Published in final edited form as:

Emot Rev. 2012 June 1; 4(3): 238–244. doi:10.1177/1754073912439763.

Basic Emotions: A Reconstruction

William A. Mason and John P. Capitanio

California National Primate Research Center, University of California, Davis, USA

Abstract

Emotionality is a basic feature of behavior. The argument over whether the expression of emotions is based primarily on culture (constructivism, nurture) or biology (natural forms, nature) will never be resolved because both alternatives are untenable. The evidence is overwhelming that at all ages and all levels of organization, the development of emotionality is epigenetic: The organism is an active participant in its own development. To ascribe these effects to “experience” was the best that could be done for many years. With the rapid acceleration of information on how changes in organization are actually brought about, it is a good time to review, update, and revitalize our views of experience in relation to the concept of basic emotion.

Keywords

basic emotion; component schemas; development; early experience; nature–nurture; New Paradigm

Emotions are a common component of behavior. Any mammal actively engaged with its environment will show signs of emotional arousal. For hundreds of years making sense of such phenomena was chiefly the concern of philosophers. By the 19th century, however, the emotions were beginning to be studied scientifically. A landmark event in this development was the publication in 1872 of Charles Darwin’s *The Expression of the Emotions in Man and Animals*.

Darwin had already published *On the Origin of Species* (Darwin, 1859/2008) and *The Descent of Man, and Selection in Relation to Sex* (Darwin, 1871) and was ready to extend his revolutionary concepts of natural selection and evolution to expressive behavior in humans and animals. He believed that there were distinctly different kinds of emotional expression, that they evolved gradually, served a useful purpose, were the result of actions of the nervous system, and were the external manifestations of various states of mind. He also believed the “chief” expressive actions were inherited or innate, although he did not name these emotions explicitly.¹

Corresponding author: William A. Mason, California National Primate Research Center, University of California, One Shields Avenue, Davis, CA 95616, USA. wamason@ucdavis.edu.

¹To the reader interested in first-hand acquaintance with *The Expression of the Emotions in Man and Animals* and the historical context of this work, we recommend the third edition (Oxford University Press, New York, 1998), chiefly because of the excellent Introduction, Afterword, and Commentaries by Paul Ekman.

Basic Emotions

The identity of Darwin's chief emotions, the *basic emotions*, as we refer to them here, has been the subject of considerable discussion and debate. Although opinions vary as to their precise kind and number, the lists are usually short and use terms from the common language, typically including fear, anger, sadness, happiness, and love (Nesse, 1990; Ortony & Turner, 1990). In keeping with Darwin's original view, basic emotions are assumed to be subjective states (feelings) expressed in species-typical behaviors. They are typically believed to provide the biological foundations for all emotions, to be genetically determined, and to have acquired their adaptive functions in response to recurrent challenges to the individual and the species over generations of evolutionary history (Tooby & Cosmides, 1990). The major features of this perspective are evident in Plutchik's psychoevolutionary theory of emotion (Plutchik, 2001). The theory postulates eight basic emotion dimensions, arranged in four pairs: joy versus sorrow, anger versus fear, acceptance versus disgust, and surprise versus expectancy. Plutchik hypothesized that basic emotions were combined to produce mixed emotions, personality traits, and psychopathology. Other theories, such as the various forms of *constructivism*, place more emphasis on the importance of social origins, such as cultural expectations or beliefs, in shaping emotional expression (Averill, 2009).

The pursuit of basic emotions has produced much important and useful new information. Nevertheless, the central and still unresolved question is: Are basic emotions an inherent part of the makeup of humans and other animals? Are they biologically given, like vision and blood pressure, ready to be discovered? Or are they human creations like bracelets and use of fire? (Barrett, 2006). While there is little doubt that what we call fear, anger, and sadness refer to real (i.e., observable) phenomena and important parts of human experience, the weight of scientific opinion appears to be shifting away from the view that a few specific emotions are natural and universal kinds, laid down in the biology of humans and other animals (nature), in favor of a larger place for experience (nurture) in all emotions (Averill, 2009; Ekman, 1999).

Doubts about the reality of basic emotions are not new. More than 20 years ago, after a careful review of the topic, Ortony and Turner asked whether a satisfactory criterion of "basic-ness" was possible (Ortony & Turner, 1990). More recently, Nesse and Ellsworth concluded that "the clear taxonomy of emotions sought for so long by so many may not exist" (Nesse & Ellsworth, 2009, p. 132). Russell and Barrett in a series of articles go a step further and seemingly question the very validity and utility of the basic emotions concept (Barrett, 2006; Russell, 2003; Russell & Barrett, 1999). They propose an alternative model comprising two major dimensions. One dimension is *core affect*, a neurophysiological state experienced as feeling good (pleasure) or feeling bad (displeasure). Their second proposed dimension is called *activation*, which represents the degree of arousal or intensity of the affective state. Core affect is a primitive, biological universal present in other animals, as well as humans. Specific emotions, such as those usually regarded as basic, stem from core affect. The perceived causes of specific emotional responses to objects, situations or events, presumably are based on concepts taken from folk psychology (Lindquist & Barrett, 2008; Russell, 2003).

Although opinions continue to differ among emotion theorists about the relative contributions of biology and experience to the expression of emotions, a consensus seems to be building that both factors must be included in an integrated theory of emotional expression (Ekman, 1999; Izard, 2007; Panksepp, 2007; Plutchik, 1983). At a conceptual level this change may reflect a growing unease with conventional views and the spreading influence of a new scientific paradigm that has been building for decades.

The contributions of animal research to this New Paradigm have been especially significant. By supporting innovative experimental approaches and a strong multidisciplinary thrust, comparative developmental research has produced (and continues to produce) important new ideas and information on the ontogeny, organization, and adaptive functions of an extensive range of phenomena, including emotions. The primary concerns of this article are the implications of these contributions for the ongoing shift in the new scientific paradigm in psychology and for the concept of basic emotions.

Changing Paradigms

Disagreement over the nature of basic emotions, in our view, relates in part to different scientific paradigms. From ancient times, two ways of looking at the natural world have existed as general models or metaphors, reflecting contrasting views of reality. Contemporary psychologists will recognize them as two sharply different scientific paradigms, the *mechanistic* and the *organismic* (Altman, 1967; Mason, 1979; Overton & Reese, 1973; Reese & Overton, 1970).

The *mechanistic paradigm* dominated scientific psychology for many years and continues to have enthusiastic supporters. It assumes a world order in which behavior, like all natural phenomena, is governed by natural laws. A fundamental concept is *homeostasis*. Organisms are quiescent until their equilibrium is disturbed, either by an event originating on the outside, a predator for example, or by a change within, say hunger or thirst, whereupon they react in some appropriate fashion and continue to react until equilibrium is restored. Given sufficient relevant information about an individual's heredity, its state of need, its experience, and its current environment, it follows that its behavior can in principle be predicted with complete reliability. This is the perspective of the traditional S-R formula of radical behaviorism. Adherents tend to avoid mentalistic terms and draw their inspiration from such seminal thinkers as Watson, Pavlov, Hull, and Skinner. This paradigm is characterized by a rigorous experimental approach to psychological phenomena, including emotions, using objective measures, such as behavioral expressions or muscle tension. Basic emotions, thought of as innately programmed responses to biologically determined releasing stimuli, are readily accommodated within this paradigm.

The *organismic paradigm* departs from the mechanistic alternative in many ways. Some sense of the differences is conveyed in this quotation by Bertalanffy, a major contributor to the New Paradigm:

It used to be the general trend of psychology to reduce mental happenings and behavior into a bundle of sensations, drives, innate and learned reactions or whatever ultimate elements are theoretically presupposed. In contrast, the system

concept tries to bring the psychophysiological organism as a whole into the focus of the scientific endeavour. (Bertalanffy, 1968, p. 193)

The individual is viewed as an evolved, self-organizing system, functioning probabilistically, in continuous interchange with an uncertain world (Brunswik, 1955; Monod, 1971).

In this paradigm, psychology is considered a biological science, distinguished from other biological sciences by its focus on mind. A basic premise is that mind is important to study, but can only be approached indirectly. As Hebb put it in his 1960 presidential address to the American Psychological Association entitled *The American Revolution*: “Mind and consciousness, sensations and perceptions, *feelings* and *emotions* [emphasis added] all are intervening variables or constructs and properly part of a behavioristic psychology” (Hebb, 1960, p. 740). Behavior figures prominently in the paradigm not only because it is important in its own right, but also because it is a principal source of information about mental phenomena, including the emotions. An organismic perspective on the question of the origins of basic emotions might conclude that, in essence, the question is wrong. Rather, a more relevant one might be, how do emotions emerge in organisms, and what accounts for the consistencies between organisms that have given rise to the notion of basic emotions in the first place?

Ontogeny of Emotions from an Organismic Perspective

The most radical and sweeping changes within the organismic perspective have occurred in the field of ontogeny. The study of emotions has been deeply involved in these changes. Historically, the role of emotions was manifested in two discrete approaches, one focusing on the effects of early experience on emotional responsiveness, defined operationally in terms of locomotion and defecation in an open-field situation, for example (Newton & Levine, 1968). Frequently, these measures were supplemented by sophisticated assessments of changes in endocrine and central nervous system variables (Levine, 2005), an impressive illustration of Bertalanffy’s focus on “the psychophysiological organism as a whole.” The second approach was broader in scope, and much closer in spirit to Darwin’s original concern with the natural history of the expression of emotions. This approach encompassed a diversity of issues, including comparative studies of the development and functions of expressive behaviors, their role in communication, and their susceptibility to environmental influences (Zivin, 1985).

A huge increase in developmental research in recent decades coincided with increasing acceptance of an organismic paradigm (Anderson, 1957; Ashby, 1960; Bertalanffy, 1968; Piaget, 1971; Schneirla, 1957). Of particular relevance to emotion development are the principles of self-organization, differentiation and integration of functional levels of organization, and emergence of new conceptual entities (Camras & Witherington, 2005; Mascolo & Harkins, 1998).

Among the most radical changes in the developmental perspective of the New Paradigm, with obvious implications for the basic-emotions question, is a fundamental revision of the heredity–environment issue. The traditional assumption that basic emotions were either “innate” or “learned,” accepted by Darwin and still held by some emotion scientists, is based

on what is currently viewed as a false dichotomy. All forms of development are epigenetic (see following lines). The phenotype is the result of complex interactions and interdependence of genetic and environmental influences (Gilbert & Epel, 2009; Gottlieb, 1991; Hamer, 2002; Mason, 2000; Moore, 2001; Pigliucci, 2010; Richerson & Boyd, 2001; West-Eberhard, 2003). This is not to say that the developmental history of variations in moods, temperament, and traits of personality, to say nothing of posited basic emotions, is understood, but rather that viable explanations will not be based on a simple nature–nurture dichotomy. “Old-fashioned metaphors like genetic blueprint and genetic programme are not only woefully inadequate but positively misleading” (Pigliucci, 2010, p. 557).

Two other conceptual changes included in the New Paradigm with profound implications for theories of emotion development are the complementary foundational concepts of *environment* and *experience*. First, the concept of the *environment of evolutionary adaptedness* (EEA) refers to the environment to which a species is adapted and in which it presumably evolved (Bowlby, 1969).² For each species there exist multiple environments of evolutionary adaptedness: Consider, for example, the contrasts between the mammalian prenatal and postnatal environments. Environments that fall within the class of evolutionary adaptedness guide and sustain development in species-typical ways. Those that fall outside of it do not. Second, the concept of experience in the context of emotion development has also changed significantly. Traditionally the concept has been construed as stimulation of sensory systems. For many purposes this is adequate. As research has extended to novel forms of events, conditions, and contexts, however, it has become necessary to include phenomena that do not fit within traditional categories. A broader and more useful term that includes the conventional meaning of “experience,” as well as other causal factors, is *information* (Oyama, 2000), which can be defined as any event or condition, regardless of nature or source, that makes a difference in the functioning or organization of a psychological (biobehavioral) system.

Basic Emotions: Alternative Views

The demise of the nature–nurture dichotomy might seem to mark the end of the basic emotion dispute. Recall, however, that Darwin assembled many illustrations of distinct species-typical human and nonhuman emotional expressions. Presumably these included examples of what have been called basic emotions. They are close to common experience. It is well known that household pets such as cats, for example, under some circumstances will arch, hiss, snarl, purr, and scratch; dogs will bare their teeth, growl, howl, wag their tails, or snap; and that monkeys and apes, as experienced primate watchers know, can make a variety of distinctive sounds, postures, and facial expressions as they go about their daily lives. An important source of the dissatisfaction with the nature–nurture divide was evidence of considerable variability in the organization of such patterns. If they can no longer be

²John Bowlby’s professional background was that of a clinician specializing in mother–infant relations and their implications for mental health (Bowlby, 1969, Preface). He is best known for his theory of attachment, an amalgam of ideas of psychoanalysis and ethology within a general systems framework. He emphasized the interplay between biology and the environment in all aspects of phylogeny and ontogeny and believed that many different environments, which he called *environments of evolutionary adaptedness* (1969, pp. 47, 58), were required by each individual for normal development to proceed.

regarded as “innate” or “hereditary” as Darwin and many other scientists have supposed, what alternative explanations are available?

Much of the information pointing to a different view of the source of basic emotions comes from developmental research, particularly with nonhuman subjects living in arranged environments; for example, primates reared in total isolation, in a nursery, or only with peers. While conditions lack ecological validity—they fall outside Bowlby’s (1969) environment of evolutionary adaptedness—they proved to be uniquely instructive in elucidating the details of the interplay between experience and biology in the development of phenotypic attributes, including presumptive basic emotions.

Our approach to the ontogeny of basic emotions is based on the phenomenon of *component schemas*. Schemas are hypothetical information-processing units, closely linked to observed behaviors. Most if not all schemas are affectively charged. A large number of primitive schemas are present at birth or shortly thereafter in many mammalian species, where they are often categorized as *reflexes* or *fixed action patterns*. While these terms imply that such schemas are invariant, in fact they show considerable flexibility in response to conditions within the individual and its environment. The general idea of such primitive behaviors serving as components in the formation of more complex units in the ontogeny of emotions is not new (Candland, 1971; Fogel & Thelen, 1987; Mason, 2002). Its relevance specifically to the basic emotion issue, however, has apparently been overlooked.

To illustrate a component schemas approach we draw on examples mostly from nonhuman primates (Mason, 1970; 2002). The newborn monkey or ape is a textbook example of the pleasure principle. Starting at birth, individuals react positively to certain sights, sounds, tastes, movements, and touches, and they react negatively to other patterns of stimulation. The quality of their reactions is evident in posture, muscle tone, vocalizations, and heart rate, for example. Primitive sensory-motor patterns (schemas) with similar valence can merge to form higher order schemas. For instance, when an infant Rhesus monkey first contacts a small piece of fruit, it might grasp the object and convey it to its mouth (both the grasping and transporting components may earlier be performed independently and clumsily). It may mouth the object, but will probably not swallow it. With repetition the sight, taste, and smell of food will merge to form a higher order multivariate schema, which we might label BANANA. As its experience with other foodstuffs accrues, a more general category will emerge, which we label FOOD. In addition, a condition like an addiction develops. Through processes that are only beginning to be understood, FOOD acquires the ability to induce a powerful emotional state and to motivate, control, and reward behavior. Phenotypically, the outcome would seem to qualify as a basic emotion. Thus, in the appropriate context, an individual through its own activities and experience creates a positively valenced, higher order, functionally relevant schema, the generic concept of FOOD.

Another well-known primate example of the transformation of several component schemas into a larger, more complex, coherent, and functional unit is the development of an emotional attachment to an inanimate artificial “mother.” In the neonate’s initial schema, claspability essentially is the only property of the model that is relevant to the attachment, and virtually any claspable object will do. In due course, however, the artificial mother

assumes “object status.” It is recognized from a distance and at different angles of regard, its presence is able to evoke powerful emotional effects, and it can serve as motivator of behavior and a source of comfort and control. In this case too, the independence and positive valence of the constituent schemas can be demonstrated. Again as in the case of food, it is likely that the higher order schema, through a process of recruitment, perhaps of opioids or other neurotransmitters, acquires emotional properties that are stronger than those of the combined constituents. In the absence of information regarding the ontogeny of this outcome, it would seem to qualify as a “basic emotion.”

In addition to the constructive contribution of schemas to normal development, failure of the environment to provide opportunities to incorporate individual species-typical components into higher order schemas can have deleterious developmental consequences. For example, monkeys raised in a socially impoverished environment often are described as hyper-aggressive (Capitanio, 1986). Even on their first physical encounters with other monkeys they often display the specific expressive sensory-motor schemas characteristically associated with aggression in this species: threats (eyebrow flash, low-pitched vocalization, ear flap), attack (biting, slapping, grabbing), and chase. There is every indication that such individuals may also be disposed to certain actions associated with an aggressive state (e.g., anger or rage). The various behaviors they show, however, do not constitute a functionally integrated aggressive state, and in fact seem to cause confusion in more completely socialized animals. A similar lack of integration of schemas into functionally coherent patterns is seen in sexually aroused monkeys that have not been fully socialized; the raw behavior patterns are present, but the animals seem incapable of organizing them sufficiently to achieve the typical functional outcome (Capitanio, 1986).

These are a few of the data suggesting that many sensory-motor schemas can emerge during development in the absence of social experience, but that their incorporation into higher order schemas may require social input or use to drive the developing system in a particular direction. In such circumstances, the emergent quasicohesive expression of an emotional state usually incorporates the familiar elements of valence (e.g., pleasant/unpleasant), cognition (e.g., dangerous/safe), motivation (e.g., flight/fight), expressive behavior (e.g., frown/smile), and awareness of the situation (e.g., familiar/unfamiliar).

We need not be reminded, however, that development begins at conception. There are clear indications that important organizational events that influence emotional development can occur during prenatal life. For example, a Rhesus monkey mother that has been iron deprived during the last trimester of pregnancy produces an infant that displays reduced fear and inhibition at 4 months of age, even though the infant received an iron-sufficient diet starting on the day of birth (Golub, Hogrefe, Germann, Capitanio, & Lozoff, 2006; see also Clarke & Schneider, 1997; Coe & Lubach, 2005).

New Biological Directions in Emotions Research and the New Paradigm

At a fundamental level, the processes that we think of as emotions are related to the functioning of a brain. While it is seductive to think of specific emotions as emanating from particular brain regions (e.g., the amygdala is responsible for fear), such an approach is

inappropriately reductionistic. How can the exciting developments in genetics and neuroscience be incorporated into the New Paradigm? Here we speculate on three recent developments in psychobiology.

Epigenetics

“Epigenetics” is a term with multiple meanings. In biology, epigenesis was a view that stood in opposition to the preformationist positions on development, and described how cells differentiate and retain their phenotype through multiple cell divisions. In psychology, the word emphasized that behavior developed through a process involving “the continuous dynamic exchange of energy between the developing organism and its environment, endogenous and exogenous” (Kuo, 1967, p. 11). More recently the concept has become associated with specific mechanisms by which the environment can “‘program’ enduring effects on gene expression and cellular function” (Meaney & Ferguson-Smith, 2010, p. 1313). When these mechanisms operate in the germline, these environmental effects on the genome can be inherited. While use of the term is not new in biology (Holliday, 2006), it has become increasingly familiar to psychologists through the work of Meaney and colleagues, who showed that when the maternal style of mother rats involved high levels of licking and grooming, their pups showed decreased hypothalamic-pituitary-adrenal activity to stressors and grew to be less fearful as adults. This style of mothering was associated with altered methylation of promoter regions in the glucocorticoid receptor gene (Kaffman & Meaney, 2007). Methylation of DNA is one of several epigenetic mechanisms.

The growing awareness of epigenetic mechanisms has provided psychologists with one plausible explanation of how the environment can get into the genome and create relatively lasting changes in psychological organization and behavioral expression. If this environment contains important elements of the environment of evolutionary adaptedness, then emotional development will likely be species-typical, and “basic emotions” may be inferred. But in unusual environments, such as the early rearing environments described before for nonhuman primates, epigenetic changes may alter how component schemas develop. There is scant evidence for this as yet, although a recent paper has shown the beginnings of such a link. The serotonin transporter gene produces a protein responsible for the reuptake of the neurotransmitter serotonin, and numerous studies have demonstrated that possession of a specific allelic variant (the “short” allele) in the promoter region of this gene can be a risk factor for affective disorders when the individual experiences an adverse environment (Lesch, 2011). Kinnally et al. (2010) demonstrated that for monkeys that were reared in a nursery instead of with their mother, individuals with higher methylation of the serotonin transporter gene also showed heightened activity in response to a social separation, suggestive of greater responsiveness. Methylation status was unrelated to responsiveness among mother-reared monkeys. Importantly, this result was independent of serotonin transporter genotype, suggesting that the environmental factors that altered gene expression were more important than the “usual” risk factor—genotype—for the organization of this behavioral system.

Mirror Neurons

Mirror neurons become active when an individual performs a specific action and sees the same action being performed by another (Fabbri-Destro & Rizzolatti, 2008). These neurons, discovered in the premotor cortex in monkeys, were first examined in the context of simple motor acts, such as grasping food items. Being able immediately to perform an action observed by another is seemingly adaptive. In addition, however, the firing of the cells while observing another's action may be a mechanism for creating an internal representation of the act (Rizzolatti, Fadiga, Gallese, & Fogassi, 1996).

How might a mirror neuron system figure into the New Paradigm, when on its surface, such a system would appear to represent a classic example of a mechanistic perspective? As in the area of behavioral epigenetics, there is little direct research on the role of the mirror neuron system in emotional development, nor do we yet know the limits of the mirror neuron system in the brain (Fabbri-Destro & Rizzolatti, 2008; Keysers & Gazzola, 2009). There has been growing interest, however, in the phenomenon of intersubjectivity, and specifically in the close interactions that take place between a caregiver and a neonate (e.g., Meltzoff & Moore, 1977). Recently, reports have emerged that within the first several days following birth, a Rhesus monkey mother interacts with directed gaze and exaggerated lip smacks (a display of affiliative gestures) toward her infant, who also responds with lip-smacking gestures (Ferrari, Paukner, Ionica, & Suomi, 2009). These intense interactions decrease substantially after the first month of life. In humans, this early pattern of interaction, involving active participation on the part of both participants, has been linked to development of emotion regulation (Tronick, 1989), and in monkeys, when mothers are not available (as in nursery-rearing conditions), poor emotion regulation does typically result. The evolution of a mirror-neuron-like system could underlie the phenomenon of intersubjectivity, and lead to stable, species-typical patterns of emotional expression when the young infant's environment contains critical elements of its EEA, such as a responsive mother.

Cytokines

In the past 15 years, it has become increasingly clear that the relationship between the brain and the immune system is bidirectional (Maier & Watkins, 1998). There has been substantial interest in the mechanisms by which illness leads to so-called sickness behaviors, which include reductions in activity, social interaction, and mood. The principal mechanism appears to involve proinflammatory cytokines, which cross the blood-brain barrier and interact with receptors on cells in the brain, leading to depressed mood (e.g., Eisenberger, Inagaki, Mashal, & Irwin, 2010). The idea that immune responses can modulate affective and behavioral manifestations of emotion has even generated a "cytokine hypothesis of depression" (Schiepers, Wichers, & Maes, 2005).

In the context of emotional development, there is growing evidence that fetal exposure to maternal infection, or proinflammatory cytokines, can affect brain development and behavioral reactivity, and links have been made with affective disorders. Experimental work with monkeys that were given a low dose of lipopolysaccharide early in the third trimester of pregnancy showed that in early infancy, animals were more emotionally reactive than

individuals in the control condition, but later in infancy displayed a pattern more consistent with behavioral inhibition (Willette et al., 2011). While the specific mechanism remains unknown, the example illustrates not only the importance of the prenatal period, but reminds us that the continuous interaction between an organism and its environment consists of events and involves physiological systems that one would not normally associate with particular outcomes such as emotional dispositions.

Conclusions and Future Directions

Darwin's publication of *The Expression of the Emotions in Man and Animals* helped make the topic of emotion a subject of scientific scrutiny, and placed its study squarely into a comparative framework. When psychology returned to the study of mental processes, the study of emotions (and other phenomena) proceeded apace, but the growing appreciation of a developmental perspective helped counter the simplistic either/or thinking that had stalled progress on many fronts. Experimental work, primarily with animals, revealed an important distinction between the expression of emotions, in terms of discrete behavior patterns, and the organization of emotions, which emphasizes ontogenetic processes and functional outcomes. From a developmental systems perspective, basic emotions are not innate. They are not illusory. Nor are they created by the forces of culture or custom. Instead it seems more likely that what are usually construed as basic emotions are the outcome of a natural developmental process that depends on an appropriate enabling environment (e.g., an environment of evolutionary adaptedness), and the proper genome interacting in ways that are "customary" based on the evolutionary history of the species. A large number of primitive sensory-motor units (schemas) are present in the neonatal period. These may be affectively charged only in a broad sense of positive/negative. Based on opportunity, use, functional affinity, and mutual compatibility, however, primitive schemas can merge into higher order, quasicohesive systems (i.e., components not tightly linked), which, overall, are characteristic of the species. Is it possible that this is the functional level that is the usual focus in the basic emotions debate? Throughout this process, of course, the environment and experience of each individual, both of which provide information, are influential in forming the operating characteristics of that individual's specific emotional system, and the effects of many of these influences may become incorporated into the genome by epigenetic mechanisms. We believe that the ongoing genomics and neuroscience revolutions will continue to make major contributions to our understanding of the mechanisms underlying emotional development, and will further help in putting to rest simplistic ideas of the origins of complex psychological phenomena.

Acknowledgments

Author note: The authors were supported by grants RR019970 and RR000169 from the United States National Institutes of Health.

References

Altman, J. Organic foundations of animal behavior. New York, NY: Holt, Rinehart and Winston; 1967.

- Anderson, JE. Dynamics of development: System in process. In: Harris, DB., editor. The concept of development: An issue in the study of human behaviour. Minneapolis, MN: University of Minneapolis Press; 1957. p. 25-46.
- Ashby, WR. Design for a brain: The origin of adaptive behaviour. 2nd. New York, NY: John Wiley & Sons; 1960.
- Averill, JR. Constructivism (psychological perspectives). In: Sander, D.; Scherer, KR., editors. Oxford companion to emotion and the affective sciences. New York, NY: Oxford University Press; 2009. p. 98-99.
- Barrett LF. Are emotions natural kinds? Perspectives on Psychological Science. 2006; 1:28–58. [PubMed: 26151184]
- Bertalanffy, LV. General system theory Foundations, development, applications. Edmonton, Canada: University of Alberta; 1968.
- Bowlby, J. Attachment and loss Volume I: Attachment. New York, NY: Basic Books; 1969.
- Brunswick E. Representative design and probabilistic theory in a functional psychology. Psychological Review. 1955; 62:193–217. [PubMed: 14371898]
- Camras LA, Witherington DC. Dynamical systems approaches to emotional development. Developmental Review. 2005; 25:328–350.
- Candland, DK. The ontogeny of emotional behavior. In: Moltz, H., editor. The ontogeny of vertebrate behavior. New York, NY: Academic Press; 1971. p. 95-168.
- Capitanio, JP. Behavioral pathology. In: Mitchell, G.; Erwin, J., editors. Comparative primate biology: Volume 2A Behavior, conservation, and ecology. New York, NY: Alan R. Liss; 1986. p. 411-454.
- Clarke AS, Schneider ML. Effects of prenatal stress on behavior in adolescent Rhesus monkeys. Annals of the New York Academy of Sciences. 1997; 807:490–491. [PubMed: 9071378]
- Coe CL, Lubach GR. Prenatal origins of individual variation in behavior and immunity. Neuroscience and Biobehavioral Reviews. 2005; 29:39–49. [PubMed: 15652253]
- Darwin, C. On the origin of species. New York, NY: Sterling; 2008. (Original work published 1859)
- Darwin, C. The descent of man, and selection in relation to sex. London, UK: John Murray; 1871.
- Darwin, C. The expression of the emotions in man and animals. London, UK: John Murray; 1872.
- Eisenberger NI, Inagaki TK, Mashal NM, Irwin MR. Inflammation and social experience: An inflammatory challenge induces feelings of social disconnection in addition to depressed mood. Brain, Behavior, and Immunology. 2010; 24:558–563.
- Ekman, P. Basic emotions. In: Dalgleish, T.; Power, M., editors. Handbook of cognition and emotion. Sussex, UK: John Wiley & Sons; 1999. p. 45-60.
- Fabbri-Destro M, Rizzolatti G. Mirror neurons and mirror systems in monkeys and humans. Physiology. 2008; 23:171–179. [PubMed: 18556470]
- Ferrari PF, Paukner A, Ionica C, Suomi SJ. Reciprocal face-to-face communication between Rhesus macaque mothers and their newborn infants. Current Biology. 2009; 19:1768–1772. [PubMed: 19818617]
- Fogel A, Thelen E. Development of early expressive and communicative action: Reinterpreting the evidence from a dynamic systems perspective. Developmental Psychology. 1987; 23:747–761.
- Gilbert, SF.; Epel, D. Ecological developmental biology: Integrating epigenetics, medicine and evolution. Sunderland, MA: Sinauer Associates; 2009.
- Golub MS, Hogrefe CE, Germann SL, Capitanio JP, Lozoff B. Behavioral consequences of developmental iron deficiency in infant Rhesus monkeys. Neurotoxicology and Teratology. 2006; 28:3–17. [PubMed: 16343844]
- Gottlieb G. Experiential canalization of behavioral development: Theory. Developmental Psychology. 1991; 27:4–13.
- Hamer D. Rethinking behavior genetics. Science. 2002; 298:71–72. [PubMed: 12364769]
- Hebb DO. The American Revolution. American Psychologist. 1960; 15:735–745.
- Holliday R. Epigenetics: A historical overview. Epigenetics. 2006; 1:76–80. [PubMed: 17998809]
- Izard CE. Basic emotions, natural kinds, emotion schemas, and a new paradigm. Perspectives on Psychological Science. 2007; 2:260–280. [PubMed: 26151969]

- Kaffman A, Meaney MJ. Neurodevelopmental sequelae of postnatal maternal care in rodents: Clinical and research implications of molecular insights. *Journal of Child Psychology and Psychiatry*. 2007; 48:224–244. [PubMed: 17355397]
- Keysers C, Gazzola V. Expanding the mirror: Vicarious activity for actions, emotions, and sensations. *Current Opinion in Neurobiology*. 2009; 19:666–671. [PubMed: 19880311]
- Kinnally EL, Capitanio JP, Leibel R, Deng L, LeDuc C, Haghighi F, Mann JJ. Epigenetic regulation of serotonin transporter expression and behavior in infant Rhesus macaques. *Genes, Brain, and Behavior*. 2010; 9:575–582.
- Kuo, Z-Y. The dynamics of behavior development: An epigenetic view. New York, NY: Random House; 1967.
- Lesch KP. When the serotonin transporter gene meets adversity: The contribution of animal models to understanding epigenetic mechanisms in affective disorders and resilience. *Current Topics in Behavioral Neurosciences*. 2011; 7:251–280. [PubMed: 21225411]
- Levine, S. Stress: An historical perspective. In: Stecker, T.; Kalin, NH.; Reul, JMHM., editors. *Handbook of stress and the brain*. Vol. 15. Amsterdam, The Netherlands: Elsevier B. V.; 2005. p. 3–23.
- Lindquist KA, Barrett LF. Constructing emotion. The experience of fear as a conceptual act. *Psychological Science*. 2008; 19:898–903. [PubMed: 18947355]
- Maier SF, Watkins LR. Cytokines for psychologists: Implications of bidirectional immune-to-brain communication for understanding behavior, mood, and cognition. *Psychological Review*. 1998; 105:83–107. [PubMed: 9450372]
- Mascolo, MF.; Harkins, D. Toward a component systems approach to emotional development. In: Mascolo, MF.; Griffin, S., editors. *What develops in emotional development?*. New York, NY: Plenum Press; 1998. p. 189–217.
- Mason, WA. Early deprivation in biological perspective. In: Deneberg, V., editor. *Education of the infant and young child*. New York, NY: Academic Press; 1970. p. 25–50.
- Mason, WA. Ontogeny of social behavior. In: Marler, P.; Vandenbergh, JG., editors. *Handbook of behavioral neurobiology*, Vol 3: Social behavior and communication. New York, NY: Plenum Press; 1979. p. 1–28.
- Mason, WA. Early developmental influences of experience on behaviour, temperament, and stress. In: Moberg, GP.; Mench, JA., editors. *The biology of animal stress: Basic principles and implications for animal welfare*. New York, NY: CABI; 2000. p. 269–290.
- Mason, WA. The natural history of primate development: An organismic perspective. In: Lewkowicz, DJ.; Lickliter, R., editors. *Conceptions of development: Lessons from the laboratory*. New York, NY: Psychology Press; 2002. p. 105–134.
- Meaney MJ, Ferguson-Smith AC. Epigenetic regulation of the neural transcriptome: The meaning of the marks. *Nature Neuroscience*. 2010; 13:1313–1318. [PubMed: 20975754]
- Meltzoff AN, Moore MK. Imitation of facial and manual gestures by human neonates. *Science*. 1977; 198:74–78. [PubMed: 897687]
- Monod, J. *Chance and necessity An essay on the natural philosophy of modern biology*. New York, NY: Vintage Books; 1971.
- Moore, DS. *The dependent gene: The fallacy of nature vs nurture*. New York, NY: Henry Holt; 2001.
- Nesse RM. Evolutionary explanations of emotions. *Human Nature*. 1990; 1:261–299. [PubMed: 24222085]
- Nesse RM, Ellsworth PC. Evolution, emotions, and emotional disorders. *American Psychologist*. 2009; 6:129–139. [PubMed: 19203145]
- Newton, G.; Levine, S., editors. *Early experience and behavior (the psychobiology of development)*. Springfield, IL: Charles C. Thomas; 1968.
- Ortony A, Turner TJ. What's basic about basic emotions? *Psychological Review*. 1990; 97:315–331. [PubMed: 1669960]
- Overton, WF.; Reese, HW. Models of development: Methodological implications. In: Nesselroade, JR.; Reese, HW., editors. *Life-span developmental psychology: Methodological issues*. New York, NY: Academic Press; 1973. p. 65–86.

- Oyama, S. The ontogeny of information. Developmental systems and evolution. 2nd. Durham, NC: Duke University Press; 2000.
- Panksepp J. Neurologizing the psychology of affects: How appraisal-based constructivism and basic emotion theory can coexist. *Perspectives on Psychological Science*. 2007; 2:281–296. [PubMed: 26151970]
- Piaget, J. Biology and knowledge. Chicago, IL: The University of Chicago Press; 1971.
- Pigliucci M. Genotype-phenotype mapping and the end of the “genes as blueprint” metaphor. *Philosophical Transactions of the Royal Society B*. 2010; 365:557–566.
- Plutchik, R. Emotions in early development: A psycho-evolutionary approach. In: Plutchik, R.; Kellerman, H., editors. *Emotion—Theory, research and experience, Vol 2: Emotions in early development*. New York, NY: Academic Press; 1983. p. 221-257.
- Plutchik R. The nature of emotions. *American Scientist*. 2001; 89:344–350.
- Reese, HW.; Overton, WF. Models of development and theories of development. In: Goulet, LR.; Baltes, PB., editors. *Life span developmental psychology: Research and theory*. New York, NY: Academic Press; 1970. p. 115-145.
- Richerson PJ, Boyd R. Built for speed, not for comfort. *Darwinian theory and human culture. History and Philosophy of the Life Sciences*. 2001; 23:425–465. [PubMed: 12472064]
- Rizzolatti G, Fadiga L, Gallese V, Fogassi L. Premotor cortex and the recognition of motor actions. *Cognitive Brain Research*. 1996; 3:131–141. [PubMed: 8713554]
- Russell JA. Core affect and the psychological construction of emotion. *Psychological Review*. 2003; 110:145–172. [PubMed: 12529060]
- Russell JA, Barrett LF. Core affect, prototypical emotional episodes, and other things called emotion: Dissecting the elephant. *Journal of Personality and Social Psychology*. 1999; 7:805–819. [PubMed: 10353204]
- Schiepers OJG, Wichers MC, Maes M. Cytokines and major depression. *Progress in Neuro-Psychopharmacology & Biological Psychiatry*. 2005; 29:201–217. [PubMed: 15694227]
- Schneirla, TC. The concept of development in comparative psychology. In: Harris, DB., editor. *The concept of development An issue in the study of human behaviour*. Minneapolis: University of Minnesota Press; 1957. p. 78-108.
- Tooby J, Cosmides L. The past explains the present. *Emotional adaptations and the structure of ancestral environments. Ethology and Sociobiology*. 1990; 11:375–424.
- Tronick EZ. Emotions and emotional communication in infants. *American Psychologist*. 1989; 44:112–119. [PubMed: 2653124]
- West-Eberhard, MJ. *Developmental plasticity and evolution*. New York, NY: Oxford University Press; 2003.
- Willette AA, Lubach GR, Knickmeyer RC, Short SJ, Styner M, Gilmore JH, Coe CL. Brain enlargement and increased behavioral and cytokine reactivity in infant monkeys following acute prenatal endotoxemia. *Behavioral Brain Research*. 2011; 219:108–118.
- Zivin, G. Separating the issues in the study of expressive development: A framing chapter. In: Zivin, G., editor. *The development of expressive behavior Biology–environment interactions*. New York, NY: Academic Press; 1985. p. 3-75.