

Manifestations of chronic and acute stress in dogs

Bonne Beerda, Matthijs B.H. Schilder^{*}, Jan. A.R.A.M. van Hooff,
Hans W. de Vries

Department of Clinical Sciences of Companion Animals, Faculty of Veterinary Medicine, and Department of Ethology and Socio-Ecology, Faculty of Biology, Utrecht University, Utrecht, The Netherlands

Abstract

Poor housing conditions, harsh training sessions and uncontrollable or unpredictable social environments are examples of the situations that may lead to reduced welfare status in dogs. Individuals that suffer from poor welfare presumably experience stress and may consequently exhibit stress responses. In order to evaluate stress responses as potential indicators of poor welfare in dogs, we review studies dealing with dogs subjected to stressors. The reported stress responses are categorized as being behavioural, physiological or immunological, and demonstrate the various ways stress is manifested in the dog.

Stressors such as noise, immobilization, training, novelty, transport or restricted housing conditions have been reported to elicit responses in behavioural, cardiovascular, endocrine, renal, gastro-intestinal, and haematological parameters. These and other parameters that change during stress may thus be indicative of poor welfare. However, several sources of misinterpretation have to be considered before stress responses may be used as valid indicators of welfare.

Although analogous to the human situation, especially chronic stress may impair welfare, most studies deal with acute stress and do not address chronic stress and related phenomena. Adaptation may counteract the initial stress response and render parameters of acute stress useless for assessing chronic stress. Adaptations to stress are thus in themselves indicative of reduced welfare. Such adaptations may be discovered by challenging a stress responsive system. Additional studies are recommended to investigate acute stress parameters as possible indicators of chronic stress.

Differences in stressor properties and in individual characteristics of dogs introduce variability in stress responses. Such variability will complicate a valid interpretation of stress responses with regard to welfare. Obtaining and applying fundamental knowledge of stress responses in dogs and measuring more than one stress parameter are proposed to minimize the risk of misinterpreting measurements of stress. © 1997 Elsevier Science B.V.

Keywords: Dogs; Stress; Welfare; Behaviour; Physiology; Immunology

^{*} Corresponding author at: Department of Ethology and Socio-Ecology, Utrecht University, PO Box 80.086, 3508 TD Utrecht, The Netherlands. Tel: (31)-30-2535406; fax: (31)-30-2521105.

1. Introduction

More than ever, there is interest in the welfare of domestic animals. Poor housing or handling conditions generally accepted in the past may now be criticised for affecting animal well-being. Since little attention has been given to this subject for dogs, we focus on this species.

Poor housing conditions, harsh training sessions and an uncontrollable and unpredictable social environment are examples of situations that may seriously affect the welfare of dogs. To establish welfare problems, tools are required that measure the effects of the dog's appraisal of its environment and of its efforts to cope with it.

In humans, long lasting negative emotions that are elicited by aversive events reduce welfare. From studies in humans we also know that there are relations between negative emotions and a number of behavioural and physiological measures such as passiveness and elevated cortisol levels. Analogous reasoning justifies the assumption that causes (stressors) or indications (stress responses) of negative emotions as found in humans also apply to animals (for a discussion see Stafleu et al., 1992). In animals, emotional indications (Wiepkema and Koolhaas, 1992) such as passiveness, elevated cortisol, specific tail movements, characteristic vocalizations etc. that are elicited by stressors, may thus indicate a state of stress and possibly poor welfare. Analogous to the human situation, animals that are subjected to stressors for a longer period may especially suffer a reduced welfare. Responses that are sustained during chronic stress may, therefore, be regarded as valid indicators of canine welfare.

From findings reported elsewhere and our own data we try to deduce the behavioural, physiological and immunological changes that are consistently associated with stressors. For this purpose we review behavioural, physiological and immunological responses to experimental and 'naturally' occurring stressors. Subsequently we evaluate these stress responses with regard to their applicability as measures of poor welfare in dogs. Finally, we also point out problems in the interpretation of such measures.

2. Stressors and their behavioural, physiological and immunological effects

2.1. Behavioural stress responses induced by experimental stressors

Electric shock just below tetanizing level induces dogs to urinate, defecate, scramble rapidly and vigorously around the compartment, emit high-pitched screeches, salivate profusely and roll their eyes rapidly with dilated pupils (Solomon and Wynne, 1953). The subject's hair may show piloerection, small muscle groups may tremble and the breathing may turn into short, irregular gasping. Hyperpnea and increased salivation also occur in dogs anticipating unavoidable shock of a lesser intensity (Corson, 1971) and in dogs subjected to noise (Engeland et al., 1990). These behaviours are thought to represent compensatory actions to an increased thermogenesis (Corson and Corson, 1976). Anti-diuresis observed in dogs anticipating unavoidable shock, may furthermore help the body conserve water necessary for these thermoregulatory responses (Corson, 1971; Corson and Corson, 1976). Increased thermogenesis and subsequent thermoregula-

tory actions are exhibited in dogs of the fox terrier type, but are absent in individuals of the beagle type (Corson, 1971). Differences in thermogenic responses between breeds may reflect a predominant 'fight or flight' type of stress response (Cannon, 1929) in terriers compared with a 'conservation-withdrawal' response (Engel and Schmale, 1972) in beagle dogs (Corson and Corson, 1976). Constitutional differences in canine stress responses are in agreement with individual differences in coping strategies reported in other species such as mice, rats (Benus et al., 1987); tree shrews (Von Holst, 1986); rhesus monkey (Suomi, 1987); and pigs (Hessing, 1993).

In anticipation of signalled shock avoidance trials, when dogs remain within the experimental confinement, they develop a strong tendency for stereotyping and exhibit restlessness, agitation, whining and barking (Solomon and Wynne, 1953). In general, the studies previously discussed lack a description of precisely defined behaviours. As a result, the integration of data from different experiments is complicated. Furthermore, studies rarely report on more subtle behaviours. Small changes in the behaviour of stressed dogs may thus remain unnoticed.

2.2. Reaction to acoustic stressors

Motivated by this lack of detailed data on behavioural responses in dogs subjected to experimental stressors, we investigated the behaviour of six beagle dogs before, during and after acoustic stress. Noise was chosen as the experimental stressor, as it elicited profound responses in dogs that had been subjected to short lasting sound blasts in a study that compared different stressors (Beerda et al., in prep). Noise was presented at a frequency where dogs are sensitive to acoustic stimuli and intensities were chosen below the levels that might induce possible hearing loss. Acoustic stressors were administered intermittently and randomly to minimize the time of noise exposure, and to prevent fast habituation of the stress responses. Finally, the experimental design was chosen to enable the investigation of a possible doses-response relationship.

2.3. Methods

We chose the following experimental set up: Noise of 3000 Hz and at a level of 70, 78 and 87 dB, was presented during three trials that each lasted 30 min. Noise levels were presented to three subjects in a randomized order. During a trial, 3 min of noise was randomly presented in 18 blasts that lasted 5, 10 or 15 s. Three other dogs were subjected to a similar design, but only at a 70 dB level of noise. Also, the total duration of the treatments was much longer, namely 6, 12 or 18 min. All animals were accustomed to the experimental room for at least 40 h. Continuous behavioural observations were performed from 30 min before until 60 min after the onset of a trial. In addition, heart rate measurements were taken by means of the Holter Monitoring System and saliva was collected to assess cortisol levels. The behaviour observed during only the first 10 min of a trial was compared with pre- and post-trial observations.

2.4. Results

The observed behavioural responses showed no clear relationship with increasing noise intensities or durations for any of the animals. However, the strongest behavioural

responses were observed in the one dog inadvertently subjected to 95 dB noise. In addition to increases in the frequency of tongue out, snout lick, paw lift and body shake (Fig. 1), the posture of this animal (an index expressing the position of the ears, tail and the body) was lowered during 37.2% of the stress period. This posture was sustained during 37.5% of the recovery period. Pooled data of the other five dogs subjected to noise of an intensity of less than 95 dB showed behavioural responses with a large individual variation. But acoustic stress induced a lowering of the posture here too (Fig. 2).

In comparison with pre-noise levels, 95 dB administered to the one dog for 6, 12 and 18 min per trial, induced heart rate increases of 25, 35 and 54%, respectively. The five remaining animals showed only marginal heart rate changes that were unrelated to noise intensity or duration. When we pooled the data from 15 trials (3×5 dogs), the mean heart rate increased from 97 beats per minute (BPM) before noise presentation to 103 BPM during noise presentation. Saliva sampling increased heart rate levels only during the presentation of 87 dB. During recovery the mean heart rate returned to below the pre-trial level, namely 90 BPM.

Noise induced saliva cortisol responses were detected only in the dog subjected to 95 dB. Response magnitude showed a clear relationship with the duration of the noise (Fig. 3).

To summarize, an increased performance of tongue out, snout lick, paw lift and body shake was observed in one dog subjected to noise of 95 dB. Since behavioural responses were accompanied by heart rate and saliva cortisol increases, these behaviours may be indicative of stress. The same behavioural patterns were affected during acoustic stimulation at a lower intensity, but responses showed large individual variation. A lowered posture of dogs appears to be a more consistent indicator of stress, since it is observed following noise of both high and moderate intensity. Mouth licking, paw

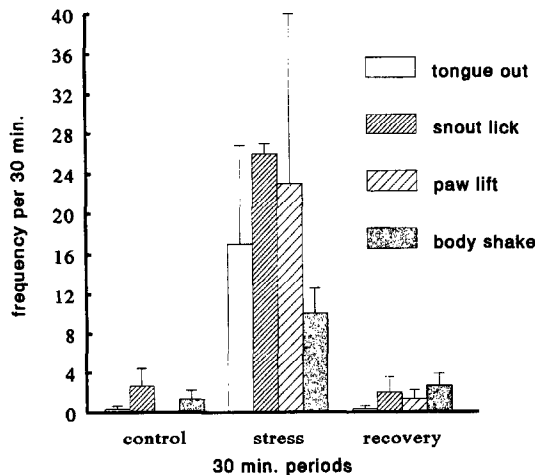


Fig. 1. The performance of several behavioural elements before (control), during (stress) and after (recovery) intermittent acoustic stress; mean values \pm SEM of three trials by one dog subjected for 6, 12 and 18 min to noise of 95 dB and 3000 Hz.

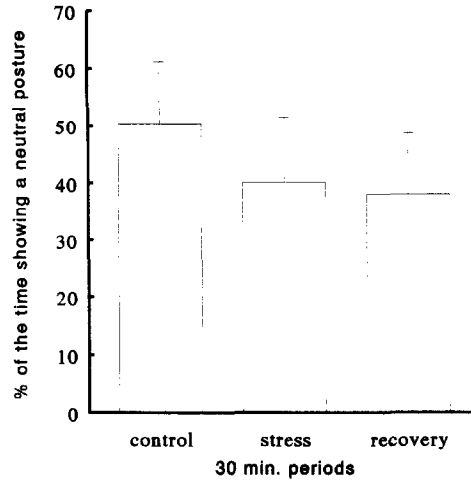


Fig. 2. The exhibition of a neutral posture (an index expressing the position of the ears, tail and body) before (control) during (stress) and after (recovery) intermittent acoustic stress; mean values \pm SEM of three trials by five dogs subjected to stress regimes of different intensity (70 to 87 dB) and duration (3 to 18 min per stress period).

lifting and lowered standing and sitting postures have been previously reported as indications of stress in dogs subjected to harsh training methods (Schwizgebel, 1982).

Noise levels below 87dB did not induce profound heart rate responses in our beagle dogs. The lack of increases in saliva cortisol supports the finding of Thalken (1971) that plasma glucocorticoid responses to noise in beagle dogs were absent. The data suggest that behavioural responses provide the more sensitive indicators for negative effects in dogs experiencing moderate noise stress.

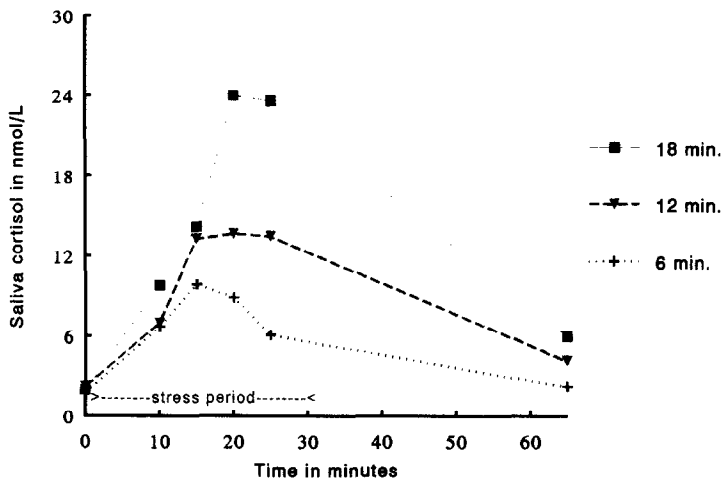


Fig. 3. Saliva cortisol responses during intermittent acoustic stress in one dog subjected for 6, 12 and 18 min to noise of 95 dB and 3000 Hz.

2.5. Behavioural stress responses induced by 'naturally' occurring stressors

Vocalizations in dogs are elicited by electrical shock (Solomon and Wynne, 1953), but also by more 'natural' stressors (Schwizgebel, 1982; Hetts et al., 1992). Dogs subjected to training methods that included acoustic and physical punishment exhibited significantly more yelping than dogs under conditions of predominantly positive reinforcement (Schwizgebel, 1982). Dogs that are socially isolated may also increasingly vocalize (Hetts et al., 1992).

Harsh training methods induce dogs to lower the standing posture, to sit in a more crouched position, to perform snout licking and to exhibit paw lifting (Schwizgebel, 1982). Schwizgebel (1982) considered these responses as submissive behaviours. However, our data on the behaviour of dogs subjected to acoustic and other non-social stressors suggest that these behaviours possibly also express an escape tendency.

Compared with dogs kept in spacious group housing systems (5–11 dogs on 744 m²), inactivity also characterizes dogs housed solitary in areas smaller than 3 m² (Hubrecht et al., 1992). As previously noted by Hubrecht, reducing the spatial area of housing systems that are already of limited size (< 4 m² per animal) does not significantly affect the dog's general activity (Hite et al., 1977; Sigg und Tobler, 1986) or play behaviour (Bebak and Beck, 1993). Reduced activity of dogs subjected to poor housing conditions or intensive racing (Kronfeld et al., 1987), is in contrast with an increased restlessness shown by dogs anticipating signalled shock avoidance trails (Solomon and Wynne, 1953). The observed discrepancy may be attributed to the fact that the latter dogs experienced anxiety, whereas in the former cases fatigue and boredom may have played a role.

Housing conditions that lack suitable stimuli to elicit behaviour and that lack adequate space to perform behaviour, may make dogs inactive without necessarily causing stress responses.

Solitary housing in restricted areas induces dogs to perform more repetitive movements such as pacing, tail chase, wall bounce and flank sucking (Hubrecht et al., 1992), as well as more grooming and more manipulation of the enclosure barriers (Hetts et al., 1992). A possible stereotyped character of the observed repetitive movements and manipulations of the enclosure barriers, would support the report on stereotypies in stressed dogs by Solomon and Wynne (1953). As in husbandry animals (for a review see Lawrence and Rushen, 1993) the performance of stereotypies in dogs may thus be indicative for prolonged situations of stress.

2.6. Behavioural stress parameters and their potential as indicators of welfare

To establish stress and subsequently welfare problems in dogs, behavioural stress parameters are of special interest since they may be measured easily and non invasively. A variety of behavioural responses have been reported to occur during acute stress; panting, vocalizing, paw lifting, snout licking, lowering of the posture etc. However, adaptation of the animal may render such indicators of acute stress useless for establishing chronic stress; especially the latter may lead to welfare problems. We have conducted additional studies to determine which acute behavioural responses are sus-

tained during prolonged stress, but these data will be published elsewhere (Beerda et al., in prep.).

2.7. Experimentally induced physiological stress responses and those induced by non-experimental stressors

Two physiological systems are particularly responsive to stress: The sympathetic adrenal medullary (SAM) axis stimulates the adrenal medulla to primarily secrete adrenaline and, to a lesser extent, noradrenaline during psychological stress (Cannon and de la Paz, 1911). The early work of Selye (1936) indicated involvement of the hypothalamic pituitary adrenal (HPA) axis. Corticotrophin releasing hormone (CRH), which originates from the hypothalamus stimulates the anterior pituitary to secrete adrenocorticotrophic hormone (ACTH), and this in turn stimulates glucocorticoid secretion by the adrenal cortex. In dogs cortisol is the primarily glucocorticoid secreted.

Experimentally induced activation of the canine SAM axis induces enhanced levels of catecholamines (Engeland et al., 1990; Parrilla et al., 1990), anti-diuretic responses (Koepke and Obrist, 1983a; Koepke et al., 1983b) and changed cardiovascular performances (for an overview see Fig. 4). Stress induced activation of the HPA axis is commonly associated with elevated levels of plasma cortisol (Dess et al., 1983; Gue et al., 1988; Knol, 1989; Palazzolo and Quadri, 1987). By way of its secreted hormones, the HPA axis exerts effects on different body functions such as gastro-intestinal motility (Gue et al., 1988; Muelas et al., 1993; Parrilla et al., 1990).

Dogs introduced into a novel environment, show enhanced sympathetic activation (Pagani et al., 1991) and enhanced HPA activity (Thalken, 1971; Vial et al., 1979). Transferring inexperienced dogs from their home cages to a surgery section, enhances the low frequency component of the inter heart beat or R-R variability (Pagani et al., 1991). A shift from a predominantly high frequency component of R-R variability in resting dogs to a low frequency component of R-R variability in stressed dogs, is proposed to result from a shift from a predominantly vagal tone to an increased sympathetic activity (Pagani et al., 1991). Admission in a veterinary hospital significantly elevates levels of plasma 11β -hydroxycorticoid in privately owned dogs when measured over night or 4 h after arrival (Vial et al., 1979). Furthermore, such hospitalization is associated with a tendency for enhanced 11β -hydroxycorticoid responses after exogenous ACTH administration. Qualitative aspects of a new environment may determine whether initial cortisol responses are sustained. Whereas privately owned dogs exhibited prolonged elevated levels of 11β -hydroxycorticoid after being caged (Vial), beagle dogs that were transported by truck to a less restricted new environment did not exhibit elevated cortisol levels the morning after transport (Kuhn et al., 1991). However, during transportation the cortisol levels were significantly elevated.

2.8. Are parameters reflecting SAM activity useful parameters of stress and indicators of welfare?

The applicability of plasma catecholamine levels as an indicator of canine welfare is problematic since the levels are easily affected by procedures of blood sampling.

	Administration of shock	Anticipation of shock	Avoidable shock	Signalled shock	Heart rate	Stroke volume	Blood pressure	Peripheral resistance	Other cardiovascular parameters	First Author
+	-	+	↑↑							Corson '71
+	+	-	↑		↑		Ao dP/dt ↑			Gaebelein '77
+	+	-	↑↗	↓↘	↑↗	↓↘	CO ↑↗			Anderson '72/73
+	+	-	↑	↑↔	↑	↘	Ao dP/dt ↓↔, CO ↑			Lawler '75
+	+	-	↑		↑		Lv dP/dtmax ↑			Galosy '79
+	+	+	↑		↔		Ao dP/dt ↔			Gaebelein '77
+	+	+	↑							Corson '71
+	+	+	↑		↑					Koepke '83b
+	-	+	↑↔							Corson '71
+	+	-	↑↑	↔	↑	↑	CO ↔			Lawler '75
+	+	-	↓↘	↓↘	↑↗	↑↗	CO ↓↘			Anderson '72/73

Fig. 4. Cardiovascular responses in dogs subjected to regimes of electric shock that differ in the presence (+) or absence (-) of four characteristics (listed in the first four columns). Arrows indicate increased (↑), decreased (↓) or unchanged (↔) performances relative to control levels whereas ↗ and ↘ indicate increases or decreases during the experimental period that are not related to control levels. Abbreviations: Ao dP/dt, maximum rate of change of aortic blood pressure from diastole to systole, an index of contractile force; CO, cardiac output = stroke volume × the number of heart beats; Lv dP/dt, maximum rate of left ventricular pressure development, an index of β -adrenergic activity.

Furthermore, catecholamine responses have only been investigated in dogs subjected to acute experimental stressors. Determining the blood pressure as a tool to establish the SAM activity may be much more advantageous since it can be measured telemetrically (Armentano et al., 1990) or non-invasively (Vincent and Michell, 1992a).

The same advantages apply to electrocardiogram (ECG) registrations which further allow the calculation of alternative indices of stress (Pagani et al., 1991). However, non-specific changes in the cardiovascular performance (Murphree et al., 1967; Lynch and McCarthy, 1969; Newton, 1969) easily complicate the measurement of stress. The sampling of more than one parameter may thus partly prevent erroneous interpretations of cardiovascular measures with regard to stress. Since cardiovascular responses may be measured non-invasively, are elicited by both experimentally and 'naturally' occurring stressors and may sustain for a longer period (Galosy et al., 1979), they may be considered useful tools to establish welfare problems in dogs.

Response variability between individuals and breeds (Corson, 1971; Koepke and Obrist, 1983a), and the necessity of invasive measuring techniques may hamper the use of renal excretory responses for establishing canine well-being. Anti-diuretic responses

may furthermore be typical for only the anticipation of severe aversive events, and last for only a limited time.

2.9. Are parameters reflecting HPA activity useful parameters of stress and indicators of welfare?

A number of experimentally and 'naturally' occurring stressors induce acute increases in plasma cortisol. Since cortisol responses reflect differences in appraisal and coping during stress (Dess et al., 1983), levels of cortisol may mirror welfare states in dogs in a sensitive way. Sampling blood may be replaced by saliva collection as a less invasive alternative for establishing cortisol levels (Vincent and Michell, 1992a; Vincent and Michell, 1992b; Beerda et al., 1996). Whether circumstances that persist and that initially elicited profound cortisol responses continue to stimulate cortisol production over time, remains unclear.

2.10. Immunological responses induced by experimentally and 'naturally' occurring stressors, and their potential as indicators of welfare states

Since very little has been published on immune activity of stressed dogs, we investigated peripheral leucocyte counts in ten Beagle dogs transported by car.

After the transport, which lasted for 50 min, the dogs were introduced into a new environment. Living conditions before and after transport corresponded in that they were spacious, enriched and social. Blood samples were taken by vena puncture before transport, immediate after arrival and 3 h after arrival. To validate transport as a stressful event saliva samples were taken and assayed for cortisol.

The mean level of saliva cortisol increased from 3.6 ± 0.4 nmol L⁻¹ before transport to 37.4 ± 8.2 nmol L⁻¹ immediate after arrival ($P < 0.01$, ANOVA for repeated measures). Responses showed great individual variation and attenuated within 1 h after arrival. Compared with pre-transport measures, total leucocyte counts were significantly elevated at 3 h after arrival (Fig. 5). The observed leucocytosis was composed of a significant ($P < 0.05$) increase in neutrophils and a nearly significant decrease in lymphocytes. This yielded a significantly elevated neutrophil:lymphocyte ratio. Mean eosinophil concentrations decreased from 0.36 ± 0.09 (SEM) before transport to 0.23 ± 0.06 3 h after arrival, but this decline was not significant.

Short lasting saliva cortisol responses and an overall leucocytosis in dogs subjected to transport are in accordance with similar findings reported by Kuhn et al. (1991). Data on leucocyte counts in humans (Weicker and Werle, 1991), make it feasible to consider the observed leucocyte responses as secondary effects of catecholamine and cortisol increases.

Specific changes in the number of peripheral neutrophils, lymphocytes and eosinophils may indicate acute stress in dogs. Whether changes in peripheral leucocytes sustain during chronic stress and thus prove valid indicators of bad welfare, remains open to further investigation. Since the assessment of altering peripheral leucocyte counts during chronic stress requires blood sampling and may become biased by seasonal fluctuations

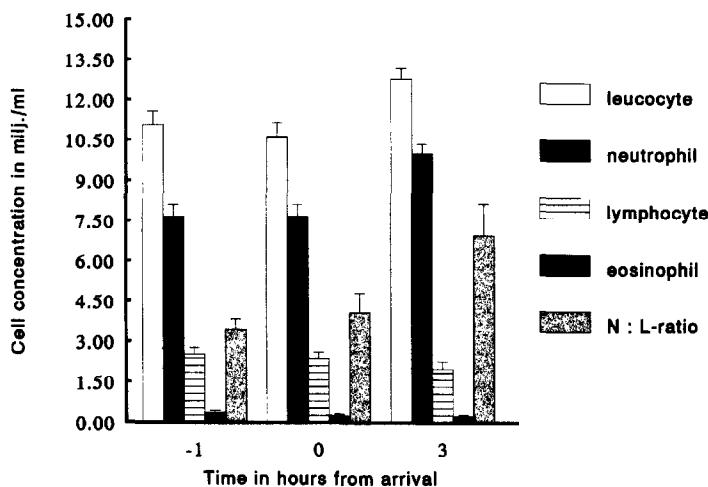


Fig. 5. Peripheral leucocyte counts before car transport (–1), immediate after arrival (0) and 3 h after arrival (+1); mean values \pm SEM in 15 Beagle dogs.

or antigen induced responses, its applicability to establish welfare problems in dogs may prove complicated.

3. Conclusions and discussion

In this paper we have reviewed how dogs show behavioural, physiological and immunological stress responses. A variety of behavioural responses has been reported in dogs subjected to different types of stressors. Part of this diversity may be attributed to differences in protocols used by the different investigators. Although still subject to individual variability, increases in frequencies of vocalizations and behavioural elements associated with fear and submission (snout licking, paw lifting and a lowered posture) may occur in dogs that experience stress. More severe stress may induce dogs to perform thermoregulatory behaviour (increased salivation, panting and anti-diuresis) and to develop stereotypies.

Similar to the behavioural responses, physiological changes in dogs experiencing stress are manifested in a wide variety of parameters. The majority of reported physiological stress responses reflect changes in HPA and SAM activity. Changes in canine HPA activity are commonly established by measurement of cortisol whereas cardiovascular performance is most frequently investigated to establish SAM activity. HPA and SAM mediated responses may be modulated by each other, and by opioid and parasympathetic systems. Some type of stressors may elicit antagonistic actions in the systems that respond to stress. This may consequently result in only marginal changes in the stress parameter under study.

Data on stress induced changes in the canine immune system are scarce and limited to peripheral leucocyte counts. It appears that acute stress induces an overall peripheral

leucocytosis that is composed of neutrophilia, lymphopenia and eosinopenia. No studies were found on canine immune responses during chronic stress.

The detection of welfare problems by measuring stress responses, requires a reliable establishment of the latter. The establishment of stress may be hampered by anticipatory and immediate responses to the sampling procedures. Anticipatory reactions can not always be prevented, but randomization of sampling times should reduce the development of time related anticipatory responses. Measures sampled non-invasively, such as behavioural observations, saliva and urinary cortisol, blood pressure and heart rate, disturb the dogs minimally and reduce unwanted side effects. Even stress responses that are established reliably may still be misinterpreted with regard to welfare. Stressor administration may evoke similar responses to those observed following events that are not likely to be aversive (Anderson and Brady, 1972; Newton, 1969). Changes in opposite directions in the same parameter (Muelas et al., 1993) or changes in different parameters (Gaebelein et al., 1977) may result when stressors with variable properties are administered. Individual differences (Lawler et al., 1975; Koepke and Obrist, 1983a) may further attribute to variability in stress responses and make interpretation difficult. Nor are the effects of breed (Corson, 1971); gender (Garnier et al., 1990); age (Palazzolo and Quadri, 1987) or earlier life experiences (Melzack, 1954) to be ignored.

The majority of studies dealing with stress in dogs report on acute responses. However, especially prolonged states of stress will be detrimental to their well-being. During prolonged stress, adaptation processes at the level of sensory input, appraisal of the stimuli and/or execution of responses, may cause stress responses to attenuate. Adaptation may render parameters of acute stress useless for establishing chronic stress (welfare). Measures of acute stress thus need to be validated as measures of chronic stress before they are used as indicators of welfare (Beerda et al., in prep.). Adaptive mechanisms, that cause specific stress responses to attenuate, may in themselves be indicative for chronic stress.

In summary, a variety of potential indicators of poor welfare in dogs subjected to acute stressors, still need to be validated with respect to chronic stress. Extending and applying basic knowledge on stress responses in dogs, measuring a range of stress parameters in each subject and testing for physiological adaptations are strategies to improve the interpretation of stress responses with regard to welfare of the dog.

Acknowledgements

The critical reading of the manuscript by B.E. Belshaw is highly appreciated. This work was supported by funds from the Ministry of Agriculture and Fishery, the Sofia Vereeniging ter bescherming van dieren and the Bond ter Bescherming van Honden.

References

- Anderson, D.E. and Brady, J.V., 1972. Differential preparatory cardiovascular responses to aversive and appetitive behavioral conditioning. *Cond. Reflex*, 7: 82–96.

- Armentano, R., Cabrera-Fischer, E., Breitbart, G., Pichel, R., Levenson, J. and Chau, N.P., 1990. Telemetry of aortic pressure in unrestrained animals: validation of the method over a wide range of blood pressure (from 40 to 200 mm Hg). *Med. Progr. Technol.*, 16: 125–129.
- Bebak, J. and Beck, A.M., 1993. The effect of cage size on play and aggression between dogs in purpose-bred beagles. *Lab. Anim. Sci.*, 43 (5): 457–459.
- Beerda, B., Schilder, M.B.H., Janssen, N.S.C.R.M., and Mol, J.A., 1996. The use of saliva cortisol, urinary cortisol and catecholamine measurements for a non-invasive assessment of stress responses in dogs. *Hormones and Behavior*, 30: 272–279.
- Benus, R.F., Koolhaas, J.M. and Van Oortmerssen, G.A., 1987. Individual differences in behavioural reaction to a changing environment in mice and rats. *Behaviour*, 100: 105–122.
- Cannon, W.B., 1929. *Bodily Changes in Pain, Hunger, Fear, and Rage*. Appleton, NY.
- Cannon, W.B. and de la Paz, D., 1911. Emotional stimulation of adrenal secretion, *Am. J. Physiol.*, 28: 64–70.
- Corson, S.A., 1971. Pavlovian and operant conditioning techniques in the study of psychosocial and biological relationships. *Society, Stress Dis.*, 1: 7–21.
- Corson, S.A. and O'Leary Corson, E., 1976. Constitutional differences in physiologic adaptation to stress and distress. In: G. Serban (Editor). *Psychopathology of Human Adaptation*. Plenum Press, NY, pp. 77–93.
- Dess, N.K., Linwick, D., Patterson, J. and Ovrncmir, J.B., 1983. Immediate and Proactive effects of controllability and predictability on plasma cortisol responses to shocks in dogs. *Behav. Neurosci.*, 97 (6): 1005–1016.
- Engel, G.L. and Schmale, A.H., 1972. Conservation-withdrawal: a primary regulatory process for organismic homeostasis. *Physiol. Emotion and Psychosom. Illness, Ciba Found. Symp.*, 8: 57–76.
- Engeland, W.C., Miller, P. and Gann, D.S., 1990. Pituitary-adrenal adrenomedullary responses to noise in awake dogs. *Am. J. Physiol.*, 258: R672–R677.
- Gaebelein, C.J., Galosy, R.A., Botticelli, L., Howard, J.L. and Obrist, P.A., 1977. Blood pressure and cardiac changes during signalled and unsignalled avoidance in dogs. *Physiol. Behav.*, 19: 69–74.
- Galosy, R.A., Clarke, L.K. and Mitchell, J.H., 1979. Cardiac changes during behavioural stress in dogs. *Am. J. Physiol.*, 236 (5): H750–H758.
- Garnier, F., Benoit, E., Virat, M., Ochoa, R. and Delatour, P., 1990. Adrenal cortisol response in clinically normal dogs before and after adaptation to a housing environment. *Lab. Anim.*, 24: 40–43.
- Gue, M., Honde, C., Pascaud, X., Junien, J.L., Alvinerie, M. and Bueno, L., 1988. CNS blockade of acoustic stress-induced gastric motor inhibition by κ -opiate agonists. *Am. J. Physiol.*, 254: G802–G807.
- Hessing, M., 1993. Individual behavioural characteristics in pigs and their consequences for pig husbandry. Ph.D. Thesis, Agricultural University, Wageningen.
- Hetts, S., Clark, J.D., Calpin, J.P., Arnold, C.E. and Mateo, J.M., 1992. Influence of housing conditions on beagle behaviour. *Appl. Anim. Behav. Sci.*, 34: 137–155.
- Hite, M., Hanson, H.M., Bohidar, N.R., Conti, P.A. and Mattis, P.A., 1977. Effect of cage size on patterns of activity and health of beagle dogs. *Lab. Anim. Sci.*, 27 (1): 60–64.
- Hubrecht, R.C., Serpell, J.A. and Poole, T.B., 1992. Correlates of pen size and housing conditions on the behaviour of kennelled dogs. *Appl. Anim. Behav. Sci.*, 34: 365–383.
- Knol, B.W., 1989. Influence of stress on the motivation for agonistic behaviour in the male dog: role of the hypothalamus pituitary testis system. Ph.D. Thesis, Utrecht University, The Netherlands, pp. 70–77.
- Koepke, J.P. and Obrist, P.A., 1983a. Angiotensin II in the renal excretory response to behavioral stress in conscious dogs. *Am. J. Physiol.*, 245: R259–R264.
- Koepke, J.P., Light, K.C. and Obrist, P.A., 1983b. Neural control of renal excretory function during behavioral stress in conscious dogs. *Am. J. Physiol.*, 245: R251–R258.
- Kronfeld, D.S., Adkins, T.O. and Downey, R.L., 1987. Nutrition, anaerobic and aerobic exercise and stress. In: I.H.X. Burger and J.P.W. Rivers (Editors). *Nutrition of the Dog and Cat*. Waltham Symposium Number 7. Cambridge University Press, Cambridge, pp. 133–145.
- Kuhn, G., Lichtwald, K., Hardegg, W. and Abel, H.H., 1991. Reaktionen von Corticoiden, Enzymaktivitäten und hämatologischen Parametern auf Transportstress bei Hunden. *J. Exp. Anim. Sci.*, 34: 99–104.
- Lawler, J.E., Obrist, P.A. and Lawler, K.A., 1975. Cardiovascular function during pre-avoidance avoidance, and post-avoidance in dogs. *Psychophysiology*, 12 (1): 4–11.
- Lawrence, A.B. and Rushen, J. (Editors), 1993. *Stereotypic Animal Behaviour: Fundamentals and Applications to Welfare*. CAB International, Wallingford.

- Lynch, J.J. and McCarthy, J.F., 1969. Social responding in dogs: Heart rate changes to a person. *Psychophysiology*, 5 (4): 389–398.
- Melzack, R., 1954. The genesis of emotional behavior: an experimental study of the dog. *J. Comp. Physiol. Psychol.*, 47: 166–168.
- Muelas, M.S., Ramirez, P., Parrilla, P., Ruiz, J.M., Perez, J.M., Candel, M.F. Aguilar, J. and Carrasco, L., 1993. Vagal system involvement in changes in small bowel motility during restraint stress: an experimental study in the dog. *Br. J. Surg.*, 80 (4): 479–483.
- Murphree, O.D., Peters, J.E. and Dykman, R.A., 1967. Effect of person on nervous, stable and cross bred pointer dogs. *Cond. Reflex*, 2 (4): 273–276.
- Newton, J.E.O., 1969. Coronary blood flow in dogs: effect of person. *Cond. Reflex*, 4 (2): 81–88.
- Pagani, M., Rimoldi, O., Pizzinelli, P., Furlan, R., Crivellaro, W., Liberati, D., Cerutti, S. and Malliani, A., 1991. Assessment of the neural control of the circulation during psychological stress. *J. Autonom. Nerv. Syst.*, 35: 33–42.
- Palazzolo, D.L. and Quadri, S.K., 1987. Plasma thyroxine and cortisol under basal conditions and during cold stress in the aging dog. *Proc. Soci. Exp. Biol. Med.*, 185: 305–311.
- Parrilla, P., Ramirez, P., Muelas, M.S., Perez, J.M., Fuente, T., Ruiz, J.M. and Ponce, J.L., 1990. Changes in small intestinal motility in acute physical stress — an experimental study. *Hepato-gastroenterol.*, 37: 140–146.
- Schwizgebel, D., 1982. Zusammenhänge zwischen dem Verhalten des Tierlehrers und dem Verhalten des Deutschen Schäferhundes im Hinblick auf tiergerechte Ausbildung. *Aktuelle Arbeiten zur artgemassen Tierhaltung*, pp. 138–148.
- Selye, H., 1936. Thymus and adrenals in response of the organism to injuries and intoxications, *Br. J. Exp. Pathol.*, 17: 234–248.
- Sigg, Von H. und Tobler, I., 1986. Motorische Aktivität von Bastardhunden in 3 verschiedenen Laborhaltung- gen. *Z. Versuchstierkd.*, 28: 157–165.
- Solomon, R.L. and Wynne, L.C., 1953. Traumatic avoidance learning: acquisition in normal dogs. *Psychol. Monogr.: Gen. Appl.*, 67 (4): 1–19.
- Stafleu, F.R., Rivas, E., Rivas, T., Vorstenbosch, J., Heeger, F.R. and Beynen, A.C., 1992. The use of analogous reasoning for assessing discomfort in laboratory animals. *Anim. Welfare*, 1: 77–84.
- Suomi, S.J., 1987. Genetic and maternal contributions to individual differences in rhesus monkey biobehavioral development. In: N.A. Krasnegor, E.M. Blass, A.M. Hofer and W.P. Smotherman (Editors). *Perinatal Development — A Psychobiological Perspective*. Academic Press, Orlando, FL, pp. 397–419.
- Thalken, C.E., 1971. The use of beagles in high intensity noise studies. *Lab. Anim. Sci.*, 21: 700–704.
- Vial, G.C., Stabenfeldt, G.H., Franti, C.E. and Ling, G.V., 1979. Influence of environment on adrenal cortical responses to ACTH stimulation in clinically normal dogs. *Am. J. Vet. Res.*, 40: 919–921.
- Vincent, I.C. and A.R. Michell, A.R., 1992a. Potential applications for non-invasive measurements in small animal epidemiology and in the detection of stress. *Proc. Meet. Soc. Vet. Epidemiol. Prev. Med.*, The Society: 102–109.
- Vincent, I.V. and Michell, A.R., 1992b. Comparison of cortisol concentrations in saliva and plasma of dogs. *Res. Vet. Sci.*, 53: 342–345.
- Weicker, H. and Werle, E., 1991. Interaction between hormones and the immune system. *Int. J. Sports Med.*, 12: S30–S37.
- Von Holst, D., 1986. Vegetative and somatic components of tree shrews behavior. *J. Auton. Nervous System. Suppl.*: 657–670.
- Wiepkema, P.R. and Koolhaas, J.M., 1992. The emotional brain. *Anim. Welf.*, 1: 13–18.