

Topics

Neonatal instinctive behaviours and parental behaviours: imprinting, early learning and social development.

1. Instinctive responses ('*Innate releasing mechanisms*' or the IRM) in nestling birds: Tinbergen and Perdeck (1950), Bachman, & Chappell (1998), Kilner, Noble, & Davies (1999), Kilner (2001), Hauber et al (2001), Butchart et al. (2003), Madden & Davies, (2006). Goth & Evans (2004) and Barry & Goth (2006) studied innate visual recognition of species in the brush turkey, which has no interactions with its parents.
2. Rapid and delayed perceptual learning of parental appearance in fowl and of song patterns in songbirds ("*Imprinting*" - Lorenz, 1937; Hess, 1973; Horn, 1998, 2004; Johnson, 1999; Bolhuis et al., 2000; Bischof, 2003; Riebel, 2003; Simpson and Vicario, 1996; Hollis et al., 1991; Burley, 2006).
3. Development of mother-infant attachment in mammals, especially primates; role of maternal and peer interactions on infant and adult behaviour in primates (Harlow, 1970; Lamb *et al*, 1984; Maestriperieri et al, 2000; Maestriperieri 2001a,b,c, Maestriperieri & Roney, 2006; Steiner et al, 2001; Zeifman, 2001; Gilmer & McKinney, 2003; Machado and Bachevalier, 2003; Farroni et al., 2004, 2005, 2006; Reid et al, 2004).
4. Theoretical accounts of these imprinting phenomena, mechanisms and functions (Bateson, 1979, 2000; Shettleworth, 1993; general theories e.g. Kraemer, 1992; Hollis et al., 1991; Bateson, 2000, Bolhuis and Honey, 1998; Horn, 2004) – conclusion that they are examples of specialized forms of learning.

Summary

It would be reasonable to expect that the behaviour of newborn animals is governed largely by innate mechanisms. However, Lorenz (1937), an ethologist, discovered that in geese and in other species where the new born are comparatively mobile, the recognition of parental appearance is **not** fully innate, but rather is strongly influenced by visual experience in the first few days after hatching. Initially it was emphasised that this process of "imprinting" differed from more general forms of learning (see "Feature of Imprinting, below), but more recently it has been suggested that imprinting is not such a special case, because most forms of learning are influenced by adaptive specializations. That is, particular species are predisposed to learn things which have functional significance for their own life-style. (Bateson, 1990, Shettleworth, 1993).

The work of Harlow (1958) on maternally deprived rhesus monkeys was at one time used to counter the view that primates are born with no instinctive social needs. Newborn rhesus monkeys have a preference for tactile "contact comfort" and well as warmth and motion (Harlow and Suomi, 1970). There is a "sensitive period" of a few weeks after which infant monkeys do not form an attachment. But normal development of the natural "species-specific" rhesus monkey behaviours involved in play, mating and maternal behaviour requires experience with peers as well as adequate maternal care in infancy.

(Futher notes are given at pages 2 and 3 of this handout)

Sample Essay

Describe and discuss the early development of social attachments in birds and primates, in the context of interactions between instinct and early forms of learning.

PARENT-YOUNG INTERACTIONS IN BIRDS

‘**Altricial**’ = ‘**Nidicolous**’ species. The common pattern: parents (usually both) bring food to young in the nest or nesting area. The young must ‘beg’ for food, at the minimum by opening their mouths.

‘**Precocial**’ = ‘**Nidifugous**’ species. Familiar in fowl: the young are mobile at birth, and feed themselves, but parents (usually both) perform protective functions.

There are mixtures: in Oystercatchers (Norton-Griffiths, 1969) the young are mobile, but the parents bring food to the nest for several days, and may continue to feed the young away from the nest for several months after hatching.

Individual recognition of parents by the young is probably widespread in both cases, also the effect of early social experience on **species-recognition** (cf the cuckoo for a purely innate case).

“**Imprinting**” = early learning by the young of the perceptual characteristics of suitably adjacent objects (in nature the parents, but fairly arbitrary artificial objects in experiments). It is studied in precocial species such as chickens and ducks, but the term is sometimes applied more loosely to other species. **Attachment** is a more general term.

Features of Imprinting

The following features of imprinting were initially emphasised to support the view that the process was not an example of general learning abilities, but a specialized functional adaptation.

- THE SENSITIVE PERIOD — imprinting is to a large degree limited to the first few days of life. (The ‘CRITICAL PERIOD’ is a stronger version.)
- Imprinting is INSTANTANEOUS – it is very rapid, but it is also associated with changes in social development that are more gradual.
- Imprinting is IRREVERSIBLE — not quite, but after a certain age the effects are very difficult to change.
- Early imprinting has important effects on MATE CHOICE, which takes in adulthood. However, it is believed that this SEXUAL IMPRINTING occurs rather later in life than the initial FILIAL IMPRINTING which influences the first social attachment, and in some species sexual imprinting is influenced by interactions with siblings. (see Bateson, 1979, 1990, 2000; Hollis *et al.*, 1991, Bolhuis and Honey, 1998).

A number of theories (e.g. Hess, 1973; Hoffman and Ratner, 1973; Bateson, 1979, 1990; Shettleworth, 1993) interpret imprinting as the interaction among several other development factors. E.g. the critical, or ‘sensitive’ period ends because imprinting narrows preferences to familiar objects, and the first preference is protected by future escape from novel objects.

Rajecki *et al.* (1978) suggested that ethological theories of imprinting are better at explaining: ‘maltreatment’ effects, the ‘secure base’ effect, and reactions to separation from the imprinted object.

Nevertheless, some current work on imprinting makes use of it in order to study the neurophysiological bases of learning and memory (e.g. Horn, 1990, 2004)

Therefore, it can be regarded as a specialized form of learning, supporting the interaction between learning and innate factors in development.

A link between parental behaviour in birds and that in mammals including primates is given by the importance of the hormone prolactin in both cases (Riddle *et al.*, 1935; Zeigler, 2000; Schradin *et al.*, 2003). Raised prolactin levels are associated with parental care giving in both males and females in species where both sexes are involved. Human fathers with higher prolactin levels and lower testosterone are more responsive to infant cries (Fleming *et al.*, 2002; see also Burnham *et al.*, 2003).

The starting point is Harlow's work on maternal deprivation in rhesus monkeys (Harlow, 1958; discussed in Jolly, 1972, Passsingham, 1982) and most general textbooks. The initial finding is merely a disproof of the view that newborns are a *tabula rasa* except for basic drives — unless “contact comfort” and more complex social needs are added to ‘basic drives.

Later work on “surrogate mothers” (artificial objects: Harlow and Suomi, 1970) suggested that —

- ☞ Lactation increases preference
- ☞ Further support for the importance of tactile contact
- ☞ Motion increases preference
- ☞ Temperature is important (cold contact comfort is rejected.)
- ☞ There is a ‘Sensitive Period’ since after 4 weeks with only a cold surrogate, it is too late for attachment behaviours to be elicited.

Work with surrogates supports the ‘protest and despair’ cycle following loss of the attachment object in primates (Mineka and Suomi, 1978). A temporary increase in attachment behaviours follow re-unions after separation.

Cloth mothers also used to study the “secure-base” effect (Harlow, 1962; Rajecki *et al*, 1978) — the secure base leads to increased exploration and investigation of novel objects, especially in the 20-40 day period (rhesus).

But, **the cloth mother as the only companion is no basis for adult social behaviour** (interactions with peers, mating and mothering: Harlow, 1962; Chamove *et al*, 1973; Ruppenthal *et al*. 1976)

Ruppenthal et al, 1976

Females reared without real mothers are inadequate and violent towards their own offspring. Male babies are most neglected. However, contact with peers prior to adulthood increases the probability of adequate mothering behaviour. Also contact with their own infant after a first birth increases the chances of adequate mothering after a second birth.

Rhesus monkeys reared without mothers in groups of 4 tended to have more normal sexual and maternal behaviour than those reared in pairs (Chamove *et al*, 1973).

Generalizations to humans

Ethological evidence was made use of by Bowlby (1969, 1973; see Rajecki *et al*, 1978), and Maestripieri (1999a) and Maestripieri and Carroll (1998) and Maestripieri (2001a,b,c) continue to make comparisons between human parenting and that of other primates but this is open to criticism. E.g.

Lamb et al (1984)

– evaluated “both the empirical evidence and the interpretation of infant behaviour in terms of principles derived from evolutionary biology” (p.127), looking at the “strange-situation” test in which infant behaviour is observed with the mother alternating with a strange person and rated for quality of attachment. They are against the suggestion that this assesses “whether the infant has developed species-appropriate adaptive behaviour as a result of rearing in an evolutionarily appropriate context”, and conclude that “interpretations in terms of biological adaptation are misguided.” They advocate attention to cultural and sociological differences in rearing patterns and “the study of learned contingencies or social cognition” (p.146).

However, their own finding was that temporal stability in security of attachment is only high when there is stability in family and caretaking circumstances.

Gilmer and McKinney (2003) continue to make use of the primate data to develop a general model in which adverse early life events such as disruptions of attachment systems will be risk factors for adult depression, while Machado and Bachevalier (2003) suggest that non-human primate models may in future assist in the understating of human childhood psychopathologies such as autism and Willams syndrome.

Main sources (Alternatives)

- Gleitman, H. (1995/99/2004) *Psychology. 4th/5th/6th Edition*. Norton, London. pp 534-544/pp576-9/506-10 “Social Development”; pp 379-412/ 405-437/416-7, “The Biological Basis of Social Behaviour”.
- Harlow, H.F. and Suomi, S.J. (1970) The nature of love simplified. *American Psychologist*, 25, 161-8.
- Jolly, A. (1972/1985) *The Evolution of Primate Behaviour. 1st and 2nd edn*. Macmillan: London. Chapter 12/14, “Mothers and Infants”.
- Lieberman, D. (1993/2000) *Learning: Behavior and Cognition*. Belmont: Wadsworth. “Learning in an Evolutionary Context”. (pp. 361-392/467-495)
- Walker, S.F. (1985) *Animal Thought*. Routledge & Kegan Paul: London. (Chapter 6 esp. pp. 194-222).
- Walker, S.F. (1987) *Animal Learning: An Introduction*. Routledge & Kegan Paul: London. (Chapter 1; pp 17-26).

Further reading (Alternatives)

- Bateson, P.P.G. (1990) Is imprinting such a special case? *Philosophical Transactions of the Royal Society, B*, 329, 125-131.
- Bateson, P. (2000). What must be known in order to understand imprinting?, In Heyes, Cecilia (Ed); Huber, Ludwig (Ed). (2000). *The evolution of cognition. Vienna series in theoretical biology*. Cambridge, MA, US: The MIT Press. (pp. 85 102: 2 copies at 156.3 EVO in Bk library).
- Bateson, P. (2003). The promise of behavioural biology. *Animal Behaviour*, 65, 11-17.
- Hinde, R.A. (1970) *Animal Behaviour: A Synthesis of Ethology and Comparative Psychology*. McGraw-Hill: London. (pp 513-27 on imprinting).
- Hollis, K.L., ten Cate, C. and Bateson, P. (1991) Stimulus representation: a subprocess of imprinting and conditioning. *Journal of Comparative Psychology*, 105, 307-317.
- Morton, J. and Johnson, M.H. (1991) CONSPEC and CONLERN: A two-process theory of infant face recognition. *Psychological Review*, 98, 164-181.
- Passingham, R. (1982) *The Human Primate*. W.H. Freeman: Oxford. (Chapter 9 “Family”, esp. pp. 262-276 on infant attachment: BK short loan at IAV [Pas])
- Shettleworth, S.J. (1993) Varieties of learning and memory in animals. *Journal of Experimental Psychology: Animal Behaviour Processes*, 19, 5-14.

Other references and lecturer’s bibliography — not for further reading

- Barry, K. L., & Goth, A. (2006). Call recognition in chicks of the Australian brush-turkey (*Alectura lathami*). *Animal Cognition*, 9(1), 47-54.
- Bastian, M. L., Sponberg, A. C., Suomi, S. J., & Higley, J. D. (2003). Long-term effects of infant rearing condition on the acquisition of dominance rank in juvenile and adult rhesus macaques (*Macaca mulatta*). *Developmental Psychobiology*, 42(1), 44-51.
- Bateson, P. & Horn, G (1994) Imprinting and recognition memory - a neural-net model. *Animal Behaviour*, Vol.48, No.3, Pp.695-715.
- Bateson, P.P.G. (1973) Preferences for familiarity and novelty: A model for the simultaneous development of both. *Journal of Theoretical Biology*, 41, 249-59.
- Bateson, P.P.G. (1979) How do sensitive periods arise and what are they for?. *Animal Behaviour*, 27, 470-86.
- Bateson, P.P.G. (1982) Preferences for cousins in Japanese quail. *Nature*, 295, 236-237.
- Bischof, H. J. (2003). Neural mechanisms of sexual imprinting. *Animal Biology*, 53(2), 89-112.
- Bole-Feysot, C., Goffin, V., Edery, M., Binart, N., & Kelly, P. A. (1998). Prolactin (PRL) and its receptor: Actions, signal transduction pathways and phenotypes observed in PRL receptor knockout mice. *Endocrine Reviews*, 19(3), 225-268
- Bolhuis, J. J., & Honey, R. C. (1998). Imprinting, learning and development: from behaviour to brain and back. *Trends in Neurosciences*, 21(7), 306-311.
- Bolhuis, J. J., Cook, S., & Horn, G. (2000). Getting better all the time: improving preference scores reflect increases in the strength of filial imprinting. *Animal Behaviour*, 59, 1153-1159.
- Bowlby, J. (1969) *Attachment and Loss. Volume 1 Attachment*. Penguin.
- Burley, N. T. (2006). An eye for detail: Selective sexual imprinting in zebra finches. *Evolution*, 60(5), 1076-1085.
- Burnham, T. C., Chapman, J. F., Gray, P. B., McIntyre, M. H., Lipson, S. F., & Ellison, P. T. (2003). Men in committed, romantic relationships have lower testosterone. *Hormones and Behavior*, 44(2), 119-122.
- Butchart, S. H. M., Kilner, R. M., Fuisz, T., & Davies, N. B. (2003). Differences in the nestling begging calls of hosts and host- races of the common cuckoo, *Cuculus canorus*. *Animal Behaviour*, 65, 345-354.

- Chamove, A.S., Rosenblum, L.A. and Harlow, H.F. (1973) Monkeys (*Macacca mulatta*) raised only with peers: a pilot study. *Animal Behaviour*, 21, 316-325.
- Farroni, T., Johnson, M. H., & Csibra, G. (2004). Mechanisms of eye gaze perception during infancy. *Journal of Cognitive Neuroscience*, 16(8), 1320-1326.
- Farroni, T., Johnson, M. H., Menon, E., Zulian, L., Faraguna, D., & Csibra, G. (2005). Newborns' preference for face-relevant stimuli: Effects of contrast polarity. *Proceedings of the National Academy of Sciences of the United States of America*, 102(47), 17245-17250.
- Farroni, T., Mansfield, E. M., Lai, C., & Johnson, M. H. (2003). Infants perceiving and acting on the eyes: Tests of an evolutionary hypothesis. *Journal of Experimental Child Psychology*, 85(3), 199-212.
- Farroni, T., Menon, E., & Johnson, M. H. (2006). Factors influencing newborns' preference for faces with eye contact. *Journal of Experimental Child Psychology*, 95(4), 298-308.
- Fleming, A. S., Corter, C., Stallings, J., & Steiner, M. (2002). Testosterone and prolactin are associated with emotional responses to infant cries in new fathers. *Hormones and Behavior*, 42(4), 399-413.
- Gilmer, W. S., & McKinney, W. T. (2003). Early experience and depressive disorders: human and non-human primate studies. *Journal of Affective Disorders*, 75(2), 97-113.
- Goodall, J. (1991) *Through a Window: Thirty Years with the Chimpanzees of Gombe*. London: Penguin.
- Goth, A., & Evans, C. S. (2004). Social responses without early experience: Australian brush-turkey chicks use specific visual cues to aggregate with conspecifics. *Journal of Experimental Biology*, 207(13), 2199-2208.
- Hailman, J.P. (1962) Pecking of laughing gull chicks at models of the parental head. *Auk*, 79, 89-98.
- Hamilton, KS, King, AP, Sengelaub, DR, West, MJ (1997) A brain of her own: a neural correlate of song assessment in a female songbird. *Neurobiology of Learning and Memory*, Vol.68, No.3, Pp.325-332 Is: 1074-7427.
- Harlow, H.F. (1958) The nature of love. *American Psychologist*, 13,673-85.
- Harlow, H.F. (1962) The heterosexual affectional system in monkeys. *American Psychologist*, 17, 1-9.
- Hauber, M. E., Russo, S. A., & Sherman, P. W. (2001). A password for species recognition in a brood-parasitic bird. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 268(1471), 1041-1048.
- Healy, S. D. (2006). Imprinting: Seeing food and eating it. *Current Biology*, 16(13), R501-R502.
- Hess, E.H. (1959) Imprinting. *Science*, 130, 133-141.
- Hess, E.H. (1973) *Imprinting: Early Experience and the Developmental Biology of Attachment*. New York: Van Nostrand (IAW).
- Horn, G. (1990) Neural basis of recognition memory investigated through an analysis of imprinting. *Philosophical Transactions of the Royal Society, B*, 329, 133-142.
- Horn, G. (1998). Visual imprinting and the neural mechanisms of recognition memory. *Trends in Neurosciences*, 21(7), 300-305.
- Horn, G. (2004) Pathways of the past: the imprint of memory. *Nature Reviews Neuroscience*, 5(2):108-20
- Ichise, M., Vines, D. C., Gura, T., Anderson, G. M., Suomi, S. J., Higley, J. D., et al. (2006). Effects of early life stress on C-11 DASB positron emission tomography imaging of serotonin transporters in adolescent peer- and mother-reared rhesus monkeys. *Journal of Neuroscience*, 26(17), 4638-4643.
- Insel, T. R. (2000). Toward a neurobiology of attachment. *Review of General Psychology*, 4(2), 176-185.
- Johnson, M.H., Dziurawiec, S., Ellis, H. and Morton, J. (1991) Newborn's preferential tracking of face-like stimuli and its subsequent decline. *Cognition*, 40, 1-19.
- Kilner, R. M. (2001). A growth cost of begging in captive canary chicks. *Proceedings of the National Academy of Sciences of the United States of America*, 98(20), 11394-11398.
- Kilner, R. M., Noble, D. G., & Davies, N. B. (1999). Signals of need in parent-offspring communication and their exploitation by the common cuckoo. *Nature*, 397(6721), 667-672.
- Kraemer, G.W. (1992) A psychobiological theory of attachment. *Behavioural and Brain Sciences*, 15, 493-541.
- Lamb, M.E., Thompson, R.A., Gardner, W.P., Charnov, E.L. and Estes, D.(1984) Security of infantile attachment as assessed in the 'strange situation'. *Behavioural and Brain Sciences*, 7, 127-71.
- Lorenz, K. (1937) The companion in the bird's world. *Auk*, 54, 245-273.
- Lorenz, K. (1952) *King Solomon's Ring*. London: Methuen.
- Lorenz, K. (1967) *On Agression*. Methuen: London.
- Lotem, A (1993) Learning to recognize nestlings is maladaptive for cuckoo *Cuculus canorus* hosts. *Nature*, Vol.362, No.6422, Pp.743-745.
- Lyon, B. (2007). Mechanism of egg recognition in defenses against conspecific brood parasitism: American coots (*Fulica americana*) know their own eggs. *Behavioral Ecology and Sociobiology*, 61(3), 455-463.
- Machado, C. J., & Bachevalier, J. (2003). Non-human primate models of childhood psychopathology: the promise and the limitations. *Journal of Child Psychology and Psychiatry and Allied Disciplines*, 44(1), 64-87.
- Madden, J. R., & Davies, N. B. (2006). A host-race difference in begging calls of nestling cuckoos *Cuculus canorus* develops through experience and increases host provisioning. *Proceedings of the Royal Society B-Biological Sciences*, 273(1599), 2343-2351.
- Maestripieri, D. (1999a). The biology of human parenting: insights from nonhuman primates. *Neuroscience and Biobehavioral Reviews*, 23(3), 411-422.
- Maestripieri, D. (1999b). Fatal attraction: Interest in infants and infant abuse in rhesus macaques. *American Journal of Physical Anthropology*, 110(1), 17-25.

- Maestripieri, D. (2001a). Biological bases of maternal attachment. *Current Directions in Psychological Science*, 10(3), 79-83.
- Maestripieri, D. (2001b). Intraspecific variability in parenting styles of rhesus macaques (*Macaca mulatta*): The role of the social environment. *Ethology*, 107(3), 237-248.
- Maestripieri, D. (2001c). Is there mother-infant bonding in primates? *Developmental Review*, 21(1), 93-120.
- Maestripieri, D. (2003). Similarities in affiliation and aggression between cross-fostered rhesus macaque females and their biological mothers. *Developmental Psychobiology*, 43(4), 321-327.
- Maestripieri, D., & Carroll, K. A. (1998). Child abuse and neglect: Usefulness of the animal data. *Psychological Bulletin*, 123(3), 211-223.
- Maestripieri, D., & Roney, J. R. (2006). Evolutionary developmental psychology: Contributions from comparative research with nonhuman primates. *Developmental Review*, 26(2), 120-137.
- Maestripieri, D., Higley, J. D., Lindell, S. G., Newman, T. K., McCormack, K. M., & Sanchez, M. M. (2006). Early maternal rejection affects the development of monoaminergic systems and adult abusive parenting in rhesus macaques (*Macaca mulatta*). *Behavioral Neuroscience*, 120(5), 1017-1024.
- Maestripieri, D., Lindell, S. G., Ayala, A., Gold, P. W., & Higley, J. D. (2005). Neurobiological characteristics of rhesus macaque abusive mothers and their relation to social and maternal behavior. *Neuroscience and Biobehavioral Reviews*, 29(1), 51-57.
- Maestripieri, D., Megna, N. L., & Jovanovic, T. (2000). Adoption and maltreatment of foster infants by rhesus macaque abusive mothers. *Developmental Science*, 3(3), 287-293.
- McCormack, K., Sanchez, M. M., Bardi, M., & Maestripieri, D. (2006). Maternal care patterns and behavioral development of rhesus macaque abused infants in the first 6 months of life. *Developmental Psychobiology*, 48(7), 537-550.
- Mineka, S. and Suomi, S.J. (1978) Social separation in monkeys *Psychological Bulletin*, 85, 1376-1400.
- Moriceau, S., & Sullivan, R. M. (2005). Neurobiology of infant attachment. *Developmental Psychobiology*, 47(3), 230-242.
- Norton-Griffiths, M. (1969) The organization, control and development of parental feeding in the oyster catcher. *Behaviour*, 34, 55-114.
- Rajecki, D.R., Lamb, M.E., and Obmasher, P. (1978) Towards a general theory of infantile attachment: a comparative review of aspects of the social bond. *Behavioural and Brain Sciences*, 1, 417-64.
- Reid, V. M., Striano, T., Kaufman, J., & Johnson, M. H. (2004). Eye gaze cueing facilitates neural processing of objects in 4-month-old infants. *Neuroreport*, 15(16), 2553-2555.
- Riddle, O., Bates, R.W., & Lahr, E.L. (1935). Prolactin induces broodiness in fowl. *American Journal of Physiology*, 111: 352-360.
- Riddle, O., Bates, R.E. and Dykshorn, S.W. (1932) A new hormone of the anterior pituitary gland. *Proceedings of the Society for Experimental Biology and Medicine*, 29, 1211-1212.
- Riebel, K. (2003). Developmental influences on auditory perception in female zebra finches - is there a sensitive phase for song preference learning? *Animal Biology*, 53(2), 73-87.
- Ruppenthal, G.C., Arling, G.L., Harlow, H.F., Sackett, G.P. and Suomi, S.J. (1976) A 10-year perspective of motherless mother monkey behaviour. *Journal of Abnormal Psychology*, 85, 341-49.
- Schradin, C., Reeder, D. M., Mendoza, S. P., & Anzenberger, G. (2003). Prolactin and paternal care: Comparison of three species of monogamous new world monkeys (*Callicebus cupreus*, *Callithrix jacchus*, and *Callimico goeldii*). *Journal of Comparative Psychology*, 117(2), 166-175.
- Simpson, H.B and Vicario, D.S. (1996) Male zebra finches can learn male-typical vocalizations from hormone-treated female tutors. *Animal Behaviour*, 52, 1119-1127.
- Slater, P J. B. (1985) *An introduction to ethology*. Cambridge: Cambridge University Press (supernormal stimulus on page 41).
- Steiner, J. E., Glaser, D., Hawilo, M. E., & Berridge, K. C. (2001). Comparative expression of hedonic impact: affective reactions to taste by human infants and other primates. *Neuroscience and Biobehavioral Reviews*, 25(1), 53-74.
- Stevenson, J., Hutchison, R.E., Hutchison, J., Bertram, B.L.R. and Thorpe, W.H. (1970) Individual recognition by auditory cues in the Common Tern (*Sterna hirundo*) *Nature, London*, 226, 562-3.
- Turati, C., Cassia, V. M., Simion, F., & Leo, I. (2006). Newborns' face recognition: Role of inner and outer facial features. *Child Development*, 77(2), 297-311.
- Waldeck, P., & Andersson, M. (2006). Brood parasitism and nest takeover in common eiders. *Ethology*, 112(6), 616-624.
- Weidman, U. (1961) The stimuli eliciting begging responses in gulls and terns. *Animal Behaviour*, 9, 115
- Winberg, J. (2005). Mother and newborn baby: Mutual regulation of physiology and behavior - A selective review. *Developmental Psychobiology*, 47(3), 217-229.
- Wynne-Edwards, K. E. (2001). Hormonal changes in mammalian fathers. *Hormones and Behavior*, 40(2), 139-145.
- Zeifman, D. M. (2001). An ethological analysis of human infant crying: Answering Tinbergen's four questions. *Developmental Psychobiology*, 39(4), 265-285.
- Ziegler, T. E. (2000). Hormones associated with non-maternal infant care: A review of mammalian and avian studies. *Folia Primatologica*, 71(1-2), 6-21.

INNATE RELEASING MECHANISMS: NEONATAL FEEDING

<i>SPECIES</i>	<i>NATURAL BILL</i>	<i>EXPERIMENTAL RELEASERS</i>	<i>REFERENCES</i>
Herring Gull	Yellow bill with red patch	Patch ✓ Head shape × Patch redness ✓ Head colour × Bill length ✓	Tinbergen and Perdeck, 1950
Laughing Gull	Plain red bill	Bill redness ✓ Head shape ✓ Shape of bill ✓ Head presence ✓	Hailman, 1962
Black Headed Gull	Plain red bill	Bill point ✓ Head shape × Bill length ✓	Weidmann, 1961
Sandwich Tern	Plain black bill	Bill blackness ✓	Weidmann, 1961
Mallard Duck	Yellow bill	Greenness ✓ (Grass?)	Oppenheim, 1966

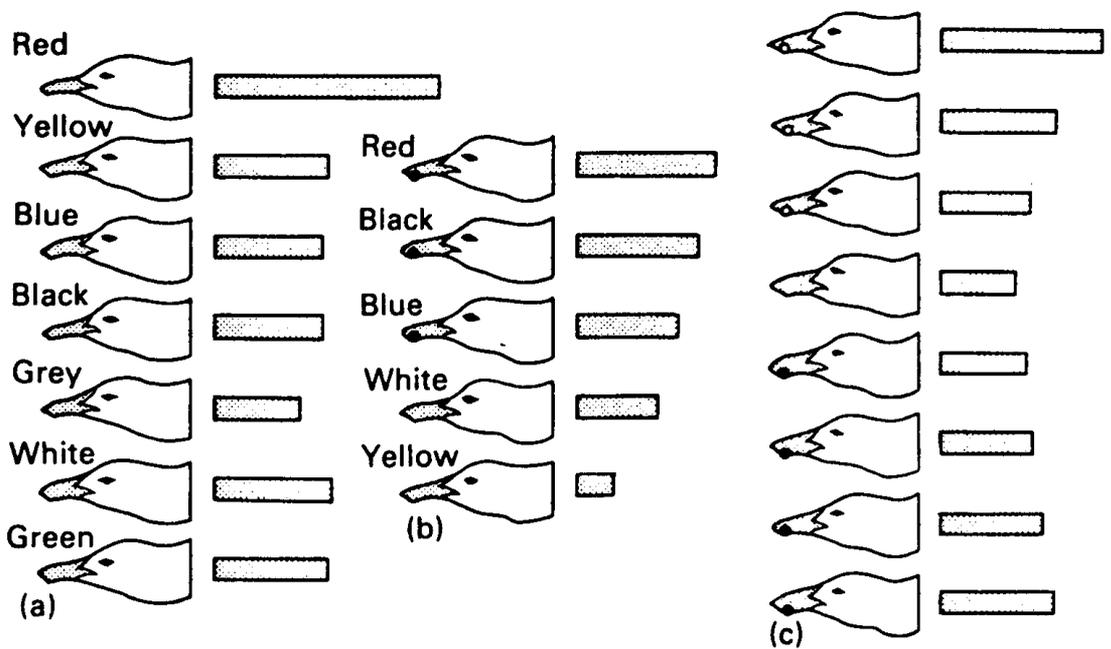


Figure 1.3 *Innate visual preferences in herring gulls.*

Three sets of model heads used to elicit pecking responses from herring gull chicks, with bars showing the relative amount of pecking elicited by each model. In (a) bill colour was varied; in (b) the colour of a patch on a yellow bill was varied; and in (c) the black/white contrast of the patch against a grey bill was varied. After Tinbergen and Perdeck (1950).

recognize a fellow member of its own species, of the opposite sex. It would therefore be foolish to deny the possibility of a very large measure of inherited control over the reactions of individual birds, in certain species. But this does not mean that *all* birds species employ the same measure of innate control, or that individual learning cannot be added on to initial innate preferences.

Tinbergen's own experimental work provides ample evidence of learned modifications to such initial preferences. For instance Tinbergen and Kuenen (1957), in their experiments on the reactions to artificial stimuli of nestling thrushes, observed that if a very natural, adult thrush-like stimulus was presented with no following feeding experience, the infants very soon refused to respond to it, whereas if an artificial non-preferred stimulus was followed by food, the young birds began to respond to it as if it was the natural

from Hinde (1970)

one species it may be different for auditory and visual stimuli (Boyd and Fabricius, 1965; Kovach et al., 1968).

The earlier limit to the sensitive period is related to the development of locomotor ability: Hess (1959b) found that the curve of increase in

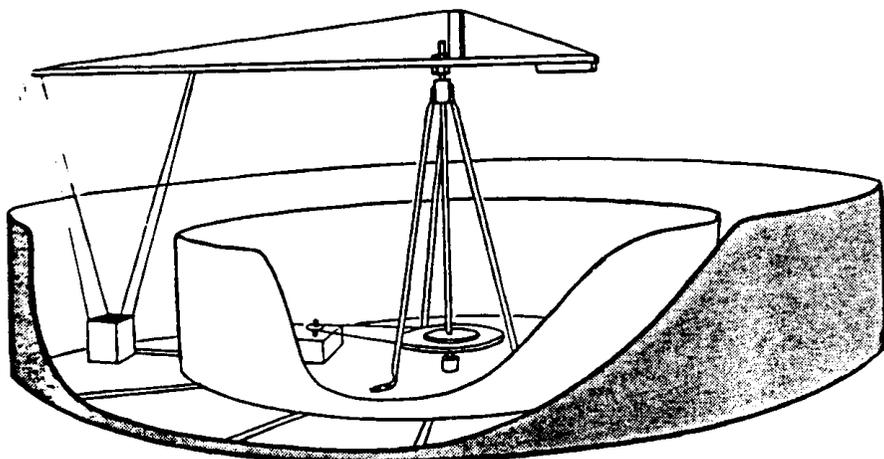


Fig. 21.3 Apparatus used for studying the following response of young chicks. The arm rotates, carrying the box round the circular runway. (From a drawing by P. Bateson.)

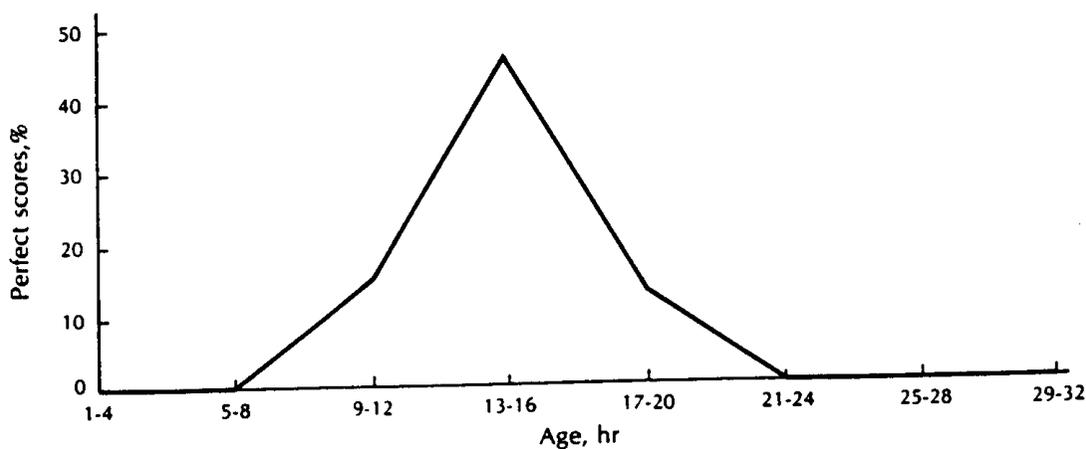


Fig. 21.4 The sensitive period for imprinting. The ordinate gives the scores of birds tested at the ages shown in hours along the abscissa. (After Hess, 1959a.)

speed of locomotion of chicks with age corresponds closely with the curve showing the onset of the sensitive period (Fig. 21.5). This, of course, does not demonstrate that locomotor ability is itself the operative factor: many perceptual and motivational changes are correlated with it, two possibilities

being the developing organization of the retina (Sackett, 1963) and the general excitability of the nervous system (Kovach, 1964). Gottlieb (1961) has shown that the beginning of the sensitive period is related to developmental age, and is little affected by posthatching experience.

There has been more disagreement over the factors limiting the end of the sensitive period. The first suggestion was that the sensitive period is

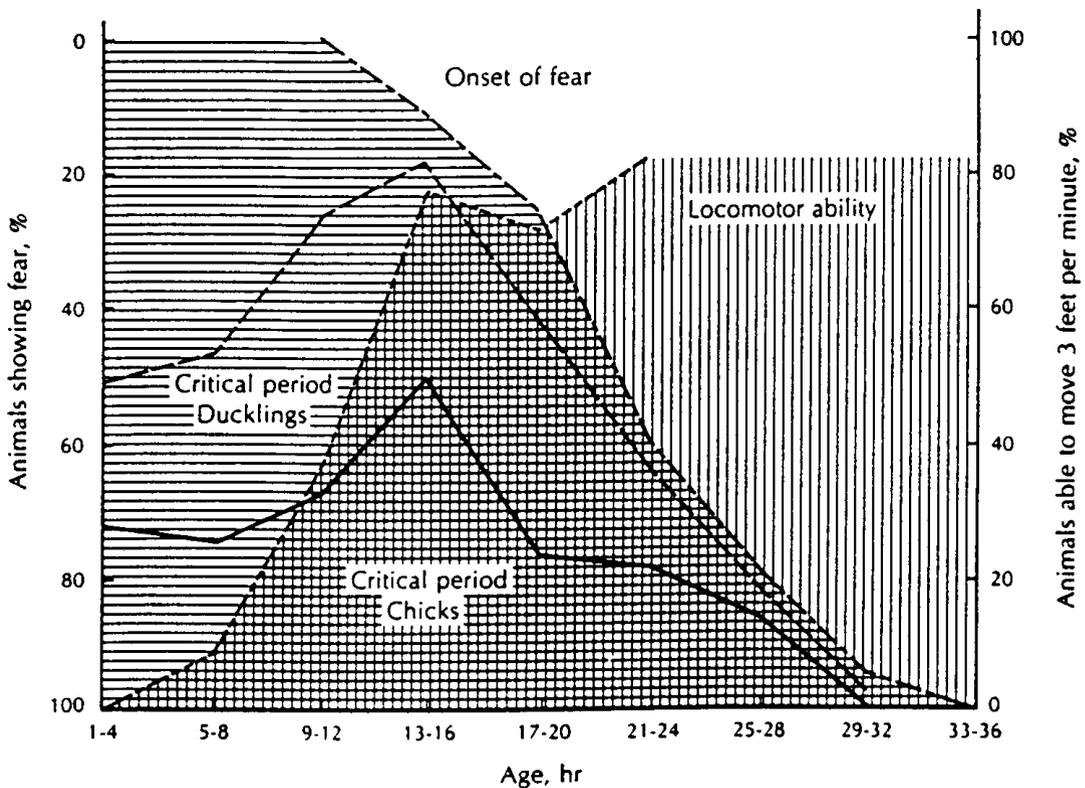


Fig. 21.5 Hypothetical and empirical curves of the critical period of chicks and mallard ducklings. (After Hess, 1959b.)

The two shaded areas show the increase with age in the proportion of birds moving more than 3 ft/min in a standard situation, and in the proportion of birds showing fear responses, the latter plotted from above downwards. The cross-hatched area under both lines is the hypothetical sensitive period on the assumption that these two factors are the limiting ones. The empirical period for chicks is shown by the continuous line, and for ducks by the discontinuous one.

limited by a waning of the tendency to follow (Lorenz, 1935; Fabricius, 1951). This carried with it the assumption that, in imprinted individuals, the specific cues learnt during the sensitive period are sufficient to elicit following later. This view was earlier associated with the assumption that the decrease in the tendency to follow was inherently determined, a hy-

Hollis, K.L., ten Cate, C. and Bateson, P. (1991) “Stimulus representation: a subprocess of imprinting and conditioning.”

Abstract “We suggest a way to reconcile imprinting and associative learning that respects the real differences between them but helps to recognise underlying commonalities... we approach learning as a combination of separate **sub-processes**. ...one of these, the **representation of stimuli** revealed striking similarities between imprinting and conditioning. <further work> 'will help us uncover the **general rules** by which combinations of stimulus features are represented in memory'.

1 Male Zebra finches raised by Bengalese finches until adult prefer Bengalese females.

2 Male Zebra finches raised with their own AND a related species prefer hybrid females.

If juvenile zebra finches are exposed to own parents for 30 days and then put individually with groups of Bengalese finches for the same length of time then, when adult, males “dither” between two over very short time periods. (Measured by directed singing)

But Ditherers actual prefer hybrid females to either species.

Conclusion

Information from double imprinting is combined in this case. This is consistent with associative theories about combinations of stimulus features.

Shettleworth, S.J. (1993) Varieties of learning and memory in animals. *Journal of Experimental Psychology: Animal Behaviour Processes*, 19, 5-14.

Can learning be neatly divided into “**general processes**” on the one hand (e.g. Habituation, Pavlovian conditioning) and “**adaptive specializations**” (e.g. imprinting, song-learning”) on the other?

Shettleworth recommends an approach in which “appreciation of specializations goes hand in hand with the study of general processes.” (p. 5)

E.g. imprinting may be an example of more general “learning rules underlying the development of a preference for — or recognition of — familiar stimuli...” (p.7)

Comments

But imprinting is clearly also an example of learning that is functionally specialized for *social identification*. Other functional areas where learning is likely to be an important process include *spatial knowledge* (learning “cognitive maps”) and *feeding strategies* (as in “optimal foraging”).

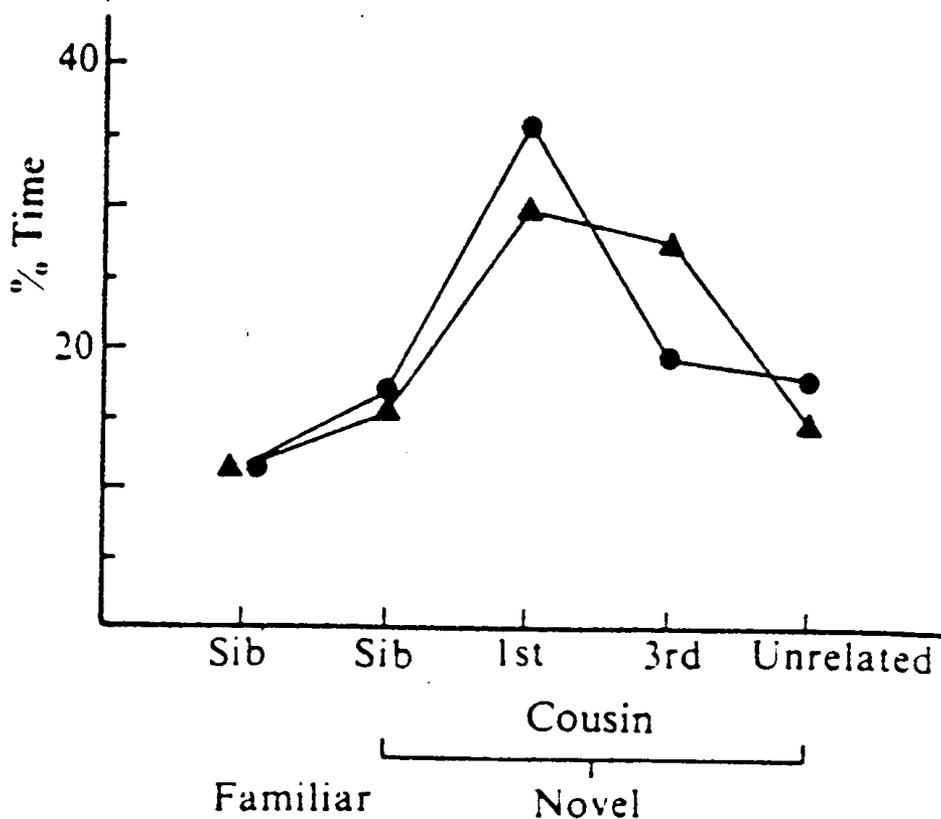


Fig. 2 The mean percentage time spent by adult Japanese quail near members of the opposite sex that were either familiar sibling (Sib), novel siblings, novel first cousins, novel third cousins, or novel unrelated individuals. The chance level is 20%. ▲, Males ($n = 22$); ●, females ($n = 13$).

kept in separate families and hatched separately. Within a day of hatching in the dark, the chicks were transferred to rearing pens and kept in true families in the same conditions as those used in previous experiments^{7,9}. The birds were isolated 30 days after hatching. Testing started at 60 days, when the quail were sexually mature.

The pedigrees of the quail in the colony were known for at least four generations and pairings had been carefully arranged. It was possible, therefore, to test all birds with a variety of members of the opposite sex that were of different degrees of relationship but of the same age. In addition, some true siblings were reared separately so that when the birds were tested, they were given choices between familiar and novel siblings, novel first and third cousins, and novel unrelated members of the

TAXONOMY OF PRIMATES (AN ORDER OF MAMMALS)

There are two sub-orders of the order of Primates. One sub-order includes humans, apes and monkeys, and the other is for Prosimians, and includes the lemurs of Madagascar, lorises (e.g. bushbabies) and tarsiers.

PROSIMII (*The older of the two suborders of Primates*)

Prosimians: = the lemurs of Madagascar, lorises (e.g. bushbabies) and tarsiers.

ANTHROPOIDEA (*A suborder of Primates*)

This includes 3 superfamilies, the superfamily of humans and apes and two superfamilies of monkeys:

Humans and Apes (*Hominoidea*). Includes extinct human species ('hominids'), modern *Homo sapiens* and the apes. "Great apes" are 2 species of chimpanzee, the orangutan and the gorilla, and "Lesser apes" are 7 species of gibbon.

Old-world monkeys: (*Cercopithecoidea* or *Catarrhines*) = dozens of species e.g. rhesus and other macaques, vervets and baboons.

New-world monkeys: (*Ceboidea* or *Platyrrhines*) = dozens of species e.g. cebus, squirrel, spider and owl monkeys and marmosets.

Table of Primate Life-Spans (After Jolly, 1972)

<i>Species</i>	<i>CEBUS (New World Monkey)</i>	<i>RHESUS (Old World Monkey)</i>	<i>GIBBON (Lesser Ape)</i>	<i>ORANG (Great Ape)</i>	<i>CHIMP (Great Ape)</i>	<i>GORILLA (Great Ape)</i>	<i>Homo Sapiens sapiens</i>
Days Gestation	180	168	210	275	225	265	266
Total yrs span	30+	28+	29+	30+	40+	35+	70+
Sub Adult till	4.0	7.5	8.5	10.5	10.0	11.0	20?
Infancy (yrs)	0.5	1.5	2.0	3.5	3.0	3?	6?
% Subadult	13%	27%	29%	35%	25%	31%	29%
% Infancy	2%	5%	7%	12%	8%	9%	9%

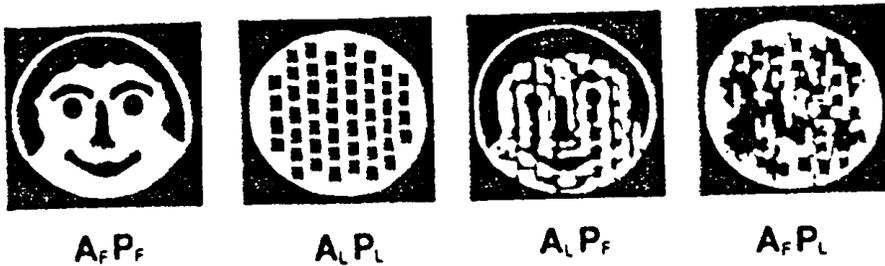


Figure 7. Approximate reproductions of the stimuli used by Kleiner (1987) and Kleiner and Banks (1987). (Stimulus A_F/P_F has the amplitude spectrum of the face and the phase spectrum of the face. Stimulus A_L/P_L has the amplitude spectrum of the lattice and the phase spectrum of the lattice. Stimulus A_L/P_F has the amplitude spectrum of the lattice and the phase spectrum of the face. Stimulus A_F/P_L has the amplitude spectrum of the face and the phase spectrum of the lattice. Note: We were unable to obtain copies of the original stimuli. From "Amplitude and Phase Spectra as Indices of Infant's Pattern Preferences" by K. A. Kleiner, 1987, *Infant Behavior and Development*, 10, pp. 54-55. Copyright 1987 by Ablex. Adapted by permission.)

turning was lower than that in Experiment 1 and corresponded more closely to that in the study by Maurer and Young (1983) than with the figures reported by Goren et al. (1975). Thus, it is likely that a certain minimal amount of mean head turning is required before a differential head-turning response can be obtained.

Because there have been three replications of the eye movement data reported in the Goren et al. (1975) study, we conclude that infants in the first hour of life are sensitive to the structure of the human face to some degree of detail. Our experiments

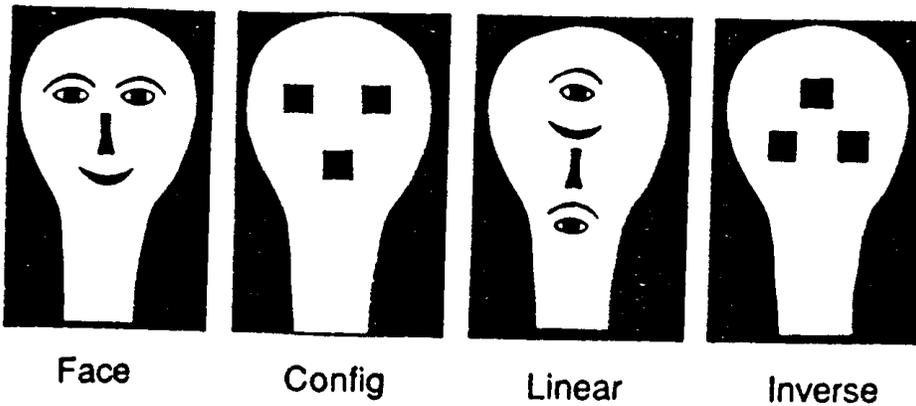


Figure 8. Stimuli used in Experiment 4 using newborn infants with a tracking technique.

between experience of a frequent response to a two-dimensional face. If this data were generalized to the experience of mother's face schematic stimuli used with

Further Experiments on Experiment 4

We have determined that the existence of a CONSPEC.

¹² We should note that these results were obtained by Kleiner (1987) herself or by her colleagues. They correspond to the accounts of Smith (1988), Dannemiller and Smith (1988), and Dannemiller and Maurer (1989). For further details see Maurer (1990).

other individuals will even

We now consider some of the questions which the young of any species must learn to describe the variety of systems. CONLERN is simply a system for specific information about the world. There are several questions. Beyond specifying the time of day, for example, examine the relationship between representations under other learning systems. A set of questions concerning

¹³ In a more recent experiment, we found more eye turning than face. The difference between the two. See Morton, Bartrip, and Johnson (1988).

¹⁴ Our use of the term *learn* changes resulting from specific changes would wish to include both "dependent learning" (Greenough and Morton, 1988).

¹⁵ We thank Annette Karmiloff-Smith for her comments.

Abstract

Evidence from newborns leads to the conclusion that infants are born with some information about the structure of faces. The structural information, termed CONSPEC, guides the preference for facelike patterns found in newborn infants. CONSPEC is contrasted with a device termed CONLERN, which is responsible for learning about the visual characteristics of conspecifics. In the human infant, CONLERN does not influence looking behaviour until 2 months of age. The distinction between these two 2 independent mechanisms allows a reconciliation of the conflicting data on the development of face recognition in human infants. Finally, evidence from another species, the domestic chick, for which a similar 2-process theory has already been put forward, is discussed. The new nomenclature is applied to the chick and used as a basis for comparison with the infant.

Other points

Exptl details are in Johnson et al 1991 Cognition paper:

1. Support for the idea of Fanz (1961) that attention is focussed on "stimuli which will later have adaptive significance." p164
2. For 20 years this has been rejected: infants said to discern only the grossest features, and to prefer the exterior boundaries over internal features.
- 3 Only at 2 months do they look longer at face-like rather than scrambled pictures. Some data suggest only at 4 months. Habituation techniques are also used.
4. But *newborns track* "face" stimuli with head and eye movements. e.g. Expt (in *Cognition*) with 24 infants only 37 mins old (mean). Stimuli either *face*, *scrambled* or *blank*. Both eye and head turn were greatest for the *face* and least for the *blank*.
5. The basis of the newborns' preference may be very general, possibly due to sensory properties of the visual system. The simplest hypothesis is that the innate specification of faces resembles the second panel in Figure 7 (uniform little squares in a circle).
6. 2-month-old infants make differential responses to schematic faces under certain procedures, but 1-month-old infants do not. (p.175).
7. At 5-months, infants show a preference for schematic over scrambled faces if the *internal* features are moving, but not if they are static. (p. 173-4: by this time, it is assumed some learning about faces has taken place.)

THE COMBINED THEORY (p.175)

There is some innate specification which directs attention to faces. The effects of this last up to about 1 month, in the peripheral visual field. There is also a learning mechanism, which is non-specialized, but which acquires knowledge about faces, which takes over from the innate mechanism during the first 2 months, and influence behaviour thereafter.

There is general agreement that neonatal perception is sub-cortical, and that cortical mechanism become more dominant after the first 2 months. Thus the innate specification (CONSPEC) is sub-cortical, and the later learning (CONLERN) is cortical.

APPLIED TO CHICKS

It has also been proposed that there are two neural mechanisms used for imprinting in the chick. There is an early predisposition to attend to objects generally similar to conspecifics. Learning about the details of the object exposed to depends on a particular forebrain region (IMHV, p.177. This is a long-term store in the left hemisphere and a buffer store in the right - Horn, 1985.)

IMHV == Intermediate and Medial portions of the Hyperstriatum Ventrale