Early determinants of behaviour: evidence from primate studies

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The idea that early experiences disproportionately influence adult behaviour has long been a fixture of mainstream developmental theory. Although unambiguous empirical support for this view at the human level is surprisingly sparse, compelling evidence from animal studies abounds. Recent studies with rhesus monkeys have demonstrated dramatic short- and long-term effects of differential early social experiences on both behavioural and physiological functioning. Early social relationships with mothers or other caregivers appear to provide especially powerful determinants of behavioural propensities throughout the lifespan.

The basic idea that certain early experiences can significantly influence adult functioning has been a central feature of many developmental theories over the past century. Throughout his career, Freud[1] argued that events transpiring during the first 5 years of life had powerful effects on personality development and intrapsychic dynamics that could last a lifetime. Konrad Lorenz[2] demonstrated that imprinting experiences in the initial hours after hatching established social preference patterns in precocial birds that were essentially permanent. Social learning theories developed by behaviourally oriented psychologists in the 1950s traced the origins of personality to a newborn's early experiences with feeding[3,4]. John Bowlby's social attachment theory postulated that all of an individual's social relationships throughout life were influenced in fundamental ways by the initial attachment relationship with one's mother[5]. Developmental neurosciences approaches of the 1980s and 1990s have focused on long-term neurobiological processes associated with events experienced during early critical or sensitive periods[6,7]. At the heart of all these approaches has been the basic belief that 'the child is the father of the man', that early experiences can and do shape adult functioning.

Given the historical prominence of these diverse theoretical traditions and their apparent convergence regarding presumed causal links between early experience and subsequent behavioural, emotional, and physiological functioning, it seems surprising that unambiguous empirical evidence for such causal links in humans is actually somewhat

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sparse[8]. While countless clinical reports over the years have interpreted the presence of various psychopathologies in adolescent and adult life as the direct consequence of specific early experiences with parents and/or other caregivers, the retrospective nature of such reports precludes scientifically acceptable conclusions regarding causality. Large-scale epidemiological studies have frequently documented statistically significant relationships between certain early life events or circumstances and characteristics, capabilities, and accomplishments expressed later in life, but these relationships are probabilistic at best and typically account for only small proportions of total variance[9]. Even the best-designed prospective longitudinal experiments in humans are almost never able to control all aspects of the subjects' physical and social environments after the initial assignment of specific subjects to specific experimental/ treatment conditions, no matter how effective the assignment procedures might be. The net result is that long-term differences between subjects that are the direct product of early treatment differences are inevitably clouded, and sometimes entirely masked, by intervening experiences that differ among subjects both within and between treatment groups. Thus, unambiguous causal links between early experiences and later functioning in humans have remained largely elusive to date.

In contrast, research with animals has permitted experimenters to carry out prospective longitudinal studies in which early experiences can be systematically manipulated and subsequent experiences can be rigorously controlled throughout the entire period of investigation. Over the past half-century there have been a wealth of prospective experiments examining the consequences of different early physical and social environments on behavioural and physiological development in animals ranging from invertebrates to many avian and mammalian species. This work has produced many compelling and convincing accounts of how specific early experiences can affect behavioural repertoires, perceptual preferences, sensory capabilities, physiological processes, neurochemical functioning, neuroanatomical cytoarchitecture, and even gene expression. Of course, the relevance of these extensive and often striking animal findings for understanding possible early experience effects in humans is largely dependent on the degree to which the specific animal phenomena in question generalize to the human case[10].

By and large, the most compelling generalizations between animals and humans occur when the animal data come from our closest evolutionary relatives — Old World monkeys and apes. Because Old World monkeys and apes share over 90% of our genes[11,12], most aspects of their morphology and physiology are homologous with humans. The basic patterns and sequences of brain development are also highly conserved across these primate species. Moreover, the rich behavioural

and emotional repertoires, advanced cognitive capabilities, and complex social organizations that characterize almost all monkeys and apes provide opportunities for modelling diverse aspects of human biobehavioural development that are simply not feasible with rodents, carnivores, and other nonprimate species[13]. Studies with captive rhesus monkeys (*Macaca mulatta*) have provided perhaps the most extensive and compelling evidence for long-term effects of differential early experience that might generalize to human phenomena.

Social organization, normative development, and individual differences in rhesus monkeys

By way of background, rhesus monkeys in their natural habitats reside in large social groups (termed 'troops'), each containing several multi-generational female lineages (matrilines), plus numerous immigrant adult males. This particular form of social organization, widespread among Old World monkey species, derives from the fact that female rhesus monkeys remain in their natal troop throughout their entire lifespans, whereas virtually all males emigrate from their natal troop around puberty, eventually joining other nearby troops[14]. Although different troops may have overlapping ranges and even daily exposure to one another, each troop represents a distinctive, cohesive social unit. Each rhesus monkey troop is also characterized by complex, multi-dimensional dominance hierarchies, based more on kin relationships and dynamic coalitions among nonkin than the relative size or strength of individual troop members[15].

The species-normative pattern of behavioural development for rhesus monkeys growing up in natural troops is well-known and thoroughly documented. Rhesus monkey infants spend virtually all of their initial days and weeks of life in physical contact with their biological mothers, during which time strong, specific attachment bonds are formed. In their second month of life, rhesus monkey infants begin to explore their immediate physical and social environment, typically using their mothers as a 'secure base' for exploration, much as Bowlby[16] has described for human infants and toddlers. Over the next few months, these infants spend increasing amounts of time engaging in extensive social interactions with other group members, especially peers[17]. From 6 months of age until puberty, play with peers becomes the predominant social activity for young monkeys. During this time, play interactions become increasingly complex, involving patterns of behaviour that appear to simulate virtually all adult social activities, including reproductive behaviours and dominance/aggressive interactions[18].

Puberty begins near the end of the third year of life (for females) and the start of the fourth year (for males) and is associated with major life transitions for both genders. Although females remain in their natal troop throughout puberty and thereafter, their interactions with peers decline dramatically as they redirect much of their social activities toward matrilineal kin, including the infants that they subsequently bear and rear. Pubertal males, by contrast, leave their natal group permanently and typically join all-male gangs for varying periods before they attempt to enter a new troop. This period of transition for adolescent and young adult males represents a major environmental stress, with mortality rates from the time of natal troop emigration to successful entry into another troop approaching 50%[19]. Some surviving males stay in their new troops for the rest of their lives, whereas other males may transfer from one troop to another several times during their adult years[20].

The above-described pattern of social group organization and sequences of behavioural ontogeny have been consistently documented not only in rhesus monkey troops living in different natural and semi-natural habitats but also in groups maintained in captivity and therefore can be considered normative for the species. Nevertheless, there are substantial individual differences among members of every troop in the precise timing and relative ease in which they make major developmental transitions, as well as how they manage the day-to-day challenges and stresses that are an inevitable consequence of life in complex social groups. Recent research has identified two subgroups of individuals born and raised in natural settings who exhibit aberrant developmental trajectories that can potentially result in increased long-term risk for behavioural pathology and even mortality[21].

Members of one subgroup, comprising approximately 20% of most populations of rhesus monkeys studied to date, consistently exhibit unusual behavioural disruption and enhanced physiological arousal in the face of a wide range of stimuli that most other monkeys in their troop find interesting and readily explore, with minimal physiological arousal. These **high-reactive** individuals typically respond instead with behavioural expressions of fear and anxiety and with significant (and often prolonged) activation of the hypothalamic-pituitary-adrenal (HPA) axis, sympathetic nervous system arousal, and increased noradrenergic turnover[22].

High-reactive rhesus monkeys can usually be identified in their first few months of life, when they typically begin leaving their mothers later chronologically and exhibit less exploratory behaviour than other infants in their birth cohort. High-reactive youngsters subsequently tend to be shy and withdrawn in their initial encounters with peers. Laboratory studies have demonstrated that high-reactive juveniles placed in novel playrooms with unfamiliar peers exhibit higher and

more stable heartrates and more elevated levels of plasma corticotropin (ACTH) and cortisol than their less reactive interaction partners[23].

When environmental perturbations are extreme and/or prolonged, behavioural and physiological differences between high-reactive and other infants and juveniles often become exaggerated. For example, virtually all rhesus monkey youngsters annually experience repeated functional maternal separations when their mothers leave the troop for several hours or even days to consort with selected males during the 2–3 month breeding season each year. Most young monkeys initially react with obvious behavioural agitation but soon begin to adapt to their mothers' repeated departures and typically expand their interactions with others in their social group while their mothers are away[24]. In contrast, high-reactive juveniles often lapse into a behavioural depression characterized by increasing lethargy and social withdrawal, apparent eating and sleeping difficulties, and a striking fetal-like huddling posture sometimes maintained for hours on end[25]. Laboratory studies have both replicated and extended these findings from the field. Relative to their like-reared peers, high-reactive rhesus monkey infants and juveniles are not only more likely to exhibit depressive-like behavioural responses to separation but also tend to show greater and longer HPA activation, more dramatic sympathetic arousal, more rapid central noradrenergic turnover, and greater selective immunosuppression[26]. These differential patterns of behavioural and physiological response to separation remain quite stable throughout development. An increasing body of evidence has demonstrated significant heritability for these differences in behavioural and physiological reactivity[27].

Recent field studies have shown that high-reactive rhesus monkey adolescent males usually emigrate from their natal troop at significantly older ages than the rest of their birth cohort[28]. When they do finally leave their home troop, high reactive young males typically employ much more conservative strategies for entering a new troop than do less reactive male peers[29]. High-reactive young females appear to be at greater risk for inadequate maternal care of their first-born offspring than are other primiparous mothers[30].

A second subgroup of rhesus monkeys, comprising approximately 5–10% of the population, can be generally characterized as unusually **impulsive** in their behavioural activities, especially those that result in aggressive interchanges; they also tend to have chronically low central serotonin metabolism, as indexed by cerebrospinal fluid (CSF) levels of 5-hydroxyindoleacetic acid (5-HIAA), the primary central serotonin metabolite in primates. These behavioural and physiological features appear relatively early in development and are notably stable from then on[31]. Impulsive individuals, especially males, seem unable to moderate their behavioural responses in rough-and-tumble play interactions,

occasionally escalating play bouts into tissue-damaging aggressive exchanges, disproportionately at their own expense. Impulsive juvenile males also display a propensity for making dangerous leaps from treetop to treetop, sometimes with disastrous outcomes. CSF samples obtained from these impulsive individuals reveal unusually low concentrations of 5-HIAA that typically remain low as these monkeys start to mature[32].

It appears that impulsive males tend to be expelled from their natal troop well before puberty, a result more likely a consequence of their social incompetence than any general aggressive tendencies *per se*[33]. Most become solitary and typically perish within a year[34]. Young females who exhibit excessive impulsive-aggressive behaviour also characteristically have chronically low CSF 5-HIAA concentrations. Unlike males, however, they are unlikely to be expelled from their natal troop (or even matriline) at any time during their lives, although laboratory studies suggest that they typically remain at the bottom of their respective dominance hierarchies. These females readily produce and rear infants, although laboratory studies suggest that they often are inept and incompetent mothers[35].

In sum, rhesus monkeys who behave impulsively (and have low central serotonin turnover) early in life tend to exhibit aberrant developmental trajectories that often result in premature death for males and chronically low social dominance for females. As was the case for high-reactive monkeys, there is increasing and compelling evidence that the behavioural and physiological features characteristic of impulsive individuals are highly heritable; certainly they are developmentally stable[36].

Effects of maternal deprivation on rhesus monkey biobehavioural development

It has long been known that early social experiences can have dramatic long-term behavioural and emotional consequences for rhesus monkeys and other nonhuman primate species. Research by Harlow and others in the 1960s clearly demonstrated that total social deprivation throughout infancy almost always results in extreme (and often permanent) behavioural abnormalities and severe social and emotional deficits, especially evident in aggressive, reproductive, and parenting activities[37]. However, the relevance of these findings for cases involving early social deprivation of human infants and young children seems unclear, given that (fortunately) virtually no human infants experience the degree of social deprivation for comparable developmental periods as the classic rhesus monkey studies entailed. More recent studies of

early social deprivation have utilized rearing environments that provide a much greater degree of social stimulation during 'deprivation' periods, e.g. access to foster mothers and/or peers, than did the early isolation experiments. Monkeys reared in such maternally deprived environments develop few, if any, of the bizarre, idiosyncratic stereotypic patterns of behaviour so characteristic of isolate repertoires; instead, most aspects of their social and emotional development generally mimic species-normative patterns[38]. Nevertheless, even relatively 'mild' forms of early maternal deprivation can have significant short- and long-term behavioural and physiological consequences.

The most commonly used rearing paradigm for these studies has involved separating infants from their mothers at birth, hand-rearing them in a nursery for the first month, and then rearing them with same-age peers until 6 months of age, after which they are moved into larger groups that also contain mother-reared agemates and sometimes older adults[39]. Both peer-reared and mother-reared youngsters continue to live in these mixed social groups at least until puberty.

Rhesus monkey infants reared according to this protocol readily develop strong attachment bonds to each other[40]. However, because peers are not nearly as effective as a typical monkey mother in providing a 'secure base' for exploration or in reducing fear in the face of novelty or stress, the attachment relationships these peer-reared monkeys develop with each other are likely to be 'anxious' in nature. As a consequence, while peer-reared monkeys show normal physical and motor development and relatively normal complex social behavioural repertoires, they seem reluctant to explore novel objects, they tend to be shy in initial encounters with unfamiliar peers, and they typically drop to the bottom of their respective dominance hierarchies when grouped with mother-reared monkeys their age[41].

In addition, peer-reared monkeys consistently exhibit more severe behavioural and greater adrenocortical and noradrenergic reactions to social separation than do their mother-reared cohorts[42]. Such differences in separation reactions persist from infancy to adolescence, if not beyond. Interestingly, the general nature of the separation reactions of peer-reared monkeys seems to mirror that of 'naturally' high-reactive mother-reared subjects, both behaviourally and physiologically. Thus early peer rearing appears to have the effect of making monkeys more high-reactive than they might have been if reared by their biological mother[43].

Early peer rearing appears to have another long-term developmental consequence for rhesus monkeys as well — it tends to make them more impulsive, especially if they are males. Like the previously described impulsive monkeys growing up in the wild, peer-reared monkeys initially

exhibit impulsive tendencies in the context of juvenile play, and as they approach puberty the frequency and severity of their aggressive episodes greatly exceeds that of mother-reared group members of similar age. Moreover, both peer-reared males and females tend toward the bottom of their respective dominance hierarchies in mixed social groups. These behavioural differences in dominance and impulsive aggression between peer-reared and mother-reared juveniles and adolescents remain robust when the monkeys are subsequently moved into newly formed social groups composed initially of strangers, and they appear to be quite stable developmentally[44].

Peer-reared monkeys also consistently show lower CSF concentration of 5-HIAA than their mother-reared agemates. These group differences in 5-HIAA levels appear relatively early (i.e. well before 6 months of age), they persist through the transition to mixed-group housing at 6 months, and they remain stable at least until adolescence, despite significant developmental drops in 5-HIAA levels for mother- and peer-reared monkeys alike[45]. Thus, peer-reared monkeys as a group resemble the impulsive subgroup of wild-living (and mother-reared) monkeys not only behaviourally but also in terms of decreased serotonergic functioning throughout development.

An additional risk that peer-reared females carry into adulthood concerns their maternal behaviour. Like all other maternally deprived rhesus monkey females, peer-reared primiparous mothers are more likely to exhibit neglectful and/or abusive treatment of their first-born offspring than are their mother-reared counterparts, although their risk for inadequate maternal care is significantly less than that of maternally deprived females who also lack early peer experience, and their maternal behaviour toward subsequent offspring tends to improve dramatically[46]. Nevertheless, certain abnormalities in both the absolute levels of and developmental changes in ventral contact of offspring are consistently shown by peer-reared primiparous females who are neither neglectful nor abusive toward their babies, and these abnormalities in ventral contact patterns persist in their care of subsequent offspring[47].

In summary, early peer-rearing seems to make rhesus monkey youngsters not only more highly reactive but also more impulsive, and the resulting developmental trajectories not only resemble those of naturally occurring subgroups of rhesus monkeys in the wild but also continue in that vein long after the differential peer-rearing procedures have been completed. Indeed, some effects of early peer-rearing seem likely to be passed on to the next generation via aberrant patterns of maternal care, as may also be the case for both high-reactive and impulsive females rearing offspring in natural settings[48].

Effects of disruptions of maternal care on macaque biobehavioural development

While most monkeys living in the wild do not experience chronic maternal deprivation from birth (if they do, they seldom survive infancy even if surrounded by peers), they inevitably experience relatively brief periods of physical, physiological, and emotional stress. To what extent do such episodic experiences have long-term developmental consequences? Some recent laboratory studies clearly indicate that seemingly 'minor' short-term environmental perturbations can have striking long-term behavioural and physiological consequences, especially when such perturbations appear to disrupt the mother–infant relationship.

Rosenblum and his colleagues studied the effects of systematically manipulating ease of access to food for mothers and their infants and found significant effects that persist at least until puberty[49–52]. The basic experimental paradigm in these studies utilized a procedure in which groups of female bonnet macaques (members of the same genus as rhesus macaques) and their infants were required to forage for their daily diet. The time and effort required for sufficient foraging to sustain the diet was manipulated experimentally, such that some groups of mothers and infants were provided with an *ad libitum* supply of food (low foraging demand, LFD), whereas food availability for other groups was switched biweekly from *ad libitum* (LFD) to a condition of relatively high foraging demand (requiring several hours of foraging each day to maintain normal dietary intake) for a total of 14 weeks, beginning when the infants were 11 weeks old (variable foraging demand, VFD). After the 14 week experimental period, both LFD and VFD groups were maintained on identical *ad libitum* feeding schedules[53].

Andrew and Rosenblum found minimal behavioural differences between the LFD and VFD mothers and their infants, respectively, during periods of differential foraging. However, when LFD and VFD dyads were subsequently challenged by brief introductions to a novel playroom, VFD infants left their mothers to explore less frequently and engaged in less social play than LFD infants, reflecting 'less secure' attachments to their mothers[54]. Surprising long-term consequences of the 14 week period of VFD treatment during infancy emerged when VFD and LFD monkeys were later challenged pharmacologically by injections with a noradrenergic probe (yohimbine) and a serotonergic probe (MCPP), respectively, when they were 3 years old. VFD monkeys were generally hyperresponsive to the noradrenergic yohimbine injection, increasing patterns characteristic of high reactivity; in contrast, they were generally hyporesponsive to the serotonergic probe[55]. Moreover, at

4 years of age, VFD monkeys exhibited persistently elevated cerebrospinal fluid levels of corticotropin-releasing factor (CRF) relative to those of LFD monkeys[56].

These findings thus demonstrate that seemingly minor environmental perturbations, e.g. 14 weeks of varied food availability, can have significant, indeed dramatic, behavioural and physiological consequences that sometimes become apparent only later in life. Presumably, these effects resulted from the differential treatment of infants by VFD and LFD mothers during the 14 week period, rather than differential foraging by the infants themselves. It is, therefore, of considerable interest that the effects of VFD on these infants seem quite similar, in pattern if not in degree, to the behavioural and physiological consequences of peer-rearing in rhesus monkeys. Both cases involved insecure early attachments, and both were associated with subsequent behavioural and physiological manifestations of increased reactivity and, to some extent, impulsivity.

Effects of unusually secure early attachments on rhesus monkey biobehavioural development

The research reviewed above clearly demonstrates that inadequate early social attachment experiences — whether the result of maternal deprivation *per se* or disruption of the mother–infant relationship — can have long-term biobehavioural consequences for macaque monkeys. But what of the reverse — are there any consequences of *enhanced* early attachment experiences for these monkeys?

A recent series of studies attempted to address this issue by foster-rearing rhesus monkey neonates who differed in temperamental reactivity with nonkin multiparous females who differed in their characteristic maternal 'style', as determined by their care of previous offspring. In this work specific members of a captive breeding colony were selectively bred to produce offspring who, on the basis of their genetic pedigree, were likely to be either unusually high-reactive or within the normal range of reactivity. These selectively-bred infants were then cross-fostered (within their first 4 days of life) to unrelated multiparous females preselected to be either unusually nurturant with respect to their attachment-related activities or within the normal range of maternal care of previous offspring (controls). The selectively bred infants were reared by their respective foster mothers for their first 6 months of life, after which they were moved to larger social groups containing both mother-reared and peer-reared agemates[57].

During the period of cross-fostering, infants with normative reactivity profiles exhibited relatively normal patterns of biobehavioural development; indeed, there were no marked differences between those cross-fostered with highly nurturant females and those foster-reared by control females. In contrast, dramatic differences emerged among high-reactive infants as a result of type of foster mothering: whereas high-reactive infants foster-reared by control mothers exhibited expected deficits in early exploration patterns and exaggerated biobehavioural responses to minor environmental perturbations, high-reactive infants cross-fostered to nurturant females actually appeared to be behaviourally precocious. These infants exhibited decreases in levels of ventral contact earlier chronologically, locomoted and explored their environment more, and displayed less behavioural disturbance during weaning than not only the high-reactive infants cross-fostered to control infants but even the 'normally' reactive infants reared by either type of foster mother. Their attachment relationships with those foster mothers thus appeared to be unusually secure[58].

Follow-up study of these selectively bred and differentially foster-reared monkeys when they were moved into larger social groups revealed additional temperament/foster-rearing interactions, marked by optimal outcomes for the high-reactive monkeys with secure previous attachment histories. These individuals became especially adept at recruiting and retaining other group members as allies in response to agonistic encounters and, perhaps as a consequence, they subsequently rose to and maintained top positions in the group's dominance hierarchy. In contrast, high-reactive individuals cross-fostered to control mothers, who had developed less secure early attachment relationships, tended to drop to and stay at the bottom of the same dominance hierarchy; no such rearing effects were evident in the control cross-fostered infants[58].

Finally, some of the cross-fostered females in the prospective longitudinal studies have since become mothers themselves, and their maternal behaviour toward their first-born offspring has been assessed. It appears that these young mothers have adapted the maternal style of their foster mothers, independent of both their own original reactivity profile and the type of maternal style displayed by their biological mother. Thus, the apparent benefits accrued by these high-reactive (by pedigree) females reared by unusually nurturant foster mothers seemingly can be transmitted to the next generation of offspring, even though the mode of cross-generational transmission is nongenetic in nature[59]. Clearly, high-reactivity need not always be associated with adverse short- and long-term outcomes. On the contrary, following certain early attachment experiences, high-reactive monkeys appear likely to have relatively normal, if not optimal, developmental

trajectories, which in turn, are apparently amenable to cross-generational transmission.

Key points for clinical practice

The research reviewed in this paper clearly indicates that early experiences can have profound and lasting effects on behavioural and physiological functioning in rhesus and other macaque monkeys. What implications might these findings have for identifying and interpreting possible effects of early experience in humans? To be sure, rhesus monkeys are not furry little humans with tails, but members of a different, albeit closely related, species. Nevertheless, there are some general principles highlighted by this research that most likely transcend species differences among advanced primates.

First, effects of early experiences are not limited to behavioural phenomena but instead can encompass a wide range of biological functioning. Indeed, research with monkeys has shown that even those behavioural and physiological processes that have highly heritable features can be substantially modified by certain early experiences.

Second, long-term consequences of specific early experiences may not be uniform across all individuals. Rather, some individuals, perhaps due to heritable predispositions, may be more sensitive to the effects of particular early experiences than are others. On the other hand, extreme early experiences, i.e. those that deviate markedly from species norms, may largely override such individual propensities.

Finally, it should be remembered that these long-term and cross-generational effects of differential early experiences were demonstrated under conditions in which subsequent environments were both highly similar, if not identical, and highly stable for all the monkey subjects. Such environmental features are rare for rhesus monkeys growing up outside of most laboratory settings, and it is therefore not surprising that, by and large, effects of specific early experiences are usually less obvious in field settings. It is no wonder that they are usually so difficult to document in most 'field environments' for humans as well.

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