being *VS* adaptations. Thus, if we presume (reasonably) that the modes of behaviour that appear at this time in the paleolithic record are connected to brain size, there seems little point in quibbling that “complex symbolic coding, more rapid and spatially diverse technological innovation, and powerfully coordinated social action such as bone architectural feats and long-distance trading [...] improved versatility and responsiveness to novel adaptive problems” (Potts, 1998a). Seen in this light, human cognitive evolution represents a seemingly excellent case-study in VS selection

However, despite an air of general plausibility, it is far from clear whether these modes of behavioural flexibility are really produced by indeterminate selective regimes. To begin to see this, consider again Potts’ foundational assumption that there is a connection between climactic volatility and highly variable adaptive problems. Although this connection does seem warranted in the ecological domain, its applicability to the social domain is altogether more dubious. This is because– in principle – it seems entirely possible that capricious ecological conditions could intensify stable and recurrent adaptive problems in the social environment. The intuitiveness of this idea can be illustrated through the following thought-experiment.

Three people survive a plane crash, and wash up on a desert island. Weather conditions on the island are incredibly volatile, and create ecological problems that never stabilize and coalesce into predictable patterns. Due to the unpredictable ways in which wind, heat, rain and cold impact their surroundings, the survivors find it impossible to generate any kind of direct, reliable solutions to any particular ecological problem they confront. For instance, after finding out that certain kinds of bait attracts certain edible fish, a sudden torrential downpour causes rough sea conditions that drive the fish to another island, thus rendering their bait useless. And so on, with every specialized-solution that they develop to an ecological problem being foiled by the weather. However, the survivors *do* find that cooperating in a reciprocal manner reliably yields good results. Consequently, year after year they focus on improving their ability to read each other's minds and enter into joint-cooperative actions. These kinds of socially directed skills thus come to represent a stable and recurrent selective pressure. Through being responsive to this selection pressure, the survivors combat climactic volatility as best they can.

This thought-experiment ought to demonstrate that it is perfectly conceivable for climactic volatility to give rise to stable and recurrent adaptive problems. However, it is crucial to emphasize that – unlike in the artificial scenario presented above – in the actual Pleistocene environment in which our ancestors evolved, climactic volatility *alone* almost certainly didn't generate selective pressure for cooperation (or indeed any other social trait).

Coalition formation, joint-parental investment and communication (to name but a few examples) would have probably created steady selection pressures for cooperation from a very early point in human evolution. Thus contextualized, it is more accurate to say that climactic volatility would have *intensified* already existent selection pressures for social competencies (like, arguably, cooperation) that could have helped combat the effects of Pleistocene weather shifts.

Importantly, the idea that stable selective pressures for social adaptations were operant for long periods of hominine evolution can be empirically substantiated. Thus, the building blocks of many human social adaptations for morality (e.g. reciprocity, reconciliation, consolation and conflict mediation) [Flack & de Waal, 2001], theory of mind (Call & Tomasello, 2008), language (Fedurek & Slocombe, 2011) and face-reading (Kramer & Ward, 2012) are present in chimpanzees. Notably, there is now also a growing consensus that primate intelligence is primarily an adaptation to the complexities of social existence – something that is amply confirmed by ethnographic studies that reveal the sophisticated, often manipulative ways in which primates negotiate shifting coalitions, alliances and politically mediated intra-personal relations (Whitten & Byrne 1998, Harcourt & deWaal 1992). Finally, there is good reason to think that early hominines would not have departed from this trend,[12] and that such selection pressures would have therefore persisted into the Pleistocene.

However, another potentially problematic aspect of the thought experiment is that it rests on the tacit assumption that social skills *can* be adequately responsive to the kinds of adaptive

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[12] Traits that are shared in species that share a close genetic relationship are parsimoniously inferred to be homologies that were present in their last common ancestor (Whiten, 2011). This means that when the human lineage bifurcated from the last common ancestor that we shared with chimpanzees, our ancestors would have already possessed (roughly) similar social traits to those displayed by chimpanzees (McGrew, 2010)

problems brought about by climate oscillation.[13] Many may find this claim to be speculative at best. Fortunately, though, such a claim rests on more than just intuition, and can be paleoanthropoligcally substantiated. In this respect, consider the following example provided by Foley & Gamble (2009):

> [...] across the course of human evolution, one of the strongest trends is that human 'society' has evolved to cope with more and more 'fissioning'. If the community is one of the most basic building blocks of human society—a group with shared dialects, kin bonds and political organization—then it is clear that humans have the capacity to maintain these in the absence of close social proximity, and with long periods where there is no contact. The social and cognitive apparatus that has evolved provides the mechanisms for this. However, from a socioecological perspective, the fissioning potential (which may become permanent as groups do diverge and form new ones) provides ecological flexibility to human communities and to individuals pursuing their reproductive and other goals. Human society is essentially a chimpanzee community with exploded fission–fusion; a society that has achieved release from the constraints of proximity (Rodseth et al.1991) that dominate the negotiation and often daily affirmation of social bonds and hierarchies among primates. Social extension in time and space was not achieved by all hominins. It appeared late in human evolution, as indicated by overwater dispersal to Australia and then throughout Polynesia as well as coping in the extreme continental environments of boreal Siberia with longer periods of fission, and very low population densities owing to highly seasonal resources.

Other equally compelling examples can be listed. Whiten & Erdal (2012) note that cooperation allows humans to coalesce into 'group-level predators' (or hunting-bands) that are structured through a division of labour which allows for a wider variety of plants and animals to be accessed.[14] More particularly, the cooperative socio-cognitive competencies involved in such kinds of group-level predation can be reconstructed through examining the hunting-stratagems of the San, in which group discussion of hunting plans, sign language (as

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[13] Crucially, in making this claim I do not mean to imply that social adaptations provide the only adaptive solutions to climactic volatility. Other physiological (and psychological) adaptations can clearly also provide solutions as well, and so selective pressures for them could also be feasibly generated by a volatile climate. For example, it is plausible to imagine that ecologically orientated adaptations designed for predator/prey interactions (Barrett, 2005) and navigation (Silverman et al., 2007) could become especially significant during such periods of instability.

[14] Following Whiten & Erdal (2012) I am assuming that many of the proximal cognitive mechanisms that foster this cooperation are derived from our shared ancestory with chimpanzees. Thus, chimpanzee hunting, foodsharing, raiding and coalitionary behaviour are all underscored by significant degrees of cooperation (Boesch, 1994; Boesch & Boesch, 1989; Mitani & Watts, 2005; de Waal, 2002; Mitani, 2010). Additionally, it is important to note that Whiten & Erdal's understanding of hunter gatherer- cooperation needn't depend on any notion of group selection, as hunter-gatherer cooperative hunting allows for individuals to gain a variety of foodstuffs that they would have been unable to gain in isolation. Thus, as with reciprocal altruism in general, cooperative hunting can be analysed in terms of zero sum logic.

hunters approach prey), coordinated searching, and analysis of the results of attacks on prey feature prominently (Lee, 1979). As Whiten & Erdal correctly observe, these kinds of practices are saturated through and through with competencies connected to theory of mind and language.[15]

Moreover, there are strong reasons to believe that social selective-pressures (and the adaptive problems they gave rise to) *did* indeed remain stable throughout periods of climactic oscillation in the EEA. This kind of approach has its theoretical roots in Waddington's (1957) definition of canalization as "the capacity (of development) to produce a particular definite end-result in spite of a certain variability both in the initial situation from which development starts and in the conditions met during its course". A canalized design thus acts as a buffer against environmental variation met in development (Mameli & Bateson, 2011), and leads to the development of the same phenotype regardless of circumstance. This leads to an obvious question. Under what conditions would natural selection favour phenotypes that are developmentally insensitive to environmental variation? Barrett (forthcoming) provides one standard answer, noting that canalized designs ought to be favoured by natural selection when they are responsive to aspects of the EEA in which there

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[15] As I mentioned earlier, this analysis rests on the important assumption that social adaptations can be functionally extended to combat ecological problems. Many may claim that such a phenomenon would be impossible unless social adaptations were acted upon by natural selection in such a way that their primary functions related to specific ecological problems. For example, on this view, if we are to imagine Theory of Mind (ToM) modules being used for cooperative hunting, we must also imagine that our ToM modules contain specific protocols for hunting scenarios, and that they are therefore not just designed to solve the general social problem of inferring the thoughts and intentions of conspecifics. I find this kind of concern implausible. Just as our domain-specific modules can process cultural information that they were never originally designed by natural selection to act upon (for more on this see Sperber & Hirschfeld's [2004] distinction between the 'actual' and 'proper' domain of a module), it seems perfectly reasonable that there are enough similarities between ecological and social instances of mindreading that the same modular inferences can be effective in both scenarios. Thus, when natural selection – due to climactic volatility – intensified selection pressures on social adaptations (like ToM) it most probably didn't have to generate specifically ecological protocols within our modules. Instead, it could have just kept on enhancing and refining the kinds of capacities that had been under selection for thousands of generations

is little or “no variation in that dimension of the environment across ancestral time and space”. Given that the EEA is nothing more than a statistical composite of the adaptive relevant properties and problems that our ancestors encountered, canalization thus indicates that an adaptive problem has varied little over evolutionary time – and hence that it has stably recurred in one generation after the next. The guiding logic behind this kind of claim can be illustrated through the following ‘programming’ scenario.

If a certain fitness enhancing object always appears in the same part of a room in a virtual environment, why design a lineage of virtual organisms that have the plastic capacity to search for the object on the basis of ambient environmental conditions that vary from one generation to the next? Surely the most efficient design would be one that allowed the virtual organisms to swiftly and automatically develop in such a way that they move towards the object in a straight line (i.e. in such a case the organisms would have a canalized design). In high contrast, having a developmentally plastic system only makes sense when the relevant dimensions of an adaptive problem are significantly impacted upon by environmental contingencies. In such a case, each twitch and whisper of the environment could have a bearing upon an adaptive problem, and it would make sense for natural selection to make organisms sensitive to these fluctuations.

Seen in this light, evidence of canalization has a direct bearing upon assessing whether Potts is right in assuming that climactic volatility generated wide-spread non-recurrent adaptive problems. In this respect, if many social adaptations are not developmentally plastic (and hence ontogenetically sensitive to environmental variation), it simply *cannot* be the case that climactic volatility destabilized a significant portion of the adaptive problems encountered by hominins.

However, the use of canalization to confirm the stability and invariance of the EEA may sound paradoxical given Waddington's understanding that canalization acts as a buffer *against* variability in the environment. Note, though, that not all variability that attaches itself to an aspect of the EEA is necessarily that important or definitive of the EEA. For instance, many aspects of the EEA may initially be clouded in small amounts of inconsequential variability that reliably dissipate to form a stable adaptive problem.[16] Additionally, much environmental variability could result from external forces dangerously impinging upon a stable part of the EEA (in figurative terms, imagine a butterfly pupae safely enwombed inside the stable world of its chrysalis, and yet being rocked around inside the chrysalis due to a sudden gust of wind). In both such circumstances, it would make sense for natural selection to guide an organism's developmental process in such a way that it robustly and automatically unfolds along largely predetermined lines. In contrast, to make a developmental programme plastic in such a context would be overly costly and even maladaptive. This is because such developmental plasticity may become sensitized to variability that is only a temporal or peripheral feature of an otherwise stable and invariant feature of the environment.

Empirical evidence for canalized social adaptations can be gathered from many different sources. For example, genetically identical twins raised in radically different cultural environments often have uncannily similar personalities[17] and quirks of habit (Pinker, 2003).[18] Consistent with this claim, a cortical neuroimaging study of genetically identical twins by Thompson et al. (2001) provides strong evidence that this kind of canalization is

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[16] Hence Waddington's [1942] definition of canalization as "The adjustment of developmental reactions so as to bring about one definite end result regardless of minor variations in conditions during the course of the reaction."

[17] See Buss (1996) for an adaptational account of personality types

achieved through frontal cortical areas[19] (as well as language areas) being highly heritable and thus under rather rigid genetic control– a fact which amply accounts for the way in which Pinker's twins managed to develop such strongly convergent personalities despite being raised in such divergent environments.

Another excellent example in this vein can be provided by over-imitation in young children. In this respect, the idea that over-imitation universally emerges in the second year of life (Nielson, 2006) has been questioned on the grounds that in Western societies parent-child interactions involve parents giving demonstrations that accentuate important aspects of objects (Gaskins, 2006; Rogoff *et al*.,1993). Since such demonstrations involve children receiving guided instructions, they are thus thought to prime children's expectations that "adults have tested the rationality of their actions and these actions are attempts to transmit relevant knowledge", something which creates "fertile ground in which overimitation can flourish" (Nielson & Tomaselli, 2009). However, despite the fact that Kalahari Bushmen children are mainly required to learn through observation, and that their care-givers rarely explore object use with them (Bakeman et al., 1990; Konner, 2005), 2-years Kalahari children (as well as older children) showed a pronounced tendency to over imitate in object-demonstration tasks (Nielson & Tomaselli, 2009). Here, again, considerable (relevant) environmental variability has little effect on the nature and development of a phenotypic trait which is almost certainly an adaptation to social life.

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[18] In order to illustrate this point, in a TED talk Pinker (2003) mentions the example of genetically identical twins who were separated at birth. One of the twins was raised in a Catholic family in Nazi Germany, while the other was raised in a Jewish family in Trinidad. Pinker then goes on to say "When they [the twins] met in a lab in Minnesota, they were wearing identical navy blue shirts with epaulets; both of them liked to dip buttered toast in coffee; both of them kept rubber bands around their wrists,; both of them flushed the toilet before using it as well as afterwards; and both of them liked to surprise people by pretending to sneeze in crowded elevators to watch them jump."

[19] For accounts of the involvement of frontal cortical areas in personality, see Goyer *et al*., 1994; Raine *et al*., 2000; Blaire *et al*., 2004.

Of course, many other social adaptations that appear early in development also appear to fulfil these criteria. In this respect, not only can newborn babies – some as young as 42 minutes old – imitate facial expressions (Meltzoff & Moore 1983, 1989, 1997), and not only is this capacity cross-culturally invariant (Reissland 1988), there is now even evidence that foetuses ‘practice’ facial expressions of pain/distress before they have an affective experience of pain/distress (Reissland et al., 2013). Other socially orientated competencies that emerge early in development include altruistic helping (Warneken, 2013), sensitivity to ostensive language used in pedagogy (Csibra & Gergely, 2009) and preference for native language speakers (Kinzler et al., 2011). Although such discoveries have not been tested in multiple cultures, the earliness with which they develop makes it highly likely that they are not plastically responsive to culture. Perhaps, temptingly, it could be conjectured that earliness of development (often, erroneously, taken to be evidence of innateness) is one way to insure canalization.

Needless to say, this doesn’t mean that these competencies are not developmentally enriched. However, it is crucial to note that in many cases the developmental trajectory which ensues *may* be cross-culturally universal in such a way that nearly all subjects display the same developmental progression, acquiring roughly the same developmental enrichments at roughly the same time – a fact which strongly suggests that the developmental process is not significantly impacted by the considerable environmental variation that different cultures give rise to. For example, such cross-cultural developmental invariance has been observed in the developmental phases that build upon nascent language abilities. In this respect, Lennenberg (1967) was the first to note that “children universally pass through cooing, babbling, first-words, two-word sentences, and then more complex syntax, with each milestone appearing at ages roughly as predictable as those of getting teeth or developing motor abilities" (Spelke & Newport, 1998). Since Lennenbeg's original study this developmental trajectory has been found to obtain for the developmental acquisition of even the most exotic languages (Slobin, 1985, 2013), as well as signed languages (Newport & Meier, 1985; Pettito & Marentette, 1991). Indeed, the canalization of this developmental process is perhaps most strikingly accentuated by the way in which deaf children who are not exposed to *any* conventional language invent words and sentences from gesture, and go through the early stages of acquisition on their own (Feldman et al., 1978; Goldin-Meadow & Mylander, 1984).

Finally, Frith & Frith (2003) have tentatively proposed that Theory of Mind (ToM) acquisition is also a (culturally) universal process that unfolds in a fairly uniform manner. Support for this kind of view has recently been buttressed by cross-cultural findings that confirm "a universal developmental trajectory of early false-belief understanding, one that is similar across cultures despite significant differences in language, parent-child interactions, and norms regarding others' minds" (Barrett *et al*., 2013). Interestingly, although it has yet to be cross-culturally established, work on ToM development during puberty demonstrates that most adolescents undergo similar neuroanatomical changes that facilitate improved belief attribution Blakemore (2008) – a finding which suggests that the constrained nature of ToM development is not just particular to early childhood.[20]

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[20] An outstanding question that needs to be addressed is whether these social adaptations are indeed modular. In this respect, the earliness with which over-imitation, language and theory of mind competencies emerge strongly suggests that – at least in their earliest manifestation – they are not produced by any kind of domain-general (plastic) learning process involving trial and error learning. Seen in this light, it seems that genetically heritable, functionally specialized mechanisms must be responsible for their existence. Consistent with this claim, many developmental psychologists endorse the idea that the core knowledge systems responsible for human development (e.g. systems related to space, numbers, social partners, actions, objects, language, theory of mind, personality and imitation) are indeed modular (Spelke & Kinzler, 2007; Scholl & Leslie, 1999 ; Bateson & Martin, 1999; Bjorklund & Hernandez, 2005; Van der Lely & Heather, 1997; Subiaul, 2010). Indeed, even theorists who stress the importance of domain-general Bayesian inference for early development acknowledge that such inferences are deeply reliant on evolved modules (Tenenbaum et al., 2006).

All this suggests that in the human EEA certain adaptive problems in the social domain reliably emerged and thus could be most efficiently met with a ‘fixed’ or canalized strategy. *If* social adaptive problems in the EEA had been variable, there would surely be more evidence that core developmental systems would be more plastically responsive to the considerable environmental variability brought about by culture. This – as I previously argued – suggests that climactic volatility did not cause social adaptive problems to become non-recurrent. Indeed, since there is evidence that social adaptations can be recruited in such a way that they can tackle the kinds of ecological problems that would have been attendant on climactic volatility, it is my claim that a fluctuating climate could have intensified stable selective pressures for mechanisms that solved domain-specific social problem

However, before proceeding any further, let me be clear about two things. Firstly, none of this implies that *all* modular developmental systems connected with social adaptations have narrow reaction norms – a conclusion which would clearly be absurd. Secondly, even the developmental systems that I have claimed to be canalized may be developmentally plastic in certain peripheral ways. In this respect, it is obviously a mistake to talk about any adaptive problem being completely recurrent and identical in each generation. Rather, in evolutionary terms, a recurrent adaptive problem is better envisioned as something that statistically clusters in the same area. Consequently, a little bit of plasticity may be built into even the most canalized developmental systems.

Neither of these qualifications, however, support Potts’ strong claim that recent cognitive evolution has been significantly driven by inconsistent (let alone novel) adaptive problems. This is because A) cognitive adaptations for language, theory of mind, imitation and personality surely constitute a *significant* portion of recent human cognitive evolution, and because B) even 'recurrent' adaptive problems may favour the selection of canalized designs that contain marginal plasticity to accommodate the slight variability that seeps into even the most generationally entrenched problems.

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Finally, it is worth mentioning that recent findings have cast into doubt the fossil evidence that Potts uses in order to support the notion that climactic fluctuations correlate with brain encephalization. In this respect, there is now also paleoanthropological evidence that 30% of human brain encephalization occurred in a period (400ka-300ka) in which i) humans had achieved ecological dominance though the use of projectiles, and ii) hostility existed between groups due to a scarcity of resources and space (Foley& Gamble, 2009).[21] Consistent with 'ecological dominance' theories of human evolution (Alexander, 1990; Flinn *et al*., 2005) this suggests that competition among conspecifics was the primary selective force in recent hominine cognitive evolution.[22] Consequently, it is very likely that the fixation of many human specific adaptations occurred when ecological dominance – despite the presence of

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[21] As an interesting aside, ecological dominance models also appear to account for intercontinental patterns of mammalian extinction far better than climactic fluctuation models do. For example, during the late Pleistocene (15000-12000 ka), many species of large-bodied mammals went extinct across the globe (Martin, 1967, 1984; Murray, 1991; Lessa & Farina, 1996; Flannery & Roberts, 1999; Martin & Steadman, 1999; Stuart, 1999). Although this mass extinction does correlate with a glacial-interglacial transition (Lyons et al.,2004), and although some have attributed the extinction to climate change as a result of this correlation (Guilday, 1967; Lundelius, 1967; Graham and Lundelius, 1984; Owen-Smith, 1988; Graham and Grimm, 1990; Guthrie, 1990), this still leaves open the question of why a global mass extinction only correlates with *one* of the twenty glacial-interglacial cycles that occurred in the Pleistocene (Lyons et al.,2004). Additionally, since the human colonization of Africa, North America, South America and Australia *does* coincide with this extinction event, it has been contested that the cause of the extinction is anthropogenic (Lyons et al.,2004), a view that is supported by many other findings (Coppens *et al.*, 1978; Olson and James, 1982; Martin, 1984; Farina, 1995; Farina and Vizcaino, 1997; Alcover *et al.*, 1999; Burney, 1999; Roberts *et al.*, 2001).

[22] Much additional experimental evidence supports the claim that our minds are adapted to social complexity . For instance, it is now apparent that the size of the neocortex (relative to brain volume) is positively correlated with the degree of social complexity in ungulates, carnivores and primates (Perez- Barberia et al., 2007). Studies using group size as a proxy for social complexity have thus discovered a log-linear relationship between the size of a primates brain and the size of the average population in that particular primate clade (Dunbar, 1993). Given the stock size of the human neocortex, this mathematical formula has predicted, and found, that an individual person should only be able to maintain coherent social relationships with 150 people –a number that correlates with the average size of the traditional hunter gatherer and horticultural societies (Dunbar

climactic volatility – had catalysed a process in which social skills (including cooperation[23]) were selected for on the basis of Machiavellian rather than ecological criteria.

Combined with the arguments offered throughout this chapter, these findings provide additional reasons for being sceptical of Potts' claim that hominine cognitive evolution has been driven by climactic volatility and the indeterminate ecological problems that are attendant on it.

1993, Hamilton et al., 2007; Hill & Dunbar, 2003; Roberts et al., 2009; Zhou *et al.*, 2005). Since the neocortex is the most recently evolved part of the brain, this body of empirical literature harmonizes nicely with Gamble & Foley's paleoanthropological claims.

[23] Some theorists adopt the view that cooperation and competition are mutually exclusive (Tomasello & Carpenter 2005). However, for a convincing account of why cooperation be understood as a large scale coalitional phenomenon that can aid a group in a competitive confrontations with other groups, see Boyd & Richerson, 1998.

6: Overview

I have presented a number of reasons why we ought to be sceptical of the VS hypothesis. To briefly recap, these reasons are A) there is no compelling evidence that climactic volatility triggered adaptational change across multiple species, B) recent human cognitive evolution in the Pleistocene can be explained in terms of stable, recurrent selective pressures generated by the social domain and C) the ecological versatility that buffered our ancestors from climactic volatility can (to a certain extent) be parsimoniously attributed to our social adaptations and the stable selective regime that created them. Considered in conjunction with the evidence that species – including humans – respond to climate change through shifting their geographical range (see footnote 6), it seems the VS hypothesis has a lot of loose ends to account for.

In the following sections, I shall consolidate this scepticism by critiquing a key theoretical presupposition made by the VS hypothesis and those who endorse it. In this respect, both Potts and critics of EP assume that developmentally plastic (as well as VS) cognitive adaptations generate modes of behavioural flexibility that cannot be realized via domain-specific cognitive adaptations. In what follows, by appealing first to cumulative cultural evolution and then to an enzymatic approach to modularity, I shall argue that this assumption is clearly false.

7: Cumulative Cultural Evolution and Ecological Versatility

Are Potts and critics of EP correct to assume that plastic cognitive mechanisms provide the only solution to the adaptive problems attendant on environmental novelty? In what follows, I shall argue that cumulative cultural adaptations can also be presented as plausible candidates for this function. Furthermore, although proponents of cumulative cultural evolution may appear to hold a view of the mind which is at loggerheads with EP, it shall be my claim that cumulative cultural evolution entails a mind that is crammed with functionally-specialized mechanisms. Seen in this light, it appears that a massively modular mind does indeed have everything at its disposal to deal with climactic volatility.

Theorists like Richerson & Boyd (2008) have championed the idea that culture can be seen as a powerful adaptation that can generate complex, cumulative solutions to adaptive problems. From this perspective, “we are all dwarfs standing on the shoulders of a vast pyramid of other dwarfs” (Boyd & Richerson, 2005). This is because if each individual contributes only a fractional amount to the production of a cultural artefact (e.g. a projectile), and if each one of these positive modifications is preserved, built upon, and transmitted from generation to the next, marginal individual cognitive capacity can nonetheless result in complex adaptations. Furthermore, since cultural evolution operates at a quicker rate then genetic evolution, it will be especially favoured by natural selection during periods in which environmental conditions fluctuate, (Richerson, Bettingir & Boyd, 2005) as they did indeed during the Pleistocene.

On the basis of this sketch, you may expect that theorists like Boyd & Richeson have little patience for a massively modular mind that is encumbered with myriad special-purpose mechanisms. After all, if cumulative culture can provide fine-grained informational solutions to adaptive problems, why should natural selection also go to such excessive lengths to inscribe mechanistic solutions into our brains? This kind of approach needn't rule out the counterintuitive idea that at least *some* mechanisms have been in operation during human cultural evolution. However, when culture can shoulder such a great adaptive weight, Boyd & Richerson's perspective does seem to entail that it would be naïve to suppose that a *great many* of these mechanisms exist. And yet, despite all this, their position is not as contrary to massive modularity as it may initially appear:

> Human culture allows learning mechanisms to be both more accurate and more general, because *cumulative* cultural adaptation provides accurate and more detailed information about local environments. Evolutionary psychologists argue that our psychology is built of complex, information rich, evolved modules that are adapted for the hunting and gathering life that almost all humans pursued up to a few thousand years ago. Fair enough, but *individual* humans can't learn how to live in the Arctic, the Kalahari, or anywhere else. The reason is that our information rich, evolved psychology doesn't contain the necessary information. Think about being plunked down on an arctic beach with a pile of driftwood and seal skins and trying to make a kayak. Certainly, no evolved "kayak module" lurks in the recesses of the human brain.[…] People have to acquire the knowledge necessary to construct a kayak using the same evolved psychology that people use in other environments to master other crucial technologies. No doubt that this *requires* an evolved "guidance system." People must be able to evaluate alternatives, to know that boats that don't sink and are easy to paddle are better than leaky, awkward designs. They have to be able to judge, to some significant degree, whose boats are best, and when and how to combine information from different sources. The elaborate psychological machinery that allows children to bootstrap any knowledge of the world is also clearly crucial. People can't learn to make kayaks unless they already understand something about the properties of materials, how to categorize plants and animals, the manual skills to make and use tools, *and so on and on*.

(Boyd & Richerson, 2005; my italics)

The idea here is that even cumulative cultural adaptations (e.g. kayaks) require an array of primary cognitive mechanisms that allow humans to represent and configure all the elements that are integrated in complex cultural artifacts. Although Boyd and Richerson have elsewhere confined these specialized mechanisms to theory of mind, selective social referencing, over-imitation, a functional understanding of artifacts, and an ability to construct biological taxonomies (Boyd, Richerson & Heinrich 2011), it is clear that in the domain of kayak building alone the involvement of these basic mechanisms defies easy enumeration.

Seen in this light, there appears to be no paradigmatic[24] disparity between proponents of cumulative cultural evolution and proponents of massive modularity.[25] However, although many may concede this, they may nonetheless point out that such an account glosses over a significant domain in which the theories *do* clash. More particularly, the key mechanisms that cumulative culturalists invoke to explain cultural transmission do not appear to be functionally specialized. Let me explain.

Boyd, Richerson & Henrich claim to have modelled selective processes that lead to cumulative cultural evolution in which neither replication fidelity nor domain-specific mechanisms are required. This is achieved through implanting a psychological propensity (or mechanism) for conformist transmission into their selective models. Note, this is not a sophisticated mechanism. When potential imitators try to infer and copy another individual's behaviour, they make the wrong inference most of the time. However, despite this, their results appear to show that "conformist transmission effectively corrects even large errors in transmission, even when the inferential transmission channel is 60% noise (2008)." This result is buttressed by additional "blending" models which claim to demonstrate that cumulative cultural evolution can occur when an individual forms a representation of a cultural artefact (say a bow) that is the blended average of a number of artefacts they have sampled. Importantly, this means that the averaged representation does not originate in any of the sampled artefacts, and is therefore not the result of replication. However, if we assume that the individual has a prestige bias that makes them sample the best artefacts, these models

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[24] This is not to say, however, that no disagreements exist (see Boyd, Richerson & Heinrich, 2011).

[25] Indeed, this consensus is explicitly articulated by Boyd & Richerson (2005): "Evolutionary psychologists are prone to wax eloquent over marvellous cognitive adaptations created by natural selection. And they are right to marvel; everyone should. Natural selection has created brains and sensory systems that easily solve problems that stump the finest engineers.[…] Humans are able to solve many astoundingly difficult problems as they go through daily life because natural selection has created numerous adaptive information processing modules in the human brain."

seem to support the idea that cumulative cultural evolution can occur (Cavalli-Sforza & Feldman 1981; Boyd & Richerson, 1985: 71-79). Crucially, the mechanisms driving both models of cultural transmission can be seen as crude and general purpose, a fact that Boyd & Richerson are happy to concede:

> Individuals don't have to be too smart, because simple heuristics like correlation detection and imitation of the successful can produce clever adaptations when averaged over a population of individuals and over generations of time. Even if most individuals imitate with only the occasional application of some simple heuristic, many individuals will be giving traditions a nudge in an adaptive direction, on average. Cultural transmission preserves the many small nudges, and exposes the modified traditions to another round of nudging. Very rapidly by the standards of ordinary evolutionary time, and more rapidly than evolution by natural selection alone, weak, general purpose decision-making forces generate new adaptations. The complexity of cultural traditions can explode to the limits of our capacity to imitate or be taught them, far past our ability to make careful, detailed decisions about them. We let the population level process of cultural evolution do the heavy lifting for us.

(Boyd & Richerson, 2005)

However, there is a catch. While cumulative cultural evolution may occur without strict replication, and while the mechanisms underlying it may operate using only “simple heuristics”, Boyd, Richerson & Henrich are fully cognizant that human imitation and prestige bias are anything but simple in terms of their actual manifestations. For instance, they acknowledge literature in developmental psychology that attests to the fact that children are natural born imitators (Neilson & Tomaselli, 2010; Lyons et al. 2007), and that compared to chimpanzees infants have a far greater tendency to copy the superfluous *manner* in which an instrumental action is performed (Whiten et al., 2009). In regard to prestige imitation, they are also aware of experimental data that suggests that we can decouple prestige from dominance on the basis of very slender linguistic evidence, and that our interactions with an individual who is inferred to be prestigious rather than dominant is recalled with significantly greater accuracy (Holtgraves et al., 1989).[26]

Consistent with these findings, there is also much evidence that humans are in possession of a sophisticated cortical imitation system. According to some (Iacoboni, 2009), this system is composed of a higher-order visual area that responds to biological motion and intentional actions (Allison et al. 2000, Jellema et al. 2000, Perrett et al. 1989, Puce & Perrett 2003, Puce et al. 1998), as well as parietal and frontal s mirror neuron regions that code goal-orientated and motor aspects of the action (Iacoboni et al. 1999; Iacoboni 2005; Iacoboni et al. 2005; Iacoboni & Dapretto 2006; Koski et al., 2002). It is also interesting to consider that these mirror neuron regions may have a high degree of domain-specificity, since the observation of mouth, hand and foot movements activates distinct regions of the mirror neuron system (Buccino et al., 2004)

Why do such sophisticated imitation mechanisms exist when such noisy transmission processes can nonetheless account for cumulative cultural evolution? One way to answer this question is to historicize evolutionary accounts of cultural transmission a bit more. Thus, like everything else that has ever evolved, culture must have had crude and humble beginnings. Seen in this light, Boyd & Richerson's models do a good job of illustrating how culture could have got started with a few sketchy heuristics. However, there can be little doubt that the current complexity of our imitation mechanisms is best explained by the fact that once cultural evolution *did* gather momentum, it created a selective feedback process that led to the fixation of certain genetic adaptations for culture. This process is sometimes referred to as

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[26] Interestingly, recent evidence from developmental psychology attests to the manner in which 3-4 year olds are guided by prestige biases in regard to learning. Chudek et al. (2012) have thus found that children of this age preferentially learn from models that other subjects momentarily defer to during some kind of learning task. Importantly, if the model is initially deferred to while using artifacts, the children will *not* be more likely to learn from the same model if, say, the model subsequently initiates food-learning tasks. The reverse is true if a model is initially deferred to during food-learning tasks and then initiates artefact tasks

gene-culture co-evolution. Boyd & Richerson are of course aware of this, and have elsewhere argued that language and brain size can be viewed as "genetically coded mechanisms that enable humans to host a fancy cultural system" (2010).

Furthermore, it is important to emphasize that prestige and conformity biased imitation do not exhaust the relevant ways in which cultural transmission occurs. Natural pedagogy (Gergely & Csibra 2009, 2011) is premised on the ideas that human infants are sensitive to ostensive communication in such way that the can acquire "cognitively opaque cultural knowledge that would be hard to acquire relying on purely observational learning mechanisms alone" (Gergely & Csibra 2009).Gaze direction, for example, provides perhaps the most intuitively obvious example of ostensive action (e.g. If I am looking directly at you perhaps my intentions and actions are being performed for your sake). In line with this, neuro-imaging evidence suggests that 4 month year olds *do* interpret eye contact as an ostensive signal. Thus, both eye contact and raised eye-brows (another classic ostensive signal) trigger similar brain regions in infants (Grossmann, 2008). Even more convincingly, though, the neural structures that are stimulated in infants by eye contact correlate with the neural structures that are stimulated in adults when they perceive communicative actions (Kampe et al., 2003). Crucially, ostensive actions also seem to modulate infants expectations about the object that is being referred to. In this respect, Gergely & Csibra theorize that infants have the expectation that they can learn something generalizable and enduring about an object that is being ostensively referred to – an idea that seems to be borne out by other experiments as well (see Egyed et al., 2007; Yoon, 2008).

Although Gergely & Csibra refer to natural pedagogy as a culturally universal 'adaptation' (2011), it is more than likely that it is a functionally integrated system of adaptation*s*. This is because natural pedagogy manifests multiple epistemic, cognitive and motivational sensitivities in both instructors *and* learners. The idea that a single adaptation could do all of this seems computationally implausible. Seen in this light, natural pedagogy could constitute an integrated complex of domain-specific adaptations that facilitates cultural transmission, and hence contribute to cumulative cultural evolution. Given that there is paleoanthropological evidence that apprenticeship structured the construction of stone tools (Tehrani & Riede 2007), it seems deeply improbable that imitation alone is sufficient to explain the spread and stability of culture. Indeed, in current communities in which informal pedagogy regulates the production of complex cultural artifacts (like carpets), copying fidelity of certain motifs has remained stable for many hundreds of years (Tehrani & Collard, 2002).

Once again, then, despite outward appearance, there seems to be nothing substantive that makes cumulative cultural evolution incompatible with the idea of massive modularity.

*

Where, exactly, does all this leave us in regard to the question that was posed at the beginning of this section? The first thing to note is that the cognitive mechanisms responsible for generating cumulative cultures needn't be plastic. In this respect, it is prima faci obvious that a reservoir of constantly updated cultural *information* provides a direct source of behavioural flexibility and therefore a means to combat ecological indeterminacy or novelty. However, in contrast, the cognitive *mechanisms* that allow us to acquire culture don't need to be plastically sensitive to ecological indeterminacy. So long as the social environment is stable in such a way that imitation or natural pedagogy offer reliable means to acquire cultural information, our cultural acquisition devices can tick away in their customary way, no matter what the weather is doing.

Furthermore, a cumulative approach to cultural evolution provides an excellent reason why conformity and prestige biased imitation – as well as natural pedagogy – emerge at such an early developmental point. To see why this is, consider that the more culture accretes the more adaptively salient information pools within its domain. And the more this occurs, the more advantageous mutations will be that ‘fix’ cultural learning strategies at a young age, thus making infants more cognitively primed to acquire the ever growing, ever more sophisticated body of cultural knowledge that determines human survival and reproductive success. This model of gene-culture co-evolution thus stresses that cumulative culture not only provides a constant selection pressure, it also provides a constant selection pressure that gets heavier and heavier the more culture accretes. These two factors could powerfully combine to favour the selection of highly-specialized and canalized social adaptations.

As a final note, there should be nothing empirically controversial about the claim that cultural adaptations did indeed help our ancestors confront not only climactic volatility, but also whole ecologies that were *completely novel*. In this respect, there is considerable evidence that the most ecologically inhospitable corners of the planet were rapidly colonized during the Pleistocene (see Mourre et al., 2010; Klein, 2009; Rowe et al., 2008), and that once our tropic foraging ancestors migrated out of Africa 70000 years ago, they adapted to brutally cold regions like Northern Eurasia using cultural adaptations (e.g. tailored clothes, shelters, and technologies connected to the generation of heat and light) [see Boyd, Richerson & Henrich, 2011].

8: Module Bundling and Cognitive Flexibility

Cumulative culture and developmental plasticity do not exhaust the ways in which behavioural flexibility can be attained. In this respect EPs (Tooby & Cosmides, 1992; Barrett, forthcoming) hold the view that the *proliferation* of functionally-specialized mechanism can also bring such flexibility about. This thesis has its roots in the claim that domain-general cognitive systems cannot be made neatly equivalent with behavioural flexibility. Tooby & Cosmides (1992) vividly capture this concern in the following passages:

> From a traditional point of view [...] it seemed sensible to regard generality as an enhancement of the capacity of a system: The system is not prevented from assuming certain states or kept from doing what is adaptive (or desirable) by a "rigid" or "biased" architecture. Generality of application seems like such an obvious virtue and content-independence seems like such an obvious road to flexible behavior, what could possibly be wrong with them? In this view, content-specificity in evolved psychological design is imbued with all the legendary attributes of "biology"-rigidity, inflexibility, and constraint. It is viewed as preventing the system from achieving advantageous states that would otherwise naturally come about.... [however] by widening the problem domain that a mechanism must address, strategies that worked correctly on only a subset of problems must be abandoned or subtracted from the repertoire because they give incorrect answers on the newly included problems in the enlarged domain. As problem domains get larger and more broadly defined, a smaller and smaller set of residual strategies is left that remains applicable to the increasingly diverse set of problems. At the limit of perfect generality, a problem solving system can know nothing except that which is always true of every situation in any conceivable universe and, therefore, can apply no techniques except those that are applicable to all imaginable situations. In short, it has abandoned virtually anything that could lead it to a solution
>
> (100 & 104)

Contrary to received wisdom, then, it is perhaps mistaken to believe that domain-generality is a hotline to cognitive flexibility. However, this doesn’t automatically imply that domain-specific mechanisms are the answer to the problem, and that they have therefore been mistakenly aligned with rigidity. Importantly, domain-specific mechanisms acquire their processing power through having very stringent input criteria. As such, it appears they obtain this efficiency at the cost of being completely blind to the many other adaptive problems that fall outside the purview of the specialized sub-classes of information that they are designed to process. This gives rise to the horns of a computational dilemma, in which either narrow success or broad failure seem possible. EPs, however, claim that a middle road is possible:

> The solution to the paradox of how to create an architecture that is at the same time both powerful and more general is to bundle larger numbers of specialized mechanisms together so that in aggregate, rather than individually, they address a larger range of problems. Breadth is achieved not by abandoning domain-specific techniques but by adding more of them to the system. By adding together a face recognition module, a spatial relations module, a rigid object mechanics module, a tool-use module, a fear module, a social-exchange module, an emotion-perception module [....], and so on, an architecture gains a breadth of competences that allows it to solve a wider and wider array of problems, coming to resemble, more and more, a human mind. The more a system initially "knows" about the world and its persistent characteristics, and the more evolutionarily proven "skills" it starts out with, the more it can learn, the more problems it can solve, the more it can accomplish. In sharp contrast to the Standard Model, which views an absence of content-specific structure as a precondition for richly flexible behavior, the analysis of what computational systems actually need to succeed suggests the opposite: that the human capacity for adaptive flexibility and powerful problem-solving is so great precisely because of the number and the domain-specificity of the mechanisms we have. Again, this converges on William James's argument that humans have more "instincts" than other animals, not fewer (James, 1 892; Symons, 1987).

(Tooby & Cosmides, 1992; pp.113)

This approach is vindicated by more than just intuitive appeal. For instance, many AI researchers now agree that artificially duplicating the complexity of human intelligence requires modular computational systems (Minsky 1985; Kortenkamp et al., 1998; Thorrison 1999; Sengers 1999; Hexmoor et al., 1997; Bryson 2000, 2003; Bacchus & Kabanza, 2000). Furthermore, although neuroscience is implicitly committed to the idea that different brain regions perform different functions – and hence that the anatomical localization of cognitive mechanisms is an obvious and rather uninteresting truth[27] – recent neuroimaging work has begun to accentuate just how varied, populous and neurologically fine-grained these mechanisms are, especially in relation to reading (Deheane & Cohen, 2007), language (Bookheimer, 2002; Binder et al., 2009) theory of mind (Saxe, Carey & Kanwisher, 2004;

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[27] As the philosopher Richard Samuels pithily points out, a significant degree of cognitive modularity is a banal truth since even a general purpose Van Neumann’s computer is made up of modular bits and pieces (Samuels, 2006).

Frith & Frith, 2003), face-recognition (Haxby et al., 2000) and memory (Baddeley, 2000, 2007).

Despite this resonance, the *theory* of massive modularity put forth in the above excerpt is little more than a sketch. Many outstanding questions remain about precisely what ‘modules’ are, and how they communicate with one another. As many are no doubt aware, it is precisely in these areas that the massive modularity thesis has sparked huge controversy. Indeed, as it will turn out, without addressing these concerns, it is simply naive to think that stockpiling modules gets us any closer to cognitive flexibility than general-purpose mechanisms do.

In a literal sense, a module refers to a separable or self-contained component of something – for instance the “isolable sub-components” of a hi-fi system (Carruthers, 2005). On basic definitional grounds, then, we can immediately see why such a mechanism harmonizes with EP’s stance on cognition. Like an adaptation that has evolved to solve a domain-specific problem, a tape-deck or amplifier – or indeed any modular structure in a well-designed information processing system – acts upon a specific class of information in a highly efficient manner. Although this concern is often glossed over, the spatially discrete nature of modules also maps onto a crucial aspect of the mechanisms that interest EP. Of course, discreteness does not imply that modules are like miniaturized neural versions of cogs and wheels that are sharply individuated from one another – using Pinker’s metaphor, modules are much more likely to resemble “roadkill, sprawling messily over the bulges and crevasses of the brain” (1997). Nevertheless, adopting this more realistic view certainly does not rule out that modules can be conceived of as neurologically bounded entities (even roadkill has a boundary, albeit a smeared and irregular one). Distinguishing modules on these anatomical grounds is very important as it "presupposes that a module has a distinct history in the development of the individual brain, and this in turn presupposes some genetic and evolutionary story about the conditions that make such an individual development possible" (Sperber, 2005). For self-evident reasons, this is crucial for an account of modules as fully biologized entities that are robustly distinguishable from the idealized 'boxes' used in diagrams that illustrate the flow and regulation of information in cognitive processes (Sperber, 2005). Moreover, in a broader paradigmatic sense, anatomically localizing modules boosts the scientific prospects of understanding mental adaptations. In the words of the evolutionary developmental biologists Wolfgang and Gunther Wagner:

> In general, the idea of modularity is the hypothesis that reality can be packaged into more or less discrete units with characteristic properties. If this is possible there is the hope that a class of natural processes may be understood as interactions and reactions among those natural units. Within the sciences the paradigm for such an approach is certainly chemistry, which has a small hierarchy of such units that define the universe of classical chemistry
>
> (2003)

However, ever since Fodor's groundbreaking (1983) analysis of modules, his philosophically derived conclusions about the features that a module ought to possess have been accepted to such a great extent that - in many people's minds –Fodorian modularity has become synonymous with modularity per se. This has led to much acrimony and conceptual confusion (Barrett & Kurzban, 2006), and is surely unwarranted, since, as Sperber (1993) correctly points out, modules are empirical entities whose nature is something to be discovered rather than conceptually stipulated. Of course, Fodor's work on modularity has proven controversial not just because it has been adopted as an orthodoxy. Even more importantly, it advocates a view of modules that abnegates the very heart of massive modularity. Let us see why.

In Fodor's original analysis of modularity, something counts towards being a module if it fulfils the following criteria: 1) domain specificity, 2) mandatory operation, 3) limited central accessibility, 4) fast processing, 5) informational encapsulation, 6) shallow outputs, 7) fixed neural architecture, 8) characteristic and specific breakdown patterns, 9) characteristic ontogenetic pace and sequencing. Crucially, Fodor took information encapsulation to be the most essential feature of a module (Robbins, 2009).[28]. However, while Fodor (1983) famously argued for the modularity of sensorial input systems, he nonetheless rejected the idea that central-cognition could be modularized. Fodor's main argument against central-modularity derived it's impetus from the way in which he envisioned a modular system's cognitive architecture. Specifically, Fodor (2000) reasoned that modules would struggle to preserve the true properties of their informational output unless that output was immediately posted into a vertical transmission chamber that fed into the input of another module. Crucially, in this architecture, information processing is bottom up, that is, once information gets sucked up a tube it cannot be re-integrated into the system at large.[29] Clearly, this rigidly encapsulated 'pipe' like system doesn't cohere with the phenomenology of central cognition, in which distal thoughts bleed into one another and are combined on the fly in endless associative patterns. To cash this idea out more technically – as Fodor himself puts it – central cognitive beliefs are determined through global processes. Thus, when we form or confirm any belief we draw upon our entire epistemic landscape, a process that requires the mixing and matching of ideas in a manner that is far too unconstrained for Fodor's rendering of our cognitive architecture to facilitate.

However, while Fodor's arguments for the defining characteristics of perceptual modules were appropriate and empirically rigorous – and while they continue to be supported by current neuroscience – his argument against central-modularity only gets going if we

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[28] Spelt out more fully, ' "A cognitive system is informationally encapsulated to the extent that in the course of processing a given set of inputs it cannot access information stored elsewhere" (Robbins, 2009).

[29] See Appendix, Diagram 3

accept that his architectural schema is a *necessary* conceptual requirement for any modular processing system. However, the *biological* fact of the matter is that Fodor's architectural constraints – although well motivated – are far from inexorable. To begin to see this, consider the following example. Opposing a vertical pipe-line Fodorian architecture, Barrett (2012) conceptualizes a kind of' bulletin board' modular system in which the informational outputs of modules are posted in a public space that all modules monitor and have access to. Moreover, when the informational output of one module fails to meet the input requirements of another module, the information is returned to the 'board' unaltered. However, when the information does meet the input requirements of a module it can either be A) re-posted in its original form or B) reposted with an additional informational tag that can provide further information to another module.[30] Although it seems implausible that any kind of truth preservation could occur in such an 'open', elaborately interconnected and transformative system, Barrett (2012) points out that enzymes can be fruitfully compared to specialized computational devices that achieve just this, since

> […] enzymes use a template to detect specific substrates; they are passive, monitoring a pool of substrates until a match is found; and when they encounter a substrate that matches their template, they systematically transform it into something new, in a rule-like fashion. Thus, enzymes have the three basic properties of specialized computational devices: [they] accept information of a particular kind […] perform specific operations on the information they admit […]output the resulting information in a format useable by other systems. [Furthermore] One can have an enzymatic system in which all of the enzymes in the system have access to all of the substrates, and in which only the 'correct' reactions are catalyzed.[31]

(268-270)

Barrett's argument needn't entail that every modular processing network in our brain resembles an enzymatic system. The point, rather, is that pace Fodor, it does at least seem biologically *possible* for modular processing to take place within an architecture in which

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[30] See Appendix, Diagram 4.

[31] See Appendix, Diagram 5 & 6

strict information encapsulation is not required. Most intriguingly, though, in certain domains, the enzymatic approach appears to map onto empirical neuroscience rather neatly. In this respect, consider face-processing. According to fMRI scans, face processing is facilitated by two groupings of anatomically localizable and functionally-specialized mechanisms. While the first ‘central’ network processes static and dynamic features of faces, the second ‘extended’ network uses visually perceived face to extract salient information about the person (e.g. their mood, intentions, etc.) [Haxby et al., 2000].[32] Amazingly, this psychological information can then loop back into the face perception system to enhance our perceptual classification of a face. Studies have thus found that the emotional ‘tone’ of an expression appears to contribute to the accurate *perception* of that expression (Calder et al, 1996; Adolphs et al., 1994). Not only does such a processing system directly violate the one-way vertical transmission that occurs in Fodorian architecture, it also seems to suggest that some kind of sophisticated enzymatic tagging process must be taking place. Furthermore, there is now also evidence that such collaborative processing relies on the fact that independent mechanisms–like the ones in the face-processing network–communicate with one another by having common access to bulletin-board like cognitive nodes (Bullmore & Sporns, 2009). All of this empirical evidence strongly suggests that an enzymatic approach can be credibly extended to understand modular information processing in the brain.

However, if all this is indeed correct, does such a departure from Fodor’s original characterization of modularity mean that the current modularity concept is talking about a set of mechanisms that are only termed modules due to semantic laziness? The answer to this question must be no. As we’ve already seen with the face-processing network, enzymatic

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[32] See Appendix, Diagram 7

systems can retain the key notions of Fodorian modularity – functional specialization (or domain-specificity) and anatomical localization.

Seen in this light, contemporary accounts of modularity *can* account for flexibility without shifting the goal posts and imbuing modules with properties that make them general-purpose or neurologically unbounded. Of course, while it is true that encapsulation was integral to Fodor's original characterization of modularity, its importance was only due to his meta-assumptions about the kind of cognitive architecture that could enable truth preservation. If it is indeed true – as I have hopefully demonstrated – that biological systems do not require such an architecture in order to be modular, it seems only fair to conclude that there is no compelling reason to suppose that strict information encapsulation ought to be a defining property of modules.

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Since there are justifiable reasons to suppose that modules can flexibly communicate with one another and augment each other's processing procedures, the 'bundle' hypothesis does seem to solve Tooby & Cosmides' paradox without biting off more than it can chew. A remaining question, though, is how such a flexible cognitive system contributes to the adaptive problems attendant on climactic volatility. In my view, this question can only be answered in a general way. This is because a massively modular brain could generate an almost inexhaustible range of solutions. To get a sense of this, consider Barrett's (forthcoming) suggestion that our object parsers, animacy detectors, face recognition systems and action detector mechanisms are seamlessly integrated in an enzymatic manner. How could this enhance the flexible behaviour of a hunter-gatherer group who need to hunt and cooperate in novel conditions because of climactic disturbances? To take just one example, the look of pain on a hunter's face could help a fellow hunter's animacy detector reassess an alien object that was initially taken to be inanimate and benign; the outputs of these mechanisms could then enable the hunter's action parser to assess that the fellow hunter is not standing still but is backtracking at a slow and extremely cautious pace. Throw a few cultural adaptations into the mix and some nascent language and theory of mind abilities, and the possibilities simply explode.

Thus, while it is undoubtedly true that cognitive and developmental plasticity exist and that they help with environmental indeterminacy, it is not at all clear why the cognitive flexibility achieved by a system that is crammed with highly interconnected special-purpose machinery cannot also deal with these problems. Even if these mechanisms are adapted to the recurrent, task-specific adaptive problems of an environment that has no direct bearing upon the variable and novel adaptive problems brought about by climactic volatility, to rule out their efficacy on the basis of this alone seems unwarranted. It would, for instance, be akin to saying that a suburbanite who ends up stranded on a desert island has no chance of successfully adapting to his radically altered environment. Needless to say, such an assumption would be presumptuous at best.

9: Conclusion

I have presented four interconnected arguments which seek to critique the VS hypothesis and its consequent claim that EP has seriously mischaracterized both the EEA and the cognitive architecture of the human mind. It is crucial to emphasize that each argument – barring the first– has been designed in such a way that its rejection of the VS hypothesis lends automatic credence to EP's rendering of the EEA. As a further methodological note, it is also important to stress that the arguments, while interrelated, do not depend on one another for their truthfulness. Thus, even if half of them are deemed implausible, the remainder ought to do enough to usher in a broad scepticism about Potts' thesis and the manner in which EP's critics have used it to buttress their claims about modularity. Of course, on a more gratifying note, if all the arguments presented are strong enough to resist close scrutiny, this surely does enough to show that the VS hypothesis ought to be rejected.

However, this leads to an important caveat. Implicit to the VS hypothesis is the claim that climactic volatility and the evolution of VS adaptations have been the *dominant* theme in hominine evolution. A rejection of the VS hypothesis does not therefore entail that no VS adaptations to climactic volatility occurred in human evolutionary history. In actual fact, I am happy to concede that many such adaptations could indeed exist. The idea I think we should resist is that these adaptations are statistically *significant* compared to the special-purpose adaptations produces by recurrent adaptive problems.

Finally, it must be pointed out that this study does not purport to offer a full defence of how EPs have reconstructed the EEA. As I mentioned at the outset, a whole variety of objections have been levelled against the EEA, with philosophers of biology in particular posing some hard questions (Franks, 2005; Griffith, 1996; Sterelny & Griffiths, 1999) that have not been as easy to answer as others.[33] Still, unlike many of these objections the VS hypothesis offers a critique of the EEA which

A) has an immediate bearing on EP's thesis of massive modularity
B) is informed by a sophisticated paleoanthropological theory
C) has been widely influential in the critical literature
D) has received little critical attention itself.

On these grounds alone, it surely deserves to be singled out as perhaps the most intriguing objection that has been raised against the EEA. By seeking to decisively assess it, then, this thesis hopes to make a substantive defence of the manner in which EP has conceptualized the EEA.

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[33] But see Atkinson & Wheeler (2001) for an account of how EP and its conception of the EEA can be defended against the 'grain-problem' raised by Sterelny & Griffiths (1999).

Diagram 1: Potts’ Modelling of Variability Selection

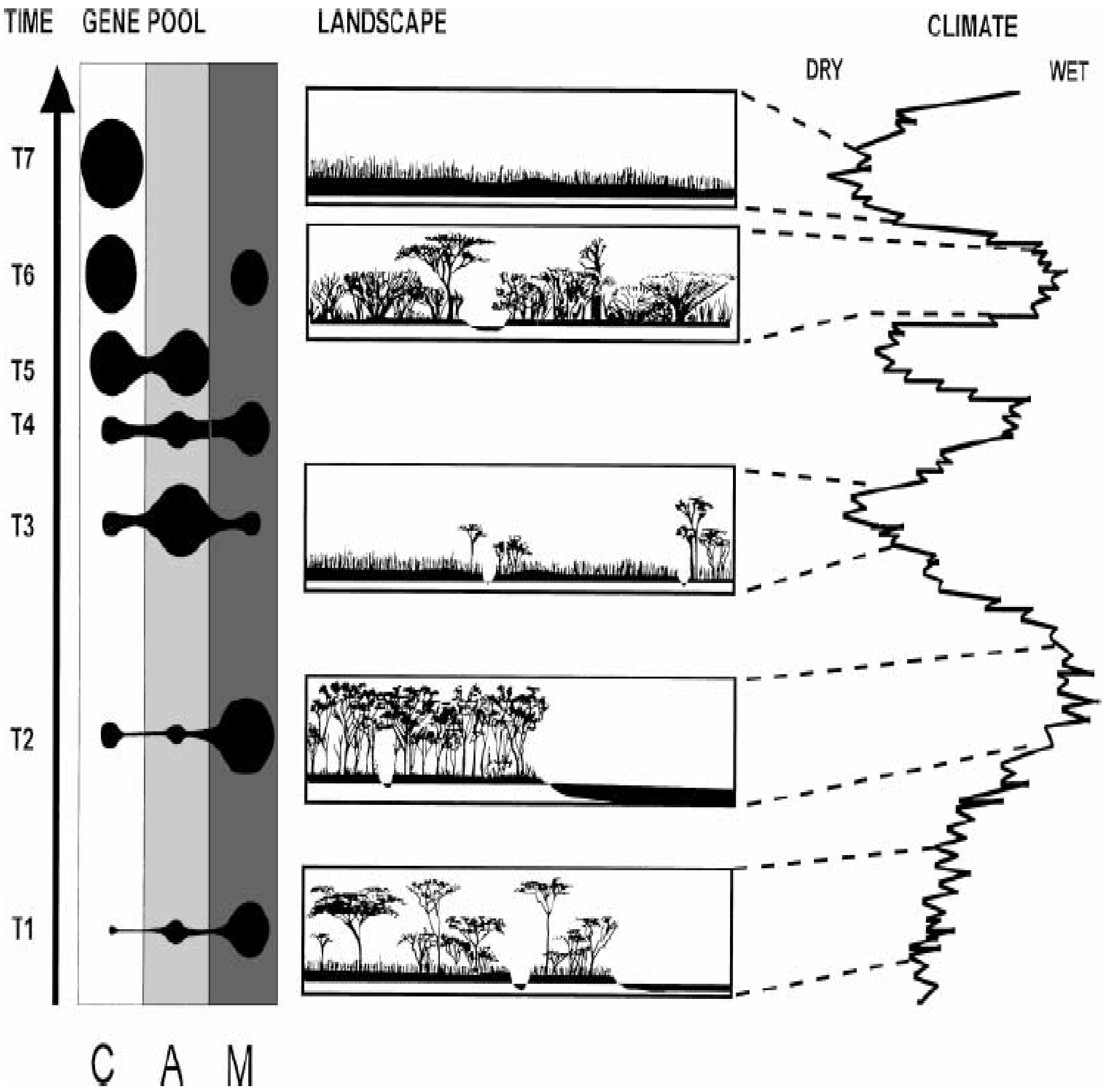


Figure 2. Variability selection in a Mendelian population (based on Potts[40]). Pleistocene environmental oscillation (Climate) causes fluctuation in vegetation and surface water (Landscape). At t1, a modest-sized lake is fed by a meandering fluvial system in open woodland. After a series of wet phases, when tree cover and surface water are abundant, and dry phases, when grassland and low lake levels prevail, surface water disappears from the area (t7). Shifts in important parameters of natural selection such as food distribution influence the genetic options of a population. The model assumes the existence of multiple genetic, developmental, and phenotypic options. Over time, three alleles, not necessarily at the same locus, play critical roles: *M* affects a structure or function that offers competitive advantage in moist, highly vegetated settings. Allele *A* governs a behavior that yields higher fitness in dry, open habitats. And *C*, though at greater metabolic cost than the other alleles impose, contributes to the organism's versatility in response to resource changes by, for example, increasing digestive flexibility or providing larger memory regarding alternative food sources. The size of the shapes under Gene Pool depicts the relative fitness of these three alleles in specific time intervals. Significant adaptive change is usually thought to arise by consistent selection from one generation to another (e.g., t1 to t2). *M* and *A* have periods of high relative fitness within certain environments. Environmental oscillation and related inconsistency in selective conditions, however, ultimately favor versatility (fixation of allele *C*) at the expense of habitat-specific responses (elimination of *A* and *M*). By t5 to t7, the relative advantage of allele *C* is apparent but cannot be extrapolated from the short-term fitness results of any single interval earlier in time. Over several hundred thousand years of oscillation, a wide suite of alleles affecting multiple aspects of an organism's diet, cognition, sociality, and other functions may become dominant because they enhance environmental data processing and novel problem solving.

Diagram 2: Comparison Between Extinct Large Herbivores and Closely Related Surviving Taxa

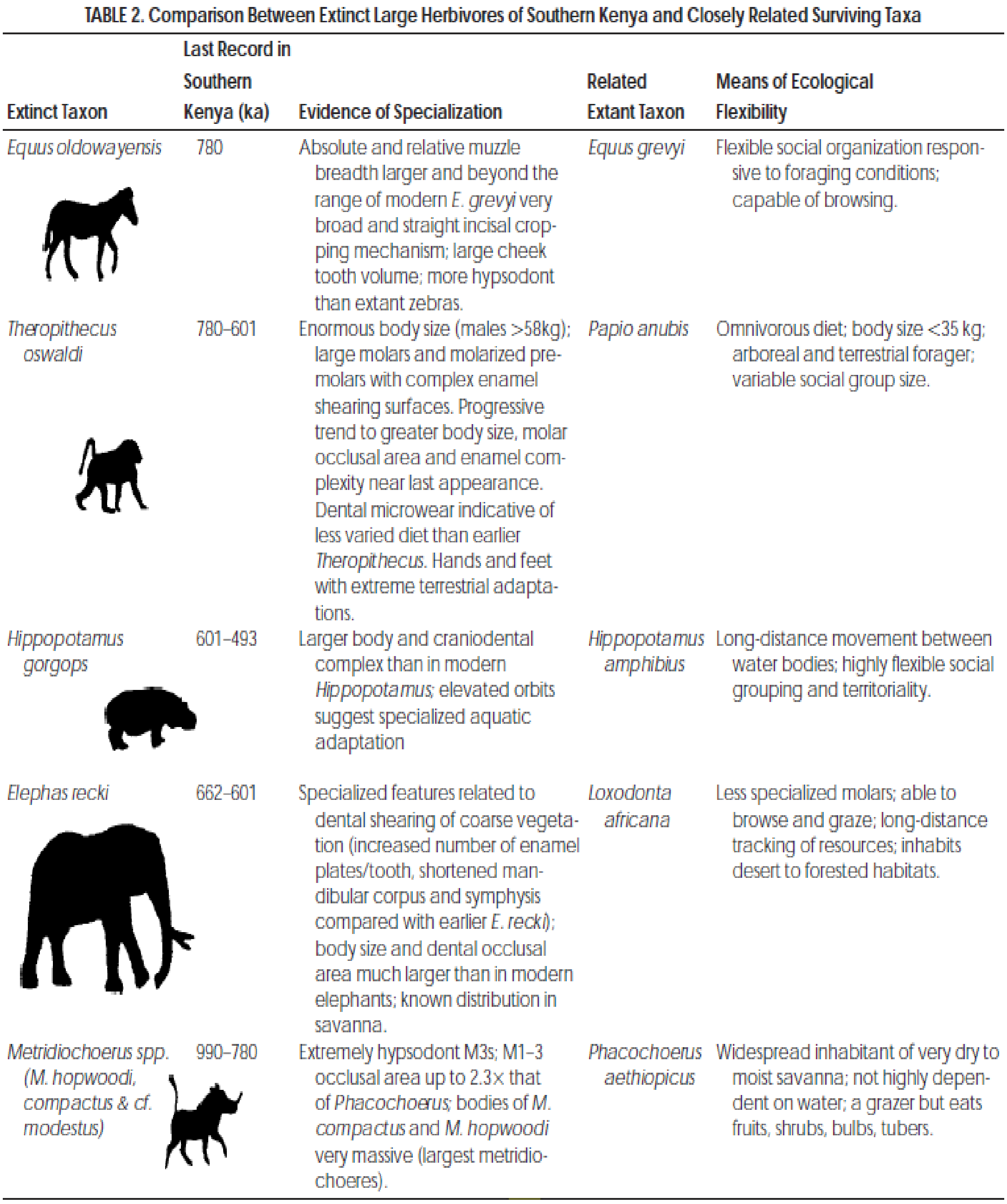


TABLE 2. Comparison Between Extinct Large Herbivores of Southern Kenya and Closely Related Surviving Taxa

Extinct Taxon	Last Record in Southern Kenya (ka)	Evidence of Specialization	Related Extant Taxon	Means of Ecological Flexibility
Equus oldowayensis	780	Absolute and relative muzzle breadth larger and beyond the range of modern *E. grevyi* very broad and straight incisal cropping mechanism; large cheek tooth volume; more hypsodont than extant zebras.	*Equus grevyi*	Flexible social organization responsive to foraging conditions; capable of browsing.
Theropithecus oswaldi	780–601	Enormous body size (males >58kg); large molars and molarized premolars with complex enamel shearing surfaces. Progressive trend to greater body size, molar occlusal area and enamel complexity near last appearance. Dental microwear indicative of less varied diet than earlier *Theropithecus*. Hands and feet with extreme terrestrial adaptations.	*Papio anubis*	Omnivorous diet; body size <35 kg; arboreal and terrestrial forager; variable social group size.
Hippopotamus gorgops	601–493	Larger body and craniodental complex than in modern *Hippopotamus*; elevated orbits suggest specialized aquatic adaptation	*Hippopotamus amphibius*	Long-distance movement between water bodies; highly flexible social grouping and territoriality.
Elephas recki	662–601	Specialized features related to dental shearing of coarse vegetation (increased number of enamel plates/tooth, shortened mandibular corpus and symphysis compared with earlier *E. recki*); body size and dental occlusal area much larger than in modern elephants; known distribution in savanna.	*Loxodonta africana*	Less specialized molars; able to browse and graze; long-distance tracking of resources; inhabits desert to forested habitats.
Metridiochoerus spp. (*M. hopwoodi, compactus & cf. modestus*)	990–780	Extremely hypsodont M3s; M1–3 occlusal area up to 2.3× that of *Phacochoerus*; bodies of *M. compactus* and *M. hopwoodi* very massive (largest metridiochoeres).	*Phacochoerus aethiopicus*	Widespread inhabitant of very dry to moist savanna; not highly dependent on water; a grazer but eats fruits, shrubs, bulbs, tubers.

Diagram 3: Fodorian Vertical Pipe Architecture

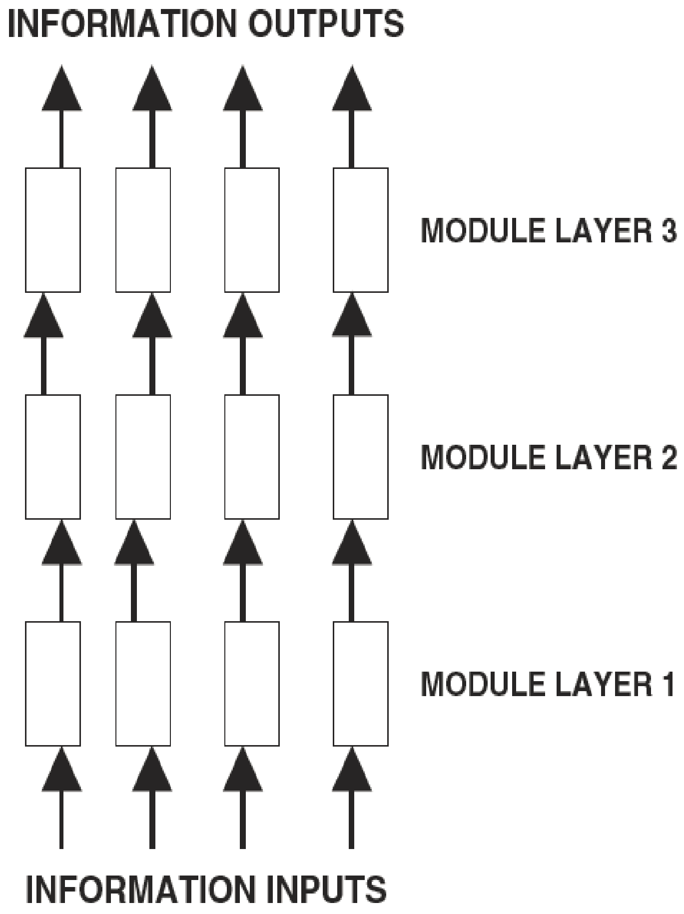


Figure 1 *Vertical pipe architecture*

Diagram 4: Bulletin Board Achitecture

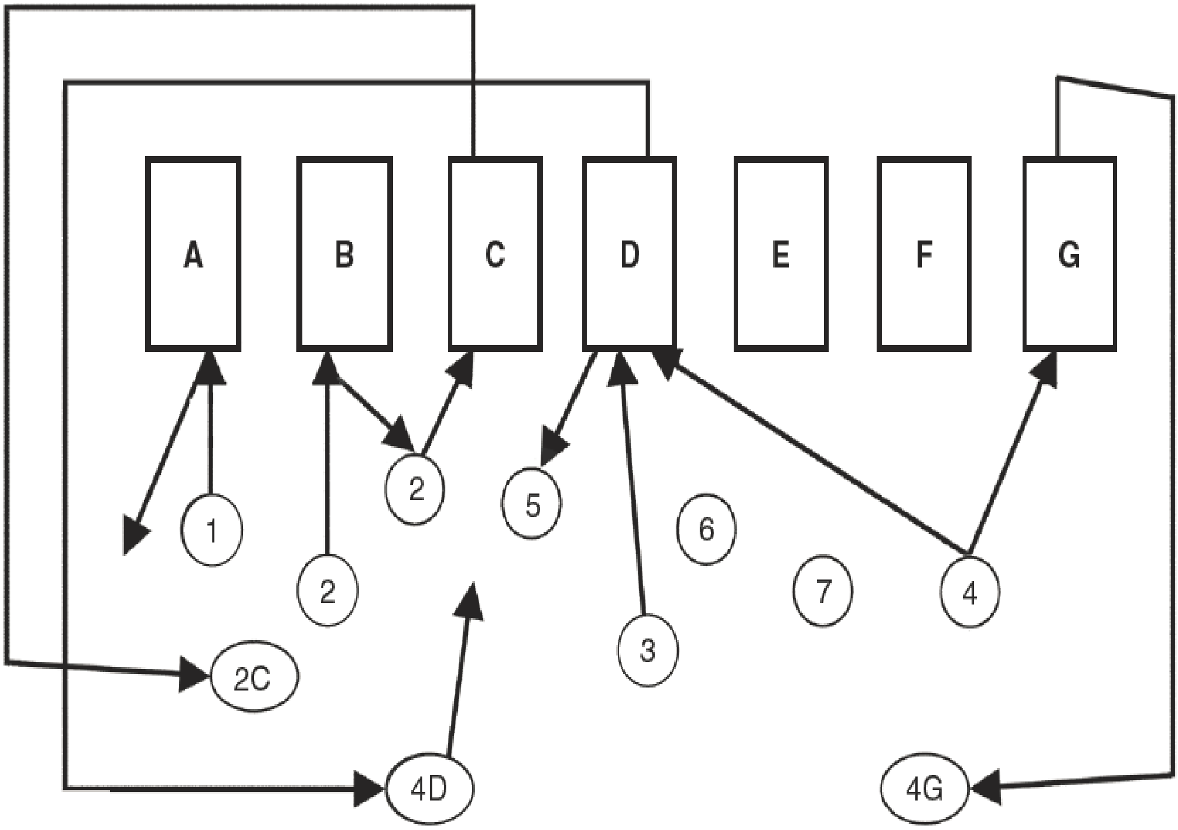
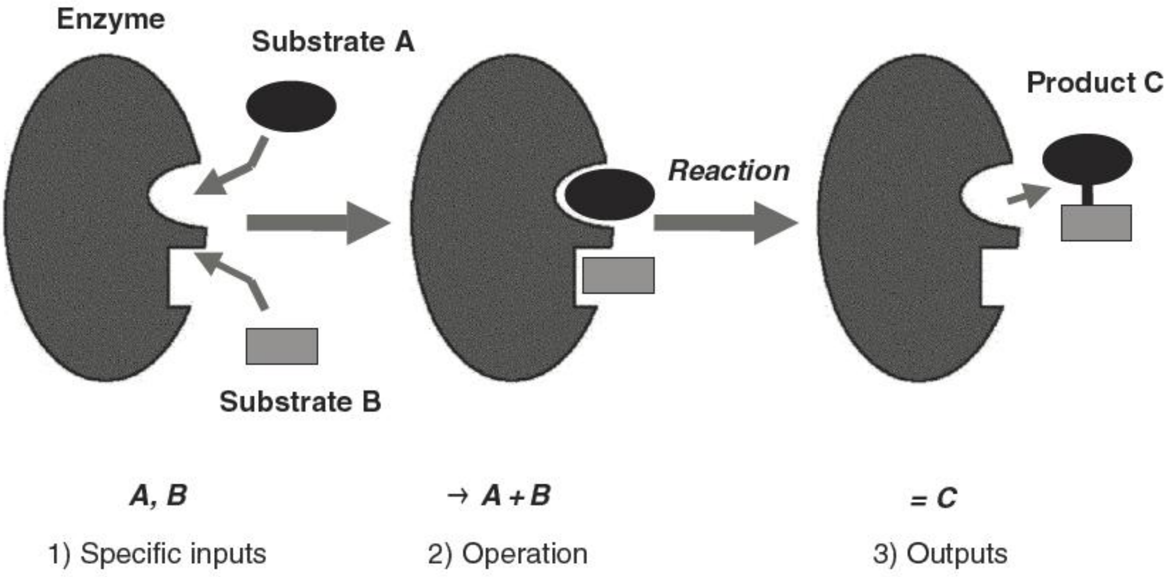


Figure 2 *Bulletin board architecture*

Information packets (labeled 1 through 7) are posted on a 'bulletin board' or public representational space that is visible to all modules (modules are labeled A through G). Modules constantly monitor the bulletin board for representations that they are able to process

Diagrams 5 & 6: Enzymatic Processing



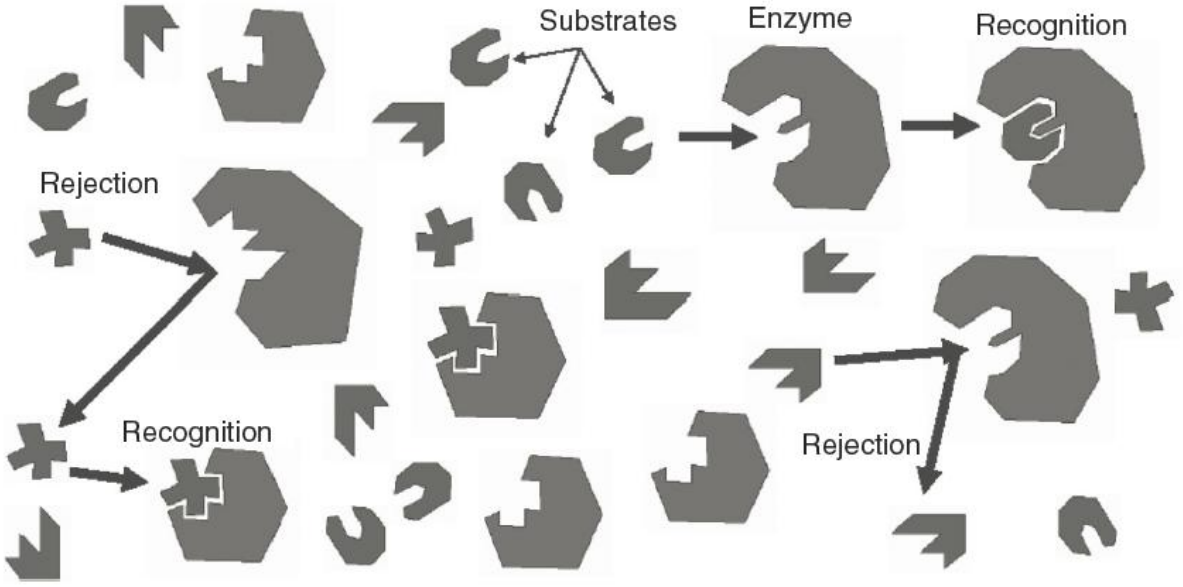


Figure 5 *Binding specificity*

Diagram 7: Face Processing Modular Network

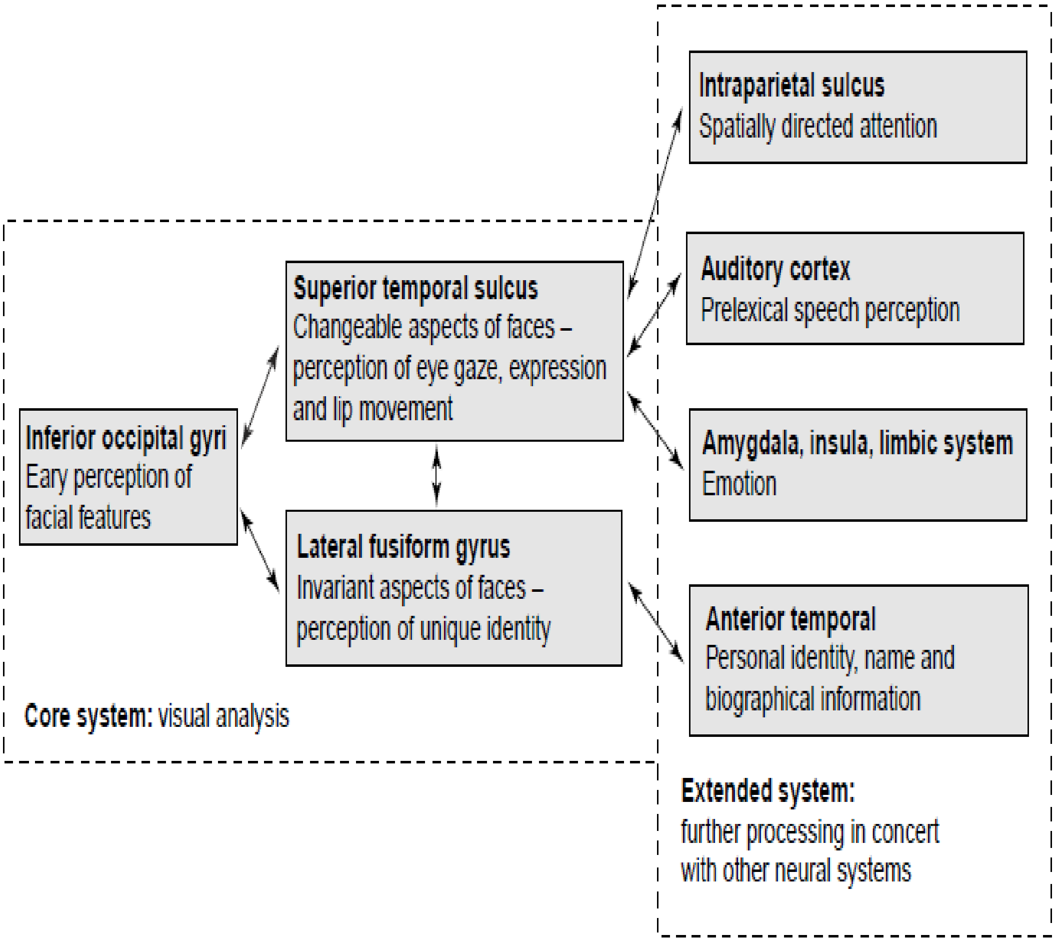


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Fig. 5. A model of the distributed human neural system for face perception. The model is divided into a core system, consisting of three regions of occipitotemporal visual extrastriate cortex, and an extended system, consisting of regions that are also parts of neural systems for other cognitive functions. Changeable and invariant aspects of the visual facial configuration have distinct representations in the core system. Interactions between these representations in the core system and regions in the extended system mediate processing of the spatial focus of another's attention, speech-related mouth movements, facial expression and identity.

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