A Comparison of the Sensory Development of Wolves (*Canis lupus lupus*) and Dogs (*Canis lupus familiaris*)

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Abstract

Little is known about the development of the sensory systems of wolves. The timing of sensory development in wolves is usually extrapolated from studies on dogs, since they are members of the same species. However, early developmental differences between these two subspecies have already been identified. For example, wolves tend to approach and investigate objects in their environment 2 wk before dogs. These changes in developmental timing may play an important role in the behavioral differences between adult wolves and dogs. The purpose of this study is to compare the development of the sensory systems in wolves and dogs.

Responses of seven wolf pups and 43 dog pups to familiar and novel olfactory, auditory, and visual stimuli were tested weekly from 2–7 wk of age. Eleven wolf pups were also observed for orientation towards auditory and visual stimuli during 2-h sessions, 5 d a week, from 2–8 wk of age. These observations were supplemented by the daily records of caretakers.

The results suggest that wolves and dogs both develop olfaction by 2 wk, audition by 4 wk, and vision by 6 wk on average, despite the 2-wk shift in their ability to explore. This means that when wolves begin to explore at 2 wk, they are blind and deaf, and must rely primarily on their sense of smell. Thus, there is a significant alteration of how these subspecies experience their environment during the critical period of socialization. These findings lead to an alternative explanation for the difference in dogs' and wolves' abilities to form interspecies social attachments, such as those with humans.

Introduction

Olfaction, audition, and vision play important roles in mammalian behaviors such as hunting, reproduction, hazard avoidance, and communication. The development of the sensory system is also an important component of the critical period of socialization, during which mammals form social attachments that are the basis for proper species identification (Scott et al. 1974). While there have been a number of studies on the sensory development of dogs (Scott 1958; Fox 1964, 1968, 1971; Scott & Fuller 1965; Fox & Weisman 1970; Ashmead et al. 1986; Strain et al. 1991), little if anything has been reported on the development of the sensory systems of wolves. Since wolves and dogs are members of the same species

(Wilson & Reeder 1993; Nowak 2005), the timing of sensory development in wolves is usually extrapolated from studies on dogs (Scott & Marston 1950; Harrington & Asa 2003).

Olfaction in dogs becomes functional between 8 and 13 d (Scott et al. 1974). Dog pups respond to chemosensory cues from birth (Fox 1971; Wells & Hepper 2006). However, these responses are most likely dependent on taste, since pups less than a week old are not capable of finding their mother without thermal-tactile input (Scott & Marston 1950; James 1952; Fox et al. 1968). Dogs begin to respond to sound at 19.5 d on average, with the opening of the ear canals, which are sealed shut before this point (Scott 1958; Fox 1968; Strain et al. 1991); however, they do not reliably respond to sound until 25 d of age (Fox 1964, 1971;

Ashmead et al. 1986). Dog pups' eyes open at approximately 13 d, but it is not until 25 d on average that dog pups begin to see forms (Fox 1964; Scott & Fuller 1965). Dogs can display visually guided behavior at 4 wk, but their vision is not mature until 6 wk (Fox 1968; Fox & Weisman 1970), when rapid growth of the central nervous system is complete (Fox 1964, 1968).

Given the ability of dogs and wolves to have fertile hybrid offspring, it would seem reasonable to assume that they acquire their senses on the same developmental schedule. Yet, previous comparisons of dogs and wolves have found significantly different timing of their locomotory development. Wolves begin to walk in a coordinated manner and investigate their environment at 2 wk of age (Frank & Frank 1982; Packard 2003), while dogs do not exhibit this behavior until 4 wk of age (Walking: Rheingold 1963; Fox 1964; Investigating: Scott & Fuller 1965). These changes in the timing of early development have been proposed as the cause of the behavioral differences between adult dogs and wolves (Coppinger & Schneider 1995; Saetre et al. 2004).

Determining the developmental timing of wolves' senses in comparison to dogs' may help to explain the large behavioral differences between these subspecies. The senses play a large role in the development of adult behavior. The early development of sensory input, motor output, and the synthesis of this information plays a role in the foundation of adult behavior. For example, early in their development mammals experience a critical period of socialization (e.g. Carnivores: mink, Gilbert & Bailey 1969; sea lions, Schusterman et al. 1992; cats, Karsh & Turner 1988; Ungulates: Sheep: Tallet et al. 2009; pronghorns, Autenrieth & Fichter 1975; other, Bateson 1966; Hediger 1968; Rodents: rats, Hol et al. 1999; Guinea-pigs, Sluckin 1968; Hess 1973; Primates: rhesus macaque, Harlow 1962). During this critical period, exposure to novelty results in long-term familiarity (Scott et al. 1974). In the wild, this critical period allows for the development of proper species identification and later avoidance of novelty (Lorenz 1937; Hess 1959; Scott et al. 1974). In captivity, exposure to other species during this period can result in interspecies social attachments (Lorenz 1937; Hess 1959; Scott et al. 1974). The critical period of socialization commences with the ability to explore (approach and investigate novelty) (Hess 1959; Scott & Marston 1950). Once the critical period begins fear gradually increases until it inhibits the exploration of novelty, bringing the critical period of socialization to a close (Scott & Marston 1950; Hess 1959; Freedman et al. 1960; Scott & Fuller 1965). Changing the timing of any of the components in relationship to one

another can affect adult behavior (e.g. exploration of novelty, species recognition).

The fact that wolves begin to walk and investigate their environment 2 wk before dogs leads to two hypotheses regarding the development of their sensory systems:

1. Wolves are able to orient to olfactory, auditory, and visual cues by 2 wk of age when they begin to approach and investigate novelty. This would imply that wolves and dogs both develop the ability to use their sensory systems before they begin to explore their environment, but wolves go through the process 2 wk before dogs.

2. Wolves develop their sensory abilities at the same time as dogs. This would mean that wolves would be exploring while still deaf and blind, resulting in a different quality of early experiences and an alternative developmental trajectory than dogs.

The purpose of this study is to compare the timing of the development of the sensory systems in wolves and dogs. This will be accomplished by comparing observational data from wolves with previous observational data on dogs. Dogs and wolves will also be tested for their ability to orient towards different stimuli in order to eliminate confounding variables of the observational dog studies and control for the effect of human rearing on wolves.

A better understanding of the development of the sensory systems of wolves will not only fill a gap in our knowledge but will allow us to better understand the differences between adult behavior in dogs and wolves.

Methods

Subjects/Test site

Pups from ten litters were observed from approximately 2–8 wk of age (Table 1). Three litters of wolves, totaling eleven pups (two females, nine males) were reared by humans from approximately 10 d of age. The first litter of wolf pups (one female and three males) was included in the observational data, but not in the experimental data.

Forty-three dog pups from seven litters (24 females, 19 males) were observed. Dog pups were split into two groups: (1) 33 pups from five litters were reared by their mothers with regular human contact (caretakers engaged in daily human socialization beyond standard husbandry). Two of these litters, totaling fifteen pups, were border collies and the other three litters, totaling eighteen pups, were German shepherds. (2) The second group was human-reared, to control for the effect of human rearing on the wolves,

Table 1: Subjects

Litter Type	Number mother-reared pups observed	Number hand-reared pups observed	Age of first test in days	Data collected: Observational (Obs.) experimental (exp.)
Wolf	–	4	15	Obs.
Wolf	–	4	14	Obs. and exp.
Wolf	–	3	14	Obs. and exp.
Border collie	8	–	17*	exp.
Border collie	7	–	15	exp.
German shepherd	8	–	14	exp.
German shepherd	4	–	14	exp.
German shepherd	6	3	16*	exp.
German shepherd	–	3	14	exp.
German shepherd	–	4	21*	exp.

*Dogs that were not tested by 15 d of age were excluded from olfactory orientation analysis.

and consisted of ten German shepherd pups from three litters. Three of these pups were littermates to six pups in the mother-reared group (Table 1).

All pups were tested at the subject's rearing site. The rearing site of mother-reared pups was the private residence of the breeder; the rearing site of hand-reared pups was the private residence of the human caretaker. The rearing site of wolves was the facility that owned the pups (litter 1:Parc Safari, QC; litter 2: Wolf Park, IN; litter 3: SPCA, QC/Wolf Creek, IN).

Procedure

Experimental

The response of seven wolf pups and 43 dog pups to familiar and novel olfactory, auditory, and visual stimuli were tested once a week from 2–7 wk of age.

Pups were individually placed on a white flannel sheet (158.5 by 166.5 cm), which was marked to ensure that the placement of the stimulus and pup were the same for each trial. The sheet was in a room physically separated from the rest of the litter.

Pups were then exposed to olfactory, auditory, and visual stimuli, one at a time. The order of the tests was counter-balanced so that pups in a litter received stimuli in a different order on any given day, and each pup received different orders during consecutive

weeks. All tests were videotaped using a Panasonic S-VHS Reporter AG450 or a Canon Elura 100 digital video camcorder.

Each pup's ability to orient towards stimuli was scored by two observers from the video recording. Definitions of orientation for each sense are provided below. Percent agreement was 89% and any discrepancies were coded a second time by the first observer. This method is designed to control for confounding variables, but can only be conducted weekly, due to the potential of habituation. Therefore, it is not possible to determine a specific day of onset using this method. Furthermore, this experimental method requires that pups not only be able to sense the stimulus, but also selectively attend to the test stimulus. Therefore, the results from this experiment will provide the age at which pups reliably respond to olfactory, auditory, and visual stimuli rather than when they are first capable of sensing each stimulus.

Olfactory responsiveness

Pups were exposed to two olfactory stimuli weekly:
1. 1 ml of the shampoo used by the experimenter or caretaker
2. 1 ml of novel liquid, starting with the 2nd wk of testing.

The novel scent was included to control for habituation to the original scent. Novel scents included vanilla extract, eucalyptus oil, fish oil, grape juice, lavender oil, and mint extract. None of these ingredients were present in the shampoos used as the standard olfactory stimulus. Pups were exposed to one novel scent a week, and experienced each scent by the end of the 6th wk. The order was the same for all pups within a litter, but was randomized between litters, so that each litter received the novel olfactory stimuli in a different order.

All scents were rubbed onto a 13 cm^2 piece of terry cloth, which could not be swallowed by subjects. To begin each test pups were placed with their backs towards the stimulus and their back feet 0.9 m from the scented cloth. Observers considered pups to orient towards the scent if they demonstrated visible sniffing.

Auditory responsiveness

Pups were exposed to two auditory stimuli weekly:
1. A tone with a frequency of 440 Hz, a maximum amplitude of 88 db, and a duration of 3 s.
2. A novel auditory stimulus of the same duration and with the same speaker positions as the original

auditory stimulus, starting with the 2nd wk of testing. This novel stimulus was included to control for potential habituation to the tone played every week. Novel sounds included a wavering tone, a cat's meow, a siren, applause, office sound effects, and a rattle.

Before each sound was played, pups were placed so that their backs were towards the speakers, and their back feet were 0.9 m away from the speakers. All sounds were played from a Macintosh Powerbook G4 through an Optimus moisture-resistant mini speaker system. A pup was considered to orient towards the auditory stimulus if it turned its head so that its eyes and ears were directed towards the sound at its onset.

Visual responsiveness

Pups were exposed to two visual stimuli weekly:
1. A laser pointer light held approximately 1 m from the floor and shone in one place on the floor.
2. A laser shone at the floor from approximately 1 m and moved back and forth slowly for 3-s.

If the pup failed to find either stimulus the experimenter placed the light in the pup's direct line of sight and continued to move it back and forth. The moving stimulus was included to avoid habituation to the still light, and to increase the likelihood of the pup being attentive to such a small stimulus.

At the beginning of each test pups were placed with their front feet 0.9 m away from the spot where the light would be shone. Pups were placed facing towards where the stimulus would appear. A pup was considered to orient towards the visual stimulus if it turning its head so that its eyes and ears were directed at the light. If an animal was not seen to orient during testing it was given the maximum latency (7 wk).

Observational

Eleven wolf pups were videotaped from 2 to 8 wk of age for 2 h a day, 5 d a week. Daily notes were also taken by human caretakers on the wolves' responses to auditory and visual stimuli, from 10 d until 8 wk. The caretakers were in 24 h contact with pups from 10 d of age through 4 wk of age. After 4 wk, caretakers spent 16 h a day with the pups.

An experimenter observed the videotapes of the pups and recorded the earliest response to auditory and visual stimuli captured on video. The earliest mention of auditory response and visual response for each wolf pup was also extracted from the caretakers' notes.

If there was a discrepancy between the video and the caretaker notes, the earliest date for each stimulus was used. Because pups should have functional olfactory abilities from the day they were retrieved from the den, only auditory and visual abilities were recorded observationally. Observational data were deemed unnecessary for dogs because the timing of the onset of visual and auditory systems is well established and previous experiments are comparable to these methods (Fox 1964, 1968, 1971; Scott & Fuller 1965; Fox & Weisman 1970; Ashmead et al. 1986).

Analysis

All statistical analyses were carried out in the statistical package R (R version 2.6.2; R Development Core Team 2008). Frequency distributions of the age (in weeks) at which pups first oriented towards each sensory stimulus were compared using Fisher's exact test. Analyses were completed for pups' first response to olfactory, auditory, and visual stimuli.

Comparisons were made between the two border collie litters and the two largest mother-reared German shepherd litters. These four litters provided an estimate of litter effect, since most litters were too small for comparison. Border collies were compared to mother-reared German shepherds to determine breed effects. Hand-reared German shepherds were compared to mother-reared German shepherds to determine rearing effect. If rearing effect was present, hand-reared German shepherds were compared with wolves. Finally, all dogs were compared to wolves.

To create frequency distributions, age categories were combined when there were fewer than five pups in a given category in the entire data set. For auditory orientation, onsets were categorized as occurring during the 3rd wk, 4th wk, or 5th wk and later. For visual orientation towards the laser light, onsets were categorized as occurring at 5 wk and earlier, 6 wk, or 7 wk.

In order to compare all three *Canis* groups simultaneously (border collie, German shepherd, and wolf), Kruskal-Wallis rank sum tests were performed for each sensory modality. Pair-wise comparisons between breeds that yielded significant results in the Kruskal-Wallis test were subsequently subjected to a *post-hoc* Nemenyi-Damico-Wolfe-Dunn test (Hollander & Wolfe 1999).

Observational data were compared to the observational results from previous literature (visual: Fox 1964; auditory: Fox 1964; Scott & Fuller 1965). A one-sample *t*-test was used to compare current findings

to the mean of previous findings for visual data. Descriptive statistics were used for auditory data, due to the lack of normality and the extremely low variance in these data. Normality was determined using a Shapiro-Wilk normality test.

A *post-hoc* power analysis was performed on non-significant results to determine the effect sizes these tests could detect. Given the lack of availability of computational devices to determine the power of nonparametric calculations (i.e. Fisher's exact and Kruskal-Wallis rank sum tests), the effect size of Fisher exact tests were calculated using $r_{equivalent}$ (Rosenthal & Rubin 2003). Effect sizes of less than or equal to 0.21 were considered small. Effect sizes from 0.22 to 0.35 were considered medium, and effect sizes greater than 0.35 were considered large.

Results

Olfactory responsiveness

All pups that completed their first test at 2 wk oriented toward the olfactory stimulus on their first test. Therefore, due to this lack of variability it was not possible to conduct a Fisher's exact test on these frequency distributions.

Auditory responsiveness

Experimental

No litter effect was found in the timing of the two border collie litters to orient to sound (Fisher's exact test: p = 0.16, $r_{equivalent}$ = 0.38). Nor was there a significant difference in the timing of the two largest mother-reared German shepherd litters to orient to sound (Fisher's exact test: p = 0.59, $r_{equivalent}$ = 0.16). No breed effect was found between border collies and hand-reared German shepherds (Fisher's exact test: p = 0.13, $r_{equivalent}$ = 0.27). Mother-reared German shepherds did orient to sound before hand-reared German shepherds (Fisher's exact test: p = 0.04) (Fig. 1). There was also a significant difference between hand-reared German shepherds and wolves (Fisher's exact test: p = 0.02). However, there was no significant difference in the timing of dogs and wolves to orient towards sound (Fisher's exact test: p = 0.10, $r_{equivalent}$ = 0.24; Kruskal-Wallis test: H_2 = 0.58, p = 0.75) (Fig. 2).

Observational

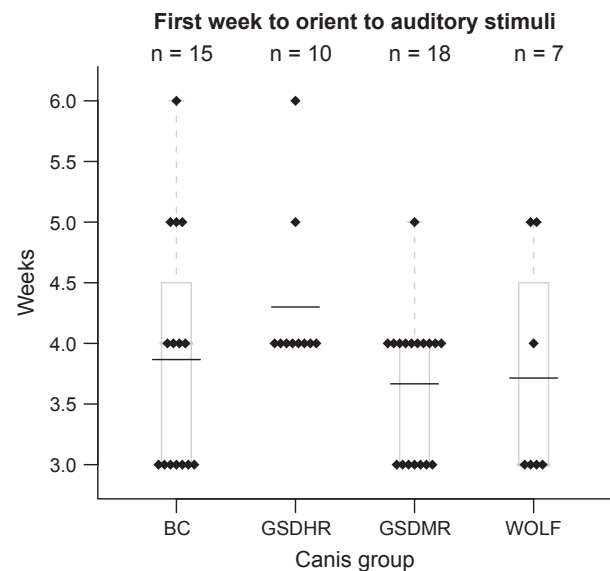Wolves first oriented toward auditory stimuli at 18.8 d (SD = 0.60).

Fig. 1: First week pups oriented towards auditory stimuli during the test by breed and rearing type. Individual dots represent data for individual pups (BC = mother-reared border collies, GSDHR = hand-reared German shepherds, GSDMR = mother-reared German shepherds, WOLF = hand-reared wolves), with box plot overlay (box represents first and third quartile, grey line represents median, the black line represents the mean, the dotted line extends to maximum if outside of box).
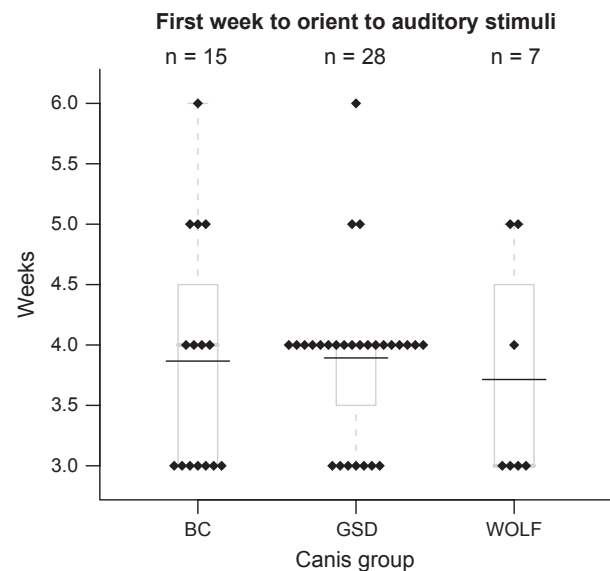

Fig. 2: First week pups oriented towards auditory stimuli during the test. Individual dots represent data for individual pups (BC = border collies, GSD = German shepherds, WOLF = wolves), with box plot overlay (box represents first and third quartile, grey line represents median, the black line represents the mean, the dotted line extends to maximum if outside of box).

Visual responsiveness

Experimental

No significant litter effects were found in the time at which pups oriented toward the light (border collies: Fisher's exact test: $p = 0.14$, $r_{equivalent} = 0.22$; German shepherds: Fisher's exact test: $p = 0.33$, $r_{equivalent} = 0.28$). There was a significant difference between border collies and mother-reared German shepherds (Fisher's exact test: $p = 0.03$). However, there was no significant difference in the age at which hand-reared and mother-reared German shepherds first oriented to the laser pointer light (Fisher's exact test: $p = 0.14$, $r_{equivalent} = 0.28$). German shepherds did orient towards the light significantly earlier than border collies (Kruskal-Wallis test: $H_2 = 15.84$, $p < 0.001$; Nemenyi-Damico-Wolfe-Dunn test: $p < 0.001$) and wolves (Nemenyi-Damico-Wolfe-Dunn test: $p < 0.001$) (Fig. 3). There was no significant difference in the age at which dog and wolf pups first oriented towards the laser pointer light (Fisher's exact test: $p = 0.60$, $r_{equivalent} = 0.08$).

Observational

Wolves first oriented to visual stimuli at 26.6 d (SD = 1.36), which is significantly later than the 25 d

First week to orient to visual stimuli

Fig. 3: First week pups oriented towards visual stimuli during the test. Individual dots represent data for individual pups (BC = border collies, GSD = German shepherds, Wolf = wolves), with box plot overlay (box represents first and third quartile, grey line represents median, the black line represents the mean, the dotted line extends to maximum if outside of box).

mean found in dogs by Fox (1964), (one-sample t-test: t = 3.99, p = 0.003).

Discussion

The current data refute the first hypothesis that wolves develop their senses 2 wk before dogs. However, the results support the second hypothesis by showing that the sensory development of wolves and dogs appear to be very similar. The experimental data also match well with previous data on the development of reliable responses to olfactory, auditory, and visual stimuli in dogs, while the observational data match well with previous data on the first response of dogs to auditory and visual stimuli.

There were some significant differences between groups of dogs. Hand-reared German shepherds were less likely to orient to sound at 3 wk than mother-reared German Shepherds or wolves. The hand-reared German shepherds experienced more human handling before their 3rd wk of age than did mother-reared German shepherds, due to bottle-feeding. Increased human handling has been shown to reduce reactivity in dog pups (Fox & Stelzner 1966; Gazzano et al. 2008), and laboratory animals (Morton 1968). Thus, mother-reared German shepherds were more likely to startle at the auditory stimulus played during the test.

While the current experiment attempted to eliminate startle reactions by not using loud sudden noises, a more fearful or reactive pup could startle at any novel noise, leading to orientation toward the stimulus. The wolf pups were also bottle-fed. However, early intensive handling does not have the same effect on wolves as it does on dogs (Fentress 1967; Klinghammer & Goodman 1987; Zimen 1987). While socialized wolves are less fearful of humans than unsocialized wolves, they do not generalize this tameness to all humans and they are more fearful of novelty in general than dogs (Fentress 1967; Klinghammer & Goodman 1987; Zimen 1987). Thus, wolf pups were also more likely to react to sound at 3 wk than hand-reared dogs. These findings also suggest that hand-reared wolves are more directly comparable to mother-reared dogs, despite the differences in early handling.

It is important to note that the earliest a pup from any group was ever found to respond to sound was at 3 wk, the date previously found for the initial response to sound in dogs (Scott 1958; Fox 1968; Strain et al. 1991). Furthermore, the average time at which hand-reared German shepherds reliably responded to sound was less than a week different
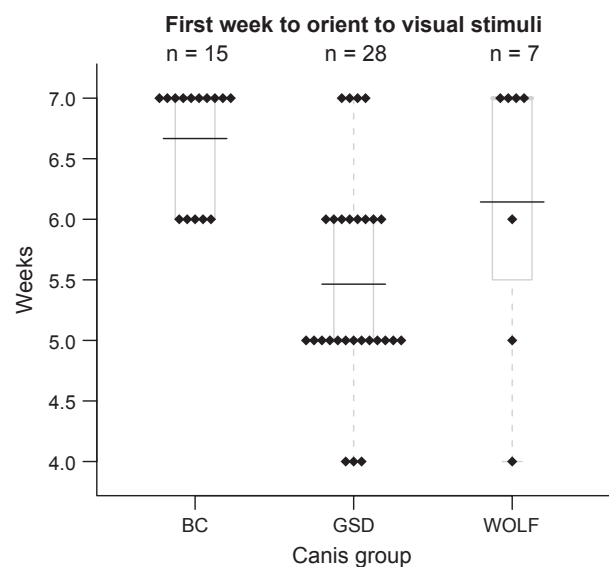
from mother-reared German Shepherds and wolves (Hand-reared German shepherds: 4.3 wk; Mother-reared German shepherds: 3.7 wk; Wolves: 3.7 wk) and matches well with previous literature (Fox 1964, 1971; Ashmead et al. 1986).

The group differences in visual response were most likely an artifact of methodology. The experimenter stood on the mat while showing the laser pointer light for the first three litters tested (one wolf litter and both border collie litters) and sat on the mat for the remainder of the litters (one wolf litter and all of the German shepherd pups). Sitting on the mat increased the pups' attention in the area of laser pointer light. This change in methodology would explain why mother-reared German shepherds (tested in the seated position) responded to visual stimuli significantly earlier than border collies (tested in the standing position). It would also explain why German shepherds (all tested in seated position) responded to visual stimuli significantly earlier than border collies (tested in standing position) and wolves (1 litter tested in standing position). The effect of this methodological difference is supported by the fact that there was no difference in visual response between wolves tested when seated and German shepherds tested when seated (Fisher's exact test: p = 1.00). Furthermore, the only pups that never attended to the laser light were pups that were tested while the experimenter was standing, two wolves from the first litter tested and two border collies. Since these animals responded normally to other visual cues and were highly focused on other stimuli during the test, it is believed that this was due to distraction rather than visual impairment.

It is important to note that while German shepherds reliably responded to visual stimuli a week earlier on average than border collies, they responded under a week earlier than the wolves (means in weeks ± SD: wolves = 6.1 ± 1.2, BC = 6.7 ± 0.5, GSD = 5.5 ± 0.9). All groups were less than a week different from the previous finding for dogs, which were reported as reliably orienting towards visual stimuli at 6 wk of age (Fox 1968; Fox & Weisman 1970). Furthermore, the earliest any individual animal responded to the visual stimuli was 4 wk, the age previously identified as when dogs first orient towards visual stimuli (Fox 1964; Scott & Fuller 1965).

The observational data on visual response show wolves orienting to visual stimuli for the first time at 26.6 d on average (± 1.36 SD). This is 1 d later than previously found in dogs, which begin to visually track forms at 25 d on average (Fox 1964; Scott & Fuller 1965). While these findings are statistically different, a

1-day shift would not be expected to result in any functional differences given that the development of the visual system is notoriously plastic (Shatz 1992).

Implications for wolves' critical period of socialization

The finding that dogs and wolves develop their senses at the same time suggests that they have different early experiences. Dogs begin to approach and investigate objects in their environment at 4 wk of age (Rheingold 1963; Fox 1964; Scott & Fuller 1965). Wolves, on the other hand, begin to explore their environment at 2 wk (Frank & Frank 1982; Packard 2003). The current data support previous finding that dogs begin to explore once their senses are operational. However, these data also provide new evidence that wolves are still blind and deaf when they begin to explore. Therefore, wolves are exploring primarily using olfaction, while dogs are exploring using olfaction, audition, and vision. This different quality of early experience in wolves is likely to result in an alternative developmental trajectory from that of dogs.

Since this difference in experience is occurring during the critical period of socialization, it is likely to have a profound effect on the development of adult behavior. The critical period of socialization is largely based on the ability to explore and occurs early in the ontogeny of mammals. Exposure to novelty during this time results in long-term familiarity (Scott et al. 1974). The critical period of socialization allows for the development of proper species identification in the wild (Scott et al. 1974) and exposure to other species during this period can result in interspecies social attachments (or socialization) in captivity (Scott et al. 1974). The critical period of socialization begins with the ability to approach and investigate novelty and ends with avoidance of novelty (Scott & Marston 1950). Differences in the sensory input of an individual during this period could produce significant differences in adult behavior (Fox & Stelzner 1966; Fox et al. 1968; Wright 1983; Gazzano et al. 2008; Pluijmakers et al. 2010). The development of what is familiar and what is novel is the foundation of later exploratory behavior and species recognition, which in turn affects adult reproduction, hazard avoidance, and foraging behavior.

For example, this change in the relationship between exploration and sensory development should be investigated for its effect on the perception of novelty and familiarity. Dogs begin to explore at 4 wk when all of their senses have at least onset. They have their entire critical period to explore and become

familiar with the olfactory, auditory, and visual aspects of their environment, and the animals and objects in that environment. The current data suggest that when wolves begin exploring at 2 wk of age they are doing so olfactorily. Therefore, for their 1st wk wolves only become familiar with the olfactory stimuli of their environment, including their species. Thus, the formation of species identification starts with olfactory familiarization when pups are still highly reliant on their mother. When further exploration occurs (auditory, and visual) it could be limited by the need for a familiar scent. In this way proper social behavior can develop without the risk of improper species identification or reduced flight response toward other potentially dangerous species. Dogs on the other hand are released from these constraints allowing them to form a reduced flight distance and easily form bonds with other species present in their early environment.

These data also call into question the assumed timing of the critical period in wolves. Wolves begin the critical period of socialization at 2 wk. It has been previously assumed that their critical period ends at 18 d (Miklósi 2007). This is largely based on Zimen's (1987) report that wolves show an initial fear response at this age. If wolves' critical period does end at 18 d they would have a 4-d critical period of socialization, which would end before they were able to hear reliably and see forms.

Upon closer investigation of Zimen's (1987) data, the display of fear at 18 d better matches the description of the startle reaction found in dog pups when their ears open (Scott 1958; Fox 1964), than the more permanent avoidance of fear, which marks the end of the critical period. This is supported by the current data, which show that wolves begin to hear at 18 d. Both Zimen (1987) and other authors report a more permanent avoidance of novelty in wolves at 6 wk of age (Scott & Marston 1950; Fentress 1967; Woolpy & Ginsburg 1967). Therefore, the current data suggest that wolves have a 4-wk long critical period beginning at 2 wk and ending at 6 wk. This is the same length as dogs' critical period, but occurring 2 wk earlier.

Dogs' critical period begins at 4 wk when dogs are not fearful of novelty and readily approach it (Freedman et al. 1960; Scott & Fuller 1965). Their critical period ends at 8 wk at which point it takes several days of exposure before the pup will approach a novel object (Scott & Marston 1950; Freedman et al. 1960). However, fear of novelty continues to increase until approximately 14–16 wk of age (Freedman et al. 1960; Fox 1971). Therefore, the effects of the critical period of socialization can be prolonged by artificially

enforcing extended exposure to novelty up until 16 wk of age. Even so, maximum generalization occurs between 4 and 8 wk when dogs would be encountering novelty on their own accord (Freedman et al. 1960; Fox & Stelzner 1966, 1967; Cairns & Werboff, 1967; Fox 1969; Wright 1983).

By shifting the beginning and end of the critical period while leaving sensory development the same, dogs are effectively liberated from the interruptions of sensory development. Dogs have four full weeks to interact with their environment with adult-like sensory modalities. Alternatively, I suggest that wolves have 4 wk to explore olfactory stimuli, 3 wk to explore auditory stimuli, and 2 wk to explore visual stimuli (Fig. 4a, b).

A shift in the timing of the critical period between dogs and wolves also fits well with previous work on the evolution of the dog from the wolf. Belyaev found that selection for reduced flight distance was sufficient to explain other major differences between dogs and
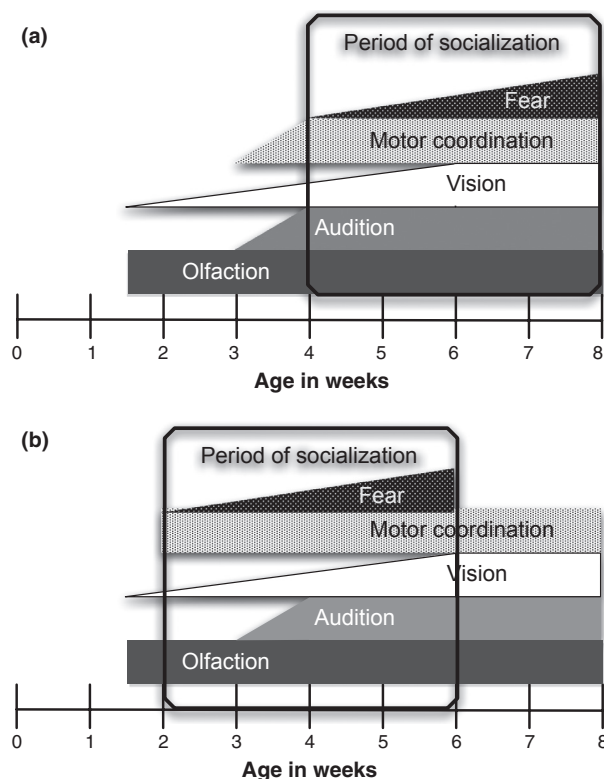

Fig. 4: (a) Classification of early development in dogs based on findings from previous literature (see discussion for sources) The beginning of a bar represents the first appearance; the maximum width of a bar represents maturity. (b) Classification of early development in wolves given current data.

wolves (Trut, 1999). In an attempt to create more tractable foxes for a fur farm in Siberia, Belyaev bred together foxes with the shortest flight distances (Trut, 1999). After approximately ten generations (20 yr) the progeny of the selected foxes not only allowed humans to approach them, but solicited human contact. Furthermore, they had two-toned coats, flipped up tails, floppy ears, and diestrus cycles (Trut, 1999), all characters that distinguish dogs from wolves. Belyaev concluded that domestication was the result of changes in the timing of gene expression, which then had wide reaching effects on other related ontogenetic systems.

Perhaps this wide reaching change in gene expression is a 2-wk delay in the beginning and end of the critical period of socialization. It is interesting to note that Belyaev et al. (1984/1985) found that unselected foxes reach their onset of fear at 40 d, while domesticated foxes reached their onset of fear after 60 d.

Further experimentation on the development of fear in wolves is needed, but a simple change in the timing of the critical period combined with conservation of sensory development would be sufficient to explain the relatively speedy evolution of reduced flight distance in dogs and the resulting ease with which they form interspecies social bonds.

Conclusion

Given that the statistically significant differences between dogs and wolves were not meaningful functionally, and the tests that revealed nonsignificant differences between dogs and wolves had the power to detect medium (auditory orientation: $r_{equivalent} = 0.24$) or small effects (visual orientation: $r_{equivalent} = 0.08$), the results suggest that wolves' sensory systems develop at the same rate as dogs'.

The current data support previous findings that dogs begin to explore once their senses are operational. These data also provide new evidence that wolves are still blind and deaf when they begin to walk and explore at 2 wk (Frank & Frank 1982; Packard 2003). Therefore, wolves are initially exploring primarily using olfaction, while dogs are exploring with using olfaction, audition, and vision. This different quality of early experience in wolves is likely to result in an alternative developmental trajectory from that of dogs.

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