Hormones and Behavior 55 (2009) 484–487

Contents lists available at ScienceDirect

Hormones and Behavior

journal homepage: www.elsevier.com/locate/yhbeh

Father of mothering: Jay S. Rosenblatt

Daniel Lehrman Lifetime Achievement Award 2006

Jay S. Rosenblatt was the recipient of the first Daniel S. Lehrman Lifetime Achievement Award. We cannot imagine a person more deserving to be the first recipient of the award.

Jay is a person who, in the modern period starting around 1960, virtually created a field of inquiry: the study of the psychobiology of mammalian maternal behavior. Jay provided the framework and the foundation for much of the work on maternal behavior that has taken place in the past 45 years. Although this work and its framework were very much Jay's own, there were many people who influenced Jay's thinking throughout his career, including T. C. Schneirla and Daniel Lehrman. However, Danny Lehrman's influence on Jay's career was perhaps the greatest and most meaningful. Theirs was a friendship that lasted until Danny's untimely death in 1972. Jay and Danny Lehrman were graduate students together at New York University and also were colleagues at the City University of New York as assistant professors, as well as associates of the Department of Animal Behavior at the American Museum of Natural History (AMNH), where both of them did their doctoral research.

Jay began his work on rat maternal behavior after arriving at Rutgers-Newark in 1958 and after joining Danny in his newly established Institute of Animal Behavior (IAB). This work was what he spent most of his intellectual energy on for the next 45 years and for which he was honored in 2004 by becoming an elected Fellow of the American Association for the Advancement of Science.

Jay became Director of the IAB in 1972 following Danny Lehrman's death and remained Director for more than 17 years. Perhaps one of the most characteristic settings for Jay occurred at lunch time in the IAB conference/lunch room. Jay, sporting suspenders and with a pocket knife in hand, would sit down at the conference table with an apple and piece of cheese and proceed to dice the apple and slice the cheese (his lunch) as he engaged students, postdocs and faculty in research discussions. His mild and unassuming demeanor served as the backdrop for numerous theoretical discussions relevant to ongoing behavioral and biological research issues. Jay was always approachable and never too busy to talk science, or art for that matter. His perspective was an open one, and he was willing to entertain other viewpoints, ones that needed substantive data to modify a preexisting conceptual framework.

For a little historical perspective, note that at the time Jay was doing his seminal work on maternal behavior in the late 1960s and

doi:10.1016/j.yhbeh.2009.01.001

1970s, the other two major senior investigators in this area were Mike Zarrow at the University of Connecticut and Howard Moltz at the University of Chicago. The nominees for Jay's Lehrman Award and authors of this article were graduate students under the mentorship of Rosenblatt, Moltz, and Zarrow, respectively. Importantly, Bob Bridges and Michael Numan subsequently did postdoctoral research with Jay during the 1970s. The mixing of research ideas, strategies, and methodologies that eventually occurred laid the groundwork for the many important findings of our field.

It is not possible to discuss each and every one of the more than 150 papers and chapters that Jay has written in his more than 60 years as a scientist, many of which were seminal to the field of the psychobiology of parental care. We will, however, describe some of the primary themes that have grown out of his work and the primary influences he has had on the field and on his students. These themes involved behavioral synchronies, developmental transitions, and hormone–environment interactions, representing Jay's view that behavioral processes and their physiological underpinnings are complex and multilayered. It is not surprising that similar themes also characterized Danny's work on courtship and parental behavior in the ring dove.

In Jay's work there are two, and perhaps three, principal ideas that have come to be identified with his overarching perspective, which is developmental in nature; these principal ideas have had an impact on the field in general and on the direction of our own work.

One of Jay's major areas of research and renown focused upon infant development and maternal behavior and with the mechanisms regulating maternal behavior.

The first major contribution to this field was his recognition that given the right ecologic and naturalistic context one can demonstrate learning by the neonate at ages that are considerably younger than believed possible at the time this work was first done in the 1960s (Rosenblatt et al., 1969). The sensory modalities recruited for this early learning were initially single modalities, thermal and tactile, but through associative processes, kittens came to depend heavily on the olfactory sense and eventually the learning became truly multimodal. Jay's early kitten work illustrating these processes provided the groundwork for an entire field of study that focuses on learning within naturalistic contexts and by neonatal animals (Rosenblatt et al., 1969; Rosenblatt, 1971). This idea, tested well before its time, is reflected in more recent work called 'the constraints on learning'.

Although Jay is most famous for his work on rat maternal behavior, which he began when he joined Lehrman's IAB at Rutgers in 1958, his prior work on kittens, initiated at the AMNH, epitomizes his approach to the organization of behavior and the influence of Schneirla's approach—withdrawal theory (Schneirla and Rosenblatt, 1961; Schneirla, 1952). To understand development one must understand the transition between dependence on basic sensory-motor reflexes, which occurs first, to the development of affectively-based perceptual–motivational relations. Hence through learning, simple responses to primary stimuli (thermal and tactile) develop into approach or withdrawal responses from affectively laden multimodal stimuli (often including olfactory information, Rosenblatt, 1971).

When asked what his most exciting personal moment in his career was, Jay described these kitten discoveries, which were, in fact, quite serendipitous. While weighing kittens on a daily basis he had noted, and later set Gerry Turkewitz to study, that whenever kittens were replaced back into their home environments (after removal of the mother), the kittens would return to the home corner and do so more rapidly each day. Since the kittens seemed to know where to go, despite having no vision, this could only be based on early learning of the olfactory characteristics of the area where mother normally nurses her young (Rosenblatt et al., 1969; Rosenblatt, 1983).

He says of this work and the kitten work that followed, "It seemed to me all the problems of early development could be studied in the development of home orientation of kittens — development of sensory capacities and developmental transition in the use of sensory systems, development of motor capabilities, and the effect on sensory system use (when kittens rise off the floor [crawling to walking] they can't use olfactory stimuli as well or as continuously and need to shift to vision with olfactory support, etc.), transition from use of socially conditioned stimuli (nest odors) to social stimuli (mother), development of learning and cognitive structures (internalization of pathtaking) and of course, their emotional development indicated by their distressed vocalization and its termination" (Fleming, interview with Rosenblatt). This work was followed up in 1978 by Jay's student, Natalie Freeman (Freeman and Rosenblatt, 1978) and is summarized in Rosenblatt (1983).

The second set of ideas or themes that have come to be identified with the Rosenblatt framework is reflected in the concepts of behavioral transitions in the maternal behavior cycle and behavioral synchrony between mother and young. Since these concepts have had such an impact on our own work and are by now part of the vocabulary of the study of maternal behavior ('onset vs. maintenance'), they will now be discussed in some detail (Rosenblatt, 1970).

Although the study of maternal behavior is not primarily about early development, Jay treated the phases in the maternity cycle much as he would any developmental problem, as a series of developmental transitions. He became very interested in the phenomenology and then the mechanisms that mediated the development of maternal responsiveness from mating through pregnancy, to pregnancy termination, through the postpartum period and into and through weaning. Each of these phases was characterized, and for each he established the role of sensory factors, the associated physiological changes, the feedback effects of behavior, the role of endocrine factors, and then the role of shifts in hedonic and affective mechanisms. For each phase the mother undergoes there occurs a synchronized set of behavioral and physiological changes in the offspring. While in his rodent work, the emphasis was on the mother, the developmental status and needs of the offspring changed accordingly, so that mother and offspring were mutually adapted in their behavior to one another (Rosenbaltt, 1980; Lott and Rosenblatt, 1969).

The next transition in the maternity cycle that Jay and his students have studied most intensively occurs at the end of pregnancy and was first described in a chapter by Rosenblatt and Lehrman (1963). While Jay did not know which hormones 'turned on maternal behavior' initially his 1972 studies with Joseph Terkel on the role of blood borne factors in the functional parabiotic manipulation showed that the relevant factors were present during the last 48 h of gestation (Terkel and Rosenblatt, 1968, 1972). These studies with Terkel were followed up with studies by Harold Siegel and other students and postdocs working at the IAB. This work described the pregnancy effect, in which mothers undergo elevations in maternal responsiveness across pregnancy, peaking close to parturition. Furthermore, through the use of the hysterectomy–ovariectomy (pregnancy termination) endocrine manipulation, which was sometimes combined with steroid hormone administration, Jay and his students established the importance of mid-pregnancy endocrinology and the subsequent decline in pregnancy progesterone levels and rise in estradiol for the onset of maternal behavior (Bridges et al., 1978; Siegel and Rosenblatt, 1975a,b). These studies led to the recognition by researchers that estrogen priming is essential for the activational effects of oxytocin and prolactin in the initiation of maternal responsiveness.

Although Jay's research had a tremendous impact on our understanding of the hormonal basis of the onset of maternal behavior in rats, he is perhaps most famous for his 1967 study which defined a nonhormonal basis for maternal behavior in rats (Rosenblatt, 1967). That is, the neural basis for maternal care is present independent of pregnancy and parturition. Virgin female rats could be induced to show maternal behavior through constant exposure to pups over a

period of 6–8 days, and the display of such maternal behavior even occurred in ovariectomized or hypophysectomized females. This work led to the idea that processes exist which will allow for the occurrence of maternal behavior in naive virgin female rats after prolonged infant contact. Working with Fleming and Terkel, the view was developed that the virgin initially avoids and withdraws from novel pups but that after an extensive habituation (fear-reduction) period, pup stimuli come to evoke approach behavior (Fleming and Rosenblatt, 1974a). The influence of Schneirla on such an approach-avoidance motivational analysis was enunciated by Jay in 1995. The hormonal events of late pregnancy came to be viewed as modifying brain function so that infant stimuli were capable evoking immediate approach responses in the primiparous puerperal female on her first exposure to young.

With respect to the third phase in the maternity cycle, the 'maintenance phase', Jay did some landmark experiments on the role of experiences acquired during the postpartum on the subsequent expression of the behavior at a time when the parturitional hormones were no longer playing a role (Rosenblatt and Lehrman, 1963; Rosenblatt, 1980). These experiments suggested the existence of a sensitive period for the long term effectiveness of a postpartum experience with young. This work formed the foundation for what is now called the maternal experience effect or maternal memory, as outlined below.

Work initiated by Bob Bridges and then by the Fleming and Stern laboratories explored in more specific detail the role of the expression of the behavior and of somatosensory versus olfactory experiences with the pups in the maintenance of the motivation to show maternal behavior (Bridges, 1975; Fleming et al., 1996; Stern, 1990; Morgan et al., 1992). The importance of the timing and duration of the maternal experience, and, as with other forms of learning, the importance of the interval during which pups are not present on responsiveness at retention test (the retention interval) were recognized. These behavioral flexibilities are reflected by flexibilities in brain function and structure.

Jay's research on the maintenance phase of maternal behavior also contributed to the currently accepted view that although the immediate onset of maternal behavior at parturition in rats is regulated by hormones, its maintenance is free of hormonal control and is regulated solely by the mother's responsiveness to infant stimuli. Just when this important transition occurs, mothers are particularly susceptible to the formation of a 'maternal memory'.

The end of the maternity cycle, weaning, was also of considerable importance to Jay but it remains to this day the least studied phase (Reisbick et al., 1975). Jay's early work on weaning by a mother cat of her kittens is a true classic and describes behavioral synchronies between mother and kittens, where the mother cat actively withdraws from her growing and proactive litter prior to weaning (Rosenblatt and Schneirla, 1962), providing a facile analogy for our own experiences as parents of teenage children!

Jay's laboratory has also made important contributions to the study of maternal aggression and the developmental impact of mothering (Moore and Morelli, 1979; Williams et al., 1980). This research, along with his approach-withdrawal concept, set the stage for the current high interest in emotional processes associated with maternal behavior, which includes the study of stress and anxiety factors and their relevance to the development and then the onset and maintenance of maternal behavior.

In short, Jay explored the psychobiology of maternal behavior and aspects of infant learning from many angles, at multiple analytic levels, using multiple technologies and techniques, as they became available, and from proximal, functional, developmental, comparative and, more recently, evolutionary perspectives. He was among the first to study maternal behavior from the perspectives of its humoral (hormonal) bases (Terkel and Rosenblatt, 1968, 1972); he explored the role of sensory factors, starting with somatosensory stimulation of mammary gland development during pregnancy derived through self-licking (Roth and Rosenblatt, 1968) and the role of chemosensory cues in its organization and regulation (Fleming and Rosenblatt, 1974b,c; Mayer and Rosenblatt, 1993a,b). His work on experiential factors (which harks back to his studies on the role of experience in the mating behavior of male rats following castration) was a key study in this research area, and was highlighted by his famous chapter with Danny Lehrman in 1963 (Rosenblatt and Lehrman, 1963). It should also be noted that Jay's students and postdocs also explored the role of neural and neurochemical factors, and led by Michael Numan together with Barry Komisaruk, they were among the first to demonstrate the importance of the medial preoptic area in the regulation of maternal behavior (Numan et al., 1977; see Numan and Insel, 2003). This work on the neural and neurochemical control of maternal behavior, starting in 1975, was very fruitfully pursued over the years by other students and postdocs and eventually taken over by Joan Morrell and her students when she arrived at IAB (Felton et al., 1998; Mattson et al., 2001; Olazábal et al., 2004), and by students of IAB and their students (Giordano et al., 1989; Lonstein and Stern, 1997). Overall, studies on the analysis of the neural and neurochemical mediation of maternal behavior produced as much as 25% of all research papers published by members of the Institute of Animal Behavior/Neuroscience Institute at Rutgers.

It cannot be overstated that Jay's theoretical formulations based on his behavioral and hormonal work had a tremendous impact on those more directly involved in examining the neural control of maternal behavior and the field of behavioral neuroendocrinology. In particular, his approach-withdrawal views of the onset of maternal behavior have set the foundation for exploring dual neural circuits which regulate maternal behavior, with the function of these circuits mapping on nicely to the concepts of approach and avoidance.

Finally, Jay maintained a comparative approach in his thinking and research. He did not restrict his work to rats, but worked with multiple species over his career, starting with cats, hamsters, and, most productively, and in an active collaboration with Gabriela González-Mariscal and Carlos Beyer, with rabbits (González-Mariscal et al., 1994). His approach was to explore the similarities and differences in behavioral phenotypes across species; this comparative and evolutionary perspective, seen already in 1989, is best formulated in a paper in the New Directions in Child Development on the evolution of behavioral and non-behavioral patterns of parental care and physiology in mammalian and avian species.

Jay accomplished all this by working very hard, by giving his students guidance (but with a very long leash), by thinking deeply about issues, by being an excellent experimental scientist and methodologist, and by being inherently complex and seeing the world as complex. He was both willing to exploit unexpected serendipitous findings and remain programmatic and somewhat dogged in his pursuit of a problem. He was not a trend follower and rarely pursued the 'sexy' ideas. Perhaps unbeknownst to him (or maybe he did know) he was a trend-setter himself; many careers have grown out of his conceptualizations and his work.

Those of us who have had the opportunity to have worked with Jay, and our students and theirs, are very lucky indeed.

Acknowledgments

Some of the descriptive text comes from: Fleming, A.S., 2007. The three faces of Jay S. Rosenblatt. Devel. Psychobiol. 49, 2–11, part of an issue (ed. G. González Mariscal) in honor of Jay, based on a symposium at the 2005 meeting of the International Society for Developmental Psychobiology.

Because of the space constraints for this article, we have not been able to reference all the work produced by all the excellent students and post-doctoral fellows who worked with Jay directly; nor the many scientists who have been influenced by him both within and outside the Institute for Animal Behavior. We are all honored to be part of the same scientific community.

References

Bridges, R.S., 1975. Long-term effects of pregnancy and parturition upon maternal responsiveness in the rat. Physiol. Behav. 14, 245–249.

Bridges, R.S., Rosenblatt, J.S., Feder, H.H., 1978. Serum progesterone concentrations and maternal behavior in rats after pregnancy termination: behavioral stimulation after progesterone withdrawal and inhibition by progesterone maintenance. Endocrinology 102, 258–267.

Felton, T.M., Linton, L., Rosenblatt, J.S., Morrell, J.I., 1998. Intact neurons of the lateral habenular nucleus are necessary for the nonhormonal, pup-mediated display of maternal behavior in sensitized virgin female rats. Behav. Neurosci. 112, 1458–1465.

Fleming, A.S., Rosenblatt, J.S., 1974a. Maternal behavior in the virgin and lactating rat. J. Comp. Physiol. Psychol. 86, 957–972.

Fleming, A.S., Rosenblatt, J.S., 1974b. Olfactory regulation of maternal behavior in rats. I. Effects of olfactory bulb removal in experienced and inexperienced lactating and cycling females. J. Comp. Physiol. Psychol. 86, 221–232.

Fleming, A.S., Rosenblatt, J.S., 1974c. Olfactory regulation of maternal behavior in rats. II. Effects of peripherally induced anosmia and lesions of the lateral olfactory tract in pup-induced virgins. J. Comp. Physiol. Psychol. 86, 233–246.

Fleming, A.S., Morgan, H.D., Walsh, C., 1996. Experiential factors in postpartum regulation of maternal care. In: Rosenblatt, J.S., Snowdon, C.T. (Eds.), Advances in the Study of Behavior, Vol 25. Academic Press, San Diego, pp. 295–332.

Freeman, N.C., Rosenblatt, J.S., 1978. Specificity of litter odors in the control of home orientation among kittens. Dev. Psychobiol. 11, 459–468.

Giordano, A.L., Siegel, H.I., Rosenblatt, J.S., 1989. Nuclear estrogen receptor binding in the preoptic area and hypothalamus of pregnancy-terminated rats: correlation with the onset of maternal behavior. Neuroendocrinology 50, 248–258.

González-Mariscal, G., Díaz-Sánchez, V., Melo, A.I., Beyer, C., Rosenblatt, J.S., 1994. Maternal behavior in New Zealand white rabbits: quantification of somatic events, motor patterns, and steroid plasma levels. Physiol. Behav. 55, 1081–1089.

Lonstein, J.S., Stern, J.M., 1997. Somatosensory contributions to c-*fos* activation within the caudal periaqueductal gray of lactating rats: effects of perioral, rooting, and suckling stimuli from pups. Horm. Behav. 32, 155–166.

Lott, D.F., Rosenblatt, J.S., 1969. Development of maternal responsiveness during pregnancy in the rat. In: Foss, B.F. (Ed.), Determinants of Infant Behavior IV. Methuen, London, pp. 61–67.

Mattson, B.J., Williams, S., Rosenblatt, J.S., Morrell, J.I., 2001. Comparison of two positive reinforcing stimuli: pups and cocaine throughout the postpartum period. Behav. Neurosci. 115, 683–694.

Mayer, A.D., Rosenblatt, J.S., 1993a. Contributions of olfaction to maternal aggression in laboratory rats (*Rattus norvegicus*): effects of peripheral deafferentation of the primary olfactory system. J. Comp. Psychol. 107, 12–24.

Mayer, A.D., Rosenblatt, J.S., 1993b. Peripheral olfactory deafferentation of the primary olfactory system in rats using ZnSO4 nasal spray with special reference to maternal behavior. Physiol. Behav. 53, 587–592.

Moore, C.L., Morelli, G.A., 1979. Mother rats interact differently with male and female offspring. J. Comp. Physiol. Psychol. 93, 677–684.

Morgan, H.D., Fleming, A.S., Stern, J.M., 1992. Somatosensory control of the onset and retention of maternal responsiveness in primiparous Sprague–Dawley rats. Physiol. Behav. 51, 541–555.

Numan, M., Insel, T.R., 2003. The Neurobiology of Parental Behavior. Springer-Verlag, New York.

Numan, M., Rosenblatt, J.S., Komisaruk, B.R., 1977. Medial preoptic area and onset of maternal behavior in the rat. J. Comp. Physiol. Psychol. 91, 146–164.

Olazábal, D.E., Abercrombie, E., Rosenblatt, J.S., Morrell, J.I., 2004. The content of dopamine, serotonin, and their metabolites in the neural circuit that mediates maternal behavior in juvenile and adult rats. Brain Res. Bull. 63, 259–268.

Reisbick, S., Rosenblatt, J.S., Mayer, A.D., 1975. Decline of maternal behavior in the virgin and lactating rat. J. Comp. Physiol. Psychol. 89, 722–732.

Rosenblatt, J.S., 1967. Nonhormonal basis of maternal behavior in the rat. Science 156, 1512–1514.

Rosenblatt, J.S., 1970. Views on the onset and maintenance of maternal behavior in the rat. In: Aronson, L., Tobach, E., Rosenblatt, J.S., Lehrman, D.S. (Eds.), Development and Evolution of Behavior: Essays in Memory of T. C. Scheirla. Freeman, San Francisco, pp. 489–515.

Rosenblatt, J.S., 1971. Suckling and home orientation in the kitten: a comparative developmental study. In: Tobach, E., Aronson, L., Shaw, E. (Eds.), The Biopsychology of Development. Academic Press, New York, pp. 345–410.

Rosenblatt, J.S., 1980. Hormonal and nonhormonal regulation of maternal behavior: a theoretical survey. Reprod. Nutr. Dev. 20, 791–800.

Rosenblatt, J.S., 1983. Olfaction mediates developmental transition in the altricial newborn of selected species of mammals. Dev. Psychobiol. 16, 347–475.

Rosenblatt, J.S., Schneirla, T.C., 1962. The behavior of cats. In: Hafez, E.S.E. (Ed.), The Behavior of Domestic Animals. Ballière, Tindall and Cox, London, pp. 455–488.

Rosenblatt, J.S., Lehrman, D.S., 1963. Maternal behavior in the laboratory rat. In: Rheingold, H.L. (Ed.), Maternal Behavior in Mammals. John Wiley & Sons, New York, pp. 8–57.

Rosenblatt, J.S., Turkewitz, G., Schneirla, T.C., 1969. Development of home orientation in newly born kittens. Trans. N.Y. Acad. Sci. 31, 23–250.

Roth, L.L., Rosenblatt, J.S., 1968. Self-licking and mammary development during pregnancy in the rat. J. Endocrinol. 42, 363–378.

Schneirla, T.C., 1952. A consideration of some conceptual trends in comparative psychology. Psychol. Bull. 49, 559–597.

Schneirla, T.C., Rosenblatt, J.S., 1961. Animal research. I. Behavioral organization and genesis of the social bond in insects and mammals. Am. J. Orthopsychiatry 31, 223–253.

Siegel, H.I., Rosenblatt, J.S., 1975a. Estrogen-induced maternal behavior in hysterectomized–ovariectomized virgin rats. Physiol. Behav. 14, 465–471.

Siegel, H.I., Rosenblatt, J.S., 1975b. Latency and duration of estrogen induction of maternal behavior in hysterectomized–ovariectomized virgin rats: effects of pup stimulation. Physiol. Behav. 14, 473–476.

Stern, J.M., 1990. Multisensory regulation of maternal behavior and masculine sexual behavior: a revised view. Neurosci. Biobehav. Rev. 14, 183–200.

Terkel, J., Rosenblatt, J.S., 1968. Maternal behavior induced by maternal blood plasma injected into virgin rats. J. Comp. Physiol. Psychol. 65, 479–482.

Terkel, J., Rosenblatt, J.S., 1972. Humoral factors underlying maternal behavior at parturation. J. Comp. Physiol. Psychol. 80, 365–371.

Williams, C.L., Hall, W.G., Rosenblatt, J.S., 1980. Changing oral cues in suckling of weaning age rats: possible contributions to weaning. J. Comp. Physiol. Psychol. 94, 472–483.

Alison S. Fleming
University of Toronto at Mississauga, Canada
E-mail address: afleming@utm.utoronto.ca.
Corresponding author.

Michael Numan
Boston College, USA

Robert S. Bridges
Tufts University - Cummings School of Veterinary Medicine, USA