Review Article

NEURO-BEHAVIORAL ONTOGENY. A SYNTHESIS OF ETHOLOGICAL AND NEUROPHYSIOLOGICAL CONCEPTS

M. W. FOX

Thudichum Psychiatric Research Laboratory, Galesburg State Research Hospital, Galesburg, Ill. (U.S.A.)

(Received March 4th, 1966)

INTRODUCTION

The hypothesis of the critical period of socialization as originally presented by Scott and Marston[81] was reviewed and extended by Scott[78] in describing the behavioral development of non-precocial mammals, in other words, those born relatively immature. In this way, the term critical period originally used in embryology was applied to ethology, the objective study of animal behavior[92]. For purposes of this review the mouse, dog and cat are considered as examples of the non-precocial group and correlations in other parameters of neurological development common to all these animals will be used to extend the critical period hypothesis. Other critical periods, dependent on neuro-endocrine and environmental factors are seen during later life, notably in the onset of sexual and maternal activities. These activities are themselves greatly influenced by the developmental processes underlying the establishment of primary social relationships during the critical period of socialization.

In much of the research on behavior undertaken by earlier American psychologists, theoretical conclusions were drawn from empirical observations restricted to one species observed in a synthetic laboratory environment. Indeed plasticity and adaptibility of behavioral development were considered undesirable variables and animals not conforming to the rigid theoretical model were often discarded. At about the same time, in Europe, the students of animal behavior were, in contrast, developing a discipline for studying adaptive behavior within the natural environment, as shown for example, by the increased focus of research within the field of behavioral development, resulting from the earlier work of Lorenz[61] on imprinting. With a fundamental knowledge of the processes underlying behavioral development we may formulate systematic criteria of development within a species and make comparisons between groups of species; *e.g.* precocial and non-precocial birds or mammals. Recent reviews on imprinting[44,45,84], on the effects of early experience[13,59] and on environmental enrichment or deprivation[4] emphasize the extrinsic and intrinsic variables both dependent and independent which may modify ontogeny. The approach/withdrawal theory of Schneirla[77] which closely resembles similar observations on approach/avoidance (active and passive defensive reflexes) described by Krushinskii[56], and Anokhin's[2] theory of systemogenesis as a regulator of development and adaptation are major contributions to this field of research. Such theoretical foundations provide a basis for the advancement of theories which regard development not as a rigid progression, but as a plastic and adaptive sequence of events.

EMBRYOGENESIS

On the basis of earlier classical studies of Coghill[9] and of Hooker[47], Hamburger[41] has piesented new and stimulating observations on the embryogenesis of behavior. He recognized two components of motility, namely, spontaneous and reflexogenic, the former being the primary component. Reflexogenic activity develops later, and because of the lack of stimulation *in utero*, is less important in the prenatal moulding of behavior. He regarded spontaneous motility as the major factor in organizing behavior during embryogenesis. This activity was characterized by rhythmicity with short phases of activity followed by longer phases of inactivity. Although not organized or integrated in the embryo, it may be the embryonic antecedent of the spontaneous component in adult activity. The development of patterned integrated and adaptive behavior from the unintegrated generalized motility of the embryo is still poorly understood. But from the basic observations of Hamburger[41] we may postulate that rhythmicity with widely varying phases of activity is a natural phenomenon of organisms and is of adaptive and survival value. At the time of birth or hatching the sudden increase in afferent stimuli evoke reflexogenous activities which can be rapidly elaborated or modified from the innately organized spontaneous motility. As postnatal development progresses cortical control of movement emerges, and although overtly overshadowing these earlier activities, is nonetheless dependent upon them for integration of function both in the immature and adult organisms. The ability of the duck embryo to show components of action patterns, for example, wingbeating in response to self-induced proprioceptive and tactile stimulation, led Gottlieb and Kuo[36] to stress that self stimulation may be an important process in prenatal behavioral development. Lorenz[62] states that the organism can learn (or more correctly, organize) important elements of behavior before being hatched or born. Information in the genome may be doubly decoded, first by morphogenesis and subsequently by trial and error learning making use of morphological structure. Further research is needed on the ontogeny of circadian activities and of the homeostatic mechanisms which are characteristic of a species. These mechanisms are in part genetically determined and are adaptively 'triggered' by the environment shortly after or at the time of birth[40].

DEVELOPMENT OF REFLEX ACTIVITY

As has been pointed out by many observers, ontogeny does not follow a series of sharply defined developmental phases, but a more gradual, sequential unfolding of neural units organized into more complex integrated patterns of activity. The concepts of Coghill[9] and the similar views of Anokhin[2] embrace the notion that localized, specialized acts are secondary manifestations of the initial total pattern or functional systems, that is, reflex activity at its functional onset is composed of integrated total acts. This theory has been called the total pattern theory. Windle[99] and Barcroft and Barron[3] in contrast maintained that reflex activity develops from simple to complex reactions (local pattern theory).

Sedlacek *et al.*[82] ascertained the effects of CNS transection at various levels on washing, licking, combing and shaking reactions elicited by cutaneous stimulation at different ages in rats, guinea-pigs and dogs. His results are comparable to those obtained by Fox[19,23] in pups (dog) of different ages subjected to spinal cord transection and decerebration[28]. Sedlacek and his colleagues[82] support the conception of Volokhov[94] which attributes the development of reflex activity to qualitative and quantitative evolution of the CNS. Their concept equates with the animal behaviorist interpretation of initial 'units' of behavior being integrated into complex specialized acts. The development of 'unit' systems (components of fixed action patterns) in the neural organization of behavior in non-precocial mammals is an important step in the maturation of reflex responses.

Accordingly, Sedlacek *et al.*[82] divided the development of reflex activity into 7 evolutionary phases which were closely associated with rostral progression of function in the developing nervous system (Fig. 1). Sedlacek's[82] hypothesis can be corre-

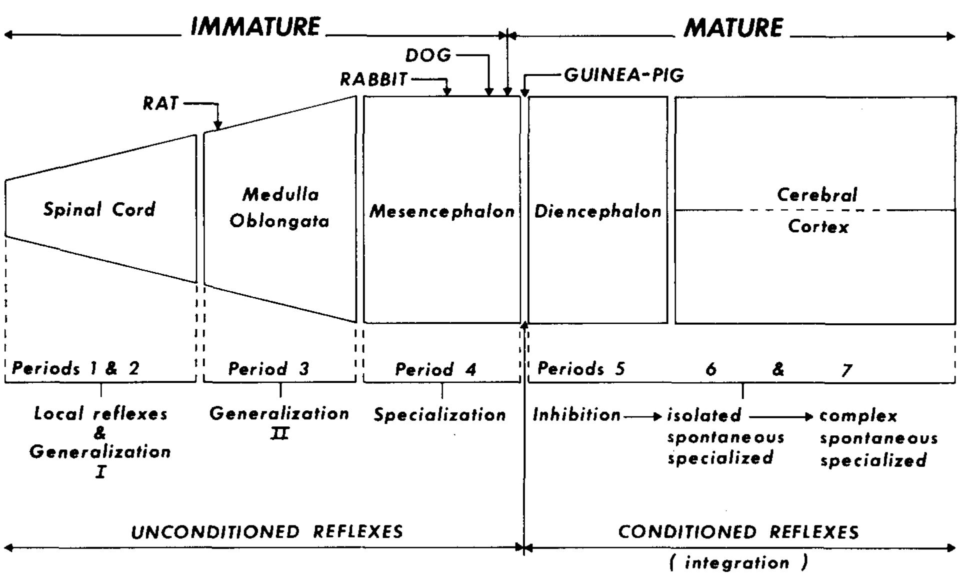


Fig. 1. Ontogenetic organization of behavior: note differences in various species according to degree of development at time of birth. After Sedlacek *et al.*[82].

lated with the postnatal emergence of conditioned responses and the ontogenesis of unconditioned reflex responses. Tuge[88] stated that negative conditioned reflexes in the ontogeny of internal inhibition show a pattern of development similar to unconditioned and conditioned reflex activities but occur at a much later age. These reactions are at first diffused and generalized and later acquire a localized and refined form. Sedlacek *et al.*[82] divided the development of these 7 phases into 2 stages: first, the development of unconditioned (spontaneous) reflex mechanisms progressing to the phase of specialization of reflex action, and second, the development of conditioned reflex mechanisms starting with inhibition of specialized reflexes. Thus unconditioned specialized reflexes occur in the 4th and 5th phase and complex natural conditioned specialized reflexes in the 6th and 7th phase (Fig. 1). It must be emphasized that the division of reflex development as described by Sedlacek *et al.*[82] is not absolute, for components of one phase are evident in succeeding phases[23].

A neuro-ontogenetic study of the postnatal development of reflex responses in relation to behavior in mouse, cat and dog has been described by Fox[21,23,25], following the basic observations of Scott and Marston[81] on the dog, Williams and Scott[98] on the mouse, and the less complete observations of Rosenblatt and Schneirla[73] on the cat. The changes in the nature of these reflex responses when chronologically charted showed that discrete periods of neurologic development are present in each of these 3 species with similar patterns of neuro-ontogeny being evident. The sequential changes in these responses precede and underlie developmental changes in behavior (Fig. 2). In these species primitive reflexes are inhibited as they are super-

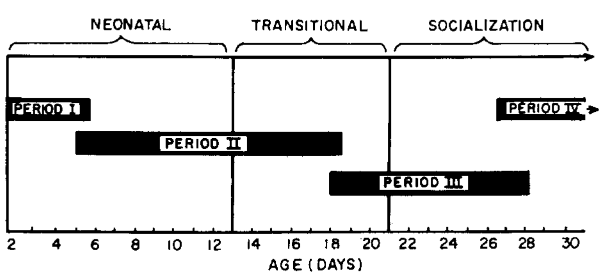
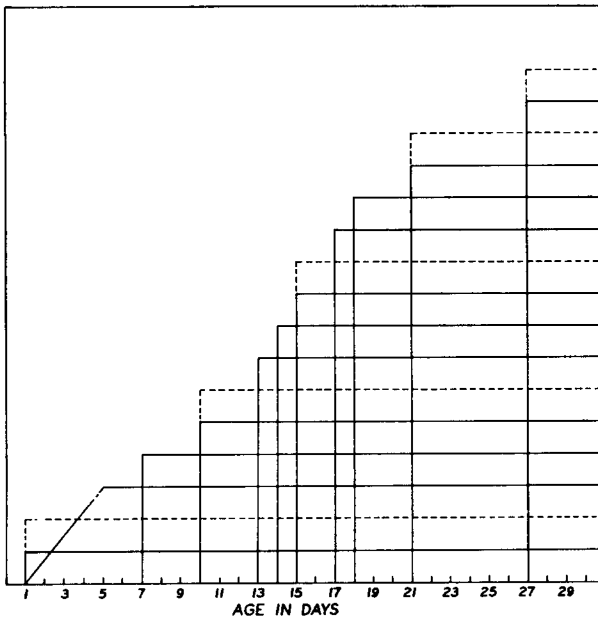


Fig. 2. Neurological and behavioral periods of development in the dog. Note that changes in reflex responses precede changes in overt behavior. (From Fox[23]).

seded by the more complex responses which appear as the brain develops and matures.

Several parameters of the postnatal development of dog, cat and mouse have been reviewed from multidiscipline studies and charted chronologically (Figs. 5, 6 and 7). In all 3 species of animals studied, the most dramatic alterations in CNS morphology in terms of cell density, axonal and dendritic development, etc. occur during the neonatal and transitional periods. After this time, morphological changes are less easily detected and the changes that do occur are the more gradual processes of maturation as contrasted to the initially explosive developmental changes. The development of myelin has been well correlated with behavior in the kitten[57,58] but not as



SENSE ANALYZER	RESPONSE	REFERENCE
AUDITORY	LEG WITHDRAWAL	50
VISUAL	DEFENSE	94
AUDITORY	HEAD ORIENTATION	50
VISUAL	WITHDRAWAL FOOD MOTOR	34, 94
AUDITORY	WITHDRAWAL	34
DERMAL (TEMP.)	DEFENSE	94
OLFACTORY AND TACTILE PROPRIOCEPTIVE	DEFENSE	94
AUDITORY	FOOD MOTOR	94
TASTE	WITHDRAWAL	34
OLFACTORY	WITHDRAWAL	34
TACTILE (AIR PUFF)	WITHDRAWAL	10
VESTIBULAR	FOOD MOTOR	94
DERMAL (TEMP.)	FOOD MOTOR	94
TASTE	SUCKING	84b
TACTILE PROPRIOCEPTIVE	FOOD MOTOR	94
OLFACTORY	FOOD MOTOR ORIENTATION	30, 94

Fig. 3. Age of first appearance of positive conditioned responses in the dog. (Time of stable conditioning not included). Note early emergence of food–motor responses at the rhinencephalic level and later development of withdrawal responses.

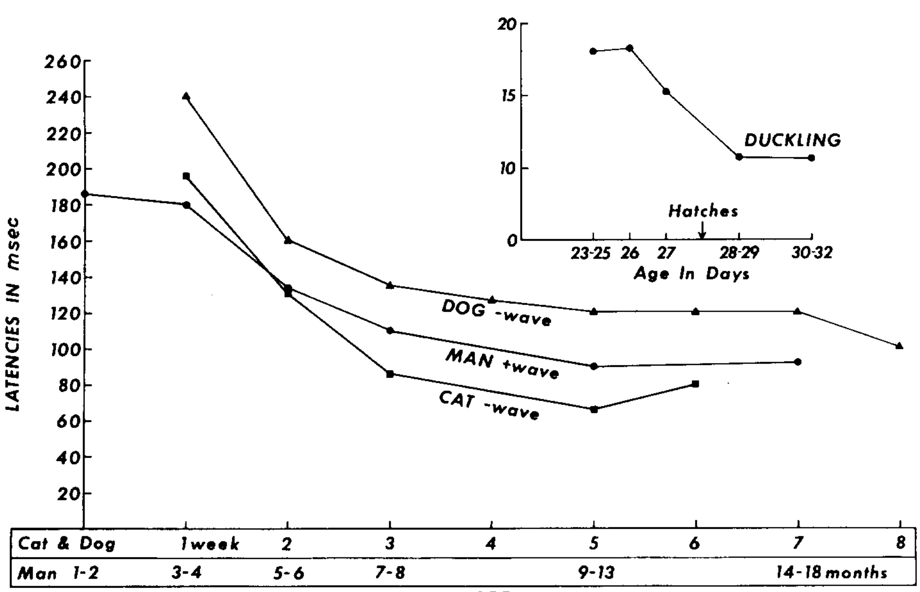


Fig. 4. Ontogeny of visual evoked responses. Note similarity in curves for cat[17], dog [27] and human[16]. Perceptual maturation in dog corresponds with critical period of socialization and 8½ month anxiety period in human infant. Duckling's responses[70] illustrate rapid maturation in precocial animals. (Cat under Nembutal: other subjects conscious).

yet in the dog or the mouse. Nutritional variables may severely interfere with normal development[67] and should be carefully controlled in developmental studies. On the behavioral side of the problem considerable information is available on the conditioned reflex responses in the dog. In this animal the responses at the higher levels of sensory organization are not stable until the end of the transitional period (Fig. 3). Biochemical changes in the developing brain have only recently attracted intensive analytical investigation. Certain biochemical events appear to precede the appearance of electrophysiological and behavioral events[15]. Electrophysiological studies[17,55,69,76] have been well documented in all three species and indicate that direct correlates with behavioral development can be made in relation to the development of spontaneous EEG activity and evoked electrical brain potentials of various sensory modalities (Fig. 4). From these findings, structuro-functional changes in the CNS may be directly correlated with periods of behavioral development. Changes in behavior must be considered on a physiological basis and are consequential to structural and biochemical changes (Figs. 5, 6 and 7).

Studies of the postnatal development of reflex responses in the human infant have shown that changes in the nature of these responses, such as the disappearance of primitive reflexes, *e.g.* Magnus reflex, and the emergence of visual orientation and fixation not only indicate the level of neurologic maturity attained but also may be

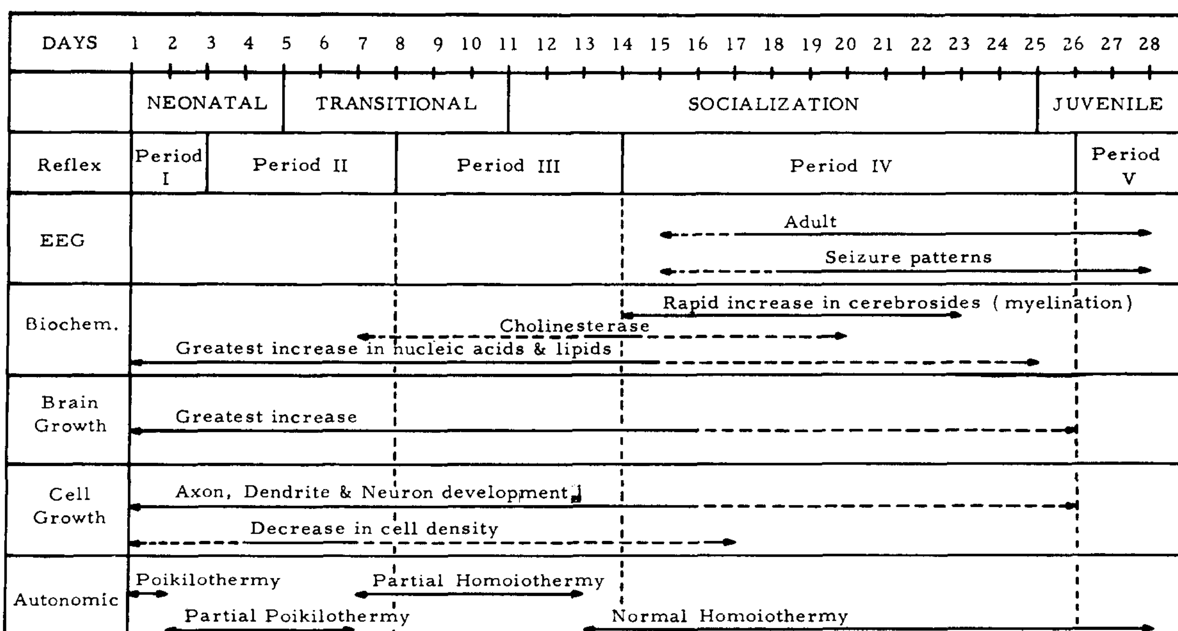


Fig. 5. Neuro-ontogeny of the mouse. Solid line indicates most rapid development, dotted lines more gradual. Arrow direction to left indicates first onset, arrow to the right indicates continuation of development beyond the age shown.

For references, see bibliography. Behavioral periods[98], reflex periods[21,22], EEG[55], biochemistry[35,89], brain growth and axodendritic development[54], cell density[39] and thermo-regulation[91].

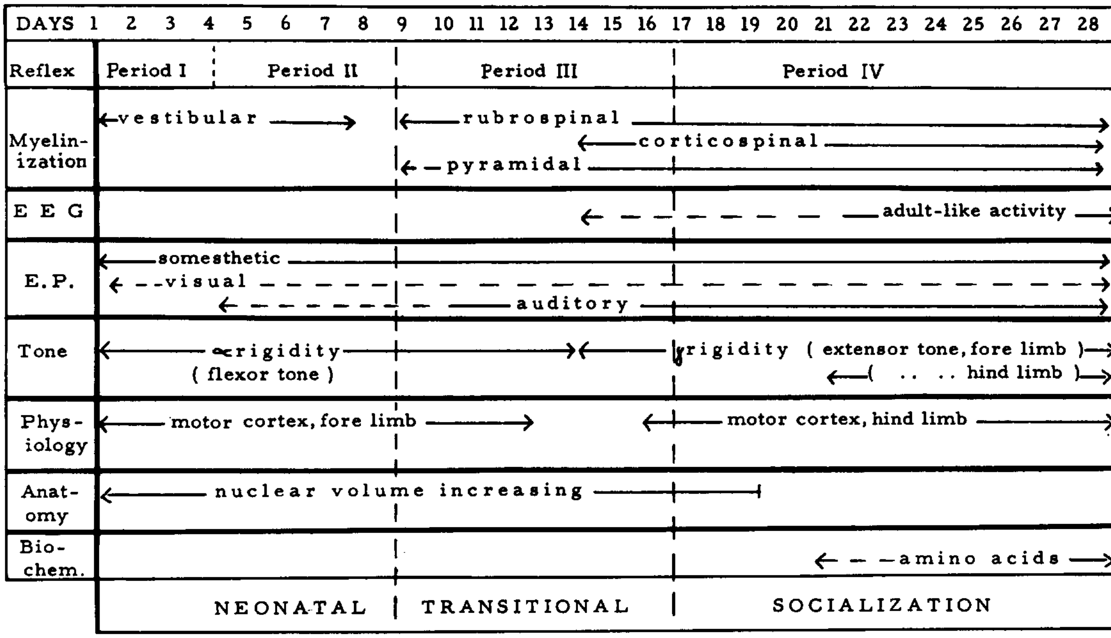


Fig. 6. Neuro-ontogeny of the cat. Solid line indicates most rapid development, dotted line more gradual. Arrow direction to left indicates first onset, arrow to the right indicates continuation of development beyond the age shown.

For references, see bibliography. Myelinization and physiology[57,58], EEG[38,64,71,75], E.P. (evoked potential)[17,90], changes in muscle tone[83], biochemistry[5], reflex periods[25,87], and anatomy[6].

correlated with behavior[11,95]. In a study of reflex development in non-precocial mammals (Ref. 19, *et seq.*) the sequence of events in dog, mouse and cat correlated closely with the development of human infant (Table I). Although many aspects of development are quite different, several parameters of neuro-ontogeny follow similar patterns in the postnatal development of these phylogenetically diverse mammals. Similar phenomena such as hyperkinetic tremors and extensor hypertonia in the human infant have been observed in the dog, cat and mouse as part of the normal spectrum of activities in the postnatal period.

These data support the critical period hypothesis in confirming that various aspects of neuro-ontogeny, in addition to the development of overt behavior patterns, are organized and integrated in a definite interdependent sequence of events. This sequence is common to the three species of non-precocial mammals discussed here as well as to man. Because of the close similarity of these sequences, cross species identification of the periods of behavioral development and the underlying neuro-ontogenetic changes can be made.

THE CRITICAL PERIOD HYPOTHESIS

The precocial mammals (*e.g.* sheep, guinea-pig), being neurologically mature at birth, are able to interact with their environment and with members of their own

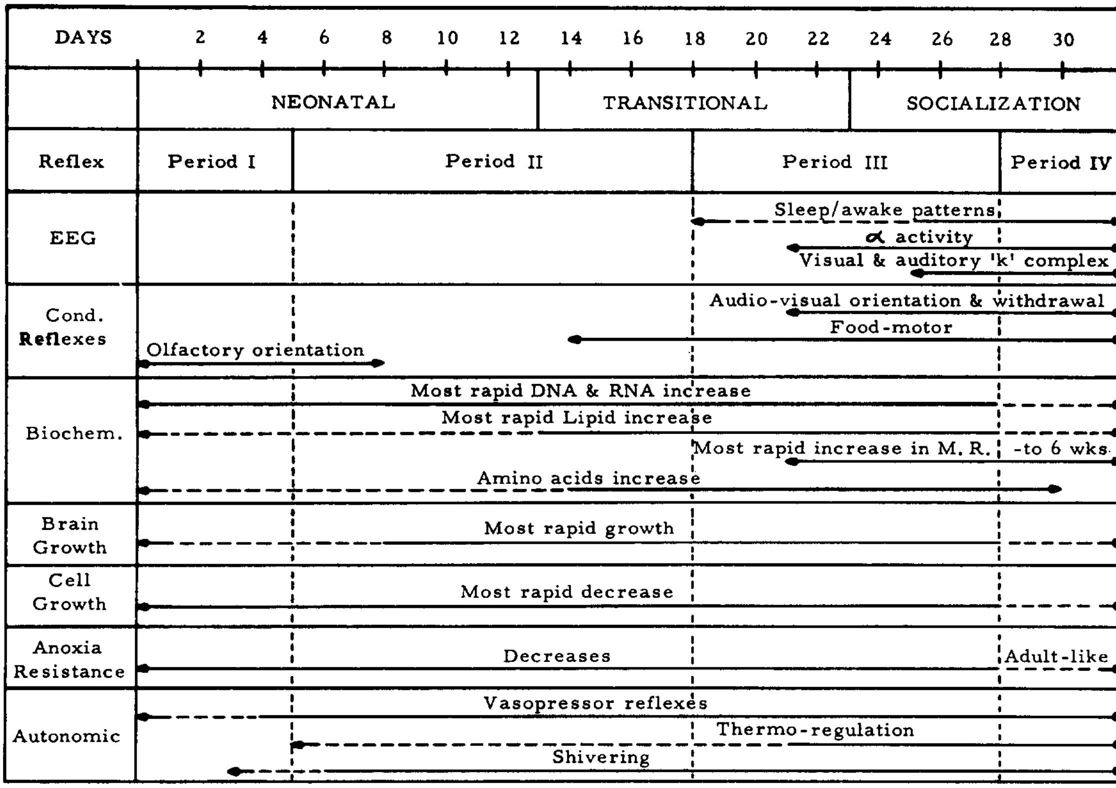


Fig. 7. Neuro-ontogeny of the dog. Solid line indicates most rapid development, dotted lines more gradual. Arrow direction to left indicates first onset, arrow to the right indicates continuation of development beyond the age shown.

For references, see bibliography. Behavioral periods[81], reflex periods[23], EEG[7,69,71], conditioned reflex[10,30,50,93], biochemistry[14,26,46,63], anoxia resistance[52], vasopressor reflexes[8,49] and thermoregulation[51], brain growth[24,29].

species immediately after birth and thus to establish primary social relationships[78]. This rapidly developing phenomenon is termed imprinting. In contrast, the non-precocial mammals develop more slowly postnatally and have a clearly defined neonatal period during which they are dependent on the mother for shelter and food. It is only after this period when sensory and locomotor development have reached a certain point that primary social relationships can be established (Fig. 8). This later emergence of a phenomenon having the same characteristics as imprinting but occurring over a longer period of time has been termed the 'critical period of socialization'[78]. Essentially these two phenomena are similar in that there is an initial period which allows emotional attachment to any object (normally to mother) after which strong avoidance behavior to novel stimuli develops. Such avoidance behavior acts as a natural survival mechanism for the young animal. The early dominance of approach behavior facilitates the establishment of primary social relationships (resembling the following response of imprinting[37]). In accordance with the approach/withdrawal theory of Schneirla[77] there is a gradual emergence of withdrawal or avoidance behavior

TABLE I

APPROXIMATE AGE WHEN RESPONSE CHANGES (DISAPPEARS OR ADULT-LIKE)

Reflex	*Man*[11] *(months)*	*Dog*[23] *(days)*	*Mouse*[21] *(days)*	*Cat*[25] *(days)*
Rooting	11–12	24	9	20
Hyperkinesias (coarse tremors)	2	21	10	—
Magnus (tonic neck and labyrinthine)	3– 6	21	6– 8	15
Mass movements (generalized responses, *e.g.* to pain)	3	21	9	—
Postural flexion (in vertical suspension)	3– 4	4	6	—
Postural extension (-do-)	4– 6	19	10	—
Righting (otolith)	2– 3	birth	birth	birth
Crossed extensor	3– 4	15	4	15
Mature relaxed phase	—	26	12–14	—
Primitive stepping	7	1	1	1
Forelimb placing (visual)	5– 6	27	12–14	21
Forelimb contactual placing	—	4	1	1
Subcortical and spinal responses weaken (cortical dominance)	3	16–21	8–10	11–14
Reciprocal kick reaction	4	15	5	—
Voluntary elimination	22–24	23	12–14	5– 6 wk
Emotional reactions	6–12	21	12	15–21
Eyes open	at birth	10–13	11–12	5– 9
Visual fixation	4	28	—	17
Auditory startle	at birth	25	12–14	15
Visual orientation (following response)	at birth	26	—	17
Auditory orientation	4	26	16	16

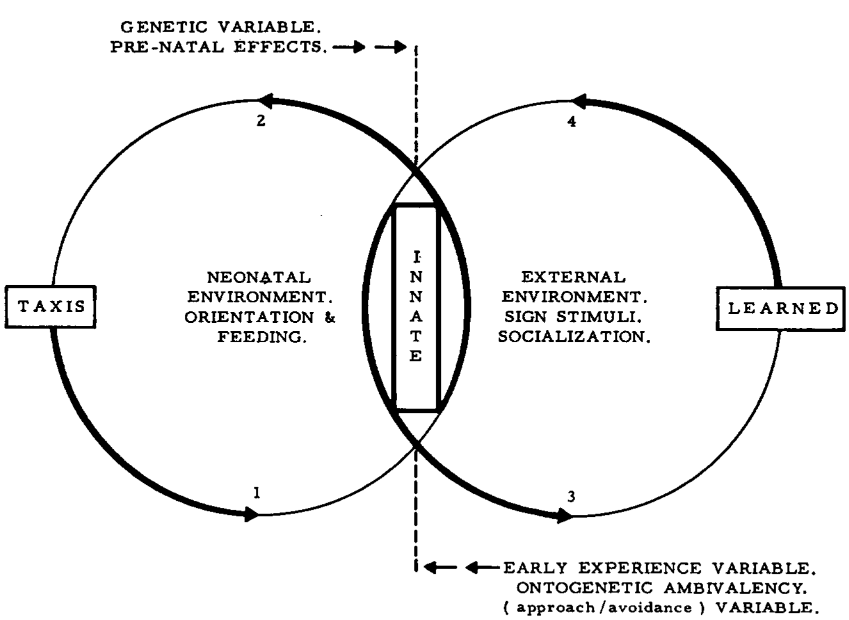


Fig. 8. Postnatal ontogenetic relationships of various levels of behavioral organization in a typical non-precocial mammal. Taxes predominate in early life followed by emergence of innate, species specific behavior patterns and learned responses.

and the development of fear/escape reactions. These findings have been observed in the dog[32,33] and compared with a similar phenomenon in the human infant[79], and may be represented by the 'jumpy' period or overgeneralized responsiveness in the mouse[21]. The adaptive and protective mechanisms of such an ambivalent behavior mechanism are obvious, ensuring early socialization with like species, and protection against potential predators at a later age, until learning and discrimination can be established.

It should be emphasized that the critical period is the time when neural organization is sufficiently developed to permit perceptual interaction and adaptation to the environment and the establishment of primary social relationships. The extension of this hypothesis leads to the idea that at specific periods during postnatal development the animal is particularly sensitive to changes that in turn affect behavior patterns in later life. Each period is dependent on the neural organization of behavior at that specific age. The most important period, however, is the critical period of socialization when neural organization at the higher levels of behavior are integrated to permit the establishment of emotional (or affectional) bonds, learned responses, and more complete behavioral interaction with the environmental milieu. In terms of animal behavior this period may be regarded as the time when the inherited characteristics of the organism (the genome[62]) facilitate adaptation to the environment with concurrent learning or acquisition of additional adaptive modifications of behavior (Fig. 9).

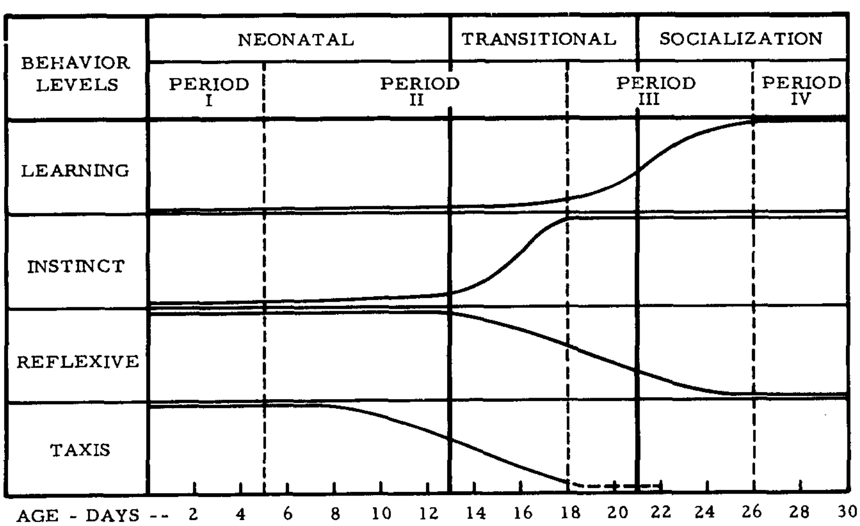


Fig. 9. Schema of major changes in adaptive behavior in ontogeny of the dog.

The implications of genetic and environmental variables in the normal and abnormal social development of the dog have been recently reviewed by Krushinskii[56], Fox[20], and Scott and Fuller[80].

Although some of these 'units' of the nervous system reach maturity prior to the onset of the critical period of socialization, they do not become functional until other dependent structures reach maturity and can be organized with these more precocial units. Anokhin[2] postulates that each phase of postnatal development is synchronized heterochronously, *i.e.*, differential rate of neural maturation paralleling specific behavioral maturation to promote maximal adaptation and survival of the organism at each phase of ontogeny. This heterochronous sequence of events means a selective maturation of receptor apparatuses in correspondence with ecological factors[2]. In essence, this theory is similar to the views of Sackett[74] where responsiveness to specific visual stimuli is attributed to differential rates of sensory maturation paralleling the maturation of certain behavior patterns. At this point we can trace the link with other theories based on information theory, filtering systems (perceptual abilities) and genetic coding of innate behavior reviewed by Thorpe[86] and Lorenz[62]. It has been rightly emphasized by Ames and Ilg[1] that behavior patterns of the immature organism do not give way to more mature patterns in a linear and gradually weakening fashion, but instead tend to alternate repeatedly and recurrently. Thus, the development of mature behavior patterns reflects the neural organization of earlier patterns, and their ontogenetic relationships and dependency resemble the principle of reciprocal neuromotor interweaving[1].

In a field as broad and diffuse as the development of behavior it is inevitable that some confusion as to the precise definition and meaning of the critical period hypothesis has arisen, especially since 'critical period' is a term taken from embryology and applied to behavior. For the purpose of this review it is defined as the time when early experience has the greatest effect on later behavior[78]. To recapitulate, the critical period hypothesis *per se* parallels phenomena contingent upon normal perceptual and motor development. In other words the onset of the critical period of socialization is marked by an almost mature CNS with perceptual and motor development sufficient to enable the young organism to interact fully with its environmental milieu. Phenomena resulting from experimental manipulation of the normal processes of ontogeny tend to show other sensitive or critical periods which are to be segregated as factors arising from unnatural variables influencing development. Such phenomena appear to be the basis for Denenberg's[12] statement that there are as many critical or sensitive periods as there are experimental variables at different ages. He concluded, on this basis, that the critical period hypothesis must be seriously reconsidered. In defense of the critical period hypothesis, it is well known that pre- and postnatal stimuli may greatly modify later behavior, and these stimuli whether experimentally induced or occurring in the natural environment do constitute variables. They, therefore, have no place in the critical period hypothesis which is concerned with the *normal* sequences of development under *normal* conditions. It is also well known that subnormal or supranormal stimulation may cause morphological[53], physiological[65], behavioral[31], endocrine and biochemical[4,31,59,60] changes and consequently may alter the onset of the critical period of socialization. Admittedly many parameters of development are divisible into several periods, *e.g.* the fact that neurologic changes precede behavioral ones[23] (Fig. 3) and the heterochrony of the CNS[2]. False ideas, however, can be drawn if conclusions are based only on indices of normality from the results of experimentally induced stressors. In adapting to such stressors which widely deviate from the normal environmental conditions, it is logical that the ontogeny of behavior may be altered and no definable 'critical period' can be demonstrated. Until we know more fully how near these experimental variables are to those affecting development in the natural environment, we should reserve the term 'critical period' for the natural sequence of ontogeny and 'sensitive periods' for the other category of experimentally induced modifications in behavior.

ENVIRONMENTAL DEPRIVATION STUDIES

Much valuable information pertinent to the critical period hypothesis is available from studies on the effects of environmental deprivation. Although some attempts have been made to separate innate ('instinctive') from learned behavior, the two types are interdependent. Responses may be modified or undergo spontaneous regression by interference of learning processes (such as stimulus substitution or deprivation). Mature behavior patterns are composed of interdependent units, where innate responses are adaptively modified (or discarded) by learning processes and in turn may facilitate, modify or restrict learning processes. This interdependency is demonstrated in isolation rearing where innate responses if not experientially reinforced by adaptive learning may undergo spontaneous remission. Essentially, the deprivation experiment underlines the information that is relayed by the genome, *i.e.* 'unlearned' behavior[62].

In deprived animals learning at a later age is rendered difficult or impossible[18,68], for it is especially during the critical period that the innate-learned associations mostly readily affect the adaptive organization of behavior. If the normal adaptive sequences of development are omitted, severe deficits in later life may therefore occur (refs. 33b, 42, 66). An innate pattern when not expressed may be impossible to elicit once the critical period for its development and consolidation has passed. Conversely if abnormal stimuli are given, abnormal behavior patterns may emerge as in Padilla's[68] studies, or maladaptive pathological reactions develop. The original species-characteristic behavior pattern is then extremely difficult to re-educate or re-establish due to conditioned inhibition or spontaneous remission of normal actions. Thompson and Schaefer[85] have discussed these problems and conclude that primacy, plasticity, differentiation and critical periods in development represent the most crucial characteristics of the young organism. The effects of early environmental influences are susceptible to analysis for the generality of change (number of functions affected), extent of change in a particular function and the reversibility or permanence of the change in relation to the initial behavioral change (Fig. 10).

A major problem in the deprivation experiment is the provision of an adequate stimulus situation. Lack of an adequate stimulus may lead to the incorrect conclusion that certain behavior patterns are defective, whereas the abnormality or absence of the pattern may be actually the result of information being withheld from the animal. It may be surmised that although the mechanisms involved in postnatal development appear rigid and stereotyped, they are actually adaptive and are geared to promote survival. Adaptation may not be possible, however, if the environment is drastically

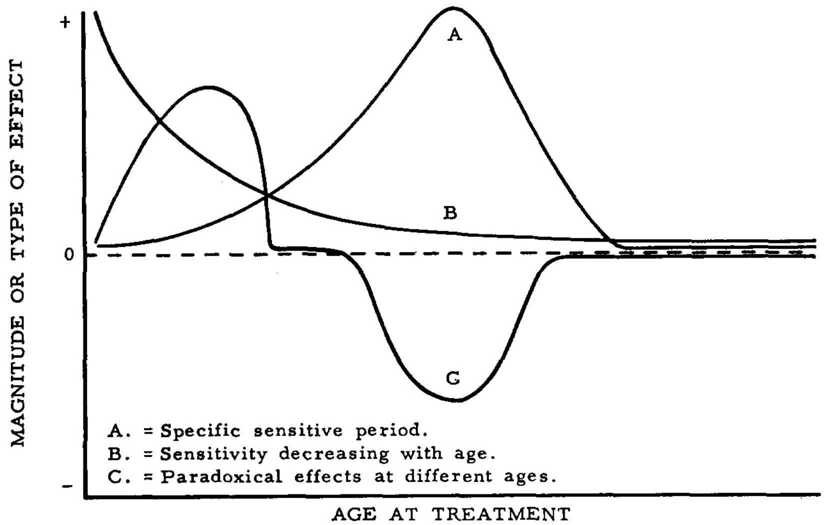


Fig. 10. Relationships between age and theoretical effects of early experiences (Modified from Thompson and Schaefer[85]).

altered or experience denied as occurs in social isolation or envii onmental deprivation. Such vaiiables affect early experience by disrupting the normal sequences of ontogeny and may arrest or disrupt both structural and functional components of behavior[96,97]. The onset of the critical period of socialization may similarly be affected and have long-term effects on the development of adult behavior patterns and acquisition of learned responses in non-precocial mammals. Riesen[72] in his classical studies on the effects of light deprivation on retinal and neuronal degeneration in the lateral geniculate observes that the rate of degeneration is negatively correlated with the age when first deprived and concludes that the more complex the later behavior the more dependent is that behavior on cumulative changes in earlier behavior. Riesen[72] recognized 4 categories of behavioral building blocks, namely, innate response, perceptual learning (or sensory preconditioning), sensory–motor and motor–sensory integrations and motor preconditioning or response–response learning as in pure motor skills. Innate responses include stimulus generalization, discrimination and innate emotional (fear) responses to novel stimuli. Held and Hein's[43] work support these concepts on sensory–motor and motor–sensory integrations, where several modalities (multiple afferent feedback) are required for visual learning. Thus early deprivation of one modality can affect many behavior patterns in later life as neurobehavioral organization is disrupted with consequent motivational, sensory and perceptual manifestations of abnormality. Hubel and Wiesel[48] have elegantly demonstrated in a series of neurophysiological studies in the kitten that if visual stimulation is denied, neuronal disorganization ensues—thus stimulation is essential for the maintenance, development and maturation of neural systems.

In future research we must clearly define what constitutes a 'normal' stimulus and elucidate the variables of innate responses and the afferent perceptual mechanisms of the filtering systems involved. (See also Lorenz[62], critique of deprivation experiments).

A POINT OF SYNTHESIS: THE PERIOD OF INTEGRATION

As has been shown in this paper, when structuro–functional relationships of neural elements begin to reach adult-like levels, a period of neuro-physiological integration occurs, which underlies the critical period of socialization. In precocial animals, neural integration occurs shortly before or at the time of birth and in the behavioral sense is associated with early perceptual maturity, responsiveness to specific sign stimuli and results in the phenomenon of imprinting. In non-precocial animals neural organization continues after birth (as exemplified by the 'neonatal' and 'transitional' periods of overt behavior) and is followed by the period of integration. This period of integration of neural components also embraces the concept of integration and adaptation of the organism to its environment since at this time, with almost adult-like perceptual abilities, more complete interaction with the environment is possible. Normal behavioral development is dependent upon environmental stimulation, notably exposure learning[84], and maturation reflects the stimuli which were present during development.

Stimulation is a primary need and the period of integration is a sensitive time in development when the organism is receptive to this stimulation. Early plasticity affords greater adaptability and without appropriate stimulation, rigid, stereotyped and maladaptive responses may emerge in later life, affecting many patterns of behavior. Innate characteristics of the organism and learning processes are brought into play at the onset of integration, which represents a crucial phase in adaptation and underlies the critical period of socialization and imprinting, on which almost all subsequent behavior is dependent.

SUMMARY

Behavioral development is discussed from several points of view in this review and the events incorporated into a broad concept of neuro-behavioral ontogeny. From the organization of innate reflex patterns of behavior in the embryo and neonate, and sequential ontogenetic phases in both structural and functional parameters of the CNS, there is evidence that similar phenomena of neuro-behavioral ontogeny are to be found in the three species considered here (mouse, cat and dog). Chronologically related, environmentally adaptive phases of reflex and behavioral development and structuro-functional changes in the CNS have been identified for these species. They show similar sequences in development of neural components which reach adult-like levels at the period of integration. Development is discussed in relation to stimulus dependent maturation and experimental manipulations which have demonstrated other critical periods which would be more appropriately termed experimentally 'sensitive' periods. In an attempt to synthesize many parameters of behavioral development on the basis of several theories from various disciplines, the multidisciplinary concept of neuro-behavioral ontogeny is presented. This concept regards the common sequences of neuro-ontogenetic changes in various non-precocial mammals as adaptive periods of behavioral development, the most dramatic and clearly defined period being the period of integration, which underlies the critical period of socialization.

ACKNOWLEDGEMENTS

The author wishes to express his gratitude to Dr. Williamina A. Himwich of this laboratory, Dr. John Paul Scott, Professor of Psychology, Bowling Green University, Ohio, and Professor Jaromir Myslivеček Department of Physiology, Charles University, Prague (Czechoslovakia) for their helpful advice and criticism in the preparation of this manuscript.

REFERENCES

1 AMES, L. B., AND ILG, F. L., The developmental point of view with special reference to the principle of reciprocal neuromotor interweaving, *J. genet. Psychol.*, 105 (1964) 195–209.
2 ANOKHIN, P. K., Systemogenesis as a general regulator of brain development. In W. A. HIMWICH AND H. E. HIMWICH (Eds.), *The Developing Brain, Progress in Brain Research, Vol. 9,* Elsevier, Amsterdam, 1964, pp. 54–86.
3 BARCROFT, J., AND BARRON, D. H., Movement of the mammalian foetus, *Ergebn. Physiol.*, 42 (1939) 107–152.
4 BENNETT, E. L., DIAMOND, M. C., ROSENZWEIG, M. R., AND KRECH, D., Chemical and anatomical plasticity of the brain, *Science*, 146 (1964) 610–619.
5 BERL, S., AND PURPURA, D. P., Postnatal changes in amino acid content of kitten cerebral cortex, *J. Neurochem.*, 10 (1963) 237–240.
6 BRIZZEE, K. R., AND JACOBS, L. A., Postnatal changes in volumetric and density relationships of neurons in cerebral cortex of cat, *Acta anat.*, 38 (1959) 292–303.
7 CHARLES, M. S., AND FULLER, J. L., Developmental study of the electroencephalogram of the dog, *Electroenceph. clin. Neurophysiol.*, 8 (1956) 645–652.
8 CLARK, G. A., The development of blood pressure reflexes, *J. Physiol.*, 73 (1934) 391–400.
9 COGHILL, G. E., *Anatomy and the Problem of Behavior*, Cambridge University Press, New York, 1929.
10 CORNWELL, A. C., AND FULLER, J. L., Conditioned responses in young puppies, *J. comp. physiol. Psychol.*, 54 (1961) 13–15.
11 DEKEBAN, A., *Neurology of Infancy*, William and Wilkins Company, Baltimore, 1959.
12 DENENBERG, V. H., Critical periods, stimulation input and emotional reactivity: A theory of infantile stimulation, *Psychol. Rev.*, 71 (1964) 335–351.
13 DENENBERG, V. H., The effects of early experience. In E.S.E. HAFEZ (Ed.), *The Behaviour of Domestic Animals*, Bailliere, Tindall and Cox, London, 1962, p. 109.
14 DRAVID, A. R., AND HIMWICH, W. A., Biochemical studies of the central nervous system of the dog during maturation. In W. A. HIMWICH AND H. E. HIMWICH (Eds.), *The Developing Brain, Progress in Brain Research, Vol. 9*, Elsevier, Amsterdam, 1964, pp. 170–173.
15 DRAVID, A. R., HIMWICH, W. A., AND DAVIS, J. M., Some free amino acids in dog brain during development, *J. Neurochem.*, 12 (1965) 901–906.
16 ELLINGSON, R. J., Studies of the electrical activity of the developing human brain. In W. A. HIMWICH AND H. E. HIMWICH (Eds.), *The Developing Brain, Progress in Brain Research, Vol. 9,* Elsevier, Amsterdam, 1964, pp. 26–53.
17 ELLINGSON, R. J., AND WILCOTT, R. C., Development of evoked responses in visual and auditory cortices of kittens, *J. Neurophysiol.*, 23 (1960) 363–375.
18 FOLEY, J. P., First year development of a Rhesus monkey *(Macaca mulatta)* reared in isolation, *J. genet. Psychol.*, 45 (1934) 39–105.
19 FOX, M. W., A phylogenetic analysis of behavioral neuro-ontogeny in precocial and nonprecocial mammals, *Canad. J. comp. Med. Vet. Sci.*, 28 (1964) 196–202.
20 FOX, M. W., *Canine Behavior*, Thomas Publishing Company, Springfield, 1965.
21 FOX, M. W., The development of reflexes and neuro-ontogeny of the mouse, *Anim. Behav.*, 13 (1965) 234–241.
22 FOX, M. W., The neuro-ontogeny of some neuromuscular mutant mice. *J. Hered.*, 56 (1965) 55–60.
23 FOX, M. W., The ontogeny of behaviour and neurologic responses in the dog, *Anim. Behav.*, 12 (1964) 301–310.

24 Fox, M. W., The postnatal growth of the canine brain and correlated anatomical and behavioral changes during neuro-ontogenesis, *Growth*, 28 (1964) 135–141.
25 Fox, M. W., The postnatal neuro-ontogeny and reflex development of the cat, Submitted to *Brain Research* (1966).
26 Fox, M. W., Total lipid content of pons medulla, cerebellum, midbrain and cerebrum of dog during development. Unpublished data. Galesburg State Research Hospital, Galesburg, Ill. (1966).
27 Fox, M. W., Development of visual evoked responses in the dog, Unpublished data. (1966).
28 Fox, M. W., Age differences in the effects of decerebration and spinal cord transection in the dog: Theoretical and clinical implications, *J. small Anim. Pract.*, 7 (1966) 91–98.
29 Fox, M. W., Inman, O., and Himwich, W. A., Postnatal development of neocortical neurones in the dog, *J. comp. Neurol.*, (1966) In Press.
30 Fox, M. W., and Stelzner, D., Olfactory responses in the neonate dog and conditioned reflex ontogeny. (1966) In preparation.
31 Fox, M. W., and Stelzner, D., The behavioral effects of differential rearing in the dog, *Anim. Behav.*, (1966) In Press.
32 Fox, M. W., and Stelzner, D., Approach/withdrawal variables in the development of social behavior in the dog, *Anim. Behav.*, (1966) In Press.
33 Freedman, D. G., Elliot, E., and King, J. A., Critical period in the social development of dogs, *Science*, 113 (1961) 1016–1017.
33b Fuller, J. L., The effects of experimental deprivation upon behavior in animals, *Proc. 3rd World Congr. Psychiat.*, University of Toronto Press, 1964, pp. 223–227.
34 Fuller, J. L., Easler, C. A., and Banks, E. M., Formation of conditioned avoidance responses in young puppies, *Amer. J. Physiol.*, 160 (1950) 462–466.
35 Gerebtzoff, M. A., Development of cholinesterase activity in the nervous system. In H. Waelsch (Ed.), *Biochemistry of Developing Nervous System*, Proc. 1st International Neurochem. Symposium, Academic Press, New York, 1955, p. 315.
36 Gottlieb, G., and Kuo, Z. Y., Development of behavior in the duck embryo, *J. comp. physiol. Psychol.*, 59 (1965) 183–188.
37 Gray, P. H., Theory and evidence of imprinting in human infants, *J. Psychol.*, 46 (1958) 155–166.
38 Grossman, C., Electro-ontogenesis of cerebral activity, *Arch. Neurol. Psychiat.*, 74 (1955) 186.
39 Haddara, M., A quantitative study of the postnatal changes in the packing density of the neurons in the visual cortex of the mouse, *J. Anat.*, 90 (1956) 494.
40 Hague, E. B., Photo-neuroendocrine effects in circadian systems with particular reference to the eye, *Ann. N.Y. Acad. Sci.*, 117 (1964) 1–645.
41 Hamburger, V., Some aspects of the embryology of behavior, *Quart. Rev. Biol.*, 38 (1963) 342–365.
42 Harlow, H. F., and Harlow, M., Social deprivation in monkeys, *Sci. Amer.*, 207 (1962) 137–146.
43 Held, R., and Hein, A., Movement produced stimulation in the development of visually guided behavior, *J. comp. physiol. Psychol.*, 56 (1963) 872–876.
44 Hess, E. H., Imprinting, *Science*, 130 (1959) 133–141.
45 Hess, E. H., Imprinting in birds, *Science*, 146 (1964) 1128–1139.
46 Himwich, H. E., and Fazekas, J. F., Comparative studies of the metabolism of the brain of the infant and adult dogs, *Amer. J. Physiol.*, 132 (1941) 454.
47 Hooker, D., *The Prenatal Origin of Behavior*, University of Kansas Press, Lawrence, Kansas, 1952.
48 Hubel, D. H., and Wiesel, T. N., Receptive fields of cells in striate cortex of very young, visually inexperienced kittens, *J. Neurophysiol.*, 26 (1963) 994–1002.
49 Hutchinson, E. A., Percival, C. J., and Young, M., Development of cardiovascular responses in the kitten, *Quart. J. exp. Physiol.*, 47 (1962) 201–210.
50 James, W. T., and Cannon, D., Conditioned avoiding responses in puppies, *Amer. J. Physiol.*, 168 (1952) 251–253.
51 Jensen, C., and Ederstorm, H. E., Development of temperature regulation in the dog, *Amer. J. Physiol.*, 183 (1955) 340.
52 Jilek, L., Personal communication, Department of Physiology, Charles University, Prague, Czechoslovakia, 1965.
53 Klosovskii, B. N., *The Development of the Brain and its Disturbance by Harmful Factors*, MacMillan Company, Pergamon Press, New York, 1963.
54 Kobayashi, T., Brain to body ratios and time of maturation of the mouse brain, *Amer. J. Physiol.*, 204 (1963) 343–346.

55 KOBAYASHI, T., INMAN, O., BUNO, W., AND HIMWICH, H. E., A multidisciplinary study of changes in mouse brain with age. In J. WORTIS (Ed.), *Recent Advances in Biological Psychiatry*, Vol. 5, Plenum Press, New York, 1963, p. 293.
56 KRUSHINSKII, I. V., *Animal Behavior*, Consultant Bureau, New York, 1962.
57 LANGWORTHY, O. R., Histological development of cerebral motor areas in young kittens correlated with their physiological reaction to electrical stimulation, *Contr. Embryol. Carneg. Inst.*, 19 (1927) 177–207.
58 LANGWORTHY, O. R., A correlated study of the development of reflex action in fetal and young kittens and the myelinization of tracts in the nervous system, *Contr. Embryol. Carneg. Inst.*, 20 (1929) 127–171.
59 LEVINE, S., Plasma-free corticosteroid response to electric shock in rats stimulated in infancy, *Science*, 135 (1962) 795.
60 LEVINE, S., The psychophysiological effects of early stimulation. In E. BLISS (Ed.), *Roots of Behavior*, Harper, New York, 1962, p. 246.
61 LORENZ, K., Der Kumpan in der Umwelt des Vogels, *J. Ornithol.*, 83 (1935) 137–213; 289–413.
62 LORENZ, K., *Evolution and Modification of Behavior*. University of Chicago Press, 1965.
63 MANDEL, P., REIN, H., HARTH-EDEL, S., AND MANDEL, R., Distribution and metabolism of ribonucleic acid in the vertebrate CNS. In D. RICHTER (Ed.), *Comparative Neurochemistry*, Pergamon Press, New York, 1962, p. 149.
64 MARLEY, E., AND KEY, B. J., Maturation of the electrocorticogram and behavior in the kitten and guinea-pig and the effects of some sympathomimetic amines, *Electroenceph. clin. Neurophysiol.*, 15 (1963) 620–636.
65 MEIER, G. W., Infantile handling and development in Siamese kittens, *J. comp. physiol. Psychol.*, 54 (1961) 284–286.
66 MELZACK, R., AND SCOTT, T. H., The effect of early experience on the response to pain, *J. comp. physiol. Psychol.*, 50 (1957) 155–161.
67 MEYER, A., PAMPIGLIONE, G., PLATT, B. S., AND STEWART, R. J. C., Neurological, EEG and neuropathological changes in dogs with experimental malnutrition. VII. International Congress of Neurology, Rome, *Excerpta med., Int. Congr. Series, No. 39*, 1961 p. 15.
68 PADILLA, S. G., Further studies on the delayed pecking of chicks, *J. comp. Psychol.*, 20 (1935) 413–443.
69 PAMPIGLIONE, G., *Development of Cerebral Function in the Dog*, London, Buttersworth, 1963.
70 PAULSON, G. W., Maturation of evoked responses in the duckling, *Exp. Neurol.*, 11 (1965) 324–333.
71 PETERSEN, J., DIPERRI, R., AND HIMWICH, W. A., The comparative development of the EEG in the rabbit, cat and dog, *Electroenceph. clin. Neurophysiol.*, 17 (1964) 557–663.
72 RIESEN, A. H., Stimulation as a requirement for growth and function in behavioral development. In D. W. FISKE AND S. R. MADDI (Eds.), *Functions of Varied Experience*, Dorsey Press, Inc., Homewood, Ill., 1961.
73 ROSENBLATT, J. S., AND SCHNEIRLA, T. C., The behavior of cats. In E. S. E. HAFEZ (Ed.), *The Behavior of Domesticated Animals*, Bailliere Tindall & Cox, London, 1962.
74 SACKETT, G. P., A neural mechanism underlying unlearned, critical period and developmental aspects of visually controlled behavior, *Psychol. Rev.*, 70 (1963) 40–50.
75 SCHEIBEL, A. B., Studies of dendrite development in cat and EEG. In J. WORTIS (Ed.), *Recent Advances in Biological Psychiatry*, Vol. 4, Grune & Stratton, New York, 1962, p. 313.
76 SCHERRER, J., AND OECONOMOS, D., Cortical somesthetic responses of newborn mammals compared with adult, *Etud. néo-natal.*, 3 (1954) 199.
77 SCHNEIRLA, T. C., Aspects of stimulation and organization in approach/withdrawal processes underlying vertebrate behavioral development. In D. S. LEHRMAN, R. A. HINDE AND E. SHAW (Eds.), *Advances in the Study of Animal Behavior*, Vol. 1, Academic Press, New York, 1965, Ch. I.
78 SCOTT, J. P., Critical periods in behavioral development, *Science*, 138 (1962) 949–958.
79 SCOTT, J. P., The process of primary socialization in canine and human infants, *Monographs of the Society for Research in Child Development*, 28 (1963) 1–47.
80 SCOTT, J. P., AND FULLER, J. L., *Genetics and Social Behavior of the Dog*, Chicago University Press, Chicago, 1965.
81 SCOTT, J. P., AND MARSTON, M. V., Critical periods affecting normal and maladjustive social behavior in puppies, *J. genet. Psychol.*, 77 (1950) 25–60.
82 SEDLACEK, J., SVEHLOVA, M., SEDLACKOVA, M., MARSALA, J., AND KAPRAS, J., New results in the ontogenesis of reflex activity. In P. SOBOTKA (Ed.), *Functional and Metabolic Development of the Central Nervous System*, Pilsen Symposium, Plzen. lek. Sbor., Suppl. III, 1961, p. 167.

83 SKOGLUND, S., On the postnatal development of postural mechanisms as revealed by electromyography and myography in decerebrate kittens, *Acta physiol. scand.*, 49 (1960) 299–317.
84 SLUCKIN, W., *Imprinting and Early Learning*. Aldine Publishing Company, Chicago, 1965.
84b STANLEY, W. C., CORNWELL, A. C., POGGIANI, C., AND TRATTNER, A., Conditioning in the neonatal puppy, *J. comp. physiol. Psychol.*, 56 (1963) 211–214.
85 THOMPSON, W. R., AND SCHAEFER, J., Early environmental stimulation. In D. W. FISKE AND S. R. MADDI (Eds.), *Functions of Varied Experience*. Dorsey Press, Homewood, Ill., 1961, pp. 81–105.
86 THORPE, W. H., *Learning and Instinct in Animals*, Harvard University Press, 1956.
87 TILNEY, F., AND KUBIE, L. S., Behavior in its relation to development of the brain, *Bull. neurol. Inst. N.Y.*, 1 (1931) 231.
88 TUGE, H., Comparative study of ontogenetic development of unconditioned and conditioned reflexes. In P. SOBOTKA (Ed.), *Functional and Metabolic Development of the Central Nervous System*, Pilsen Symposium, Plzn. lek. Sbor., Suppl. III, 1961, pp. 147–154.
89 UZMAN, L. L., AND RUMLEY, K. M., Changes in the composition of the developing mouse brain during early myelinization, *J. Neurochem.*, 3 (1958) 171–185.
90 VALATX, J. L., JOUVET, D., ET JOUVET, M., Evolution électroencéphalographique des différents états de sommeil chez le chaton, *Electroenceph. clin. Neurophysiol.*, 17 (1964) 218–233.
91 VERLAG, B., The postnatal development of homoiothermy and cold resistance in mice, *Experientia*, 18 (1962) 282.
92 VERPLANK, W. S., A glossary of some terms used in the objective science of behavior, *Psychol. Rev.*, Suppl. 64, No. 6, Part 2, 1957.
93 VOLOKHOV, A. A., Comparative-physiological investigation of conditioned and unconditional reflexes during ontogeny, *Pavlov. J. higher nerv. Activ.*, 9 (1959) 49–60.
94 VOLOKHOV, A. A., On the significance of various levels of the central nervous system in the formation and development of motor reaction in embryogenesis. In P. SOBOTKA (Ed.), *Functional and Metabolic Development of the Central Nervous System*, Pilsen Symposium, Suppl. III, 1961, p. 141.
95 WHITE, B. H., AND CASTLE, P. W., Visual exploratory behavior following postnatal handling of human infants, *Perceptual and Motor Skills*, 18 (1964) 497–502.
96 WIESEL, T. N., AND HUBEL, D. H., Effects of visual deprivation on morphology and physiology of cells in the cat's lateral geniculate body, *J. Neurophysiol.*, 26 (1963) 978–993.
97 WIESEL, T. N., AND HUBEL, D. H., Single-cell responses in striate cortex of kittens deprived of vision in one eye, *J. Neurophysiol.*, 26 (1963) 1002–1017.
98 WILLIAMS, E., AND SCOTT, J. P., The development of social behavior patterns in the mouse in relation to natural periods, *Behaviour*, 6 (1953) 35–64.
99 WINDLE, W. F., Reflexes of mammalian embryos and fetuses. In P. WEISS (Ed.), *A Genetic Neurology*, University of Chicago Press, Chicago, 1950, p. 214.