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## Critical Period: A History of the Transition from Questions of When, to What, to How

ABSTRACT: Although age appears to be the defining characteristic of the concept of critical period, central to its investigation is the recognition that there are specific events which must occur in a particular order for the typical development of certain characteristics to occur. A brief history of some research on critical periods reveals that our questions have shifted from those of: is there a critical period and, if so, when does it occur; to questions of what contributes to the criticality of the period; and finally to how is criticality controlled during development. Abandoning age as a defining component of development has permitted the discovery of exactly how previous and current events construct subsequent events in the process of development. The shifts in questions about critical periods mark an increasing sophistication in understanding how development can be controlled.

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Development is an historical phenomenon in which previous events affect the manifestation of both current and subsequent events and current events become the previous events that affect subsequent events. Hence, there is a serial order to developmental phenomena that has a cumulative aspect. Consequently, development must be defined by the illumination of the factors creating and governing the serial order and the processes of change and stability of that order over time (Michel & Moore, 1995).

The serial order of development reflects both logical and empirical characteristics. For example, given that cell division is a doubling process, a two cell stage must logically precede a four cell stage. However, a 16 cell stage can precede a subsequent 8 cell stage only if there is empirical evidence of cell death between the 16 and 8 stage events. Thus, development is a serially ordered process that is identifiable across time, but it is not defined by time. This distinction is often overlooked in research. Too often, especially in research on psychological characteristics, comparison across time (as represented by age) serves as

the only indication that the research is developmental. A brief historical examination of the concept of critical period may help illustrate why time should not be a defining characteristic of development.

Morphological and behavioral characteristics of an individual emerge over time. Development typically exhibits both regularity in the serial order for the appearance of specific characteristics (stages) and regularity in the time from conception for when the "stages" in the serial order occur. The regularities of order and time are identified by their similarity across individuals and the patterns of behavioral and morphological development are identified in part by both the sequence and time course of the appearance of new characteristics. For example, "limb buds" appear before "limbs" and "stepping" appears before "walking" and the time from conception to the appearance for each of these characteristics is fairly similar across members of the same species. Since the time of appearance of each morphological structure is closely associated with the "age" (time since fertilization of the organism), it is not surprising that the timing of development (the when) became a major focus of research. Thus, cross-individual and within-species regularity of the appearance of morphological structures and the within species regularity of the time (or age) of appearance of such structures helped create the field of embryology and developmental biology. The regularity in

Received 30 July 2004; Accepted 30 November 2004 Correspondence to: G. F. Michel Published online in Wiley InterScience (www.interscience.wiley.com). DOI 10.1002/dev.20058 age of appearance within a species rapidly became the marker of normal development and any variations in age of appearance marked abnormal development.

Early in the history of embryology, investigators wanted to determine whether the embryo was an "unfolding" of some preformed being or a constructed entity. Manipulations shortly after the initial divisions of the zygote, demonstrated that dividing the zygote resulted in the development of two half-organisms. This seemed to support the notion of an unfolding of some preformed entity. Subsequent studies demonstrated that such division resulted in the development of two separate whole individuals. This seemed inconsistent with the notion of a preformed entity. Debate about the contradictions of these studies was ended when it was discovered that the timing of the division (or age and stage of the organism at the time of division) was associated with the difference in outcome. Thus, there seemed to be a period of time that was critical to whether or not dividing the embryo would result in the development of two half-organisms or two whole-organisms.

Spemann (1938/67) demonstrated that the developmental outcome (what type of tissue characteristics a cell begins to manifest) of embryonic cells is determined by their location. Signals from the local environment induce cells to adopt a particular developmental "fate". That is, a normal organism (e.g., a frog) will develop even when its tissue has been rearranged (e.g., skin and brain cells exchanged during the gastrula stage). However, the timing of the exchange became critical when it was noted that if the exchange occurred when the cells were in the late gastrula stage, the organism developed with inappropriately placed patches of tissue. The cells seemed committed to a particular fate. Thus, questions about "when" (i.e., the age of the embryo when manipulations did or did not affect the outcome of development) became the main focus of experimental embryology.

Ultimately, this led to the establishment of the field of teratology—the investigation of factors that would disrupt "normal" (the regularities of) development. Developmental questions focused on whether or not there was a critical period for exposure to certain events which would affect the course of development and, if there was a critical period, what were its time/age boundaries. Embryologists identified critical periods for the exposure to many atypical environmental (particularly chemical) conditions that had profound effects on the morphological development of the organism. They discovered, also, that certain manipulations had negative consequences despite the age of the embryo at the time of the manipulation. Thus, the latter did not exhibit a critical period for their impact.

As embryology grew as an experimental/manipulation science, the definition of "abnormal" development became directly related to any variation in the typically regular age of developmental events. "Normal" development was defined as the typical sequence of events occurring at the typical age/time. Failure of the normal sequence, as a result of exposure to conditions at particularly sensitive periods or as a result of not being exposed to appropriate conditions at their optimal times, was abnormal development. Hence, a maturational time-table became a guide to the distinction of normal and abnormal development. Physicians adopted developmental milestones to represent normal development against which abnormal development could be identified. Anything that delayed or advanced aspects of the typical pattern of development was defined as producing abnormal development.

In contrast to considering such variability in the timing of developmental processes as simply abnormal, de Beer (1958) and Gould (1977) argued that such variability was the foundation for the evolution of species variability. Comparisons of the patterns of development among closely related species revealed that the origin of morphological differences, with important adaptive consequences, derived from differences in the timing of typical sequences of developmental events. Since these related species were not necessarily at a disadvantage in living, both de Beer and Gould considered the variability in the course and timing of developmental events as a "natural" aspect of living systems.

Of course, specific developmental outcomes can be more or less advantageous for the individual. If some outcome is disadvantageous for the individual, it should prompt attempts at rehabilitation (for those with the disadvantageous outcome) and prevention (for those who may be at risk for such an outcome). Placing too much emphasis on the timing of development could result in a more pessimistic approach to the building rehabilitation and prevention programs (Bateson, 1979; Bateson & Hinde, 1987). The metaphor of development as a train moving on a track according to a time-table with a limited number of switching stations can lead to the notion that redirection of the outcome (rehabilitation) is unlikely because a switching station has been passed. Knowledge of those factors responsible for the sequential order of developmental events and those that influence when they occur can generate a more optimistic approach.

As biologists began to investigate the "natural" behavior of animals (sometimes referred to as instinctive behavior), some investigators chose to pose the issue of behavioral development within the framework of developmental biology. For example, Konrad Lorenz (1937/57) subjected to more systematic investigation the common barnyard phenomenon that ducklings, goslings, and chicks often mistakenly follow a human (usually a child) instead of following their parent shortly after hatching. To find out why, he chose the developmental biological technique of manipulating the age at which newly hatched ducklings

and goslings were exposed to various potential parental substitutes. These studies led him to conclude that there was a critical period for the development of the pattern.

During a particular age period (within hours after hatching), the young bird had to be exposed to a moving object and thereafter it would follow that same object. Subsequently in adulthood, objects with characteristics similar to those of the object followed, were courted for mating. This process of forming a perceptual pattern for selecting mates from exposure shortly after hatching was translated in to English as "imprinting". Lorenz's definition of imprinting included a rigidly defined critical period. Lorenz proposed that the onset and offset of this period was determined by intrinsic processes of development under control of the organism's genes. Therefore, the age of occurrence of the critical period could vary across the species but vary little within a species. Lorenz proposed that critical periods might exist for the development of other species-typical behavior patterns.

Indeed, research on bird song by W. H. Thorpe (e.g., 1961) and Peter Marler (e.g., 1970) revealed that males of many species of birds acquire their species-typical song pattern by hearing the song of their father when nestlings. For some species, there seemed to be a critical age period for exposure to the species-typical song. Isolation from that song during that age and exposure to the song subsequently did not result in the development of the species-typical song.

Not long after Lorenz's work on the critical periods for the establishment of social behaviors in birds, John Paul Scott (1962) reported a critical period for the development of socialization in dogs and cats. Unless encouraged to interact with humans at a particular early age, certain breeds of dogs and cats would not be able to be socialized to human interaction. For other breeds the critical period appeared to be much longer or non-existent. Since this pattern seemed to mimic the pattern of filial imprinting reported by Lorenz, Scott proposed that critical periods for socialization may underlie the social development of many species of bird and mammal, including humans. Harry Harlow (c.f., Harlow & Harlow, 1965) also reported a series of studies on the development of social abilities in Rhesus monkeys that indicated that social deprivation during the infant monkey's first three months had rather catastrophic long term developmental consequences. Similar deprivation after six months of age resulted in relatively mild developmental disturbances.

In the late 1950s, Austin Riesen (c.f., 1975) reported a series of studies with monkeys and cats that showed that the absence of light or patterned visual stimulation during infancy led to blindness in adults. He went on to describe much of the anatomy and physiology that was disrupted by the patterned light deprivation which was responsible for the blindness. The functional blindness was created

only when kittens were reared without patterned light during their first four months. A similar period of four months without patterned light after the kittens were older than 6 months did not affect their sight. Hence there seemed to be a critical period for the development of functional sight. Similar results of rearing without patterned light were obtained with monkeys.

Drawing on the results of imprinting, bird-song development, development of visual ability, and socialization, combined with the evidence on language development in humans and the effects of various kinds of brain damage on such development, Eric Lenneberg (1967) proposed a critical period for language development. Indeed, his proposal included a critical period for the development of both language and the specialization of the left hemisphere for language processing. Interestingly, Leneberg proposed a 10-12 year window (from birth to puberty) for the critical period of language acquisition and the development of hemispheric specialization for language skills.

Similarly drawing on the literature of ethology and animal behavior, Bowlby (1969) proposed a critical period for the formation of an attachment relationship between the mother and child which if disrupted resulted in the development of adult psychopathology. From birth to approximately three months, the infants can recognize their caregivers but they do not seem to be socially attached specifically to them. From 3 to 6 months, infants exhibit caregiver preference. However, the period from 6 months to 3 years seemed to be critical for the formation of an attachment relationship that would become the basis for all future social partnerships and the capacity for the individual to form emotional bonds with others or to exhibit either sympathy or empathy.

Not long after Leneberg's and Bowlby's publications, critical periods began to be proposed for the development of a host of human characteristics including sensory and perceptual abilities, social skills, motor skills, language and second language acquisition, critical reasoning skills, etc. (Bornstein, 1989). Most often the evidence for the critical period consisted of some relatively minimal demonstration that a weakness of skill was associated with an unusual event or a particular kind of experiential deprivation that occurred early in the individual's life. Educators had long proposed that educational experiences should be restricted to certain age periods because it is believed that these periods represent the time when children are "ready" for such experiences to have their developmental impact. The empirical investigations of the concept of critical period provided support for such proposals.

While critical periods were flourishing in the study of behavior, embryologists had come to focus less on the timing or age of the exposure and more on processes that were associated with time or age. That is, time and the status of the developmental process were intimately related for those aspects of development that exhibited the regularity that attracted investigation by developmental biologists. For example, a morphological structure such as the corpus callosum in the mammalian brain is composed of hundreds of millions of the axons of pyramidal cells of the cortex. Pyramidal cells on the right side of the cortex project their axons to the left side of the cortex and pyramidal cells on the left side project their axons to the right side of the cortex. The criss-crossing of these axons over the third ventricle create the corpus callosum. The timing of the growth of the projections that create the corpus callosum is well specified and several events can disrupt the formation of this structure. Thus, studies focused on the "when" of development revealed a critical period during which several factors (including some known teratogens) can disrupt the formation of the corpus callosum.

However, as developmental biologists examined this critical period it was discovered that a major factor that created the criticality of the timing was the formation of certain forms of glial cells called "bridge" cells at the border of the third ventricle. When the axons approached the area of the third ventricle, if the bridge cells were present, the axons would extend across the ventricle to the opposite side. If the bridge cells were not present, then the axons continued to project to other areas within their own hemisphere (c.f., Silver, Lorenz, Wahlsten, & Coughlin, 1982).

The bridge cells themselves had a relatively delimited time of existence and, as with all developmental phenomena, this time was a consequence of previous events and the current conditions. Bridge cells are formed at one time from certain glial cells and then after some time (and for reasons not yet completely known) they die. As this process was examined, it became clear that the formation of the corpus callosum could be disrupted by any combination of factors that sped-up or slowed-down the growth of the axons, sped-up the formation or the death of the bridge cells, or caused bridge cells to form in the wrong place in the brain. Hence, developmental biologists began to examine the criticality of the sequence of events for the formation of some morphological characteristic. They asked questions about what characteristics composed the sequence of events of development and how these were disrupted by the manipulations that seemed to mark a critical period. Questions of "when" were replaced by questions of "what".

In the study of imprinting and bird song, questions of "when" also were being replaced by questions of "what". Many studies showed that the onset and ending of the critical period for imprinting could be altered by various sorts of environmental manipulations. For example, dark

rearing would delay the offset of the critical period. The onset of the "critical period" seemed to be determined by the sensory and motor abilities of the individuals and these had developmental courses that were influenced by the manipulation of certain ubiquitous experiences and conditions which then altered the onset of the critical period. Moreover, the end of the critical period for song learning and imprinting seemed to be a self-terminating process in some species (Bateson, 1987; Eales, 1985; ten Cate, 1989). That is, the acquisition of the percept of the object or the song during the process of imprinting or song acquisition prevented any further acquisition of other percepts.

Patrick Bateson (1966, 1987) showed that the termination of the critical period could be created by the experimental conditions used to test the critical period. Chicks would imprint on the perceptual characteristics of their cages if their deprivation from exposure to "imprintable objects" did not occur in darkness. Thus, having been exposed to a stimulus, a percept would be acquired for the discrimination of familiar from non-familiar. Familiar stimuli would be approached and attended to whereas the exposed chick would withdraw from unfamiliar stimuli and thereby fail to become familiar with its characteristics. With this knowledge, other investigators showed that deprivation during the critical period could be overcome by specific patterns of exposure at later ages. Critics claimed that such manipulations only affected "taming" and not imprinting. Nevertheless, the filial and mating preferences of certain species could be altered by manipulations that occurred outside of the supposed critical period for imprinting.

Investigations of the critical period for bird song acquisition also revealed that some of the criticality depended on the experimental conditions of investigation. Species who were exposed only to the sound of a song exhibited a critical period for acquisition that did not occur if they were exposed to the presence of a singer. In some species, the singer needed to be a familiar companion whereas in other species the singer could be a stranger (c.f., Petrinovich, 1988). Again, the investigation of bird song acquisition was replacing the "when" of exposure with investigations of "what": What was it about the conditions of the individual that made timing relevant?

Interestingly, at the time of Scott's 1962 report of critical periods for socialization, Schneirla and Rosenblatt (1963) reported that the development of species-typical social behavior in cats exhibited a cascading set of events in which the experiences associated with each social event was critical for the cascade. That is, the kitten begins to adjust to the mother at birth using the behavioral systems available, in part through the prenatal fetus-mother relationship. As new behavioral systems emerge through

changes in both the kitten's and mother's systems, new social adjustments are made. By separating kittens from their mother and litter mates and keeping them on an artificial brooder, Schneirla and Rosenblatt showed that the kittens had difficulty adjusting to the mother at reunion. The mother's system had changed during the separation, in part by her adjustment to the remaining kittens in the litter, and the kitten's system had been altered by the separation and adjustment to the brooder. At reunion, the kitten behaves toward the mother in ways more appropriate to an earlier phase of their interaction, thereby producing discordant interactions between them.

All separated kittens manifested difficulties in their social adjustments, no matter when during development their separation occurred. No single period during development appeared to be more crucial for social adjustment than any other. However, the particular difficulties manifested at reunion depended on the level of social ability achieved by the kitten before separation and the degree of changes in the mother induced by her experiences during the separation. The degree of difficulty at reunion depends on the degree of discrepancy between the level of the kitten's social ability and that of its mother. Thus, the timing of the events seemed to emerge from the logic of the sequence rather than from some intrinsic clock. Hence, Schneirla and Rosenblatt argued against the notion of critical periods in development and more for critical sequences for the emergence of specific social skills and abilities. Although this research was a serious challenge to research focused on questions of "when" in the development of behavior, it had little impact at the time.

One reason for the lack of impact was that critics argued that the Schneirla and Rosenblatt study was not the appropriate type of experiment for evaluating whether there is a sensitive period in cat socialization (i. e., whether the impact of a controlled stimulus varies with the age of the individual). Schneirla and Rosenblatt did not examine whether age modified the response to a specific type of stimulus. Instead, they deconstructed the process of social development to identify why separations for different lengths of time and at different stages in the relationship between the mother cat and her offspring led to different developmental outcomes in the social relationship between the mother and offspring.

Scott's (1962) study examined the responsiveness to humans of puppies who were at different ages when they were first exposed to a human. Hence, it met the critics' criterion for the identification of a critical period. Although Scott proposed that there was a critical period for socialization in dogs, only the socialization of puppies to humans was examined. More importantly, the age of the puppy at exposure to humans seemed to be the explanation for why "socialization" did or did not fail.

Obviously, social behavior involves social interactions between individuals. That is, since the mother behaves differently at different points in the relationship (which does occur across time), the reunion at different "times" presents a different stimulus to the kitten. However, it is only as a result of the Schneirla and Rosenblatt (1963) study that the discrepancies between mother and offspring can be identified as the reason for the failure of the reestablishment of the relationship. Once those discrepancies are identified, research can be begin to seek ways of providing compensatory manipulations that promote a developmental pathway that results in the desired outcome. This is important to the rehabilitation aspect of developmental research and it was put to excellent use by Mason in his research on the types of social and non-social experiences that rehabilitate the social skills of Rhesus monkeys who were raised on a cloth "mother" (Mason & Capitanio, 1988). Nevertheless, the Schneirla and Rosenblatt study was dismissed as not appropriately investigating the concept of critical period

Of course, it was (and is) still clear that at some periods (stages) of development, exposure to certain conditions more easily affected development than exposure to those same conditions at other periods (stages). However, the notion of some process controlled by the timing or age of the individual did not seem appropriate for comprehending the historical contingency of developmental phenomena. Hence, the notion of critical period was replaced by the notion of a "sensitive" period. Sensitive periods are not clock-like, built-in or predetermined periods in development but are themselves the product of development. Thus, we should expect the variability in onset/ offset (timing), specificity, etc. evident in their study. Replacement of critical periods by sensitive periods should operate as a "promissory note" that future research will be designed to reveal exactly why the development of some characteristic was sensitive to a particular pattern of experience at a particular time in the individual's life. Replacing "critical" with "sensitive" marked the recognition that once the "what" of development was discovered, timing alone would not be critical for manipulating the developmental outcome.

Nevertheless, the use of the concept of sensitive period permitted many investigators to retain the notion that there are biological processes that normally unfold at a certain age and that they dictate the neural response to experience. Therefore, even if the timing of these biological processes was sensitive to experience, this did not imply that age/time was not important. These investigators argue that such factors just make it much more difficult to define the temporal limits of sensitive periods. By adding the notion that any sensitive period may be a reflection of multiple sequential sensitive periods that interact with one another, these investigators believe that they have accounted for

why different manipulations and dependent measures often yield different results about the temporal limits of the sensitive period. That is, different stimuli engage specific neural processes to a greater or lesser degree than others, and different dependent measures are more or less affected by the various interacting processes that impact responsiveness to a particular experience. Thus, sensitivity may appear greater or lesser depending upon the salience of the stimuli delivered during the experimental manipulation and the pattern of overlap among interacting sensitive periods.

However, in a somewhat Ptolemaic manner, it may be that it is only the attempt to retain the importance of time as a defining aspect of development that prompts such a convoluted notion of sensitive period. All phenotypic traits (including sensitive periods of experiential vulnerability) are generated during individual ontogeny because particular aspects of the temporal and spatial arrangements of individuals and their contexts reliably occur at times when the organism is in particular developmental states, having had a particular developmental past (Michel & Moore, 1978). Therefore, when accepted as simply a promissory note for further investigation of exactly why some events affect development at certain stages more than at other stages rather than as an explanation of development, sensitive periods need not become burdened with unnecessary complexity.

In the past two decades, developmental biology has shifted from questions of "when" and "what" creates the regularities of development to questions of "how" regularity is achieved. Research is focused on how processes of intra- and intercellular communication produce the various "pathways" of development that result in both individual differences and inter-individual similarities of characteristics. Revealing these mechanisms will permit both the identification of developmental pathways with potentially unacceptable outcomes and identification of places in the pathway in which either simple or complex interventions can be undertaken to establish more acceptable pathways. In other words, investigations of the "how" of morphological development is providing us with more sophisticated control techniques and opportunities. Thus, age/time is no longer the defining aspect of developmental phenomena (c.f., Gilbert, 2003).

There are too few current investigations of the "how" of behavioral development (but see additional articles in this issue). Most investigations of the "how" of development have relied upon the presumed indirect behavioral consequences of developmental biological investigations of the development of gross brain structures and their general physiology. That is, the "how" of development is thought to require reduction to a physiological or molecular level of biological investigation. However, as we become more sophisticated in the understanding of

organism-environment interaction in behavioral development, we will begin to achieve greater understanding of the pathways responsible for individual differences and inter-individual similarities of psychological characteristics (c.f., Gilbert, 2001). Such understanding will provide us with greater control of our offspring's destiny and greater responsibility for our exercise of such control.

## REFERENCES

- Bateson, P. P. G. (1966). The characteristics and context of imprinting. Biological Reviews, 41, 177–220.
- Bateson, P. P. G. (1979). How do sensitive periods arise and what are they for? Animal Behaviour, 27, 470–486.
- Bateson, P. P. G. (1987). Imprinting as a process of competitive exclusion. In J. P. Rauschecker & P. Marler (Eds.), Imprinting and cortical plasticity: Comparative aspects of sensitive periods (pp. 151–168). New York: Wiley.
- Bateson, P. P. G., & Hinde, R. A. (1987). Developmental changes in sensitivity to experience. In M. H. Bornstein (Ed.), Sensitive periods in development (pp. 19–34). Hillsdale, NJ: Erlbaum.
- Bornstein, M. H. (1989). Sensitive periods in development: Structural characteristics and causal interpretations. Psychological Bulletin, 105, 179–197.
- Bowlby, J. (1969). Attachment and loss (Vol. 1). Attachment. New York: Basic Books.
- de Beer, G. R. (1958). Embryos and ancestors (3rd Ed.). London: Oxford University Press.
- Eales, L. A. (1985). Song learning in zebra finches: Some effects of song model availability on what is learned and when. Animal Behaviour, 33, 1293–1300.
- Gilbert, S. F. (2001). Ecological developmental biology: Developmental biology meets the real world. Developmental Biology, 233(1), 1–12.
- Gilbert, S. F. (2003). Developmental biology (7th Ed.). Sunderland, MA: Sinauer Associates, Inc.
- Harlow, H. F., & Harlow, M. K. (1965). The affectional systems. In A. M. Schrier, H. F. Harlow, & F. Stollnitz (Eds.), Behavior of nonhuman primates (Vol. 2, pp. 287–334). New York and London: Academic Press.
- Lenneberg, E. H. (1967). The biological foundations of language. New York: Wiley.
- Lorenz, K. (1937/57). The conception of instinctive behavior. In C. H. Schiller (Ed. and Trans.), Instinctive behavior (pp. 129–175). New York: International Universities Press. (Original work published 1937.)
- Marler, P. (1970). A comparative approach to vocal learning: Song development in white-crowned sparrows. Journal of Comparative and Physiological Psychology, 71, 1–25.
- Mason, W. A., & Capitanio, J. P. (1988). Formation and expression of filial attachment in rhesus monkeys raised with living and inanimate mother substitutes. Developmental Psychobiology, 21, 401–430.
- Michel, G. F., & Moore, C. L. (1978). Biological perspectives in developmental psychology. Monterey, CA: Brooks/Cole.

- Michel, G. F., & Moore, C. L. (1995). Developmental psychobiology: An interdisciplinary science. Cambridge, MA: The MIT Press.
- Petrinovich, L. (1988). The role of social factors in white-crowed sparrow song development. In T. R. Zentall & B. G. Galef (Eds.), Social learning (pp. 255–278). Hillsdale, NJ: Erlbaum.
- Riesen, A. (1975). The developmental neuropsychology of sensory deprivation. New York: Academic Press.
- Schneirla, T. C., & Rosenblatt, J. S. (1963). "Critical periods" in the development of behavior. Science, 139, 1110–1115.
- Scott, J. P. (1962). Critical periods in behavioral development. Science, 138, 949–958.
- Silver, J., Lorenz, S. E., Wahlsten, D., & Coughlin, J. (1982). Axonal guidance during development of the great cerebral commissures: Descriptive and experimental studies, in vivo, on the role of preformed glial pathways. Journal of Comparative Neurology, 210, 10–29.
- Spemann, H. (1938/67). Embryonic development and induction. New York: Hafner. (Original work published 1938.)
- ten Cate, C. (1989). Behavioral development: Toward understanding processes. In P. P. G. Bateson & P. Klopfer (Eds.), Perspectives in ethology (Vol. 8, pp. 243–269). New York: Plenum Press.
- Thorpe, W. H. (1961). Bird song. Cambridge: Cambridge University Press.