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*Sensory development in puppies (*Canis lupus f. familiaris*): implications for improving canine welfare*

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Abstract

*Despite an auspicious start from which lasting theories were generated (eg critical periods hypothesis, Scott & Marston 1950), and despite recent modern technology enabling biological investigations of sensory development (eg EEG, fMRI), in the last fifty years little attention has been devoted to the development of puppies' (*Canis lupus f. familiaris*) sensory abilities. Attention to puppies' sensory development is needed for both theoretical and applied purposes, because understanding puppies' early experiences depends on understanding their perceptual world. This paper reviews the chronology of sensory development in puppies, looking at each sense individually. It then examines the relationships among phases of sensory and neural development and the critical periods proposed by Scott and Marston (1950). With improved knowledge and awareness of canine sensory development, researchers and other practitioners that work with puppies can better assess and improve puppies' welfare. Therefore, this review should be of interest not only to researchers, but should also be of use to others that interact with dogs (eg shelter workers, dog breeders). By knowing what puppies are able to see, practitioners can visually enrich puppies' environments. By knowing what puppies are able to taste and smell, practitioners can better predict the preference-related impact of introducing dietary variation to puppies. Knowing when puppies are first, and best, able to hear, see, and otherwise sense people and other animals, practitioners can design and customise programmes of socialisation and systematic exposure of young puppies.*

Keywords: *animal welfare,* Canis lupus f. familiaris*, critical periods, puppy, sensory development, socialisation*

Introduction

More than a century ago, Mills (1898, as reported in Scott & Marston 1950) conducted observational studies in which he observed that puppies (*Canis lupus f. familiaris*) showed behavioural responses to loud sounds 18 days after birth. This study was followed by numerous observational and experimental studies that were conducted in the 1930's through into the 1970's (eg Menzel & Menzel 1937; Scott 1958, 1963; Fox 1964, 1966), many of which were conducted in affiliation with Jackson Laboratories (eg Scott & Fuller 1965). Despite this strong and precocious beginning, from which lasting theories were generated (eg critical periods hypothesis, Scott & Marston 1950), and despite recent modern technology enabling biological investigations of sensory development (eg EEG, fMRI), little attention has been devoted to the development of puppies' sensory abilities since the conclusion of Scott and Fuller's (1965) studies.

According to the theory presented by Scott and colleagues (eg Scott & Marston 1950; Scott 1958, 1962, 1963; Scott & Fuller 1965), there exist critical periods when puppies have a heightened level of sensitivity to certain aspects of their surroundings. During these periods, experience is most likely to have either a positive or a negative life-long impact on puppies (Scott & Marston 1950; Fuller 1967). These critical periods show patterned relationships with puppies' phases of sensory and neural development (eg Fox 1966) such that the beginning of most critical periods correspond to advances in sensory or neural development.

Breeders, pet owners, and practitioners working with dogs have long held the belief that dogs' early experiences are important. Early experiences are believed to shape animals' later behaviour, reactions to the environment, and personalities. Beliefs about the influence of early experiences on dogs have lead to enrichment programmes for guide dog puppies and other working dog puppies, in addition to debate over the ideal age at which to remove a puppy from littermates and dam (eg Slabbert & Rasa 1993). Groups interested in these issues have ranged from private dog owners and breeders to professional working dog breeding and training institutes.

Understanding puppies' early experiences is dependent upon understanding the puppies' perceptual world. Without knowing whether, or what, puppies are able to see, one cannot be certain whether puppies' environments are enriched by visual stimuli. Without knowing when puppies are able to taste or smell, one cannot predict the preference-related impact of introducing dietary variation to puppies.

Without knowing when puppies are able to hear, see, and otherwise sense people, one can neither logically begin a programme of socialising young puppies to humans, nor understand all of the intricacies and variations in puppies' behaviour and learning. Historically, much of dog socialisation and training (eg early training of sheepdogs) has been done through trial and error – which may be inefficient for both dog and trainer, and also stressful and detrimental to the dog's social and psychological well-being.

An examination of the current state of knowledge of how phases of sensory and neural development may underlie the critical periods will allow a greater understanding of the dynamic development of puppies. A reasonable point at which to begin examination of development is the sensory state of newborn puppies, and so this review begins by describing the sensory state of newborn puppies. What senses are newborn puppies able to use? What implications does this have for the puppies' early experiences? Clearly, what puppies are able to experience also depends upon their neurological development, and, as such, the development of myelin in puppies' brains will be discussed. The review will then cover the development of each of the senses, in approximately the order that they become of use to puppies: tactile and thermal, vestibular, taste, olfaction, vision, and audition. When puppies are born, their eyes and ears are closed and their senses of vision and audition are most limited. As a consequence, vision and audition undergo the most development postnatally and will be given the most attention in this review. Next, the development of puppies' sensory systems will be examined in terms of phases or periods, termed here 'developmental phases'. Finally, relationships between these sensory and neural developmental phases and critical periods of behavioural and social development will be discussed in order to draw a larger picture of puppies' development.

Although it is a synthesis of past research which even draws from past reviews (eg Fox 1966; Braezile 1978), this review aims to draw attention to the lack of research attention that puppies' development has recently received. This review is pertinent both to those who work with dogs in applied domains and those interested in them for more theoretical reasons. Relevant applied practitioners include those interested in the practical tasks of selecting levels of enrichment for litters of potential working dog (eg guide dog, explosive detection dog) puppies, and those interested further understanding early dog-human interactions. The review will also be informative and useful to dog shelters and rescue groups, which often need to care for orphaned puppies and select the appropriate age at which to place puppies in homes. The review can also be of use to the growing body of researchers interested in personality and temperament assessment in the domestic dog, providing insight into why puppy temperament tests fail, when puppies may be most malleable, and how to design a test such that the puppy perceives stimuli in a predictable fashion. Finally, the review will be important to the growing body of research scientists interested in using animal models to examine basic issues of human personality and psychology (Gosling 2001) and animal behaviour (Dugatkin 2004).

Sensory state of neonate puppies

Puppies are altricial mammals; at birth, their neural organisation, sensory abilities, and motor abilities are limited and immature (Fox 1966). Neonatal puppies show evidence of a developed tactile and thermal sense, responding to touch, pain, heat and cold (Scott 1958, 1963; Braezile 1978). Vestibular reflexes (eg gravitational senses, head-righting) are also present at birth (Scott 1963; Braezile 1978), although puppies show weak motor abilities (Braezile 1978). Puppies are also able to detect and react to olfactory stimuli at birth, showing avoidance of oil of anise and dog repellants, despite immaturity (including lack of myelination) of olfactory tracts and bulbs at birth (Scott 1958). Further investigation might reveal that these stimuli may act on the trigeminal system, which is known to be more developed at birth (eg Harman, as reported in Scott 1958, 1963; Fox 1970). Due to the immaturity of the olfactory system, some researchers (eg Harman, as reported in Scott 1958, 1963) propose that these reactions to olfactory stimuli are mediated by the sensory system associated with taste, not true olfaction. There is evidence that puppies are able to not only detect tastes, but acquire conditioned responses to tastes, as early as day one (Fox 1966). In contrast, puppies appear unable to detect visual and auditory stimuli at birth, as their eyes and ears are closed.

Myelination in neonate puppies

Myelin, which wraps around neuronal axons in the central and peripheral nervous systems, provides insulation for the axon and facilitates the faster propagation of impulses down the axon (Bear *et al* 2001). Examination of myelination of puppies' brains immediately after birth reveals myelin to be virtually absent from these immature brains, and present only surrounding the trigeminal nerves, the facial nerve, and the non-acoustic (ie vestibular) portion of the eighth nerve (Harman, as reported in Scott 1958, 1963; Fox,1970). The trigeminal and facial nerves, which connect to the jaw, face and tongue (Bear *et al* 2001), are clearly associated with the most frequent activity in the neonate puppies' lives: nursing (Harman, as reported in Scott 1958, 1963).

Fox (1970) found that between birth and 21 days of age there is a gradual increase in myelin covering the spinal cord first in the cervical region and motor areas, then in the sensory areas. By 21 days of age, the myelination of puppies' optic nerves has been described as adult-like (Fox 1964). Between 21 and 35 days after birth, the thalamo-cortical afferent nerve fibres that carry primarily tactile information from the body to the brain (Bear *et al* 2001) become myelinated (Fox 1970). During this period, at 28 days of age, Fox (1970) reports that myelination is first detected in the somatosensory area. By 48 days after birth, myelin is more evenly distributed over the visual and auditory cortex. Still, myelination of the brain continues to increase slowly until approximately nine months of age, at which point the myelination of the brain resembles that of an adult dog.

Puppies' postnatal sensory development

This section details puppies' postnatal sensory development. Some sensory systems (eg tactile and thermal sensation, vestibular orientation) appear to be mature at birth, functioning like those of the adult dog despite puppies' overall, and, in particular motor, immaturity. Neonatal puppies may react severely to and readily sense cold, but, for example, be unable to get up and move because their muscle and motor cortices are not yet well developed. On the other hand, some sensory systems (eg olfaction, taste) appear functional and mature judging from behavioural observation, but immature judging from myelination of the association neural pathways. These systems have not been thoroughly investigated. In these cases, and because taste and olfaction are so closely related, it is difficult to determine the maturity of the sensory systems. The visual and auditory systems, on which this section will primarily focus, are clearly the least mature of the sensory systems when puppies are born: the eyes and ears are both closed and puppies have been described as blind and deaf.

Tactile and thermal sensation

At birth, puppies show behavioural reactions (eg movement, yelping) in response to touch, pain, heat, and cold (Scott 1958, 1963). Their tactile responses, however, are largely or entirely limited to stimulation of the head and the body (Braezile 1978). Stimulation of the forelimbs does not elicit a response until seven to 14 days of age, and stimulation of the rear, or pelvic limbs does not elicit a response until puppies are 14 to 21 days of age (Braezile 1978).

Shortly after birth, however, a variety of stimulation of the head or body can elicit reflexes and responses from puppies. Pricking neonate puppies' skin with a pin elicits vocalisations and attempts at withdrawal from the stimulus, implying more than minimal maturation of the afferent sensory system of the pain sensory system (Braezile 1978). In addition, the twitching of the skin, called cutaneous twitch or panniculus, in reaction to stimulation of the thoracic and abdominal wall can be elicited from birth (Braezile 1978). Immediately after birth, many puppies also show a 'wink reflex' when their eyelids are touched; nearly all puppies show this reflex by seven days of age (Scott 1958). One to two days after birth, puppies shake their heads in response to stimulation of the pinna (external ear flap), regardless of whether pain is induced, as well as to stimulation of the external ear canal (Braezile 1978). At two days of age or older, repeated pin pricking or scratching of the thoracic wall or neck elicits a scratch reflex (Braezile 1978). Braezile (1978) observed that, even though the movement of puppies' pelvic limbs corresponds with the side of the body that is stimulated (and resembles adult dogs' scratch rate and rhythm), puppies lack the co-ordination required to bat away the offending object. As mentioned above, early responses to tactile stimuli occur primarily in reaction to contact with the head or body. Limb withdrawal reflexes, in response to pain-inducing stimuli, can sometimes be elicited in neonate puppies, but the reactions are very slow and accompanied by distress vocalisation (Braezile 1978).

Braezile (1978) also observed that when puppies are one to two days old, tactile stimulation of the trunk of the body or the side of the face elicits movement in that direction and puppies press against the stimulus. Braezile (1978) further observed a few behavioural patterns that seem contradictory. The first behavioural pattern is that puppies' response to move towards tactile stimuli becomes more intense during the first 14 days of age, even exhibiting an 'after effect' in which the puppies seem to continue to attempt to make contact with the stimulus once it has been removed. Between 21 and 28 days after birth these responses become more dependent upon puppies' 'attitude' toward the individual in question. If a stranger (eg a veterinarian) touches the puppies, the puppies might not attempt to press against the stimulus. According to Braezile (1978), if a familiar person touches the puppies, the response of leaning against the stimulus continues into adult ages. The notion of the 21-day-old puppies' responding to touch based upon the familiarity of the person who is touching them contradicts Braezile's (1978) statement that puppies are unable to recognise their owner or mother, as indicated by vocal or behavioural signals from the puppies, until at least 28 to 35 days after birth.

Vestibular orientation

At birth, puppies show adult-like behavioural reactions (eg head-righting) indicating that they are aware of their orientation in space (Scott 1963; Fox 1964; Braezile 1978). Shortly after birth, a variety of physical manipulations of puppies elicit responses indicative of a developed vestibular orientation system. In one-day-old puppies, vestibular head-righting is observed when the puppies are held with their heads up, tilting the body forward and backward (Braezile 1978). The puppies will tilt their heads to maintain their heads upright. In addition, holding one-day-old puppies upside down results in weak attempts to right their heads (Fox 1964; Braezile 1978). This response also strengthens during the first postnatal week until, at seven days of age, the response is quick and accompanied by full-body struggles (Braezile 1978). Braezile (1978) reports that adult-like vestibular reflexes occur when the somatic motor system is more mature; at 21 to 28 days after birth. If puppies are placed on their backs, they will show a relatively strong head-righting response. If puppies are righted, they will not only cease to struggle to right their heads, but will also extend their forelimbs. This reflex quickly strengthens until, at 14 to 21 days, the rear limbs are also used. Braezile (1978) noted that the vestibular apparatus is already differentiated when puppies are born and proposed that the maturation of the vestibular righting reflexes during the first 35 days after birth was a reflection of the maturation of somatic motor control, as opposed to the vestibular apparatus.

In addition to the head-righting reflex, eye movements can also be elicited by alterations of head position in young puppies, as soon as eyelids are open (Braezile 1978). These eye movements are elicited by tilting the head. The visual system appears to be inadequately developed to produce this response until puppies are at least 21 days old (to be discussed further when we address the development of the visual system). Thus the puppies' responses to this test are based on the development of the vestibular system.

Taste

As early as the day of birth, puppies can acquire a conditioned response to taste (Stanley *et al* 1963; Fox 1966). Acquiring a conditioned response to taste requires the ability to perceive taste, and thus puppies' ability to acquire conditioned responses to taste indicates they can perceive the taste stimuli. Puppies are able to acquire approach responses to taste stimuli significantly sooner than withdrawal responses. The withdrawal response to the taste stimulus cannot be conditioned until around day 14 (Fuller *et al* 1950). It is possible that both of these responses can be acquired around the same time due to puppies' cognitive maturation, in addition to or instead of improvements in sensory abilities.

Olfaction

At birth, puppies show behavioural reactions (eg withdrawal) from certain odours, which may be detected primarily through use of taste as opposed to olfaction (Scott 1963). For example, even shortly after birth, puppies will move towards and lick fish-scented drops (Scott & Marston 1950), suggesting they are able to detect the stimuli, whether through taste, olfaction, or both. It is unclear which system (taste or olfaction) is used to detect these stimuli (Scott 1963). In a study reported by Scott (1958), puppies tested shortly after birth consistently showed avoidance responses to two substances: oil of anise and a drug used as dog repellent (related to citronella). Two hundred puppies were examined. Eighty-three percent showed avoidance responses to the dog repellent, and a 'smaller number' showed avoidance responses to the oil of anise. Due to the lack of myelination of olfactory tracts and bulbs when these responses to anise and repellent are shown (Harman, as reported in Scott 1958, 1963), Scott suggests that the reactions to odour are due to detection by sense of taste, not by olfactory detection.

Scott (1958) also reported observational evidence that hungry neonatal puppies show a response to the smell of milk, but did not claim evidence for it. It has also been suggested that puppies are able to smell and taste because they will move towards fish-scented drops, even just shortly after birth (Scott & Marston 1950). These observations are in accordance with Fox's (1966) later report that approach (motor orientation towards food) can be conditioned to an olfactory stimulus as early as the day of birth. In contrast, withdrawal in response to an olfactory stimulus cannot be conditioned until around 13 days after birth (Fuller *et al* 1950; Fox 1966). Clearly, if an animal can be trained to approach in response to stimulus, the animal can detect that stimulus. Inability to acquire the avoidance response must be due to other aspects of the task, beyond initial detection. Fox (1966) and others theorise that this may be due to the cognitive complexity of the withdrawal response.

Vision

At birth, puppies' eyelids are closed (Scott 1963; Braezile 1978) and, as the retina is poorly differentiated (Braezile 1978), they are blind. Estimates of the age at which puppies' eyes open vary from between seven days in a few puppies examined by Scott (1963) to more than 14 (Scott 1963; Braezile 1978). In a sample of 195 purebred puppies (of various breeds), only two showed the eye completely open seven days after birth (Scott 1963). Two-thirds had opened their eyes by 14 days, however. The mean time until the puppies' eyes opened in this group was 13 days. This fits with Braezile's (1978) report that the eyelids open between 10 and 15 days of age. Scott and Marston (1950) report that puppies open their eyes anywhere between 11 and 19 days. However, Strain *et al* (1991a) reported that his subjects (all beagles) had all opened their eyes at eight to 10 days of age; somewhat earlier than Braezile (1978), Scott (1963), and Scott and Marston (1950) report. It has been suggested that this is due to variability in the length of gestation period: puppies may be born more or less immaturely (Scott & Marston 1950). A more consistent estimate might be obtainable by counting from the day of conception. When the eyes open, responses to light and moving objects are weak and variable (Braezile 1978), but some patterns can be observed across the literature.

Behavioural tests of visual capacity

Even before puppies' eyes open, a blink reflex in response to light can be shown under certain conditions (eg Braezile 1978; Scott 1958). Scott (1958) reported that some puppies will 'wink' in response to light as early as immediately after birth; at least seven days before the eyes open. He further observed that this response was most often elicited from breeds with red hair and light skin pigment. This may be due to the light pigment doing less to impede the passing of light through the closed eyelid. Similarly, Braezile (1978) reports that a bright light shown through the eyelid before the eye is open will elicit a slow blink and that, if the light is maintained in front of the eye, will elicit a withdrawal response from the puppy. He reported that the blink reflex in response to a bright light remains slow compared to that of an adult dog until puppies reach at least 35 days of age. Once the puppies' eyes are open, blink reflexes in response to tactile stimulation of the cornea (eg a puff of air) are immediately present (Braezile 1978).

The pupillary reflex (ie constricting of the opening of the pupil) to strong light usually appears as soon as the eye opens (Scott 1958, 1963). Ophthalmoscopic examination of the eye when puppies are 14 to 21 days old reveals that the pupillary reflex in response to light is weak and not as complete as in adult dogs (Braezile 1978). By 28 to 35 days of age, puppies' pupillary reflex in response to light appears like that of an adult dog (Braezile 1978).

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As soon at the eyes are open, the nystagmus reflex can also be observed (Scott & Marston 1950; Scott 1958; Braezile 1978). If puppies' heads are slowly rotated, the eyes move from side-to-side quickly. Scott (1958) theorises, however, that this reflex is controlled by the non-auditory (eg vestibular) portion of the acoustic nerve, not by sight. Braezile (1978) agreed, stating that the visual system is not mature enough to produce this response until 21 to 28 days of age and that it is likely that the vestibular system controls this reflex. In support of this idea, Scott (1958) observes that puppies do not show the nystagmus reflex in reaction to visual observation of moving objects. Scott (1958) suggests that puppies are able to perceive only light and darkness, not images, until 28 to 35 days of age.

During the seven days following the opening of puppies' eyes, visual tracking of moving objects improves (Braezile 1978). By 21 to 28 days (Braezile 1978) or 26 days (Fox 1964), visual tracking becomes stable and similar to that of the adult dog (Braezile 1978). Visual fixation in puppies is reportedly similar to that of an adult dog at 28 days after birth (Fox 1964).

Other tests of visual capacity

When puppies are born, not only is the eyelid closed, but the structure of the eye is yet to develop entirely. At birth, the retina itself is not yet entirely formed, or 'differentiated' (Braezile 1978). Histological examinations reveal that, despite the fact that the eye shows various responses to bright light, the retina is still not fully developed when the eyes open, nor at 21 days of age (Scott 1958). Later histological examinations reveal that at 28 days of age the retina is still not completely developed, indicating that the eye is still not able to function in the same way as the adult eye (Parry 1953; Scott 1963).

Braezile (1978) reported on a study of electroretinographic (ERG) activity, starting at birth and continuing through more than 32 days, or four and a half weeks, after birth. There was no ERG activity at birth, reflecting a low level of receptor cell response to light. By 10 days after birth, ERG activity is present but poorly developed and with a long latency of 12 to 20 msec (compared to the adult latency of about 0.07 msec). In addition, these early wave patterns are significantly different from adult patterns. Between 11 and 18 days, the ERG waves recorded show their greatest increase in size (amplitude), and Braezile explained that this corresponds with the point where the retina is extremely close to demonstrating an adult pattern of organisation. By 21 days after birth, the puppies' wave patterns are similar to those of adult dogs, and latency has shown a clear trend towards the adult dogs' typically low level. When the puppies reach 28 days of age, the adult pattern of amplitude and latency of ERG is observed.

An early study of the development of puppies' electroencephalogram (EEG), starting at birth and continuing through to 56 days after birth (Charles & Fuller 1956), revealed a more conservative estimate of the time by which the puppies' visual system reaches its adult level of functioning. The EEG allowed researchers to examine alpha rhythms, thought to be indicative of the functioning of the visual cortex (Charles & Fuller 1956). In Charles and Fuller's (1956) study, puppies examined immediately after birth show a virtual complete absence of the alpha rhythm, with no discernable difference between waking and sleeping states. At about 21 days after birth, the EEG begins to show differences between waking and sleeping states, and an alpha rhythm appears. The final adult EEG is developed between 49 and 56 days after birth, indicating that visual function is not fully developed until even later.

In a more recent study, Strain *et al* (1991a) examined visual-evoked potentials from 13 beagle puppies between the ages of seven and 100 days. The researchers induced potentials by flashing white light 20 cm in front of the puppies' eyes. Responses were recorded between needle electrodes strategically placed on the puppies, allowing researchers to record five alternative positive and negative peaks (3 positive, 2 negative). Two of the puppies were tested before their eyes were opened. Peak latencies were very similar to those of the adult dogs by day 11 for positive peak 1 and day 38 for negative peak 1 and positive peak 2. Positive peak 3 did not reach the amplitude revealed in adult dogs prior to day 100, but did plateau around day 43. The amplitude between positive peak 1 and negative peak 1 reached the level shown in mature dogs by day 14, and the amplitude between negative peak 1 and positive peak 2 did so by day 32. The amplitudes of other parts of the wave pattern reached plateaux that exceeded adult amplitudes by day 58.

Audition

At birth, the external meatus (or pinna) of the ear is folded over the ear canal such that the ear appears closed (Scott 1963; Braezile 1978). In addition, the ear canal itself is closed (Braezile 1978). The external ear canal opens around 12 to 14 days, and further enlargement and opening of the canal continues until puppies reach about 35 days after birth, at which time the ear canal appears proportional to other external structures of the ear (Braezile 1978). Despite the fact that the ear is closed when puppies are born, the middle and inner ear structures in the newborn puppies appear to be well differentiated (Braezile 1978).

Behavioural measure of auditory capacity

Mills (1898, as reported in Scott & Marston 1950) reported that puppies showed behavioural responses to sound at about 18 days after birth. Other early observations of behavioural evidence of hearing in puppies suggested that boxers were able to hear as early as 15 days after birth, but that most boxer puppies showed behavioural responses to sound at around 21 days (Menzel & Menzel 1937). More recently, researchers have focused their behavioural studies of puppies' hearing abilities on the startle response (eg Scott 1958, 1963; Braezile 1978). A startle response is characterised typically by puppies moving away from the auditory stimulus and flattening their bodies to the floor, but some have been observed simply erecting their ears instead (Scott

& Marston 1950). In one-day-old puppies, loud noises (intensity not reported) elicit a generalised response (Braezile 1978). This response, though, does not occur immediately after the noise, unlike the startle-reaction. Braezile (1978) suggests that this reflects a general immaturity of the CNS structures which, by 14 days after birth, are mature enough to support a rapid startle response to auditory stimuli.

Scott (1958) did not find such precocious response to sound. In examination of 200 purebred puppies of various breeds, he found that only 1% of puppies gave a startle response to sound by 14 days after birth. Scott and Marston (1950) observed that they had never witnessed the startle response before 21 days after birth. By this age, however, 74% of puppies examined by Scott (1958) demonstrated startle responses. Scott thus estimated that the average age at which the startle response emerges is 19.5 days (Scott 1958, 1963). However, in the five breeds that Scott examined, he found considerable differences between breeds, with wire-haired terriers showing the earliest startle responses. Fox (1964) reported that puppies show adult-like auditory startle responses at 25 days after birth, and that they orient towards the source of sounds in an adult-like fashion by 26 days. Scott (1963) further suggested that there is doubt as to whether puppies are able to discriminate complex sounds as early as they demonstrate startle responses to sudden auditory stimuli, but states that it is clear that the ability to see develops sooner than the ability to hear.

Other measures of auditory capacity

Despite the appearance that the middle and inner ear structures are well differentiated and developed in neonate puppies, auditory cortical-evoked potentials cannot be recorded until puppies are 12 to 14 days old, at which point their amplitudes and latencies correspond to those of visual-evoked potentials (Braezile 1978). This correspondence may indicate that earlier responses are absent because puppies' ear canals are yet to fully open. When puppies are 21 to 28 days old, their auditory-evoked potentials are very similar to those of adult dogs (Braezile 1978).

Strain *et al* (1991b) examined brain stem auditory-evoked potentials using 'clicks' as stimuli from 13 beagle puppies, documenting their postnatal development between the ages of one and 76 days. Responses were recorded from measurements taken between needle electrodes, performed without sedation (for details of the procedure, see Strain *et al* 1991b). Low-amplitude responses to high intensity stimuli of 105 dB normal hearing level (nHL, 0 dB is the normal hearing threshold for young adult humans) were recorded from puppies even prior to the opening of the ear canals. The brain stem auditory-evoked potential thresholds were similar to those of an adult dog by 20 days after birth.

The results of Strain *et al* (1991b) correspond to those of Poncelet *et al* (2002), despite the fact they used slightly different stimuli. Poncelet *et al* (2002) conducted a study to build an audiogram from the threshold of brainstem tone-evoked potentials in dogs. In this more recent study, the researchers elected to use pure tones as stimuli instead of the clicks used by researchers such as Strain *et al* (1991b) because the click contains a larger variety of frequencies. Researchers thus view the pure tone as the more precise stimulus for threshold-isolating studies in which they wish to identify the minimum intensity at which an animal can reliably detect a given frequency (Poncelet *et al* 2002). The subjects of this study were nine beagles, examined between 10 and 47 days after birth. Three puppies were examined on days 10, 13, 19, 25 and 45. The four other puppies were examined at 16 days. The data from seven puppies examined between 42 and 47 days after birth were combined to yield an audiogram for 1.5 month-old puppies.

This study revealed extreme increases in sensitivity in the first month and a half after birth (Poncelet *et al* 2002). The best auditory threshold lowered from about 60 dB sound pressure level (SPL) at about 13 days to around 0 dB SPL at about 25 days, then stabilised. In addition, the audible frequency range widened to include 32 kHz from day 19 onward. The audiogram of the seven 1.5 month-old puppies shows that their auditory threshold decreased by about 11 dB per octave from 0.5 to 2 kHz, was lowest and relatively steady from 2-8 kHz, and increased by 20 dB per octave from 8 to 32 kHz.

Initial stages of learning as related to each sensory system

Many studies of early learning in puppies have examined how early puppies can be conditioned to show an approach, withdrawal, or defensive response to a given stimulus. Fox (1966) reviewed many of these studies, pulling together, among other findings, those shown in Table 1. Examination of when conditioned responses to stimulation of the various sensory systems can be elicited is of interest for many reasons. First, when a conditioned response is possible, it is necessary that the sensory system is developed enough to detect the stimulus. Hence this information provides an upper age limit at which puppies are able to detect various types of stimulation. Second, the ability to associate with a given stimulus implies further development of the cortices than examined in most other studies. Hence this information may give an insight into the upper age limit at which puppies are able to integrate sensory information to alter their behaviour. This is an upper limit because puppies may be able to respond to a stimulus before they are able to develop a conditioned response; conditioning requires some degree of memory in addition to sensation. Third, the order in which puppies acquire approach, withdrawal, and defensive conditioned responses may provide insight into the puppies' further cognitive development.

Column one of this table, entitled 'Sensory system', lists the system utilised for detection of the stimulus used in conditioning. An example of a tactile stimulus is gently poking the puppies' abdomens. This stimulus could be an indicator of presence of food and, if the puppies are capable of detecting the stimulus and forming the association, indicate that food is present. Column two, entitled 'Response type', categorically lists the three types of responses that were conditioned: approach, withdrawal (or avoidance), and

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Table 1 Age at which conditioned responses to stimulation of a sensory system have been elicited.

Sensory system	Response type	Conditioned response	Day	System maturity (day)
Tactile	Approach	Move/orient towards food	1	1
	Withdrawal	Avoid puff of air	10	
Thermal	Approach	Move/orient towards food	7	1
	Defensive	Defensive reaction (eg struggle)	17	
Vestibular	Approach	Move/orient towards food	10	1
Taste	Approach	Sucking response	1	1
	Withdrawal	Move away	14	
Olfactory	Approach	Move/orient towards food	1	Undetermined
	Withdrawal	Move away	13	
Vision	Approach	Move/orient towards food	21	49-56 days[a]
	Withdrawal	Move away	21	Eyes open: 7-19 days
	Defensive	Defensive reaction (eg struggle)	27	
Audition	Approach	Head orientation	21	20 days[b]
	Withdrawal	Move away	18	Ears open: 12-14 days[c]
	Withdrawal	Withdraw leg	27	

Columns 1 to 4 adapted from Fox (1966), who points out that food-motor responses at the rhinencephalic level develop early, with withdrawal responses developing much later. [a] This is the most conservative estimate of visual system maturity from Charles and Fuller's (1956) EEG study.
According to this study, puppies do not show EEG activity until at least 49 to 56 days after birth.
[b] This is a fairly conservative estimate of auditory system maturity, derived from Strain *et al*'s (1991b) examination of brain stem auditory-evoked potentials.
[c] The ear canals continue to open after the external meatus has opened. The ear canals appear entirely open 35 days after birth (Braezile 1978).

defensive. Approach responses involve moving or orienting towards something (eg food) when the conditioned stimulus (eg touch) is presented. Withdrawal responses involve moving the entire or part of the body, such as a limb, to avoid something (eg a puff of air, a shock) when the conditioned stimulus (eg touch) is presented. Defensive responses are a form of withdrawal response and may include struggling, stiffening, and pushing away from or against something in the environment in order to avoid an unpleasant experience (eg a shock, a pin prick) when a conditioned stimulus (eg cold) is presented. The conditioned response (column three) is the puppies' response to the conditioned stimulus; these responses are categorised into the three types just discussed. Column four lists the earliest day (from birth) at which the conditioned response could be trained and elicited. These range from day 1 for conditioned approach responses to tactile, olfactory, and taste stimuli, to day 27 for conditioned withdrawal responses to auditory stimuli. Overall, approach responses appear to be established first. With the exception of the vestibular system, for which a withdrawal response has not been conditioned, and the auditory system, which is known for the startle response (Scott 1958, 1963; Braezile 1978), all sensory systems show the conditioning of an approach response at the same time as (eg visual system) or prior to (eg tactile, thermal, olfactory, taste) the conditioning of a withdrawal response.

Column five lists relatively conservative estimates (from the review above) of when each sensory system appears to mature. This information may be of particular importance in making sense of the time delay between conditioning approach and withdrawal responses to tactile, thermal, olfactory, and taste stimuli, a pattern which is not as clear in conditioning responses to visual and auditory stimuli. At birth, some of the puppies' sensory systems are relatively well developed, thus puppies are able to detect stimuli. Puppies also appear able to acquire approach responses. However, withdrawal responses cannot be acquired until later. This difference may be due to the puppies' cognitive ability, not their sensory ability. Puppies are able to acquire conditioned withdrawal responses to tactile, thermal, taste and olfactory stimuli before they are able to acquire approach responses in response to visual and auditory stimuli, around the age at which the eyes and ears open.

Developmental phases and critical periods

This section deals first with the idea that the development of sensory systems and associated neural development fit into four developmental phases, as proposed by Fox (1964). Next it deals with the idea that the behavioural development of puppies also falls into phases, or critical periods, as proposed by Menzel and Menzel (1937) and later by Scott and Marston (1950). The possibility of the relationship between these developmental phases and critical periods is then explored.

Developmental phases

The previously discussed maturation of sensory and other physiological systems have been fitted into four developmental phases (Fox 1964). The first developmental phase spans from birth to five days afterwards. Developmental phase I is characterised by a lack of sensory responses of the audiovisual system, until a slow blink response to light can be elicited. The second developmental phase spans from five to 18 days after birth. During days five through 13 of developmental phase II, adult postural reflexes appear. During days 15-18, some puppy reflexes (eg crossed extensory and Magnus reflexes) fade. During this phase, the eyes begin to open, but the blink response is not adult-like until the end of the phase. A weak startle response may also appear. The third developmental phase spans from 18 to 28 days after birth. Developmental phase III is marked by the emergence of positive orientation responses towards visual and auditory stimuli, which are strong by day 25. In addition, the puppies' reflexes of rooting and urination on stimulation disappear, and adult sensory reactions (eg startle response, avoiding the edge of a visual cliff) and motor activities emerge. The fourth developmental phase characterised by Fox (1964) begins at 28 days and continues into adulthood. In this phase, adult behaviour emerges. The puppies avoid visual cliffs reliably, recognise littermates and humans both visually and auditorily, and begin to show both approach and avoidance behaviours in response to stimulation of all sensory systems.

The integration of the developed neurophysiological systems, according to some (eg Fox 1966), underlies the critical period of socialisation, to be discussed in the next section. In precocial mammals such as sheep (*Ovis aries*) or Guinea pigs (*Cavia porcellus*) (Scott 1962), neural integration occurs around the time of birth and is associated with early perceptual maturity, responsiveness to stimuli immediately after birth and is related to the early formation of attachment in social relationships, or imprinting (Scott 1962; Fox 1966). In altricial mammals, as exemplified by puppies' development, neural and physiological organisation continues long after birth and, once the sensory and neural systems have reached a relatively mature state, integration of the systems occurs.

Critical periods

In order to understand how the early stages of puppies' physiological development influence adult dogs' interactions with the environment, it is useful to consider the classic idea of critical periods, originally derived from research with other animals (eg the Greylag goose [*Anser anser*], jackdaw [*Corvus monedula*]; Lorenz 1965). The idea of critical periods has been explored extensively in both observational and experimental studies of puppies (eg Scott & Marston 1950; Fox & Stelzner 1967; Slabbert & Rasa 1993). As defined by Fox (1966; p 12), the critical period begins "when neural organization is sufficiently developed to permit perceptual interaction and adaptation to the environment and the establishment of primary social relationships." Defined more generally (Scott *et al* 1974; p 490), critical periods theory states that "the organization of a system is most easily modified during the time in development when organization is proceeding most rapidly." In agreement with both of these definitions, various researchers (eg Fox 1966; Scott 1958, 1962, 1963; Scott & Fuller 1965) have extended the hypothesis of what occurs after the integration of the developed neural systems to suggest that there are specific periods during postnatal development during which puppies have a heightened level of sensitivity to changes, and that experiences during these periods have a long-lasting impact on the adult dog's behaviour patterns.

There have been at least two different sets of critical periods proposed, both originating from observational research of the behaviour of puppies (eg Menzel & Menzel 1937; Scott & Marston 1950). As they focused on slightly different aspects of behaviour and development, both sets of critical periods differ slightly. Menzel and Menzel (1937) divided the development of puppies into five periods. The first period, called the vegetative period, lasts from birth to 14 days. The second period, in which the puppies are able to become aware of and respond to their environment, lasts from 14 to 42 days. The third period, called the whelp period, lasts from approximately 49 days to the end of the fourth month. It should be noted that this may leave a gap between the second and third critical periods; it is not necessary for critical periods to follow-on immediately after one another. The fourth period, called the pre-pubertal stage, lasts from the end of the fourth month to the end of the sixth month. The fifth period, the pubertal stage, lasts from the end of the sixth month to the end of the tenth month.

Scott and Marston (1950) divided the development of puppies into four periods: 1) the neonatal period, lasting from birth until the opening of the eyes (11-19 days, observed by Scott and Marston 1950); 2) the transitional period, lasting from when the eyes open until puppies are able to crawl out of the nest or whelping box at 21 to 28 days after birth; 3) the socialisation period, lasting from when puppies leave the nest until they are weaned by the dam at 56 to 70 days, or eight to ten weeks, after birth; and 4) the juvenile period, lasting from when puppies are weaned until they reach sexual maturity anywhere between seven and 14 months after birth. Scott and Marston's proposed critical periods do not draw divisions in the development of the puppy between weaning and sexual maturity, perhaps because they focus largely on sensory development. After weaning, most of the puppy's development is social; the sensory systems have already largely developed. Most later work that discusses critical periods and developmental periods in puppies refers back to Scott and Marston's four periods in puppy development.

As is apparent after reviewing the sensory capacities of neonate puppies, new-born puppies predominantly employ thermal and tactile senses, avoiding cold and moving towards physical contact (eg Scott & Marston 1950). During this stage, puppies appear concerned mainly with nutrition and body temperature (Fox 1964). Smell and taste are probably present, as reflected by puppies' responses to oil of anise, fish, milk, and dog repellant (Scott & Marston 1950; Stanley *et al* 1963; Fox 1966). However, it is not entirely apparent whether or not puppies use these senses early on. With exception of experimental manipulation, puppies take in no food except their dam's milk, and appear to do little smelling when in the neonatal period (Scott & Marston 1950). Puppies' eyes and ears are closed, and thus hearing and sight are both either extremely limited (as

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implied by blink responses to light, eg Scott 1958; Braezile 1978), or entirely absent (eg Scott & Marston 1950). Early research investigating the influence of traumatic experiences (ie extremely painful experiences) during the neonatal period have not revealed any lasting negative effects on puppies (eg Scott *et al* 1951), and researchers have described neonatal puppies as 'insulated' from the world and most environmental stimuli (Scott 1958).

The opening of the eyes serves as a distinct dividing line between the end of the neonatal period (period I) and the beginning of the transitional period (period II) (eg Scott & Marston 1950). However, the opening of the eyelids was not observed by Scott and Marston (1950) to significantly impact the behaviour of the puppies. Perhaps this is because the opening of the eyes reveals a still immature retina and, behind it, a brain not yet capable of processing complex visual stimuli.

Scott and Marston (1950) report that the opening of the eyes, which marks the end of the neonatal period and the onset of the transitional period, is quite variable, occurring anywhere between 11 and 19 days after birth. Other researchers have found that the eyes open even earlier, expanding the window during which opening may occur to between seven and 19 days. This variability is due possibly to differing lengths of gestation periods (Scott & Marston 1950). Once the eyes are open, puppies show limited visual responses. Shortly after visual responses appear, behavioural evidence of audition appears (eg startle reflex; Scott & Marston 1950; Scott 1958; Braezile 1978). By the end of the transitional period, all sense organs are functional to some degree, and visual, auditory, and olfactory senses begin to dominate tactile and thermal senses (Scott & Marston 1950). At the end of the transitional period, puppies are able to crawl out of their whelping boxes or nests (Scott & Marston 1950). At this point, the most dramatic growth and organisation of the CNS morphology (with respect to cell density, axonal development, dendritic development) comes to an end as such growth slows (Fox 1966).

Puppies enter their third period of development, the socialisation period, with all senses apparently functional (Scott & Marston 1950). Scott and Marston (1950), among others, believe this period of development to be the most important stage of development in puppies' lives and report several observations of behaviour during this period. At the beginning of the period, puppies appear extremely fearful, crouching down and shrinking away from any loud sounds or sudden movements. By 42 days after birth, the puppies begin to attempt to follow scent trails, and they use their eyes, nose, and mouth to explore novel objects in their environments. According to Scott and Marston (1950), puppies in this stage of development seem to become simultaneously aware of the dangers and helpful aspects of their surroundings, and have little to no control over their responses to their environments (ie cannot inhibit behaviour). This period is viewed as being the most important for puppies' development because the puppies' appear more emotionally sensitive to their surroundings (eg they yelp when left alone or otherwise distressed), and because puppies are, for the first time, open to forming social relationships that will have long-term impacts on their adult behaviour (Scott & Fuller 1965). Prior to this age, experimental isolation from either other dogs or people, or both, has not been shown to have long-lasting impact (eg Freedman *et al* 1961; Slabbert & Rasa 1993). However, isolation puppies which are isolated from human contact during the socialisation period behave differently towards people after emergence than puppies exposed to people during the socialisation period (Freedman *et al* 1961). In particular, puppies exposed to people between 49 and 63 days after birth are friendlier towards people after emergence. In addition, puppies separated from their dams during this period show poorer health (ie diarrhoea, low weight gain, higher mortality) than puppies allowed to remain with their dams (Slabbert & Rasa 1993).

The fourth period begins when the dam weans the puppies (which may vary from 56 to 70 days) and continues on until sexually maturity (Scott & Marston 1950). Scott and Marston (1950) report no change in sensory systems during this period. In contrast, Charles and Fuller's (1956) EEG study in which puppies did not display adult-like EEG patterns even at 49 to 56 days after birth, suggests their visual cortices were not yet mature at this age. Thus, it is uncertain whether sensory development is complete at the onset of the juvenile period.

The relationship between developmental phases and critical periods

Each of the developmental periods described by Scott and Marston (1950) and extended by others (eg Scott 1962) depends on the underlying neural organisation at that age (Fox 1966). As Ames and Ilg (1964) emphasise, behavioural patterns in immature organisms do not give way to mature patterns linearly, nor gradually. The differential rate of neural maturation – which influences the sequence of critical periods because it forms the basis of the neural abilities, which form the basis of behaviour – may promote maximal adaptation and survival of the organism at various phases of ontogeny (Anokhin 1964). For example, it may be highly adaptive for puppies in the socialisation critical period to have an elevated fear response to novelty, because this elevated fear response may cause puppies to avoid not only harmless novel situations, but also novel situations that are dangerous.

The developmental periods of neural organisation described by Fox (1964) and the broader developmental, or critical, periods described by Scott and Marston (1950) are listed sequentially, but their relationship to one another is not so simple. First, each stage of neural organisation and development seems to straddle the end of one critical period and the beginning of another. In this way, it is clear that it is possible the developmental phases lay the groundwork for new behavioural patterns and sensitivities to emerge in each approaching critical period. Second, neither the neural organisational periods nor the critical periods have definite and clear on-set and off-set times, partially complicated by variability between puppies that may be a consequence of variation in gestation time (Scott & Marston 1950), partially due to complications that may be a consequence of breed-specific genetic difference (eg Fuller & Clark 1966), and partially due to the relatively arbitrary nature of subdividing a continuous process.

Impact of critical periods on adult interaction with environment

The critical periods discussed here are not the last critical periods in a dog's life, nor do they yield an inflexible dog. They are theorised, however, to have a great impact on later critical periods. Other critical periods, dependent on neuroendocrine and environmental factors (eg nutrition, shelter) are observable later in life, notably at the onset of sexual and maternal activities. Both mating and the attachment formed by a dam towards her puppies are influenced by the developmental processes underlying the establishment of primary social relationships during the critical period of socialisation (Fox 1966). Dogs reared without conspecifics but with another species during the socialisation period may show sexual interest in animals of the other species (eg cats; Fox 1969). Bitches failing to form relationships with conspecifics as puppies may show fear or aggression towards, or minimal interest in, conspecifics later in life, which may interfere with maternal care towards a litter (Fox 1969).

Discussion and conclusions

This review shows that puppies go through tremendous developmental changes with respect to sensory abilities, CNS myelination, and behaviour in a relatively short period of time after birth. Puppies are born immature, able to sense contact, temperature, and their orientation in space. They may also be able to taste and smell. It is not clear if neonate puppies are able to detect sound and light at all; these senses are extremely limited. By 19 days at the latest, puppies' eyes and ears are open and all of their senses are, to a certain extent, functional. The precise days at which eyes and ears open, and the precise days at which visual and auditory abilities are mature, are unclear. This may be due, in part, to the variability in gestation period between litters, and even between puppies within a single litter. This variation in speed of development may also be due to genetic variation related to breed.

Implications for the treatment, socialisation and welfare of dogs

It appears that puppies' neural and sensory development fits into four developmental periods, as proposed by Fox (1964). These four developmental periods may provide the basis for the behavioural changes observable in each of the critical periods described by Scott and Marston (1950) and later expanded by Scott (1962). If the notion of critical periods in puppies' development is accepted, and the idea that experience during these critical periods can have life-long impact on dogs' interactions with their environment, then the implications of combining Fox's (1964) and Scott and Marston's (1950) ideas to illustrate puppies' dynamic development could be highly useful. Potential applications include improved design of early rearing quarters (ie whelping beds) to minimise stress to newborn puppies by making the environments best suited to their early senses; improving tactile and thermal comfort. Once puppies enter the transitional period in which their visual and auditory senses begin to dominate, it might be possible to improve puppies' subsequent tolerance of visual and auditory stimuli by slowly introducing lights and sounds in ways that do not disturb the puppies. Perhaps the startle response that characterises the beginning of the socialisation period could be minimised by careful desensitisation during the transition period. Modern problems identified with dogs' personalities are not that they do not fear enough dangerous stimuli, but rather that they are too fearful. Fearfulness leads to dogs' being unable to serve, for example, as guide dogs (eg Goddard & Beilharz 1984). Hence minimisation of fear-related issues, for example, through age- and sensory-appropriate early exposure and environmental enrichment could be highly beneficial but is possible only given a further understanding of the sensory abilities of developing puppies.

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