

Transformations of the Maternal–Fetal Relationship in the Twentieth Century

From Maternal Impressions to Epigenetic States

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2.1 Introduction

During the 1960s and 1970s, a new understanding of the fetus emerged at the intersection of demographic changes: high fertility and reduced infant mortality in the ‘baby boom’ era; new medical visual technologies and the expansion of mass media; and the rise of the feminist movement and the liberalisation of abortion. These social shifts spurred scholarly and lay interest in public representations and private perceptions of the fetus [1–4], the rise of the fetus as a subject [5, 6], the politics of abortion [7], and the uses of fetal bodies in research [3, 8]. A century ago, scholars argued that the mother and the fetus were one; maternal experiences ‘imprinted’ the malleable fetus and maternal testimony was central to the understanding of pregnancy until the hidden fetus was revealed at birth. But starting in the nineteenth century and especially during recent decades, an increasingly visible and autonomous fetus has emerged, the mother has been erased from the picture, and the experience of pregnancy has come to be more contingent and technologically mediated.

This compelling and broad narrative glosses over subtler shifts in the way that the fetus, the mother, and, especially, the relationship between them have been conceptualised. And yet, a closer look at medical and scientific literature shows that over the course of the twentieth century, the maternal–fetal relationship has been reinterpreted and redrawn multiple times. For this chapter, I have used published sources from diverse medical and scientific disciplines, such as obstetrics, fetal physiology, evolutionary biology, developmental science, and epigenetics, to draw attention to the changing ways in which the maternal–fetal relationship has been understood. This close reading has helped me uncover underlying assumptions – shifting and competing even within a single discipline – that fed into scientific and clinical research. For example, in the 1960s, physiologists who stressed fetal autonomy when describing fetuses as lone mountaineers and astronauts also worked on questions related to the fetal control of processes within

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the fetal and maternal bodies, such as the onset of labour and fetal growth. The diverse assumptions, metaphors, and research questions tell us something about changing social views of and attitudes towards motherhood, pregnancy, and the relationship between the mother and the fetus, including and especially maternal influences on the developing organism.

Covering the long twentieth century, I have identified several key concepts and periods: the abandoning of maternal impressions, strong hereditarianism, and the fetus as the parasite in the early decades of the twentieth century, the era dominated by eugenics; the ‘maternal effects’ of the mid-twentieth century, when concerns over adequate nutrition and trauma of long-standing effect that emerged around the Second World War supported the idea of the ‘critical’ or ‘sensitive’ periods and revived interest in maternal influences; the autonomous fetus of the 1960s and 1970s civil rights movement era followed by the selfish fetus imagined by evolutionary biologists of later decades of the twentieth century; ending with the latest rapprochement between the mother and the fetus supported by developmental approaches and epigenetics. While it may be tempting to regard this latest development as a return of maternal impressions, I want to show that similarities are superficial: the fetal–maternal relationship was redrawn according to new rules, and it cannot be fully understood without insight into its recent history.

2.2 The Fetal Parasite

Well into the 1800s, the developing organism was seen to be malleable by external influences, and the mother was both the mediator and the source of these cues. Anything the mother ate, saw, touched, or even imagined, collectively known as maternal imagination or maternal impression, was understood to have the capacity to affect the child [9, 10]. Yet during the nineteenth century, this close bond between the mother and the fetus was broken. The concept of heredity, which reduced the mother to little more than a passive vessel transmitting elements collected from previous generations to the offspring, first appeared in the early decades of the nineteenth century and quickly gained popularity [11]. In the 1880s, the German biologist August Weismann explained how heredity worked using the tools of experimental biology [12]. According to Weismann, ‘germplasm’ (preserved in the germline but unfolding its potential in the body during development) was resistant to influences exerted by ‘soma’, so changes in somatic cells had no effect on the germline. While Weismann did allow the possibility of direct environmental influence on the germ cells, scholars who followed in his footsteps by and large reduced development to a robust pre-programmed sequence of stages. Influences received in development, unless extreme to the point of threatening maternal or fetal survival, were secondary to heredity.

Weismann’s work had a major impact outside academic biology. The early twentieth century is usually seen as the high point of eugenics, a broad movement that distilled nineteenth-century concerns over rapid socio-economic change into modernist visions of society reformed through rational reproduction [13, 14]. Eugenics preceded the cellular explanation of heredity: it relied, initially, on the mid-century concept of degeneration, whereby ‘organic’ and social factors acted on the organism to produce a reverse evolution, cumulative over generations, taking a lineage to a downhill slope of no return [15]. Weismann’s work provided it with scientific cachet.

So if we take that strong hereditarianism saw the mother as a passive vessel, rather than an active agent in the formation of the new organism and the mediator of external influences, then the appeal of the model taken from another cutting-edge scientific discipline of the period, parasitology – the relationship between a parasite and its host – begins to make sense. The parasite depended on its host for shelter and food but was also remarkably protected from the fluctuations in the host's circumstances and environment, even if the host itself suffered. Accordingly, the fetus was understood to thrive in all except the most extreme circumstances, with maternal homeostatic mechanisms maintaining environmental factors at a near-constant level and the placenta providing protection from many noxious substances [16, 17]. Yet, for the mother, the pregnancy could be precarious, as 'the increasing demands of the parasitic fetus will make the diet deficient for the mother' [18, p. 1].

There were traces of the idea of the parasitic fetus in earlier times: in the eighteenth century, Denis Diderot wrote in his *Eléments de physiologie* that 'the child is at all times an inconvenient guest for the womb' and described delivery as 'a sort of vomiting' [19, p. 406]. However, it was not until the turn of the twentieth century that the idea gained full prominence. Scientists travelled across colonial empires to study the life cycles of organisms causing frightening diseases, such as malaria and sleeping sickness, killing people, and damaging imperial economies. The idea of the parasite was engrained in public imaginations. It was also politically helpful: as civilians faced severe food shortages in the First World War, reassurances that the fetus (as well as the infant/lactating mother) would be unaffected by maternal starvation might have been seen as comforting [20].

Yet there were voices critical of strong hereditarianism. Some came from relatively marginal movements such as prenatal culturism, associated with theosophy and drawing on the notion of prenatal impressions. It argued that heredity could be influenced by a pregnant woman's thoughts and behaviour, and thus those had to be controlled [5]. Others were mainstream physicians. They used examples of conditions such as congenital syphilis to argue against a sharp distinction between hereditary and communicable (environmentally caused) diseases [21]. The best known among them was the Edinburgh obstetrician John William Ballantyne, who gave teratology – the science of collecting and studying births with congenital abnormalities – clinical significance and reinvented it as antenatal pathology [22, 23]. For Ballantyne, the maternal body provided the immediate point of medical and research interest as 'we can only reach the unborn infant through the mother who carries him, and so the pre-natal life and the life of the woman in pregnancy are closely bound together and depend one upon the other' [24, p. x]. Indeed, he defined the relationship between the mother and the child in the following manner: 'although he [the infant] is hidden from sight in the womb of his mother, he is not beyond the influences of her environment, nay, her body is his immediate environment' [24, p. xii].

The rise of hereditarianism through the nineteenth and early twentieth centuries thus influenced the view of the maternal–fetal relationship. The concept of maternal impressions, or indeed any influences received from or through the mother, was relegated to second place, after heredity. 'The mother marks her infant, not with the fanciful imagery of birthmarks, but with the ancestral tendencies,' wrote a Chicago professor of obstetrics in this period [25]. But as the narrow notion of heredity was forged around 1900, the notion of prenatal or antenatal came into being [26]. This new

concept accounted for the contingencies of conception, gestation, embryogenesis, birth, and breastfeeding, now disconnected from heredity [27].

2.3 Critical Periods

‘The existence of a profusion of myths and superstitions has probably somewhat inhibited until modern times scientific thought and investigation into maternal–fetal relationships from the standpoint of how fetal development may be influenced by varying maternal factors. During the last twenty years, however, many facts and some very interesting hypotheses accumulated in the literature of various fields’,

wrote the American physician Lester Sontag, who between the 1930s and 1960s studied the ways in which cues received during development – from maternal nutrition to emotional states – influenced the offspring [16, p. 996]. By the 1930s, eugenics was in retreat: in the increasingly unstable political-economic climate, the impact of environment, physical as well as social, on human health and disease could not be ignored. Genetics, an experimental discipline studying mechanisms and rules of heredity, had matured since the early 1900s, and its specialists criticised harshly what they perceived as eugenics’ sloppy grasp of genetic concepts and research methods [28]. During the economic depression and in the shadow of the looming war, concerns about feeding human and animal populations in the likely conditions of severe shortage occupied politicians as well as scientists [29]. Those who subscribed to the notion of the parasitic fetus worried that poorly nourished mothers would perish under the demands of pregnancy. Others argued that in a malnourished mother, the growth and development of the fetus would suffer too. While food was seen as a prime example of outside exposures impinging upon the developing organism, other influences – microorganisms, toxins, but also maternal emotional states – came under the scrutiny of experimental and clinical scientists.

Throughout the 1930s, nutritionists and physicians, faced with deprivations caused by economic depression, studied the impact of maternal undernutrition on the offspring of cohorts of working-class women, but the results were negative or inconclusive [30, 31]. In the Second World War, however, large civilian populations suffered sieges and blockades of food shipments, providing scientists with ‘natural experiments’: previously well-fed women exposed to severe famines of limited duration [32]. Early findings came from the Leningrad siege, between September 1941 and January 1944, during which the urban civilian population experienced prolonged and severe famine [33]; smaller but more precise data came from Western Holland during the German siege between September 1944 and May 1945, in what became known as the Dutch Winter Famine [34]. Data showed that if the mother starved around conception, then the fetus had a greater chance of being miscarried or born malformed, and if famine struck in the last months of pregnancy, the baby was likely to be born small and light.

Wartime observations were carried forward into the lean post-war years: the British scientist Elsie Widdowson studied the birthweight of babies and milk production in hospitals, as well as the growth of children fed small and monotone food rations in orphanages in war-ravaged Germany [29]. She found that not just food but also emotions affected children’s growth: children living in an orphanage directed by a strict matron lagged behind their peers raised in an institution run by a kind person [35]. Back in Cambridge laboratories, Widdowson and her collaborator Professor Robert McCance transformed clinical observations into hypotheses for experimental animal studies: they manipulated maternal nutrition

and the size of the litter (which determined the amount of mother's milk received by each pup) to test how undernutrition during pregnancy and early postnatal period affects the offspring's growth and development. They found that the impact was permanent, making adult animals smaller, more prone to infections, and even changing their facial structure.

Widdowson's research supported the notion of 'critical periods' that emerged across disciplines in the 1930s and 1940s, most importantly in teratology, behavioural studies, and fetal physiology, to describe the relationship between chronological time and developmental milestones. Teratology in this period transformed from a museological discipline engaged in collecting and classifying malformed births into an experimental science that sought to explain how certain noxious agents – especially microorganisms such as the rubella virus and certain toxins – acting at well-defined developmental stages produced specific effects [36]. Other studies explored how the lack or excess of physiological substances, such as vitamins or hormones, could influence development.

Hormones offered a way to explain a problem of long-standing concern: how maternal emotional states influence the psychological set-up of the child. In the late nineteenth century, France Charles Féré had argued that external stimuli, such as loud sounds or maternal emotions, caused uterine contractions, which in turn stimulated the fetus to move [27]. Féré based his argument on the observations made on a cohort of children born to women who had suffered from 'mental shocks' while pregnant during the siege of Paris, 1870/71 [37]. In the 1940s, Lester Sontag observed a connection between increased fetal movement and fetal weight gain [38]. Heightened fetal activity, he claimed, was caused by maternal emotional states, which were then transmitted to the fetus by hormones such as adrenaline. And while loud noises and maternal fatigue did increase fetal activity, these (intermittent) factors were less significant than maternal emotional states. Sontag published cases, such as that of a mother with a 'religious and moralistic' background who during pregnancy learnt about her husband's infidelity. Her 'almost continual emotional turbulence' resulted in an 'extremely active' fetus and, finally, a short and light infant. In another case, the father developed a psychosis during the fifth month of the mother's pregnancy, causing her to live in constant apprehension of physical violence and worry about her husband's health as well as their future as a family. The infant was light for its length and 'extremely active and irritable' [38, p. 629].

While just a few decades earlier, the focus was on fetal resistance to changes in the maternal environment, the decline of eugenics, experiences of economic depression, and especially war moved the emphasis onto the ways in which the fetus was sensitive to its environment. I have argued elsewhere how broader social concerns with recovery from early trauma – nutritional, emotional, and psychological – so pertinent in post-war Europe provided the background to the idea of sensitive periods [29]. While the idea of the fetus as a parasite did not quite go away, the concept of pregnancy as a plastic, open state and the fetus in constant exchange and communication with the environment gained currency.

2.4 The Autonomous Fetus

In 1965, the prestigious *Life* magazine published a series of photographs by the Swedish photographer Lennart Nilsson, documenting human development over the nine months of pregnancy [39]. These photographs were hailed as the unprecedented celebration of the 'drama of life before birth'. Nilsson's images, showing the childlike fetal form floating on the 'starry sky' background, without the maternal body anywhere in sight, signalled the new status of the fetus as an autonomous being. The growing distinction between

mother and fetus was evident everywhere: in the way that the fetuses were portrayed in the media, for lay audiences, but also in textbooks and research papers; in their acquisition of the status of the patient in their own right; and in the language used to talk about them. By the 1960s, society was no longer preoccupied with survival and war trauma but rather with questions of identity, subjectivity, and agency. Could it be that the severance of the umbilical cord in the representation of fetuses reflected a broader social shift?

The use of fetal images has been extensively studied in the context of feminist history (visual), politics of abortion, as well as the broader political and social history of this period [1, 2, 40]. Nilsson's photographs – the most famous and best studied – were created within a gynaecological campaign in Sweden to restrict the abortion law and published in a popular colour magazine to entertain and educate its audience; in the 1970s, they were recruited by the growing pro-life movement in the United States to teach its prospective supporters about the 'humanity' of the fetus. And in addition to Nilsson's vivid images, pro-life advocates could also draw on less attractive yet increasingly ubiquitous ultrasound scans. By the 1970s, ultrasound technology, first developed in the 1950s, had become a standard part of antenatal medicine.¹

Historians of medicine have noted that the deployment and popularity of fetal images corresponded with the emergence of the fetus as a patient in its own right. The increased prosperity of the post-Second World War and the rise of public healthcare systems worldwide meant that more women than ever were receiving antenatal care. Yet with improved control of infectious disease and better socioeconomic conditions, both maternal and infant mortality – at least in the developed world – were falling. The medical focus now turned to relatively rare cases of congenital anomalies, prematurity, and conditions that developed in pregnancy. In this period, a leading obstetrical scientist, William Liley, pioneered a therapy targeted at the fetus to treat the hitherto incurable fetal haemolytic disease, which emerged when the mother, who did not have Rh antigen on her red blood cells, developed antibodies to the Rh antigen-bearing red blood cells of the fetus [43]. Under ultrasonic guidance, Liley performed a blood transfusion into the fetal belly – a method previously done only on children. Liley's work marked the beginning of the field of fetal medicine, which in the following decades gave rise to the highly precarious and controversial area of fetal surgery [6].

The obstetricians' increased interest in the fetus and their positioning as fetal, rather than maternal, advocates became sharply evident as the debate over the legalisation of abortion deepened in the late 1960s and 1970s. Around that time, many countries liberalised their abortion laws, but the debate continued, and obstetricians frequently stood on the 'conservative' side, against the liberal laws. Ian Donald was a prominent opponent of the legalisation of voluntary abortion and a campaigner against the 1967 Abortion Act, and he employed vivid images produced by the ultrasound technology that he had pioneered in anti-abortion campaigns. Even when his campaign failed and Britain legalised abortion, he continued to fight elsewhere, for example taking his images to Italy that in the late 1970s was in the swing of the anti-abortion debate [42, p. 243]. At the same time, alarmed by the developments in Britain, William Liley

¹ Roentgen was employed to visualise the fetus, but its use was limited to the skeleton and to the fetuses with sufficiently calcified skeleton to permit X-ray visualisation, so usually from the second trimester onwards. But the use of X-rays became tainted with danger, especially after Hiroshima and Nagasaki, and the final blow was a 1956 study showing that children X-rayed as fetuses had a higher risk of childhood cancer [41, 42].

launched the Society for the Protection of the Unborn Children (SPUC) in New Zealand in 1970. In contrast to most other pro-life activists, Liley was not religious but rather held a firm belief that the fetus is a being independent of its mother, 'our new individual' residing in a 'suitable host' [5, p. 114]. Yet while fetal advocacy in matters of abortion prohibition produced little in the way of results, in other areas, fetuses increasingly came to be seen as needing legal protection from the actions of their mothers [5]. From the 1970s onwards, especially in the United States, conflicts between fetal rights and the rights of women – as patients, workers, and citizens – steadily increased.

One aspect of the increasing visibility of the fetus that has hitherto been little studied is how scientists – rather than practising obstetricians – viewed the fetus. Examining their language and research topics reveals a clear shift towards the autonomous fetus. Starting from the 1960s, science books and articles no longer described the fetus as a passive parasite but rather as a fearless pioneer in extreme conditions. Metaphors drew on new technologies of ocean, space, and land exploration, calling the fetus a submarine sailor, 'a weightless astronaut in utero' [44, p. 307], or a mountaineer. At the time when Edward Hilary and Sherpa Tenzing captured the public imagination by 'conquering' Mount Everest, the fetal environment began to be described as 'Mount Everest in utero' [45]. From the 1960s until 1990, scientists met at conferences tellingly titled 'Foetal autonomy', 'The fetus and independent life', and 'Foetal autonomy and adaptation' [46–48]. Indeed, the introduction to the 1969 Foetal Autonomy Conference Proceedings said that 'it [the fetus] demonstrates its innate capacity for influencing its external and maintaining its internal environment – that is, its autonomy' [47, p. 1].

The language of fetal autonomy closely corresponded to the type of research questions that interested scientists in this period. In the 1940s and 1950s, McCance and Widdowson experimented with maternal nutrition and the size of the litter to show how the antenatal environment shaped development before and after birth. In contrast, in the 1960s and 1970s, the focus moved from external influences to the ways in which the fetus controlled its development. Research methods were developed – named chronic preparation or chronic method – that allowed precise monitoring of physiological parameters throughout the course of pregnancy, using electrodes and catheters inserted into the pregnant animal [49]. And, indeed, the fetus seemed remarkably autonomous. It could regulate its sleep patterns and its behaviour. It moved, and it appeared to breathe. It oversaw its growth through a finely balanced cascade of hormones [50]. But its agency did not stop at the boundaries of the fetal body: the fetus was also seen to 'participate in, or is responsible for, the sequence of events that ends in its birth' because 'it would be a logical feature of reproductive design if the initiation (of labour) were under fetal control, so that the other systems necessary for postnatal survival were normally mature before birth. In this sense fetal autonomy would be a necessary feature of development' [51]. Testifying before the US Congress in support of pro-life legislation, William Liley described the fetus as being 'very much in charge of the pregnancy'. The fetus, it seemed, was in control.

2.5 Neighbours at Odds

The idea of the fetus as a cosmonaut or a mountaineer implied agency and self-sufficiency. But scientists and physicians went even further: the feminist historian Ann Oakley quoted from Frank Hytten's 1976 obstetrics textbook, describing the fetus as

an egoist and by no means an endearing and helpless little dependent as his [*sic*] mother may fondly think. As soon as he has plugged himself into the uterine wall, he sets out to make certain that his needs are met, regardless of any inconvenience he may cause. He does this by almost completely altering the mother's physiology, usually by fiddling with her control mechanism [41].

This 'selfish fetus' could not help itself: it was a machine governed by its selfish genes. The 1970s and 1980s were the heyday of the disciplines of sociobiology and evolutionary psychology. They explained behaviour – human and animal – using the mid-twentieth-century 'superdiscipline' of Modern Synthesis. Modern Synthesis was Darwin's theory of evolution by natural selection unified with population and experimental genetics [52]. Evolution was defined as a change in the allele (gene) frequency, and although the evolutionary environment acted upon the phenotype of the whole organism, it was the passage of the gene across generations that mattered.

And genes, as suggested persuasively in the title of Richard Dawkins' famous book, were selfish [53]. They looked after their own interests using the organism as a convenient vehicle to ferry them around, meet prospective mates, and secure survival for the next generation. One was fond of his or her parents because they shared 50 per cent of their genes but cared progressively less for his or her siblings, half-siblings, and cousins, as the percentage of shared genes dropped [54]. In 1974, the American sociobiologist Robert L. Trivers built on this concept to explain the apparent conflict over resources arising between parents and their children [55]. According to him, children demand more from their parents than the latter are willing to give because their evolutionary interests differ: individual children want all of their parents' attention (and food), yet parents have other – extant or future – children to consider. Trivers supported his hypothesis with data on the social behaviour of mammals, mostly around the time of weaning. The young aggressively demanded more food and care than their parents, who wanted to reserve their energy for other or future offspring, were willing to give.

Trivers' model met enthusiastic reception among evolutionary biologists. Steven Pinker saw the conflict as 'inherent to the human condition' [56]. Richard Dawkins described Trivers' model of parent–offspring conflict as 'brilliant' [53, p. 127]. At the same time, behavioural scientists criticised Trivers: in many species, the offspring weaned itself, while in others mothers responded to its requests. But the model remained popular. It inspired the Harvard evolutionary biologist David Haig to extend it to pregnancy and development, arguing that the mother and the child each have their own interest in mind; interests that are partially aligned (because they share 50 per cent of their genes) but substantially differ (because the remaining 50 per cent is different). Pregnancy, in Haig's view, was not a romantic alliance of 'one body and one flesh, a single harmonious unit in which conflicts of interest are impossible' – a perspective that, according to Haig, was the received view. But neither was it correct to see the mother and the fetus locked in a relationship where 'the fetus is an alien intruder within its mother's body: a parasite whose sole concern for its host is to ensure an uninterrupted supply of nutrients' [57, p. 226]. Rather, he likened this 'most intimate human relationship' to a constant negotiation, 'a tug-of-war' where 'two teams attempt to shift a flag a small distance either way, yet there is high tension in the rope and the system would collapse if either side stopped pulling' [58, p. 496].

Haig first applied the parent–offspring conflict concept to development and pregnancy to explain the phenomenon of genomic imprinting, in which for some genes only

the maternal (or paternal) copy is expressed, while the copy that came from the other parent is silenced [59]. Because the mammalian mother is equally related to all of her offspring, her interests are best served by controlling resource allocation to her offspring, making sure as many survive as possible; but because the father of the fetus in the current pregnancy may not also father a future fetus or litter, it is in his interest to promote the growth of this particular fetus [60]. The hypothesis was persuasively supported by the insulin growth factor 2 (IGF2) system, in which the growth factor (promoting growth) was paternally expressed as the growth factor receptor (controlling growth) was maternally expressed. But Haig soon expanded his concept to other aspects of pregnancy, in the first place the communication between the mother and the fetus by means of chemical messages through hormones [61]. In Haig's words, this communication was a devious game played by both sides to advance their own interests: 'a response that is beneficial for a sender need not be beneficial for the responder, and vice versa' [61, p. 358]. Mothers were 'able to extract some information from placental hormones' [61, p. 374], yet placental hormones were 'fetal attempts to manipulate maternal metabolism for fetal benefit' [61, p. 357].

While Haig's hypothesis of placental hormones as tools of fetal subterfuge has remained without empirical support, the concept of maternal–fetal relationship as a state of unresolved conflict has held much attraction. For instance, clinical researchers have used it widely – moving slickly from selfish genes to selfish organisms and back – to explain various pathological phenomena of pregnancy, such as gestational hypertension and severe chronic infections [67]. The attraction of the concept may be explained by the broader social view of the maternal–fetal relationship in the last decades of the twentieth century. It was recognised that for the fetus the mother presented the immediate environment, but the idea of an autonomous fetus, whose needs and interests need not overlap with its mother's, remained in full force. Yet, the strong hereditarianism implied in the conflict model, with both the mother and the fetus seen as machines governed by their genes, left little room for considerations of environmental influences received in development [62–64].

2.6 Maternal Environment and Fetal Exposure

By the end of the twentieth century, many of the paradigms that had dominated the twentieth century came under scrutiny. As 'the century of the gene' ended with the publication of the Human Genome draft (and, a few years later, full sequence), it became obvious that the knowledge of the genome sequence was only the beginning, rather than the end, of the quest for understanding life, health, and disease [65]. The notion of the autonomous fetus was questioned too. 'We have been dazzled by the very strong control by the fetus' wrote the fetal physiologist Graham Liggins, when decades of research into the onset of birth revealed enormous interspecies variation and the fact that, in humans, the mechanism firing off labour had little direct input from the fetus [66]. The research programme studying fetal respiratory movements came to a dead end in the late 1980s. Fetal physiologists looked for inspiration elsewhere and found it in the work of David Barker, the British epidemiologist who argued that the conditions of early life – indeed, even before conception – shaped the disease risk in adulthood [48, 67]. Barker was certainly not the first to stress the importance of prenatal influences: there were studies coming from social medicine and epidemiology throughout the 1960s and 1970s, such as

those by Zena Stein and Mervyn Susser [68], examining the impact of maternal nutrition on cognitive development in youth. Yet as long as the genetic paradigm and the idea of the autonomous fetus prevailed, this approach remained restricted to public health fields.

The move away from the close focus on the fetus back to the mother and the environment of the pregnancy and early life fitted well with the renewed interest in development, manifested, for example, in the return of development into evolutionary studies named ‘*evodevo*’ [69]. It also had to do with an increased anxiety about the environment changed by human action and its impact on human health, which had been growing since the 1960s. Older research, such as the previously described work of Robert McCance and Elsie Widdowson or studies of the cohort of women who were pregnant during the Dutch Winter Famine, was reappraised and integrated into the new paradigm [70]. The reappraisal included the previously little recognised research across the Iron Curtain, by the East Berlin endocrinologist Günter Dörner, who in the 1970s compared the risk of obesity and cardiovascular diseases in the cohorts of young men born before, during, and after the Second World War [71, 72]. The difference was that, around the turn of the twenty-first century, the long-term impact of the early influences had to be expressed in molecular rather than late-nineteenth-century physiological or twentieth-century endocrinological terms.

The solution was offered by the new, rapidly growing area of biomedical research, epigenetics, which has been variously described as ‘the study of mitotically or meiotically heritable changes in gene function that cannot be explained by changes in genetic sequence’ or, in a less technical language, ‘the molecular memory of past stimuli’, the signals allowing cells to ‘remember past events, such as changes in the external environment or developmental cues’ [73]. Epigenetics holds the promise of explaining what genetics could not; it clarifies how, under (even slightly) different environmental influences, switching certain genes on and off may allow the same genetic code to produce different phenotypes. There seem to be many mechanisms through which genes may be turned on (and off) – some involving small RNAs and others spatial changes to the DNA–protein complex in the nucleus – but the best studied is the addition of methyl groups to promoter regions of the gene [21].

It may seem that, with developmental approaches and epigenetics, ‘maternal impressions’ have returned to medicine and society. Yet, while the mother was certainly brought back into the picture, her return took place in a reductionist manner, befitting the way that science operates today. The perception of the mother is evident in expressions of ‘maternal effects’ and ‘maternal environment’. Maternal experiences are required (1) to be, or to be made, amenable to experimental, molecular approaches (2) to show a quantifiable change in parameters that may be measured using epigenetic methods.

Most research is focused on two categories of influences or exposures: nutrition and stress [21]. The impact of changes in diet is modelled in a relatively straightforward manner in animal models, by restricting nutrition or changing proportions of food groups or particular nutrients in experimental animal diets. Yet the relevance of results to human physiology has not always been obvious. There is very little ‘natural’ about the standardised diets fed to laboratory animals, bred in laboratory environments for generations, so the implications of experimental findings for human nutrition are not always clear. Epigenetic research has also complicated the previously established therapeutic regimens: folate, a B vitamin that has been supplemented to pregnant women to prevent neural tube deficit, is a powerful methyl-group donor, which thus changes the epigenetic state at multiple locations in the organism and possibly has widespread effects.

Even more controversial and complicated than nutritional epigenetics are the attempts to show how maternal psychological traumas and emotional states influence development. Féré once explained them with nervous reflex reaction and Sontag with hormones such as adrenaline; epigenetic research largely focuses on the expression of genes coding receptors for corticosteroid stress hormones. 'Stress' here refers to a large group of very different experiences – from parental neglect in early life to the situations where the mother is exposed to environmental stress, for example experiencing the 9/11 terrorist attack. The best-known animal model was the 'high/low licking/grooming' model. In this model, rat dams are divided into those that exhibit either frequent licking and grooming behaviour towards their offspring (thus modelling a caring mother) or opposite – infrequent licking and grooming – behaviour [74]. The caring mother is supposed to provide a positive, low-stress environment for the offspring, which in turn is understood to affect the functional activity of a group of genes involved in the production and activity of corticosteroids, stress hormones, evident in the epigenetic state of stress hormone receptors and in the level of the hormone.

In short, the new approach to the ways in which the mother modulates and transmits influences received during development is highly reductionist, made amenable to experimental physiological and molecular approaches, with very different experiences expected to produce the same chemical effect in the organism. It is thus entirely different from maternal impressions. One aspect, however, remains by and large unchanged, and that is the responsibility of the mother for the child's health – and not just in childhood, but throughout life, and even, if the transmission of epigenetic marks across generations proves true, to future generations. The way that the results of epigenetic studies are reported – by journalists but also in some cases by scientists who did the research – places the burden of guilt for a child's poor health squarely on the shoulders of the mother [75]. Maternal behaviour during pregnancy is scrutinised to an unprecedented level, with an ever-increasing list of prohibited foods, the prohibition of any alcohol, strict scrutinising of weight gain, and a growing list of medical checks. The focus on the mother may seem baffling if we know that many of the animal studies cannot be easily extrapolated to humans, that paternal effects (through the epigenetic changes in sperm cells) may play an equally important role, and that many influences are really of societal or broadly environmental nature. Yet if we keep in mind the older as well as more recent history of the maternal–fetal relationship, on the background of which these studies are conducted and results are presented, then this picture of an ambivalent association makes sense. Rather than seeing the mother and the fetus as a team, a pair working together towards a common goal, they are viewed as two parties uneasily united: the fetus requiring protection and the mother needing control.

2.7 Conclusion

In this chapter, I have argued that the focus on the maternal–fetal relationship, rather than the mother or the fetus alone, provides a richer, more instructive picture than the focus on the fetus or on the mother alone. For example, Sara Dubow's close attention to the medical and legal status of the fetus in twentieth-century America painted an image of ever-increasing autonomy and rights ascribed to the fetus, paralleled by the continuously diminishing status and control of the mother [5]. This view agrees with the older feminist critique of women's loss of authority in medicine today, for example by Barbara Duden

[4]. Yet shifting the lens slightly to capture the interaction between the two tightly connected organisms also changes, or complicates, our view of the history of the fetus, of the mother, and indeed of ‘maternal impressions’. Rather than a linear process, we see an image where the importance of maternal experiences, and of influences received through the mother, periodically strengthens and weakens. These shifts tell us as much about social changes – women’s position in the society, war trauma, standpoints on human identity, agency, and rights – as they do about developments in obstetrics and fetal physiology. In the era of ‘hard heredity’, eugenics, and the early days of genetics at the beginning of the twentieth century, the fetal parasite got what it needed from the mother to survive, but, beyond the bare minimum necessary for survival, maternal influences had no impact. But in the economic depression and political upheaval of the 1930s, which brought unprecedented civilian suffering and famines, the idea of a fetus sensitive to maternal experiences – from her diet to the psychological trauma – prevailed. By the 1960s, however, in the newly affluent society, the main concerns revolved around the issues of human rights and subjectivity. The fetus – made visible through the new technology of ultrasound and enjoying media exposure in colour magazines – was seen as an autonomous organism, able to breathe, move, and control its growth and possibly even the timing of birth. Fetal rights came to be understood as opposed to women’s rights in the era of liberalisation of abortion laws; obstetricians increasingly positioned themselves as fetal rather than women’s advocates. Mothers and fetuses, it seemed, were uncomfortable neighbours whose interests only partially overlapped; evolutionary biologists provided an explanation of this relationship that drew on their sharing only some of their genes. But as the genetic paradigm began to lose some of its power around the turn of the twenty-first century and concerns about the environment changed through human action strengthened, approaches emphasising the importance of environmental influences began to grow in importance. The mother is now seen as the primary environment, as well as the mediator of cues coming from the broader environment. While these approaches may be understood as more inclusive and accurate, they also carry the load of the recent history of maternal–fetal relationship. They imply – and sometimes explicitly state – that the mother, through her behaviour and her choices, is responsible for the health of her future child, but that she cannot be trusted and requires close supervision and control, preferably before the pregnancy has even begun. So rather than viewing the mother and the fetus as a unit, a team working towards a shared goal, their relationship remains ambivalent. Finally, while it may be tempting to see the epigenetic approach as the return of maternal impressions – with the Internet and newspapers brimming with titles such as ‘you are what your mother ate’ – the similarity is only superficial. The mother, in epigenetics terms, is a molecular environment, a source, and a mediator of exposures, where what matters is not the actual experience but whether it activates the gene or not.

References

1. Petchesky RP. Fetal images: The power of visual culture in the politics of reproduction. *Feminist Studies* 1987; 13: 263–292.
2. Jülich S. Fetal photography in the age of cool media. In: Ekström SA, Jülich FL, Wisselgren P, eds. *History of Participatory Media: Politics and Publics, 1750–2000*. London, Routledge, 2011; 125–141.
3. Wilson EK. Ex utero: Live human fetal research and the films of Davenport Hooker. *Bulletin of the History of Medicine* 2014; 88: 132–160.

4. Duden B. *Disembodying Women: Perspectives on Pregnancy and the Unborn*. Cambridge, MA, Harvard University Press, 1993.
5. Dubow S. *Ourselves Unborn: A History of the Fetus in Modern America*. Oxford, Oxford University Press, 2011.
6. Casper M. *The Making of the Unborn Patient: A Social Anatomy of Fetal Surgery*. New Brunswick, Rutgers University Press, 1998.
7. Reagan LJ. *Dangerous Pregnancies: Mothers, Disabilities and Abortion in Modern America*. Berkeley, University of California Press, 2010.
8. Pfeffer N, Kent J. Framing women, framing fetuses: How Britain regulates arrangements for the collection and use of aborted fetuses in stem cell research and therapies. *BioSocieties* 2007; 2: 429–447.
9. Huet MH. *Monstrous Imagination*. Cambridge, Cambridge University Press, 1993.
10. Shildrick M. Maternal imagination: Reconceiving first impressions. *Rethinking History* 2000; 4: 243–260.
11. López-Beltrán C. The medical origins of heredity. In: Müller-Wille S, Rheinberger HJ, eds. *Heredity Produced: At the Crossroads of Biology, Politics and Culture, 1500–1870*. Cambridge, MA: MIT Press, 2007; 105–132.
12. Müller-Wille S, Rheinberger HJ. *A Cultural History of Heredity*. Chicago, University of Chicago Press, 2012.
13. Levine P, Bashford A. Introduction: Eugenics and the modern world. In: Levine P, Bashford A, eds. *The Oxford Handbook of the History of Eugenics*. Oxford, Oxford University Press, 2010; 3–24.
14. McLaren A. *Reproduction by Design: Sex, Robots, Trees and Test-Tube Babies in Interwar Britain*. Chicago, University of Chicago Press, 2012.
15. Pick D. *The Faces of Degeneration: A European Disorder, c. 1848–1918*. Cambridge, Cambridge University Press, 1989.
16. Sontag LW. The significance of fetal environmental differences. *American Journal of Obstetrics and Gynecology* 1941; 42: 996–1003.
17. Martin A, Holloway K. ‘Something there is that doesn’t love a wall’: Histories of the placental barrier. *Studies in History and Philosophy of Biological and Biomedical Sciences* 2014; 47: 300–310.
18. Ebbs KH, Scott WA, Tisdall FF, et al. Nutrition in pregnancy. *The Canadian Medical Association Journal* 1993; 46: 1–6.
19. Diderot D. *Éléments de physiologie*. In: Assézat J, ed. *Oeuvres complètes*. Vol. 9. Paris, Hachette, 1875; 236–430.
20. Members of the Department of Experimental Medicine, Cambridge, and associated workers. *Studies of undernutrition, Wuppertal 1946–1949*. Special Report Series 1951; 275.
21. Gluckman PD, Hanson MA, Beedle AS, Buklijas T, Felicia ML. The epigenetics of human disease. In: Hallgrímsson B, Hall BK, eds. *Epigenetics: Linking Genotype and Phenotype in Development and Evolution*. San Francisco, University of California Press, 2011; 398–423.
22. Al-Gailani S. ‘Antenatal affairs’: Maternal marking and the medical management of pregnancy in Britain around 1900. In: Helduser U, Dohm, B, eds. *Imaginations of the Unborn: Cultural Concepts of Prenatal Imprinting from the Early Modern Period to the Present*. Heidelberg, Winter, 2018; 153–172.
23. Al-Gailani S. *Teratology and the clinic: Monsters, obstetrics and the making of antenatal life in Edinburgh, c. 1900*. Unpublished PhD thesis, University of Cambridge, 2011.
24. Ballantyne JW. *Expectant Motherhood: Its Supervision and Hygiene*. London, Cassell, 1914.
25. Adair FL. The interrelationship of mother and fetus. Chairman’s address. *Journal of American Medical Association* 1932; 99: 433–437.
26. Arni C. Vom Unglück des mütterlichen “Versehens” zur Biopolitik des “Pränatalen”. Aspekte einer Wissensgeschichte der maternal-fötalen Beziehung. In: Sänger E, Rödel M, eds.

- Biopolitik und Geschlecht: zur Regulierung des Lebendigen. Münster, Westfälisches Dampfboot. 2012; 44–66.
27. Arni C. The prenatal: The contingencies of procreation and transmission in the nineteenth century. In: Brandt C, Müller-Wille S, eds. *Heredity Explored: Between Public Domain and Experimental Science*. Cambridge, MIT Press. 2016; 285–310.
28. Kevles D. *In the Name of Eugenics: Genetics and the Uses of Human Heredity*. New York, Knopf, 1985.
29. Buklijas T. Food, growth and time: Elsie Widdowson's and Robert McCance's research into prenatal and early postnatal growth. *Studies in History and Philosophy of Biological and Biomedical Sciences* 2014; 47; 267–277.
30. Sontag LW, Pyle SI, Cape J. Prenatal conditions and the status of infants at birth. *American Journal of Diseases of Children* 1935; 50: 337–342
31. Williams S. Relief and research: The nutrition work of the National Birthday Trust Fund, 1935–1939. In: Smith DF, ed. *Nutrition in Britain: Science, Scientists and Politics in the Twentieth Century*. London, Routledge. 1997; 99–122.
32. Susser M, Stein Z. *Eras in Epidemiology: The Evolution of Ideas*. New York, Oxford University Press. 2009; 208–210.
33. Antonov AN. Children born during the siege of Leningrad in 1942. *The Journal of Pediatrics* 1947; 30: 250–259.
34. Smith CA. Effects of maternal undernutrition upon the newborn infant in Holland (1944–1945). *Journal of Pediatrics* 1947; 30: 229–243.
35. Widdowson EM. Mental contentment and physical growth. *Lancet* 1951; 257: 1316–1318.
36. Kalter H. Teratology in the Twentieth century: Environmental causes of congenital malformations in humans and how they were established. *Neurotoxicology and Teratology* 2003; 35: 131–282.
37. Arni C. *Psychischer Einfluss und generationelles Trauma. Pränatale Prägung als Problem der Transmission, oder: Die Kinder des Année terrible 1870/1871*. In: Helduser U, Dohm, B, eds. *Imaginations of the Unborn. Cultural Concepts of Prenatal Imprinting from the Early Modern Period to the Present*. Heidelberg, Winter. 2018; 133–152.
38. Sontag LW. Effect of fetal activity on the nutritional state of the infant at birth. *American Journal of Diseases of Children* 1940; 60; 621–630.
39. Buklijas T, Hopwood N. 'The lonesome space traveller'. *Making Visible Embryos*. 2008–2010. www.sites.hps.cam.ac.uk/visibleembryos/s7_4.html (Accessed 16 June 2023.)
40. Hughes L. Burning birth certificates and atomic Tupperware parties: Antiabortion movement in the shadow of the Vietnam war. *Historian* 2006; 68: 541–558.
41. Oakley A. *The Captured Womb: A History of the Medical Care of Pregnant Women*. New York, Basil Blackwell, 1984.
42. Nicolson M, Fleming JEE. *Imaging and Imagining the Fetuses: The Development of Obstetric Ultrasound*. Baltimore, Johns Hopkins University Press, 2013.
43. Gluckman PD, Buklijas T. Sir Graham Collingwood (Mont) Liggins. 24 June 1926–24 August 2010. *Biographical Memoirs of Fellows of the Royal Society* 2013; 59: 195–214.
44. McCance RA. Summary of session I: Food reserves and food requirements of the newborn. In: Jonxis JHP, Visser HKA, Troelstra JA. *Nutricia Symposium on the Adaptation of the Newborn Infant to Extra-Uterine Life*. Leiden, Stenfert Kroese. 1964; 305–307.
45. Dawes GS. *Foetal and Neonatal Physiology: A Comparative Studies of the Changes at Birth*. Chicago, Year Book Medical Publishers, 1968.
46. Dawes GS. *The fetus and independent life*. Introduction. *Ciba Foundation Symposium* 1981; 86: 1–4.
47. Wolstenholme GEW, O'Connor M. *Foetal Autonomy*. London, Churchill, 1969.

48. Dawes GS, Borruto F, Zacutti A, eds. *Fetal Autonomy and Adaptation*. Chichester, Wiley, 1990.
49. Rudolph AM, Heymann MA. The circulation of the fetus in utero: Methods for studying distribution of blood flow, cardiac output and organ blood flow. *Circulation Research* 1967; 21: 163–184.
50. Gluckman PD, Liggins GC. Regulation of fetal growth. In: Beard RW, Nathanielsz PW, eds. *Fetal Physiology and Medicine: The Basis of Perinatology*. New York, Dekker. 1984; 511–557.
51. Dawes GS. The fetus and birth. Introduction: A historical perspective. *Ciba Foundation Symposium* 1977; 47: 1–4.
52. Bowler PJ. *Evolution: The History of an Idea*. Berkeley, University of California Press, 1984.
53. Dawkins R. *The Selfish Gene*. Oxford, Oxford University Press, 1976.
54. Hamilton WD. The genetical evolution of social behaviour. *Journal of Theoretical Biology* 1964; 7: 1–16.
55. Trivers RL. Parent–offspring conflict. *American Zoologist* 1974; 14: 249–264.
56. Pinker S, Bloom P. Natural language and natural selection. In: Barkow JH, Cosmides L, Tooby J, eds. *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*. New York, Oxford University Press. 1992; 451–494.
57. Haig D. Altercation of generations: Genetic conflicts of pregnancy. *American Journal of Reproductive Immunology* 1996; 35: 226–232.
58. Haig D. Genetic conflicts in human pregnancy. *Quarterly Review of Biology* 1993; 68: 495–532.
59. Haig D. The kinship theory of genomic imprinting. *Annual Review of Ecology and Systematics* 2000; 31: 9–32.
60. Moore T, Haig D. Genomic imprinting in mammalian development: A parental tug-of-war. *Trends in Genetics* 1991, 7; 45–49.
61. Haig D. Placental hormones, genomic imprinting, and maternal–fetal communication. *Journal of Evolutionary Biology* 1996; 9: 357–380.
62. Abrams ET, Meshnick SR. Malaria during pregnancy in endemic areas: A lens for examining maternal–fetal conflict. *American Journal of Human Biology* 2009; 21: 643–650.
63. Hollegaard B, Byars SG, Lykke J, Boomsma JJ. Parent–offspring conflict and the persistence of pregnancy-induced hypertension in modern humans. *PLOS One* 2013; 8: e56821.
64. Muehlenbachs A, Mutabingwa TK, Edmonds S, et al. Hypertension and maternal–fetal conflict during placental malaria. *PLoS Medicine* 2006; 3: e446.
65. Fox Keller E. *Century of the Gene*. Cambridge, Harvard University Press, 2000.
66. Ciba Foundation. The fetus and birth. Final discussion. *Ciba Foundation Symposium* 1977; 47: 461–472.
67. Barker DJ, Osmond CD. Infant mortality, childhood nutrition, and ischaemic heart disease in England and Wales. *Lancet* 1986; 327: 1077–1081
68. Stein Z, Susser M. Fertility, fecundity, famine: Food rations in Dutch Famine 1944–1945 have a causal relationship to fertility, and probably to fecundity. *Human Biology* 1975; 47: 131–154.
69. Gilbert SF, Opitz JM, Raff RA. Resynthesizing evolutionary and developmental biology. *Developmental Biology* 1996; 173: 357–372.
70. Barker DJ. Developmental origins of chronic disease: The Richard Doll lecture. *Public Health* 2012; 126: 1–15.
71. Dörner G, Haller K, Leonhardt M. Zur möglichen Bedeutung der prä- und/oder früh postnatalen Ernährung für die Pathogenese der Arteriosklerose. *Acta Biologica et Medica Germanica* 1973; 31: 31–35
72. Dörner G, Rodekamp E, Plagemann A. Maternal deprivation and overnutrition in early postnatal life and their primary prevention: Historical

- reminiscence of an ‘ecological’ experiment in Germany. *Human Ontogenetics* 2008; 2: 51–59.
73. Landecker H, Panofsky A. From social structure to gene regulation, and back: A critical introduction to environmental epigenetics for sociology. *Annual Review of Sociology* 2013; 39: 333–357.
74. Meaney MJ. Maternal care, gene expression, and the transmission of individual differences in stress reactivity across generations. *Annual Review of Neuroscience* 2001; 24: 1161–1192.
75. Richardson SS, Daniels CR, Gillman MW, et al. Don’t blame the mothers. *Nature* 2014; 512: 131–132.