SENSITIVE PERIODS IN THE DEVELOPMENT OF BEHAVIOURAL ORGANIZATION IN THE DOG AND THE ROLE OF EMOTIONAL HOMEOSTASIS

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Introduction

It is generally agreed that experiences during a sensitive period of canine behavioural development, from 2.5-3 weeks to some time between 12 and 14 weeks, have a more profound and lasting effect than those that occur in later life (Freedman *et al* 1961; Scott & Fuller 1965; Fox 1978; Bateson 1979; Serpell & Jagoe 1995; Overall 1997; Scott & Marston 1950). Exposure to benign novelty during this period appears to be essential to the development of sound temperament (Scott & Fuller 1965; Appleby 1993, 1999; Overall 1997; Appleby *et al* 2002; Campbell 1975; Serpell & Jagoe 1995) and optimal welfare (McCune *et al* 1995). Although these studies have remained influential (Serpell & Jagoe 1995; Hubrecht 1995) some of the earlier findings have been questioned in respect of being context-specific, and also in terms of experimental design (Webster 1997; Overall 1997; Appleby 1999) and interpretation of results (Lehrman 1970; Webster 1997). This paper proposes an alternative explanation for the development of inappropriate avoidance and fearful behaviour by examining how behavioural organisation is influenced by the emotional development of the dog, and furthermore, suggests that the three to five week period of development forms the foundation for the whole of the sensitive period.

Emotional states

Current thinking suggests that animals have emotional states such as fear, euphoria, anxiety etc., which can be defined as a cohesive set of behaviourally and physiologically integrated responses to environmental experiences (Spruijt 2001). They have an organizing effect on other brain structures, and induce an internal state which may be indirectly recognized by observing behaviour patterns and by the presence of internal organizing signals such as hormones (Spruijt 2001; Fraser & Duncan 1998). Brain structures involved in the selection of responses integrate cue and context-related information with the emotional state of the animal (Spruijt 2001; Fraser & Duncan 1998).

Emotional states are not hedonically neutral but are experienced as either positive or negative (Fraser & Duncan 1998; Frijda 1988) and may occur because of a match or mismatch between events and interests (Fraser & Duncan 1998; Frijda 1988).

Behavioural organisation, emotional homeostasis and maintenance sets

Behavioural organisation allows an organism to achieve emotional homeostasis, which is defined as neurophysiological stability, in a varying environment, equipping it with an independent capacity to cope and adapt (Vincent 1986). The dog's capacity to remain in emotional homeostasis develops throughout the sensitive period for behavioural organisation, as part of the process whereby mental representations of stimuli are formed and linked to associations and responses. Some of those associated with parasympathetic activity, the means whereby emotional homeostasis is achieved, become part of a maintenance set of animate and inanimate objects. Emotional dependence upon these objects or stimuli associated with them is formed and maintained by exposure (Pageat 1998; Bateson 1981; Cairns 1966; Scott 1963) and, for social stimuli, may not depend upon but may be enhanced by the presumed primary reinforces, such as suckling (Harlow & Zimmerman 1959; Igel & Calvin 1960; Pageat 1998) and physical contact (Cairns & Johnson 1965).

Whether a stimulus becomes part of a maintenance set and the extent to which dependency upon it develops is determined by cue salience, duration of exposure, context (Cairns 1966), the stimulation the object provides (Cairns 1966; Gross 1996; Gubernick 1981) and the extent to which a maintenance set has developed and enabled behavioural organisation (Scott 1968). During the sensitive period for behavioural

organization the process is rapid and easily influenced, but is initially regulated by stages of sensory and neurophysiological development during which higher levels of neural organisation build upon more primitive mechanisms (Fox 1971). Therefore disturbance at an earlier stage of neural development will have negative consequences for subsequent development (Fox 1971).

In the first 16 weeks of life periods of decreased and raised heart rate occur (Scott 1958). These correlate with parasympathetic (three to five weeks) and sympathetic dominance (week five to a peak at seven/eight weeks followed by gradual decline) respectively, and are manifested in changes in approach-avoidance behaviour (Lindsay 2000). The three to five week dip in heart rate results from integration of neural connections and the development of emotional responses to social and non-social stimuli (Lindsay 2000).

Disruption of homeostasis

Disruption of behavioural organisation, and therefore disruption of emotional homeostasis, can cause frustration, anxiety and/or fear. Reduction in parasympathetic autonomic system activity results in activation of regulatory mechanisms with the aim of re-establishing emotional homeostasis. If the challenge to these mechanisms is too great the organism will experience a sense of loss of control, reducing its capacity to cope and adapt.

Disruption of homeostasis can be caused by:

1. Unconditioned (innate/prepared) threatening stimuli: Animals may react fearfully towards a stimulus because of its physical characteristics (ie intensity, duration, suddenness).
2. Conditioned threatening stimuli: the stimulus is associated with a threatening event as a result of learning.
3. Novel stimuli: as the level of behavioural organization increases, the presence of novel stimuli and stimuli that do not perform to expectation may lead to a negative emotional state.
4. The loss of stimuli from the maintenance set which leads to a feeling of reduced control and disruption of responses to subsequent events. The extent to which the behaviour is disrupted will increase with the combined salience of the lost stimuli.

Furthermore, these factors can combine and their effect accumulate through a process of sensitisation.

Development of behavioural organisation

Behavioural organisation in the ontogenetic **initial phase** is largely reflexive and concerned with survival (Lindsay 2000). Only rapid changes in physical stimulation, such as sudden loss of support (hunger, cold, lack of contact, pain), cause distress (Kagan 1970). There is no wariness of novelty (Smith 1979) and limited capacity for conditioning (Lindsay 2000; Fox 1971). The **initial phase** of behavioural organisation and normal maintenance set development results in a puppy becoming emotionally dependent upon its mother and to a lesser extent on its littermates and nest-site. This is inevitable because of the availability and salience of the stimuli, sensory and cognitive development (Scott 1992; Fox 1978) and absence of opportunity to attach to other stimuli due to limited drive and mobility. Initial behavioural organisation, manifested as dependency on the maternal figure is not simply an affectional bond but a way of maintaining homeostasis of the autonomic nervous system (Cairns 1966; Bourdin 1999; McFarland 1999).

The **second phase** of development reduces dependence upon the very narrow and salient maintenance set already established by increasing the number and variety of stimuli for behavioural organisation after perceptual and locomotor abilities develop and reflexive behaviour declines. Stability developed in the first phase establishes the confidence to explore other stimuli and develop parasympathetic responses through further learning (Bradshaw *et al* 2002). There are two mechanisms involved in the seeking system and development of behavioural organisation at this stage; perceptual learning and response selection (Smith 1979). Perceptual learning involves recognition of new stimuli and variations in familiar stimuli (Carlson 1998) but this is only useful in conjunction with other forms of associative learning. This learning involves the acquisition of cue properties for stimuli that elicit the organization of behaviour (Carlson 1998; Cairns 1966). Exploration is driven by the seeking components of the brain, which were without intrinsic cognitive content in the initial phase of development but now exhibit spontaneous learning.

Seeking (Panksepp 1998) is aroused by:

- Regulatory imbalances that drive consummatory reflexes, leading to general arousal and motor output of forward locomotion.
- External stimuli. These can be subdivided into biologically relevant stimuli which are unconditioned and are relevant for survival, and biologically irrelevant cues. The former have a strong innate interaction with the system. The latter have weak interactions with the system prior to conditioning because they are not indicators of environmental events that promote survival. The motor output consists of exploration, approach-sniffing behaviour, investigation and species-typical foraging.
- Cues associated with incentives. The seeking system interacts with higher brain circuits that mediate the ability to anticipate rewards. Animals exhibit expectancies in response to cues which have been previously associated with arousal of this system, and display anticipatory approach towards them (Panksepp 1998). Consummatory behaviour results in disarousal of the system (Panksepp 1998).

Behavioural organisation is also developed through exposure to different contexts, and novel and challenging stimuli (Fox 1978; Serpell & Jagoe 1995) that disrupt it and result in the learning of responses that maintain emotional homeostasis. Expectation of these outcomes increases the sense of control and reduces emotionality.

The **third phase** is reached when a broad maintenance set is established and behavioural organisation to the known environment is achieved. Subsequent change is more likely to upset than to benefit the system. However, the composition of stimuli in maintenance sets is variable because their effect can diminish, extinguish or be superseded by more salient or more available stimuli.

An expectation based on learned associations is an important cause of fear (Smith 1979). Cumulative experience will increasingly become a determinant of fearful and non-fearful responses during the rest of life. Stimuli which are moderately difficult to assimilate – for example, those that are somewhat unpredictable - will generally bring about exploratory responses, so long as other contextual factors are reassuring and that the animal has a preference to investigate novel stimuli or locations over those that are familiar (Smith 1979).

The ability of the individual to maintain contingent behaviour sequences or control is (probably) very important (Smith 1979). The individual may readily learn specific fears of eg unfamiliar stimuli, and retain and generalise them, because of their initial discrepancy in visual appearance, and/or noncontingent or unpredictable sequencing of behaviour (Smith 1979).

The sensitive period of behavioural organisation: An alternative view to the present concept of socialisation and habituation

The previous model of the development of fear responses to novel stimuli (Scott & Marston 1950; Freedman *et al* 1961; Scott & Fuller 1965) and subsequent research based on it (Fox 1971), clearly showed that behavioural development in the dog takes place during identifiable phases. Isolation experiments to determine the timing of the development of behavioural problems due to a lack of socialisation have limited use, and may even be slightly misleading because they are based on observation of behavioural change. In fact, these changes follow a period of development of the relevant brain structures, their integration and most importantly a period of behavioural organisation that makes subsequent response to novel stimuli possible (Fox 1964; Fox 1971). In other words, before an animal is in the position to identify a stimulus or event as being "novel", it must have formed a cognitive representation of the world in which it lives, making it possible to form expectations (Gray 1971; Williams *et al* 1997).We propose that the underlying mechanism involves representations of stimuli to which the animal has been exposed being stored in the pre frontal cortex up to the age of five weeks, after which integration with the hippocampus enables comparison between these stored representations of stimuli and incoming stimuli for the detection of novelty (Lindsay 2000).

Between three and five weeks approach and investigative behaviour is directed equally to novel and familiar objects but most attention is paid to rapidly changing stimuli, eg movement and sounds. As the formation of maintenance sets becomes more sophisticated, greater attention is paid to moderately discrepant stimuli that evoke investigative behaviour, and very discrepant stimuli that evoke fear. Conversely, attention to familiar stimuli declines (Kagan 1970). Discrepant events in the environment will lead to arousal and

attempts to compare with previous events, and to find a suitable coping response (Kagan 1970). Successful assimilation will lead to behavioural organisation and reduced attention.
During this second stage recognition and recall memory develops (Smith 1979). Search behaviour for missing social or non-social objects start to appear (Kagan 1970) and latency of approach to a novel object starts to increase. Evaluation and attempted assimilation of context, rather than arousal by stimuli in isolation also starts to occur (Smith 1979). Therefore, introduction of a new stimulus in a familiar context may cause a positive emotion, whereas introduction of the same stimulus in an unfamiliar context may cause a negative emotion (Smith 1979).

Conclusion

Changes in behaviour and increases in emotionality both result from the maturation and integration of structures in the brain. The increase in bi-directional interchange of information between the various areas of the brain, but especially between the hippocampus and neocortex, make more detailed information processing possible. Once parasympathetic dominance has declined and the maintenance set has been formed, unfamiliar stimuli encountered may cause sympathetic arousal. The characteristics of these stimuli and the characteristics of the maintenance set will determine the extent of sympathetic arousal, and the particular behaviour displayed. The presence of an effective maintenance set also increases the individual's confidence to explore and broaden that maintenance set over the ensuing weeks. It follows that a failure to develop an adequate maintenance set during the period of parasympathetic dominance between three to five weeks and beyond should have a detrimental effect on the development of subsequent behaviour, and by implication on welfare, and will increase the probability that behavioural disorders will develop.

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