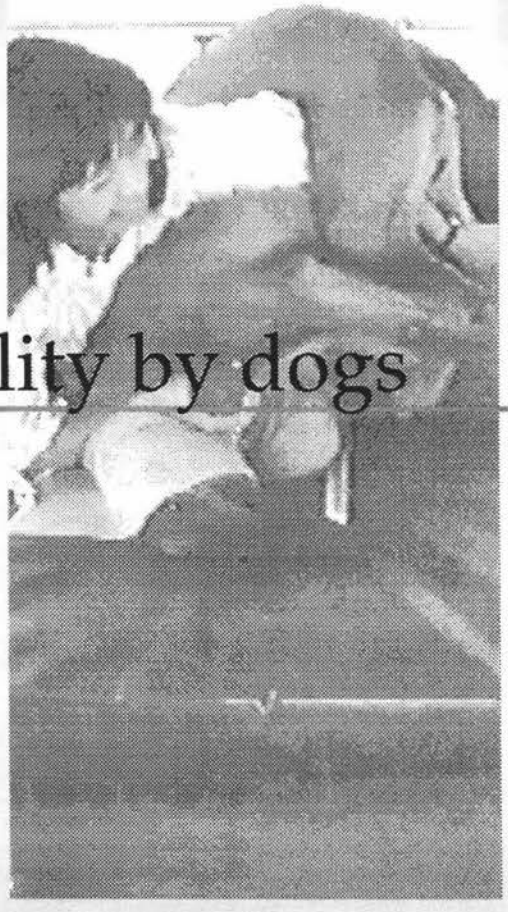
Tonic immobility by dogs



Tonic Immobility by Dogs

A thesis presented
in partial fulfilment of the requirements
for the degree
of Master of Veterinary Science
in Veterinary Ethology
at Massey University.

ONG Rae Ming
1993

Abstract

Tonic immobility (TI) is a state of relative immobility induced by restraint and presumed to function as a terminal defensive reaction. Although TI has been reported in a wide spectrum of species ranging from invertebrates to mammals, there have been very limited studies on TI by dogs.

The aim of this thesis was to determine the susceptibility and characteristics of TI in dogs so that the feasibility of using TI as a humane, quick, easily reversible, non-chemical and safe method of restraint for veterinary procedures could be assessed.

In an initial survey, 132 dogs were tested twice. Once by inversion and 30s restraint in the lateral position and once with an additional treatment (stroking, scruffing, blanket over head, cuff around ears or light into eyes) during the 30s restraint. Based on the criterion of remaining in the position restrained, without lifting its head off the test surface, for a minimum of 10s after release from restraint, 10 of the 132 dogs (7.6%) exhibited TI.

The characteristics of the dogs during TI were similar to those reported in other species, as the dogs remained very still, with the exception of occasional repositioning of heads and limbs, muscle tremors, twitches and paw movements. Swallowing, lip licking, blinking and occasional periods of eye closure were also observed but dogs had their eyes open throughout most of the TI episodes and appeared to be continually monitoring their environment as eye and ear movements, muscle twitches and changes in respiration rate were observed in response to auditory and other stimuli.

Many TI episodes were not terminated by intense stimulation such as loud auditory stimuli or physiological testing that included pinching between the dog's toes and inserting a thermometer into the dog's rectum. Respiration rate, heart rate, withdrawal reflexes and temperature were monitored on these dogs. These physiological parameters were all within normal limits.

Susceptibility to TI appeared to be a dog effect rather than a technique effect. Timid dogs or dogs that eliminated during testing were more susceptible to TI, indicating that susceptibility may be related to the dog's temperament or fearfulness. It was also found that proestrous bitches were more susceptible to TI than the other dogs.

A potentiation effect with repeated testing was observed when the intertrial interval was between 20 - 80s. No order or carry-over effect was however found when a 3 min intertrial

interval was used. No difference in susceptibility to TI was found between techniques but the cuffing technique resulted in longer TI durations than the others.

Results should however, be interpreted with caution due to the small number of dogs exhibiting TI. More extensive investigations of the characteristics and physiological changes during TI and the effect of individual variables on TI susceptibility and durations are also required to determine the safety and extent of procedures that may be conducted while dogs are in TI. The results from this initial study are promising as they show that dogs do exhibit TI. The duration, characteristics and physiological changes observed during TI also indicate the potential for using TI as a quick, non-chemical, easily reversible and safe method of restraint in some dogs, for routine clinical examinations or even veterinary procedures.

Acknowledgements

I would like to thank and acknowledge the collaboration of the Animal Health Service Centre at Jennersmead, Palmerston North SPCA and the dog breeders and owners that allowed me to test the dogs in their care. Special thanks to Olive Judd who introduced me to the dog breeding scene and to the breeders whose friendliness made the study more enjoyable. Approval of the Massey University Animal Ethics Committee is acknowledged.

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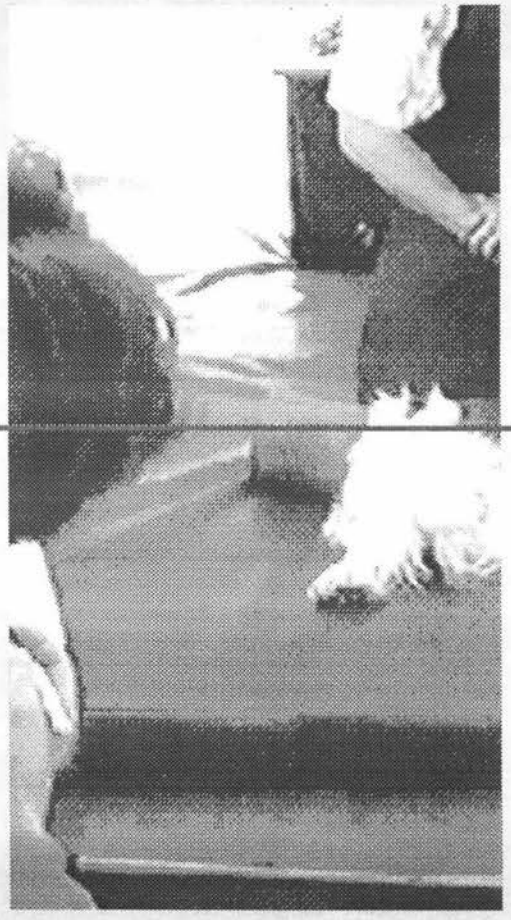


Introduction

Tonic immobility or TI is a state of relative immobility induced by restraint and presumed to function as a terminal defensive reaction. Although it has been reported in a wide spectrum of species ranging from invertebrates such as insects, spiders and crustaceans to fish, amphibia, reptiles, birds and mammals including humans, there have been very few studies on TI by dogs. This is believed to be the first specific study of TI in non-experimental dogs. The aim of this thesis is to study the phenomenon of TI in dogs to determine the susceptibility and characteristics of TI in the species.

If dogs were susceptible to TI, the feasibility of using TI as a humane, quick, easily reversible, non-chemical and safe method of restraint for veterinary procedures could then be assessed. The advantages of being able to perform simple tasks like blood sampling or injections, that don't usually justify chemical methods, without having to fight with a struggling dog and risk damaging a vein or being bitten and stressing the dog, veterinarian, nurse and owner are self evident.

It may even be possible to perform other procedures such as minor stitch-ups or sugery (eg. grass seed or lump removal), ophthalmic or aural examination, adbominal or rectal palpation, catheterisation, nail clipping, skin scraping and radiology while an animal is in TI. Elimination of manual restraint for a struggling dog in radiology would mean sparing two to three people from possible irradiation. Clearer and fewer exposures would also result as the dog would be unlikely to move or struggle during the vital exposure period.

Although chemical restraint can be used, it may be contraindicated on some occasions, for example if the dog is in shock, with compromised circulatory or cardiac functions or has severe liver or kidney disease. Using TI as a form of restraint also means not having to worry if dog has recently been fed and so alleviates the need to wait 12-24 h before anaesthetising an animal for assessment, radiology or treatment. Owners could also bring their pets in for minor procedures without the need to starve the dog beforehand or to wait till the dog recovers sufficiently from anaesthesia before returning home. This would decrease the costs associated with overnight stays and anaesthesia.

In order to evaluate if TI could be used as a method of restraint for veterinary procedures in dogs, the first step was to determine whether dogs exhibit TI and the proportion of dogs that are susceptible. The duration and depth of TI were assessed to determine how long a dog remained immobile and the intensity and type of stimulation that caused termination of TI.

The characteristics and physiological changes during TI (eg. whether there is analgesia associated with TI) also need to be assessed to determine the safety and feasibility of performing certain procedures during TI. Tonic immobility may for example, affect the cardiovascular, respiratory or nervous system in some dogs, thus making it unsafe for certain subjects. Whether TI interacts with drugs such as sedatives, analgesics, anaesthetics or other medications also needs to be evaluated.

The dog's behaviour at termination of TI is also important, as some species exhibit aggressive behaviour towards the investigator at termination. Behaviour at termination may also indicate how aversive TI is to the dog and thus whether TI is an humane alternative form of restraint for dogs. This is especially important if TI is to be induced several times in the same dog. The effects of repeated testing on TI susceptibility and duration need to be determined if TI is to be re-induced on several visits or perhaps even during a single visit if the response is not deep, or the duration of immobility is not long enough (eg. for several re-positionings for radiology).

Finally, other variables (eg. testing conditions, induction method, age, breed or temperament) affecting TI need identification in order to examine how they affect TI susceptibility and duration. Different methods of inductions may for example be more successful at inducing TI in certain categories of dogs. This information could then be used to identify susceptible dogs (eg. pups only) or be used to potentiate TI susceptibility or increase durations as a certain duration and depth of TI would be required for different procedures.

Extensive research is therefore required before it can be determined if TI is useful as a routine method of restraint for veterinary procedures. This study of TI in dogs attempted to determine the susceptibility of dogs to TI and its characteristics. From this, an indication of the proportion of dogs susceptible to TI, duration and depth of TI, characteristics and physiolgical changes during TI were ascertained. Some of the variables affecting TI susceptibility and duration were also identified and examined.

Chapter two

Literature review

Literature Review

2.1 INTRODUCTION

Tonic immobility or TI is a fascinating phenomenon that has been reported in a wide spectrum of species ranging from invertebrates such as insects, spiders and crustaceans to fish, amphibia, reptiles, birds and mammals including humans (Figure 2.1). It is a state of relative immobility induced by restraint and presumed to function as a terminal defensive reaction. This immobility may last for only a few seconds or persist for up to several hours.

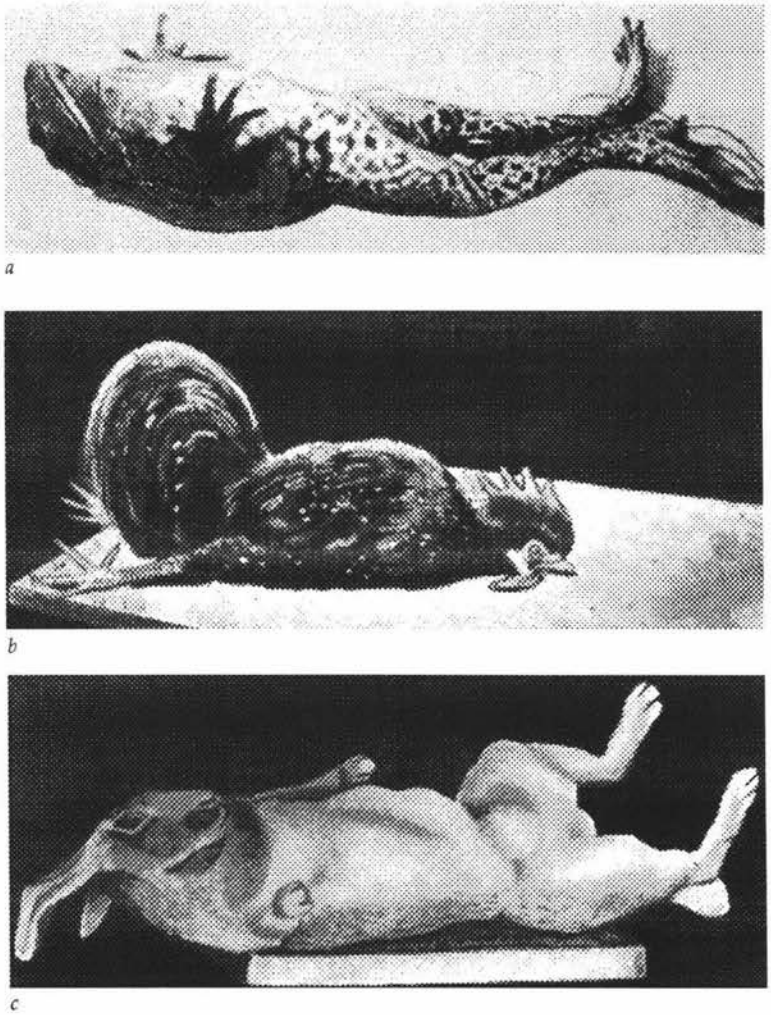


Figure 2.1 Tonic immobility in a a. amphibian, b. bird and c. mammal (Volgyesi 1966).

Examples of common knowledge of TI or "animal hypnosis" include the farm yard trick of "hypnotising" chickens by stretching them out on the ground. (Figure 2.1b) When released after a few seconds restraint, the chicken remains immobile for several seconds or even minutes. Fishermen are also familiar with the resultant immobility when they

place their thumb inside a fish's mouth to remove a hook. This and the familiar effect of turning a frog on its back and stroking its stomach are examples of folk knowledge of "animal hypnosis". Similar procedures are also used in rodeos and alligator wrestling (Ratner 1967).

TI has also found its way informally into laboratory procedures and animal husbandry. For example, injections and blood samples are often taken from animals such as rabbits by inverting them into a V-shaped trough, holding them briefly and then working on them while they are immobile (Figure 2.2). Handbooks on banding wild birds also typically warn novices that a bird may appear to have died while held for banding (Figure 2.3), but will fly away if thrown into the air (Ratner 1967). Naturalistic observations also commonly describe instances of "death feigning" in prey animals when attacked by a predator.

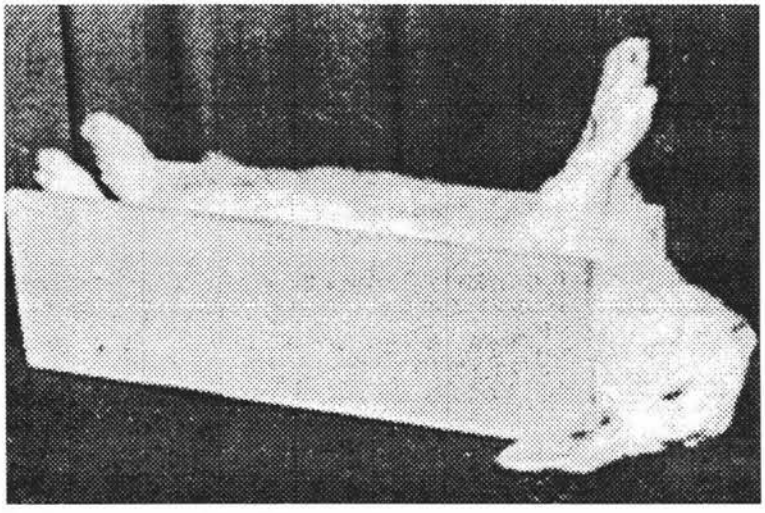


Figure 2.2 Rabbit exibiting TI in a U-shaped wooden holder (Klemm 1966b).

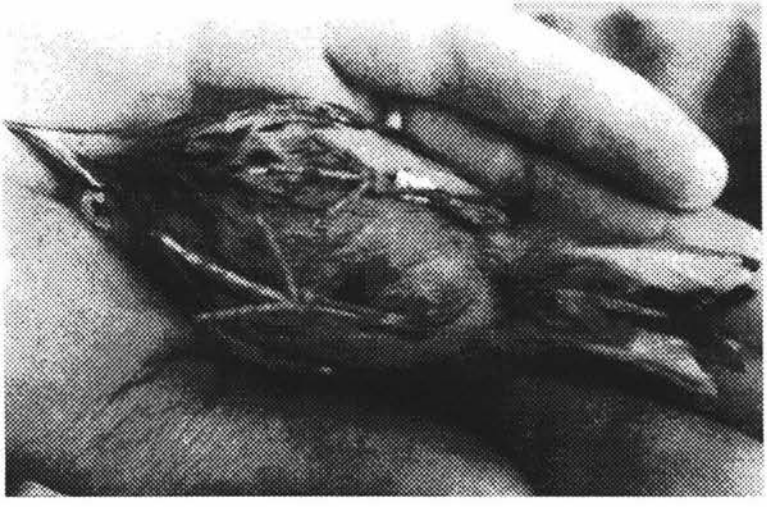


Figure 2.3 Bird displaying TI while held for banding (Volgyesi 1966).

Although a state of immobility might not seem particularly intriguing, TI has fascinated ethologists, naturalists, zoologists, physiologists, neurologists, psychologists, psychiatrists, pharmacologists and even theologians for over three centuries. Until today, there is still considerable debate regarding its mechanisms, characteristics and even the most appropriate term to describe this state.

This literature review aims to provide a brief historical overview of TI, discuss some of the terms that have been used to describe this phenomenon and then with a working definition of TI, review the species, methods of induction, characteristics and physiological changes during TI. A discussion on the variables that can affect TI and the theories that have been postulated in an attempt to explain TI will then follow, with emphasis on areas that are most relevant to this thesis. For example, as the thesis does not attempt to elucidate a specific neural pathway or neurotransmitter involved in TI, only a cursory review of this area of the literature will be covered as the scope of this relatively new area of TI is beyond the limitations of this thesis's preliminary survey of the susceptibility and characteristics of TI in the dog. Finally the review will examine the very limited literature available on TI in dogs, highlighting the need for further research in this species.

To begin, a brief historical overview of tonic immobility or as it was more commonly referred to, "animal hypnosis" is presented. This illustrates the diversity and controversy surrounding this phenomenon in regard to the terms used to describe it, the different methods of induction, the wide variety of species that show this phenomenon and especially the controversy that surrounds the theories behind TI. Even its history is controversial, with differing reviews being evident from European and American papers.

2.2 HISTORICAL OVERVIEW

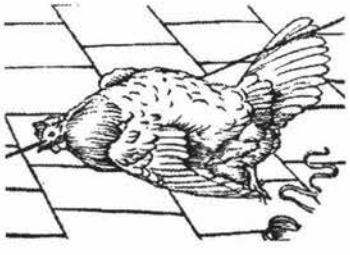


Figure 2.4 Father Kircher's TI experiment in a chicken (Volgyesi 1966).

Early written accounts of TI date back to the Ancient Egyptians, The Old Testament and The Talmud where references were made to the immobilisation of snakes, lizards and scorpions (Klemm 1971c). The first specific study on TI however, was not reported until 1636 when Daniel Schwenter, a mathematics professor and orientalist at the University of Altdorf induced immobility in a chicken by "pressing it gently to the ground, holding the head immobile and drawing a chalk line rapidly away from the head and beak" (Gilman and Marcuse 1949). Father Athannasius Kircher an Austrian Jesuit priest also repeated Schwenter's experiment in 1746 and his paper titled "Experimentum mirabile de imaginatione gallinae Kircher" is often credited as the first publication on TI (Figure 2.4).

Despite the novelty of Schwenter's and Kircher's discovery, whether due to lack of interest or lack of information, scientific interest in TI did not resurge until Frank Mesmer (1766-1842). Mesmer is best known for his seemingly magical methods for healing or hypnotising by waving his hands or "magnetised objects" in front of his subjects (Gilman and Marcuse 1949).

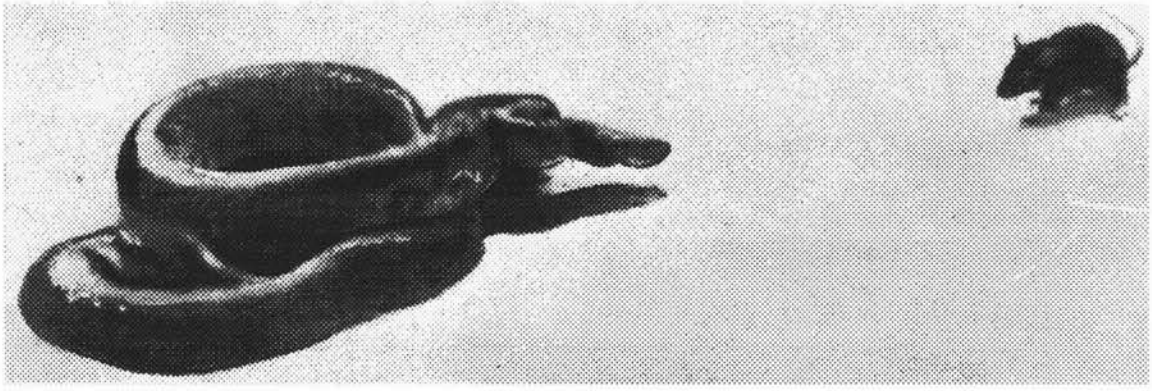


Figure 2.5 A giant snake entrancing its prey, a rat (Volgyesi 1966).

Abbe Faria, one of Mesmer's followers, applied Mesmer's techniques to animals and popularised the idea that animals could entrance others by looking steadily into the eyes of their prey (Klemm 1971c) (Figure 2.5). It was believed that some magnetic material emanated from the magnetiser to the magnetised by means of "passes" and that animals could be magnetised by placing them into peculiar positions (Figure 2.6) and stroking from the head to the tail to "magnetise" it and were "demagnetised" by stroking in the opposite direction (Chertok 1964).

Figure 2.6 Tonic immoblity in a chicken placed in the bizarre position shown (Chertok 1964).

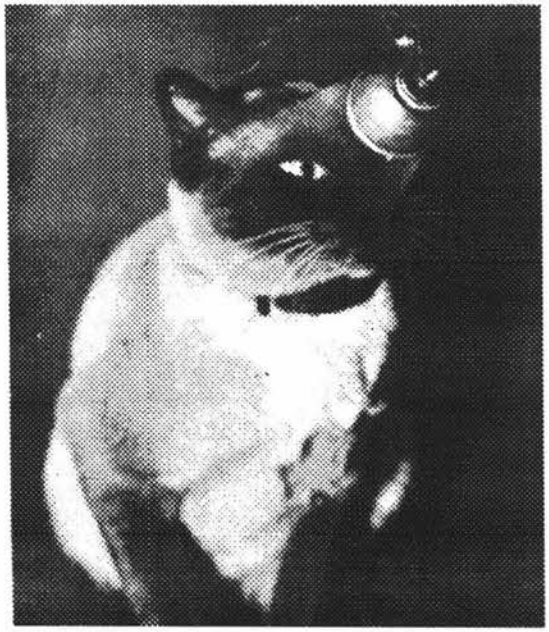


Figure 2.7 "Hypnosis" of cat by eye fixation on a light (Volgyesi).

Then in 1840, TI research in France came to an abrupt halt as the French Academy of Science forbade its members from investigating human or animal magnetism as it was deemed to be an unscientific supernatural procedure (Klemm 1971c). During this period, an English ophthalmic surgeon, James Braid (1795-1860), noticed the importance of eye fixation during a stage show in which a Frenchman was putting people and animals into a trance. Braid introduced the use of prisms and was among the first to popularise the use of human hypnosis for medical purposes. He also dispelled a lot of the mystery surrounding hypnosis by demonstrating that simply staring at a prism or light (Figure 2.7) is sufficient to induce a trance in certain subjects without the need for magical waving of arms or incantations by the experimenter (Klemm 1971c).

Braid is also often credited with the observation that a phenomenon similar to human hypnosis occurs in animals during moments of extreme danger (Preyer 1881). As an example, Braid cited the attraction of a bird to the slow movements and stare of a snake (Ratner 1967). Braid called this phenomenon "monoidesmus" (Figure 2.8) which was believed to be a combination of cataplexy, hypnosis, fascination and all other phenomena which temporarily disturb the nervous system because of the limitations imposed on it by a focussed attention (Gilman and Marcuse 1949).

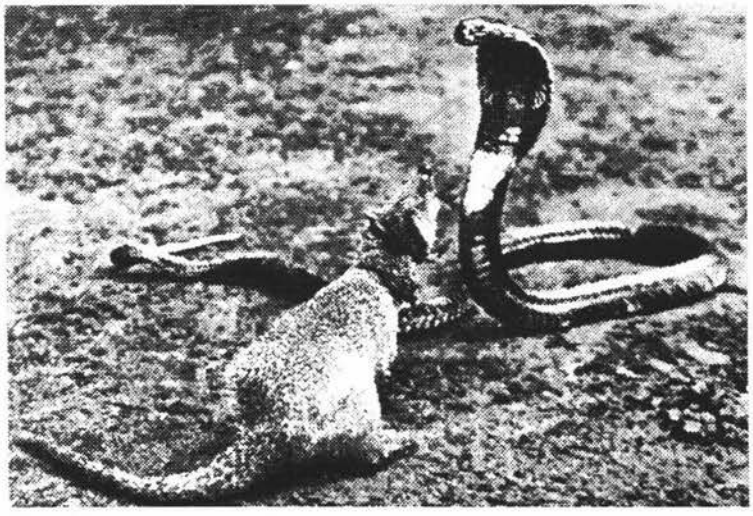


Figure 2.8 "Monoidesmus" between a snake and a mongoose (Volgyesi 1966).

The importance of fixation in animal hypnosis was further developed by Preyer (1881) but he believed that only special fear-producing objects could elicit this fixation and the resultant immobility. Preyer is therefore often credited for introducing the concept that fear may be an important aspect of animal hypnosis (Ratner 1967). Preyer based this theory on demonstrations where immobility could be produced by suddenly grabbing an animal rather than by gentle passes of hands or by staring into its eyes (Klemm 1971c). This theory and method of induction is still in vogue today.

Later, Darwin (1900) interpreted the immobility reactions he observed when animals are grabbed by a predator in terms of death feigning and the adaptive significance of this behaviour (Gilman and Marcuse 1949). Although this interpretation caused considerable debate and opposition at the time, this concept has been incorporated into several theories regarding the function and mechanisms of tonic immobility.

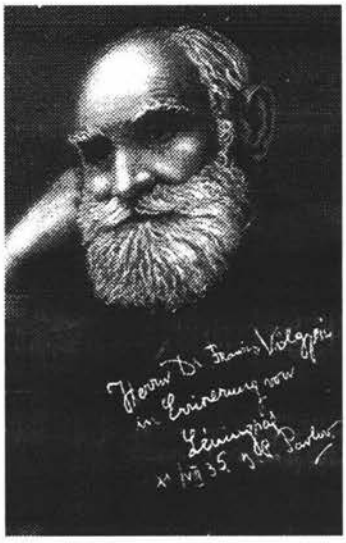


Figure 2.9 IP Pavlov (Volgyesi 1966).

Another notable scientist who has been intrigued by TI was Pavlov (Figure 2.9) who encountered TI during his studies on conditioned reflexes. He reported that two of his experimental dogs would lapse into a hypnotic state (Figure 2.10) when placed into their experimental apparatus (Pavlov and Petrova 1934). Pavlov interpreted this phenomenon as "a self-protecting reflex of an inhibitory character" arising due to inhibition from cortical cells induced by monotonous stimulation such as occurs during his conditioning experiments or by sudden and intense stimulation such as during attack by a predator (Ratner 1967). Volgyesi who worked with Pavlov is another scientist who was fascinated by TI. Volgyesi conducted extensive research on human and animal hypnosis and published an excellent review entitled "Hypnosis of Man and Animals" (Volgyesi 1938) which made accessible a wealth of European literature which would have otherwise been inaccessible.

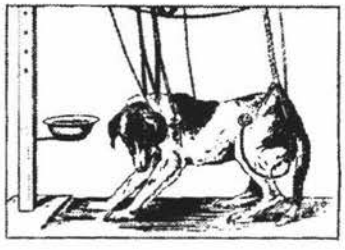


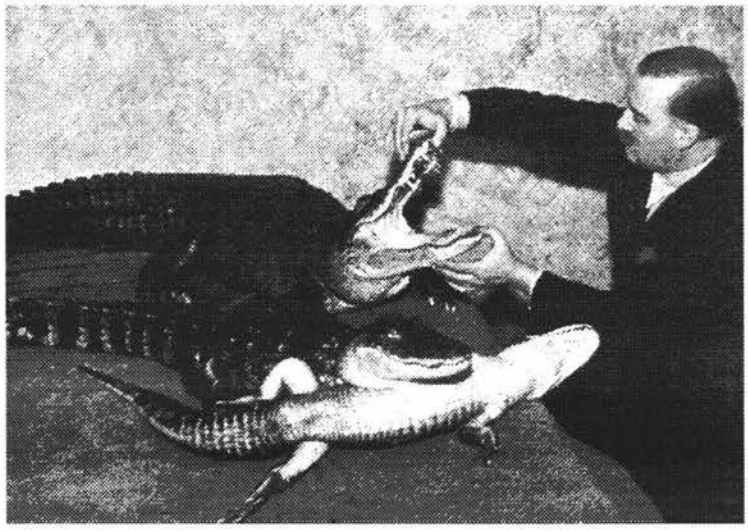
Figure 2.10 "Hypnosis" in one of Pavlov's dogs (Volgyesi 1966).

Another review of older literature (Steiniger 1936) listed 240 publications on TI. Most of these early reports were not in English and dealt mainly with empirical observations, TI characteristics, induction methods and phylogenetic distribution of susceptibility. Many of these early experiments however were pseudoscientific being dominated by concepts such as mesmerism and animal magnetism (Klemm 1971c).

Besides Volgyesi's book which provided a comprehensive account of hypnosis in humans and animals along with fascinating pictures of Volgyesi hypnotising various animals including a lion, crocodiles and a bear (Figure 2.11); several other excellent reviews written in English have been published by Gilman and Marcuse (1949), Chertok (1964), Ratner (1967), Klemm (1971c) and Gallup (1974a).

a

c



b

Figure 2.11 "Hypnosis" in a a. lion b. crocodile c. bear (Volgyesi 1966).

The largest review of TI however, was published in 1977 in a special issue of the Psychological Record titled "Animal Hypnosis: Research and Theory". This special issue of the Psychological Record included 12 papers by various leading authors on TI. The investigators agreed on many points but argued about terminology, aetiology, homology or analogy across species and about the various explanatory theories for TI. This special volume also included a partially annotated Tricentennial Bibliography from 1636 - 1976 by Maser and Gallup (1977) which included approximately 500 references in English, 69 in French, 175 in German and 56 in Slavic languages.

Since 1977 however, there have not been any reviews on TI in general. Scientific literature on TI prior to 1970 tended to be more review orientated covering history, species, methods, characteristics and explanatory theories for TI. Investigations then became more concerned with variables affecting TI and the various explanatory theories or hypothesis regarding the mechanisms behind TI.

As is evident from the colourful history of TI, numerous theories and terminology have been proposed for TI over the centuries and have often included a wide variety of immobility behaviours such as death feigning, freezing, catalepsy and hypnosis. These numerous theories and labels however, may be describing different immobility phenomena.

2.3 TERMINOLOGY

Traditionally, various immobility behaviours have been considered as one phenomenon and the different terms attached to immobility in animals have been considered mere synonyms for one another and have been used interchangeably depending on a given author's fancy or the current trend in animal hypnosis research.

Maser and Gallup (1977) noted approximately 30 terms in their review of TI literature and reported that the common names span at least 9 languages: Czechoslovak, English, German, Hungarian, Italian, Latin, Russian and Spanish. Table 2.1 lists over 50 terms that have been used to describe various immobility reactions considered to be TI.

Many of these terms reflected the current trends and hypothesis regarding TI. For example, bewitchment, entrancement, fascination, mesmerism and trance originated during Mesmer's period when there were still strong mystical beliefs. Even today many terms (eg. "immobility reflex" Klemm 1971a) reflect the author's favourite theory for TI. Other terms either describe the behaviour that is characteristic of the state (eg. action inhibition, akinesis, hypertonicity, immobilisation, immobility and still reaction) or the assumed cause of the state (eg. bewitchment, animal hypnosis and death feigning) or both the behaviour and the assumed causation (eg. reflex immobility, fright or terror paralysis).

In order to categorise any behavioural pattern, it is necessary to incorporate a minimum of several criteria including presumed function, causation and motor pattern (Beer 1973). When developing a word or phrase to describe a behavioural pattern, as many of these criteria should be represented as accurately as possible. Concentrating on one criterion at the expense of the others would limit the types of questions which may be raised concerning the behavioural pattern. However, if too little is known concerning one of the criteria, then its inclusion may lead to ambiguity and subsequent anthropomorphism (eg. animal hypnosis, death feigning or fright paralysis).

The most commonly used terms today are animal hypnosis, immobility reflex and tonic immobility. "Animal hypnosis" is the most familiar and frequently used term but is anthropomorphic and by assuming a similarity to human hypnosis, can result in oversimplification, reductionism and confusion. "Tonic immobility" and "immobility reflex" are more behaviouristically descriptive as the most prominent feature of the state which these terms describe is virtual immobility. "Tonic immobility" however, concentrates only on the motor aspect of response and therefore has limited heuristic value. "Tonic" is not entirely accurate as the immobility may only last a very brief period. Klemm (1976b) therefore suggested the use of the phrase "phasic immobility". Another point of

confusion is that the term "tonic immobility" has also been used by physiological psychologists to describe other forms of immobility such as conditioned emotional responses to conditioned stimuli previously paired with electric shock (eg. Thomas et al 1968). This form of immobility however, neither shares the same causal stimuli nor underlying neural mechanism (Woodruff et al 1975; Woodruff and Lippincott 1976).

Terms used to describe "tonic immobility"

action inhibition	feigning death	phasic immobility
akinesis	fright paralysis	playing possum
animal hypnosis	hypertonicity	pretended death
apparent death	hypnosis	reflex immobilisation
bewitchment	immobilisation	reflex immobility
catalepsy	immobilisation reflex	restraint immobility
cataplexy	immobility reaction	rho
catatonia	immobility response	shammed death
catatonic trance	immobility reflex	still reaction
clipnosis	inhibition	terror paralysis
conditional akinesis	inhibitory state	thanatomimesis
conscious simulation of death	letisimulation	thanatosis
contact defence immobility	mesmerism	Totstell's reflex
death feigning	monoideism	totstellung
death feint	monoideismus	trance
entrancement	myotonia congenita	tonic immobility
fascination	paralysis of fear	withdrawal
feigned death	paroxysmal inhibition	

Table 2.1 Terms used to describe "tonic immobility".

"Immobility reflex" the term used by Klemm (1971a) is behaviouristically descriptive and as intended by Klemm fosters thinking along the neurophysiological lines. The term "reflex" however, has too many connotations as although the initiation of the immobility response may be reflexive, termination is probably under considerable conscious control (O'Brien and Dunlap 1975). More recent research (eg. Gallup et al 1980) has also indicated that this form of immobility is an integrated functional behavioural act in which several sensory modalities participate and is in fact a very complex phenomenon and not just a simple reflex as might be implied by the term "immobility reflex".

The most descriptive and least misleading term is Woodruff's (1977) "contact defense immobility". Compared to other terms, "contact defense immobility" is behaviouristically descriptive and distinguishes this type of immobility from others by including in the label its presumed function and causation. There is now considerable evidence supporting the theory that this form of immobility has a defensive role against predation and that the most important causal stimuli appears to be restraint and consequent pressure on body parts (eg. Sargeant and Eberhardt 1975) as will be discussed in section 2.8.

This terminology therefore meets all of Beer's (1973) criteria by including the behaviour's presumed function, causation and motor function. Because it is specific, it distinguishes this form of immobility from other forms which for example, do not include contact (eg. freezing behaviour which Woodruff (1977) termed "distance defense immobility") or are not of defensive nature (eg. drug induced immobility). Other terms such as "animal hypnosis" can and have been applied to a wide variety of immobility responses even though the responses may have very little in common besides a diminished responsiveness or immobility. The duration of the immobility may range from several seconds to several hours and the necessary eliciting stimuli, overt response characteristics, accompanying physiological changes and controlling mechanisms are so exceedingly variable that it would be beyond the scope of this thesis to review all these immobility reactions.

This literature review will therefore be limited to the group of immobility behaviours best described as *a state of relative immobility induced by restraint and presumed to function as a terminal defensive reaction*. Even this is no small task as evidenced by the wide range of methods used for inducing this phenomenon in the seemingly unlimited numbers of species exhibiting this response.

2.4 SPECIES

Based on this criterion for TI, recent research (20th century) has concentrated primarily on TI in the domestic chicken with almost 50% of papers reporting on TI in chickens. The rest of the literature consists of approximately 20% on rabbits, 10% on rodents, 5% on lizards,

3% on frogs or toads and less than 3% on dogs. As is evident from the following list however, it can be seen that TI has been reported in a wide range of animals including:

Animals reported to exhibit TI

INVERTEBRATE	REPTILES, AMPHIBIAN, FISH	BIRDS	MAMMALS
beetle	anole	bobwhite quail	cat
caterpillar	boas	buzzard	cow
cockroach	chameleon	canary	coyote
crab	crocodile	chicken	deer
crayfish	frog	crow	dog
cricket	fish	cuckoo	elephant
lobster	gecko	duck	fox
mantid	iguana	falconet	goat
octopus	lizard	finch	guinea pig
pill bug	newt	goose	horse
shrimp	salamander	guinea fowl	human
spider	snake	gull	lion
scorpion	tadpole	hawk	mice
tarantula	toad	heron	monkey
water beetle	tortoise	Japanese quail	opossum
wood louse		owl	pig
		oyster catcher	rabbit
		parrot	rat
		partridge	sheep
		peacock	squirrel
		pigeon	
		robin	
		sparrow	
		swan	
		turkey	
		vulture	

Table 2.2 Animals reported to exhibit TI.

The wide range of subjects exhibiting this immobility response indicates a general phylogenetic spread of the phenomenon. Ratner (1977) believed that immobility reactions reported in invertebrates and vertebrates are the same phenomenon, as although they have been studied by independent scientists, the same behavioural responses of prolonged immobility and reduced responsiveness to stimulation has been reported. Induction procedures are also similar especially considering the differences in size and sensory processes of the two groups of animals. In addition the variables of repeated testing and intensity of stimulation during induction have similar and expected effects on duration of immobility for both vertebrates and invertebrates.

A similar immobility reaction in humans has also been reported by Armstrong (1965) who described cases of humans who were immobilised and analgesic during terrifying experiences. This is analogous to the common description of people being "scared stiff", " frozen with fear" or soldiers being "shell shocked" when in combat. Suarez and Gallup (1979) also believed that rape-induced paralysis in humans may represent the same phenomenon as TI as reactions by rape victims are often isomorphic with behaviours shown by immobilised animals. That is, full consciousness along with motor inhibition, tremors, suppressed vocal behaviour, apparent analgesia, cold sensation, abrupt onset and termination and aggressive reactions at the termination of an episode. Fear, overtones of predation, contact and restraint are also common denominators to rape and the induction of tonic immobility.

Hoagland (1928) and Crawford (1977) also reported that a state similar to TI has been described in children by Pieron (1913) and Peiper (1963) who induced immobility in young children by inversion, restraint and rhythmic stimulation. Hoagland induced immobility lasting several seconds in adult humans by getting his subjects to bend forward from the waist at an angle of 90 degrees and then be "man-handled" by two men who would suddenly throw the subjects backwards through 180 degrees. Crawford (1977) also attempted to induce immobility by rapidly inverting his students who were restrained in a specially designed tilt chair which allowed rapid inversion. The students all reported muscular contraction, sweating, flushing, shallow breathing and irregular pulse but none became immobilised.

Although most investigators (eg. Frolov 1937; Gilman and Marcuse 1949) believed that "the capacity of becoming immobile under the influence of compulsory restriction of movement is characteristic of all species", others (eg. Danilewski 1890, Svorad 1956) have reported that certain species for example cats, dogs, rats and mice are refractory to "hypnosis". It is however more likely that different species vary in their susceptibility to TI and also in the best induction technique required for inducing TI, as other investigators (eg. Mangold 1914) have been able to induce TI in these species (Figures 2.12 and 2.13).

Even though TI is generally considered to have a common underlying basis, it is possible that the mechanisms are different in different species (Lefebvre and Sabourin 1977a). The differences in susceptibility between species may be explained by differential morphology, physiology or requirements for certain environmental conditions, age and longevity of the subject, induction methods such as degree of restraint or other variables (Crawford 1977) as will be discussed in section 2.7. Different methods of induction will be discussed in the following section.

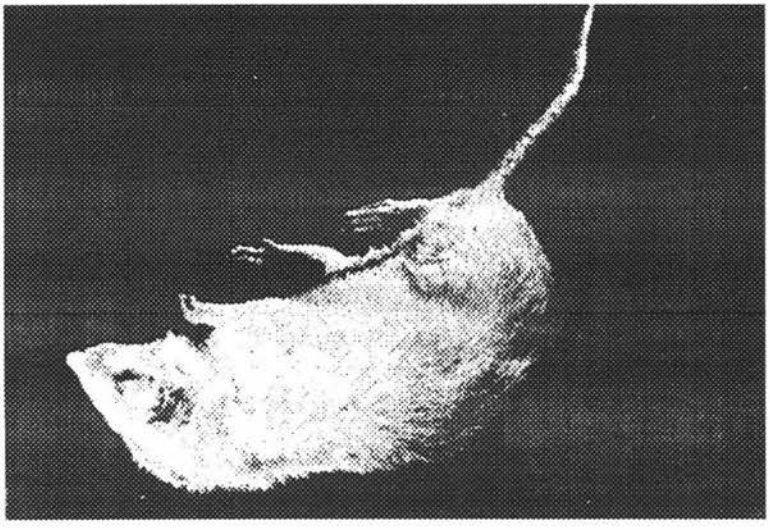


Figure 2.12 Tonic immobility in a rat (Klemm 1971).

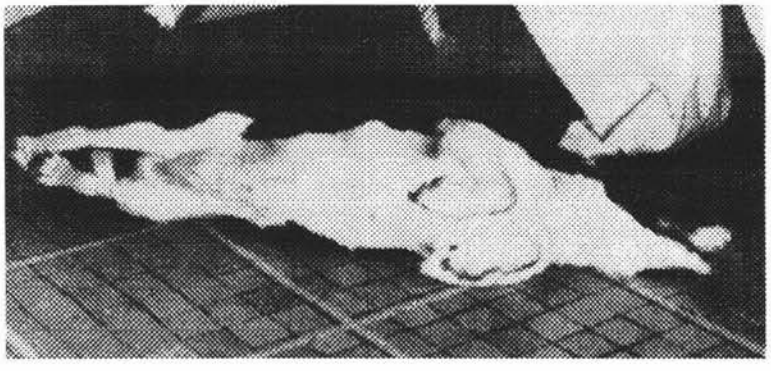


Figure 2.13 Tonic immobility in a dog (Fox 1978).

2.5 METHODOLOGY

As evident from the historical review, many different methods have been used to induce tonic immobility or to "hypnotise" animals. These ranged from superstitious methods such as mesmeric passes of the hand or fixation of the subjects gaze on a prism or chalk line (Figure 2.14) to the more conventional or so called classical methods of inversion and restraint.

Figure 2.14 Hypnosis of a peacock by Schwenter-Kircher's chalk line method (Volgyesi 1966).

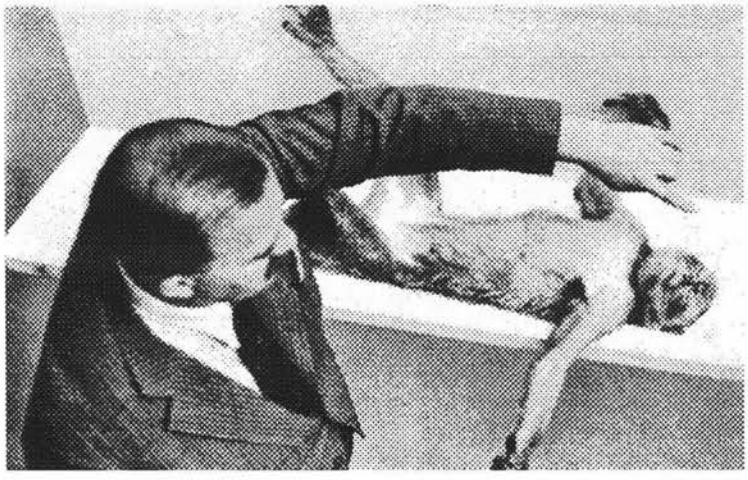


Figure 2.15 Hypnosis of a mandril by eye-fixation (Volgyesi 1966).

The common techniques reported include eye fixation (Figure 2.15), use of a light or a prism, swaying the subject back and forth, stroking or waving the hands to create monotonous tactile or visual stimulation, grabbing the subject with or without sudden inversion and pressing on the thorax or abdomen of an inverted subject. Although at first glance, these induction techniques do not necessarily fit into the definition of TI as "a state of relative immobility induced by restraint ....", they all have features in common that can be grouped into 4 categories (Foley 1938).

1. Repetitive stimulation
2. Pressure on body parts
3. Inversion
4. Restraint.

Most methods use 2 or more of the above stimuli in combination and the common denominator in most of these techniques is restraint. For example, to be able to stroke, sway, apply pressure or invert an animal, some degree of restraint is necessary. Restraint is also integral part of the induction of TI in natural conditions when a prey animal is grabbed by a predator (Armstrong 1965; Franq 1969; Sargeant and Eberhardt 1975). Many investigators (eg. Ratner 1967) believed that "the production of hypnotic reactions in animals requires restraint and novelty or unfamiliarity of the restraining stimulus". This review will focus primarily on the more recent publications that induce TI by the so called classical methods of inverting and restraining the subject in a specific position.

It is generally reported that the less profound the restraining stimuli in terms of strength, duration and physical proximity, the weaker the response (Ratner 1967). The effectiveness of a particular induction procedure to cause TI is however, affected by many other variables as will be discussed in detail in section 2.7. For example, species differ in the type

of stimuli that will have the greatest effects; that is, different methods of induction in one species may give rise to different responses (Lefebvre and Sabourin 1977a).

For example, there is an increase in TI duration in frogs (Figure 2.16) if induced belly up (Mangold and Eckstein 1919) and placing a rabbit (Figure 2.2, p 6) in a V-shaped trough (Ratner 1967, Carli 1977) has been shown to potentiate TI. Klemm (1971c) provided detailed description of the different methods he has found to work best for inducing TI in the frog, rabbit and rat. Some of these differences however, may just reflect the different species morphology or characteristics. For example, frogs are usually restrained on their backs because it would be almost impossible to balance a frog on its side and tarantulas are usually inverted in a glass container to avoid direct handling. There are however, also species differences in optimal restraint periods or testing apparatus and surfaces.

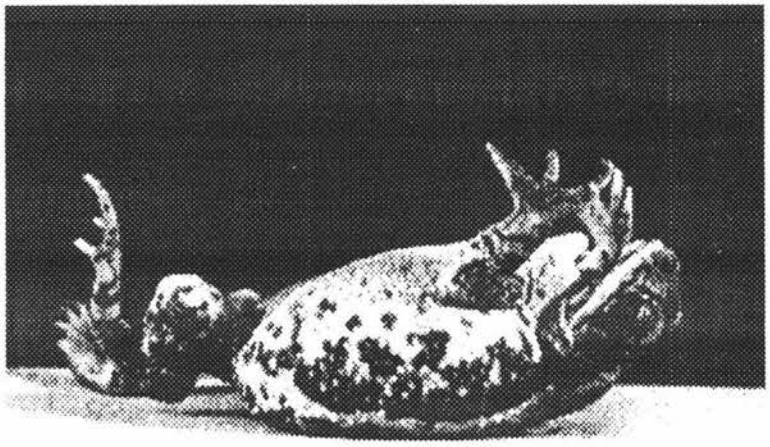
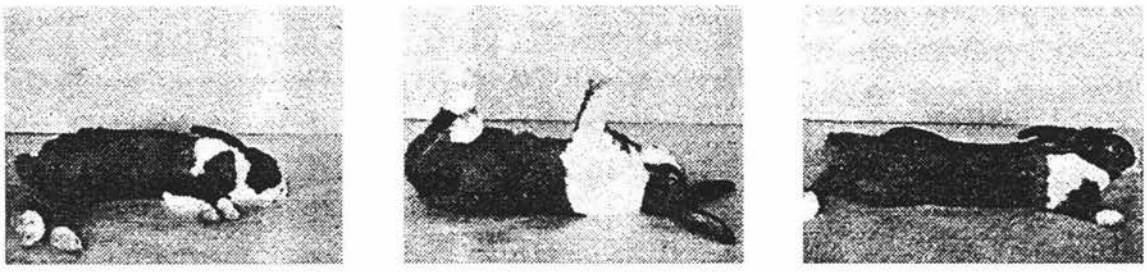


Figure 2.16 Tonic immobility in a toad induced in the dorsal position (Klemm 1971c).

This section will discuss different methods of induction in terms of position and duration of restraint, various restraining apparatus or surfaces and the measures that are recorded during TI experiments.

2.5.1 POSITION OF RESTRAINT

Three basic restraint positions used for inducing TI are the lateral (Figure 2.17a), dorsal (Figure 2.17b) or ventral (Figure 2.17c) position. Gilman et al (1950) immobilised chickens by restraining the chicken's head and feet while it was lying in a lateral position or in the prone (ventral) position. For dorsal induction, the chicken's wings were held down while it was lying on its back. Although the differences between these methods were not always statistically significant, Gilman et al (1950) reported that the ventral method resulted in fewer trances and shorter durations than the lateral and dorsal techniques. Consequently, the two most commonly used methods of restraint today are in the lateral and dorsal positions.



a *b* *c*

Figure 2.17 Tonic immobility in the a. lateral position b. dorsal position c. ventral position (Flannigan and Whishaw 1977)

With dorsal restraint however, unless the subject has a flat or broad back, it tends to passively roll over onto its side which may result in the termination of TI. To overcome this problem, investigators either place their subject in an apparatus that prevents them from rolling over, for example a V-shaped trough (Klemm 1966b Figure 2.2, p6), or use a sawdust test surface and create a small depression into which the subject can be placed (Oakley and Plotkin 1977; Whishaw et al 1978; Wishaw, Flannigan and Barnsley 1979).

A similar procedure has also been used by Braud and Ginsburg (1973a) with day old chicks restrained in the ventral position. The chicks were restrained in a small cardboard box either on the bare floor or in a cloth trough made from a folded white laboratory coat which contoured the chick's body and kept it from falling over to the side and "awakening" itself. Ventral restraint has also been used by Rovee and Kleinman (1974) to induce TI in 3 day old chicks by applying palmar pressure over the chick for 5s with its head tipped forward and down, legs bent beneath the body and the wings firmly restricted to the side.

2.5.2 BODY PARTS RESTRAINED

Pressure may also be applied to various parts of the subject's body. Depending on the species, common areas of restraint are the head or neck and body (Gallup, Nash and Wagner 1971). Tarantulas for example, are not manually restrained but instead are rapidly inverted in a petri dish (Ternes 1977). To immobilise toads however, Ternes (1977) rapidly inverted them and applied constant light pressure on their thorax while holding their front legs in a flexed position against their body. In comparison to Ternes who did not restrain hind legs, Crawford (1977) induced TI in crickets by grasping their 2 hind legs and holding their legs together at the knees. Rabbits have also been immobilised by gentle pressure on their ears which were hanging over the edge of a trough (Oakley and Plotkin 1977).

To prevent biting and scratching from rats, pressure can be applied on the rat's body with one hand while the other hand holds the rat's head firmly in place by pressure on its lower jaw (Hennig and Dunlap 1977a). Hennig (1977) reported that this method may simulate natural predatory episodes as predators seize their prey in the region of the head. Thompson et al (1981) also observed that TI was not induced in birds unless the cats held

or bit the birds around the neck region. This method has also been reported to maximise TI responses in squirrel monkeys. Restraint on the rat's body is then gradually reduced so that only its head is held rigid. However, if the rat begins struggling at this stage, the hand on the body is replaced until struggling ceases. Hennig and Dunlap (1977a) maintained restraint until immobility was evident or until 30s had elapsed. Thirty seconds was chosen as Ratner (1967) had reported that 30s was the optimal induction period for TI in rats.

2.5.3 DURATION OF RESTRAINT

The duration of restraint used by investigators varied from a few seconds up to a minute. Many did not specify the duration of restraint and just reported restraint until struggling ceased. Crawford (1977) for example, considered induction complete when his crickets' legs and antennae stopped moving. Other investigators restrained their subject until it was still or until a specified time had elapsed (eg. Whishaw, Schallert and Kolb 1979 - 10s and Wishaw et al 1978 - 15s in rabbits; Hennig and Dunlap 1977a - 30s in rats).

The optimum period of restraint is reported to vary between species. For example, Gallup, Nash and Wagner (1971) reported that in chickens, 15s of manual restraint yielded the most durable reactions whereas Simonov and Paikin (1969) reported that in rabbits 60s restraint resulted in the longest response as compared to Ratner's (1967) 30s optimum induction period for TI in rats or Lefebvre and Sabourin (1977b)'s 10s optimum restraint for fish.

The duration of restraint required however, may also depend on the restraining position. Klemm (1971c) for example, only restrained his rabbits for a few seconds when on their backs but needed 15s restraint if they were positioned on their side. Although most investigators released restraint immediately after the specified restraint period (eg. Braud and Ginsburg 1973a; Rovee and Kleinman 1974), others (eg. Gallup, Nash and Wagner 1971) gradually released their grip over the restraint duration or as Oakley and Plotkin (1977), applied gentle pressure for 15s and then gradually released restraint over another 15s.

In some cases the duration of restraint does not necessarily correlate with the period of restraint on a flat surface. Prestrude (1977) for example, held his subject, an iguana, above the testing surface for 10s before placing it ventral side down on the test surface. It was then grasped so that the iguana's feet were held along its body and tail for another 10s before it was finally inverted about its long axis until it rested on its side or back and is held for a further 10s. Each induction procedure therefore involved 30s handling and restraint. A similar procedure was also used on chickens by first gently holding each chick in the standing position for a few seconds before abruptly placing it on its right side in the

induction box and applying manual restraint for a further 15s Gallup, Nash and Wagner (1971).

2.5.4 INDUCTION APPARATUS

Investigators may test their subject on a flat surface or use special apparatus such as an induction box or a trough to prevent the subject from rolling over onto its side when restrained in the dorsal position.

Induction boxes are usually simple cardboard (Braud and Ginsburg 1973a), plastic (Oakley and Plotkin 1977) or wooden (Gallup, Nash and Wagner 1971) boxes that function primarily to standardise the immediate testing environment and to reduce extraneous visual stimulation. The size and type of the induction boxes varies with the species being tested. For example, Gallup, Nash and Wagner's (1971) induction box for chickens consisted of a 3 sided plywood box 0.35m high x 0.61m wide that was placed on top of a table. In comparison, tarantulas were tested in a cylinder (Crawford 1977) or petri dish (Ternes 1977) and goldfish were placed in a chute and inverted onto a soft rubber foam to prevent injury to the fish (Lefebvre and Sabourin 1977b).

The testing surface, whether on a table (Gallup et al 1976), on level ground (Montevecchi 1978) or inside an induction box may include various substrates such as cloth (Braud and Ginsburg 1973a), newspapers (Prestrude 1977) or sawdust (Whishaw et al 1978; Wishaw, Flannigan and Barnsley 1979). In addition to the ability of sawdust or cloth substrates to mould and support the subject, the type of substrate has also been reported to affect the duration of TI in other ways as will be discussed in section 2.7.

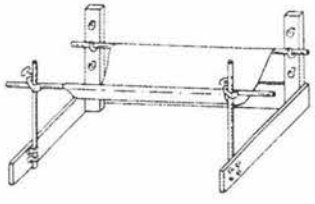


Figure 2.18 Canvas sling used by Reese et al (1985)

Other methods used to prevent subjects induced in the dorsal position from rolling over include various V-shaped troughs as have been used for rabbits (Figure 2.2, p6 - Klemm 1966b; Oakley and Plotkin 1977), rats (Hennig and Dunlap 1977a), chickens (Jones and Faure 1981a) and dogs (Reese et al 1985 - Figure 2.18). The trough may be a U-shaped wooden cradle (Jones and Faure 1981a); a close-fitting wooden holder with two sides and a bottom (Klemm 1966b) or made from 2 sheets of aluminium joined at right angles and lined with paper towel (Oakley and Plotkin 1977). Whatever the construction, it prevents subjects from rolling onto their sides and possibly terminating immobility episodes prematurely. Klemm (1966b) believed that the trough enhanced the depth and duration of TI as it restrained the subject in an inverted position as well as applying pressure on the subject's body.

Jones and Faure (1981a) tested various substrates and methods for inducing TI in the chicken found that although TI was induced in every situation, the use of a cradle rather than flat surface significantly decreased the number of inductions required to induce TI, increased the latency to first head movement and increased the durations of TI probably by providing greater support and restraint. The use of a cloth repeatedly folded in the wooden cradle was found to be most effective method for potentiating TI.

2.5.5 MEASURES OF TONIC IMMOBILITY

The parameters used to quantify TI can be divided into three categories.
1. Susceptibility of an individual or group to enter into TI (eg. duration of restraint required to induce immobility, number of inductions required to induce immobility or the percentage of animals becoming immobile).
2. Duration of the immobility response.
3. Depth of the immobility response
(eg. the intensity or duration of stimulation required to terminate the immobility response).

Although some experiments record several different parameters (eg. Jones and Faure 1981a), the most frequently used measure of TI is duration of the immobility response.

2.5.5.1 Duration of Immobility

This usually refers to the time a subject remains in a single position after immobility has occurred. It is typically measured from the time the subject is released by the investigator until it regains mobility (eg. Gallup 1974a) or is back on its feet (eg. Ratner and Thompson 1960). This is often referred to as "self-paced" immobility (Ratner 1967). There are however studies which impose an upper limit on the duration of immobility (eg. Prestrude 1977) and others which include the restraint period in their estimate of the duration of the immobility (eg. Salzen 1963).

Figure 2.19 Rabbit immobilized in the sitting position.
(Flannigan and Whishaw 1977)

For this measure to be used objectively, it is important for the subject to be immobilised in a standard manner and that there be a set criterion for judging the termination of the immobility response. For example if the subject is immobilised in a sitting (Figure 2.19), standing position or in the ventral position, its feet are already on the ground thus making it unreliable if not impossible to use the criterion of "back on its feet" or righting response to indicate the termination of the immobility period.

Whishaw et al (1978) and Whishaw, Flannigan and Barnsley (1979) for example, used righting response in rabbits as the criterion for ending a trial from dorsal, lateral and ventral position but displacement of the paw for the sit position. Using ventral restraint, Rovee and Kleinman (1974) discontinued timing as soon as a chick stood up or for 12h-post-hatch chicks which were not capable of standing upright completely, timing was discontinued when the chicks exhibited ambulatory movements of both feet while sitting upright. Besides the very young, other subjects may also have difficulty righting themselves especially from the dorsal position. Termination criteria should therefore be set at the time subjects begin struggling in an attempt to right. For example kicking of legs for toads and tarantulas (Ternes 1977).

Rakshit and Klemm (1980) believed that the high variability in TI durations is attributable to the usual method of scoring TI duration from release of restraint to spontaneous righting. In addition to spontaneous righting, they therefore also recorded the time to first movements even if these abortive righting movements did not lead to righting. These brief "flinching" movements are thought to represent termination of TI but may also reinduce TI so quickly that righting does not occur.

There are also often minor movements of the subjects limbs, eyes and neck during an immobility episode but most investigators did not regard this as an indication of termination of the immobility response providing the subject maintained its posture. Some investigators however (eg. Jones and Faure 1981a) recorded latency to these movements as well as the latency to righting as will be discussed later in this section.

2.5.5.1.1 Arbitrary Limits

As immobility in some subjects may last well over an hour, many investigators place an arbitrary upper limit on the duration of the immobility response (eg. Crawford 1977) after which the subject is lifted by the experimenter and the trial terminated. This arbitrary maximum duration varies between investigators, from experiment to experiment and also with the species tested. Oakley and Plotkin (1977) for example terminated any episode lasting longer than 3 min, whereas Braud and Ginsberg (1973a) set their arbitrary maximum duration at 15 min.

2.5.5.1.2 Habituation Training

Although setting an arbitrary maximum trial duration saves vital experimental time, this procedure may in some situations result in the loss of important data as the effect of certain manipulations may be so pronounced that the use of a time limit or ceiling might mask the influence of procedures designed to enhance the duration of immobility (Gallup, Creekmore and Hill 1970). Gallup, Nash, Potter and Donegan (1970) therefore devised a habituation training procedure to circumvent this problem.

This habituation procedure involved restraining a subject repeatedly over several days until a low level of responsiveness was achieved (Habituation will be discussed in section 2.7). Gallup, Nash, Potter and Donegan (1970) manually restrained birds on their sides for 15s, 5 times in succession each day until they remained immobile for 60s or less on the first habituation trial for 2 consecutive days. If the subject remained immobile for greater than 60s, the response was externally terminated by gently prodding the subject. A 2 to 5 min intertrial interval was allowed between successive inductions to preclude the possibility of punishing the chicken for rising to its feet by administering another induction procedure.

As habituation decreases TI duration, the use of habituation training provides a more homogeneous population of subjects prior to the introduction of independent variables. This therefore circumvents the problems often faced in TI research designs caused by the extreme variability in TI durations. Gallup, Nash and Wagner (1971) for example, reported a mean TI duration in chickens of 577.9s with a standard deviation of 712.59s. Habituation training also provides subjects that are more sensitive to procedures designed to produce changes in arousal (eg Gallup, Nash and Ellison 1971). This procedure is now commonly used by others. Rakshit and Klemm (1980) for example, induced TI approximately 25 times in each rabbit until the average duration of immobility stabilised before starting their main study.

In addition to recording the actual duration of immobility following release from restraint, most investigators also set a criterion for an operational definition of susceptibility to TI.

2.5.5.2 Susceptibility

2.5.5.2.1 Duration Criteria

The most commonly used susceptibility criterion is a minimum duration of immobility. Any immobility below this set duration criterion is not considered to be TI. This susceptibility criterion for TI ranges from 4s (McGraw and Klemm 1969; Hennig and Dunlap 1977a) to 10s (Jones and Faure 1981a) of immobility, the most common being 5s (Gilman et al 1950; Rovee and Kleinman 1974; Lefebvre and Sabourin 1977b). In the latter case, a subject is only considered susceptible if it remains immobile for 5s or more after release from a predetermined period of manual restraint.

In an exploratory study, Gilman et al (1950) observed that nonsusceptible birds righted 2-3s after release from restraint (3s being for the heavier, slower moving birds). To allow for a margin of error, 5s was therefore chosen as the determination point for susceptibility. In over 350 immobilisations, the criterion of 5s had to be applied to a judgement of

susceptibility in only 4 instances. They therefore did not consider the determination of the exact end point a major difficulty.

In comparasion to Gilman et al (1950) who determined susceptibility from a single induction attempt, other studies allow induction attempts to be repeated several times before a subject is considered to be insusceptible.

2.5.5.2.2 Number of Inductions

Provided that a standard period of manual restraint is used and inductions are repeated over several attempts, the number of successive inductions required to elicit TI (as predetermined by the duration criterion) can also be used as a measure of susceptibility to TI (Gallup 1974a). That is, the fewer the number of inductions required to elicit TI, the more susceptible the subject (Gallup, Nash, Donegan and McClure 1971).

Usually, a maximum number of inductions is allowed after which the subject is considered insusceptible to TI. The maximum number ranges from 5 (Lefebvre and Sabourin 1977b) to 20 (Hennig and Dunlap 1977a) attempts. Hennig and Dunlap (1977a) for example, allowed 20 30s induction attempts and only if the subject did not remain immobile for at least 4s (their duration criterion for TI) within these 20 attempts was it considered insusceptible and received a duration score of 0s. In comparison, Crawford (1977) only allowed six attempts for each trial and if TI had not been induced in a subject after 6 attempts on a single trial the subject was deemed insusceptible and the trial recorded as a zero duration.

2.5.5.2.3 Time to Induce Immobility

The susceptibility criterion may also be set on the basis of the time required to induce TI. Klemm (1971c) for example, considered a subject insusceptible if it failed to become immobile within 10 minutes of induction attempts.

The duration of restraint required to induce TI has also been used as a measure of TI (eg. McGraw and Klemm 1973). This measure is rarely used today as it can be difficult to obtain this measure objectively in practice as investigators must invariably release their grip or pressure on the subject to determine whether immobility has occurred.

As discussed above, there are species as well as individual differences in optimal restraint periods. For example in chickens 15s of manual restraint yielded the most durable reactions (Gallup, Nash and Wagner 1971), whereas in rabbits 60s provided for the longest response (Simonov and Paikin 1969). Ratner (1967) believed that there is a negative relationship between the time required to induce immobility and the resulting duration of the response.

2.5.5.2.4 Percentage of Subjects Becoming Immobile

Some subjects may fail to exhibit TI even with repeated inductions or prolonged restraint (Gallup 1974a). This measure therefore refers to the proportion of animals in a particular group that become immobile for some minimum period. It involves using a standard induction procedure and the establishment of some minimum duration criterion for TI as discussed previously. Some investigators (eg. Prestrude 1977) believe that this measure of the proportion responding to be the most informative dependent variable.

This measure also has the advantage of being very economical of experimental time as durations greater than the specified duration that defines TI can be terminated by the experimenter. It however is not amenable to complex statistical analysis as individual scores are lost in obtaining the percentages (Ratner 1967). Many authors therefore often use this measure in conjunction with duration measures by allowing the animal to remain immobile until it spontaneously terminates the response. Ratner and Thompson (1960) indicated that the percent of animals responding and the duration of the response are positively correlated but that the duration of the response is a more sensitive measure when TI susceptibility is high.

Another measure of TI that is perhaps more useful at the stronger level of responsiveness is a measure of the depth of the response. This is usually measured as the intensity of stimulation required to terminate the immobility reaction.

2.5.5.3 Stimulation Required for Termination

Changes in external stimulation can cause TI to terminate. A variety of stimuli such as loud noise, sudden visual presentation or electric shock may lead to termination of TI, particularly if the stimulation is intense and the onset is abrupt (Ratner 1967).

These stimuli (eg. light, sound, touch and temperature) can be utilised to test the depth of TI as the amount of stimulation can be used as an index of the intensity of the immobility response (Gilman and Marcuse 1949). The methodology for using this measure as a quantitative index of immobility involves stimulating the immobile animal and measuring the amount of stimulation required to terminate immobility. In general it assumes that the greater amount of stimulation required to terminate immobility, the greater the depth of the immobility response.

Mangold and Eckstein (1919) for example, reported that hypnotised frogs took many more electric shocks than normal frogs before they sprang away and that frogs hypnotised on their backs were in a deeper trance than those hypnotised belly down as they endured more shocks.

Rakshit and Klemm (1980) also examined the relationship between the duration of TI and its depth in the rabbit by measuring the resistance of the state to disruption by external stimulation (ie. arousal threshold) and reported a progressive decrease in depth as the duration of a given episode progressed. Depth was determined by measuring the amount of electrical stimulus required to disrupt TI. Similar methods have also been used by Klemm (1965) and Tompkins (1974) to test the effects of tranquillisers and stimulants on TI arousal thresholds.

In order to examine the intensity of stimulation required to terminate TI however, an initial high level of TI is required. This is sometimes achieved by giving each subject a preinduction shock (Hatton and Thompson 1975). The principal problem with this method is that the application of any intense stimulus might serve to prolong rather than terminate immobility by increasing the subject's fearfulness as fear has been shown to be an important variable affecting TI susceptibility and duration (discussed in section 2.7). Ginsburg, Braud and Taylor (1974a) reported that a stimulus applied during an immobility episode served to abbreviate the reaction in chickens that had been habituated to TI but that similar stimuli either had no effect or intensified the response in naive subjects.

In addition, different loci, frequencies or intensites of stimuli may have special effects and confound interpretations on the amount of stimulation when used as indices of the intensity of the TI reaction. This measure is therefore not commonly used and if used, is often used in conjunction with other measures such as duration or others listed below.

2.5.5.4 Other Observations and Measurements

Other measures commonly recorded during TI experiments include physiological measures, such as respiration and heart rate, minute to minute records of duration of eye closure or rate of vocalisation (Rovee et al 1973; Rovee and Luciano 1973; Rovee and Kleinman 1974). The measurements and observations recorded varied between investigators depending on what aspects of TI they were investigating. Most investigators however, tended to include a measure of the duration of immobility and a measure of susceptibility.

Jones and Faure (1981a) for example measured:-

1. The number of inductions necessary to obtain TI.
Each induction involved 15s of inversion and restraint and the bird had to remain immobile for a minimum of 10s.
2. The latency to the first head movements,
(ie. alert scanning movements rather than postural change).
3. The number of head movements.
4. The duration of TI, (ie. till the bird righted itself or in the second experiment, up to a maximum duration of 1200s).

They suggested that the latency to first head movement may be a more sensitive measure of disinhibition or immobility than righting time and that it may be more appropriate to refer to "righting time" than the "duration of TI" as the term TI implies complete lack of movement whereas the majority of their birds made alert head movements before righting themselves.

There are varying opinions as to the best methods for inducing TI as well as the best measures to record when investigating TI. There are also many other variables (eg. type and duration of restraint or handling before induction, environmental conditions, presence and position of the experimenter) that affect the effectiveness of a method of induction. All these variables need to be taken into consideration when designing the methodology for testing TI. These variables will be discussed in more detail in section 2.7. In the next section, the characteristics of TI and how these may change with different stages of the immobility response are reviewed.

2.6 CHARACTERISTICS OF TI

The most conspicuous characteristic of TI is immobility and suppression of responses to external stimulation such as auditory, visual, tactile and possibly even painful stimuli (Gilman and Marcuse 1949). This immobility may last for several seconds up to several hours. As mentioned in the previous section however, animals are not completely immobile during this period as vital physiological functions such as respiration continue and most investigators also report small movements of the subject's head or limbs during TI (eg. Gilman and Marcuse 1949; Salzen 1963).

In addition to the immobility, there are reports of accompanying physiological and behavioural changes such as changes in heart rate, respiration rate, blood pressure, temperature, EEG patterns, muscle tone and reflexes as well as variable observations on eye and limb positions, defaecation, vocalisation, colour changes, Parkinsonian-like muscle tremors and analgesia (Gallup 1977, Jones 1986a). There is however, little agreement over the direction or significance of some of these reported changes. Moreover, there has also been debate over the degree of "unresponsiveness" and analgesia during TI, as it has been shown that considerable central processing of the external environment occurs during TI (eg. Sigman and Prestrude 1981) and that subjects may be more responsive than normal during TI (Draper and Klemm 1967).

The wide discrepancy in results may be partially due to the different species and methods used. The stage of TI during which these measurements and observations were made may also be important as several different stages with some different characteristics have been described (Rovee and Luciano 1973; Prestrude 1977).

This section will describe the various stages of TI, their associated gross and physiological changes and also discuss the apparent "unresponsiveness" and analgesia reported during TI.

2.6.1 STAGES OF TONIC IMMOBILITY

Several investigators have attempted to divide TI into different stages. Prestrude (1977) depicts TI as a sequence of events as illustrated in Figure 2.20 below, where an animal in a normal state may enter into a state of immobility following restraint and some struggling by the animal. During the immobility episode, certain behavioural and physiological changes occur and the episode finally terminates with the subject returning to a normal state eventually.

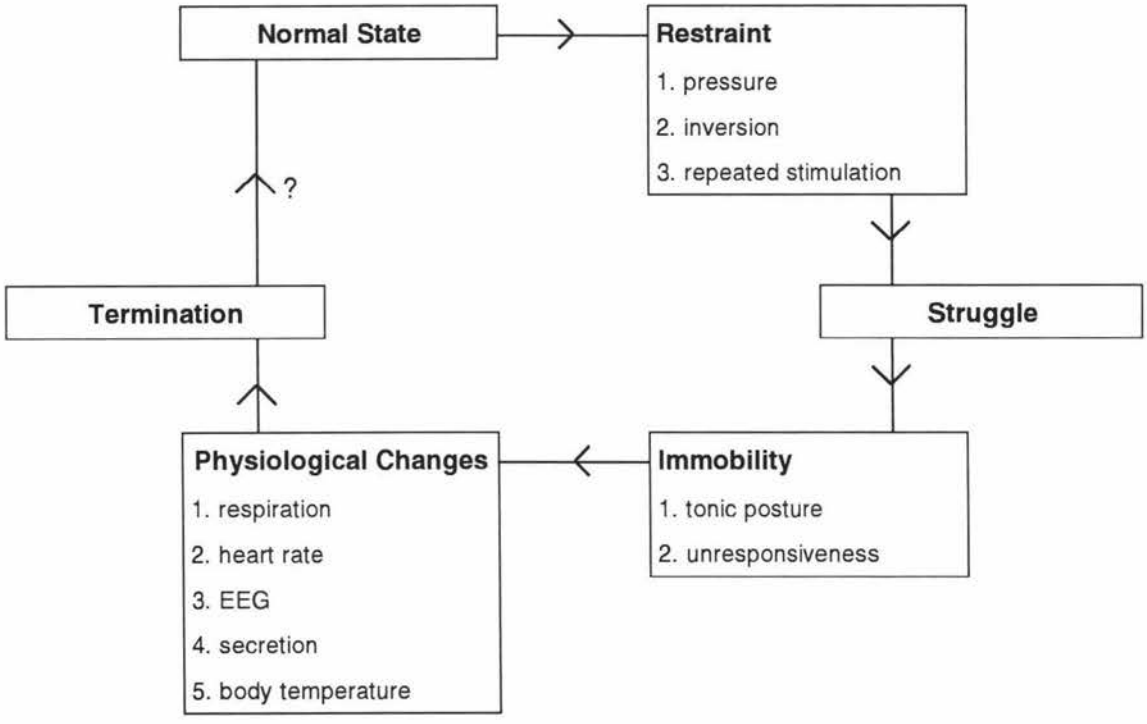


Figure 2.20 Stages of tonic immobility (Prestrude 1977).

The following sections will describe the characteristics of subjects at onset of TI, during TI and at termination of TI.

2.6.1.1 Characteristics at Onset

Compared to the differences in characteristics described during other stages of TI, remarkable agreement exists among the reports of behaviours of animals just prior to onset of immobility. Generally during induction, subjects struggle, attempt to scratch or

bite the investigator and try to escape from the restraint. These frantic responses however, usually subsides after approximately 15s and the subjects will assume a relatively motionless posture which will be maintained even in the absence of further restraint. Restraint therefore seems to be necessary for the initiation of the response but not for its continuation (Gallup 1975). The brief period of struggling may also be an essential part of the eliciting conditions (Lefebvre and Sabourin 1977a).

As indicated by Prestrude's diagram (Figure 2.20), various physiological changes occur during TI. Even during induction and at the onset of TI following the struggle and fight against the restraining agent, many investigators (eg. Ratner 1967; Klemm 1971c) have reported an increase in heart rate and respiration rate and occasionally vocalisations and muscle tremors. Hypertension, pupil dilatation and EEG desynchronisation has also been reported during induction (Carli 1974). Colour change at onset may be observed in some species such as the octopus (TenCate 1928) and toad-fish. The toad-fish is reported to begin to pale all over at the onset of immobility and then rapidly lose its colour until it becomes yellow instead of its normal mottled brown colour (Gunter and McCaughan 1959). Following these changes at the onset of TI, immobility usually intervenes.

2.6.1.2 Characteristics During Immobility

In contrast to the activity during induction and onset of TI, the most obvious characteristic of the next stage is the immobility and apparent unresponsiveness. This immobility may last for only a few seconds to over several hours as its duration varies enormously between species and also between and within individuals. Gallup, Nash and Wagner (1971) for example, reported that the mean duration of self- paced immobility in their chickens was 577.79s with a standard deviation of 712.59s. Chickens averaged approximately 500 - 600s (Gallup 1974a) and the record in Gallup's laboratory for a single uninterrupted immobility reaction was reported to be 5h 45min. In comparison, Prestrude (1977) reported immobility episodes of 8h or more in lizards.

During this period of gross immobility, absence of righting reflexes and suppression of overt responsiveness, the posture of the animal can be extremely variable depending on the species and methods of induction (Figure 2.21). Generally, the posture of the animal during TI is very similar to the posture during induction. Characteristic postures for some species have however, been reported (Ratner 1967). Birds for example, usually have their heads, back and legs extended and frequently show gross muscle tremors (Figure 2.21c).

Extended legs have also been reported to be characteristic of immobility in frogs (Figure 2.16, p19) and guinea pigs whereas spiders (Ratner 1967) and crustaceans (Gunter and McCaughan 1959) have their appendages drawn up tightly against their bodies. The

position of the limbs however, are not fixed as they may be extended or flexed or one flexed and the other extended depending on the muscle tone.

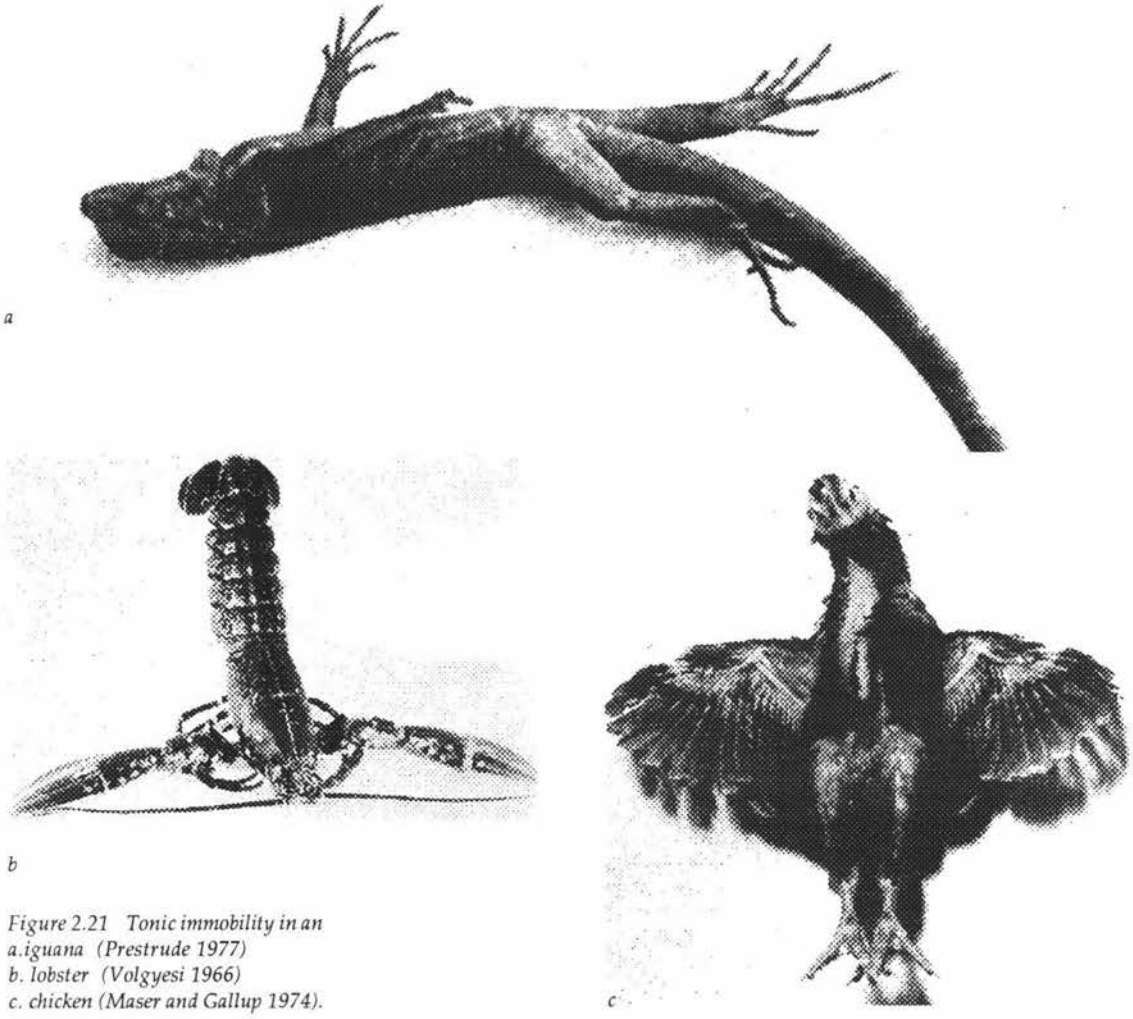


Figure 2.21 Tonic immobility in an a.iguana (Prestrude 1977) b. lobster (Volgyesi 1966) c. chicken (Maser and Gallup 1974).

The muscle tone during TI can be difficult to assess (Carli 1974) and has been described as tetanic, atonic or resembling waxy flexibility or plastic tonus (Gilman and Marcuse 1949). It is reported to be either increased or decreased originally but to become more relaxed as TI progresses (Klemm 1966a). This finding was supported by Ookawa (1972) who found that there is an increased tonic EMG discharge of neck muscles at the transitional stage at the beginning of restraint but that the EMG decreases in amplitude during TI.

Klemm (1971cd) also reported that muscle tone varies with species and induction method. For example, in the chicken, TI is reported to be characterised by tremors, hypertonicity and waxy flexibility (Hicks et al 1975) whereas rabbits are reportedly hypotonic but usually not completely atonic (Carli 1969a; Galeano et al 1979). Rabbits often have their

limbs extended in the early stages followed by relaxation but mild arousing tactile stimuli, which do not disrupt the reflex, will elicit a transient increase in muscle tone. Sometimes during the early post-induction stages, a fine tremor of the hind limbs occurs in rabbits and a coarse clonic tremor can be induced by touching the hind feet or tapping the patellar tendon or other body parts such as the abdomen (Schaeppi and Rubin 1965).

Other characteristics seen during TI include small movements of the subject's head and limbs. Muscle tremors that resemble those of Parkinsonism may also be seen in the extremities. Suppression of vocalisation is characteristic in some species, although others (eg. chicks) occasionally make distress calls and vocalise intermittently towards the end of an episode (Gallup 1974a).

Both birds and guinea pigs have been observed to eliminate during immobility (Bayard 1957) and Liberson (1948) report that guinea pigs exhibit exopthalmus during TI. The subjects' eyes may open or close intermittently during an immobility episode and they may appear to be asleep or dead but there is no loss of consciousness despite the apparent lack of responsiveness, as will be discussed later in section 2.6.3. Because of the tremors, eye movements, occasional head turns and vocalisations, TI cannot be described as absolute immobility even though there is a profound state of response inhibition. This state is however, subject to environmental changes and a surprisingly dynamic internal physiology which will be discussed in the following section 2.6.2

The wide variation in characteristics during TI has led some investigators to further categorise the immobility period. Rovee and Luciano (1973) proposed a 3 stage analysis of TI based on qualitatively different states of immobility in the chicken.

Stage 1

Appears at the beginning of immobility and also immediately prior to spontaneous termination and is characterised by shrill distress calls and continuously open eyes.

Stage 2

A slightly deeper stage characterised by occasional vocalisations and fluttering eyelids.

Stage 3

Predictive of long immobility and characterised by complete eye closure, head bobbing, sporadic generalised body twitches and no vocalisations.

Jones and Faure (1981a) identified 2 stages during the immobility response. The first stage was one of inhibition characterised by complete immobility and lasting from induction to the first head movement. In the second stage, the bird was alert and may have made several head movements before righting itself. As the term TI implies complete lack of movement, Jones and Faure (1981a) believed that it should strictly only apply to the first

stage and the term "righting time" be applied to the time until the bird was back on its feet. They believe that latency to first head movement may be a more sensitive measure of disinhibition than righting time.

It is difficult to compare Jones and Faure's stages with Rovee and Luciano's, as Jones and Faure tested adults which do not vocalise and Rovee and Luciano used ventral restraint which did not allow any leg movement to determine "righting time". Termination of the immobility period however, is usually sudden and complete and generally difficult to predict.

2.6.1.3 Characteristics at Termination

Termination of an immobility episode may be self-paced or externally induced. Self-paced termination is usually abrupt with the subject making an almost immediate transition from the immobile to an upright mobile state and attempting to escape (Ratner 1967; Gallup 1974a). Some animals however may lapse back into TI especially if they have difficulty righting themselves from the dorsal position. Externally induced termination is also usually associated with sudden and complete recovery but occasionally, recovery may be incomplete. In this case, the subject rights itself or is placed onto its feet but then slumps back into immobility, sometimes even while upright.

Following the conclusion of an immobility episode, some birds exhibit complex defensive responses such as injury feigning displays. Ground-nesting birds for example, may limp away dragging one wing behind (Armstrong 1965) but a more common response in naive subjects is an immediate attempt to attack or escape from the experimenter (Ratner and Thompson 1960).

Many investigators have attempted to identify specific characteristics preceding termination which could be used as predictors of termination. Gunter and McCaughan (1959) reported that the toad-fish "finally gives a convulsive gasp and revives". However, although they tested more than a dozen fish, they did not specify how many of their subjects showed this change just prior to termination.

Hoagland (1928) reported that the recovery of activity in the lizard, *Anolis carolinensis*, is generally heralded by the progression of a wave of activity starting at the tip of the tail and passing forward to the lumbar region when the animal springs violently into activity. He further reported that if the lizard is lying on its back, recovery is always characterised by vigorous leg movements and immediate struggles to turn its ventrum downwards.

Generally self paced termination is sudden with few indicators that it is about to occur, but several reported predictors of the duration of TI exits. Duration of eye closure and latency

to vocalisation are reported to be good predictors of the duration of an immobility episode in adult (Gallup 1974a) and young chickens (Rovee and Luciano 1973). That is, lengthy eye closure and little or no vocalisation during immobility is predictive of longer durations and vocalisations usually indicate that the response is about to terminate (Rovee, Agnello and Smith 1973). Gallup, Nash and Wagner (1971) reported that birds which defeacated during or shortly after termination remained immobile longer than comparable non-defeacators.

In addition to these gross behavioural changes during TI, changes in various physiological parameters have also been reported.

2.6.2 PHYSIOLOGICAL CHANGES DURING TONIC IMMOBILITY

During TI, accompanying physiological and neurophysiological changes in respiration rate, heart rate, blood pressure, temperature and EEG are observed. As TI is potentiated by aversive stimuli one might expect to find correlated psychophysiological changes. There is little agreement over the direction or significance of some of these reported changes.

2.6.2.1 Respiration Rate

There are reports that respiration is increased (Hofer 1970), decreased (Klemm 1977) or unchanged (Gilman et al 1950) during TI. Ratner (1967) reported that he has seen all 3 respiratory states at some time during the course of an immobility reaction. His observations however were based on nonquantitative observations.

Quantitative studies of respiration during TI are few and conflicting in their findings. Prestrude and Crawford (1970) reported that there is an initial elevation in respiration rate immediately following induction in the green iguana, followed by a gradual decline so that prior to response termination, the respiration rate is below normal values. This finding is supported by Nash, Gallup and Czech (1976) who also found an initial increase in chickens' respiration rate which then gradually decreased during TI. In contrast, Klemm (1966) reported that there is an initial decrease in respiration rate in rabbits, followed by further decreases as the response continues and that a return to normal does not occur till after TI termination.

Some of these differences could be a due to species variation or more likely due to differences in methodology resulting in different degrees of struggling during induction as the initial rise in respiration rate may be associated with struggling during induction. Ratner (1967) observed that compared to animals that are immobilised quickly, those that

struggle for prolonged periods during restraint tend to have an initial increase in respiration rate which then gradually approaches that of a normal animal during TI.

It therefore seems that despite the differences reported in initial respiration following onset of TI there is a consensus that respiration decreases during TI and may reach rates that are lower than normal. Similar results and confusion have also been reported on heart rate changes during TI.

2.6.2.2 Heart Rate

Although heart rate is generally increased upon exposure to a fear inducing stimulus, the relationship between heart rate and TI, a fear related phenomenon, is still unclear. There have been reports of increases (Ratner 1967), decreases (Ookawa 1972; Reese et al 1982) and no change (Rijlant 1933; Gilman et al 1950) in heart rate during TI. These discrepancies may be due to species differences, different methodologies, recording methods, times or stages of TI. Schneiderman (1970) reported that rats show an increase in heart rate in response to electric shock whereas the same stimulus resulted in a decrease in heart rate in pigeons.

One might expect an initial post-induction rise in heart rate on behavioural (struggling) and physiological (alarm reaction) grounds as reported by Ratner (1967) and Nash, Gallup and Czech (1976). This is usually followed by a gradual return to control levels, reaching their lowest point just prior to termination (Ratner 1967; Ookawa 1972; Nash, Gallup and Czech 1976).

Similar changes have also been reported by Carli (1974) who observed heart rate oscillations during induction, with tachycardia reaching its peak when the rabbit was on its back but still trying to escape. The highest values were recorded during the initial few seconds of the episode. Heart rate then gradually decreased to control rates and some reduced even further during long TI episodes. Moore and Amstey (1963) believed that an extended period of immobilisation might be required for a reduction in heart rate during TI as they reported that heart rate would drop to below the base rate if immobility exceeded 70s.

The oscillations in heart rate during induction reported by Carli (1974) may account for Klemm's (1966) report of a decrease in heart rate at the beginning of TI followed by a further reduction when TI continues. Nash, Gallup and Czech (1976) also recorded an initial decrease in heart rate during induction that is followed by an abrupt post-induction and post-termination rise in heart rate. This post-termination rise in heart rate is also supported by Reese et al (1982) who reported a decrease in heart rate during TI followed

by a marked increase when released from the inverted position. In addition to these changes, there have also been reports of cardiac arrhythmias during TI (Hofer 1970).

It appears that there are oscillations in heart rate during induction followed by an immediate post-induction increase in heart rate which then decreases during the immobility episode and may even become lower than preinduction or control rates. This is reversed at termination when there is often a marked increase in the subject's heart rate.

2.6.2.3 Blood Pressure

Blood pressure was reported to show a series of oscillations during induction resulting in considerable hypertension during the initial few seconds of TI (Carli 1974). It then gradually decreased from the beginning of TI to control pressures and in longer episodes, a slow decrease in blood pressure to below control pressures was recorded (Carli 1977). Subsequently, it was reported that systolic and diastolic pressures were not modified during TI except at times of induction and termination (Carli et al 1984). Hatton et al (1979) reported that induction but not termination resulted in a sharp rise in blood pressure. Although inconclusive, these blood pressure studies support the hypothesis that reflexive baroreceptor activity occurs as a consequence of the induction procedure for TI as both inversion and restraint would be expected to increase blood pressure and as a consequence, baroreceptor activity.

2.6.2.4 Temperature

There have been limited studies on temperature changes during TI. Nash, Gallup and Czech (1976) reported that the body temperature of chickens remained lowered throughout the TI response. There is however, an immediate post-immobility increase in temperature after TI, possibly due the to extensive motor involvement accompanying the typical escape reaction at response termination.

2.6.2.5 Reflexes

In addition to the immobility and absence of righting mechanisms during TI, there are associated inhibitory influences affecting spinal motor neurones and their reflexes as evident from the hypotonia and depression of mono- and poly-synaptic reflexes throughout TI (Carli, Lefebvre et al 1976). Withdrawal reflexes to pin pricks and deeper assault are usually absent (Carli 1977) but if the eyes are open, the corneal reflex is usually active (Schaeppi and Rubin 1965) and the pupillary light reflex is present (Ratner 1967). Some species variability in spinal reflexes may exist, as Carli (1968) reported that polysynaptic reflexes are depressed in frogs but not in guinea pigs.

2.6.2.5 EEG

Early reports of EEG during TI described the pattern as being identical to sleep (Svorad 1956; Lievens 1960). Schwartz and Bickford (1956) reported that within 10s and usually simultaneously with the onset of TI, the EEG showed 50-100 microvolt, 5-7 Hz waves which replaced the normal background 7-9 Hz rhythm. That is, the normal background alpha rhythm was replaced by slower frequencies characteristic of drowsiness. This then changed to one that resembled awake controls at termination (Schwartz and Bickford 1956).

More recent research (Ookawa 1970; Carli 1977; Carli et al 1984) reported that there was a clear cut desynchronisation of the EEG, with low voltage fast wave activity during induction (Carli, Lefebvre et al 1976). Then, as TI continued in the absence of any external stimulation, this pattern was gradually replaced by high voltage slow wave activity in the EEG identical to that occurring during spontaneous synchronised sleep.

Occasionally however, the EEG remained desynchronised even in long lasting episodes (Carli 1969a) or the characteristic high amplitude slow wave activity was interrupted by sudden, spontaneous desynchronisation with low voltage fast activity without any apparent movement by the subject (Klemm 1966a; Carli 1969a; Carli, Lefebvre et al 1976). These episodes were interpreted as EEG arousal reactions and not REM sleep because whenever observed, there was a marked pupil dilatation and absence of eye movements (Klemm 1966a; Carli 1969a). These episodes of arousal could also easily be elicited by any form of sensory stimulation which did or did not cause termination (Carli 1969a; Klemm 1970). The spontaneous termination of TI was usually preceded by 1-3s of desynchronisation in the EEG.

The EEG during TI is affected by the EEG pattern immediately preceding TI and tends to be opposite to that occurring during the preceding control period. There appears to be no typical EEG pattern during TI (eg. Carli 1969a) as the EEG during TI is determined by the general EEG and behaviour occurring in the preinduction control period.

The EEG changes, like all the other physiological changes during TI, are extremely variable as described by Liberson et al (1961) who found EEG changes ranging from those characteristic of extreme excitation to those indicating deep sleep. The variable EEG and its sustained sensitivity to stimulation is compatible with the view that the EEG is not uncoupled from normal behavioural correlates during TI and that animals are consciously monitoring their environment during TI.

2.6.3 CENTRAL PROCESSING

The reported EEG desynchronisation in response to external cues presented during TI (Klemm 1971a, b and c) is contrary to the reports of subjects "unresponsiveness" during TI. There is also considerable evidence that central processing of the external environment occurs during TI (Carli et al 1974) and the subject may be more responsive than normal while in TI (Draper and Klemm 1967).

The fact that TI is almost always interrupted by intense stimulation such as major surgery and may be interrupted by mild tactile or auditory stimuli (eg. Gruber and Amato 1970) supports the notion that subjects are responsive to the external environment during TI (Danneman et al 1988). Even when TI is not interrupted, perception of such stimuli is suggested by the occurrence of mydriasis and changes in the EEG (eg. Carli, Farabollini and Fontani 1976) or tachycardia even if no overt response in the form of a startle or orientation reflex is exhibited (Ratner 1967).

Prestrude and Crawford (1970) have shown that even though head movements elicited by a rotating black and white barred pattern is not present during TI, the optokinetic reflex persists. Imprinting experiments demonstrated that chicks can be imprinted during TI (Sigman and Prestrude 1981) and that the duration of TI in chicks can be reduced if an imprinted auditory stimulus is presented during TI (Hodges and Prestrude 1978).

The ability of subjects under TI to monitor their environment and to respond selectively to environmental test conditions by attenuated response in the presence of familiar shapes and stronger reactions to unfamiliar shapes (Rovee et al 1973) or differential responses to the presence and proximity of experimenter (Gallup, Cummings and Nash 1972), predator (Gallup, Nash, Donegan and McClure 1971), artificial eyes (Gallup, Nash and Ellison 1971; Gagliardi et al 1976), other birds (Jones 1982a; Jones and Faure 1982) or escape opportunities (Hennig et al 1976) all support the view that animals are consciously monitoring their environment during TI.

Furthermore, animals can undergo classical conditioning during TI (Draper and Klemm 1967; Carli et al 1974; Gallup et al 1980) and can learn to interrupt TI to perform a conditioned response (Carli, Lefebvre et al 1976). All this indicates that subjects are not "unresponsive" during TI but only appear to be due to the suppression of behavioural responses to stimulation, which result in the seemingly passive immobile state.

This however does not necessarily indicate that there is "disconnection of overt motor functions" (Draper and Klemm 1967) or "sensory-motor dichotomy and uncoupling of motor control" (Klemm 1971b) as Gallup et al (1980) have demonstrated that subjects are

able to suppress minor movements during TI in response to conditioned aversive cues. It is therefore proposed that certain overt motor functions are subjected to considerable influence from stimuli during TI and that the motor inhibition associated with TI is only relative and confined mainly to efferent processes without much reduction in afferent activity or the central processing of information.

The reactivity of animals during TI appears to be depressed, since the effective thresholds to most stimuli, including noxious pain stimuli, seem to be much higher than normal (Klemm 1971c). Many people have therefore questioned whether analgesia is present during TI.

2.6.4 ANALGESIA

Although many investigators (eg. Darwin 1900; Holmes 1906; Marcuse and Moore 1944) believed that analgesia is present during TI, there is no unanimity of opinion. Coriat (1912) reported that he did not observe any signs of analgesia in the frog or guinea pig during TI.

Similarly, although Danneman et al (1988) reported that the distress associated with noxious electrical and pressure stimulation was significantly reduced by TI, they found that even in rabbits that did not withdraw in response to noxious stimulation, physiological changes suggestive of distress was sometimes exhibited during TI. They therefore concluded that TI should not be considered as a reliable or humane alternative to analgesic / anaesthetic drugs for laboratory rabbits. Steineger (1936) also believed that sensation is unimpaired during TI and that pain is felt but not overtly manifested because the subject is unable to move.

There is however, both direct and circumstantial evidence that TI may involve an element of analgesia. Most animals show decreased overt responsiveness to pain stimuli during TI and some investigators have found that behavioural reactions to noxious stimuli can be interrupted by TI (Carli, Farabollini and Fontani 1976; Carli, Lefebvre et al 1976; Carli et al 1981). It has been possible to perform minor surgical procedures on animals restrained solely by TI (Ten Cate 1928; Stroder 1938; Rapson and Jones 1964; Gruber and Amato 1970) without any apparent pain reactions (Mangold 1914; Haberland 1926).

Observations that TI resembles other conditions which apparently reduce pain perception such as pressure immobility (Carli et al 1984), pinch induced catalepsy (Amir 1986; Fleichmann and Urca 1988b) an acupuncture induced state in animals (Takeshige et al 1976; McLennan et al 1977; Galeano et al 1979) and the cataleptic state induced by opiod drugs in various species (Carli, Farabollini and Fontani 1976; Chaillet et al 1983) further suggests that TI itself may be analgesic.

Conversely, Mauk et al (1981) reported hyperalgesia during and immediately after termination of TI in response to tail-flick test in the lizard, *Anolis carolinensis*. Therefore, like with the other characteristics observed during TI, there is still considerable debate over whether subjects experience analgesia during TI. The many discrepancies discussed in this section may however be explained by a closer examination of the variables that affect TI.

2.7 VARIABLES INFLUENCING TI

As is evident from previous sections, numerous conflicting results have been reported in the TI literature. There has been debate over the best methods of induction, the physiological changes that occur during TI and even whether TI encompasses different phenomena (Crawford 1977). These difficulties have occurred as a result of generalised comparisons being made across a wide range of species and different experimental conditions, without taking into account the many variables that can affect TI and the confounding effects of these variables. Although most papers describe the methods and procedures, very few list or describe the variables that can affect TI.

It is vital to identify these variables as they can affect the degree of TI in terms of duration, time to induce, percent of animals responding or amount of stimulation required to terminate the reaction. They may help to explain the numerous confounding results reported in the literature. It is also important to identify and keep these variables in mind when designing experiments in order to avoid or control them.

Some variables such as species and age may be easily controlled whereas others such as circadian rhythms and the spacing of trials may be easily overlooked. Many variables interact and may confound each other. In this review, the variables affecting TI have been loosely grouped into two categories:

1. animal variables
2. variables due to experimental design.

2.7.1 ANIMAL VARIABLES.

2.7.1.1 Individual Variation

The first and most vague animal variable is "individual variation". Investigators (Gallup 1974a; Crawford 1977) accept that there is variation between individuals of the same species and that the "susceptibility in any one subject is variable" (Gilman and Marcuse 1949).

Although this individual variation must be considered (Marcuse 1951), it is important to ensure that the variability observed is not due other factors interacting with each other. Jones (1982) reported that dominant hens show longer TI durations than subordinates. This variation could be attributed to individual variation or on closer examination, may be due to previous experience, fear or age related variables. Although there is a great deal of variability between individuals, this variability is not as great as the variation reported between species (Hoagland 1928; Crawford 1977).

2.7.1.2 Species

Different species vary in their susceptibility (Crawford 1977), ontogeny (Vestal 1975), best induction methods (Klemm 1971c; Crawford 1977), induction times and even in TI responses. Crawford (1977) reported that it is easier to induce TI in crickets than tarantulas and that the times for induction and durations were much shorter in the cricket. Likewise, although the rabbit is reported to be a very susceptible species and many investigators have reported 100% susceptibility in their rabbit subjects (eg. Klemm 1971c; Carli 1977), cats, dogs, mice and rats have been reported to be refractory to TI (Danilewski 1881; Svorad 1957).

This variation in susceptibility has been demonstrated between closely related species such as between species of spiders (Robertson 1904), sandfleas (Holmes 1903), snakes (Crawford 1977) and rodents (Webster et al 1981). Ratner (1967) reported that although coyotes showed strong immobility reactions, red foxes did not, even when subjected to the same conditions of restraint.

It is reported that species susceptibility varies negatively with phylogenetic rank (Coriat 1912; Gilman and Marcuse 1949; Fraser 1960; McGraw and Klemm 1969). That is, higher animals with more developed neocortices are less susceptible than lower animals like birds or invertebrates (McGraw and Klemm 1969; Klemm 1971c). Klemm (1971c) demonstrated a decreasing susceptibility from the rabbit, to the guinea pig, to the rat and that this corresponds to the gradation in neocortical development. This he believed was due to the more developed neocortex in the rat inhibiting "hypnogenic centres" of the brain.

The importance of evolutionary variables in TI reactions has been noted by a number of biologists (Palmer 1909; Hoagland 1928; Nice 1943; Armstrong 1955) as it appears that some species have evolved immobility and associated reactions to a higher degree than others. Armstrong (1955) noted that the European Wren, which is characterised by great activity and nimbleness, has never been observed to show TI.

The stimuli that elicit TI may also have an evolutionary basis, as different specific stimuli may be most effective in different species and these sensitivities may have evolutionary origins. TI in the mantid for example, seems to be elicited most readily by the attack of another mantid (Crane 1952) and immobility in some spiders by movements of the male spider (Savory 1928).

It is therefore not surprising to find that different species respond best to different stimuli or induction methods. Klemm (1971c) reported that the best method for inducing TI in frogs was to place them on their backs with their rear legs pressed against their body and front legs left free to extend whereas it was necessary to immobilised rats on their sides. In rabbits, the best method was to place them on their backs.

Whishaw et al (1978) also reported that the longest duration of TI in rabbits (*Oryctolagus cuniculus*) occurred when they were placed in the back posture. TI in the cottontail (*Sylvilagus nuttalli*) and hare (*Lepus townsendi*) however, tended to be longer when placed in the front posture and most difficult to induce when on their backs. This was possibly due to their sharp backs causing balancing difficulties as compared to the rabbit's relatively broad back which made it easy to place them in this position.

Different species exhibit different characteristics during TI. Ratner (1977) demonstrated this in 2 species of woodlice that are often found together in one small area, *Armadillidium vulgare* and *Porcellio scaber*. Specimens of *A vulgare* curl up into a tight ball and maintain this posture for a minimum period of 2 min whereas specimens of *P scaber* flatten themselves against the ground for a brief period. Brodie et al (1974) reported that different species of salamanders show variations in the posture adopted during TI.

Unrelated species show more variable responses during TI. Opossums lie on their sides with a posture characterised by a ventral flexure of the body and flexure of their digits (Franq 1969). Ducks have their heads extended maximally with their eyes open and wings held tight against their bodies (Sargeant and Eberhardt 1975) and snakes become kinked with the appearance of being desiccated (Liner 1977).

Species differences in susceptibility, methods of induction and characteristics during TI do not necessarily indicate evolutionary differences specific to TI, as they may be related to differences in morphology, physiology or another unrelated characteristic of the species. Within a species however, differences between strains, breeds or genetic lines have been reported.

2.7.1.3 Strain / Genetics

Descendants of domesticated strains often appear less responsive to various stimuli (including TI induction techniques) than descendants of wild strains. Domesticated animals are also considered less emotional or timid than their wild progenitors and are reportedly less susceptible to TI (Hennig 1979a).

Differences in TI susceptibility have been reported between domesticated strains. Within domestic chickens, White Leghorns show immobility responses that last 2-3 times longer than Production Reds (Gallup et al 1976; Nash 1978) and Brown Leghorns exhibit considerably shorter TI durations and latency to first head movements than Rhode Island x Light Sussex or White Leghorn lines (Jones and Faure 1981a).

These differences between strains may be due to strain-specific emotionality or fearfulness, as casual observations indicate that White Leghorns are more emotional than Production Reds's both prior to and after immobility testing (Gallup et al 1976; Nash 1978) and Brown Leghorns appear less fearful than Rhode Island x Light Sussex or White Leghorn lines (Jones and Faure 1981a). Jones and Mills (1983) reported that chicks of a flighty White Leghorn strain showed longer TI reactions than their more placcid Rhode Island Red x Light Sussex counterparts. Birds bred for long TI durations tended to be more timid and less aggressive than those bred for brief responses (Gallup et al 1976).

There however does not appear to be strain differences in susceptibility to TI, indicating that duration and susceptibility may be independent TI parameters (Gallup et al 1976). Gallup (1974b) reported that birds from parents with long TI durations have average reactions lasting over 30 min longer than offspring of parents with brief responses, but neither of these groups differed in susceptibility.

In rats however, strain differences in susceptibility as well as duration of TI occurred (McGraw and Klemm 1973). The spontaneous durations of TI in Tyron maze-bright rats averaged approximately twice those of Tyron maze-dull rats and the time required to induce TI in Tyron maze-bright rats was also significantly shorter. Tyron maze-bright rats appeared more fearful, showed lower ambulation scores and had longer TI durations than maze dull strains. Ambulation scores in chickens also clearly indicated that White Leghorns are more fearful/hesitant than Production Reds (Gallup et al 1976).

Tyron maze-bright rats have been shown to be more fearful than Tyron maze-dull rats based on commonly accepted indexes of fear such as urination and defecation. It therefore appeared that rat strains, genetically selected for differences in one aspect of behaviour (maze performance) could simultaneously differ in their susceptibility to TI indicating that the differences in TI may be in part related to genetic factors (McGraw and Klemm 1973).

This is further supported by Gallup (1974b) in chickens and Benoff and Siegel (1976) in quail, as they showed that animals can be selectively bred to show differences in TI durations (McGraw and Klemm 1973; Gallup 1974b; Benoff and Siegel 1976) and susceptibility (McGraw and Klemm 1973; Benoff and Siegel 1976). Cross breeding between strains resulted in hybrids that exhibited intermediate responses.

Gallup (1974aandb) reported an unusually robust effect of selective breeding in chickens. After only one generation of breeding birds to show either prolonged or brief TI reactions, heritability estimates of between 0.7 and 0.9 were found, with F1 offspring from parents exhibiting long reactions remaining immobile an average of over 30 min longer than those derived from parents showing brief immobility times. Both types of offspring were reared under identical conditions in artificial incubators and commercial brooders, thus ruling out sources of pre- and post-hatch variation.

Although this extremely high heritability seems to support the notion that TI is an evolved predator defence, it is in opposition to the principle that the size of the heritability coefficient should be inversely proportional to the survival value of the trait (Falconer 1960).

The domestication of the chicken may have reduced the selective pressure for the stabilisation and maintenance of TI, resulting in the reinstatement of considerable genetic variability. Alternatively the survival value for TI may relate to the probability of becoming immobile initially rather than to the subsequent duration of the reaction. This interpretation is consistent with Gallup's (1974b) finding that there is no heritable difference in susceptibility to immobility, despite large duration differences between offspring bred to show long and short immobility reactions. These F1 differences in duration may therefore merely reflect a differential fear of humans.

Other investigators (eg. Benoff and Siegel 1976) report that non-additive genetic effects and / or maternal effects are more important than the additive genetic effects. Kabai and Csanyi (1979) reported heritability values of between 31 and 33% in 2 subspecies of fish *Macrpodus opercularis opercularis* and *M o concolor*. The average number of gene differences between the 2 subspecies was only 1.0 suggesting that the genetics influencing the duration of TI in fish are not complex. Benoff and Siegel (1976) found that the additive genetic variation affecting TI in quail was also low to moderate in magnitude, suggesting that there had been prior natural selection for TI and indicating that this trait is associated with fitness.

Whatever the genetic mechanism, these studies all provide clear evidence that genetic factors are important variables affecting TI.

2.7.1.4 Sexual Status

The sex of the subject however, is not considered to be an important variable affecting TI as most investigators report that there is no sexual dimorphism for susceptibility to or duration of TI. (Borchelt and Ratner 1973; Benoff and Siegel 1976; Mills and Faure 1986 - in the quail and Gallup 1974b - in the chicken).

Jones and Faure (1981a) found no significant sex difference in the duration of TI, but males in 2 out of 3 lines of chickens exhibited greater latencies to first head movements and fewer subsequent alert head movements than females. This is consistent with Jones's (1977a and b;1978) finding that female chicks are less fearful than males. Jones and Faure (1981a) postulated that perhaps the females allowed themselves more time to "explore" the environment for possible dangers before righting and flight whereas the males tended to right themselves without prior head movements. Mills and Faure (1986) however, found that gender had little effect on TI or several other "fear" behavioural responses including emergence test, the open field and the response to a bell test in Japanese quail chicks

Possible sexual dimorphism in TI was reported in female lizards which exhibited longer TI than males of the same size during the non-breeding season (Cashner et al 1981). This difference was however, non-significant during the breeding season (Cashner et al 1982). This effect could be the result of an interaction with endogenous hormones affecting TI mechanisms which may be mediated through other reproductive hormones or behavioural mechanisms. Weight was also found to be a factor in male lizards with males weighing 4.0g or more showing significantly longer TI durations during the non-breeding season (Cashner et al 1982).

The size of subject may also be related to age factors.

2.7.1.5 Age

The age of the subject appears to be a very important variable affecting TI as most investigators report that TI responsiveness decreases with age (McGraw and Klemm 1969; Klemm 1971c; Prestrude 1977). In ground nesting birds, TI is absent in neonates until approximately 7-8 days of age. The response then remains constant until about 7 weeks before declining with age (Ratner and Thompson 1960; Salzen 1963; Borchelt and Ratner 1973; Hughes 1979).

It was therefore postulated that TI requires a maturation period that is related to the development of fear responses in domestic and other precocial fowl as the appearance of TI coincides with the development of fear responses in these animals (Ratner and Thompson 1960; Salzen 1963). Imprinting literature however, reports that fear develops

as early as 20 - 25 hours of age and certainly by 3 - 4 days in the domestic chick (Hess and Schaefer 1959) which is more supportive of Rovee and Luciano's (1973) and Prestrude's (1977) finding of TI in chickens from 3 or 5 days of age.

With the exception of Rovee and Luciano (1973) all the studies that reported a maturational delay in the onset of TI attempted induction using either dorsal or lateral restraint. Using ventral restraint, Rovee and Kleinman (1974) induced TI in White Leghorn chicks within 12 hours post-hatch. Braud and Ginsburg (1973a) also induced TI in chicks as young as one day old using dorsal restraint, provided testing was conducted on a cloth depression which contoured to the chicks body or provided the experimenter's hand was kept within close proximity of the chick (Ginsburg 1975).

They therefore suggested that day old chicks were capable of exhibiting TI provided effector disruption (rolling over) was prevented or if increased physical contact or close spatial proximity during induction augmented fear or produced a "prolonged zero" in the animal's defensive distance. The previous failures to induce TI in chicks less than 7 days old could therefore have been due to inappropriate testing conditions instead of the absence of fear, insufficient hormonal functioning or non-functioning "releasing nervous mechanisms" (Braud and Ginsburg 1973a).

Variation in TI susceptibility and duration with age has also been reported in other species. Herring gulls for example, exhibit TI around 15-20 days post-hatch (Montevecchi 1978) and possums from 120 days of age, which corresponds to weaning and emergence from its mother's pouch. Adult possums are also reported to respond less readily than ones under 8 months of age (Franq 1969).

This declining susceptibility with age is also seen in the rat where the period of susceptibility is said to last till approximately 15 days in Wistar rats (Klemm 1971c), 11 days in albino rats and 9 days in the hooded rat (Prestrude 1977). As this period coincides with the maturation of the neocortex, it has been postulated that the neocortex may inhibit TI (McGraw and Klemm 1969). From this period, duration of TI declines progressively with age till 3.5 weeks and susceptibility does not return until the rats age and pass their "prime of life" (Klemm 1971c).

Characteristics of an animal during TI also change with age as reported in the oyster catcher (Dewar 1920), turkey vulture (Vogel 1950), black-headed gull (Kirkman 1937), sparrow (Nice 1943), curved bill trasher (Rand 1941) and a variety of other species (Palmer 1909). Rovee and Kleinman (1974) also observed marked qualitative changes in TI responses over the first few days post-hatch. The duration of immobility and eye closure increased with age while distress calls and vocalisations decreased. This negative

relationship between duration of vocalisation and duration of eye closure is consistent with Gallup, Nash and Wagner's (1971) report in adults and Rovee and Luciano (1973), Rovee et al's (1973) and Rovee and Kleinman (1974) reports in the very young.

Age has also been reported to affect the way a subject responds to environmental novelty (Rovee et al 1973), temperature changes (Whishaw, Flannigan and Barnsley 1979; Whishaw Schallert and Kolb 1979) during TI and even in the methods of induction necessary to elicit TI (Oakley and Plotkin 1977). It is therefore clear that biological development and age of the subject are important variables affecting TI. These changes with age however, may also be affected by the subject's experience, as experience, especially early experience, plays an important role in determining an animal's behaviour.

2.7.1.6 Previous experience

Previous experience affects both the incidence and duration of TI (Ratner and Thompson 1960). It is commonly reported that subjects used to human handling or which have been tamed, are less susceptible or insusceptible to TI (Gilman et al 1950) and that the duration of TI and susceptibility decreased as the number of days feeding and other associations with the experimenter increased (Ratner and Thompson 1960). This has been confirmed in many species including chickens (Gilman et al 1950; Ratner and Thompson 1960), hawks (Crawford 1977), opossums (Franq 1969) and frogs (Boice and Williams 1971).

These results are consistent with the reports that longer immobility durations occur in wild compared to domestic animals (Whishaw et al 1978) and that TI is not elicited in family pets when they are tested by a member of the family in a familiar environment, although members of the same or related species do exhibit TI under more suitable stimulus conditions (Ratner 1967).

The method of rearing may also be important as lambs reared by ambivalent fostermothers and subjected to varying periods of butting and hardships are reported to have TI durations that are 7 times shorter than control animals. Moore and Amstey (1962) believed that this was because the fostered animals had become adapted to fear or threatening stimuli (including humans) and therefore did not develop normal TI responses.

TI is also reported to be reduced by familiarity with the test situation or experiences that lead to general adaptation of fear (Ratner 1967). This effect was evident in socially reared chicks which exhibited greater immobility than chicks reared in isolation, when tested individually (Salzen 1963; Rovee and Luciano 1973). When tested with a group of chicks nearby, socially reared chicks failed to show TI whereas isolates were unaffected by the presence of other chicks. Salzen suggested that the fear response enhancing TI in the socially reared chicks was due largely to the separation of chicks from their conspecifics.

The role of social interactions on TI was also demonstrated by Crawford (1977) and Jones and Faure (1982) even though they obtained contradictory results. Crawford (1977) found that more dominant chickens exhibited shorter durations and were more resistant to induction than subordinates whereas Jones and Faure (1982) found that dominant hens showed longer TI durations, which suggested that dominants were more fearful than subordinates. Crawford's birds were however tested at 4 weeks of age and as peck orders are generally not established till at least 5 weeks of age, his heirachies may not have been stable (Jones 1986a).

While comparing fearfulness in laying hens housed in cages or in pens, Jones and Faure (1981b) demonstrated an effect of housing conditions on social interactions and TI. Although susceptibility was similar in both groups, there was a decrease in TI duration and latencies to first leg and head movements in pen-housed birds as compared to caged birds suggesting that caged birds are more fearful than pen-housed ones. Kujiyat et al (1983) also reported shorter immobility reactions among birds housed socially in pens rather than in cages.

Hennig and Dunlap (1978) reported that naturalistic housing conditions such as foliage in the housing environment can affect the duration of TI in anoles on certain days of testing. Keeping males in groups is also reported to reduce the duration of TI in comparison with solitary individuals or those accompanied only by a female (Regalado 1985).

It can therefore be seen that many variables need to be considered when designing and planning TI experiments. Firstly, it is necessary to choose the subject carefully taking into consideration variables such as species, strain/breed and age of the subject. Having chosen a group of subjects it is also important to consider their background and previous experiences as well as how the subjects will be housed and handled prior to experimentation as all these variables discussed in this section have the potential to affect TI.

2.7.2 EXPERIMENTAL VARIABLES

Once the subjects have been chosen and appropriately housed, variables arising due to experimental design and conditions need to be considered, since methods of induction, duration of restraint, time of day, environmental conditions, distribution of trials, arousal and fear can affect TI and the experimental results.

2.7.2.1 Pre-testing Conditions

Pre-testing conditions such as the amount of handling or chase time required to capture and transport the subject to the test area can increase the probability that the subject will exhibit TI and also increase the duration of the response (Tortora and Borchelt 1972; Eyer

and Ratner 1975). Gallup, Nash and Wagner (1971) found pretest holding conditions to be a potent source of variation in naive, unhabituated birds as subjects carried to the experimental area in a cardboard box showed significantly longer TI durations than hand-held subjects.

2.7.2.2 Methods of Induction

As discussed in section 2.5, different methods of induction in one subject may result in different responses (Lefebvre and Sabourin 1977a). There is for example, an increase in TI duration in frogs if induced belly side up (Figure 2.22) (Mangold and Eckstein 1919) and hooding or placing a rabbit in a V-shaped trough (Figure 2.23) (Ratner 1967, Carli 1977) will result in an abrupt recovery of TI even after the response has nearly disappeared as a result of several days testing.

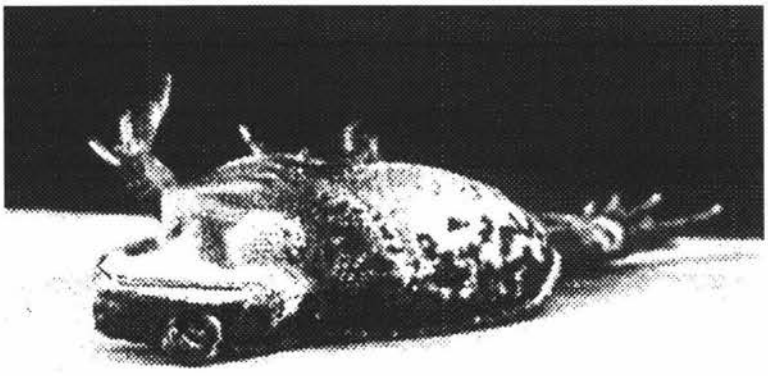


Figure 2.22 Frog exibiting TI from dorsal induction (Klemm 1971c).

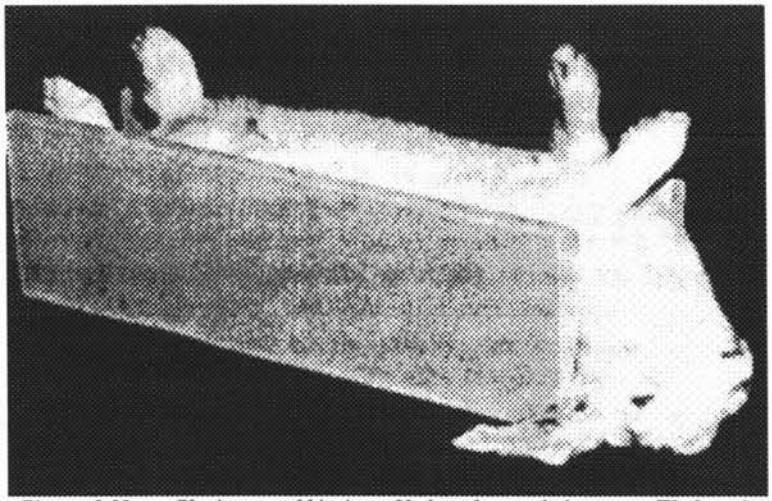


Figure 2.23 Placing a rabbit in a V-shaped trough increases TI duration (Klemm 1971c).

Generally, the less profound the restraining stimuli in terms of strength, duration and physical proximity, the weaker the response (Ratner 1967). This however is affected by other variables such as the species and age of the subject. For example, the reported optimum restraint period is 60s for rabbits (Simonov and Paikin 1969) but only 15s for chickens (Gallup, Nash and Wagner 1971) and Oakley and Plotkin (1977) have shown that during first 2 weeks post partum, TI can be induced just by inverting the subject without any restraint whereas from 4 weeks onwards 15s restraint in the inverted position was required.

The method by which TI is measured, in terms of the criteria set for TI susceptibility or termination of TI, also affects the way results are presented and interpreted, and so must be considered when reading TI literature or designing TI experiments. The details on how different methods can affect TI have already been discussed in previous sections. Other variables such as drug manipulations and neural ablations all have the potential to affect TI susceptibility and duration but will be discussed later in section 2.8.

2.7.2.3 Distribution of Trials

Another important variable to consider when designing TI experiments is the effect of repeated testing on the duration and susceptibility of a subject to TI. There was initial confusion over the effect of repeated testing on TI with reports of increased (Liberson 1948), decreased (Holmes 1906; TenCate 1928), unchanged (Gilman et al 1950), rhythmic cycles (Hoagland 1928; McBride and Klemm 1969) or fluctuations (Holmes 1906; Gilman et al 1950) in TI in response to repeated testing.

Closer examination of the literature however, revealed certain patterns in TI susceptibility and durations with repeated testing. Generally, TI responses decreased (habituated) as the amount of prior testing increased (Ratner 1967). Such results have been reported in the shrimp, toad fish (Gunter and McCaughan 1959), goldfish, rabbit, clawed toad (Lefebvre and Sabourin 1977), octopus (TenCate 1928), frog (McBride and Klemm 1969), tarantula, cricket, isopod, oscar (Crawford 1977), chicken (Braud and Ginsburg 1973a), rat, chaffinch, pigeon (Gilman et al 1950; Ratner and Thompson 1960) and opossum (Franq 1969).

The greatest decline in responsiveness to TI occurred when there was a maximum temporal distribution of trials. That is, 1 trial/day for 24 days resulted in stronger habituation than 4 trials/day for 6 days, which habituated more than the 12 trials/day for 2 days (Crawford 1977). Habituation was also stronger when TI was allowed to run its full course without premature external termination (Nash and Gallup 1976).

In some circumstances, TI responsiveness increased instead of decreased with repeated testing. This occurred when TI was reinduced immediately after termination of an immobility period or when a subject was repeatedly tested with short intertrial intervals. An intertrial interval of at least 15s is usually recommended (Nash and Gallup 1976) to avoid this sensitisation or potentiation effect of massed trials, which has been reported in guinea pigs (Liberson 1948; Bayard 1957), iguanas (Prestrude 1977) and chickens (Nash and Gallup 1976).

The influence of repeated trials is therefore a function of intertrial interval. Long intervals result in habituation with a decrease in TI response whereas short intervals result in potentiation producing longer TI durations. Like variations in methodology however, the effects of repeated testing also varies with species as it has been reported that the rabbit (Ewell and Cullen 1981), bobwhite quail (Eyer and Ratner 1975), green iguana (Prestrude 1977) and lizard (McKnight et al 1978) do not habituate with repeated testing.

Generally however, as repeated testing and habituation usually coincides with an increase in familiarity with the experimenter and environment and a corresponding change in the subject's behaviour from one of initial general agitation to docility when being handled (Gilman et al 1950), many investigators (eg. Ratner and Thompson 1960; Boice and Williams 1971; McKnight et al 1978) believed that the decrease in TI responsiveness is a result of taming and not testing *per se*. Others however, (Nash and Gallup 1976; Nash 1978) believed that repeated elicitation of TI and not just handling resulted in the reduced response susceptibility and durations.

Whatever the cause of the declining responsiveness to TI, it appears that the habituation of TI is durable and may represent a relatively permanent effect with no evidence of spontaneous recovery for up to 6 weeks in chickens (Nash 1978; Nash, Ronci and Girdaukas 1976). Recovery of TI responsiveness may however be achieved by nociceptive stimulation (Smith and Klemm 1977) or changing the testing environment or experimenter (Gilman et al 1950). The effect of environmental variables will be discussed in the following sections.

2.7.2.4 Periodic / Circadian Rhythms

Another variable that has been reported to affect TI is the time of testing as circadian rhythms for TI have been documented in several species including toads (Ternes 1977), tarantulas (Ternes 1977), chickens (Rovee et al 1976), lizards (Hoagland 1928; Hennig and Dunlap 1977b), rats (Hennig and Dunlap 1977a) and woodlice (Ratner 1977). There however, does not seem to be any obvious pattern to these variations in susceptibility and durations of TI in the different species.

For example, longer durations during night than day have been reported in chickens (Rovee et al 1976), toads and tarantulas (Ternes 1977), and rats (Hennig and Dunlap 1977a), even though chickens are diurnal and the other species are nocturnal. Likewise, Hennig and Dunlap (1977b) reported that 2 species of lizards, the anole (*Anolis carolinensis*) and the gecko (*Hemidactylus turcicus*) exhibited similar responses even though they have opposite activity cycles with the gecko being a nocturnal species.

The finding that circadian rhythms in TI are not tied to rhythms in normal activity indicates separate underlying mechanisms controlling theses two behaviours which is supportive of the view that TI is an important predator defence and so, might be expected to supersede normal periodicity in activity.

However, in contrast to chickens, toads, tarantulas and rats, Hennig and Dunlap's (1977b) lizards exhibited longer immobility durations in the light than in the dark. This is similar to Ratner's (1977) findings in 2 species of woodlice. It was postulated that the visible presence of experimenters in the light may have enhanced TI (Gallup 1973b, Hennig 1977) whereas the dark may have provided possible escape, thus decreasing TI durations (Hennig et al 1976).

The importance of light is evident from the numerous reports that manipulation of lighting schedules can alter the susceptibility and durations of TI (eg. Hennig and Dunlap 1977a - in the rat; Hennig and Dunlap 1977b - in lizards; Rovee et al 1976 - in chickens).

The effect of other periodic rhythms on TI has also been reported. Hoagland (1928) for example demonstrated that TI in lizards shows a rhythmical distribution, with a declining duration with increasing environmental temperature. Observations of variation in TI with temperature has also been reported in frogs (Dabrowska and Manikowski 1982), rabbits (Whishaw, Flannigan and Barnsley 1979; Whishaw, Schallert and Kolb 1979), salamanders (Dodd and Brodie 1976) and water bugs (Holmes 1906).

Cashner et al (1982) also reported seasonal variations in TI durations in lizards in response to breeding seasons. This was thought to be due to interactions of endogenous hormones affecting TI mechanisms, mediated through reproductive hormones or behavioural mechanisms.

These periodic variations in TI duration and susceptibility are probably related to seasonal or circadian changes in temperature, light, humidity, magnetic forces or even other variables undetected by human senses. Ethologists have long maintained that environmental factors are important in understanding the behaviour of animals, especially behaviours such as habitat selection, feeding, predator defence and social organisation. It

is therefore not surprising to find that TI is influenced by environmental factors such as light and temperature. These environmental conditions must therefore be controlled during TI experiments.

2.7.2.5 Experimental Environment

In addition to environmental conditions such as temperature and light, other environmental factors such as layout of the testing area are also important and have been shown to affect TI. Jones (1986b) emphasised the need to maintain a uniform auditory environment within TI studies as it was found to be an intervening variable when comparing silence with white noise, traffic noise and the background noise of a poultry house. Although standardisation may not be necessary between experiments the environmental conditions should be described and kept constant during a single experiment as novelty has been demonstrated to affect TI responses (eg. Rovee et al 1973).

2.7.2.5.1 Familiarity

Generally, the more familiar the restraining stimulus and testing environment, the weaker the TI response (Ratner 1967). If subjects are tested in their natural habitat (Holmes 1903), near their home cage (Ewell and Cullen 1981), or in a familiar environment especially if they can still see and hear their conspecifics, there is an attenuation of the TI response (Jones 1984) as compared to when tested in an open unfamiliar area (Suarez and Gallup 1981). The presence of a familiar imprinting stimulus also shortens the duration of TI (Hodges and Prestrude 1978) while withdrawal of the same stimulus will lengthen the duration of the response relative to baseline (Berns and Bell 1979).

Subjects tested in isolation in an unfamiliar environment show longer TI durations. Gilman et al (1950) demonstrated the effects of familiarity with aspects of the test situation by regularly testing a group of birds for 25 days during which TI habituated and reactions greatly diminished. On the 26th day specific items associated with the test situation (eg. table or experimenter) were changed. Each item of change led to an increase in TI with the changing of the experimenter leading to the largest increase of all. Similar results have also been reported by Rovee et al (1973) and Jones (1984).

Other aspects of the testing environment such as the testing surface or presence of foliage can also affect TI responses. These effects have been demonstrated to be related to the subject's escape opportunities.

2.7.2.5.2 Opportunity for escape

O'Brien and Dunlap (1975) reported that TI durations in blue crabs tested on sand were half that of controls tested on a solid surface as the sand provided easy burrowing escape routes. This observation was supported by Garrison (1976) in crayfish tested on sand or mud.

The presence of large bushes during testing also decreased the duration of TI in anoles, while testing in an open area increased the duration of immobility (Hennig et al 1976). This effect was enhanced when a potential predator was nearby and was most evident the closer thepredator was to the prey. Flight latency in anoles after termination of TI was also significantly shorter in anoles housed in terraria containing foliage, while greater incidence of freezing was shown by anoles housed in empty terraria (Hennig 1979a).

Other aspects of the testing environment such as the presence or absence of predators or conspecifics have also been reported to affect TI.

2.7.2.6 Presence of Conspecifics

When socially reared subjects are tested in the presence of conspecifics there is an attenuation of the TI response (Liberson 1948; Ratner 1967; Gallup 1972; Jones 1984) whereas subjects reared in isolation are unaffected by the presence of their conspecifics (Salzen 1963). Salzen suggested that this is a result of an increased fear in the socially reared chicks when separated from their imprinted social companions. Rovee and Luciano (1973) also reported that social isolation prolonged TI in the young chick.

In older chickens the social ranking of the subject also affects TI as Jones and Faure (1982) reported that presence of subordinate in a nearby cage reduced the TI response in the dominant from the same group but presence of the dominant did not alter its subordinates response. They suggested that the subordinate may represent a familiar fear reducing cue thus attenuating the dominant's TI response whereas the acquired threatening properties of the dominant would override its value as a familiar cue.

Conspecific vocalisation also affects the duration of TI as covey calls (call to regroup members after a predator has departed ie. safety signal) and "Ku" calls (which are normally associated with feeding) result in a decrease in TI duration as compared with warning calls (such as the aerial predator call, the ground predator call or the fear squawk) which significantly prolongs TI (Eyer and Ratner 1975; Jones 1986a). Thompson and Liebreich (1987) also reported that chicks remained in TI longer when they were exposed to conspecific fear squawks and aerial or ground predator alarm calls than when exposed to an equally novel attraction call or white noise.

2.7.2.7 Presence of predator / experimenter

While the presence of conspecifics generally attenuates TI responses, presence of predators or the experimenter potentiates TI responses. Duration of TI is increased by the presence of a simulated predator (stuffed Cooper's hawk - Figure 2.24) in domestic chickens (Gallup, Nash, Donegan and McClure 1971; Gallup, Nash and Ellison 1971; Gallup, Cummings and Nash 1972) and anoles (Edson and Gallup 1972, Gallup 1973b, Hennig 1977) and the closer the predator is to the subject, the longer the duration of immobility .

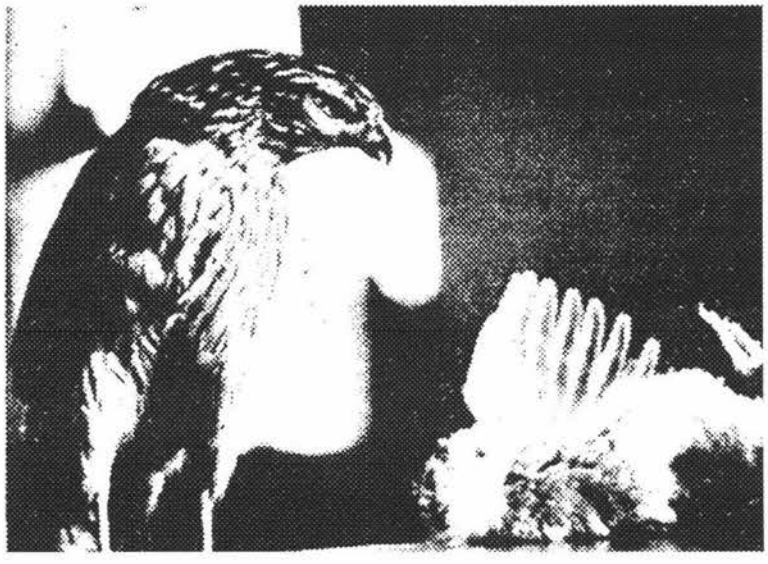


Figure 2.24 A chicken exibiting TI in the presence of a stuffed Cooper's hawk (Gallup 1975).

The importance of eye contact in increasing susceptibility and prolonging TI has been demonstrated by covering the stuffed hawk's eyes and by the use of glass eyes to simulate the presence of predators in chickens (Gallup, Nash and Ellison 1971), anoles (Gallup 1973b) and blue crab (O'Brien and Dunlap 1975).

A similar effect of experimenter proximity has also been reported in chickens (Gallup, Nash, Donegan and McClure 1971; Gallup, Nash and Ellison 1971; Gallup, Cummings and Nash 1972; Ginsburg 1975), anoles (Hennig et al 1976a; Hennig 1979a) and rabbits (Ewell and Cullen 1981) with a potentiation effect on TI the closer the experimenter was to the subject.

Gallup Cummings and Nash (1972) for example, reported that chickens restrained in the presence of an experimenter remained immobile over twice as long as those separated from the experimenter by a plywood barrier. Moreover, experimenter proximity as well as visual orientation (direct gaze, averted gaze or no eye contact) to the chicken were found

to appreciably affect the duration TI. Therefore, like the stuffed hawk, the experimenter's eyes were important in sustaining TI and the experimenter probably represents a potential predator in TI experiments (Suarez and Gallup 1982).

The interaction between the many variables affecting TI was also demonstrated by Hennig et al (1976a) and Hennig (1979a) who reported that close proximity between anoles and the experimenter produced longer durations of immobility in an open area but with bushes nearby, this relationship is reversed with shorter durations when the anoles were close to the experimenter. This indicates that animals do monitor their environment during TI and stimuli presumably associated with the absence of a predator or opportunity to escape decreases the duration of TI whereas the presence of a predator (including human experimenters) increases the duration.

This increase in duration caused by the presence of a predator may be related to an increase in fear which is another important variable affecting TI susceptibility and duration.

2.7.2.8 Fear

Fear is an important variable as it is believed by many (eg. Gallup 1977, Ratner 1977) to be an important factor in the induction and mechanism of TI. The effect of fear on TI will be discussed in greater detail in section 2.8.

Generally, TI is potentiated by procedures designed to increase fear such as exposure to electric shock (Gallup, Creekmore and Hill 1970; Gallup, Nash, Potter and Donegan 1970; Hughes 1979), loud noise (Gallup, Nash, Potter and Donegan 1970; Nash et al 1970; Edson and Gallup 1972) or suspension over a visual cliff (Gallup and Williamson 1972) and is attenuated by manipulations which reduce fear, such as taming (Gilman et al 1950; Gallup 1974a; Crawford 1977), conditioned safety signals (Maser et al 1973), habituation (Nash 1978) and tranquillisers (Gallup, Nash and Brown 1971).

Other investigators however question whether fear or arousal is the potentiating factor in these experiments.

2.7.2.9 Arousal

Leftwich and May (1974) postulated that increased arousal confounded all the fear experiments and proposed that increased arousal and not fear potentiated TI. Kaufman and Rovee-Collier (1978) supported this when they demonstrated that chicks subjected to either predator pursuit or food deprivation exhibited enhanced TI reactions. Gallup and Williamson (1972) however, were unable to increase TI levels when they raised arousal by non-fearful methods. This however, does not mean that arousal could not be another

variable that may affect TI and so, any experimental design proposed should attempt to control arousal levels as well as all the other variables discussed in this section.

2.7.3 CONFOUNDING VARIABLES

Although this section has attempted to identify separate variables that can affect TI, it is obvious from the review that most of these variables interact and confound each other and should be considered collectively. For example, although some investigators report that the rat is not susceptible (eg. Marcuse 1955), others (eg. Ratner 1967) have induced TI using the usual method of restraint, provided the rats were not tamed to handling. Others report that TI can be induced in rat pups but not in adult rats until they have aged (Klemm 1971c; Prestrude 1977). Therefore, although species variations in susceptibility exist, the insusceptibility reported for some species may actually reflect other confounding variables.

Examination of the many variables affecting TI can help in the interpretation of previous conflicting reports in the TI literature, by bringing to attention the many variables affecting TI and how these variables may interact to affect TI. Keeping these variables in mind when designing new experimental protocols will also assist in understanding the complexities of tonic immobility.

2.8 THEORIES

As evident from the literature review so far, numerous theories have been postulated to explain the phenomena of tonic immobility. Although initial attempts tended to focus on the supernatural, with references to "bewitchment" and "magnetism", aspects of some early theories are present in current theories. The numerous theories proposed can be grouped into at least six discernible, though not mutually exclusive categories.

2.8.1 HYPNOSIS

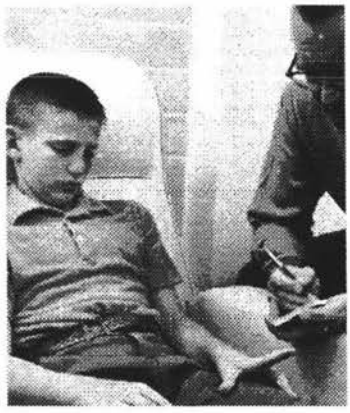


Figure 2.25 A person undergoing hypnosis (Volgyesi 1966).

The association of TI with human hypnosis (Figure 2.25) probably arose from the gross similarities in the behaviours associated with these two states and from the use of the anthropomorphic term "animal hypnosis". Considering the vastly different procedures used to induce the states (eg. use of suggestion in human hypnosis), with the exception of certain individuals (eg. Volgyesi 1938) the consensus of opinion is that human hypnosis and TI are unrelated phenomena and only bear superficial resemblance to each other.

2.8.2 SLEEP

The hypothesis that TI may be a form of sleep arose from early EEG studies (eg. Svorad 1956; Lievens 1960) which described the EEG during TI to be similar to sleep EEG patterns. The arousal EEG during TI is however different from REM sleep as whenever observed, there is always marked pupil dilatation and lack of eye movements (Klemm 1966a; Carli 1969a). This and other differences between these two states have brought this theory into disregard.

2.8.3 SPATIAL DISORIENTATION

As TI is often induced by inverting the subject, it had been postulated that TI may be caused by spatial disorientation (Rabaud 1916; Hoagland 1928). However, as TI can be induced without inverting the animal and ablation of an animal's inner ear and vestibular organ does not affect TI (Hoagland 1928, McBride and Klemm 1969), spatial disorientation is an unlikely cause of TI. It may however be a feature of induction that contributes to the unfamiliarity of the situation and may therefore facilitate TI.

2.8.4 NEURAL THEORIES

As the onset of TI occurs rapidly, it is proposed that the proximate cause must be neuronal (Rakshit and Klemm 1980) and not hormonal even though hormones do modulate TI (to be discussed in the following section). Many investigators (eg. Holmes 1906; Hoagland 1927; Pavlov 1955) believed that some aspects of the induction procedure triggers cerebral inhibition resulting in TI. Klemm (1977) reviewed various senses that might be involved and concluded that it is most likely somatosensory input during manual restraint that plays a crucial role in the generation and maintenance of TI as procedures that increase body contact with surrounding surfaces enhance TI durations (Klemm 1966b; McBride and Klemm 1969; Rakshit and Klemm 1980).
Brain transection studies in frogs (Danilewsky 1881; Svorad 1957; McBride and Klemm 1969), chickens (Maser, Klara and Gallup 1973; Gentle et al 1985), rats (McGraw and Klemm 1969; Klemm 1971a), rabbits (Carli 1971) and guinea pigs (Speigel and Goldbloom 1925; Klemm 1971b) have all indicated that the cerebral cortex is not involved in TI but that the TI control centre is located in the brain stem or spinal cord.

In fact, the cerebral cortex has been shown to antagonise TI as decerebrate animals are more susceptible to TI and exhibit longer durations than intact subjects (McGraw and Klemm 1969; Gentle et al 1985) and depression of cortical electrical activity by applying a potassium chloride solution results in greater TI susceptibility and longer durations (Teschke, Maser and Gallup 1975). That the cortex exerts inhibitory effects on TI is also supported by the observation that phylogenetically advanced species with better devel-

oped neocortex are poorly susceptible (Chertok 1964; Ratner 1967; McGraw and Klemm 1973) and that susceptibility decreases in young animals at about the time the neocortex matures (McGraw and Klemm 1969).

Along with brain transection studies, electrophysiological studies have identified an anatomical locus for TI in the medullary portion of the brainstem as multiple unit activity of numerous neurones in the medulla and pons increase immediately at TI onset and persists through the duration of TI (Klemm 1969; 1976b; Braun and Pivik 1983). Electrical stimulation of several sites in the pons also enhanced TI (Klemm 1965). The role of the ponto-medullary reticular formation in TI is supported by the fact that these areas are known to provide global descending and non-reciprocal inhibitory influences on movement (eg. Magoun and Rhines 1946).

These results have led to the development of a model for the neural basis of TI in which somesthetic input during induction triggers the motor inhibitory areas of the bulbar reticular formation to send diffuse descending inhibitory influences on the spinal motor neurones resulting in immobility (Klemm 1971c). In addition, Klemm (1976a) proposed that forebrain areas (especially the limbic system which mediates affective behaviour such as fear) can also modulate TI via its connections to the reticular system. Woodruff (1977) further postulated that within the limbic system, the cingulate cortex enhances TI whereas the hippocampal and septal areas act to inhibit TI. More recently, it was reported that although spinal cord lesions interrupting somesthetic ascending tracts attenuated TI responses, it did not affect TI susceptibility indicating that somesthetic input is important for the maintenance but not the initiation of TI (Woodruff and Baisen 1985).

Even with the extensive studies attempting to identify neural pathway for TI, to date there is still no unanimous agreement as to the neural pathways involved in TI. This is also the case with the attempts at identifying the neuropharmacological basis for TI.

2.8.5 NEUROPHARMACOLOGICAL THEORIES

Numerous investigators have attempted to identify the neuropharmacological changes underlying TI and have shown the involvement of at least four neurotransmittor systems: adrenergic (Hennig 1980; Hennig et al 1981 and 1984), cholinergic (Thompson et al 1974; Woodruff and Lippincott 1976; Hughes 1982), dopaminergic (Ettinger and Thompson 1978; Wallnau 1979) and serotonergic (Maser et al 1975; Harsten et al 1976; Gallup et al 1977; Wallnau and Gallup 1977; Boren et al 1979; Hennig 1980; Wallnau et al 1981a). A detailed review of this area of the literature is beyond the scope of this thesis but interested readers can refer to Gallup et al's (1983) review on the psychopharmacology of TI.

Briefly, several investigators (Thompson et al 1974; Hughes 1982) have proposed a cholinergic (ACh) inhibition system as the basis for TI since various cholinergic agonists and antagonists such as scopolamine, atropine and physostigmine have been shown to affect TI. Other investigators favour a serotonergic (5-HT) control mechanism for TI based on the effect of psychomimetic drugs, monoamine oxidase inhibitors, serotonin blockers, serotonin and its precursors on TI (reviewed by Wallnau and Gallup 1977). Wallnau and Gallup (1977) proposed a mid-brain-raphe model of TI in which TI durations are negatively related to the rate of firing by 5-HT neurones in the raphe area. This model has now been modified with a shift in emphasis from the effects of serotonin on raphe activity in the brain to its action at the postsynaptic serotonin receptors (Boren et al 1979; Wallnau 1979; 1981; Wallnau et al 1981a and b; Hennig et al 1988).

Support for the catecholamine involvement in TI has been based on the findings that both adrenalin and noradrenaline potentiate TI durations (Thompson et al 1977; Thompson and Joseph 1978) thus indicating that adrenergic neurochemical systems can affect TI. Hennig et al (1981 and 1984) for example, reported that drugs that stimulate alpha2 adrenoceptors potentiate TI whereas drugs that stimulate alpha1 adrenoceptors attenuate TI.

Other investigators have also implicated the dopaminergic (dopamine) system in TI. Ettinger and Thompson (1978) demonstrated that L-DOPA, a precursor of dopamine potentiates TI while Wallnau (1979) showed that haloperidol, a dopamine blocker, enhances TI and that apomorphine, a dopamine receptor agonist attenuates TI.

All this indicates that several different neuropharmacological systems are involved in TI and that they are likely to interact with each other as indicated by recent reports of interactions between the serotonergic and dopaminergic systems (Wallnau 1981; Wallnau et al 1981aandb; Klemm 1983a). The neuropharmacological mechanisms of TI however, still remain as much of a mystery as the neural pathways for TI.

What is clear however, is the importance of fear in TI and the notion that TI may participate in predator-prey relationships under natural conditions.

2.8.6 FEAR THEORY

There is considerable evidence supporting the importance of fear in TI. Preyer (1891) was probably the first investigator to implicate fear in TI when he reported of "fear induced catalepsy". From then the "fear hypothesis" developed with the proposal that TI represents an innate fear potentiated response.

This was based on observations where procedures which are assumed to reduce fear such as handling, taming, repeated testing (Ratner and Thompson 1960; Gallup, Creekmore and Hill 1970; Boice and Williams 1971; Jones and Faure 1981c) and tranquillisation (Gallup, Nash and Brown 1971) result in an attenuation of TI whereas rough handling (Parker 1971), novel or unfamiliar test environments (Gilman et al 1950) and adrenalin (Hoagland 1928; Braud and Ginsberg 1973b; Thompson et al 1977) potentiate TI.

Reports where social animals tested in isolation exhibited longer durations than those immobilised in the presence of their conspecifics (Liberson 1948; Salzen 1963) were also interpreted as evidence that TI was related to the fear associated with separation from imprinted or familiar conspecifics. Defecation during TI (Bayard 1957; Gallup, Nash and Wagner 1971), weight loss with repeated testing (Liberson et al 1971) and occasional deaths when subjects were tested under conditions which increased fear (Gallup 1974a) also provided indirect evidence of possible stress or fear-like autonomic involvement in TI.

More direct evidence was provided in experiments where exposure to primary aversive stimuli such as brief electrical shock (Gallup, Creekmore and Hill 1970; Edson and Gallup 1972), loud noise (Gallup, Nash, Potter and Donnegan 1970; Nash, Gallup and McClure 1970; Edson and Gallup 1972) or suspension over a visual cliff (Gallup and Williamson 1972) prior to induction resulted in potentiation of TI susceptibility and durations in chickens, lizards and guinea pigs. Moreover the more intense the shock, the greater the potentiation of the response (Gallup, Nash, Potter and Donnegan 1970; Gallup 1973a).

To overcome the possibility that the use of electric shocks or loud noise may have resulted in tetany thus confounding fear, Gallup, Rosen and Brown (1972) developed an aversive conditioning paradigm and found that a neutral stimulus previously paired with shock increased TI durations even when presented without shock and that the conditioned fear signal may be more effective at prolonging TI than application of the shock itself. Once again stimuli paired with stronger shocks resulted in greater potentiation of TI than stimuli paired with weaker shocks (Gallup 1973a).

In addition to this, Maser et al (1973) reported that a similar conditioning procedure based on shock termination resulted in attenuation of TI thus indicating that TI is amenable to both enhancement and disruption by conditioning procedures designed to increase or alleviate learned fear. Leftwich and May (1974) however, failed to find any effect of conditioned aversive stimuli on TI in guinea pigs and believed that most fear experiments were confounded by increased arousal. Increase in arousal by food deprivation (Gallup and Williamson 1972) or amphetamines however either had no effect on TI or diminished

the response (Gallup1974a). It has also been demonstrated that the TI induction procedure itself is fear producing or aversive in its own right (Nash and Gallup 1975a).

It has however been observed that some tame birds are susceptible whereas some wild ones are not (Gilman et al 1950). Reports where surgical ablation of so called fear centres of the brain still allow induction of TI (Carli 1968, 1971; McBride and Klemm 1969) and reports of chlorpromazine (a fear reducing drug in humans) enhancing rather than inhibiting TI (Klemm 1977) also seem to negate the fear hypothesis. Some investigators also question whether fear has any tangible status (Klemm 1971c; Gallup 1974a) especially in lower vertebrates and invertebrates (Ratner 1967).

The effect of fear on TI in higher vertebrates is however well documented but although fear has been shown to be important in TI as fear manipulations dramatically affect TI, fear alone is not sufficient to produce TI as physical restraint is what invariably triggers the reaction. Fear is therefore not postulated to be the cause of TI but just an intervening variable and the fear theory useful as a predictive framework for TI (Gallup 1977).

The widespread acceptance of the role of fear in TI has resulted in the use of TI as a method of estimating fearfulness in chickens (Jones 1987) as TI is considered positively related to fear (Jones 1986c). This has been based on observations where chickens which exhibited long TI durations were also likely to exhibit high levels of fearfulness in other potentially frightening situations such as exposure to a novel environment and / or a loud noise (Suarez and Gallup 1981; Jones and Mills 1983).

2.8.7 PREDATOR-PREY THEORY

Related to the idea that TI may be an innate fear reaction is the Darwinian notion that TI may represent a predator defence. Although Darwin's (1900) death feigning theory (an animal in the face of danger, instinctively succumbs to immobility as a protective guise) was widely criticised (Gilman and Marcuse 1949; Prestrude and Crawford 1970) because of its theological overtones, his basic notion of TI as an adaptation to predation has been further developed by Ratner (1967) and is now widely accepted.

The main theme of Ratner's (1967) theory is that immobility is one of the final responses made by a prey in a sequence of responses that occurs when a prey is approached and attacked by a predator. The response a prey makes depends on the "defensive distance" between the prey and its predator. (Figure 2.26) As the defensive distance is decreased the prey exhibits in succession responses such as freezing, fleeing, secreting, fighting and finally the immobility response.

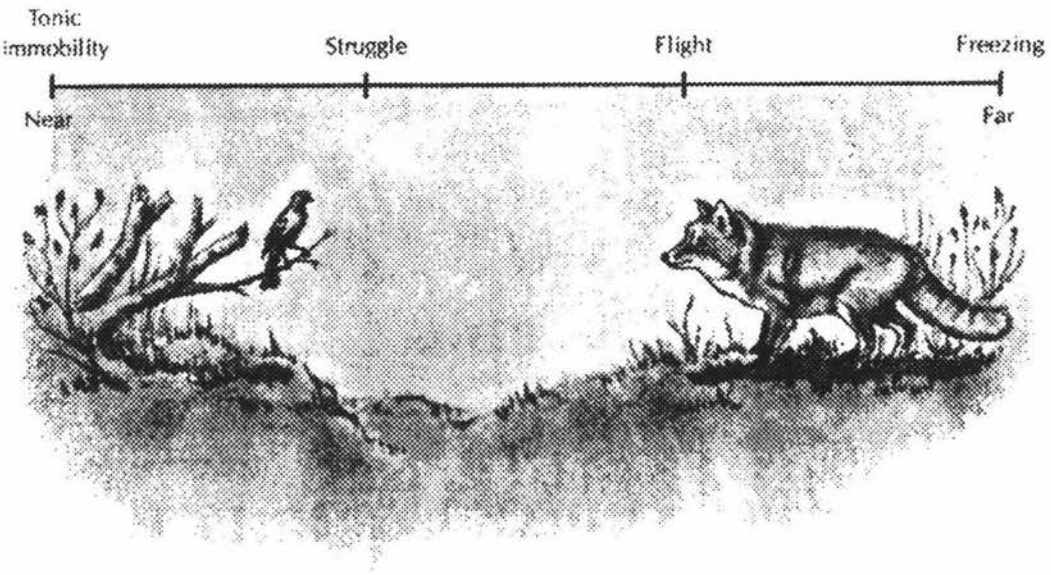


Figure 2.26 Diagramatic representation of Ratner's (1967) predator-prey theory (Gallup and Maser 1977).

That is, at an appreciable distance from a predator, the typical prey reaction is to freeze in order to reduce detectability. However, if the predator then approaches, thus reducing the defensive distance, flight becomes more likely as the prey attempts to escape. This is then followed by fighting and struggling at close quarters if physical contact is made in a further attempt to escape or deter additional predatory advances. Finally, at zero defensive distance, if contact with the predator is prolonged, TI which represents the terminal defensive reaction in this sequence of distance-dependant predator defence often ensures. It is postulated that TI may reduce stimulation for further attack or cause the predator to lose interest in the prey.

When viewed in this manner, TI is no more mysterious than injury feigning, distraction display or biting as all of these behaviours function as specialised responses to stimulus aspects of an approaching or attacking animal. In the case of TI, the predator or predator-like stimulus (including experimenters) must have touched or grasped the prey.

Numerous studies supporting this theory have been conducted in species including chickens (Gallup, Nash, Donegan and McClure 1971; Gallup, Nash and Ellison 1971; Gallup, Nash, Potter and Donegan 1971; Ginsburg et al 1974b), lizards (Edson and Gallup 1972; Gallup 1973b) and crabs (O'Brien 1973). The presence of just a simulated predator in the form of a stuffed hawk (Figure 2.24, p56) not only prolonged immobility but also produced distance-dependent effects with increased susceptibility and durations the closer the predator is to the subject (Gallup, Nash, Donegan and McClure 1971).

Selectively manipulating the facial characteristics of the hawk, using a hood or pieces of black tape indicated that visual contact with the predator's eyes was essential for attaining increased immobility times (Gallup, Nash, Donegan and McClure 1971; Gallup 1973b). More direct support for the importance of eye contact was evident from the similar results obtained using artificial eyes suspended over the subject during immobility testing (Gallup, Nash and Ellison 1971; O'Brien and Dunlap 1975) indicating that the effect of eye contact is contextually independent of other facial or bodily features of potential predators.

Gagliardi et al (1976) further reported that only pupil-to-eye size ratios resembling the average vertebrate predator eye was effective in potentiating TI in chickens. Jones (1980) also found that monochromatic, two-dimensional eye shapes elicited avoidance and fear in chicks and that horizontal orientation, pairedness and the presence of both an iris and a pupil were important recognition cues with the shape rather than the size of eye-like stimuli being more important .

Eyes are probably important because during conditions of eye contact, the predator's attention is focussed on its prey, thus any attempt at escape would be maladaptive. This is supported by Gallup, Cummings and Nash (1972) who reported that not only did the visual presence and vicinity of an experimenter in the testing area potentiate TI but that the orientation of the experimenter's gaze also had significant effects on TI with longer durations when the experimenter maintained direct eye contact with the subjects than when his gaze was averted or eye contact avoided (Suarez and Gallup 1983).

All this indicates that subjects are continuously monitoring their environment during TI and may be awaiting opportunities to escape as discussed in section 2.7.2 where increased opportunities to escape into nearby foliage decreased TI durations as compared to when TI was tested in an open area (Hennig et al 1976).

It has also been observed that in comparison to subjects tested without any visual contact with a predator, those tested in the presence of a predator showed exceptionally intense escape reactions and often attempted to attack the experimenter before fleeing (Gallup, Nash and Ellison 1971). This suggests that a reversal of Ratner's (1967) defensive distance sequence may occur at termination of TI. Further support is provided by Hennig et al (1976) who observed that the reactions after termination is affected by the distance from the potential predator. At 270 cm from the experimenter, their subjects (anoles) always froze while at shorter distances, half froze and half fleed.

In the presence of nearby plants, the anoles were also more likely to freeze at short distances from the experimenter than in an open area and those that did flee showed a high tendency to climb onto plants. Therefore, escape opportunities can affect the applicability of Ratner's (1967) defensive distance theory, once again indicating the complexity of TI.

The enhancing effect of conspecific warning call (aerial and ground predator alarm calls) as compared to covey calls (safety signal) which attenuate TI responses also provide support for the theory that TI may act as a predator defence (Eyer and Ratner 1975; Jones 1986a; Thompson and Liebreich 1987).

Figure 2.27 Chicken immobilized in the presence of a live Savannah hawk (Gallup 1977).

Viewing TI as an evolved predator defence is also dependant on the idea that on some occasions, an immobile animal is more likely to escape a predator than a mobile animal. That is, some selective advantage is associated with TI thus allowing it to evolve as a consequence of selective pressure exerted by predation. Naturalistic observations reveal that a number of prey do exhibit TI when captured by predators (Armstrong 1965 - birds; Sargeant and Eberhardt 1975 - ducks; Franq 1969 - opossums; Brodie et al 1974 - salamanders) and it is likely that the adoption of an immobile posture might minimise or at least reduce stimulation for further attack and allow for escape when the predator is distracted as many predators appear to be innately programmed to respond to specific stimuli such as movement and struggling or vocalisations to maintain orientation and attack (Figure 2.27) (Fox 1969; Askew et al 1970; Kaufman 1974; Drummond 1979).

Support for this theory is evident from reports of TI decreasing the probability of meal worms being eaten by lizards (Hoagland 1928) or lizards being spared by cats if they became immobile after capture (Gallup 1974a). Wild ducks have also been observed to escape unharmed if they enter into a state of TI when attacked by red foxes (Sargeant and Eberhardt 1975). Sargeant and Eberhardt (1975) then conducted a series of experiments with captive foxes and found that the ducks could survive capture and handling by virtue of assuming an immobile posture (Figure 2.28). They therefore concluded that "death feigning appears to be a highly developed anti-predator behaviour in ducks that facilitates the escape of some birds after capture by red foxes". It was also noted that the immobile ducks appeared alert and often took advantage of escape opportunities.

Similarly, Thompson et al (1981) reported that TI in quails deters predation by cats and that the total time a cat spent stalking, attacking and handling a bird was negatively related to the total time the bird spent in TI as TI seemed to eliminate the movement stimuli that sustains further attack. Furthermore, they noted that a bird's initial response to an approaching cat was to flee or freeze and that mere physical contact such as paw batting

by the cat was not sufficient to induce TI but that TI was only observed when the cat held or bit the bird, especially around the neck region. Then once TI was induced, the cat would usually drop the bird to stalk other moving prey. Their findings therefore support the hypothesis that TI is a terminal defensive mechanism elicited by predator contact that occurs after other defences have failed and that it has adaptive value in the context of predator-prey interactions.

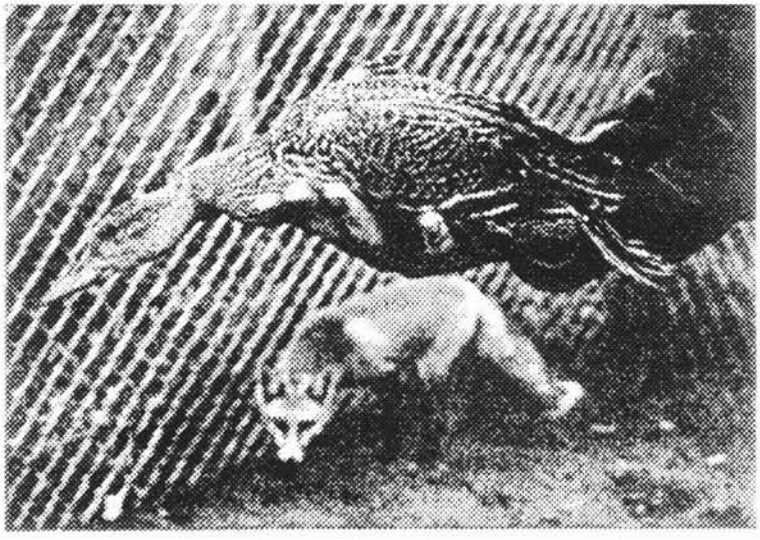


Figure 2.28 A duck exibiting TI when attacked by a red fox (Sargeant and Eberhardt 1975).

This view is also supported by various studies on the heritability estimates of TI. Besides Gallup's (1974b) extremely high estimates in domestic chickens (discussed in section 2.7.1.3) most other investigators (eg. Benoff and Siegel 1976; Kabai and Csanyi 1979) have reported low heritability estimates for TI which suggests prior natural selection for TI and that this trait is associated with fitness.

Besides the initial objection against Darwin's (1900) death feigning hypothesis, most TI investigators now agree that TI has probably evolved as a terminal defensive mechanism elicited by predator contact as there is considerable evidence supporting this theory. Although it falls short of explaining TI, in conjunction with the fear theory, this predator-prey theory seems to integrate much of the data on TI as it incorporates somatosensory input, fear and its associated limbic and neuropharmacological considerations.

Although there have been extensive studies attempting to explain TI in various species, very little work has been conducted on TI in dogs and so very little is known regarding the phenomenon in this species.

2.9 TONIC IMMOBILITY BY DOGS.

As evident from the literature, although there has been considerable research on TI in a wide variety of species, very little research has been conducted on TI in dogs. Most references to TI in dogs have been made in passing when discussing species susceptibility and give very little detail as to the methods of induction, age or breed of the dog, or even the durations of any intervening immobility.

It is generally considered that dogs are difficult to hypnotise (Chertok 1964) as many investigators have failed to induce TI in dogs (eg. Svorad 1957) and some even believe that dogs are completely refractory to TI (eg. Danilewski 1890). There are however, reports of "hypnosis" in the dog by magnetic passes or stroking (Wilson 1839), inversion (Mangold 1914, 1934; Mangold and Eckstein 1919 - dorsal and ventral restraint (Hoagland 1928) and also other methods that were not described. Some authors report that TI can only be induced in young dogs (Hoagland 1928) and not adults whereas others report that they have not even been able to induce immobility in puppies (Prestrude 1977). Due to this discrepancy in susceptibility to TI by dogs it has even been proposed that the experience and skill of the investigator may be an important variable affecting TI in dogs (Chertok 1964).

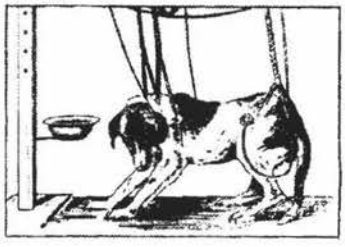
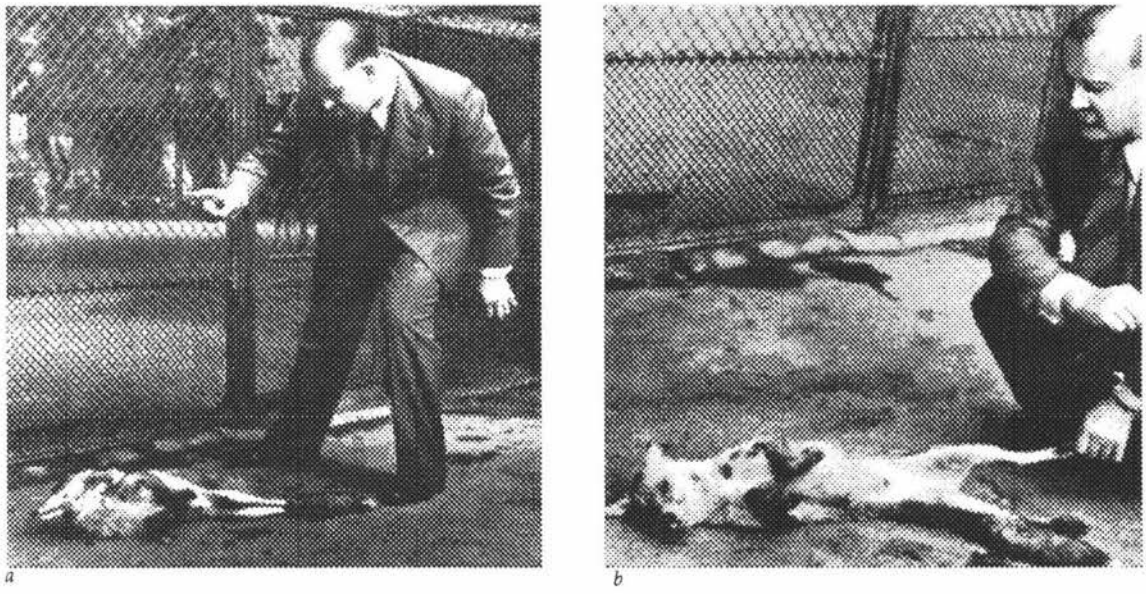


Figure 2.29 Pavlov and Petrova's (1934) dog lapsing into the "hypnotic state (Volgyesi1966).

The literature often cites Pavlov's dogs when referring to TI by dogs. Pavlov and Petrova (1934) reported that two dogs in their conditioned reflex experiments would fall into a "drowsy condition" and "continually lapse into the hypnotic state as soon as they were placed and fitted into their usual experimental surroundings" or even upon entering the experimental room (Figure 2.29). This "hypnotic state" however involved complex orientated body movements such as turning away from food and licking the wound produced by a fistula and as such the dogs were not immobile. It therefore does not fit into this thesis's criterion for TI being "a state of relative immobility induced by restraint and presumed to function as a terminal defensive reaction" even though Pavlov interpreted this phenomenon as "a self-protecting reflex of an inhibitory character". Other investigators (eg. Lefebvre and Sabourin 1977) classed this form of inhibitory behaviour as a type of altered state of responsiveness and possibly even a "mild transitory form of experimental neurosis".

Besides Pavlov's dogs the first description of TI in a canine species was reported by Ratner (1967). Very little detail was provided, with just the mention of a field experiment by Ratner and Ozoga sometime in the 1960's. This consisted of "a field experiment" where

coyotes (*Canis latrans*) and red foxes (*Vulpes fulval*) were trapped and then grasped by a choker collar that was attached to a stick. Strong TI was induced in the coyotes but not in the foxes who continued fighting during the entire procedure that included binding their legs. Armstrong (1965) however, is reported to have induced TI in the fox (species and conditions unspecified).



a *b*

Figure 2.30 Volgyesi (1966) "hypnotising" a fox by a. eye fixation on a extended finger, b. placing it unexpectedly on it's back.

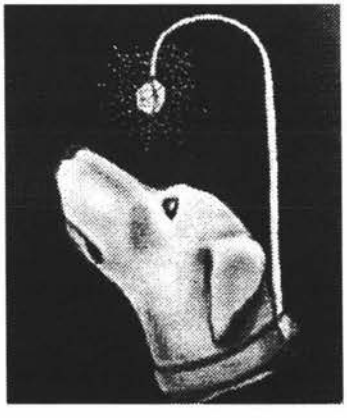


Figure 2.31 Dog "hypnotised" by a prism (Volgyesi 1966).

Volgyesi's book (1966) also contained photographs of a fox which was "hypnotised" by eye fixation on an extended finger (Figure 2.30a) or by positioning the fox "unexpectedly on its back" (Figure 2.30b). He also had a photograph of a dog "hypnotised" by a prism attached to its head (Figure 2.31). Another pictorial demonstration of TI by dogs is in a book entitled "Abnormal Behaviour in Animals" where Fox (1968) refers to TI in his chapter on "Psychomotor Disturbances" and includes a figure of an adult female beagle being put into TI by placing it suddenly on its side and then releasing it (Figure 2.32).

From the photograph, it can be seen that the dog was restrained with its head and hind legs extended and that this position was maintained at release. No further details were provided as to the duration of restraint or even the duration of the resulting TI. The same photograph also appeared in another book (Fox 1978) and Fox indicated that the beagle had originated from an extremely timid line.

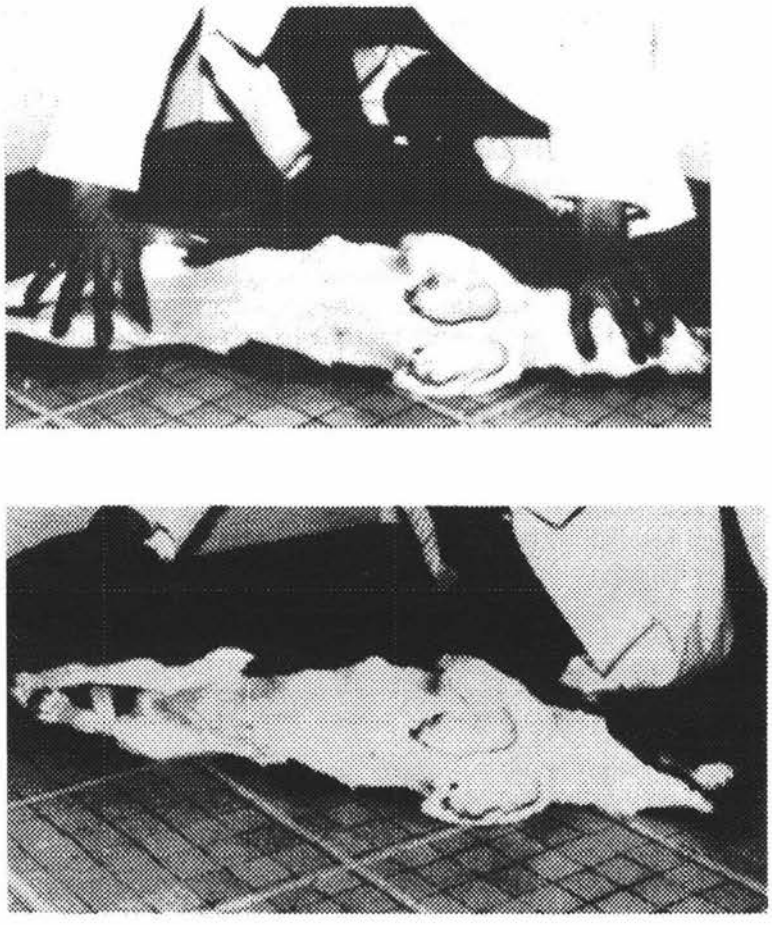


Figure 2.32 Tonic immobility in a beagle by sudden lateral restraint (Fox 1968).

Further reference to immobility in dogs was by Mery (1968) who described the ease by which veterinarians impose transient immobility while examining dogs by tipping dogs onto their sides (by grasping the dog's front and rear legs furthest away from them) or suddenly shining the light from an oculscope into the dog's eyes. Mery however did not consider this a form of "hypnosis" as the dogs jump down as soon as the intervention is completed. This was attributed to the veterinarian's authority and instinctive skill and confidence.

Mery also referred to the cataleptic state adopted by hounds, setters, pointers and spaniels when hunting or seeking out game. For example, upon exposing an immobile hare or pheasant, "pointers" take up a characteristic stance with its neck stretched forward, head held horizontal and tail held stiff and parallel to the ground. The dog appears to be in a state of motor inhibition, frozen on three rigid legs and the forth bent at the knee joint and

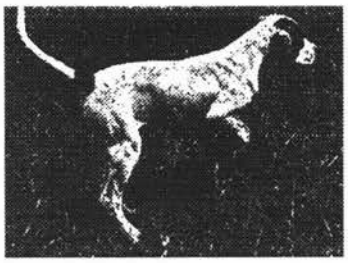


Figure 2.33 The characteristic posture of a Pointer when on a hunt (Mery 1968).

will remain in this position for several seconds or minutes on end, providing the game itself remains immobile (Figure 2.33). "Down" dogs on the other hand, will take up a position lying flat on their stomachs, head and neck outstretched and lower jaw occasionally pressed to the ground. These dogs seem to be unresponsive to environmental stimuli other than the game. Although this does not fit into our criterion for TI, it does relate to the most recent and only detailed reports of TI in dogs by Reese et al (1982, 1984 and 1985) who were conducting immobility experiments on shorthair German Pointers.

Reese et al reported that compared to the normal line of Pointers, a nervous line exhibited prolonged hypertonic immobility when inverted and restrained in an open sling (Figure 2.34). This nervous line was called the "Arkansas line of nervous Pointers". Induction consisted of grasping the dog by each leg and inverting it into an open sling. The dog was restrained for one minute with one experimenter holding its forelegs while another experimenter stroked the dog's belly at 1s intervals. Following the induction procedure, the experimenter remained standing approximately one meter from the dog and observed it for 1 (1985) or 2 (1982) min before leaving the room. Testing was terminated when the dog got out of the sling spontaneously or at the maximum limit of 4 (1982) or 9 minutes (1985) when the experimenters returned and removed any remaining dogs from the sling.

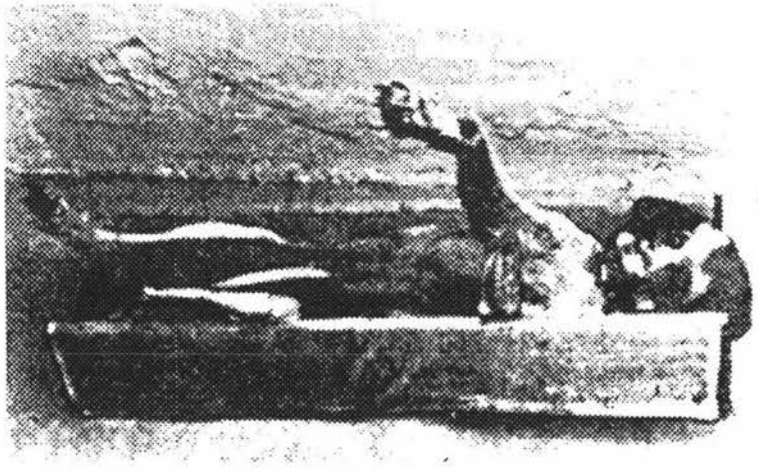


Figure 2.34 Nervous Pointer exibiting hypertonic immobiility in a sling (Reese et al 1982).

In the first experiment (1982) all 10 of the "nervous Pointers" remained in the sling for the full 4 min in a hypertonic supine position with their tails against their belly, hind legs extended, forelegs extended or rigidly flexed (Figure 2.34) and were immobile with the

exception of eye movements and occasional tremors. In contrast, 4 of the "friendly Pointers" got out of the sling immediately upon release from restraint and although the others remained in the sling for the full period, they were relaxed and moved their heads, tails and extremities freely without attempting to turn over. Similar results were also obtained in 1985 with both adult and 4 month old "nervous Pointers" exhibiting significantly longer TI durations than the "friendly Pointers".

Differences in heart rates were also recorded between these two lines as the "nervous Pointers" exhibited significant bradycardia during TI followed by a marked increase in heart rate at termination whereas the "friendly Pointers" heart rates were unchanged with a slight increase post-induction followed by a return to baseline. When tipped out of the sling at termination of TI, the "nervous Pointers" stood upright and remained stationary whereas the "friendly Pointers" actively explored the room (Reese et al 1982).

These differences between the two lines were also evident in their responses to normal human interactions as the nervous dogs showed markedly reduced activity in the presence of a human and in close quarters retreated, often urinated and defecated, attempted to hide (Figure 2.35) and when they are unable to flee stood rigidly in "ungainly" frozen postures (Figure 2.36) whereas the dogs from the friendly line approached, licked, nuzzled and moved enthusiastically about the person with their tails wagging. Heart rate changes have also been recorded with the friendly dogs showing tachycardia in response to an approaching person whereas the nervous dogs exhibited bradycardia similar to that recorded during TI in the sling. Reese et al (1985) however, were uncertain as to the difference between this immobility and the upright freezing response of the Pointers.

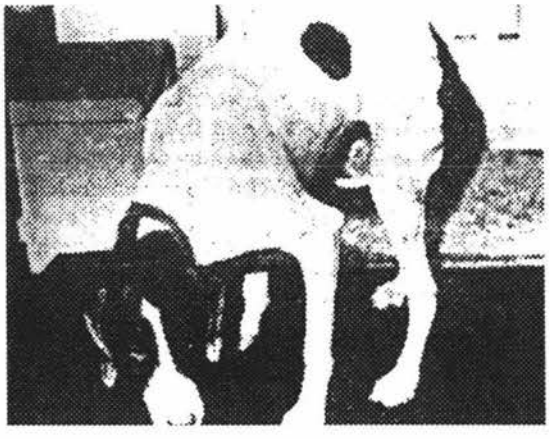


Figure 2.35 Nervous Pointer cowering a timid posture (Reese et al 1982).

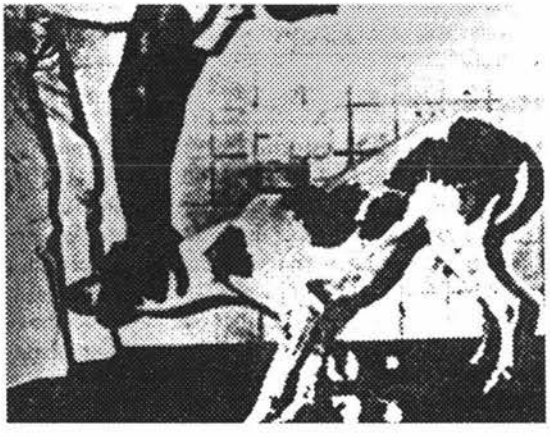


Figure 2.36 Nervous Pointer in a "frozen" posture (Reese et al 1982).

Since the literature by Reese et al (1985) there has been no further publication on TI in dogs and it appears that it has been the only systematic study of TI in dogs. Those dogs however, cannot be considered as normal representative dogs as they had been selectively inbred for either excessive timidness or friendliness. Therefore, despite the extensive research into TI, few studies have been conducted on dogs and little is known about the susceptibility of a normal population of dogs to TI, the methods that might work best, the characteristics and physiological changes that may occur during TI in dogs or the variables that may affect a dog's susceptibility to TI or duration of TI. This is therefore the purpose of this theses.

2.10 CONCLUSION

In conclusion, although there has been well over three centuries of research into TI and enough is now known about TI to describe it as a state of relative immobility induced by restraint and presumed to function as a terminal defensive reaction in a wide range of species, there are still many discrepancies in the literature concerning the best induction methods, the various physiological changes and characteristics during TI, the effect of different variables such as age and repeated testing on TI, the mechanism behind TI and even the most appropriate term to describe the phenomena.

The first stumbling block to overcome these contradictory reports is to define "tonic immobility" or decide on the criteria that will be used to decide if an immobility behaviour is to be considered as "tonic immobility". For example, it would not be productive attempting to determine the best induction method or physiological changes that occur during immobility when comparing immobility reactions such as drug induced immobility, human hypnosis, sleep or immobility caused by CNS pathology as they are different phenomena with different mechanisms and will therefore require different eliciting stimuli and will result in different characteristics or physiological changes. They will also be affected differently by variables such as age, sex or environmental conditions.

Likewise it would be just as fruitless comparing restraint induced immobility (Woodruff's (1977) "contact defence immobility") with immobility resulting from mesmeric passes, human hypnosis, drug or electrically induced catalepsy, Pavlov's dogs, open field freezing behaviour or death feigning, as although they may all have some features in common (eg. immobility and apparent reduced responsiveness), they are not necessarily the same phenomena and grouping them all under the one label of "tonic immobility" or "animal hypnosis" will not only lead to confusion but will also result in oversimplification and reductionism in an attempt to postulate a common function for these behaviours.

Another problem with previous literature is that even if TI had been defined the attempts to generalise between species has resulted in conflicting reports. Considering the wide range of species that exhibit "a state of relative immobility induced by restraint and presumed to function as a terminal defensive reaction", with their diverse morphology, physiology, lifespan, ontogeny, habitats and behaviours, it is only to be expected that different species might respond differently to different induction methods or variables such as previous experience or environmental conditions.

It is therefore critical that the variables that can affect TI (eg. species, age, experimental procedures and conditions) are identified and described if not controlled for in all TI experiments (as discussed in section 2.7) as these variables can markedly affect the results and need to be taken into consideration when reviewing the TI literature. These variables also need to be considered when planning TI experiments in order to reduce the present confusion surrounding TI literature.

Therefore although the aim of this study is to examine TI in the dog, it is also intended that more information will be gained on TI in general and that some of the discrepancies in the current literature can be solved by a thorough consideration of the variables that can affect TI.

Chapter three

Preliminary Studies

Preliminary Studies

3.1 INTRODUCTION

As discussed in the Introduction (Chapter 1), the aim of this study was to determine the susceptibility and characteristics of TI in dogs so that the feasibility of using TI as an humane, quick, easily reversible, non-chemical and safe method of restraint for routine care and veterinary procedures in dogs may be assessed.

It was therefore important to determine the proportion of dogs that are susceptible to TI and to identify the variables that may affect a dog's susceptibility (eg. induction method, age, breed and temperament). The duration, depth and effects of TI on the dog (eg. characteristics, physiological changes and state at termination) also had to be assessed in order to determine the safety and feasibility of performing certain procedures during TI. If TI is to be used more than once in a dog, the effects of repeated testing also needed to be determined.

The initial proposal was therefore to:
1. Determine the population distribution in terms of baseline susceptibility and duration of TI in response to inversion and restraint.
2. Modify the basic induction technique of inversion and restraint to determine the best methods of inducing and enhancing TI.
3. Using the best method, assess the depth of TI and determine the characteristics and physiological changes during TI.

Before deciding on the procedure however, preliminary studies were required to gain a general idea of the types of responses dogs would exhibit and to determine the feasibility of performing certain procedures.

3.2 AIM

The aim was to acquire information on how dogs respond to the handling and restraint required to induce TI. This would also indicate how susceptible dogs are to TI and allow observation of the characteristics of the TI response in dogs. This information was then used to plan and test experimental procedures to identify any problems. Experimental procedures, apparatus and record sheets were then modified as required and tested again.

For example, the best method for inverting and restraining the dogs in various positions, the duration and force of restraint required and the feasibility of performing certain procedures without any assistance from another investigator needed to be determined. These preliminary sessions also allowed determination and testing of the amount of space and time required for handling each dog and to assess the susceptibility and depth of TI in dogs. The results from these preliminary studies then influenced the experimental protocol and also helped establish criteria for defining TI.

3.3 PRELIMINARY STUDY I

3.3.1 AIM

The aim was to determine the best methods for placing dogs into dorsal and lateral recumbency and to determine the most appropriate parts of the body to restrain as well as the force and duration of restraint required to attempt to induce TI. This also provided an indication of how dogs reacted to the procedure.

3.3.2 SUBJECTS

4 dogs from the Massey University veterinary clinic were tested in this study.

3.3.3 TESTING ENVIRONMENT

These dogs were tested on a folded woollen blanket placed on the concrete floor of the dog's run. As the dog runs were separated only by wire fencing, there was continual visual, auditory and olfactory stimulation from other dogs during testing.

3.3.4 MATERIALS

The only materials used besides the woollen blanket, were an adjustable dog leash and a watch with a second hand.

3.3.5 PROCEDURES

Each dog was greeted on entering their run and several minutes were allowed for the dog to become acquainted with the investigator. Each dog was then led to the folded blanket and placed on its side or back by a variety of methods that included kneeling beside the standing dog (Figure 3.1) and pulling its fore and hind legs either towards (Figure 3.2) or away from the investigator (Figure 3.3) or by having the dog sit (Figure 3.4), drop to sternal recumbency (Figure 3.5) and then rolling it onto its side (Figure 3.6) or back (Figure 3.7). The dog was then restrained by applying pressure to various body parts including its head, neck, shoulder, back, hip and limbs.

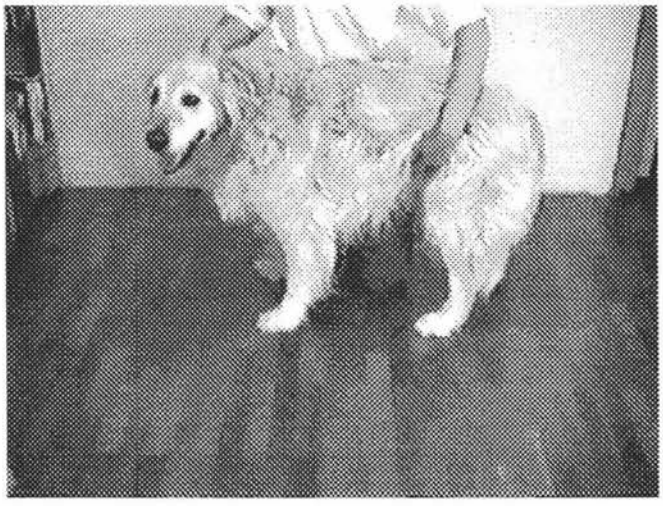


Figure 3.1 Kneeling beside the standing dog.

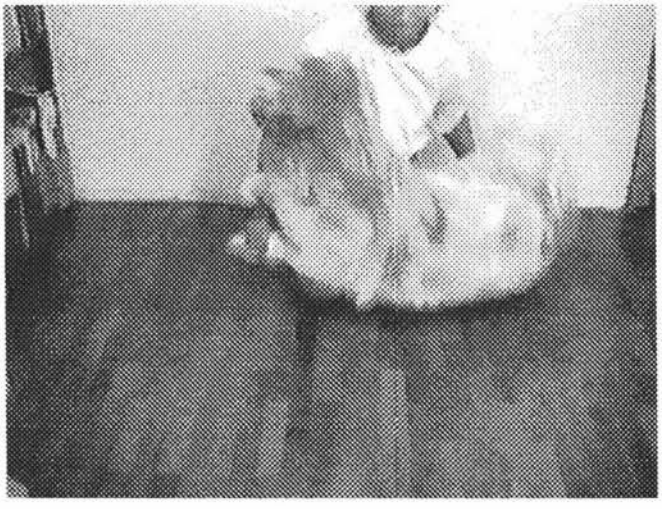


Figure 3.2 Pulling the dog's legs towards the investigator.

Figure 3.3 Swinging the dog's legs away from the investigator.

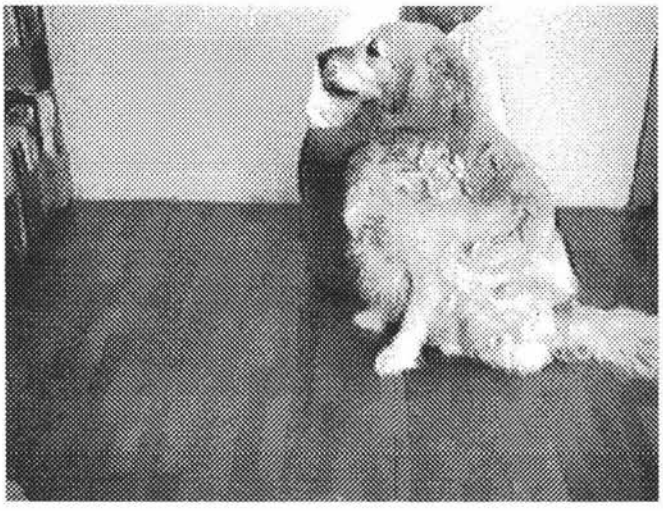


Figure 3.4 Sitting the dog.

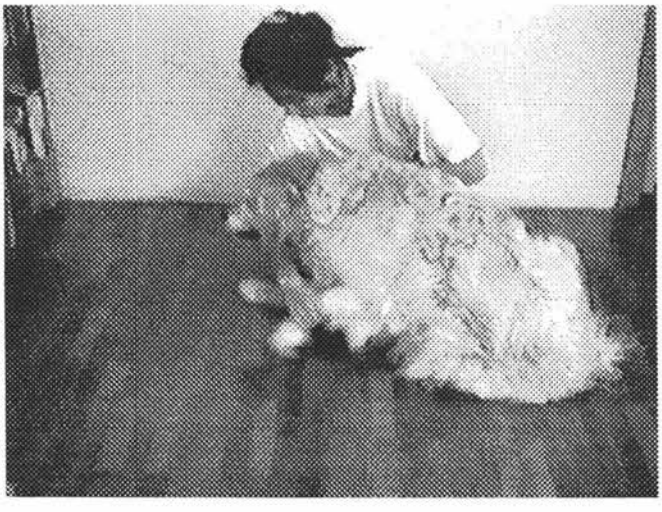


Figure 3.5 Dog "dropping" to sternal recumbency.

Figure 3.6a

Figure 3.6b
Rolling the dog over onto its side.

Figure 3.7a

Figure 3.7b
Rolling the dog over onto its back.

The degree of force required to restrain the dog and the most appropriate parts of the body to restrain were subjectively assessed. The time required for the dog to stop struggling against the restraint and the duration of any immobility was timed. The behaviour of the dog at termination of testing was also observed.

3.3.6 RESULTS

The most satisfactory method for positioning the dogs into dorsal or lateral recumbency was by kneeling beside each dog, reaching over its body to grasp the fore and hind legs closest to the investigator (Figure 3.8) and then to swing these legs away causing the dog to slide onto the investigator's thighs and knees (Figure 3.9) and then down onto the blanket. The subject could then be restrained either in the lateral position (Figure 3.10) or have their legs swung further in an arc (Figure 3.11), to position the the dog into the dorsal position (Figure 3.12).

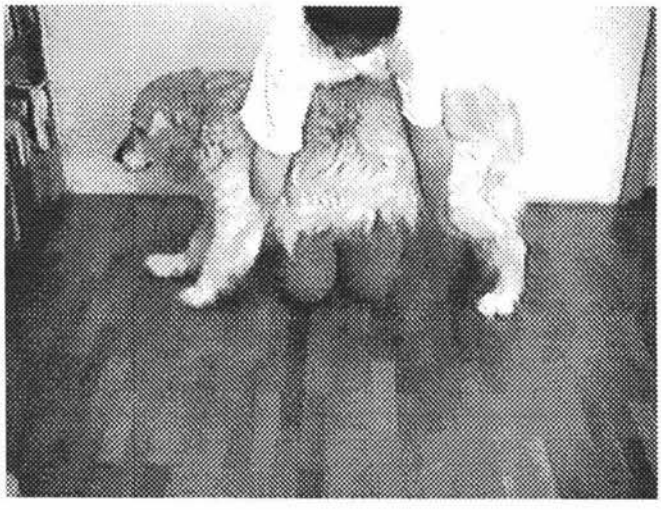


Figure 3.8 Reaching over the dog's body to grasp its fore and hind limbs closest to the investigator.

Figure 3.9 Swinging the dog's legs away, results in the dog sliding onto the investigator's thighs.

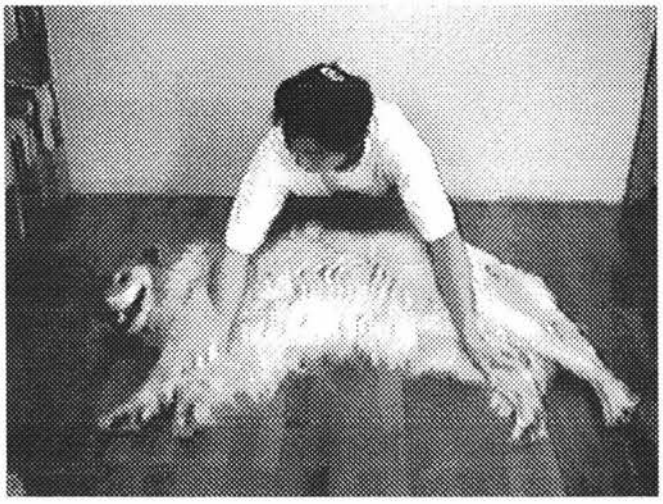


Figure 3.10 Restraint across the dog's neck and hip in the lateral position. Grip on lower limbs prevents the dog from righting.

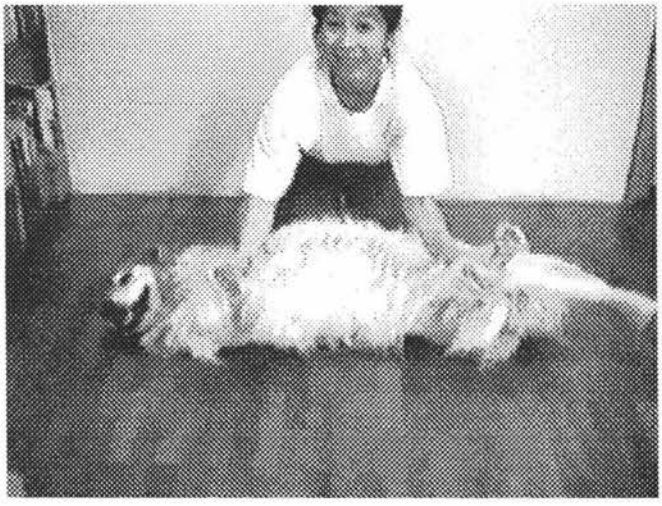


Figure 3.11 Swinging the dog's legs up to the dorsal position.

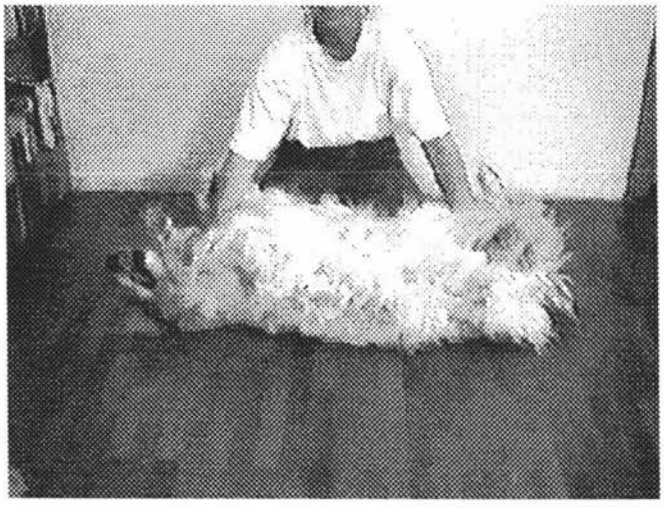


Figure 3.12 Restraint of the dog in the dorsal position.

None of the dogs objected strongly to this procedure but only struggled for a few seconds (< 10s) during restraint. The most effective method for restraint in the lateral position was to place one arm across the dog's shoulder and neck and the other across its hip. A grip on the dog's limbs was maintained to prevent the dogs from pushing off the ground (Figure 3.10). In dorsal recumbency, a grip on the limbs was also maintained but arms were placed across the dog's chest and abdomen (Figure 3.12).

As none of the dogs struggled violently against the restraint, little force was required to maintain the dogs in either the dorsal or lateral position. The resting of arms across the dog's body was sufficient to keep the dogs still. Further pressure could then be applied as necessary if a dog attempted to right itself or struggle. The dogs were unable to right themselves providing the two lower paws were prevented from contacting the blanket.

None of the dogs remained immobile any longer than 1s after release from restraint and all then appeared normal, at ease and friendly at the end of testing.

3.3.7 DISCUSSION

The three restraint positions used during TI induction are dorsal, lateral and ventral restraint. Dorsal and lateral restraint were used in this study as they are the most commonly used methods and appear to be the most successful (Gilman et al 1950). Ventral restraint is usually only used in young chicks (Braud and Ginsburg 1973a; Rovee and Kleinman 1974). It was not attempted in this study as there did not appear to be a quick and simple method of positioning large dogs in this position. In addition, as it does not involve inversion, it did not appear as novel as the other restraint methods. Since novelty and unfamiliarity of the restraining stimulus is reported to be important in the induction procedure (Ratner 1967), lateral and dorsal restraint were chosen for this study.

Compared to the other procedures such as pulling the dogs legs towards the investigator or having the dog sit and then drop before inverting it onto its side or back, the technique of kneeling beside the dog, reaching over its body to grasp and swing the two limbs closest to the investigator away was the easiest, safest and most controlled method for positioning the dogs. For example, getting the dog to sit and drop before inverting it onto its side or back relied on the dog obeying these commands or various manipulations to position it in the sit (Figure 3.13) or drop (Figure 3.14) positions. Compared to the rapid inversion techniques, this method also did not appear to be as novel to the dogs. Kneeling beside the dog and pulling its legs towards the investigator was not as easily controlled as swinging its legs away and it often resulted in the dog falling heavily onto the blanket (Figure 3.15).

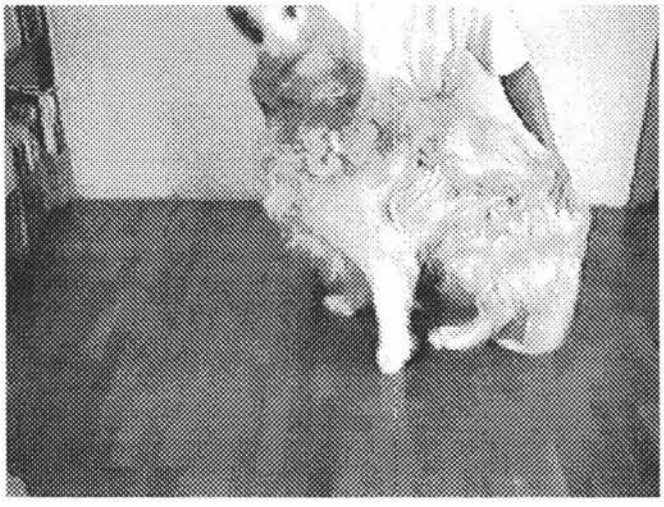


Figure 3.13 Positioning the dog into the "sit" position.

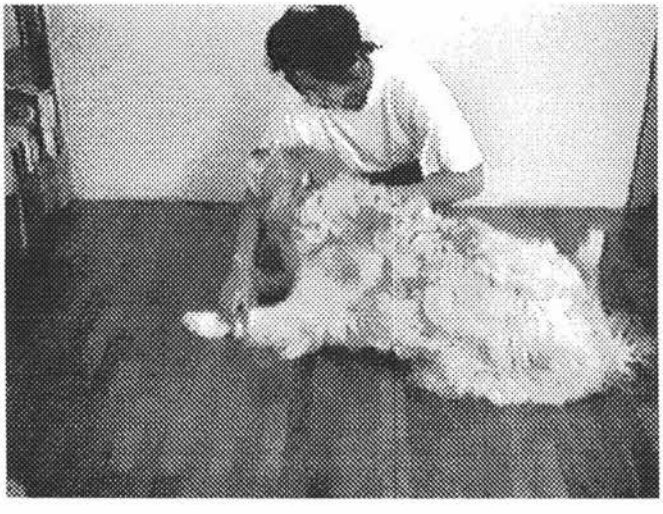


Figure 3.14 Positioning the dog into the "drop" position.

Figure 3.15 Dog falling heavily and awkwardly.

In comparison, swinging the dog's legs away resulted in the dog sliding down the investigator's body and lap prior to contacting the blanket (Figure 3.9, p82), thus breaking its fall. Finer control was also possible by adjusting the speed at which its legs were swung away and by the degree of contact maintained against the dog's body as it fell. This is similar to the procedure used by some veterinarians to place dogs onto their sides for examination and has also been described by Tuber (1986) as a method for positioning dogs onto their sides prior to a relaxation exercise.

This method allowed easier restraint, as the dog ends up lying with its back towards the investigator whose arms are resting across its neck and hip (Figure 3.10, p83). Restraint across the neck and hip region appeared to be the most effective method of restraint as dogs tend to lift their heads prior to righting. They then tuck their legs under their body in an attempt to push off the ground. Pressure across their neck and hip and maintenance of a hold on their two lower limbs during restraint (Figure 3.10) therefore impedes their attempts at righting and any struggling can suppressed as necessary by applying additional pressure across the neck and hip.

From the reports that dogs are not be susceptible to TI (eg. Chertok 1964; Svorad 1957; Danilewski 1890), it was not surprising to find than none of the dogs exhibited immobility of greater than 1s before righting. This could have been due to any number of variables such as the induction method, temperament of the dog, familiarity to the environmental conditions or the continual visual, auditory and olfactory contact with other dogs during testing. It was therefore decided that further testing would be conducted in an isolated, novel environment with limited environmental disturbance or stimuli from conspecifics or owners.

The next study also incorporated more intense stimulation as the more profound the stimulation during induction in terms of the intensity or novelty the more likely an animal is to exhibit TI (Ratner 1967). Therefore, although Gallup (1975) reported that most subjects stop struggling after 15s restraint, restraint across the dog's neck and hip (lateral position) or chest and abdomen (dorsal recumbency) was maintained for 30s in an attempt to increase this stimulation and also to ensure that most dogs would have ceased struggling. From this initial study it was also decided that best induction procedure was to kneel beside the dog and swing its legs away as this allowed better control over the procedure and was safest for the dogs.

3.4 PRELIMINARY STUDY II

3.4.1 AIM

The aim was to assess the feasibility and ease of performing various induction techniques based on the method determined in the previous study and also to observe the responses of the dogs to these procedures. These observations were designed to help establish criteria for defining TI and to determine the testing procedures to be adopted. Any problems with the procedures, apparatus or record sheets were then be modified as required.

3.4.2 SUBJECTS

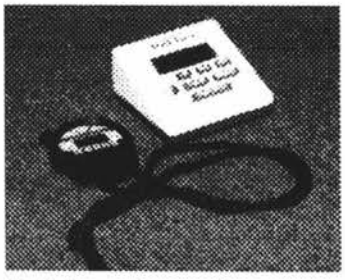
12 dogs from the Animal Health Service Centre at Jennersmead were used in this study. These dogs were all females between 1 and 6 years old and were all cross breeds ranging from a Bull terrier cross (weighing 15 kg) to an Alsatian (German Shepherd) / Labrador cross (weighing 30 kg).

3.4.3 TESTING ENVIRONMENT

These dogs were individually led from their holding quarters across a courtyard to an empty testing room. Although this removed any direct contact with other dogs, faint barking was occasionally heard in the background. Testing was once again on a folded woollen blanket placed on the concrete floor of the testing room.

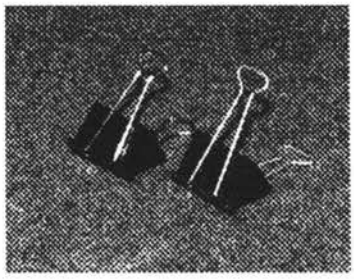
3.4.4 MATERIALS

In addition to the woollen blanket and leash used in the previous study, an electronic clock timer was used to time the period of restraint and a stopwatch to time the period of immobility after termination of restraint. Several other ancillary pieces of equipment were used to provide or inhibit additional stimulation during induction. They included a bitter deterrent spray (Leo's Bitter Spray for Pets - Leo laboratories), several metal bulldog clips (No. 3 size), a blue and black Air New Zealand eye cover, a green pressure cuff (850 x 160 mm) and a plywood box (300 x 300 x 260 mm height) with one open end and plastic flaps over one side. (Figure 3.16)



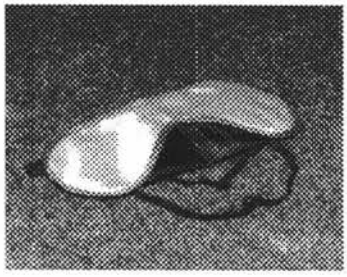
Clock timer and stopwatch.

Leo's Bitter Spray.

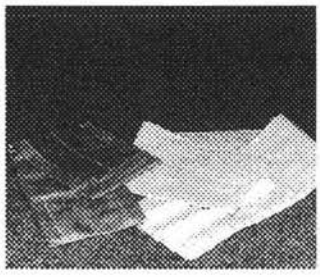


Metal bulldog clips.

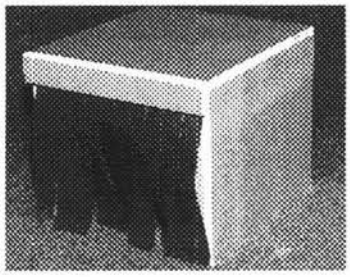
Figure 3.16 Equipment used in study ...



Eye cover.



Pressure cuffs.



Plywood box.

Figure 3.16 Equipment used in study.

Two record sheets were also prepared, one to record the dog's details/signalment (eg. owner, name, breed, sex, age, weight, temperament and health status) and the other to record environmental variables, time of testing, induction methods, ease of induction, characteristics and duration of any immobility and state of the dog after testing (Appendix 1).

3.4.5 PROCEDURES

Each dog was collected from its holding quarters and led across a courtyard to the testing room. It was allowed several minutes to investigate the room before being led to the woollen blanket. During this period, the time of testing and environmental conditions (noise, light, temperature) were recorded. The temperament of the dog was also subjectively assessed as friendly, timid or aggressive and the state of the dog before testing assessed to be quiet or excited.

Each dog was then subjected to a series of induction procedures that involved inversion and at least 30s of restraint in the lateral (Figure 3.10) or dorsal positions (Figure 3.12) as illustrated in Figures 3.8 - 3.12 (pp 82-83). To position the dogs, the investigator kneeled beside each dog and reached over its chest and abdomen to grasp the fore and hind legs that were closest to the investigator's body (Figure 3.8). These limbs were then swung away in an outwards arc causing the dog to slide down the investigator's thighs (Figure 3.9) onto the blanket. The dogs were then either restrained in this lateral position (Figure 3.10) or inverted by swinging their legs further (Figure 3.11) until they were in dorsal recumbency (Figure 3.12). The grip on the lower legs closest to the blanket was maintained to prevent the dog from getting up by pushing off the blanket.

Further restraint was applied as necessary for 30s or more by resting a forearm on the dog's neck and hip (Figure 3.10 and 12). In addition to restraint alone, during the restraint period the dog may also have had its abdomen stroked, have a blanket or box placed over its head, the blood pressure cuff around its ears, eye cover over its eyes, skin clips on its neck, be scruffed around its neck or have bitter deterrent sprayed onto its lips while in either dorsal or lateral recumbency. The stroking, blanket, box and scruffing were applied

immediately after positioning the dog into dorsal or lateral recumbency whereas the pressure cuff, eye cover, skin clips and bitter spray was applied prior to inverting the dog.

At the end of the restraint period, the investigator's arms were gently removed from the dog and the stopwatch which was worn around the investigator's neck, started. Duration of immobility was timed from release of restraint until the dog lifted its head off the blanket. This measure was chosen as the first indication that a dog was about to right. Recent investigators (eg. Jones and Faure 1981a; Rakshit and Klemm 1980) also believed that first head movements were a more sensitive measure of cessation of immobility than righting. The ease of induction and behaviour of the dogs during immobility were also recorded.

Each dog was tested with between 6 to 10 different techniques as not all treatments were tested on every dog and each treatment may have been performed with the dog in lateral and/or dorsal recumbency. In some cases, the treatments were combined (eg. blanket over the head together with stroking). (Appendix 2) The intertrial interval between successive tests ranged from 30s to several minutes.

The duration of restraint and testing procedures during this preliminary study were not standardised as the need to experiment with different induction methods and responses was paramount. For example, if a dog was still struggling after 30s restraint, occasionally restraint was continued for a further 15s or restraint for 30s was at times followed by scruffing for a further 30s. During some episodes the investigator stared directly at the dog whereas in others, direct eye contact with the dog was avoided.

3.4.6 RESULTS

The induction procedure of tipping the dog over by swinging its legs away from me worked smoothly even though the experimental dogs from Jennersmead struggled more violently than the pets from the Massey Univesity veterinary clinic. In one subject, testing was discontinued because the dog struggled continuously and violently during restraint. This Alsatian (German Shepherd) cross was the only dog to be described as timid by the handler. All the dogs were assessed to be friendly by the investigator and all except one was excited before testing.

It was also observed that some dogs fell onto their sides when released from restraint in the dorsal position. With the exception of one dog, all the others (92%) struggled more when restrained in the dorsal position than in the lateral position and also when a blanket or box was placed over their heads. In some cases, struggling was so intense that it was extremely difficult to restrain the dog and attempt to place the blanket or box over the

dog's head at the same time. 79% (11 of 14) of the attempts at placing the box over the dog's head failed because of this.

From the 90 completed inductions on 11 dogs, with the exception of 3 occasions when immobility lasted for 3, 25 and 30s, 97% of the inductions resulted in righting within 1s of release from restraint. On 71 occasions (79%) the dogs righted themselves immediately (0s immobility), after 0.5s on 12 occasions (13.5%) and after 1s on 4 occasions (4.5%).

One dog (Labrador cross) remained immobile for 25s in response to lateral restraint with the pressure cuff around its ears and another dog (Rottweiler cross) remained immobile for 3s in response to dorsal restraint with stroking and for 30s in response to dorsal restraint with the pressure cuff around its ears. During this period, the dog had its forelegs flexed, hind legs extended and its eyes were open and monitoring the environment.

3.4.7 DISCUSSION

The eye movements and posture observed are similar to that described in other species, in dogs by Reese et al (1982), as illustrated by Volgyesi (1966) in a fox, and by Fox (1968) in a beagle (Figure 3.17). These postures however, are not necessarily species specific TI postures but may just reflect the position of the subject at release from restraint. That is, when the dogs remain immobile after release from restraint, they remain in the position that they were placed in during restraint. For example, the Rottweiler cross in dorsal recumbency and the Labrador cross in lateral recumbency.

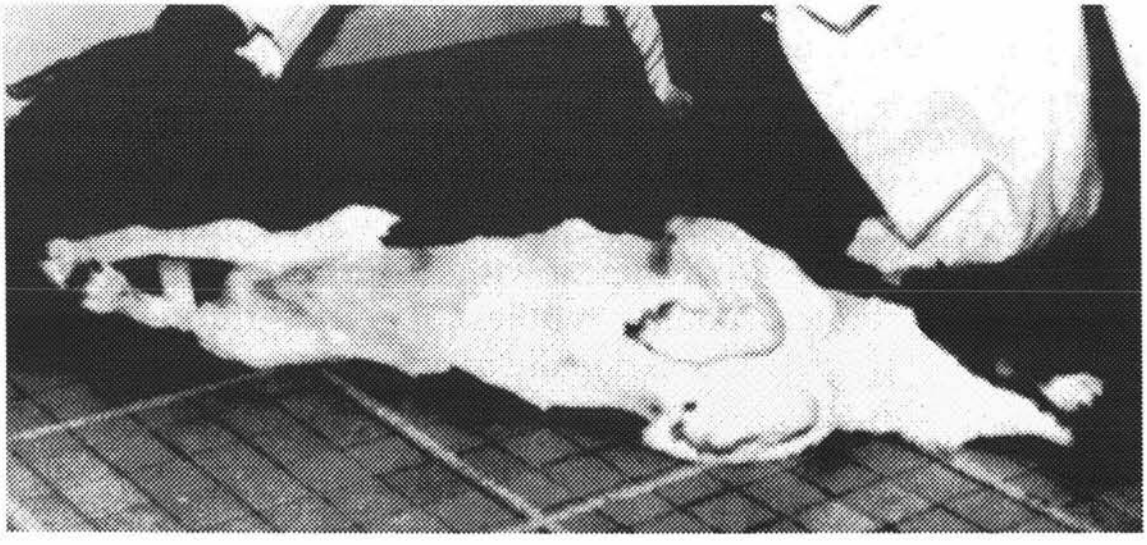


Figure 3.17 The position of a beagle in TI (Fox 1968).

With the 3s immobility by the Rottweiler cross after termination of stroking and dorsal restraint, it was unclear whether the dog was waiting for further stroking or exhibiting TI. It was possible that the dog required 3 - 5s to realise that it was free from restraint and to right itself. Thus, to allow for a greater margin for error, this time was doubled and the time required as a duration criterion to define TI was for a dog to remain immobile for 10s or longer, with the duration of immobility timed from release of restraint until the dog lifts its head off the blanket.

Ratner's (1967) criterion for TI was for the immobility to be induced by restraint resulting in immobility of "at least a minimal duration" with a species typical posture and reduced responsiveness during the immobility. The extent of the immobility, duration and degree of unresponsiveness however was unspecified as is the case for most TI studies. Reese et al (1982) reported that their criterion for TI was not irrevocably established but was based on lack of movement of body parts. Even this can lead to confusion as invariably during most reported cases of TI (including those reported by Reese et al 1982) there are slight head, eye, ear and limb movements during the "immobility" episode.

The criterion adopted to define TI in these studies was for the dog to remain in the position restrained, without lifting its head off the test surface, for a minimum of 10s after release from restraint. Eye, ear and slight movements of the head and limbs were permissible as long as the dog's head remained on the surface, as any attempts at righting were initiated by the dog lifting its head off the test surface. As discussed in section 2.6.3 animals are not unresponsive during TI but are continually monitoring their environment as suggested by their eye and ear movements and so, only appear unresponsive due to the absence of their righting response.

It was noted during this preliminary study that sudden movements by the investigator usually resulted in immediate righting by the dogs. The dogs that remained immobile therefore seemed relatively unresponsive to surrounding visual, auditory, olfactory and tactile stimuli such as releasing restraint and withdrawal of hands but not to more intense stimulation such as the investigator moving away. It was therefore decided to remain beside the dog at the end of the induction period, as attempts to move away may have terminated any TI responses. Remaining close to the dog may also have acted to enhance TI by maintaining a close proximity between the dog (prey) and the investigator (predator).

Considering the low level of susceptibility to TI in dogs as indicated from these preliminary studies and as suggested by others (eg. Chertok 1964), it was considered advantageous to attempt to potentiate TI. More intense stimulation was therefore incorporated into the induction procedures in this study with 30s restraint in either dorsal

or lateral recumbency and additional stimulation such as bitter spray, repetitive stimulation (stroking) and pressure on body parts (skin clips and scruffing) were also used as such stimuli have been reported to increase TI susceptibility (Ratner 1967). Blocking of external stimuli as occurs during hooding with the use of a blindfold, blanket or box over a subject's head has also been reported to increase TI susceptibility (Holmes 1989; Chertok 1964) and so was included in these preliminary tests.

Holmes (1989) reported that wrapping a pressure cuff over a sheep's ears and placing a box over its head was the most effective method for inducing TI in sheep. Although no success resulted with the box due to intense struggling by the dogs, the two TI episodes as defined by the criterion adopted for TI occurred in response to wrapping a pressure cuff around the dog's head. Although this treatment was only effective in 2 of the 16 attempts at inducing TI with the cuff, it was observed that on 4 occasions after having the cuff wrapped around their heads prior to induction, the dogs stood still with their heads hanging low. It was also noted that the pressure cuff was too large for some dogs and so, a smaller one was obtained for further studies.

The most important finding in this preliminary study however, was the insusceptibility of dogs to TI by inversion and restraint alone. Proceeding with the initial proposal to determine the baseline susceptibility to inversion and restraint alone would therefore be unlikely to be productive. Therefore it was decided to combine Parts 1 and 2 of the initial proposal and to test each dog twice, once with inversion and restraint alone and once with an additional treatment added in an attempt to potentiate TI and to reveal effective induction methods. Each dog was to act as its own control with respect to the technique effect.

To control for the effect of repeated testing, the order of testing (control first or first) were alternated. The next study therefore adopted this protocol and followed a more standardised procedure with fewer induction techniques. An assistant was also present to allow for easier inductions when a blanket or box was to be placed over the dog's head.

3.5 PRELIMINARY STUDY III

3.5.1 AIM

The aim of this study was to further assess the effect of various induction procedures on dogs and to familiarise the investigator and an assistant with the procedures involved in testing each dog in a caravan. This was to allow evaluation and identification of any problems associated with the testing procedure, apparatus, record sheets or testing environment so that modifications could be made prior to the major experiments.

3.5.2 SUBJECTS

8 dogs from the SPCA in Palmerston North and 1 dog from a local veterinary clinic were used in this study. They aged between 2 months and 3 years old and included 4 females and 5 males. With the exception of one dog (a Weimaraner), they were all cross breeds ranging from a terrier cross (weighing 5 kg) to a Rottweiler cross (weighing 24 kg).

3.5.3 TESTING ENVIRONMENT

Testing was conducted on a 10 cm thick foam mattress (140 x 80 cm) located on a 30 cm high platform (Figure 3.18) at the rear of a modified 4m caravan (Figure 3.19) that was towed to the testing sites. This allowed standardisation of the testing environment at different locations as well as ensuring that each dog was tested in a novel environment isolated from their owners and conspecifics.

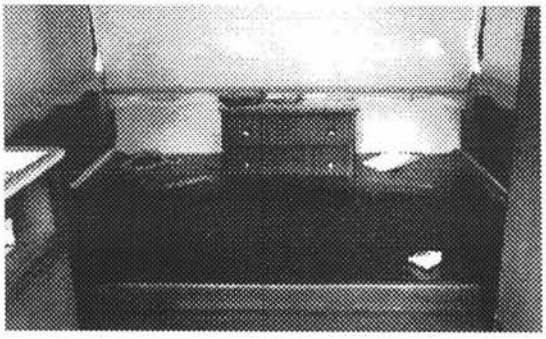


Figure 3.18 Foam mattress a on platform at rear of caravan.

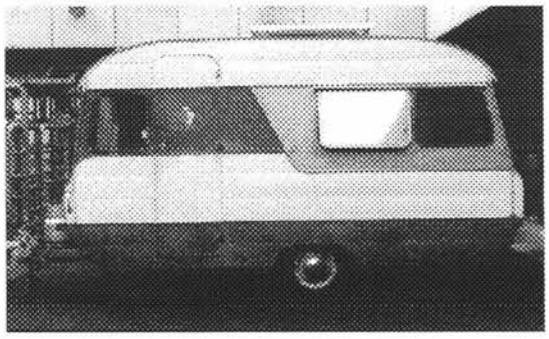


Figure 3.19 Caravan used for testing dogs.

3.5.4 MATERIALS

The apparatus used in this study were an adjustable dog leash, electronic clock timer, stopwatch, woollen blanket, No. 3 bulldog clips, plywood box, a green (850 x 160 mm) pressure cuff, a smaller grey (480 x 140 mm) pressure cuff (Figures 3.16, pp 87-88) and two record sheets (Appendix 2).

3.5.5 PROCEDURES

Each dog's signalment was obtained from its owner or SPCA attendant and recorded on the first record sheet for each dog. Each dog was met in its run (SPCA) or inside the veterinary clinic before being led to the caravan which was parked along the roadside just outside the SPCA or veterinary clinic. The dog was encouraged to enter the caravan, allowed several seconds to investigate the interior and then led up onto the platform and foam mattress located at the back of the caravan. During this period, the assistant recorded the time of testing and environmental conditions while the investigator assessed the dog's temperament (friendly, timid or aggressive) and whether it was quiet or excited before testing.

Each dog was tested twice. Once with just 30s restraint in either the dorsal or lateral position (control) and once with an additional treatment (technique) during the 30s restraint. Each dog therefore acted as its own control for the technique effect. The additional treatment were either stroking the dog's abdomen, blanket or box over the head, cuff around the ears, scruffing or skin clips applied to the neck.

The control induction procedure as illustrated in Figures 3.8 - 3.12 (pp 82-83) was similar to the previous study. The investigator knelt on the foam mattress beside the dog and started the electronic clock timer just prior to flipping the dog onto its side (Figure 3.10) or back (Figure 3.12) by swinging its legs away as described in the previous study (section 3.4.5). Restraint was maintained for 30s as before and direct eye contact was avoided. At the end of the 30s restraint period, restraint was gently released and the investigator folded their arms across their lap and remained kneeling beside the dog. At the same time, the assistant started the stopwatch and the duration of immobility was timed from the release of restraint until the dog lifted its head off the foam mattress. During testing, the assistant remained at the other end of the caravan at least 1.5m away from the dog.

The only exception was when the assistant helped to wrap the blood pressure cuff around the dog's ears or placed the blanket or box over the dog's head while the investigator restrained the dog. As for the previous study, stroking, scruffing and placing the blanket or box over the dog's head occurred immediately after positioning the dog in dorsal or lateral recumbency, whereas the blood pressure cuff and skin clips were applied prior to inverting the dog due to difficulties attaching the clips and wrapping the cuff around the dog's ears after it had been placed onto its back or side. Stroking and scruffing was only maintained during the 30s restraint period whereas the blanket, box, cuff and skin clips remained on the dog until it lifted its head off the mattress and timing was terminated.

The ease of induction (whether easy or with struggling), the duration of any immobility (as timed from release of restraint till the dog lifted its head off the mattress), the behaviour

of the dog during immobility and the state of the dog after testing (dazed or normal and friendly, timid or aggressive) were recorded.

3.5.6 RESULTS

No problems were encountered with testing the dogs on the platform in the caravan. Inductions were considerably easier with help from the assistant but there were problems associated with use of the box. Three induction attempts (dorsal recumbency with box, lateral recumbency with box and lateral recumbency with blanket) were aborted due to intense struggling by the dogs.

None of the 9 dogs, regardless of whether they were just restrained in dorsal or lateral recumbency for 30s or had additional treatment applied, showed any immobility that was greater than 1s duration. Eleven induction attempts resulted in immediate righting (0s duration immobility) and on 4 occasions (lateral restraint control, lateral restraint with blanket, lateral restraint with scruffing and dorsal restraint with stroking) the dog remained immobile for 1s.

3.5.7 DISCUSSION

Considering the reports of low TI susceptibility in dogs (eg. Chertok 1964; Svorad 1957) it was not surprising to find that none of the dogs in this study exhibited any immobility approaching the set criterion for TI of 10s. This duration criterion for TI was however not changed as only 9 dogs were tested in this study and the previous study had indicated that a dog may require 3 - 5s to realise that it was no longer restrained and to right itself. Although a criterion of 5s is commonly used (eg. Gilman et al 1950; Lefebvre and Sabourin 1977b) it was decided to maintain the criterion for TI at 10s as even including the previous study, no induction episode resulted in a possibly ambiguous duration of between 5 - 10s. The criterion for TI to be used in the following experiments therefore remained as requiring a dog to remain in the position in which it was restrained, without lifting its head off the test surface, for a minimum of 10s after release of restraint.

The low susceptibility seen in this study emphasised the need to combine the first two steps of the initial proposal as discussed in the previous study (section 3.4.7). The first main experiment, therefore involved a survey of the dog population's susceptibility to just inversion and restraint as well as other additional treatments during the restraint period. Each dog was tested twice and acted as its own control for the technique effect. Part 3 of the initial proposal to determine the depth, characteristics and physiological changes during TI was dependant on finding dogs which exhibited TI for a long enough period and deeply enough to allow certain observations and measurements to be made.

It was therefore important to identify the variables affecting susceptibility to TI in the initial survey so that enhanced TI durations and depths could be obtained for assessing characteristics and physiological changes during TI in the next part of this study. As discussed in section 2.7, major variables affecting TI are subject variables such as age, sex and breed.

In addition to the animal variables discussed in section 2.7.1, other subject variables that could possibly affect a dog's susceptibility to TI include it's weight, temperament (generally and just prior to testing), hormonal state (entire male or neuter; entire female or neuter and if entire, stage of oestrous cycle), health status, effect of any medication, previous experience in form of owner dominance, previous training, any history of fearful events or of trauma.

Initially, the subjects were to be dogs visiting or staying at veterinary clinics, in their home environments, at the SPCA, at the Animal Health Services Centre in Jennersmead, or those gathered for dog shows or obedience training. Since the goal was to determine the general dog population's susceptibility to TI, it was decided not to limit the study to a particular breed or age group of dogs.

Although this introduced many subject variables (as discussed in section 2.7.1), it was felt appropriate to survey the general dog population as the intention is to use TI on subjects of varying sex, breed, size and age. As so little was known regarding the animal variables affecting TI in dogs, it was hoped that surveying the dog population in general would provide an opportunity to identify some of the variables that affect a dog's susceptibility.

The importance of recording a complete signalment and history from each subject can therefore be seen. This caused difficulty in the preliminary studies as most of the subjects were cross breeds of uncertain breed, age and sometimes also sex status (entire or neutered). Very little information was available regarding the dog's normal temperament and history in terms of amount and type of human contact or any previous training; all of which could have had considerable effects on the dog's susceptibility to TI.

It was therefore decided not to include in further tests any dogs from which a complete signalment and history could not be obtained. This therefore ruled out using dogs from the SPCA or pounds. The requirement for testing as many dogs as possible per day also meant that locations where large numbers of dogs were gathered were needed.

Experience from this study indicated that setting up at a veterinary clinic did not allow testing of large number of dogs over a short period as it involved waiting for clients to arrive and to conclude their consultations with the veterinarian before testing. Some dogs

were also too ill to be tested and many owners only had limited time available at the veterinary clinic.

Discussions with dog breeders indicated that this would also be the case at dog shows and possibly at obedience classes. At shows, most breeders would be too preoccupied with preparing and showing their dogs to be interrupted by TI testing. The best option for testing large numbers of dogs per day was judged to be to visit owners / breeders with large numbers of dogs in their home environment, so that they were able to continue with their normal routines while their dogs were tested.

In addition to animal variables, other variables affecting a subject's susceptibility to TI are the experimental conditions including the testing environment. To keep the environmental variables as constant as possible all TI testing was conducted in a standard environment with similar fixtures and testing surface.

However, since testing would involve travel to different owners / breeders' homes to test their dogs it would have been impractical to attempt to set up identical testing conditions at each location. A caravan was therefore towed to each location for testing to reduce environmental variability by providing a constant testing area, fixtures and testing surfaces. Familiar stimuli such as the presence of the owner and other dogs were excluded during testing thus ensuring that the immediate testing environment was novel to each dog.

Environmental variables such as noise level, temperature and lighting were more difficult to keep constant as the caravan was not sound-proof and there was no power available. Barking dogs could occasionally be heard in the background during this study and the lighting intensity inside the caravan depended on the weather and time of testing. These variables, along with other variables such as time of day and fear or arousal levels were carefully evaluated and recorded.

This study also allowed assessment of the feasibility of towing the caravan to different sites, the internal layout of the caravan, space requirements for handling and testing the dogs and the dogs' reactions to the caravan. No major problems were encountered during this study.

Variables discussed in section 2.7.2 such as pre-testing conditions, experimenter, the temporal distribution of trials and fearful or arousing stimuli were controlled for by using the same investigators and using a consistent testing procedure. As the experimental procedures in this study proceeded smoothly, it was decided to continue to manually invert the dogs by swinging their legs away without additional apparatus. However, as

it was difficult to keep a dog in dorsal recumbency due to its tendency to fall over onto its side and because dorsal restraint appeared to cause more intense struggling than lateral restraint in the previous two studies, only lateral restraint was used in the following studies since the position of restraint had no measurable affect on a dog's susceptibility to TI in the preliminary studies.

Also, since a box over the head caused violent struggling and resulted in some tests being aborted, this technique was discontinued as a blanket over the dog's head caused less struggling and appeared to have the same effect of blocking visual and some auditory and olfactory stimulation. Similarly, to limit the number of treatment variables, the use of skin clips was discontinued as scruffing appeared to have the same effect. Another treatment in the form of a light shining into the dog's eyes was however included in an attempt to cover the range of induction techniques reported in TI literature.

In addition to the control treatment of inverting and restraining the dog in the lateral position, the 5 additional treatments to be used in the next study were stroking, blanket over the head, cuffing around the ears, scruffing and shining a light into the dog's eyes. The intended procedure was as for this study, with a 30s restraint period and help from the assistant as necessary. In addition to assisting with placing the blanket and box over the dog's head, during this study the assistant also helped wrap the cuff around the dog's ears prior to inversion and helped record observations such as the dog's state before testing and timing the duration of immobility. This allowed for a more accurate timing as the stopwatch could be started at the moment restraint was released, without risk of disturbing the recumbent dog.

This study also indicated that there would be some dogs that could not be tested due to intense struggling or other factors resulting in testing being aborted. Before proceeding to the first study surveying the dog population's susceptibility to TI, the record sheets were modified according to the new testing procedure.

Chapter four

Survey

Survey

4.1 AIM

The aim of this survey was to determine the susceptibility of dogs to TI in response to inversion and restraint alone and to other techniques incorporating additional treatments during restraint. From this survey the most suitable methods of induction and variables affecting a dogs susceptibility to TI were identified. Gross characteristics during TI were also observed.

4.2 SUBJECTS

Figure 4.1 Manawatu region, North Island, New Zealand.

Dog breeders in the Manawatu region (Figure 4.1) were contacted by telephone to discuss the project and if they consented, a time was arranged for testing their dogs. One hundred and fourty seven dogs from twenty breeders were tested. There were 25 breeds ranging from toy breeds such as the Chihuahua to large Bull Mastiffs and 4 dogs were of mixed breeding. Dogs of various ages (ranging from 2 months old to 14 year old), sexual status and temperaments were tested. Most were show dogs and/or breeding stock. Ten were however just kept as pets.

As expected from the preliminary studies, several dogs struggled vigorously (Figure 4.2) or vocalised loudly during the restraint period. Testing was aborted for these individuals (9 dogs) and also for 6 dogs that attempted to bite the investigator (Figure 4.3) or were assessed to be aggressive as indicated by growling, lifting of the upper lip or snarling. Testing was not completed on these 15 dogs and observations on them were not included for analysis.

Figure 4.2 Dog struggling vigorously against restraint.

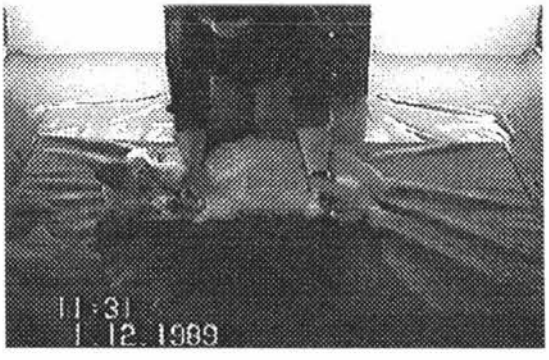


Figure 4.3 Dog attempting to bite the investigator's hand.

4.3 TESTING ENVIRONMENT

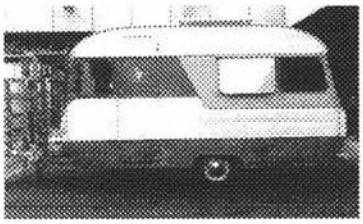


Figure 4.4 Caravan used for testing.

The dogs were tested in a 4 metre caravan (Figure 4.4) which was towed to the breeders homes and parked along the roadside, in the driveway or in a paddock near the kennels. The internal layout of the caravan is shown in Appendix 4. Besides the normal fixtures inside a caravan such as a stove, sink and cupboards, the caravan was modified by removing the two beds at the rear and replacing this area with a 30 cm high platform that spanned its width (Figure 4.5). The bed at the front of the caravan was also removed so that a video camera could be set up and a seat was placed approximately one metre from the platform so that the assistant could be seated (Figure 4.6).

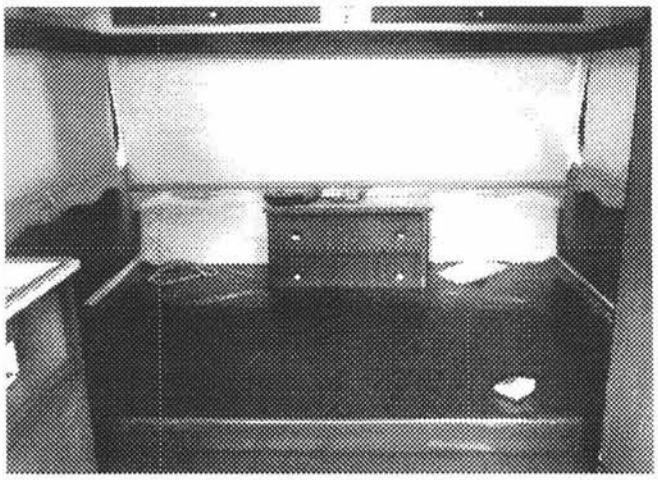


Figure 4.5 Rear of caravan modified to accommodate testing platform.

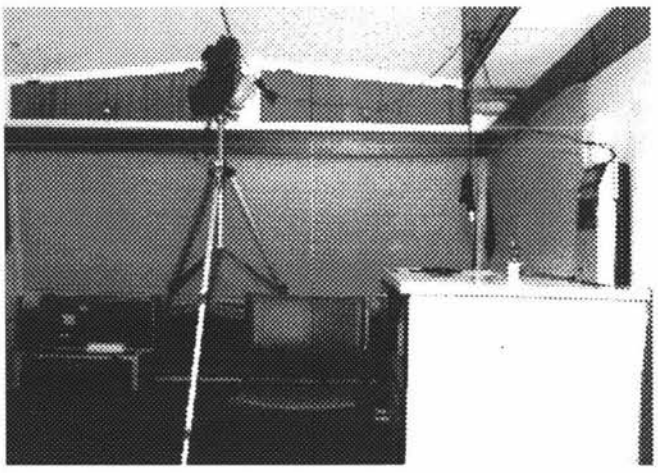
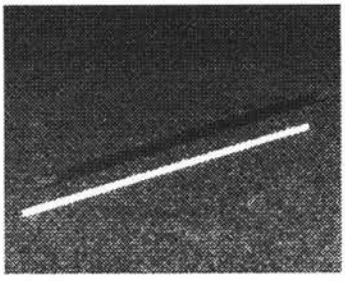
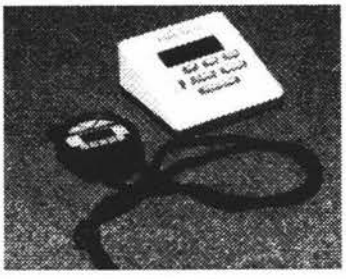


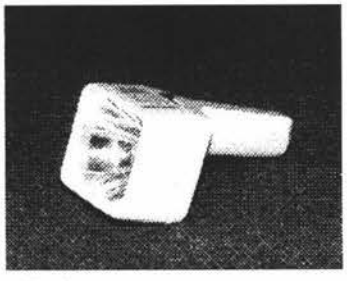
Figure 4.6 Video camera set up at front of caravan.



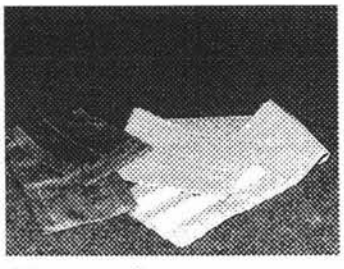
a. Thermometer



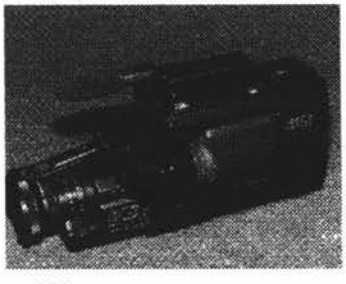
b. Stopwatch and clock timer



c. Torch



d. Pressure cuffs



e. Video camera.

Figure 4.7 Equipment used in this study.

The use of this caravan ensured standardisation of the testing environment at different sites, in terms of fixtures and testing arena. Although not sound-proof, the caravan acted to isolate the dog from its owners and other conspecifics and provided a novel environment for testing each dog. Lighting inside the caravan varied depending on weather conditions and the time of day since the only illumination was filtered light coming through the caravans blinds which were pulled down. Temperature inside the caravan ranged from 16 - 29 °C during testing.

Testing was conducted on a 10 cm thick (140 x 80 cm) foam mattress on the raised wooden platform at the rear of the caravan. The platform measured 220 x 185 cm and was 30 cm off the caravan floor. Both the platform and foam mattress were covered with a washable smooth but non-slip dark emerald green tarpaulin. There was a 30 cm high cabinet (75 x 45 cm) at the back of the platform which served as a table and storage space for some of the equipment used. (Figure 4.5)

4.4 MATERIALS

A 10 - 50 °C thermometer (Figure 4.7a) was kept in the top drawer to measure the environmental temperature inside the caravan. The duration of TI was recorded by the assistant using a battery operated electronic stopwatch that measured to one hundredths of a second. The period of restraint was timed using a battery operated electronic clock timer on count up mode (Figure 4.7b). This clock timer was positioned facing the experimenter either on the foam mattress or on the platform (Figure 4.5).

Other pieces of equipment used in this study were kept in the cabinet when not in use, including an adjustable dog leash, a rechargeable torch *(Black & Decker, France)* (Figure 4.7c), a pure wool grey blanket and 2 cotton pressure cuffs with velcro strips (Figure 4.7d). The smaller grey cuff measured 48 x 14 cm and the larger green cuff 85 x 16 cm.

The blanket was folded twice so that it became light proof but was still large enough (105 x 92 cm) to cover any dogs head.

Two record sheets were used for each dog. One for recording the dogs details/signalment (eg. owners name and address, dogs name, breed, sexual status, age, weight, temperament, history and health status) and the other to record environmental variables, time and locaton of testing, induction methods, state of the dog before and after testing, ease of induction, characteristics and duration of any immobility (Appendix 5). For more detailed analysis, a battery operated automatic focus remote control video camera (*Panasonic Series NV-MS1EA S-VHS*) (Figure 4.7e) was mounted on a tripod at the front of the caravan to record the proceedings (Figure 4.6).

4.5 PROCEDURES

Dog breeders in the Manawatu region were contacted by telephone to discuss the project and if they consented, a convenient time was arranged for testing their dogs. As natural light was required for illumination, all testing occurred between 9 am and 8 pm. On arrival at the breeders home, the caravan was parked along the roadside, in the driveway or in a paddock near the kennels and the project was discussed with the breeder. An information sheet explaining the project was also provided (Appendix 6).

The number of dogs tested at each location ranged from one to thirteen dogs. The breeders were not asked to present the dogs in any particular order but just to bring one dog at a time to the caravan to be tested. The investigator greeted each dog outside the caravan and spent a few minutes getting acquainted with it. Information regarding each subjects breed, sex, age, weight, temperament and history were obtained and recorded.

Each dog was then led inside the caravan, allowed time to investigate the interior of the caravan and was led up onto the platform and foam mattress to be tested. During this period, the assistant recorded the time of testing and environmental conditions while the dogs temperament was assessed as friendly, timid or aggressive and whether it was quiet or excited.

The dogs were each tested twice, once with inversion and 30s restraint in the lateral position (control technique - Figure 4.8) and once with additional treatment during the 30s restraint. Besides the control technique, there were 5 additional techniques. They were stroking the dogs abdomen (Figure 4.9), placing a blanket over its head (Figure 4.10), a cuff around its ears (Figure 4.11), shining a light into its eyes (Figure 4.12) or grasping its scruff (Figure 4.13) during the 30s restraint in lateral recumbency. In addition to the control

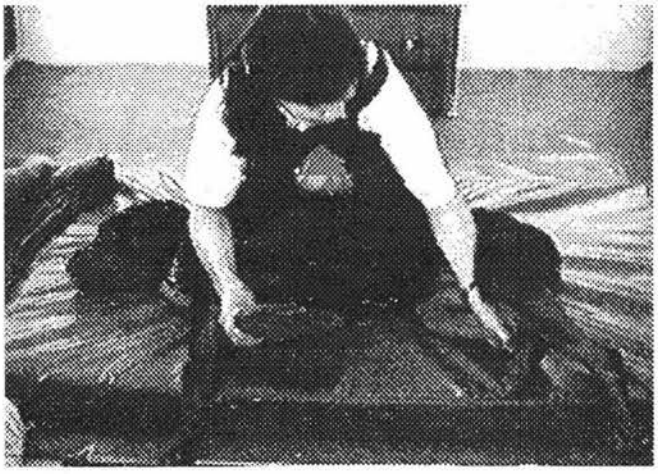


Figure 4.8 Control technique.

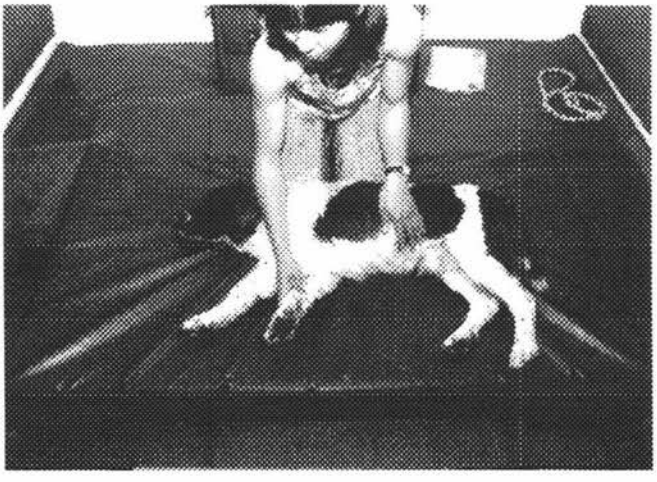


Figure 4.9 Stroke technique.

Figure 4.10 Blanket technique.

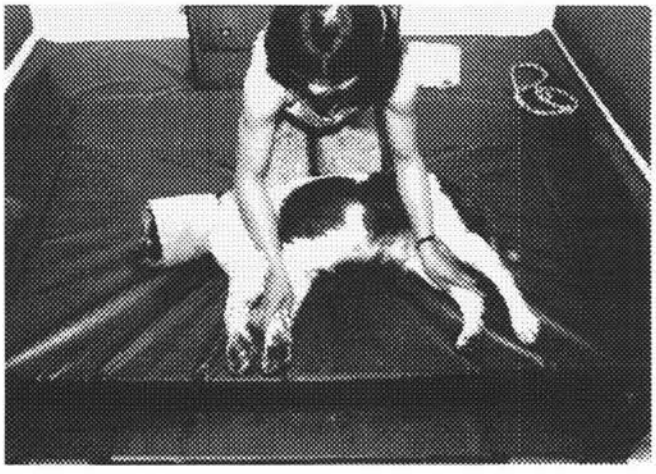


Figure 4.11 Cuff technique.

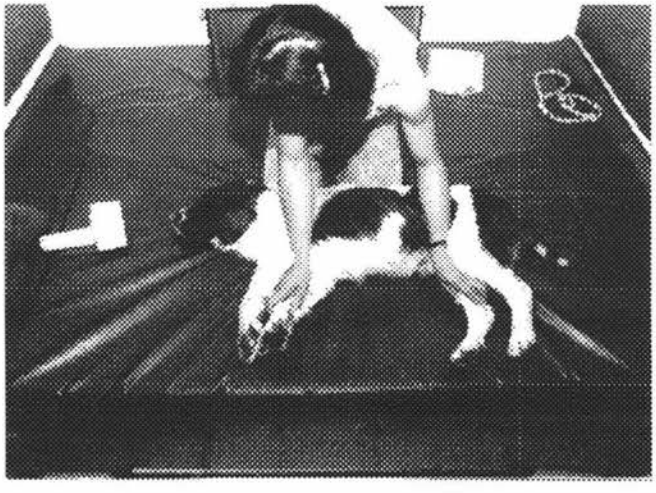


Figure 4.12 Light technique.

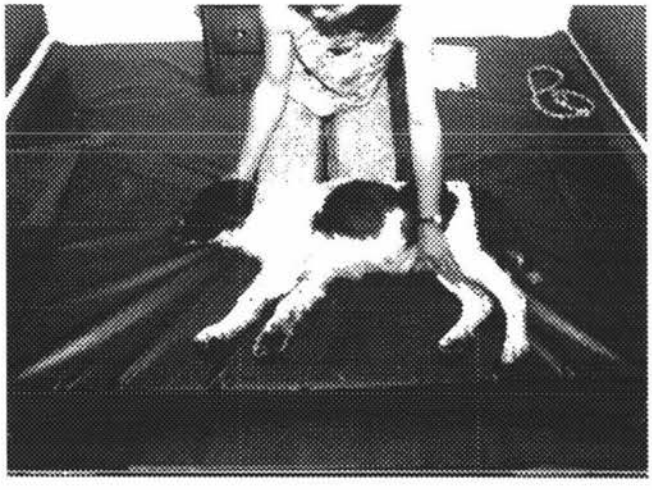


Figure 4.13 Scruff technique.

technique however, each dog was only tested with one of these additional techniques. By testing each dog twice, once with inversion and 30s restraint only and once with an additional treatment, each dog therefore acted as its own control for the additional treatment effect being tested.

Whether a dog was tested with the control technique first or with additional treatment first, was alternated between successive dogs. For example, the first dog tested was tested with the blanket technique first and then followed by the control technique. The next dog however, was tested with the control technique first followed by cuffing around its ears. There was a 20 to 80 sec interval between the termination of the first test (as indicated by the lifting of the dogs head from the mattress) and the beginning of the next test on the same dog.

As each dog was presented, the investigators worked through the 5 additional treatment techniques starting with the blanket treatment for the first dog, cuffing for the second dog, light for the third dog, scruffing for the fourth dog, stroking for the fifth dog and then returning to blanket for the sixthdog and so on; all the time alternating between control or technique first (Table 4.1).

Testing Sequence

DOG NUMBER	FIRST TECHNIQUE	SECOND TECHNIQUE
1	Blanket	Control
2	Control	Cuff
3	Light	Control
4	Control	Scruff
5	Stroke	Control
6	Control	Blanket
7	Cuff	Control
8	Control	Light
9	Scuff	Control
10	Control	Stroke
Testing sequence then repeats		

Table 4.1 Testing sequence.

If testing was aborted on a dog, the same test and order of testing was repeated on the following dog. Although there was a sequence to the order of techniques, it was not known which dog would be presented for the next technique as the breeders specified the most convenient day and time for the visits and they presented the dogs in an unspecified order.

For the control induction procedure, the dog was flipped onto its side and restrained for 30s. This involved kneeling close beside the standing dog and reaching over its chest and abdomen to grasp its closest fore and hind legs (Figure 4.14a). These limbs were then swung away in an outwards arc causing the dog to fall against the investigators lap (Figure 4.14b) and slide down her knees onto the foam mattress or to fall directly onto the mattress. The grip on the lower legs closest to the mattress was maintained to prevent the dog from getting up by pushing off the mattress (Figure 4.14c).

Further restraint was applied as necessary for 30 secs by resting forearms on the dogs neck and hip and direct eye contact was avoided. At the end of the 30s restraint period as indicated by the clock timer, restraint was gently released, arms removed from the dog and placed across the investigators lap (Figure 4.14d). The investigator remained kneeling beside the dog until it lifted its head off the mattress. The assistant remained at the other end of the caravan at least 1.5m away from the dog except when assisting to apply additional treatment.

For the 5 additional techniques (Figures 4.15 - 4.19), the same basic procedure was followed but additional treatment was provided during the 30s restraint period. With the stroking treatment, once the dog had been positioned onto its side by the above procedure, the grip on its hind limb was released and the free hand used to stroke the dogs abdomen (Figure 4.15) in a caudal to cranial direction at a rate of 3 strokes every 2s for the duration of the 30s restraint. The grip on the foreleg was maintained and restraint applied with forearms as required for the 30s period.

For the blanket induction (Figure 4.16), the blanket was placed over the dogs head by the assistant once the dog was positioned on its side. One corner of the blanket was tucked under the top foreleg of the dog (Figure 4.16d) to keep light out and to prevent the dog from dislodging the blanket. Once the blanket was positioned, the assistant returned to the other end of the caravan. The blanket remained on the dog until it lifted its head off the mattress. As for the control technique, restraint was applied as necessary by resting forearms on the dogs neck and hip.

With the cuffing treatment, the cuff was wrapped around the dogs head over its ears before flipping it onto its side (Figure 4.17a). Once on its side restraint continued as for

a

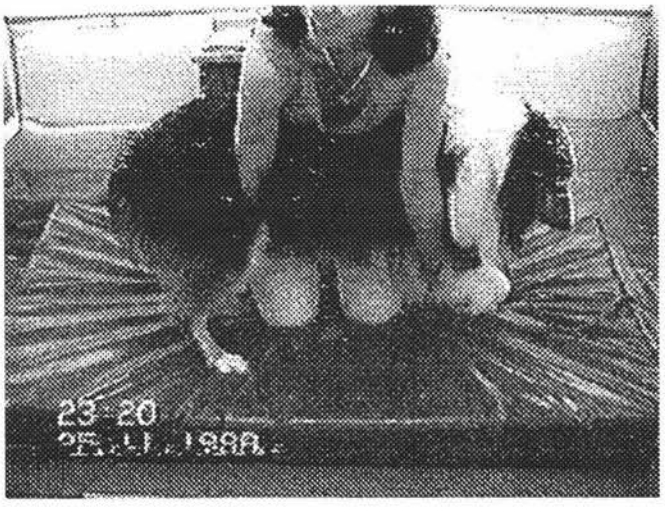
b

Figure 4.14 Control induction sequence ...

c

d

Figure 4.14 Control induction sequence.



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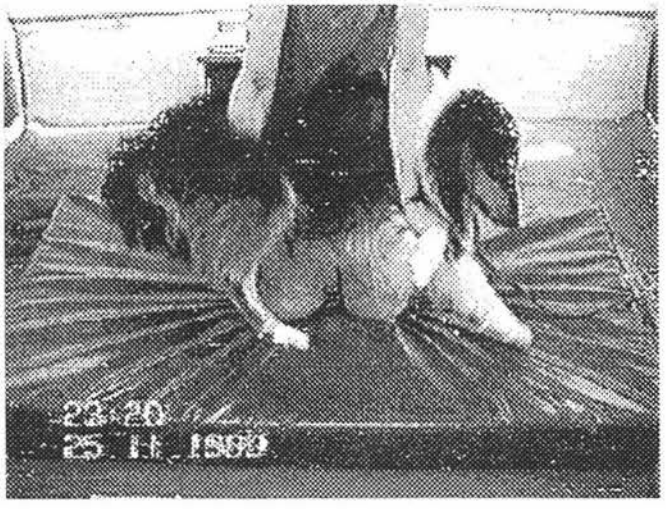

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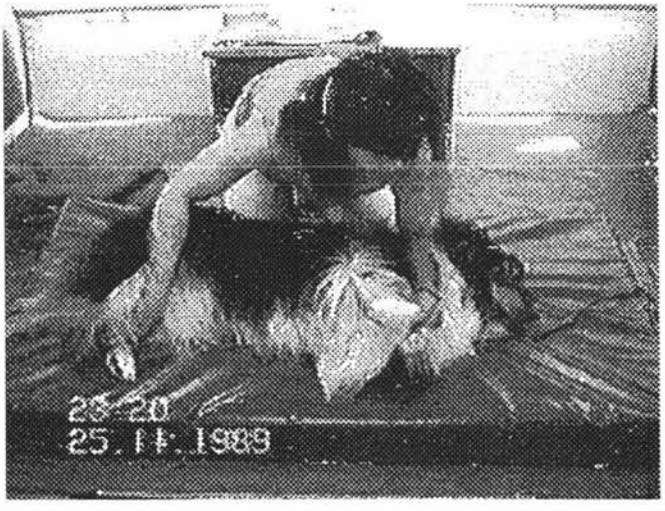
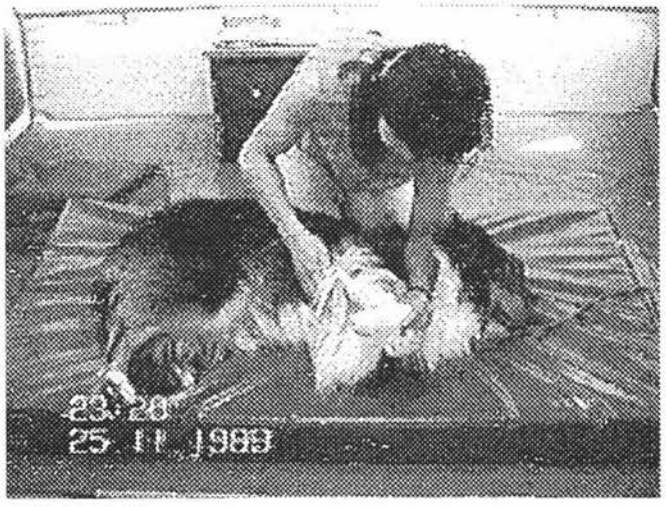


c

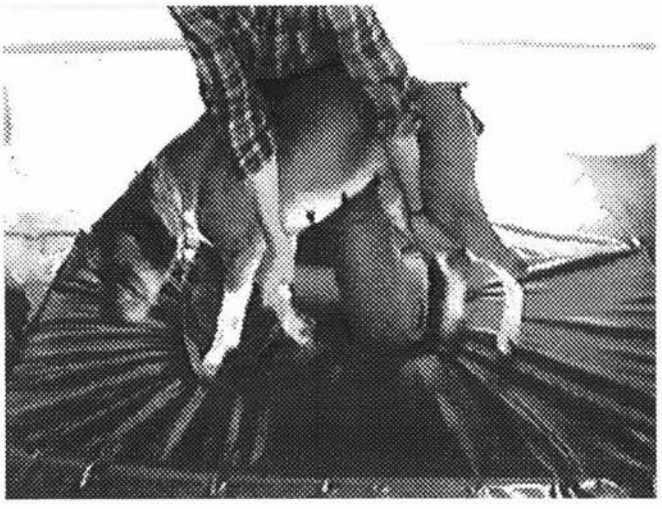
Figure 4.15 Stroke induction sequence ...



d

e

Figure 4.15 Stroke induction sequence.



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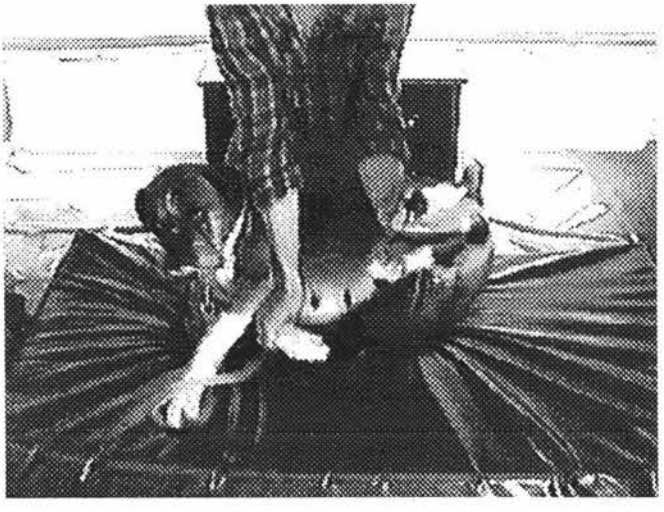

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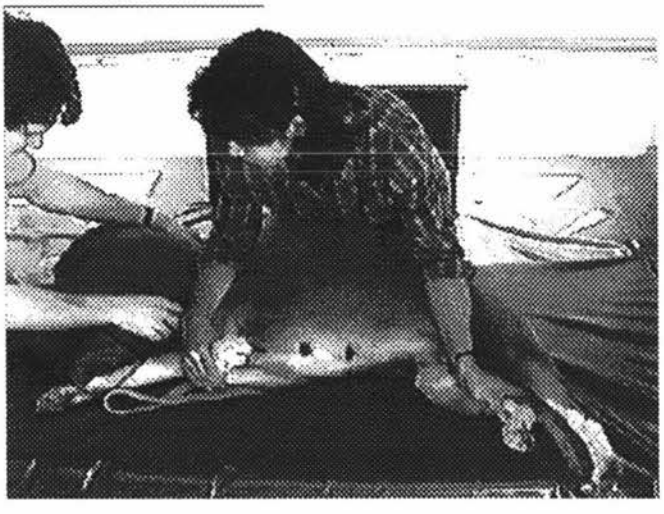
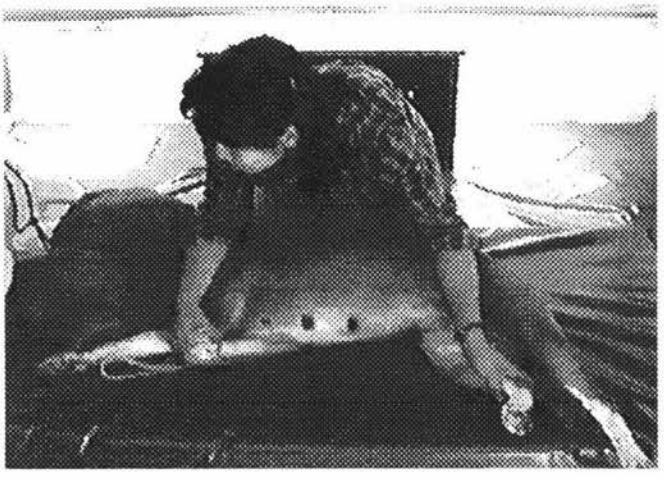


c

Figure 4.16 Blanket induction sequence ...



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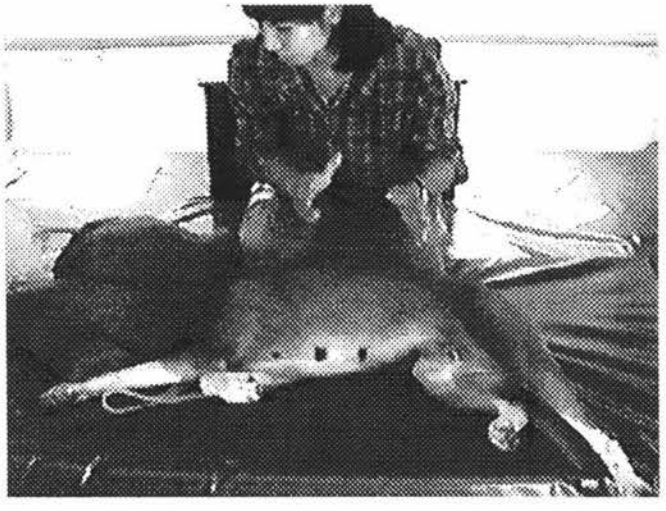

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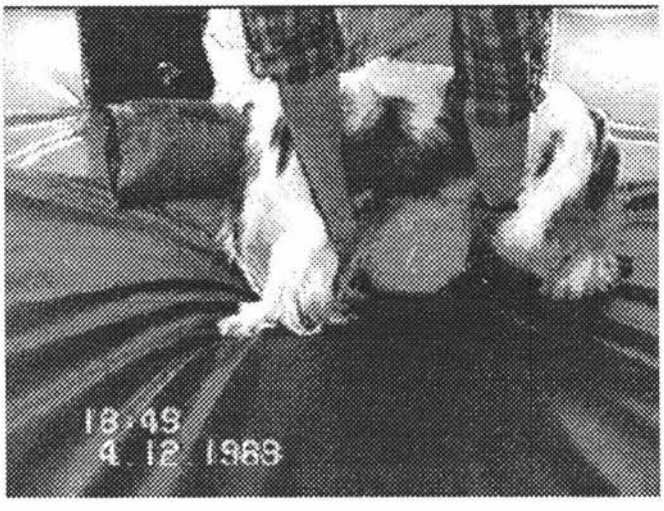
Figure 4.16 Blanket induction sequence.

a



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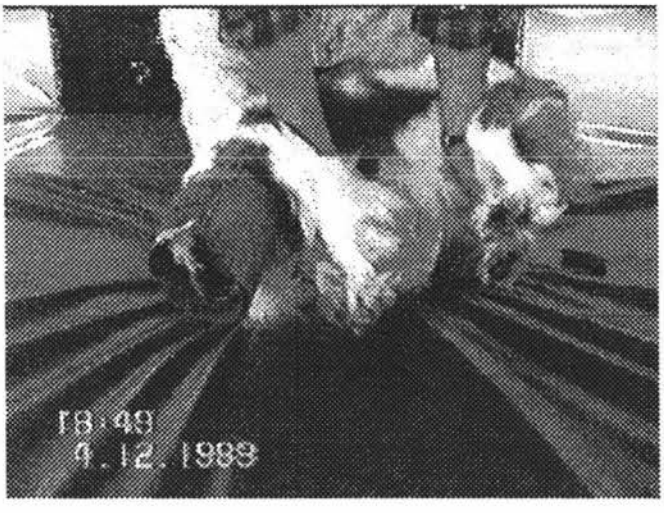
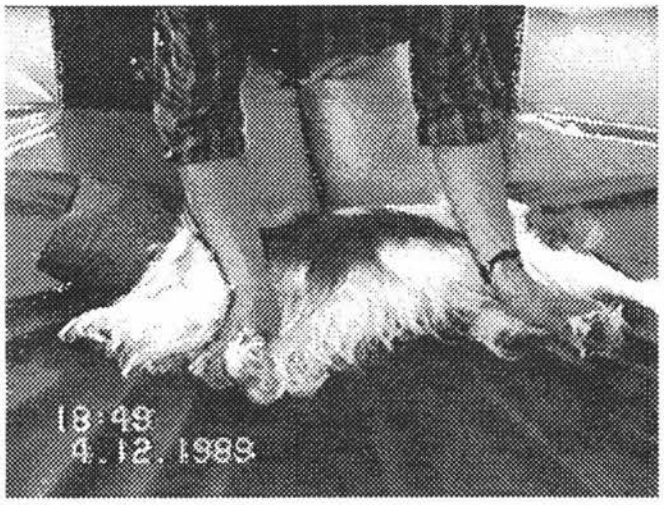


c

Figure 4.17 Cuff induction sequence ...



d

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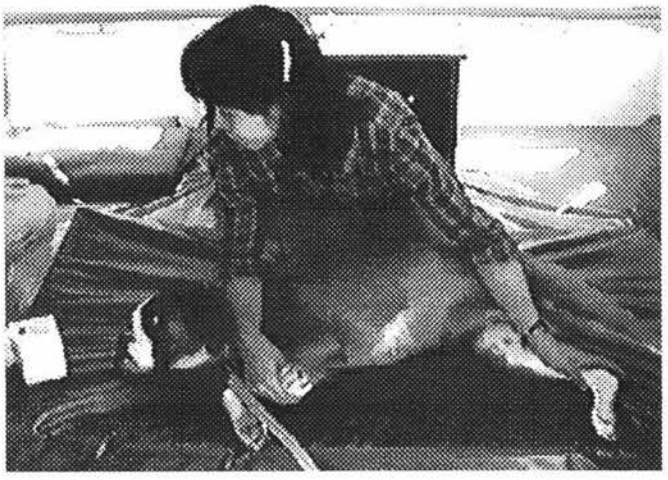
Figure 4.17 Cuff induction sequence.

a

b

Figure 4.18 Light induction sequence ...



c

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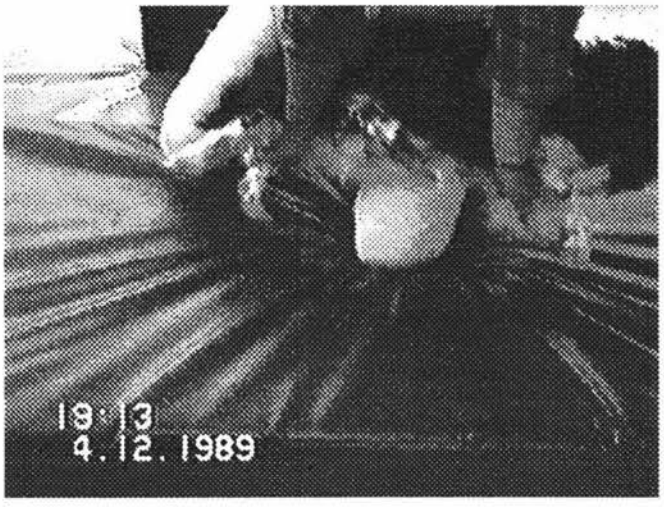
Figure 4.18 Light induction sequence.



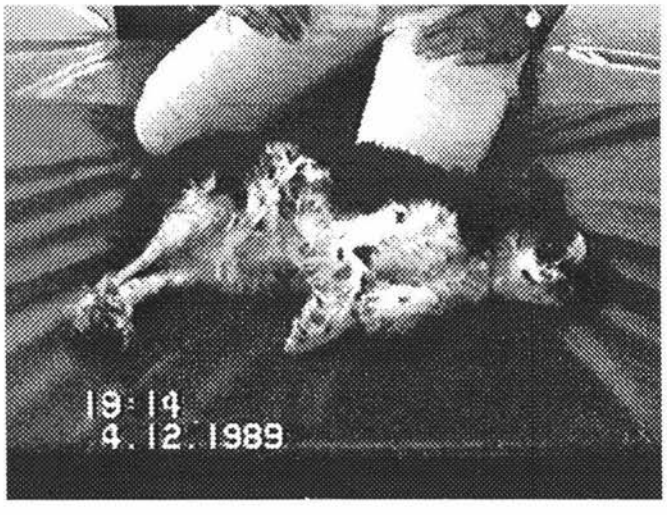
a

b

c

Figure 4.19 Scruff induction sequence ...

d



e

Figure 4.19 Scruff induction sequence.

the control technique (Figure 4.17d). The cuff was left on until the dog lifted its head off the mattress. The procedure for the light treatment (Figure 4.18) was also as for the control except that the assistant positioned the torch so that its light beam was directed into the dogs eyes once it was restrained onto its side. The torch was positioned on the mattress and kept 15 - 20 cm away from the dogs eyes (Figure 4.18c). The torch also remained on until the dog lifted its head off the mattress.

During the induction for the scruffing technique (Figure 4.19), the grip on the foreleg was released after the dog had been placed on its side. This hand was then used to firmly grasp the scruff of the dog (Figure 4.19d), maintaining enough downward pressure to restrain the dog from lifting its head off the mattress. At the end of the 30s restraint period this grip was also gently released and the arm folded across the investigators lap (Figure 4.19e).

Duration of immobility was timed by the assistant using a stopwatch from release of restraint until the dog lifted its head off the mattress. Due to time limitations and physical discomfort, if a dog was still immobile at 5 min, the investigator would begin to shift her weight or readjust her position and at 10 min, testing would be terminated by rubbing and stimulating the dog to arousal. At the termination of the test, whether spontaneously by the dog or due to external stimulation, the state of the dog after testing (dazed or normal and friendly, timid or aggressive) was recorded. The ease of induction (ie. whether it was easy to restrain the dog or it involved vigorous struggling by the dog), the behaviour of the dog during TI and any other relevant observations were recorded.

The criterion defining TI in this study was for the dog to remain in the position restrained, without lifting its head off the test surface, for a minimum of 10s after release of restraint. Each dog was also videotaped during the procedure. Video taping started at the beginning of the induction of the first test and was stopped at the termination of the second test.

The associations of TI with the large number of variables identified were examined. Associations between continuous variables (eg. age) were tested using Spearmans correlation and with categorical data (eg. breed or sex) using Chi square, Fishers exact, McNemars or logistic regression tests as required. Differences in mean durations of TI were tested using t-tests, ANOVA or Kruskal Wallis tests as appropriate.

It was originally intended to use a logistic regression model to identify predictors of TI simultaneously. The low proportion of dogs which showed TI however, (10 of the 132 dogs) limited what could be achieved statistically. This small number of susceptible dogs meant that the results had to interpreted cautiously. Any associations of other variables with TI also needed to be very strong before they could show statistical significance.

4.6 RESULTS

4.6.1 SUSCEPTIBILITY

Of the 132 dogs successfully tested, 10 dogs (7.6% with 95% confidence interval for the true percentage or 3.7 - 12.2% using the exact method) exhibited TI as defined by the criterion of remaining in the position restrained, without lifting its head off the mattress, for a minimum of 10s. 7 of these TI dogs exhibited TI in response to both the control induction technique of inversion and restraint in the lateral position as well as to the additional treatment technique. There were therefore 17 episodes of TI as illustrated in Figure 4.20.

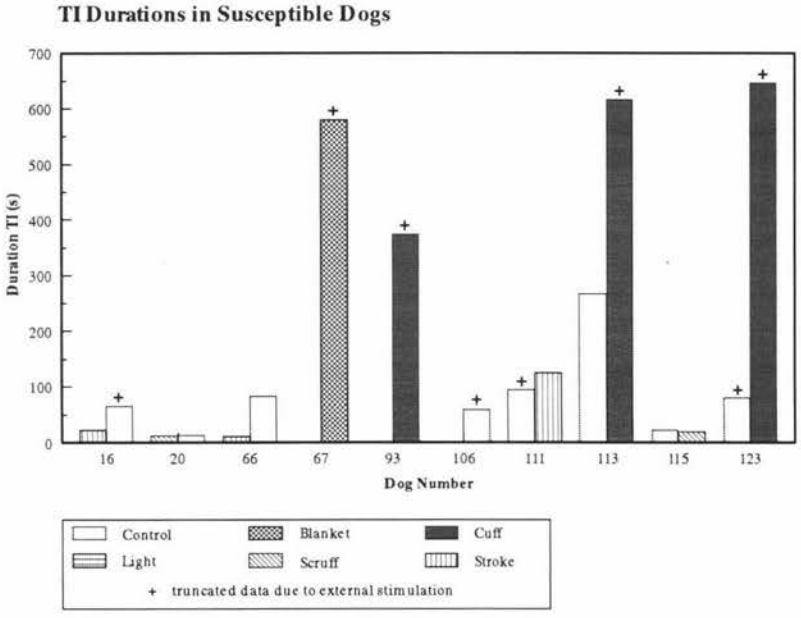


Figure 4.20 TI duration in susceptible dogs

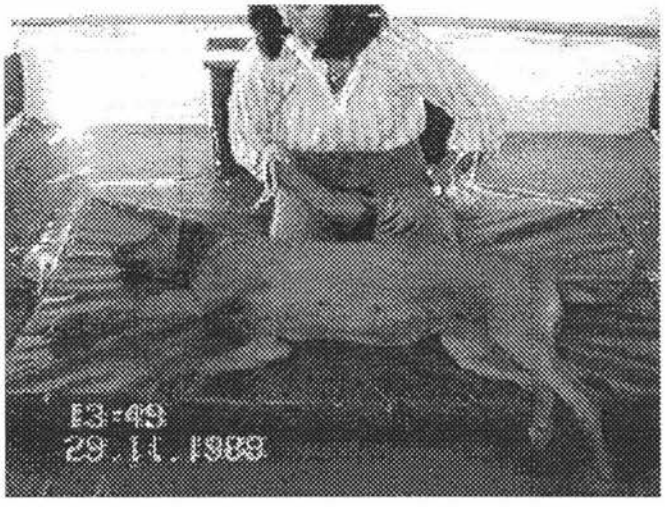
4.6.2 CHARACTERISTICS DURING TI

During the TI episodes, the dogs remained very still with the exception of occasional limb, head and tail movements in 10 of 17 TI episodes. This involved slight repositioning of the head or limbs, occasional muscle trembling or twitching especially in response to external stimulation (eg. loud noises) and paw paddling movements during four TI episodes. Figure 4.21 illustrates limb and eye movements during TI.

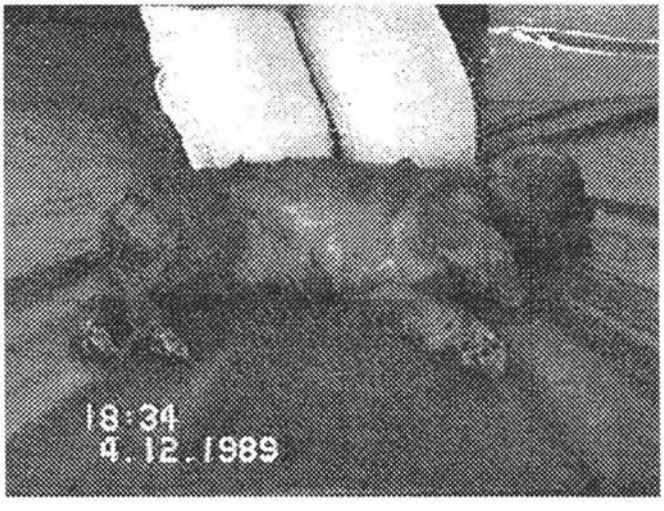
Whether the limbs were flexed or extended depended on the position of restraint and the position of the tail also reflected its position during restraint. Figure 4.22 illustrates TI positions in six dogs. The different induction techniques did not appear to affect the positions adopted during TI. Muscle tone was difficult to assess without touching the dog but was subjectively described to be tense or rigid during 3 TI episodes, relaxed in 4 episodes and could not be determined in the others.

a. Eye open, paw down.

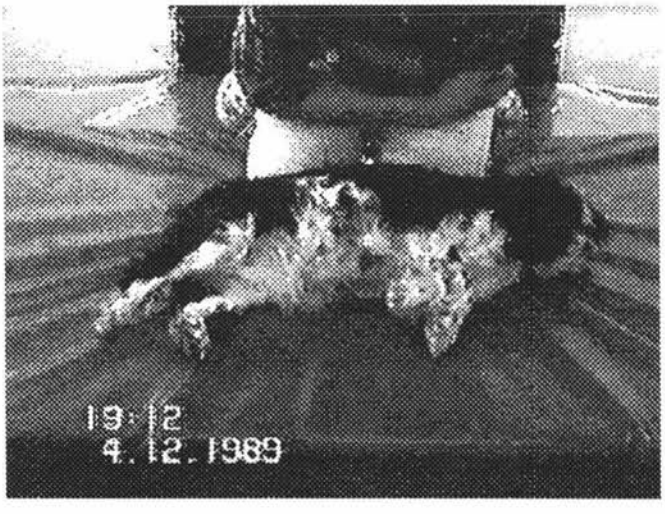
b. Eye closed, paw up.
Figure 4.21 Eye and paw movements.



TI from stroke technique (Dog 66).

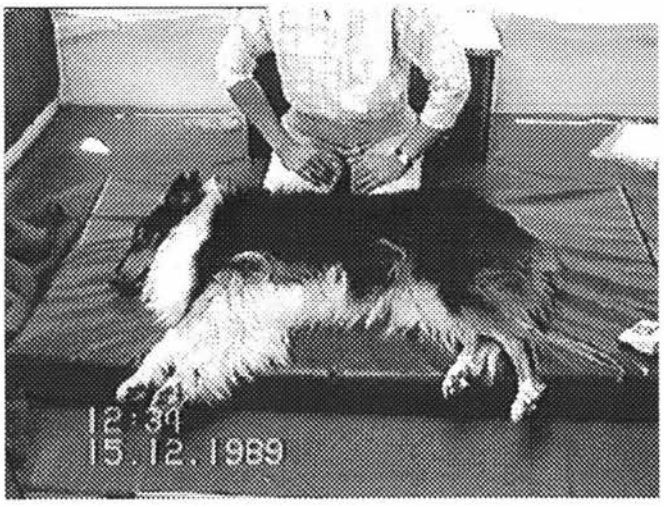


TI from stroke technique (Dog 111).



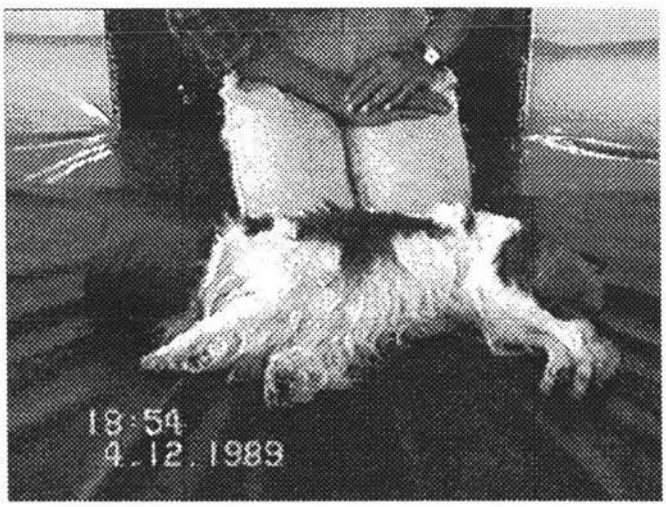
TI from control technique (Dog 115).

Figure 4.22 TI positions ...



TI from scruff technique (Dog 20).

TI from blanket technique (Dog 67).



TI from cuff technique (Dog 113).

Figure 4.22 TI positions.

The dogs face was not always visible during TI as it could have been obstructed from view due to the position of its head, hair over its face or if the dog had a cuff or blanket over its head. In over 80% (11 out of 13) of the TI episodes where the dogs eyes were visible, eye movements were observed (Figure 4.21). The dogs eyes were open throughout most of the TI episodes although blinking and periods of eye closure were observed. When the eyes were open the dogs appeared to be observing their environment. On one occasion, rapid eye movements (REM) were observed during eye closure. One dog was also observed to lick its lips several times during TI.

As can be seen from Figure 4.20, the duration of TI in successful inductions ranged from 11s to 646s (10min 46s) with a mean duration of 181.6s (3min 2s). As the caravan was parked either on the road side or near the dog kennels there was considerable auditory stimulation (eg. traffic noises, voices and barking) during testing. In addition to this, occasional coughing, whispering and weight shifting beside the dog especially after 5 min of immobility provided possible stimulation to the subjects. The dogs that were in TI therefore appeared relatively unresponsive to these stimuli (when it didnt result in termination of TI) even though they seemed to be monitoring their environment as indicated by their eye movements and slight twitching in response to loud noises. During the longer TI episodes (eg. > 4min) even intense stimulation such as noisy passing trucks, loud bangs, car horns and shouting children did not terminate TI.

When TI was terminated however, it was due to noticeable external stimulation on 8 occasions (indicated by + in Figure 4.20) and seemingly spontaneously on 9 occasions when no detectable external stimulation was observed. Two episodes of TI lasted the maximum allowed period of 10 min and were terminated by rubbing the dog. Following TI, the dogs all appeared normal. On 6 occasions, the dog appeared to be slow or reluctant to get up after termination of an episode of TI.

Figure 4.23 Dog righting as restraint is released.

All the non-TI episodes (duration < 10s) appeared to terminate spontaneously with durations ranging from 0 - 3s. In 225 inductions (85% of all inductions) the dogs righted themselves immediately after release from restraint (0s duration) (Figure 4.23). On 17 occasions the dogs righted themselves after 1s, after 2s on 4 occasions and after 3s on one occasion. The 3 TI dogs that only exhibited TI on one induction, righted themselves immediately after release from restraint during the non-TI episodes.

4.6.3 INDUCTION TECHNIQUE

As most of the dogs (122 of 132) neither exhibited TI to the control nor additional treatment technique and 7 of the 10 TI dogs exhibited TI to both the control and additional treatment technique (Figure 4.20), a highly significant association was found between whether a dog exhibits TI with control and whether it exhibits TI with the additional treatment techniques ($P < 0.001$ Fishers exact two-tailed test). That is, if a dog exhibits TI, it will with control and additional treatment techniques or else, a dog will not exhibit TI with either control or additional treatment techniques.

Using McNemars test, no significant difference was found between a dogs susceptibility to TI with either the control or additional treatment techniques ($P = 1.0$) as 8 dogs (6%) exhibited TI in response to the control induction technique and 9 dogs (7%) to the additional treatment techniques (Figure 4.20). As can be seen from Figure 4.20, 7 of the TI dogs exhibited TI to both the induction and additional treatment technique, 2 to only the additional treatment technique and 1 to the control induction technique only.

The distribution of TI durations for the TI dogs is also shown in Figure 4.20. Mean duration of TI with the additional treatment techniques was 3.5 times longer than the mean duration of TI with the control induction technique ($P = 0.07$ two-tailed t-test for paired samples). Comparison of the 6 induction methods (control and 5 additional treatment techniques) also showed that the control induction technique resulted in longer TI durations than some of the additional treatment techniques.

The induction techniques that were successful in inducing TI were stroking (3 / 26 - 11.5%), cuffing (3 / 26 - 11.5%), scruffing (2 / 27 - 7.4%), control (8 / 132 - 6.1%) and blanket over the dogs head (1 / 27 - 3.7%). The light treatment did not result in any TI in the 26 dogs tested. Figure 4.24 illustrates this variation in technique susceptibility and duration.

From Figure 4.24 it appears that the longest TI durations occurred with the cuffing induction technique but the method with the longest average TI duration per TI episode was the blanket over the head followed by cuffing, control, stroking and then scruffing. Although blanket and cuffing resulted in average TI durations that were almost 10 times the other techniques, these differences in TI duration and susceptibility with the different induction techniques could not be tested statistically due to the small number of dogs exhibiting TI.

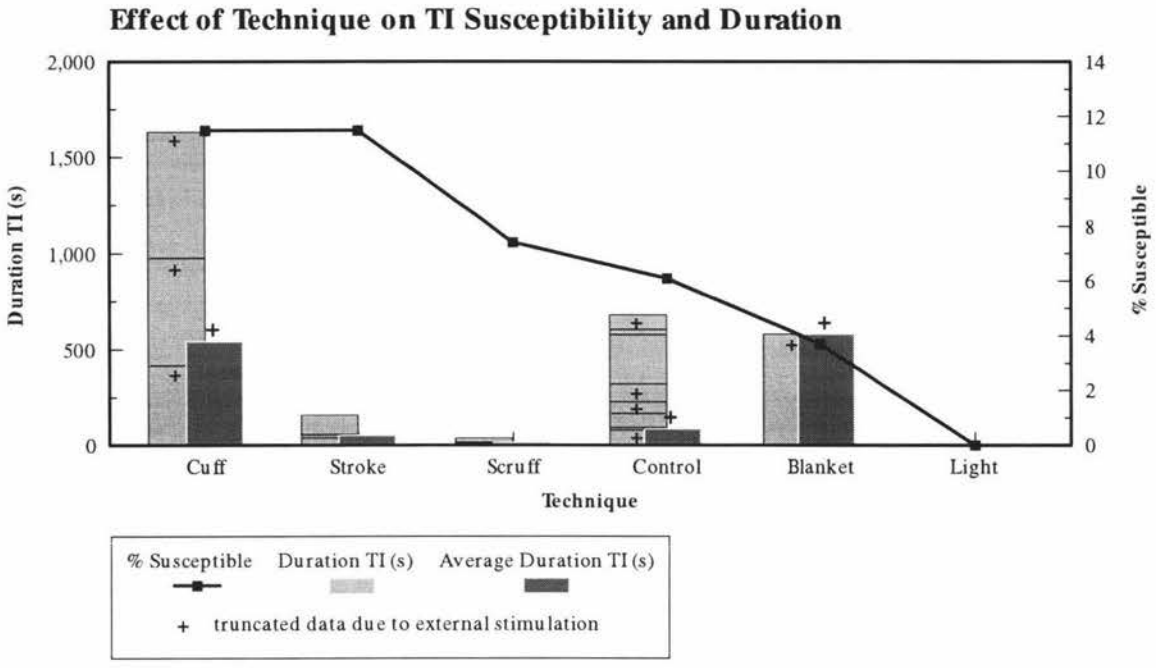


Figure 4.24 Effect of technique on TI susceptibility and duration.

4.6.4 ORDER OF TESTING

Similar problems were also encountered when examining the effect of order of testing on TI susceptibility (ie. whether dogs were more likely to exhibit TI on the first or second induction technique). Using McNemars test, there was no significant potentiation or habituation effect on TI susceptibility with repeated testing (P = 0.25)even though TI was induced from the first induction 7 times and from the second induction 10 times. This was however, severely limited due to the low number of dogs exhibiting TI and because only the 3 dogs which were discordant could be used for the test (Table 4.2).

Susceptiblity to TI in first and second test

	FIRST TEST	
SECOND TEST	TI	NO TI
TI	7	**3**
NO TI	**0**	122

Table 4.2 Susceptibility to TI in first and second test.

Whether the control technique was tested first, and then followed by the additional treatment or additional treatment first then control, also had no effect on the susceptibility to TI (P = 0.7 Fishers exact two-tailed test).

The duration of TI in the second tests were however significantly longer than the durations of TI in the first tests using a two-tailed t-test for paired samples (P = 0.03 for all dogs and P = 0.02 for TI dogs) indicating a potentiation effect with the duration of TI being 5 times longer in the second tests than the first tests.

Another effect examined was the possibility that the investigators ability to induce TI changed as the survey progressed, and thus may have affected the susceptibility and duration of TI in the dogs. From Figure 4.25 it appeared that more dogs in the later part of the survey exhibited TI and for longer durations than at the beginning of the survey (ie. increasing susceptibility and duration with record number). To examine the possibility that more dogs became susceptible and had longer TI durations as testing progressed, a Chi square test for trends (Mantel-Haenszel test for linear association) and Spearmans correlation test were used. No significant association was found between record number and susceptibility (P = 0.1) or duration of TI (Spearmans rho correlation coefficient = 0.08, P = 0.2).

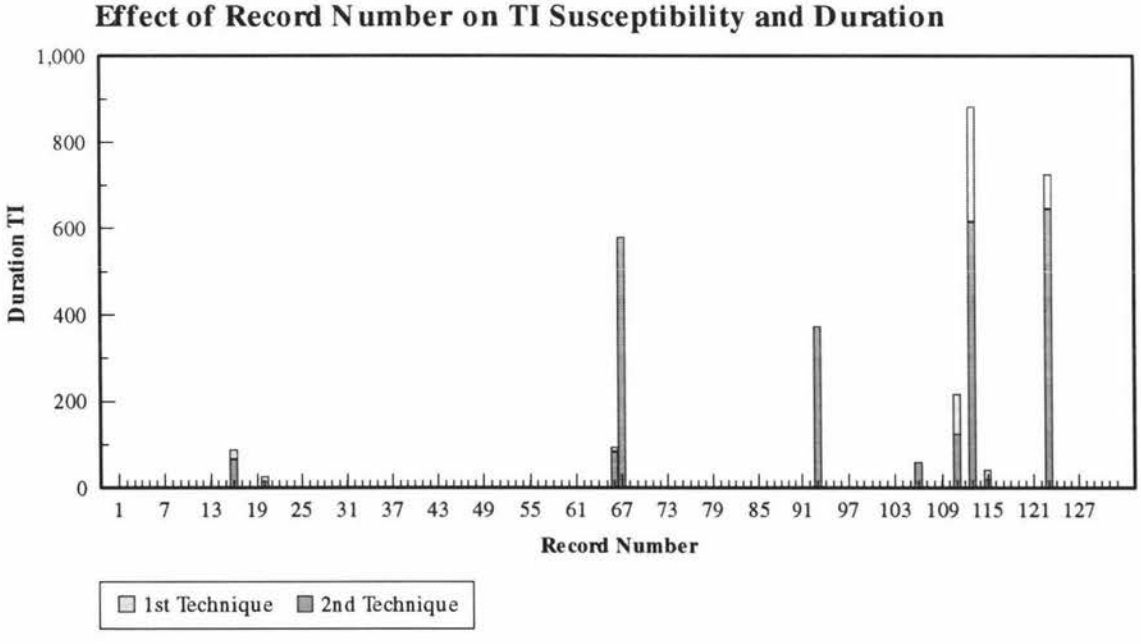


Figure 4.25 Effect of record number on TI susceptibility and duration.

4.6.5 TIME OF TESTING

The final experimental variable examined was the effect of time of testing on TI susceptibility and duration. Once again, Figure 4.26 indicates a general trend with increasing susceptibility and duration from morning to afternoon to evening. Using a logistic regression model to compare the number of dogs exhibiting TI between 9am - 12noon, 12noon - 4pm and 4pm - 8pm however, no significant difference in susceptibility was found with increasing time of day (P = 0.8). Similarly, no significant differences were found between time of testing (9am - 12noon, 12noon - 4pm and 4pm - 8pm) and duration of TI using either one-way ANOVA (analysis of variance) or the Kruskal-Wallis test (P = 0.45 and P = 0.9).

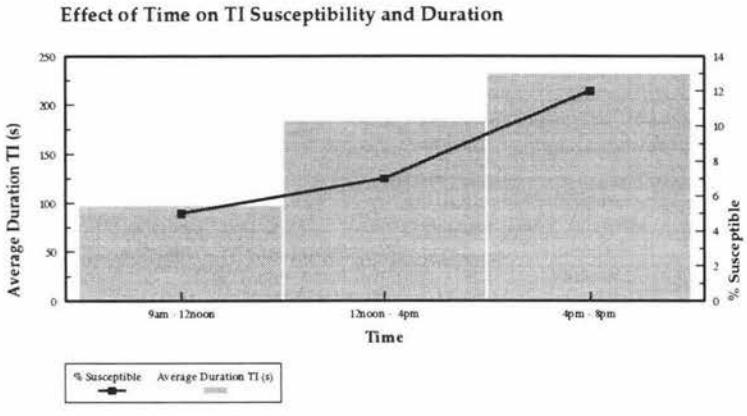


Figure 4.26 Effect of time on TI susceptibility and duration.

4.6.6 BREED

The effect of subject variables on susceptibility and duration of TI was then examined. Of the twenty breeds tested, the dogs that exhibited TI included three King Charles Spaniels, two Collies, two Rhodesian Ridgebacks, one Rottweiler, one Japanese Chin and one Pekenese. The dog breeds were grouped into different categories according to breed size (toy, small, medium or large), function (sledge, herding, guarding, retrieving or companion) and temperament (friendly, moderate or timid). The variation in susceptibility to TI and duration of TI is shown in Figures 4.27 - 4.29.

Once again however, the small number of dogs exhibiting TI along with the large number of categories severely limited the ability to obtain statistically valid results. From Figures 4.28 and 4.29 it appears that the toy breeds and companion categories were more susceptible than the other categories. No significant differences were however, found between breed sizes or functions in susceptibility using Chi square tests (P = 0.4 and P = 0.3) or in average durations of TI using either one-way ANOVA or Kruskal-Wallis test (P = 0.3 or P= 0.1 and P = 0.6 or P = 0.3).

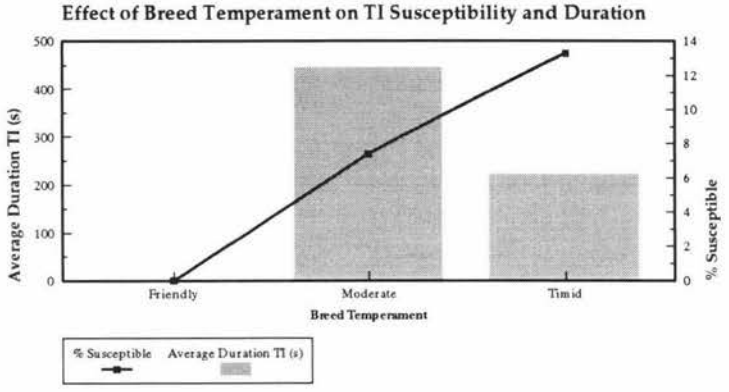


Figure 4.27 Effect of breed temperament on TI susceptiblity and duration.

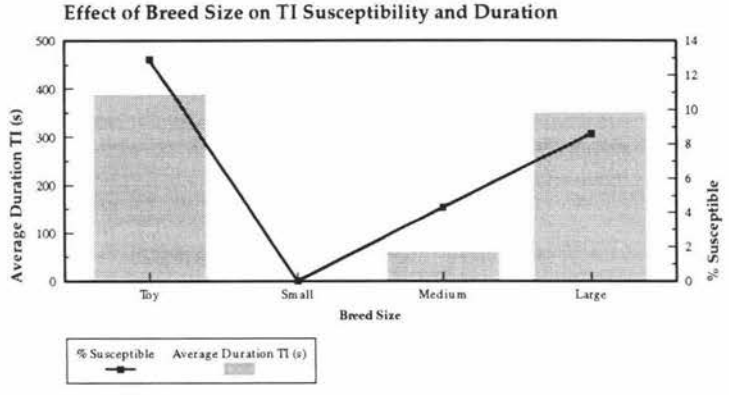


Figure 4.28 Effect of breed size on TI susceptiblity and duration.

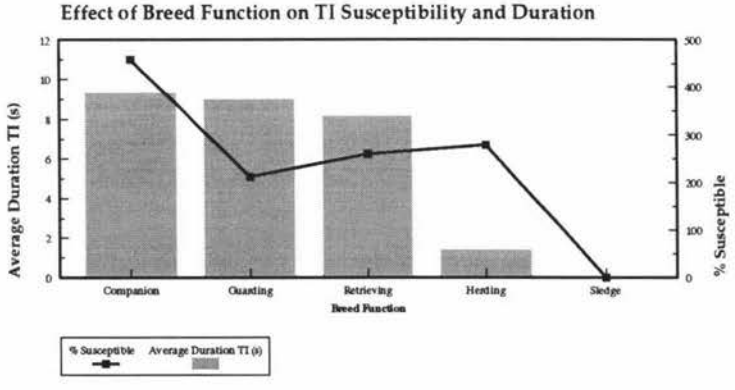


Figure 4.29 Effect of breed function on TI susceptiblity and duration.

Categorising the breed functions into companion or working breeds however, revealed a trend towards significant association between breed function and susceptibility to TI using the control induction technique (P = 0.09 Fishers exact one-tailed test). Eleven percent of the companion dogs exhibited TI compared to 3% of the working dogs. The Chi square test also indicated that more timid dogs (13%) were susceptible to TI than the moderate (7%) or friendly (0%) dogs (P = 0.03). (Figure 4.27) No significant difference was however found between the temperament of the dog and its duration of TI using either one-way ANOVA or Kruskal-Wallis test (P = 0.4 and P = 0.2).

4.6.7 AGE

The small number of dogs exhibiting TI presented problems in attempting to analyse the effect of age and sex on TI susceptibility and duration. The distribution of TI susceptibility and duration with age is shown in Figure 4.30.

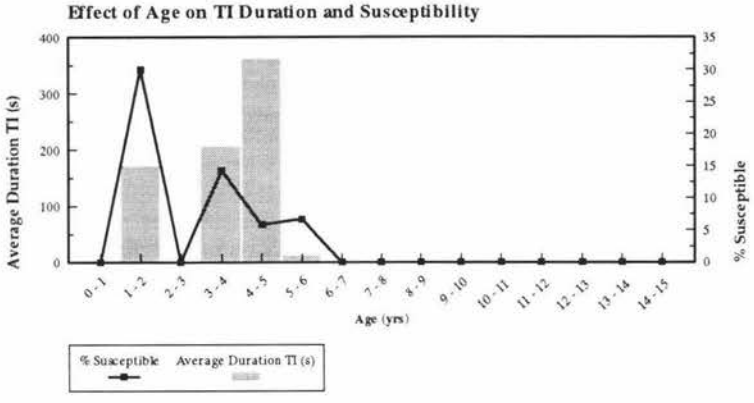


Figure 4.30 Effect of age on TI duration and susceptiblity.

From Figure 4.30 it appears that dogs are not susceptible to TI until one year of age with maximum susceptibility between 1 and 2 years old. TI susceptibility then appears to decrease with age until 6 years old. It also appears that within the susceptible dogs, there is an increase in TI durations till 5 years of age followed by a rapid decline in duration.

This changing trend in TI susceptibility and duration however, could not be adequately analysed even when the age groups were categorised into pups (< 1 year old), juveniles (1 - 3 years 11months), mature (4 - 6 years 11 months) and old (7+ years old). Grouping the dogs into greater than or less than 1 year old however, resulted in an association between the age of the dog and its susceptibility to TI which approached significance (P = 0.06 Fishers exact one-tailed test) with no dogs less than 1 year old exhibiting TI and 10% of the dogs older than 1 year old being susceptible to TI. No significant linear correlation was found between the age of the dog and its duration of TI (Spearmans rho correlation coefficient = - 0.01, P = 0.4), possibly due to the apparently increasing and then decreasing TI durations with age.

4.6.8 SEXUAL STATUS

The limited number of dogs exhibiting TI and the number of categories for sexual status limited possible statistical analysis of the effect of sexual state (male or female; pup or sexually mature; entire or neutered and if entire mature female, stage of oestrus cycle ie. anoestrous, dioestrous, oestrous, proestrous or pregnant) with either susceptibility or duration of TI. Figure 4.31 illustrates the percent of dogs in each category susceptible toTI and the average durations of TI.

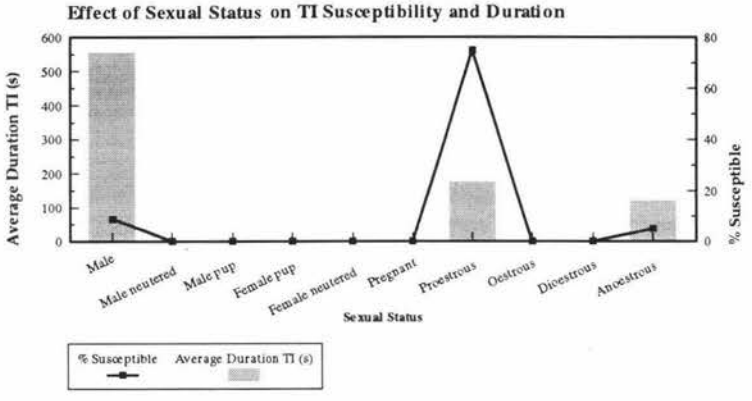


Figure 4.31 Effect of sexual status on TI susceptibility and duration.

No association was found between whether the dog was male or female (regardless of hormonal status) and its susceptibility to TI ($P > 0.9$ Fishers exact two-tailed test). Proestrous dogs were however more susceptible to TI than all the other dogs ($P = 0.001$ Fishers exact two-tailed test) with 75% of the proestrous dogs exhibiting TI as compared to 9% of the entire male dogs, 8% of the anoestrous dogs and 0% of the other dogs. As can be seen from Figure 4.31 however, the average duration of TI in susceptible dogs is more than three times longer in entire male dogs than for the other TI dogs. This difference is however not significant using a two-tailed t-test for independent samples (separate variance estimate $P = 0.2$).

4.6.9 STATE BEFORE TESTING

Association between the state of the dog before testing and susceptibility to and duration of TI was also examined. This was assessed by subjective evaluation of the dog to be quiet or excited and friendly or timid prior to testing, whether it urinated or not prior to testing and also by whether it struggled or not during induction.

Although more excited and timid dogs (17%) exhibited TI than quiet and timid (9%), quiet and friendly (5%) or excited and friendly dogs (0%), these differences were not significant ($P > 0.9$ Chi square test). Similarly, the differences in susceptibility to TI between quiet

(9%) or excited (4%) dogs and timid (10%) or friendly (2.5%) dogs were also not significant (P = 0.3 and P = 0.7 Fishers exact two-tailed tests).

Using either one-way ANOVA (P = 0.5) or Kruskal-Wallis (P = 0.2) tests, there were also no significant differences between the durations of TI in the dogs regardless of whether they were quiet or excited and timid or friendly even though the average TI durations in the quiet and timid dogs were more than 6 times longer than the average TI durations for the excited and timid dogs and more than 4 times longer than the quiet and friendly dogs. It also appeared that the quiet dogs had average TI durations almost 6 times longer than the excited dogs and that the timid dogs had average TI durations almost 4 times longer than the friendly dogs.

Dogs that struggled during induction exhibited TI durations of almost twice as long as the dogs that did not struggle during induction but these differences were not significant using the two-tailed t-test for independent samples (separate variance estimate P = 0.5). No significant association was found between the susceptibility of dogs to TI and whether they struggled (4% susceptible) or not (7% susceptible) during induction (P = 0.7 Fishers exact two-tailed test).

4.6.10 URINATION / DEFECATION

A highly significant association was found between urination or defecation ad susceptibility to TI (P < 0.001 Fishers exact two-tailed test) with 83% of the dogs that eliminated during testing exhibiting TI and only 4% of the dogs that did not eliminate exhibiting TI. Elimination was very strongly associated with TI as although dogs who exhibited TI may (50%) or may not (50%) eliminate, dogs who didnt exhibit TI were unlikely to eliminate with only 1 out of the 122 dogs that did not exhibit TI eliminating.

In contrast to susceptibility, it appeared that the average duration of TI in the TI dogs was slightly longer in those that did not eliminate (259s) than for those that did eliminate (359s), but this difference was not significant using the two-tailed t-test for independent samples (separate variance estimate P = 0.2).

The significant findings in this survey were that if a dog was to exhibit TI, it tended to with both control and additional treatment techniques, or it would not have exhibited TI with either control or additional treatment techniques. A potentiation effect occurred in second test and proestrous dogs plus dogs that urinated were more susceptible to TI than other dogs.

4.7 DISCUSSION

The low proportion of dogs that exhibited TI (10 out of 132 dogs) severely limited what could be determined statistically as the associations of other variables with TI needed to be very strong before they showed statistical significance. Additionally, as this study was an initial survey into the susceptibility of dogs to TI, the results should be interpreted cautiously as more controlled experiments are required to examine the effect of individual variables on TI susceptibility and duration.

4.7.1 SUSCEPTIBILITY

Compared to other species that are highly susceptible to TI (eg. 100% susceptibility reported in rabbits - Klemm 1971c, Carli 1977), the low number of dogs exhibiting TI in this study (7.6%) was not unexpected from both the preliminary studies and previous reports of dogs being either insusceptible (eg. Danilweski 1881, Svorad 1957, Prestrude 1977) or poorly susceptible to TI (eg. Hoagland 1928; Chertok 1964). With the exception of Reese et al (1982 & 1985), very little information has been available on the type and number of dogs tested, the percent of dogs susceptible, the methods of induction used or even the duration of immobility.

Reese et al (1982) demonstrated TI in 100% of their nervous line of Pointers but were unable to induce TI in the dogs from the friendly line. Even though 5 of their 9 friendly dogs remained in the sling for the full 4 min, they moved their heads, tails and extremities freely without attempting to turn over whereas all 10 of the nervous dogs remained in the sling for the full 4 min and were stationary with the eception of eye movements.

In a later study Reese et al (1985) reported that between 80 and 90% of their nervous dogs remained supine in a modified sling for the maximum duration of 9 min as compared to between 10 and 20% for their friendly dogs. The behaviour of the dogs while in the sling was however not described and so, it is uncertain as to whether these dogs were in TI. Reese et al did not have a criterion for establishing TI, but instead measured the total time the dog remained in the sling and also the time the dog remained supine while in the sling.

It was therefore difficult to compare the percent susceptibility of dogs in their study with the dogs in this survey as the criterion set for TI in this survey was for the dogs to remain in the position restrained, without lifting its head off the mattress, for a minimum of 10s. Examination of Reese et als (1985) data revealed that between 44 and 90% of their nervous dogs remained in the supine position for 10 or more seconds compared to between 19 and 70% of the friendly dogs. It was however uncertain if these dogs were in TI as the behaviour of the dogs while in the supine position was not described.

The within line variation in susceptibility was the result of a slight change in sling design. The lower susceptibility being due to a sling which did not completely support the smaller dogs. As even such a minor variation in experimental design had such a large effect on Reese et als results it can be seen why it is inappropriate to compare results from different experiments, especially when different experimental protocols and induction methods were used.

In addition to this, in the study of Reese et al (1985), dogs were all experimental purebred Pointers selectively bred for either extreme fearfulness or friendliness to humans, whereas the dogs tested in the current survey were of various breeds and temperaments with varying previous experiences. As most of the dogs tested in this survey were show dogs, they all would have had extensive human contact in the form of training, handling and grooming.

This extensive human contact may have contributed to the low susceptibility found in this survey as it is commonly reported that subjects that are accustomed to human handling or have been tamed, are less susceptible or insusceptible to TI (Gilman et al 1950). This same reasoning has been used by Ratner (1967) to explain why TI is not usually elicited in family pets.

Aborting testing on the 15 dogs that struggled vigorously or attempted to bite may also have affected the percentage of dogs exhibiting TI as these dogs may have been more timid, fearful or unaccustomed to handling and restraint and so may have been likely candidates for TI if testing had persisted.

The use of a 10s criterion for TI may have also contributed to the low percent susceptibility as TI studies in most other species use a 5s duration criterion for TI susceptibility (Gilman et al 1950, Rovee & Kleinman 1974, Lefebvre & Sabourin 1977b). Examination of the durations of immobility in this survey however, reveal that there were no episodes of immobility between 4 and 10s duration. The dogs therefore only exhibited immobility for greater than 10s or less than 4s with one episode of immobility for 3s, 4 episodes of immobility of 2s, 17 episodes of immobility of 1s and the remainder righting immediately after release from restraint (0s immobility). The duration criterion of 10s therefore had no effect on the percent of dogs susceptible to TI as the percent susceptibility would have been the same should the criterion been set at 5s as is commonly the case.

4.7.2 DURATION OF TI

The duration of TI in this survey ranged from 11s to the maximum allowed 646s (10min 46s) with a mean duration of 181.6s (3min 2s). In comparison, all of Reese et als (1982) nervous Pointers remained stationary in the sling for the maximum allowed 240s (4min).

Likewise, in the final 1985 experiment, all the nervous Pointers that remained supine for greater than 10s, remained supine for the maximum allowed 540s (9min). The friendly Pointers that remained supine for 10s or more however, had durations ranging from 11s to 540s, with a mean duration of 205.7s. Although this is closer to the results from this survey, these comparisons must be interpreted cautiously due to the different population samples, experimental conditions and especially because it is uncertain if these Pointers were immobile while in the supine position.

The duration of TI reported in other species, is also variable depending on the species and experimental conditions. It has been reported to range from only a few seconds to over several hours. In chickens, the maximum uninterrupted duration was reported to be 5hr 45min (Gallup 1974a), with an average duration of 578s and a standard deviation of 713s. In comparison, Prestrude (1977) has reported TI durations of over 8 hr in lizards. As an upper limit was imposed in this study, it was not possible to obtain a value for the maximum duration of uninterrupted immobility or determine an average duration of uninterrupted immobility in the dogs tested.

4.7.3 INDUCTION TECHNIQUE

Besides Reese et al (1982 & 1985) who induced TI by inverting their dogs into a sling and stroking their belly for 1 min, other investigators induced TI in canids by a variety of methods including inversion and restraint (Mangold 1934; Fox 1968) (Figure 4.32), stroking (Wilson 1839), grasping by a choker collar (Ratner 1967) and eye fixation on a finger or prism (Volgyesi 1966) (Figures 4.33). The 6 techniques (control and 5 additional treatments) used for induction in this survey all involved inversion and restraint and the additional treatments incorporated techniques that had been used in dogs and other species as discussed in section 3.5.7.

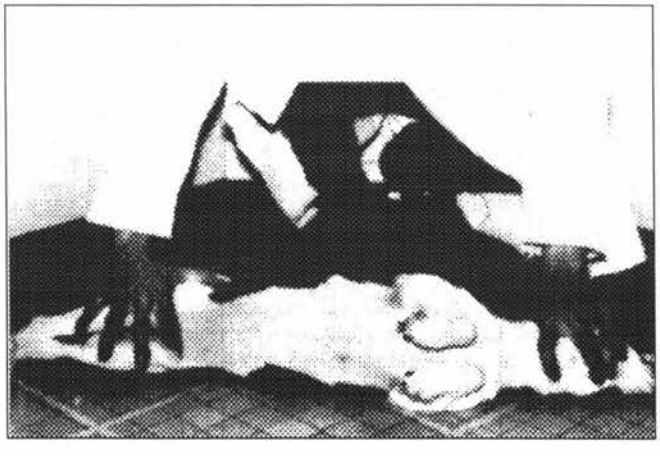


Figure 4.32 Beagle exhibiting TI from inversion and restraint (Fox 1968).

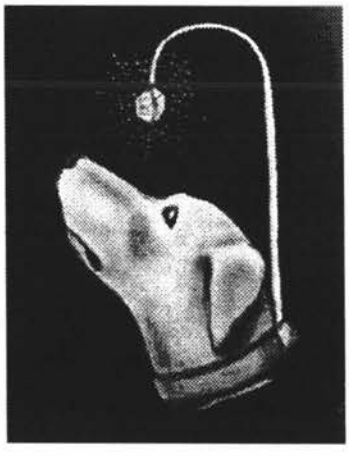


Figure 4.33 "Hypnosis" of a dog by eye-fixation on a prism (Volgyesi 1966).

No significant difference was found between the control or additional treatment techniques on the susceptibility or duration of TI. Instead, a highly significant association was found between whether a dog exhibits TI with control and whether it exhibits TI with the additional treatment techniques, indicating that if a dog was to exhibit TI, it would have with control and additional treatment technique or it would not have exhibited TI with either. It therefore appeared that susceptibility to TI was more a dog effect than a technique effect.

With the exception of the light technique, all other techniques were successful at inducing TI, with stroking and cuffing having a 11.5% success rate compared to scruffing (7.4%), control (6.1%) and blanket (3.7%). These differences however could not be meaningfully statistically compared due to the small umber of dogs exhibiting TI. Similarly, although blanket and cuffing resulted in average TI durations that were almost 10 times the other techniques, these differences were not analysed in this survey.

From the results of this survey, it appears that if a dog is likely to be susceptible to TI, the inversion and restraint technique used as the control technique and incorporated in all the other techniques is all that is required to induce TI. The important variable in the induction techniques used in other species appears to be the position and degree of restraint or support. Reese et al (1985) for example, found that modifying a sling so that it contoured to the dogs and provided additional support enhanced both TI susceptibility and durations. Similarly, placing rabbits a V-shaped trough (Ratner 1967; Carli 1977) or frogs or their back (Mangold & Eckstein 1919) potentiated TI.

The similarity seen between the techniques used in this survey may therefore be because all of the techniques involved lateral restraint on the foam mattress. This may have provided sufficient restraint and support to induce TI in the susceptible dogs. The foam mattress would have had a similar to the effect of contouring to the dogs bodies as the sawdust (Oakley & Plotkin 1977; Whishaw et al 1978; Whishaw, Flannigan & Barnsley 1979) or cloth trough (Braud & Ginsburg 1973a; Jones & Faure 1981a) used to potentiate TI in other species.

Whether the additional treatments acted to enhance the susceptibility or duration of TI was examined in a further study (Chapter 5). The results from the current survey indicate that additional treatments during induction of TI result in average TI durations more than 3 times longer than in controls ($P = 0.07$).

4.7.4 ORDER OF TESTING

The small number of dogs exhibiting TI in this survey limited the ability to conduct adequate statistical analysis on the effect of repeated testing. Although all 10 TI dogs exhibited TI in the second test whereas only 7 of the TI dogs exhibited TI on the first test, this difference was not large enough to indicate a significant potentiation effect. Whether the control technique was applied first followed by the additional treatment or vice versa also had no effect on the susceptibility to TI.

A significant potentiation effect was however seen on the duration of TI as the duration of TI in the second test was 5 times longer than in the first test. Although repeated testing usually results in habituation, with a decrease in TI susceptibility and duration, a potentiation effect with repeated testing has been reported in guinea pigs (Liberson 1948; Bayard 1957), iguanas (Prestrude 1977) and chickens (Nash and Gallup 1976). This potentiation effect occurs with massed trials, when TI is reinduced immediately after termination of an immobility episode or when a subject is repeatedly tested within a short intertrial interval.

Nash and Gallup (1976) reported that a minimum of 15s would avoid the potentiation effect of massed trials in chickens. Although the intertrial interval in this study was between 20 - 80s and testing was only repeated once, it is not surprising to find a potentiation effect, considering the different species and experimental conditions. Species variation in the effects of repeated testing has been reported in the rabbit (Ewell and Culen 1981), bobwhite quail (Eyer and Ratner 1975), green iguana (Prestrude 1977) and lizard (McKnight et al 1978). This is the first report of a potentiation effect of repeated testing on the duration of TI in dogs.

Another order effect that was examined was the possible effect of experimenter experience on the susceptibility and duration of TI. Chertok (1964) had proposed that the experience and skill of the investigator may be an important variable affecting TI in dogs. Mery (1968) believed that veterinarians authority, instinctive skill and confidence allowed them to impose transient immobility in dogs. This may account for the dogs showing TI at all. However, although there appeared to be an increase in susceptibility and duration of TI as testing progressed (increasing record number), this trend was not significant.

4.7.5 TIME OF TESTING

Circadian rhythms in TI have been reported in many species including toads and tarantulas (Ternes 1977), chickens (Rovee et al 1976); lizards (Hoagland 1928; Hennig and Dunlap 1977b), rats (Hennig and Dunlap 1977b) and woodlice (Ratner 1977). No significant association was found between time of testing and the dogs susceptibility or duration of TI even there appeared to be a slight increase in susceptibility and duration from morning to afternoon to evening.

4.7.6 BREED

Subject variables reported to affect TI were examined in this study. Strain differences in TI have been reported in chickens (Gallup et al 1976; Nash 1978; Jones and Mills 1983) and rats (McGraw and Klemm 1973). Individual breed differences to TI were not examined due to the small number of dogs exhibiting TI and the large number of breeds tested. Instead, breeds were classified into different breed sizes, function and temperament. More toy breeds and companion dogs exhibited TI than the other categories of dogs, but these differences were not significant. More timid dogs also exhibited TI than dogs classified as moderate and none of the friendly dogs exhibited TI.

This is comparable to the strain differences reported in rats (McGraw and Klemm 1973) where the fearful strains were more susceptible to TI and exhibited longer TI durations. Similarly in chickens it has been reported that the more fearful and flighty strains exhibited longer TI durations than the placid strains (Gallup et al 1976; Nash 1978; Jones and Faure 1981a; Jones and Mills 1983).

Unlike McGraw and Klemm (1973) however, Gallup (1974b) and Gallup et al (1976) found that this strain specific difference only affected TI durations and not susceptibility, indicating that susceptibility and duration may be independent TI parameters. Although contrary to their findings of strain differences not affecting susceptibility, this initial survey in dogs has also indicated that susceptibility and duration may be independent TI parameters. For xample, although breed differences in susceptibility indicate that timid dogs are more susceptible than moderate or friendly dogs, the moderate dogs that exhibited TI averaged TI durations 20 times longer than the timid dogs. Similar differences between susceptibility and duration were also found in relation to ease of induction and dogs that urinated during testing.

4.7.7 STATE BEFORE TESTING

Each dogs demeanour was evaluated by assessing its state before testing (quiet or excited and friendly or timid), whether it struggled or not during induction and whether it urinated or not during testing. Once again however, the small number of dogs exhibiting TI meant that any associations of other variables with TI needed to be very strong before they would show statistical significance.

Although no significant difference was found between the state of the dog before testing or whether it struggled during induction and the dogs susceptibility or duration of TI, the trend was for the timid dogs to be 4 times more susceptible and exhibit TI durations that were more than 4 times longer than the friendly dogs. This is similar to Reese et als (1982 and 1984) report that the nervous Pointers exhibited longer TI durations than the friendly ones. Fox (1978) also indicated that a beagle which exhibited TI had originated from an extremely timid line.

More than twice as many quiet dogs also exhibited TI than excited dogs and their TI durations were almost 6 times longer than the excited dogs. None of the excited and friendly dogs exhibited TI. The dogs that struggled during induction also exhibited TI durations almost twice as long as the dogs that didnt struggle during induction. On the other hand, the dogs that didnt struggle during induction were more susceptible to TI than the dogs that struggled.

This difference between susceptibility and duration was also seen in the dogs that urinated or defecated during the testing procedure. A highly significant association was found between elimination and susceptibility to TI with 83% of the dogs that eliminated during testing exhibiting TI. Although not significant, the TI dogs that did not eliminate however had slightly longer average durations of TI than the dogs that urinated.

As urination or defecation is often used as a measure of fear (Gray 1971; Plutchik 1971; Gallup et al 1976; Archer 1979), the increased susceptibility in dogs that eliminated during testing may be an indication of increased level of fearfulness in these dogs. Reese et al (1985) reported that their nervous line of Pointers often urinated or defecated in the presence of people. As fear is often associated with TI, this increased susceptibility to TI appears supportive of the view that fear is an important variable associated with TI.

The trend with more timid breeds exhibiting TI than moderate or friendly breeds and with more of the dogs assessed to be timid exhibiting TI than the ones assessed to be friendly also seems supportive of the fear theory. This may help explain the low susceptibility found in this study, as most investigators (Gilman et al 1950; Ratner 1967) report that subjects accustomed to human handling or tame (ie. more friendly and less likely to urinate) are less susceptible to TI.

In retrospect, instead of subjectively assessing the dogs to be timid or friendly and quiet or excited as each dog entered the caravan, a more objective assessment of each dogs temperament and fear or arousal response to human contact in the form of avoidance response (Goddard and Beilharz 1984), dog rating scale (Klein et al 1988) or human interaction test (eg. Reese et al 1982) may have been useful in defining an association between temperament, demeanour and TI. Reese et al (1985) for example, reported that in 4 month old pointers, the duration of sling immobility was positively related to the degree of behavioural pathology as determined by the human interaction test. This test was not included in the current study in order that each testing session was as quick and simple as possible.

4.7.8 AGE

Changes in the susceptibility and duration of TI with the age of the subject has been reported in many species including chickens (Ratner and Thompson 1960; Salzen 1963; Rovee and Luciano 1973; Borchelt and Ratner 1973), gulls (Montevecchi 1978), possums (Franq 1969) and rats (Klemm 1971c; Prestrude 1977). Similar trends to those reported in other species were found in this survey.

Tonic immobility was not observed in any dogs under 1 year of age, with the majority of the dogs exhibiting TI between 1 and 2 years old. This delay in the appearance of TI until a certain age, is comparable to the reports in chickens (Salzen 1963; Borchelt and Ratner 1973), gulls (Montevecchi 1978) and possums (Franq 1969). As fear responses develop in puppies from 6 - 8 weeks of age (Fox 1978), this delay in the appearance of TI in dogs is unlikely to be related to the development of fear responses as had been postulated for chickens (Ratner and Thompson 1960; Salzen 1963). The delay may instead be due to a number of other factors such as a requirement for different induction techniques for the very young, as has been reported in chickens (Rovee and Luciano 1973; Braud and Ginsburg 1973a; Rovee and Kleinman 1974; Ginsburg 1975). It may therefore have been possible to induce TI in the younger dogs if different induction techniques had been used.

Susceptibility of the dogs to TI then appeared to decrease from 2 years till 6 years of age and none of the dogs older than 6 years old exhibited TI. This is similar to the reports of decreasing responsiveness to TI with age in the chicken (Ratner and Thompson 1960; Salzen 1963; Borchelt and Ratner 1973; Hughes 1979), possum (Franq 1969) and rat (Klemm 1971c; Prestrude 1977). In rats, the duration of TI is reported to decrease with age until a certain age after which susceptibility does not return until the rats pass their prime of life. In this survey, there appeared to be an increase in the duration of TI in the susceptible dogs until 5 years of age. This was then followed by a rapid decline in TI durations at 6 years old, after which TI susceptibility ceased. Whether TI susceptibility would have returned at the older ages is uncertain as none of the dogs older than 6 years old (3 of which were greater than 12 years old) exhibited TI in this survey. It however does appear that the changes with age for TI in dogs is similar to the general trend reported in other species.

4.7.9 SEXUAL STATUS

The absence of sexual dimorphism reported in other species (Borchelt and Ratner 1973; Gallup 1974b; Benoff and Siegel 1976; Mills and Faure 1986) was found, with no significant association between the sex of the dog (male or female) and its susceptibility to TI. Proestrous dogs were however, significantly more susceptible to TI than the other dogs. Such an effect has never been reported before but this difference in TI with different stages of the breeding cycle is comparable to the report that female lizards exhibit longer TI than

males of the same size during the non-breeding season only (Cashner et al 1981 and 1982). With so little known about the neuroendocrinology of TI, this variation in TI with different stages of the breeding cycle may be due to interactions between endogenous hormones and other mechanisms affecting TI.

Contrary to Cashner et als (1981 and 1982) finding with females exhibiting longer TI than males, the susceptible entire males in this study exhibited TI durations that were 3 times longer than the other TI dogs. This is similar to Jones and Faures (1981a) finding that males in 2 out of 3 lines of chickens showed greater latencies to first head movements than females.

4.7.10 SUSCEPTIBILITY AND DURATION

Although proestrous dogs were more susceptible to TI, entire male dogs exhibited longer average TI durations. Differences found between TI susceptibility and duration with the sex and age of the subject, as well as ease of induction and urination during testing all support Gallup et als (1976) belief that duration and susceptibility may be independent parameters of TI. That is, whether a dog is susceptible to TI or not is controlled by a different mechanism than that which determines the duration of immobility.

However, many of the differences seen in this study did not reach statistical significance, probably due to the small number of dogs exhibiting TI. Results must therefore be interpreted with caution. A more detailed study examining the effect of these variables individually must therefore be conducted to properly identify the effect of the many variables on TI susceptibility and durations.

The effects seen in this study may for example, be due to the effects of some other variable not examined or controlled for. For example, it was observed that 73% of all the aborted tests occurred in 3 breeds (Boxer, Corgi and German Sheperds) from 3 breeders indicating possible breed or breeder effects or effects of previous experience. This variable was not examined or controlled for except by selecting dogs that were predominantly breeding or show dogs instead of pets.

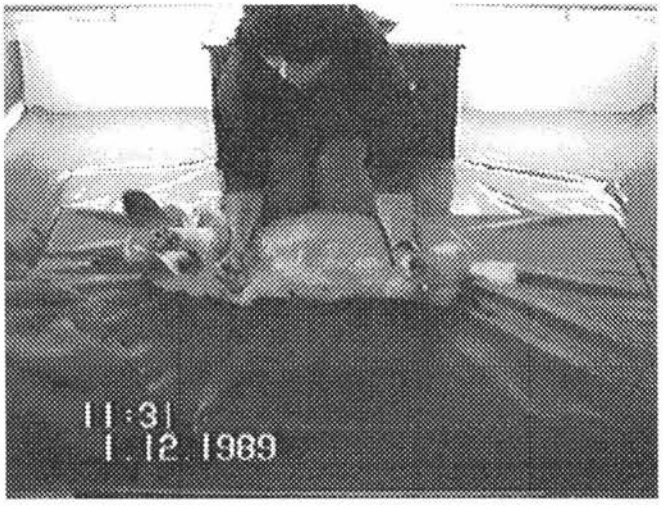
Additionally, although experimental variables were controlled from presentation of the dog till termination of testing, the immediate pre-testing and housing conditions were not controlled. The dogs therefore had varied pre-testing conditions, which have been reported to affect TI (Gallup, Nash and Wagner 1971; Tortora and Borchelt 1972; Eyer and Ratner 1975).

More control over such experimental and subject variables such as by raising experimental dogs under identical rearing and housing conditions could help to identify the effect

of such variables on TI. Such a study is beyond the scope of this thesis due to a limited supply of readily accessible dogs of a particular signalment (eg. age, breed or sex). From this initial survey however, it appears that many of the trends reported in other species are also seen in TI in dogs.

4.7.11 CHARACTERISTICS DURING TI

The characteristics seen during TI are also similar to those reported in other species as the dogs lay very still, with the exception of minor limb and head movements. As in other species (Gallup 1975; Lefebvre and Sabourin 1977a), during induction some dogs struggled against restraint and a few attempted to bite or escape from the investigator (Figures 4.34 and 4.35). Struggling however, only occurred in 20% of inductions and generally ceased within 15s of restraint. Following induction, the dogs that exhibited TI remained in the position of restraint even after release.



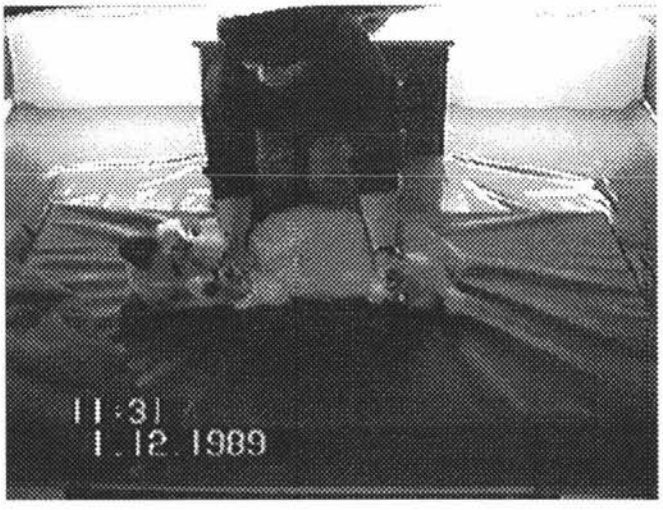


Figure 4.34 Dog struggling against restraint and attempting to bite the investigator.

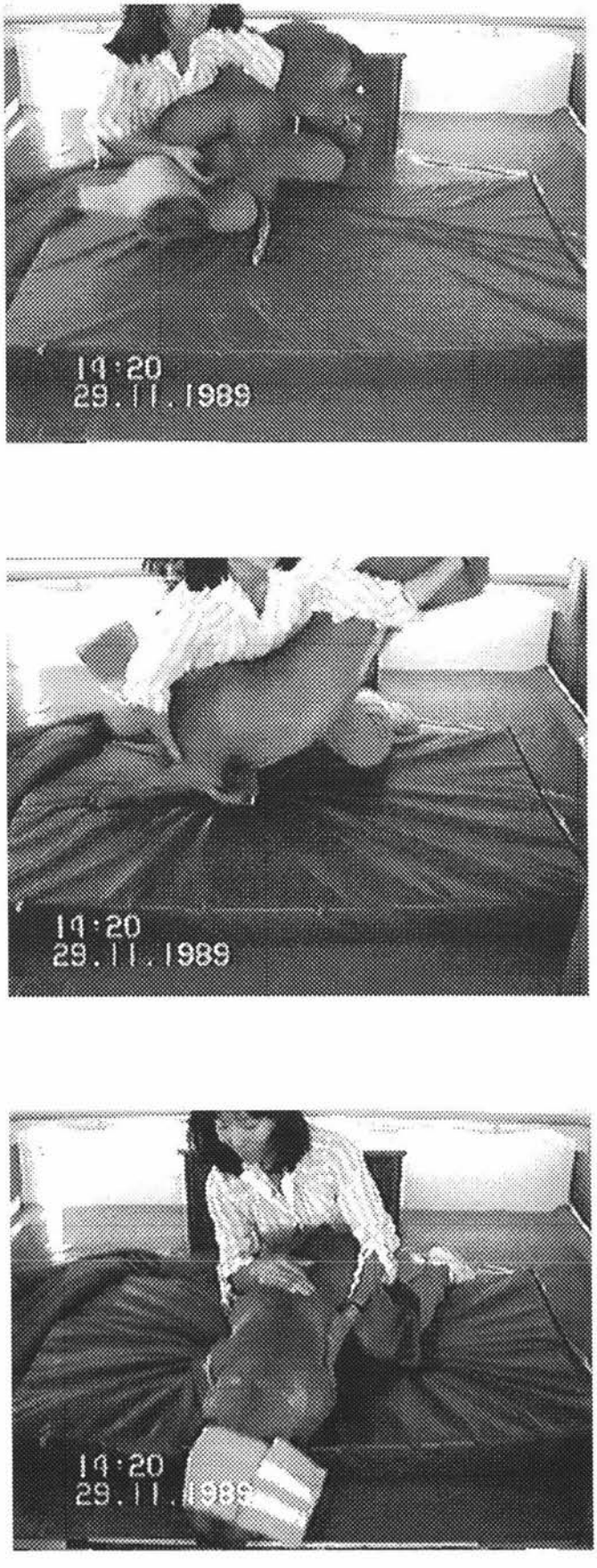


Figure 4.35 Dog struggling against restraint and attempting to escape from the investigator.

As for other species, the position of the dogs limbs were variable (Figure 4.24) depending on the final position of restraint. As with Reese et al's (1982 and 1985) Pointers (Figure 4.36), the hind limbs tended to be extended but the forelimbs either flexed or extended. Fox's (1968 and 1978) beagle was also pictured with its hind legs extended and forelegs flexed (Figure 3.17, p90). The beagle's tail was between its legs and almost curved against its belly as reported in Reese et als (1982 and 1985) Pointers. In this study, the position of the dogs tails were variable as they were extended in some cases and against the dogs belly in other cases (Figure 4.22).

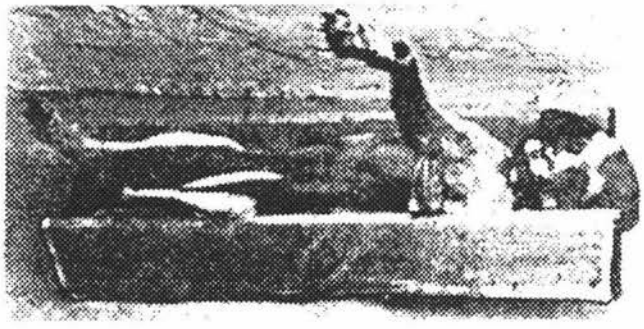


Figure 4.36 Tonic immobility in Reese et al's (1982) nervous Pointers.

Reese et als (1982) Pointers were reportedly rigid during TI. It was however difficult to assess the dogs muscle tone in this study as it appeared to be variable and occasional muscle tremors and twitches were observed, especially in response to external stimulation. Carli (1974) also found muscle tone to be difficult to assess. Muscle tremors and transient increases in muscle tone in response to mild stimuli have been reported in chickens (Hicks et al 1975) and rabbits (Schaeppi and Rubin 1965). Reese et al (1982) also described occasional muscle tremors during TI in their nervous Pointers.

As for other species (Gilman and Marcuse 1949; Gallup 1977; Jones 1986a), in addition to the muscle tremors, slight repositioning of the dogs head, limbs and paw paddling movements were observed during TI. Some of the dogs urinated during testing as has been reported in birds and guinea pigs (Bayard 1957; Gallup 1977).

Throughout the TI episodes, most of the dogs had their eyes open and appeared to be continuously monitoring the environment as blinking and eye movements were observed. This is similar to observations reported by Reese et al (1982) in their nervous Pointers and by other investigators in other species (Gallup 1977; Jones 1986a). Therefore although the dogs appeared to be unresponsive to the external environment during TI as they did not right in response to intense stimulation such as loud bangs or shouting children, the eye movements and muscle twitches in response to mild stimulation supports the view that central processing of the external environment occurs during TI (Draper and Klemm 1967; Carli et al 1974; Sigman and Prestrude 1981). The continuation

of TI despite stimulation such as coughing, talking, shouting children, barking and noisy traffic was also seen as a positive indication that TI may be used in a noisy clnical environment.

When TI terminated, it was seemingly spontaneous on 9 occasions, linked with external stimulation on 8 occasions and was terminated by the experimenter on two occasions when TI lasted the maximum allowed 10 min. Although most of the TI episodes terminated abruptly with a sudden transition from immobility to head and limb movements and lifting of the head off the mattress, none of the dogs attempted to attack the experimenter or exhibited any injury feigning displays as has been described in other species (Armstrong 1965; Ratner and Thompson 1960).

This lack of escape and attack behaviours at termination and induction of TI, most likely reflects the tameness of the subject as all the dogs would have been accustomed to being restrained and in close proximity to humans. Several dogs even appeared to be slow and reluctant to right after the TI episode was terminated when the dog lifted its head off the mattress.

No physiological parameters such as heart or respiration rate were monitored during this survey but will be conducted in the next study which will examine more closely the characteristics, depth and physiological changes during TI. As previously discussed (section 3.5.7), the feasibility of the next study was dependent on finding that dogs do exhibit TI and for a long enough period to allow certain observations and measurements to be made.

Due to the low susceptibility found in this survey, and as susceptibility appeared to be a dog effect rather than a technique effect, instead of choosing the best method to potentiate TI, it was decided that the dogs that exhibited TI in this survey would be re-tested in the next study. Otherwise, it may have required testing another 100 dogs before enough susceptible dogs that exhibited TI for a long enough duration and depth to allow physiological monitoring could be found. This would also provide an opportunity to verify that TI was not a once-off effect but actually a characteristic of some dogs or a dog effect.

As these dogs would have been tested previously in this survey, the effect of repeated testing was also examined by testing each dog several times. The different induction techniques used in this survey was again used in the next study in a further attempt to identify if there was technique effects on TI susceptibility and duration. The torch technique however, that did not result in any TI was to be omitted. The testing environment and induction techniques otherwise remained the same as they appeared to work well in this initial survey. The 10s criterion for TI also remained.

4.8 CONCLUSION

Of the dogs tested in this initial survey, 7.6% exhibited TI based on the criterion of remaining in the position restrained, without lifting its head off the test surface, for a minimum of 10s after release from restraint. The duration of TI ranged from 11s to the maximum allowed 646s. Although 7.6% susceptibility is lower than is reported in other commonly tested species such as chickens, rabbits and lizards, it was expected based on previous reports of low susceptibility in dogs and family pets that are tame and accustomed to human handling.

The characteristics of dogs during TI were similar to those reported in other species, as the dogs remained very still, with the exception of minor head and limb movements. The dogs also appeared to be continually monitoring their environment while in TI as their eyes were open and ee movements were observed. Muscle twitches were also observed in response to external stimulation.

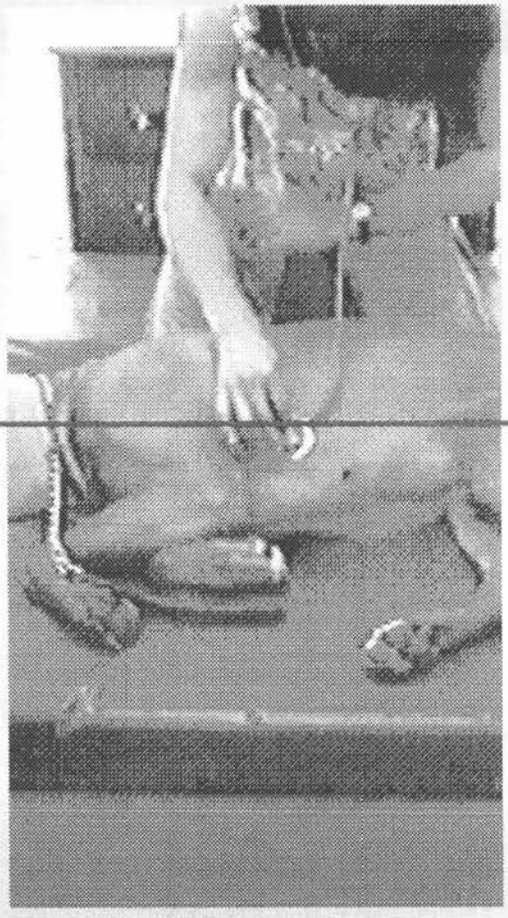
No best method of induction was found. Instead, susceptibility to TI appeared to be a dog effect rather than a technique effect as a highly significant association was found between whether a dog exhibits TI with control and whether it exhibits TI with the additional treatment techniques. The low proportion of dogs exhibiting TI however, further limited what could be achieved statistically as any associations of other variables with TI needed to be very strong before they would show statistical significance. The only other significant findings were a potentiation effect on TI duration in the second test and that timid breeds, proestrous dogs and dogs that urinated or defecated during testing were more susceptible to TI.

Trends observed in the effect of other variables on TI were also similar to those reported in other species. For example, no sexual dimorphism was observed in susceptibility to TI and there appeared to be an initial low degree of susceptibility to TI in young dogs up to 1 year old, after which susceptibility increased but then declined again as the dogs aged further.

A dichotomy between TI susceptibility and duration was also observed, with for example, male dogs and non-urinators/defecators appearing to exhibit longer TI durations than the more susceptible proestrous dogs and dogs that urinated during TI. Although this is supportive of the idea that susceptibility and duration may be independent parameters of TI, these differences were only observed trends and the results from this initial study should be interpreted with caution due to the small number of dogs exhibiting TI. More extensive studies examining the effects of variables are required in order to identify the effect of the individual variables on TI susceptibility and duration.

Chapter five

Characterisation



Characterisation

5.1 AIM

The aim of this study was to further assess the characteristics of TI, record physiological changes during TI, estimate the depth of TI and the effects of repeated testing on TI in dogs. The study also was to verify whether TI was a once-off random event and if not, whether it resulted from dog or technique effects.

5.2 SUBJECTS

Twenty of the dogs tested in the initial survey were re-used. This involved the collaboration of 6 breeders and included the 10 dogs that recorded an immobility duration of 10s or more and a matched control, selected from the same breeder. These controls were matched as closely as possible for breed, temperament (as recorded on entry into the caravan during the initial survey), age and sex. In all cases except for one pair (Rottweiler and Huntaway) they were of the same breed.

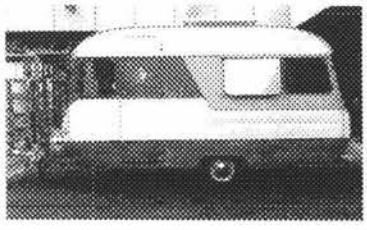


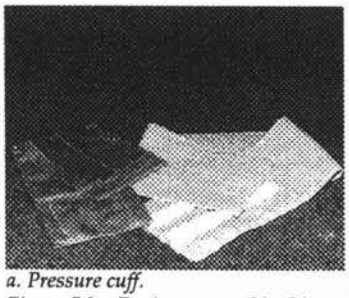
Figure 5.1 Testing caravan.

5.3 TESTING ENVIRONMENT

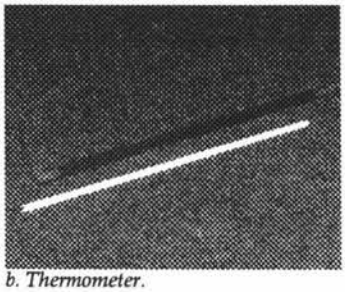
Testing was conducted inside the caravan as for the previous study (Figure 5.1). Lighting was as described in section 4.3 and the temperature inside the caravan ranged from 18 - 26 °C. Faint barking, talking and traffic noises from outside were audible inside the caravan.

5.4 MATERIALS

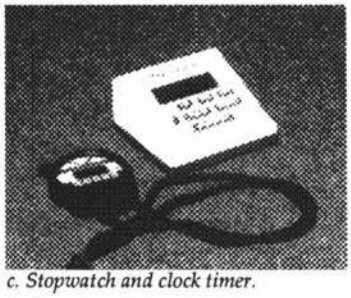
Apart from the torch, all of the materials used in the initial survey (Chapter 4) were used in this study (Figure 5.2). In addition, a stethoscope (*3M Littmann*) and a 35-42°C clinical thermometer were used to record physiological changes during TI (Figure 5.2d). Record sheets were also used to record induction methods, physiological parameters, environmental conditions and behavioural observations before, during and after TI (Appendix 7).



a. Pressure cuff.

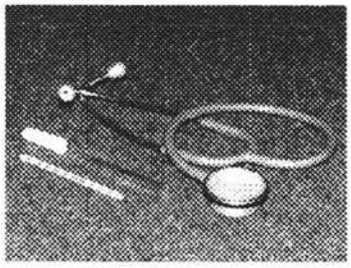


b. Thermometer.

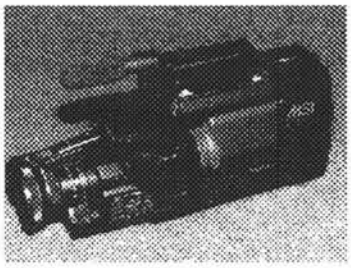


c. Stopwatch and clock timer.

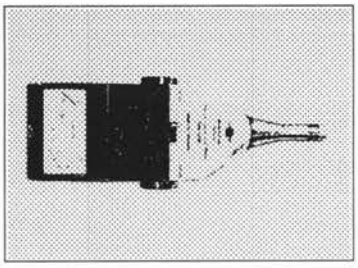
Figure 5.2 Equipment used in this study ...



d. Stethoscope and clinical thermometer.



e. Video camera.



f. Precision sound level meter.

Figure 5.2 Equipment used in this study.

A battery operated audio cassette player (*National Panasonic RQ-42IDS*) with remote control microphone was positioned on the right side of the sink (Figure 5.3) approximately 1m from the dog when on the foam mattress. It was set with both the volume and tone settings on 5. The acoustic level of the 412.4 Hz square wave signal recorded on the audio cassette (*Maxell UDI 90*) was measured using a Precision Sound Level Meter (*Bruel and Kjaer Type 2206, Denmark*) set on Fast response and on the A weighting network (Figure 5.2f). The intensity of the auditory tone at the foam mattress ranged from 44 to 83dB.

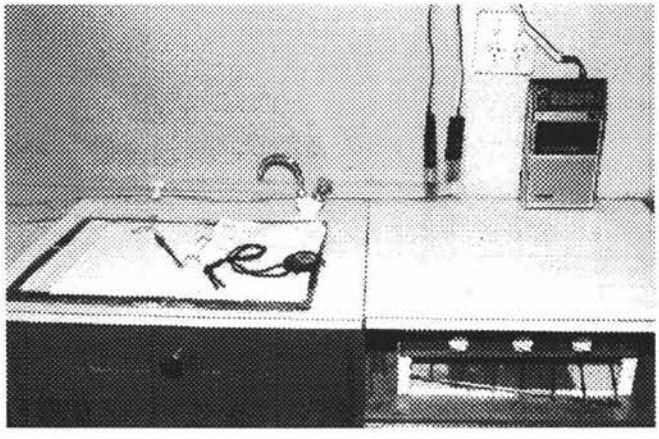


Figure 5.3 Position of audio cassette player on caravan bench top.

5.5 PROCEDURES

The 6 relevant breeders were contacted again and this part of the study explained. Suitable times were arranged for testing and the initial procedures used were as in the previous study (section 4.5). This time however, the order in which the dogs were to be presented was specified and the dogs within each pair were tested in succession. As each dog was presented, it was greeted and the investigator spent a few minutes becoming reacquainted with the dog and any additional information regarding the dog's temperament and history were obtained. Each dog was then led inside the caravan, allowed several seconds

to investigate the interior and led up onto the platform and foam mattress (Figure 5.4) to be tested. During this period, the assistant recorded the time of testing and environmental conditions while the dog's temperament was assessed by the investigator as friendly, timid or aggressive and its demeanour before testing as quiet or excited (Figure 5.5). It was also noted whether the dog urinated or defecated before testing.

Each dog was tested 5 times in succession. Once with the control induction procedure (inversion and 30s restraint in the lateral position) and once with each of the 4 additional treatment induction methods. The 4 additional treatments used in this study were stroking the dog's abdomen, placing a blanket over its head, a cuff around its ears and grasping its scruff during the 30s restraint in lateral recumbency. As none of the dogs in the previous study responded to the light induction technique with TI, it was not used in this study.

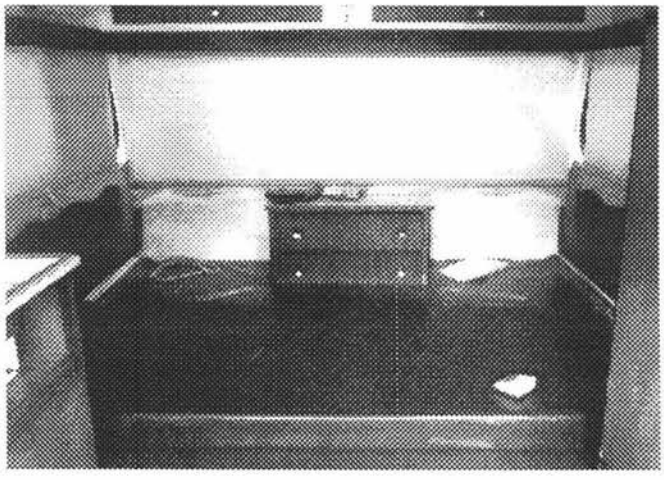


Figure 5.4 Testing platform and mattress.

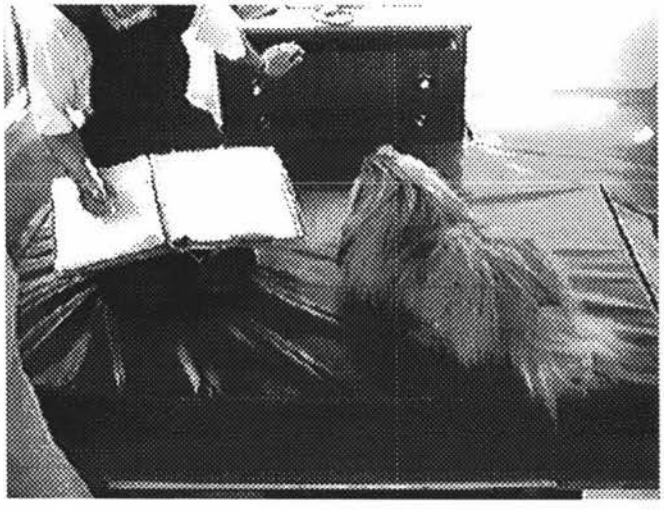


Figure 5.5 Recording observations prior to testing.

The interval between the termination of one test and the start of the next test on the same dog was set at 3 min in an attempt to avoid the possibility of the potentiation effect seen in the previous survey. To account for any possible effect of the preceding test, this part of the experiment was based on a Latin Square design balanced for residual effects (Cochran and Cox 1957). The design was made up of two latin squares (Table 5.1) and was balanced for direct order effects (ie. potentiation or habituation effect from 1st test to 2nd, to 3rd .....) and for residual or carry-over effects (ie. whether the preceding technique had an effect on the following technique). The dogs within each matched pair were tested with the 5 techniques in the same order. Whether the TI dog or the matched control was tested first was alternated as the matched pairs were tested.

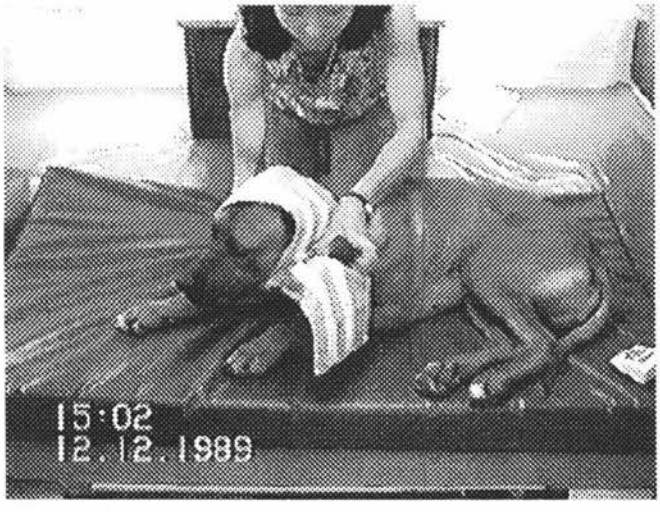
Experimental design balanced for residual effects

TECHNIQUE	DOG PAIR 1	2	3	4	5	6	7	8	9	10
FIRST	Control	Stroke	Blanket	Cuff	Scruff	Control	Stroke	Blanket	Cuff	Scruff
SECOND	Stroke	Blanket	Cuff	Scruff	Control	Blanket	Cuff	Scruff	Control	Stroke
THIRD	Cuff	Scruff	Control	Stroke	Blanket	Stroke	Blanket	Cuff	Scruff	Control
FOURTH	Scruff	Control	Stroke	Blanket	Cuff	Scruff	Control	Stroke	Blanket	Cuff
FIFTH	Blanket	Cuff	Scruff	Control	Stroke	Cuff	Scruff	Control	Stroke	Blanket

Table 5.1 Experimental design balanced for residual effects.

Prior to each test, the dog's temperament (friendly, timid or aggressive), demeanour before testing (quiet or excited), heart rate (counted for 15 secs - Figure 5.6a), whether it urinated or defecated and any other observations considered relevant were recorded. The induction procedure for all 5 induction techniques (control, stroking, blanket, cuff and scruffing) were as in the previous study except that the dogs were now consistently positioned on their right sides (Figure 5.6e) so that their left sides were uppermost to allow for easier measurement of heart rates (Figure 5.6i). Figure 5.6 illustrates an entire testing procedure for the cuffing technique.

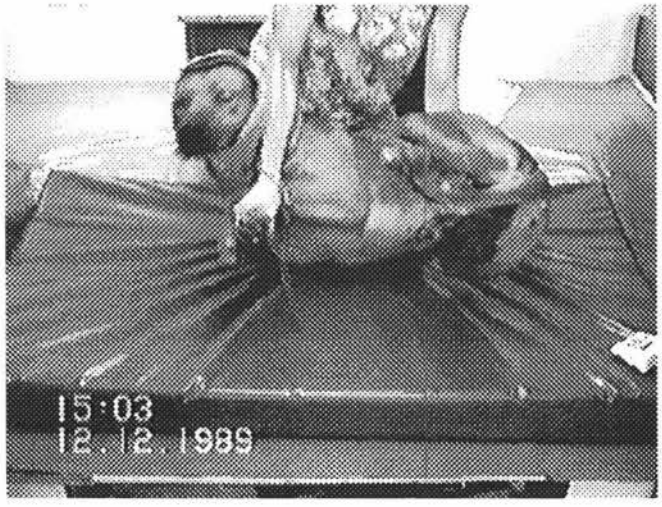
a. Recording heart rate prior to testing.



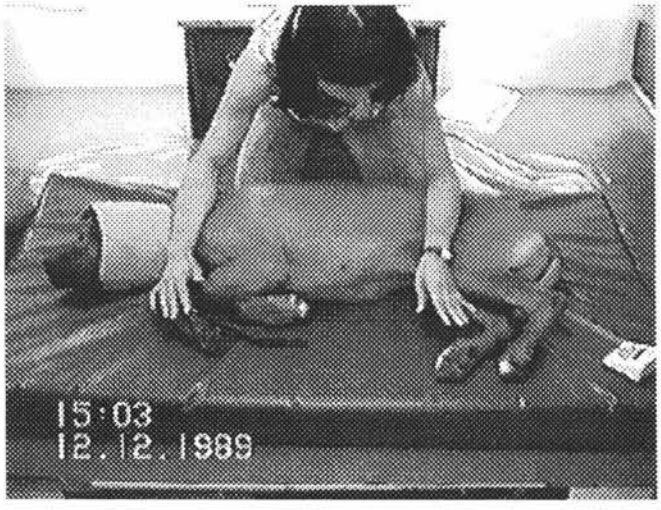
b. Wrapping pressure cuff prior to inversion.

c. Grasping dog's legs closest to investigator.

Figure 5.6 Physiological testing procedure for cuffing induction technique ....



d. Swinging the dog's legs away.

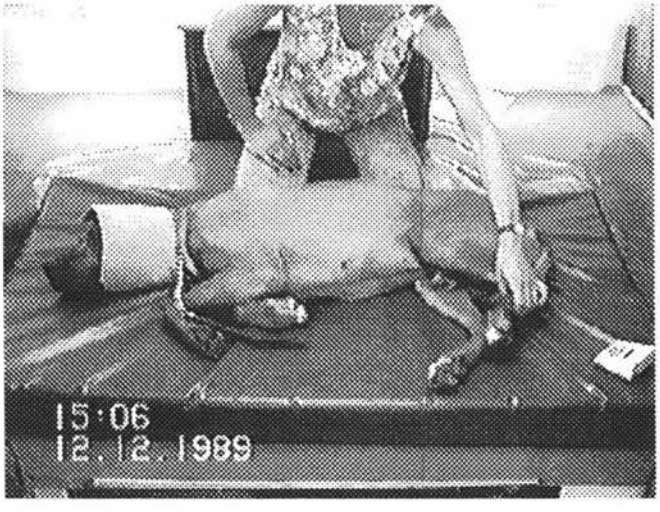


e. Lateral restraint on dog's right side.

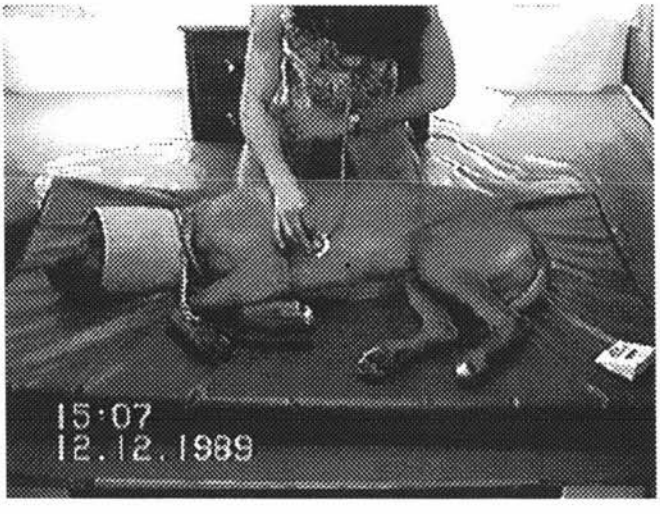
f. Counting respiration rate at 1min30s

Figure 5.6 Physiological testing procedure for cuffing induction technique ....

g. Testing muscle tone at 2 min.



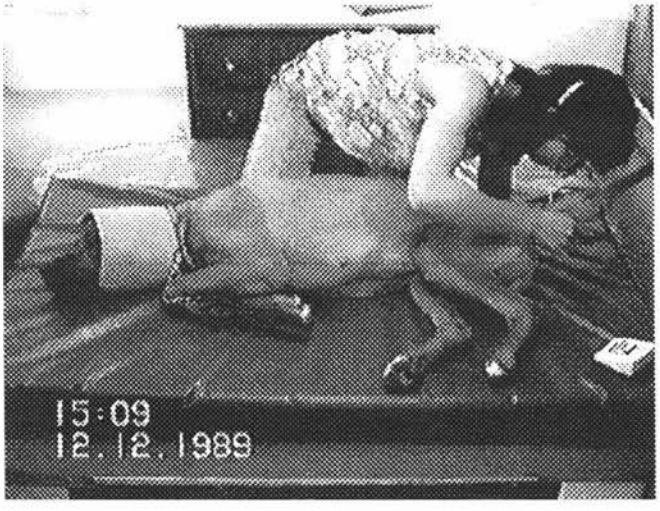
h. Flexing and extending stifle joint at 2 min.



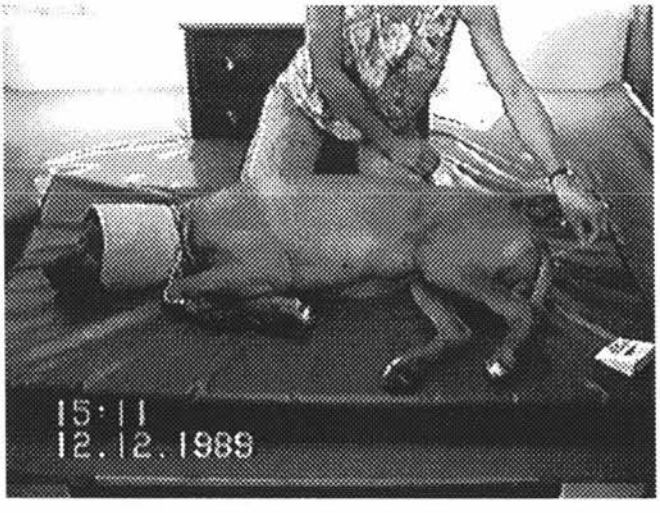
i. Counting heart rate at 3 min.

Figure 5.6 Physiological testing procedure for cuffing induction technique ....

j. Testing withdrawal reflex at 4 min.



k. Inserting thermometer at 5 min.



l. Removing thermometer at 7 min.

Figure 5.6 Physiological testing procedure for cuffing induction technique.

As for the previous test, at the end of the induction procedure, the investigator gently release restraint, placed her arms on her lap and remain kneeling beside the dog (Figure 5.6f). The assistant sat on the chair approximately 1m from the dog (Figure 5.7) when not assisting during the induction procedures (Figure 5.8). If the dog was still immobile at 55s, the assistant would switch on an audio cassette player and a 1s 412Hz square wave tone would sound at 1 min. The cassette would be left running as 1s tones had been recorded with increasing intensities at 15 and then 30s intervals. Table 5.2 illustrates the auditory stimulation and physiological testing schedule.

Physiological testing during the TI episodes also involved increasing stimulation with respiration rate being assessed at 1min 30s by counting chest movements for 15s (Figure 5.6f). At 2 min, muscle tone was tested by feeling the tone in the semi-tendinosus and semi-membranosus muscles (Figure 5.6g) as well as by flexing and extending the stifle

Figure 5.7 Position of investigator and assistant during testing.

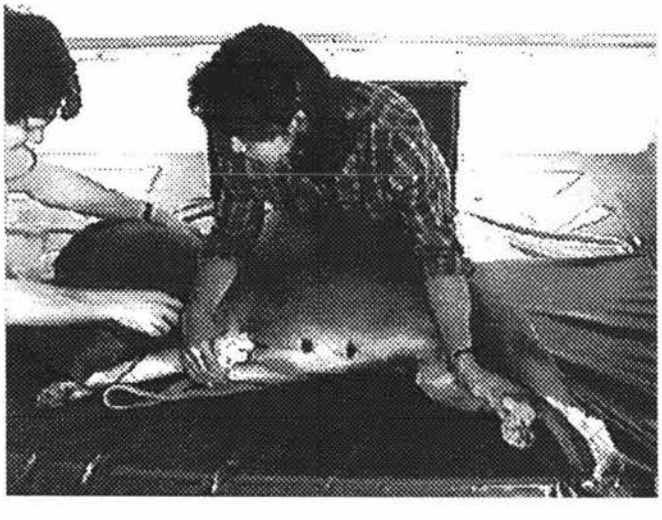


Figure 5.8 Assistant placing blanket over dog's head.

AUDITORY STIMULATION AND PHYSIOLOGICAL TESTING SCHEDULE

TIME (min)	AUDITORY STIMULATION (dB)	PHYSIOLOGICAL TESTING
1:00	44	
1:15	54	
1:30		Respiration rate
1:45	58	
2:00		Muscle tone
2:15	62	
2:45	64	
3:00		Heart rate
3:15	66	
3:45	68	
4:00		Withdrawal reflex
4:15	72	
4:45	74	
5:00		Temperature
5:15	76	
5:45	78	
6:15	80	
6:45	81	
7:00	83	Termination of test

Table 5.2 Auditory stimulation and physiological testing sequence.

joint (Figure 5.6h). Muscle tone was recorded as relaxed or tense. At 3 min if the dog was still immobile, heart rate was determined by gently resting a stethoscope or hand over its heart for 15s (Figure 5.6i) and at 4 min, the withdrawal reflex of the dog would be tested by pinching between the toes of its left upper foreleg (Figure 5.6j). Finally at 5 min, provided the dog was still immobile, a thermometer would be inserted through the dog's

anus to record its rectal temperature (Figure 5.6k). If this did not terminate TI and the dog was still immobile at 7 min, the thermometer was removed (Figure 5.6l), temperature recorded and the dog rubbed and stimulated to terminate TI.

At the termination of TI, whether spontaneously or due to external stimulation at any stage of the testing, the termination heart rate and the state of the dog at termination were recorded. In addition, the ease of induction (easy or struggling), duration of TI (from release of restraint till the dog lifted its head off the mattress), observations during TI (eg. eye movements, slight head or limb twitches, swallowing or licking), cause of termination and state of the dog after testing (dazed or normal; friendly, timid or aggressive) were also recorded.

During the 3 min interval between tests, further behavioural observations were recorded, the audio cassette was rewound (if played) and preparation for the next test occurred. The dog was patted and quietly spoken to during this period (Figure 5.9) and just prior to the next test, it's heart rate was measured and the state and demeanour of the dog assessed as calm or excited and friendly, timid or aggressive. This procedure was repeated 4 times until each dog had been tested with the 5 induction techniques (control, stroking, blanket, cuff and scruffing).

The entire procedure was videotaped for further analysis commencing once the dog stepped onto the mattress and continuing until the dog was ready to leave the caravan. This allowed a closer observation of the dog's reactions and responses during testing.

Pair, order, treatment and carry-over effects were examined using analysis of variance (ANOVA). Other associations between continuous data were tested using Spearman's correlation and Chi square or Fisher's exact tests for categorical data.

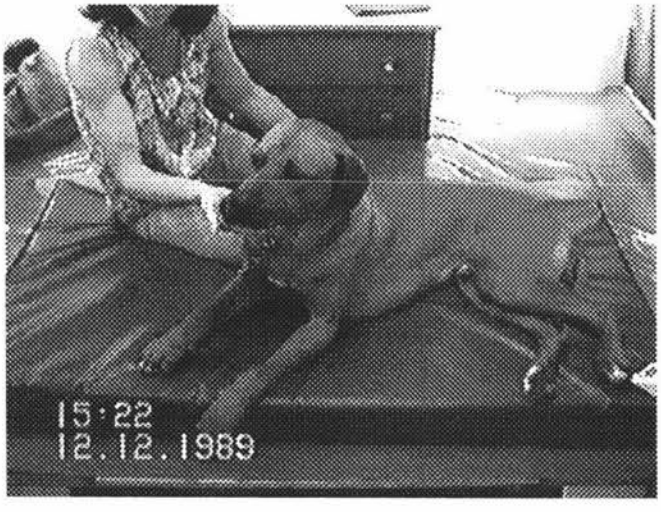


Figure 5.9 Patting the dog between tests.

5.6 RESULTS

5.6.1 SUSCEPTIBILITY AND DURATION

Of the 20 dogs tested in this study, 14 dogs exhibited TI (as defined by the criteria of remaining in the position restrained, without lifting their head off the mattress, for a minimum of 10s). All 10 dogs that exhibited TI in the previous survey (TI dogs - **bold** in Figure 5.10) exhibited TI again in this study. Four of the matched controls (*italics* in Figure 5.10) which did not exhibit TI in the survey exhibited TI in this study. Using Fisher's exact test, the dogs that exhibited TI in the initial survey were therefore more susceptible to TI during this study than those that did not exhibit TI in the previous study (P = 0.01).

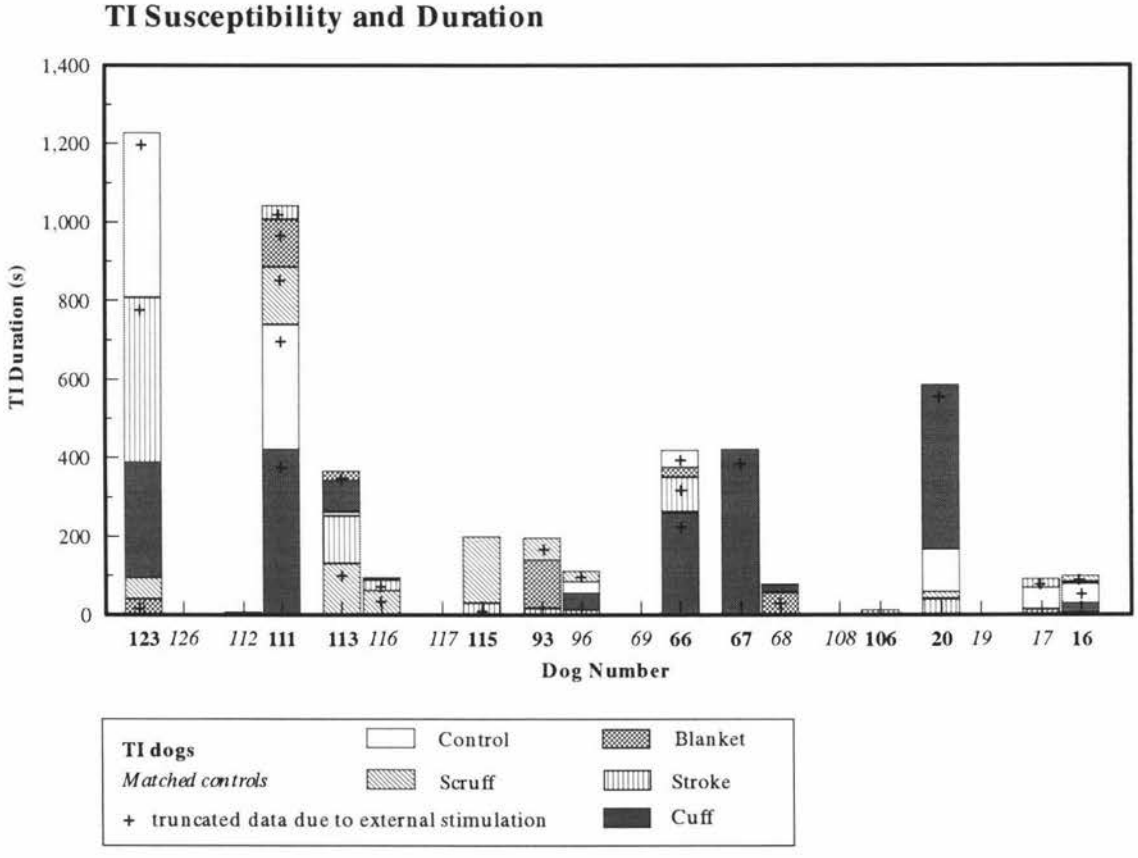


Figure 5.10 TI susceptiblity and duration.

The dogs that exhibited TI in the previous survey were also more susceptible in this study (as measured by the number of successful inductions out of the 5 induction attempts) than the dogs that previously did not exhibit TI as they exhibited TI an average of 3.3 out of the 5 induction attempts as compared to the previously non-TI dogs' average of only 1.2 successful inductions out of the 5 induction attempts in this study.

A strong correlation (P < 0.01, Spearman's $p = 0.82$) was also found between each dog's average duration of TI in the previous survey and in this study. The duration of TI in this

study ranged from 10s to the maximum allowed 7 min (420s) with an average duration of 112s. Four of the previous TI dogs exhibited TI for the maximum allowed duration of 7 min on 5 occasions. The average duration of the non-TI episodes was 0.7s with the dogs righting themselves immediately (duration 0s) after release from restraint in 80% of these episodes. The duration of immobility in the other non-TI episodes ranged from 1 - 6s.

The results from this study clearly show that the 10 dogs that exhibited TI in the previous survey had longer durations of TI, on average, than the 10 dogs that did not exhibit TI in the previous survey. The duration of TI in the dogs that exhibited TI previously were consistently longer than the duration of TI in the dogs that had not exhibited TI previously with the average duration of TI in the dogs that exhibited TI previously being almost 12 times longer than the average duration of TI in the dogs that had not exhibited TI previously. The respective average durations were 91.6s and 7.7s, giving an average difference of 83.9s. The standard error of this estimate is 15.9, so that a 95% confidence interval for the overall (TI - non-TI) difference is 83.9 ± (2x15.9), or 52-116.

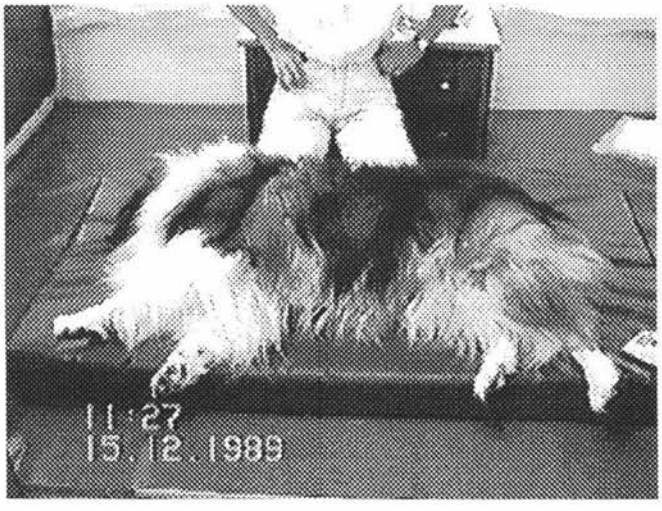
5.6.2 CHARACTERISTICS DURING TI

During TI, the characteristics of the dogs were almost identical to those observed in the previous survey. Figures 5.11 - 5.15 illustrates TI from the 5 induction techniques in 12 dogs. After release from restraint, all the dogs exhibiting TI remained very still, with the exception of occasional head, limb and tail movements which were observed in 65% of the TI episodes and in all of the TI episodes that were longer than 1 min duration. This involved minor repositioning of the dog's head (without lifting the head off the test surface) or limbs, muscle trembling or twitches and paw movements.

Whenever visible, the dog's eyes were open throughout most of TI and eye movements were recorded in over 70% of these TI episodes and in 95% of the episodes lasting longer than 1 min duration. Blinking and occasional periods of eye closure were observed but the dogs appeared to be observing their environment throughout most of the TI episodes. Muscle twitching, ear movements and changes in respiration rate were also observed in response to auditory and other stimuli. Four dogs were observed to lick their lips and/or swallow during TI.

At termination of 60% of the TI episodes, the dogs appeared normal and righted themselves immediately. Two dogs appeared to jump out of TI by righting suddenly on 3 occasions but did not attempt to attack or escape from the experimenter. There were however, occasions when the dogs appeared to be slow or reluctant to get up after termination of TI. This tended to occur especially after TI episodes of longer than a minute's duration with the dogs appearing to be slow in 67% of the TI episodes that were longer than 1 min duration.

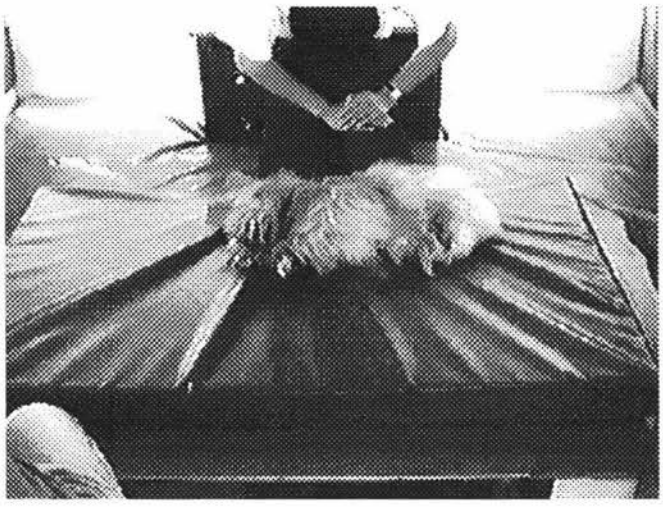
Dog 96



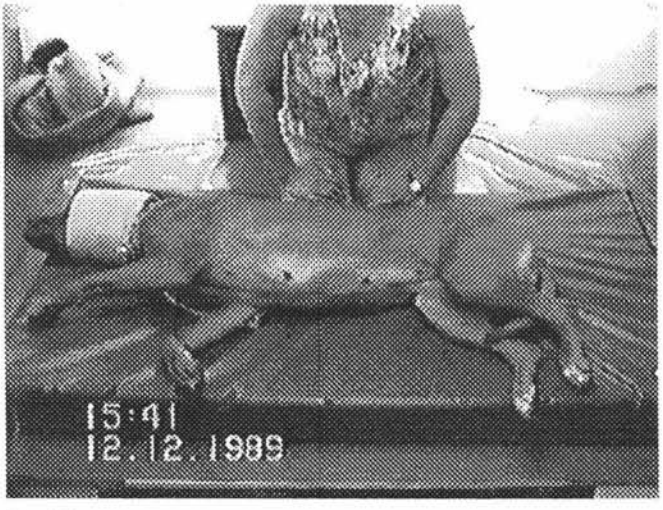
Dog 20

Dog 111

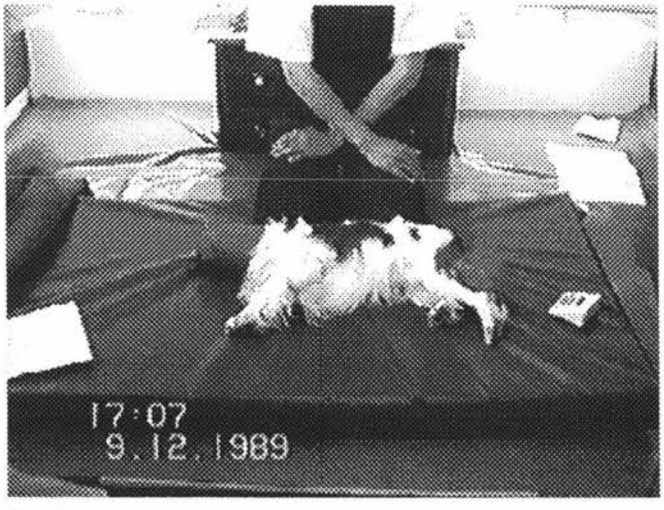
Figure 5.11 Tonic immobility from control induction technique.



Dog 123



Dog 68

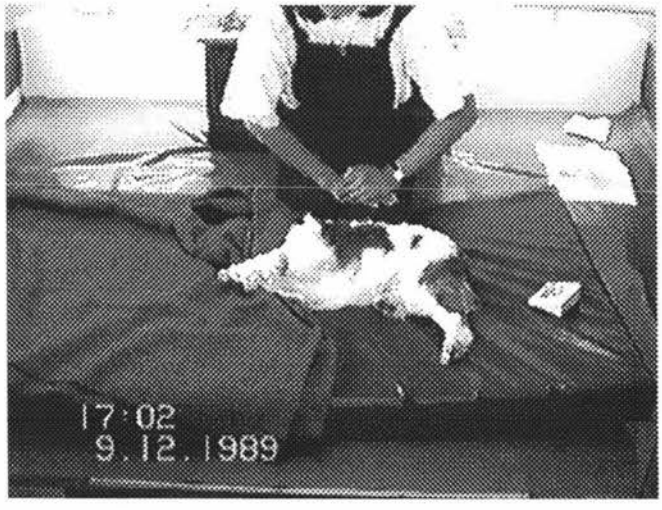


Dog 113

Figure 5.12 Tonic immobility from cuff induction technique.

Dog 17

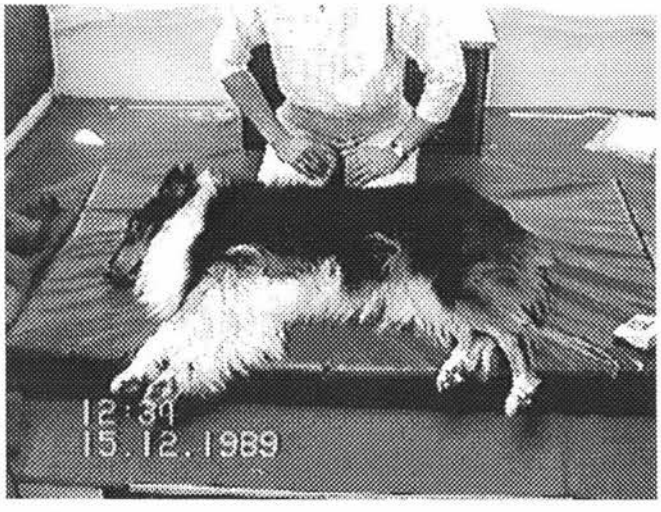
Dog 68



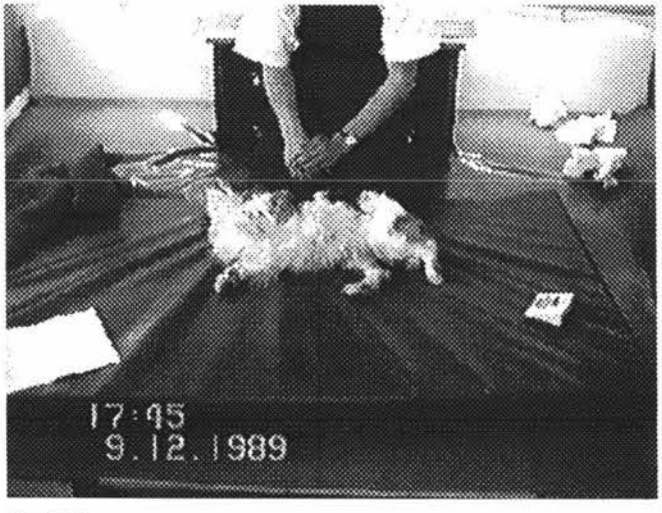
Dog 113

Figure 5.13 Tonic immobility from blanket induction technique.

Dog 115



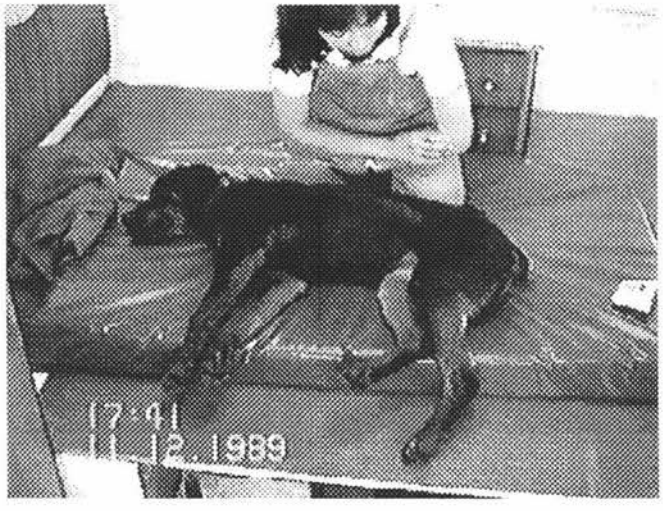
Dog 16



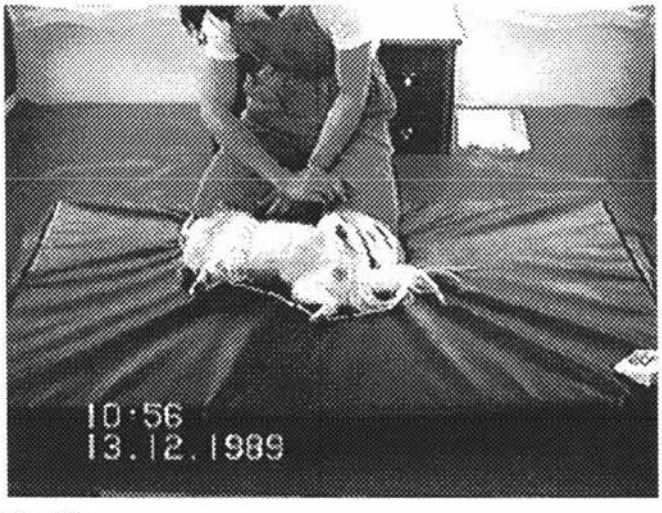
Dog 116

Figure 5.14 Tonic immobility from scruff induction technique.

Dog 115



Dog 93



Dog 106

Figure 5.15 Tonic immobility from stroke induction technique.

5.6.3 PHYSIOLOGY DURING TI

Chest movements were visible during TI and if the dog was still immobile at 1min 30s after release of restraint (15 occasions), respiration rate was counted. Respiration was variable ranging from 8 to 120 breaths per minute with an average of 29 breaths per minute across the 8 dogs. Only on 2 occasions did the respiration rate exceed 40 breaths per minute and this occurred following struggling during induction. On the other occasions respiration was less than 20 breaths per minute and induction was easy without any struggling.

As for respiration rate, heart rate was also variable as is to be expected in any dog population especially with the large range in sizes, breeds and temperaments. The initial heart rates measured prior to induction varied from 52 - 140 beats per minute and the final heart rate at termination of testing ranged from 52 - 144 beats per minute.

What was of interest was the change in heart rate during TI. In 52% of the TI episodes, heart rate decreased as compared to 14% where the heart rate remained the same and 34% where the heart rate increased. These differences were however not significant (P = 0.4, Chi square). For the TI episodes that lasted greater than 30s, there was a decrease in heart rate in 61% of these episodes as compared to 7% with no change in heart rate and 32% with an increase in heart rate. Once again however, these differences were not significant (P = 0.1, Chi square).

As there were only 8 episodes of TI which lasted for over 3 min when heart rate was being assessed, only 8 measures of heart rate were obtained during TI. In 75% of these episodes there was a decrease in heart rate from the initial rate before induction until the 3 min recording and 25% where heart rate increased. These differences were again however, not significant (P = 0.3, Binomial test).

Muscle tone was difficult to assess but was recorded as relaxed in 50% of the TI episodes and tense in 50% of the TI episodes when tested at 2 min. Withdrawal reflex on the other hand, was strong during all the episodes when tested at 4 min.

Inserting the thermometer at 5 min was more an assessment of depth than an attempt at recording the temperature. As only 5 episodes of TI lasted for the maximum allowed 7 min, only 5 temperature recordings were made. The temperature ranged from 38.5 to 39.5°C with an average of 39.2 °C.

5.6.4 DEPTH OF TI

As these episodes of TI did not terminate when the dog's tail was lifted and the thermometer inserted into the dog's rectum at 5 min, nor by the removal of the thermometer at 7 min, it appears that these dogs were in a relatively deep state of TI. The depth of TI was subjectively based on the intensity of stimulation that terminated TI.

There was continuous external stimulation during TI in the form of traffic noises, barking dogs, and people talking in the background. In addition, the dogs were continually stimulated from 1 min onwards by the 412Hz square wave tones and physiological testing. Dogs that remained in TI and were unresponsive to these stimuli therefore appeared to be in a relatively deep state of TI.

With the exception of one occasion when TI was terminated by passing traffic, all the non-TI episodes appeared to terminate spontaneously. Out of the 44 episodes of TI in this study, 25 (57%) were terminated by noticeable external stimulation and the rest (19) terminated spontaneously. The known stimuli that terminated TI before the 7 min maximum included movement in the caravan by the assistant (8x - including 3x to turn on the cassette player), by the experimenter (5x), traffic noise (3x), sneezing (1x), 72dB tone (1x), wind flapping the caravan's blinds (1x) and inserting the thermometer (1x).

All TI episodes of longer than 5 min were terminated by known external stimulation. Seventy four percent of the TI episodes that lasted for 1 min or more, terminated apparently spontaneously even though these dogs had not terminated in response to other stimuli such as the auditory tones, physiological testing, sneezing, movement in the caravan or seemingly loud traffic noises. In comparison, 56% of the episodes that were shorter than 1 min duration terminated in response to stimuli such as movement in the caravan, sneezing or traffic noises. The other 44% terminated spontaneously.

5.6.5 REPEATED TESTING

No effect of repeated testing on the susceptibility or duration of TI in subsequent was apparent tests as no habituation or potentiation effect was seen. The first, second, third, fourth and fifth test resulted in 8, 10, 10, 7 and 9 episodes of TI respectively. Examination of the durations of TI from the first to the second, third, fourth and fifth tests also did not reveal any consistent increasing or decreasing TI durations.

In addition to examining for an order effect, because different treatments followed one another, the experiment was also designed to account for the possibility of carry-over effects. That is, whether a particular treatment was affected by the immediately previous treatment. No significant order or carry-over effect on duration of TI was however found using an analysis of variance (ANOVA) examining order, carry-over and treatment effects ($P > 0.05$).

5.6.6 INDUCTION TECHNIQUE

A significant treatment effect on the duration of TI was however found ($F_{4,32}(0.95) = 2.94$, $P = 0.04$). (Table 5.3) The mean duration for the different treatments were:

Cuff (185s), Control (86s), Stroke (70s), Scruff (51s) and Blanket (27s). The standard error for comparing any two treatments was 50.2. Therefore using two standard errors as a criterion of significance, the pairwise differences that were clearly significant were (Cuff-Blanket), (Cuff-Scruff) and (Cuff-Stroke), with (Cuff-Control) being of borderline significance. That is, the cuff technique resulted in longer TI durations than the blanket, scruff and stroke techniques and marginally longer than the control technique.

Analysis of Variance examining pair, order, treatment and carry-over effects on duration of TI.				
Source	df	SS	MS	VR
Pair	9	317166	35241	2.79
Order	4	38077	9519	0.76
Treatment	**4**	**148043**	**37011**	**2.94**
Residual	32	403117	12597	
Total	49	906403		

Table 5.3 Analysis of variance examining pair, order, treatment and carry-over effects on duration of TI.

There did not appear to be any treatment effect on the susceptibility to TI as all the induction treatments/techniques were successful in inducing TI with 60% of the Stroke inductions resulting in TI, 45% of the Cuff and Scruff, 40% of the Control and 35% of the Blanket inductions resulting in TI.

5.6.7 URINATION / DEFECATION

A significant association was found between susceptibility to TI and urination, defecation or expression of anal glands during testing with all the dogs that urinated, defecated or expressed their anal glands during testing also exhibiting TI (P = 0.051, Fisher's exact test).

The significant findings from this study were that the dogs that exhibited TI in the previous survey were more susceptible to TI and also had longer durations of TI than the dogs that did not. A strong correlation was found between each dog's average duration of TI in the previous survey and in this study, indicating that TI in the initial survey was not a once-off random event but probably a dog effect.

A significant treatment effect on TI duration was however found in this study with the cuff technique resulting in longer TI durations than the blanket, scruff and stroke techniques

and being marginally longer than the control technique. There was no significant order or carry-over effect on the duration of TI but dogs that urinated, defecated or expressed their anal glands were significantly more susceptible to TI. The characteristics during TI also appeared to be the same as those described in the previous survey.

5.7 DISCUSSION

5.7.1 DURATION OF TI

The duration of TI in this study ranged from the minimum criterion duration of 10s to the maximum allowed 420s (7min) with an average duration of 112s. The shorter average duration of TI in this study compared to the previous survey (182s) was probably due to the shorter maximum duration allowed before TI was terminated. Variations in TI durations are also to be expected as it has been reported to vary enormously both between and within individuals (Gallup, Nash and Wagner 1971). Duration of immobility in the non-TI episodes ranged from 1-6s thus indicating that the 10s susceptibility duration criterion for TI once again did not markedly affect the calculated susceptibility to TI.

5.7.2 SUSCEPTIBILITY

The higher susceptibility and longer durations of TI by the dogs previously exhibiting TI compared to those that did not exhibit TI in the previous survey, along with the strong correlation between each dog's average duration of TI in the previous survey and in this study, indicates that TI in the previous survey was not a one-off random event but was probably a dog effect.

It was also observed that all dogs that urinated or defecated during the previous survey also eliminated during this study. Additionally two dogs that did not eliminate in the previous survey eliminated during this study and all of these dogs exhibited TI in this study. Thus there was a strong association between dogs that eliminated during testing and susceptibility to TI.

This is supportive of the notion of TI being a dog effect, as elimination has been reported to be a useful measure of a subject's emotionality of fearfulness (Gray 1971; Plutchik 1971; Archer 1979). Similarly, Reese et al (1985) found that nervous Pointers were more susceptible to TI and exhibited longer TI durations than friendly Pointers and often urinated or defecated in the presence of people.

This study also found that the dogs which eliminated during testing exhibited longer TI durations than the dogs that did not eliminate but the difference in duration was not significant. This is similar to Gallup, Nash and Wagner's (1971) report that birds which defecated during TI or shortly after termination, remained immobile longer than birds

that did not defecate. Gallup, Ledbetter and Maser (1976) also reported that White Leghorn chickens which appear more emotional and fearful reliably show longer TI durations than the less emotional Production Red chickens and also were significantly more prone to defecate. These findings are however, contrary to the results from the previous survey which indicated that dogs that did not urinate or defecate exhibited longer TI durations despite being less susceptible to TI than the dogs that did. These differences in TI durations were however not significant.

The increased susceptibility to TI in this study (70%) as compared to the previous one (7.6%) reflects the selective sampling from the survey population. As TI appears to be a dog effect, a 50% susceptibility may have been expected. The increase in susceptibility to TI in the previously non-TI dogs was however, not completely unexpected as the non-TI dogs were matched as closely as possible for breed, temperament, age and sex to the TI dogs. As TI appears to be a dog effect possibly related to the dog's temperament or fearfulness, it was not surprising that some of the dogs that did not exhibit TI in the previous study exhibited TI in this study since matching ensured that dogs similar in these characteristics to those exhibiting TI were tested.

Also these control dogs may have had a lower predisposition to exhibit TI and the increased number of inductions in this study and consequently increased duration of testing and prolonged contact with the experimenters may have increased the probability of their exhibiting TI. The shorter durations of TI exhibited by these dogs that did not exhibit TI in the previous study may also indicate their lower predisposition to TI.

It is unlikely that different experimental procedures potentiated TI in these previously non-susceptible dogs as almost identical experimental procedures were followed. The investigator's skill at inducing TI may have however improved despite only a slight increase in TI susceptibility and duration as testing progressed in the previous survey which was not significant. It is also unlikely that a potentiation effect of repeated testing caused the increase in susceptibility to TI in these previously non-TI dogs as contrary to the previous survey, no order effect on susceptibility or duration of TI was found in this study.

5.7.3 REPEATED TESTING

It therefore appears that increasing the intertrial interval from 20 - 80s in the previous survey to 3 min, which is 12 times the 15s reported minimum required to avoid potentiation effect of massed trials (Nash and Gallup 1976) was successful at eliminating the potentiation effect seen the previous study. No habituation effect was seen in this study either as the greatest decline in responsiveness to TI is reported to occur when trials are widely spaced (Crawford 1977). That is, 1 trial a day for 24 days as opposed to 12 trials

a day for 2 days or as for this study 5 trials a day for 1 day. No carry-over effect from the preceding technique was found in this study.

5.7.4 INDUCTION TECHNIQUE

A significant treatment effect on the duration of TI was found, with the cuff technique inducing longer TI durations than the other techniques. However, no significant treatment effect on the susceptibility to TI was found indicating again that susceptibility and duration may be independent parameters of TI (Gallup et al 1976). That is, if a dog is susceptible to TI, then any of the induction techniques used in this study would have induced TI. The duration of TI may however, be prolonged by the cuffing technique.

The increase in TI durations by the cuffing technique may have been due to the novelty of the cuff, as most dogs would never have had a pressure cuff wrapped around their head, whereas they would have been accustomed to being stroked, grabbed by the scruff and may have had a blanket or some other material placed over their heads. The cuffing technique also involved the most handling prior to testing as the dogs were restrained while the cuff was wrapped around their heads. This meant that the cuff was applied before the dogs were inverted and restrained and remained on the dogs till TI was terminated whereas the other techniques were only applied after the dogs had been inverted and restrained. Stroking and scruffing terminated after the 30s restraint period whereas cuffing and the blanket over the dogs' head remained till TI was terminated.

Any of these factors of increased novelty, handling or duration of stimulation may have prolonged TI durations using the cuffing technique as all of these factors have been reported to potentiate TI (Ratner 1967). Continuous pressure around the ears and head region may have also potentiated TI durations by giving the impression of continuous predatory contact around the head region. Thompson et al (1981) observed that TI was only induced in quails stalked by cats if the cats held or bit the quail especially around the neck region. Potentiation of TI by using a similar cuffing technique has also been reported in sheep (Holmes 1989).

5.7.5 CHARACTERISTICS DURING TI

The characteristics of TI during this study in dogs were similar to those reported in other species (Gallup 1977; Jones 1986a) and observed in the previous survey, as the dogs all lay very still, with the exception of occasional repositioning of heads and limbs, muscle trembling, twitches and paw movements. As for other species (Gilman and Marcuse 1949; Klemm 1966a; Carli 1974), muscle tone was variable and difficult to assess. Swallowing, lip licking, blinking and occasional periods of eye closure were observed but the dogs had their eyes open throughout most of the TI episodes and appeared to be observing their

environment as eye movements, ear and muscle twitches and changes in respiration rate were observed in response to auditory and other stimuli.

As reported in other species (Carli et al 1974; Sigman and Prestrude 1981), these responses indicated that considerable central processing of the external environment was occurring during TI even though the dogs appeared to be relatively unresponsive as they did not right in response to other stimuli such as the auditory tones, passing traffic or physiological testing. These stimuli have been reported to cause termination, especially if the stimulation is intense and abrupt in onset (Ratner 1967).

5.7.6 DEPTH OF TI

Although the longer TI episodes were not terminated by seemingly intense stimuli such as loud passing traffic, 80dB tones and physiological testing that involved pinching between the dog's toes and inserting a thermometer into the dog's rectum, many of the shorter episodes terminated apparently spontaneously. It was however, difficult to determine the "depth" of TI or degree of unresponsiveness as there were occasions when TI was not terminated by intense external stimulation but appeared to terminate spontaneously instead. It however did appear that the longer an animal remained in TI, the more likely it would remain in TI despite the increasing intensity of the external stimulation.

This is however, contrary to Rakshit and Klemm's (1980) report of a progressive decrease in depth as the duration of TI progressed in rabbits. Depth was assessed by measuring the resistance of TI to be disrupted by electrical stimulation. Hatton and Thompson (1975) on the other hand, investigated the effects of 60 - 90 dB tones on the duration of TI in chickens. They found that the intensity of the stimulus may be important in determining whether TI duration is decreased, unchanged or increased as at 60dB TI durations were decreased, but increased at 70dB and then decreased again at 80 and 90 dB. Two distinct effects of auditory stimulation on TI durations were therefore suggested. Firstly, an increase in duration due to increasing fear if the stimulation is intense enough then, as the stimulus further increases in intensity, a startle response which terminates TI may occur.

The apparent increased "depth" of TI as durations increased may therefore have been due to potentiation of TI by the various auditory tones and physiological testing increasing fear in the dogs. Further investigation is however required as this study was not specifically designed to test the effect of varying stimulus intensity on TI but was intended to determine the extent of clinical or physiological assessment that could be conducted while a dog was in TI.

What can be concluded from the study so far is that many of the TI episodes were not terminated by a variety of tactile and auditory stimuli (eg. talking, barking dogs and

shouting children) that would normally be present in a veterinary clinic and that it is possible to monitor respiration rate, heart rate, withdrawal reflexes and temperature on a small percent of dogs while in TI.

5.7.7 PHYSIOLOGY

Respiration rate during TI when measured at 1min 30s post induction was within the normal ranges recorded for dogs and was only elevated if induction resulted in intense struggling by the dogs. Similar findings of increased respiration rate at the onset of TI following struggling has also been reported in the chicken (Nash, Gallup and Czech 1976), iguana (Prestrude and Crawford 1970) and rabbit (Klemm 1966a).

Heart rate is also reported to be elevated following induction (Ratner 1967; Carli 1974; Nash, Gallup and Czech 1976) but is usually followed by a gradual return to pre-induction levels prior to termination (Ratner 1967; Ookawa 1972; Nash, Gallup and Czech 1976). Pre- and post-TI heart rates recorded in this study decreased in 52% of the TI episodes, remained the same in 14% and increased in 34%. Heart rate is also reported to further decrease during long TI episodes (Moore and Amstey 1963; Carli 1974). Although not significant, a decrease in heart rate was observed in 61% of the TI episodes that lasted longer than 30s duration. Seventy-five percent of the heart rates measured at 3 min were also observed to be decreased.

Reese et al (1982) reported a significant bradycardia during TI in their nervous Pointers and not in the friendly Pointers who did not exhibit TI. Fox (1978) also reported of bradycardia in canids during TI and passive submission which he believed to be an adaptive homeostatic mechanism to control for sympathetic hyperarousal. Nash, Gallup and Czech (1976) suggested that although fear induced release of adrenalin and noradrenaline acts to accelerate heart rate, the pressor response produced by the catecholamines stimulates arterial baroreceptors thus resulting in sufficient vagal tone to overcome the direct effect and produce cardiac deceleration

Beside these changes in heart rate during TI, other physiological measures appeared to be normal, as withdrawal reflexes were strong and body temperature normal. This is contrary to Nash, Gallup and Czech's (1976) report of lowered body temperature during TI in chickens and Carli's (1977) report of absent withdrawal reflexes in rabbits. Species variation in spinal reflexes have however been reported (Carli 1968).

5.7.8 TERMINATION

Another difference found in this study was the behaviour of the dogs both at induction and termination of TI. As for the previous survey, but contrary to reports in other species (Ratner 1967; Klemm 1971c; Lefebvre and Sabourin 1977), very little struggling was

observed during induction. Similarly, at termination, although two dogs appeared to jump out of TI on 3 occasions, none of the dogs attempted to attack or escape from the investigator at termination of TI. Especially with the TI episodes of greater than 1 min duration, many of the dogs appeared to be slow or reluctant to get up following termination of TI.

This lack of escape response as reported in other species (Ratner 1967; Gallup 1974a) most likely reflects the tameness of the dogs and may explain the low susceptibility to TI observed in these studies as it is commonly reported that subjects that are used to human handling or have been tamed are less susceptible to TI (Gilman et al 1950) and that TI is not usually elicited in family pets (Ratner 1967).

These differences aside, the TI observed in this study is similar to that reported in other species.

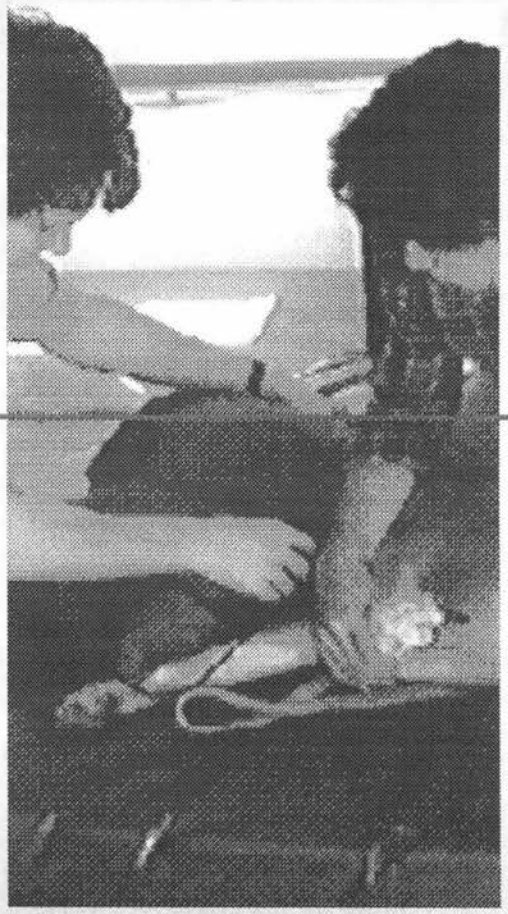
5.8 CONCLUSION

It appears from this study that the TI observed in the previous survey was not a one-off random effect but was probably a dog effect. The strong correlation found between elimination and susceptibility to TI indicates that the dog effect may be related to the dog's temperament or fearfulness.

No order or carry-over effect was found with repeated testing, but a significant treatment effect was found with the cuffing treatment resulting in longer TI durations than the other techniques. With the exception of less escape response during induction and termination, the characteristics and physiology of the dogs during TI were comparable to that reported in other species. The bradycardia reported in other species was also observed in some dogs during TI. The "depth" of TI however appeared to increase as TI progressed, possibly due to increased fear as a result of the auditory stimulation and physiological testing.

Chapter six

Overall Discussion



Overall Discussion

Tonic immobility or TI is a state of relative immobility induced by restraint and presumed to function as a terminal defensive reaction. Although it has been reported in a wide spectrum of species ranging from invertebrates such as insects, spiders and crustaceans to fish, amphibians, reptiles, birds and mammals including humans, there have been very few studies on TI by dogs.

The wide range of species reported to exhibit TI seems to indicate a general phylogenetic spread of the phenomenon (Ratner 1977) and most investigators (eg. Frolov 1937; Gilman and Marcuse 1949) believe that "the capacity of becoming immobile under the influence of compulsory restriction of movement is characteristic of all species". Others however (eg. Danilewski 1890, Svorad 1956), report that certain species for example cats, dogs, rats and mice are refractory to "hypnosis". It is however more likely that different species vary in their susceptibility to TI and also in the best induction technique required for inducing TI, as other investigators (eg. Mangold 1914) have been able to induce TI in these species.

Although there have been brief references made to TI by dogs (eg. Hoagland 1928; Wilson 1839; Fox 1968 and 1978) and 2 reports on TI in a nervous line of Pointers (Reese et al 1982 and 1985), this is believed to be the first specific study of TI in non-experimental dogs. Based on the criterion of remaining in the position restrained, without lifting its head off the test surface, for a minimum of 10s after release from restraint, 7.6% of the dogs tested in the initial survey exhibited TI.

Although this susceptibility is lower than that reported in commonly tested species such as chickens, rabbits and lizards, it was expected based on previous reports of dogs being either insusceptible (Danilweski 1890; Svorad 1957; Prestrude 1977) or poorly susceptible to TI (Hoagland 1928; Chertok 1964).

This low susceptibility of dogs to TI may be for several reasons. It is for example, commonly reported that domesticated strains or subjects that have been tamed or used to human handling are less susceptible to TI than wild subjects or subjects that have had minimal human handling (Franq 1969; Whishaw et al 1978; Hennig 1979a). This may be related to the importance of fear in potentiating TI (section 2.8.6) or the importance of predatory overtones in the induction of TI (section 2.8.7).

As all the dogs in this survey were domestic and had extensive human handling, they were not fearful of humans nor would they be expected to view the human investigator as a potential predator. Ratner (1967) reported that TI is not usually elicited in family pets

that are tame and used to human handling. The finding that the more timid or fearful dogs and those that urinated or defecated during TI were more susceptible to TI than the friendly dogs or the dogs that did not eliminate during testing is supportive of the idea that TI by dogs may be related to the degree of fear shown towards the human investigator.

It is also possible that dogs have not developed TI to the same degree as other species. Webster et al (1981) tested TI in 12 species of rodents and suggested that predatory species may be less susceptible to TI than other species. Ratner (1967) also believed that some species may have evolved immobility and its associated reactions to a higher degree than others. Armstrong (1955) for example, observed that compared to most other species of birds, the European Wren which is characterised by great activity and nimbleness has never been observed to exhibit TI.

The stimuli that elicit TI may also have an evolutionary basis, with different specific stimuli being the most appropriate to elicit TI in different species. Immobility reactions in the mantids for example, appear to be elicited most readily by the attack of another mantid (Crane 1952). The low TI susceptibility observed in this study may therefore be because inappropriate induction methods were used.

Inversion and restraint was used to induce TI as this is the "classical" and most commonly used technique for inducing TI in other species (Gilman et al 1950; Ratner 1967; Gallup, Nash and Wagner 1971). The additional treatments applied during TI (stroking, scruffing, blanket, cuff and light) were chosen as representative of the range of methods (eg. stroking, swaying, grabbing, hooding and eye fixation) reported in other species. The absence of a technique effect on the susceptibility of TI in this study may however, reflect the similarity across the different techniques (inversion and restraint across the body and limbs). Other techniques should therefore be tested in an attempt to increase the susceptibility to TI.

The potentiation effect of the cuffing technique on the duration of TI indicated that susceptibility and duration may be independent parameters of TI as suggested by Gallup, Ledbetter and Maser (1976). That is, if a dog is susceptible to TI, then any of the induction techniques used in this study could have induced TI. The duration of TI may however, be prolonged by the cuffing technique. Other examples of this dichotomy between susceptibility and duration of TI were also observed with proestrous dogs being more susceptible to TI but male dogs exhibiting TI durations three times longer than the other dogs and moderate breeds exhibiting TI twenty times longer than the timid breeds even though the timid breeds were more susceptible to TI. Therefore, although timid breeds

were more susceptible to TI, once TI is induced, the duration of TI may be controlled by other factors.

The duration of TI observed in these studies ranged from the 10s minimum duration criterion for TI to the maximum allowed 646s (10min 46s). This variation in the duration of TI is similar to that observed in other species, as the duration of TI is reported to vary enormously both between and within individuals (Gallup, Nash and Wagner 1971) ranging from a few seconds to several hours. Longer durations of TI in the dogs were not recorded as TI was terminated after 10 min in the first study and after 7 min in the second study. As previously discussed (section 4.7.1 and 5.7.1) the duration criterion of 10s did not affect the calculated susceptibility to TI.

Even though only a low susceptibility was observed, these studies have shown that contrary to reports of dogs being refractory to TI (eg. Danilewski 1890), like most other species, normal non-experimental dogs do exhibit TI. The characteristics of the dogs during TI were also similar to that reported in other species (Gallup 1977; Jones 1986a) as the dogs all lay very still, with the exception of occasional repositioning of heads and limbs, muscle trembling, twitches and paw movements. Swallowing, lip licking, blinking and occasional periods of eye closure were also observed but the dogs had their eyes open throughout most of the TI episodes and appeared to be observing their environment as eye movements, ear and muscle twitches and changes in respiration rate were also observed in response to auditory and other stimuli.

This similarity in the characteristics observed during TI across the various species, along with the similar induction procedures supports Ratner's (1977) belief that the immobility reaction reported in species ranging from invertebrates to vertebrates represents the same phenomenon. However, although the widespread phylogenetic representation of TI seems to signify its biological significance, other than the suggestion that TI has survival value in nature, no generally accepted explanation of this behaviour has been postulated.

One proposal is that TI is one of the final responses made by a prey in a sequence of responses that occurs when a prey is approached and attacked by a predator (Ratner 1967). The response a prey makes depends on the "defensive distance" between the prey and its predator. As the defensive distance is decreased the prey exhibits in succession responses such as freezing, fleeing, secreting, fighting and finally the immobility response. (Figure 6.1)

That is, at an appreciable distance from a predator, the typical prey reaction is to freeze in order to reduce detection. However, if the predator then approaches and thus reduces the defensive distance, flight becomes more likely as the prey attempts to escape. This is

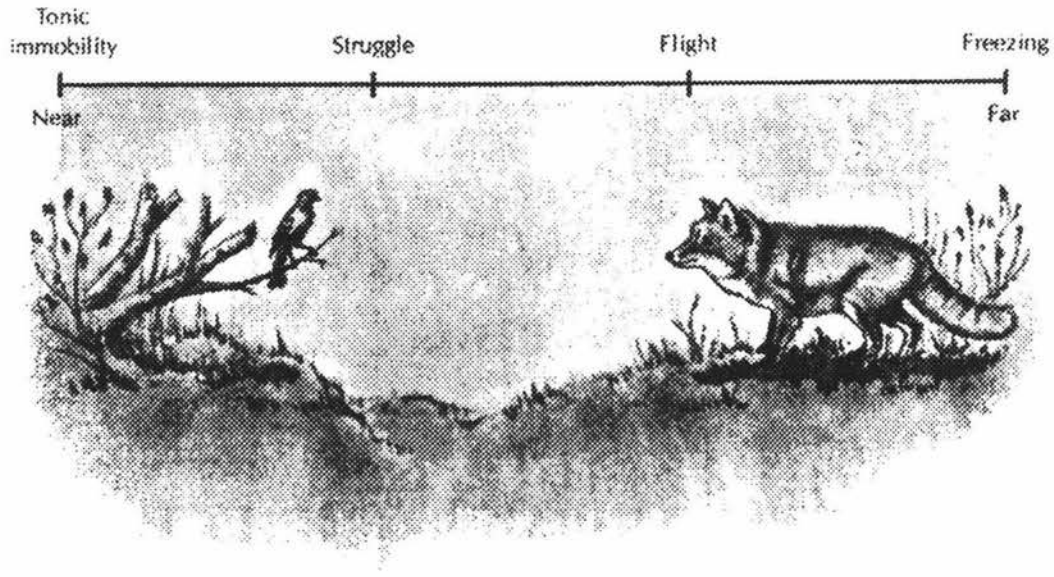


Figure 6.1 Ratner's (1967) "defensive distance" theory (Gallup and Maser 1977)

then followed by fighting and struggling at close quarters if physical contact is made in a further attempt to escape or deter additional predatory advances. Finally, at zero defensive distance, if contact with the predator is prolonged, TI, which represents the terminal defensive reaction in this sequence of distance-dependant predator defence, often ensures. It is postulated that TI may reduce stimulation for further attack or cause the predator to lose interest in the prey, thus allowing it an opportunity to escape while the predator is distracted.

The observation that the dogs in these studies appeared to be actively monitoring their environment during TI is similar to reports in other species (Carli et al 1974; Sigman and Prestrude 1981) and comparable to Sargeant and Eberhardt's (1975) findings that when attacked by red foxes, immobile ducks appeared alert and often took advantage of escape opportunities. These observations are supportive of Ratner's (1967) proposal that TI is a terminal defensive mechanism elicited by predator contact that occurs after other defences have failed and that it has adaptive value in the context of predator-prey interactions.

Although it falls short of explaining TI, in conjunction with the fear theory, this predator-prey theory seems to integrate much of the data on TI as it incorporates somatosensory input, fear and its associated limbic and neuropharmacological considerations. Further support for this predator-prey theory and the role of fear in TI has already been discussed in detail (sections 2.8.6 and 2.8.7).

The finding that the more timid dogs or the dogs that eliminated during TI were more susceptible to TI in this study than the friendly dogs or the dogs that did not eliminate during TI is also supportive of the importance of fear in TI. Similar findings of increased susceptibility to TI in more timid or fearful dogs (Reese et al 1985) and chickens (Gallup et al 1976) has also been reported. Like the dogs in this study, these subjects were also observed to urinate or defecate more during testing than the less susceptible subjects (Gallup, Nash and Wagner 1971; Reese et al 1985).

The observations from this study of TI by dogs appears to support the importance of fear in TI and the relevance of the predator-prey theory to TI by dogs, but more extensive studies into the role of fear and predatory-prey relationships on TI in dogs, such as those conducted in other species (Gilman et al 1950; Ratner and Thompson 1960; Gilman et al 1970; Gallup, Creekmore and Hill 1970; Gallup, Nash, Potter and Donegan 1970; Nash et al 1970; Boice and Williams 1971; Gallup, Nash and Brown 1971; Gallup, Nash, Donegan and McClure 1971; Gallup, Nash and Ellison 1971; Gallup, Rosen and Brown 1972; Gallup and Williamson 1972; Gallup, Cummings and Nash 1972; Gallup 1973b; Maser et al 1973; Eyer and Ratner 1975; O'Brien and Dunlap 1975; Hennig et al 1976; Gallup 1977; Jones 1980; Thompson et al 1981; Jones and Faure 1981c; Jones and Mills 1983; Suarez and Gallup 1983; Jones 1986a, b and c; Thompson and Liebreich 1987), are required. Examination of the neurophysiology and pharmacology of TI in dogs is also required before a mechanism for TI in dogs can be adequately postulated. As yet, there is still no generally accepted explanation of TI in other species.

Considering the similarities in the characteristics of TI and in the procedures effective in producing TI in a wide range of species, Webster et al (1979) postulated that a common response mechanism may be mediating TI across the various species. Lefebvre and Sabourin (1977a) however believed that although TI is generally considered to have a common underlying basis, it is possible that the mechanisms are different in different species and that the differences in susceptibility between species may be explained by differential morphology, physiology or requirements for certain environmental conditions, age and longevity of the subject, induction methods such as degree of restraint or other variables.

The similarities observed between TI and other immobility responses such as freezing behaviour (Borchelt and Ratner 1973; Suarez and Gallup 1982), retrieval response in the carried young (Webster et al 1979), lordosis in response to mating (Naggar and Komisaruk 1977) and pinch or clip induced immobility (Ornstein and Amir 1981; Fleischman and Urca 1988a and b) has caused other investigators to further speculate that a common response mechanism may be mediating these complex behavioural inhibitory states,

irrespective of the present apparent adaptive value of any particular immobility response in a particular species (Naggar and Komisaruk 1977; Webster et al 1979).

Prestrude (1977) and Herzog (1978) also believed that TI may function in intra as well as interspecific encounters as TI has been observed in many species during intraspecific confrontations (Lorenz 1952; Grant and Mackintosh 1963). Herzog (1978) further suggested that TI and submissive postures may be evolutionarily related and some submissive postures may have originated from a TI like response that reduced the probability of attack by both predators and conspecifics by removing movement cues. Another possibility is that fatigue and exhaustion as a result of fleeing or fighting might result in collapse and immobility which could spare an animal from subsequent attack. Natural selection may have then exaggerated the immobility and eventually emancipated it from its original context - exhaustion. As exhaustion is a universal physiological process in response to attack and flight, it may explain the existence of TI in such diverse taxa.

Fox (1978) also noted the similarities between TI and passive submissive behaviour in canids and reported that both of these behaviours were associated with bradycardia. Similarly, in this study, a decrease in heart rate from pre-induction values was also recorded in 75% of the dogs when heart rate was measured at 3 min into TI. Despite this bradycardia, heart rates were however still within the normal values for dogs and so would not jeopardise the health of the dog should TI be used as a form of restraint in veterinary clinics.

Klemm's (1971c) interest in TI had originated from a report (Rapson and Jones 1964) which advocated the use of TI for restraint purposes in rabbits. Extensive studies into TI in rabbits has resulted in the acceptance of the use of TI for immobilising rabbits for injections and blood sampling. It was found that the best method for inducing TI in rabbits for these procedures was to invert them into a V-shaped trough, restrain them briefly and then work on them while they were immobile.

The best methods for inducing TI in dogs and determining whether TI is a feasible method of restraint for clinical use in dogs are still to be determined. The results from this initial study into TI in dogs are promising as they show that dogs exhibit TI. As many of the TI episodes were not terminated by auditory stimuli such as talking, shouting children, barking dogs and passing traffic, it appears that TI may be used in a noisy clinical environment. The duration of TI, characteristics and physiological changes observed during TI also indicate that TI may be useful as a quick, non-chemical, easily reversible and safe method of restraint in susceptible dogs.

Although more extensive studies are required, the physiological parameters measured during TI appear to be within normal limits and the presence of reflexes would also allow a certain degree of neurological assessment during TI. It therefore appears that a general clinical examination involving a brief assessment of the dog's vital signs may be possible while some dogs are in TI.

As to whether other tests and procedures such as injections, blood sampling, skin scrapings, teeth cleaning, nail clipping or minor surgery can be conducted while the dogs are in TI still requires more assessment of the depth of TI or degree and type of stimulation that will terminate TI. The feasibility of performing many of these procedures during TI will depend on whether there is any degree of analgesia during TI. Although many investigators (Holmes 1906; Marcuse and Moore 1944) believe that analgesia is present during TI as it has been possible to perform minor surgical procedures on animals restrained solely by TI (Rapson and Jones 1964; Gruber and Amato 1970), others (eg. Dannerman et al 1988) do not consider TI to be a humane alternative to analgesia or anaesthesia.

Analgesia aside, before TI is routinely used as a method of restraint in dogs, the welfare aspects of TI need to be assessed. Nash and Gallup (1975a) for example reported that the physical restraint during induction was aversive to chickens. The low level of struggling and escape behaviour observed in the dogs during induction and termination of TI are however positive signs that the induction of TI and TI are not excessively aversive to the dogs even when tested repeatedly during the second study. Further behavioural studies are however required to determine if TI is a humane method of restraint in dogs.

Substantially more work is also required to determine if it is possible to potentiate TI susceptibility and prolong durations as although the characteristics and duration of TI in the dogs appear promising for clinical application, the susceptibility to TI needs to be enhanced to ensure that more dogs will exhibit TI. This will involve identification of the individual variables that may affect TI in dogs and a more detailed investigation into how these variables affect TI susceptibility and duration.

From the initial brief attempt at identifying the variables that affect TI by dogs in this study, it appears that subject variables are more important than the experimental variables examined. However, as previously discussed, the low susceptibility observed in this study may have been due to inappropriate induction methods for dogs. It is therefore possible that a different experimental design or induction methods different from those used in this study (eg. using a sling as Reese et al 1982 and 1985) may potentiate TI susceptibility in dogs.

Other experimental variables not examined for in this study (eg. further pre-testing conditions, testing environment, presence of conspecifics or predators, fearful or arousing stimuli) have also been reported to affect TI susceptibility and durations (eg. Gilman et al 1950; Gallup, Nash and Brown 1971; Gallup, Cummings and Nash 1972; Tortora and Borchelt 1972; Eyer and Ratner 1975; Hennig et al 1976; Ewell and Cullen 1981; Suarez and Gallup 1981; Jones 1984; Jones and Faure 1982; Kujivat et al 1983) and should be investigated. None of the experimental variables examined in this study (method of induction, order of testing, record number or time of testing) had any significant effect on the susceptibility to TI.

As discussed above, the cuffing technique did however prolong TI durations in the susceptible dogs. Although further study is required to determine exactly what aspect of the cuffing technique enhanced TI, this technique may be useful should long TI durations be required for longer clinical procedures. The maximum or average uninterrupted duration of TI by dogs was also not examined in this study and still needs to be determined.

In addition to the potentiation effect of the cuffing technique on the duration of TI, repeated testing was also found to prolong TI durations in the first study. Further investigation as to the effect of different testing schedules on TI susceptibility and duration is however still required as illustrated in this study and as previously reported (Ratner 1967; McBride and Klemm 1969; Nash and Gallup 1976; Prestrude 1977; Crawford 1977), different testing schedules may exert different effects on TI susceptibility and duration. This variable needs to be examined as TI may be used on dogs several times, whether it be once a year for vaccinations and a routine clinical examination or more regularly for a series of treatments.

Although none of the other experimental variables examined in the first study had significant effects on the susceptibility or duration of TI, it appeared that there was an increase in susceptibility and duration with record number possibly indicating that the investigator became better at inducing TI as testing progressed. In addition to potentiating TI duration it also appeared that there may have been an increase in susceptibility with repeated testing on the same dog. The additional treatment techniques also resulted in longer TI durations than the control technique indicating that some of the additional treatment techniques (eg. cuffing) may have had a potentiation effect on the duration of TI as observed in the second study. The small number of dogs exhibiting TI however limited what could be achieved statistically as associations of other variables with TI needed to be very strong before they showed statistical significance.

A similar problem was also encountered when examining the effect of subject variables on the susceptibility and duration of TI. The strong correlation found between the susceptibility and duration of the dogs that exhibited TI in the first study and the dogs that exhibited TI in the second study however, indicated that TI by dogs was not a once-off random effect but a subject effect. The significant finding across the two studies, that dogs which urinated or defecated during testing were more susceptible to TI than the dogs that did not and the finding that timid dogs were more susceptible to TI than the friendly dogs, also support the idea that susceptibility to TI may be related to the dog's temperament or fearfulness as has been reported in other species (McGraw and Klemm 1973; Gallup, Ledbetter and Maser 1976; Nash 1978; Jones and Faure 1981; Jones and Mills 1983).

As discussed above, the low susceptibility observed in this study may be because dogs are used to human handling and are thus less likely to exhibit TI. If it is found that susceptibility to TI cannot be substantially increased by different induction procedures, it may be that TI can only be used as a method of restraint in a small proportion of dogs. The ability to identify the likely candidates would therefore be important. In addition to timid dogs or dogs that urinated during testing it was also found that proestrous dogs were more susceptible to TI than other dogs. Other trends observed were that young dogs under 1 year old were not susceptible to TI using the induction methods in this study. Dogs between one and two years old appeared to be the most susceptible to TI and this susceptibility decreased from 2 years old till 6 years old, after which no dogs exhibited TI.

Even if only certain dogs (eg. 1 year old timid proestrous dogs) were found to be susceptible to TI, as long as the induction method is kept quick and simple, it would be an easy procedure to attempt to induce TI on all dogs and if found to be not susceptible, other methods of restraint could then be adopted. This is of course if further studies find that TI is safe and that the dogs remain deep enough for a long enough duration to allow the completion of procedures.

As previously discussed, this thesis reports an initial study into the susceptibility and characteristics of dogs in TI. The small number of dogs exhibiting TI and the cursory examination of the variables affecting TI means that the results should be interpreted cautiously, especially since the study was a survey. More detailed studies examining the effect of individual variables on TI susceptibility and duration are therefore required to determine if susceptibility and duration of TI can be increased. The effect of repeated testing on TI also needs to be examined.

More extensive investigations of the characteristics during TI (eg. whether there is any analgesia during TI), physiological and endocrinological changes during TI (eg. blood pressure, EEG, cortisol or any interactions with medication, sedatives etc) and the depth

of TI is also required to determine the safety and extent of procedures that can be conducted while dogs are in TI. The effects of TI on dogs, in terms of its aversiveness also need to be determined to assess how humane it is to use TI as a form of restraint in dogs.

It is therefore evident that much work is required before it can be determined if TI can be used as a routine method of restraint for veterinary procedures. The results from this study are however promising as they indicate a potential for the use of TI as a quick, non-chemical, easily reversible and safe method of restraint in dogs for routine clinical examinations or veterinary procedures such as injections, catheterisation, blood sampling, radiology, teeth cleaning, nail clipping, skin scraping, minor stitch ups or even minor surgery (eg. lump or grass seed removal).

The advantages of being able to perform simple tasks like blood sampling or injections, that don't usually justify chemical methods without having to fight with a struggling dog and risk inducing a haematoma or being bitten and stressing the dog, vet, nurse and owners is self evident. Not having to manually restrain a struggling dog in radiology also means sparing two to three people from possible irradiation. Clearer and fewer exposures would also result as the dog would be unlikely to move or struggle during the vital exposure period.

Although chemical restraint can be used, it may be contraindicated on some occasions. For example if the dog is in shock, with compromised circulatory or cardiac functions or has severe liver or kidney disease. Using TI as a form of restraint also means not having to worry if the dog has recently been fed and so alleviates the need to wait 12-24 hrs before anaesthetising an animal for assessment, radiology or treatment. Owners could present their pets for minor procedures without a need for starving the dog beforehand or having to wait till the dog recovers sufficiently from anaesthesia before returning home. This would therefore decrease the costs associated with overnight stays and anaesthesia.

For more major, painful or stimulating procedures where anaesthesia is required (especially if it is found that TI is not associated with any analgesia), TI may still be useful in order to obtain an initial period of immobility so that sedatives or anaesthetic agents can be administered without having to struggle with the dog. The effect of any interactions between TI and sedatives, anaesthetic agents, analgesics or other medication must however be investigated first.

The advantages of being able to use TI in veterinary clinics appear enormous and the encouraging results from this thesis, should stimulate further investigation into TI by dogs. Even if a 100% susceptibility is not achieved, the ability to use TI in susceptible dogs would mean saving these dogs from the unnecessary risks associated with analgesia or

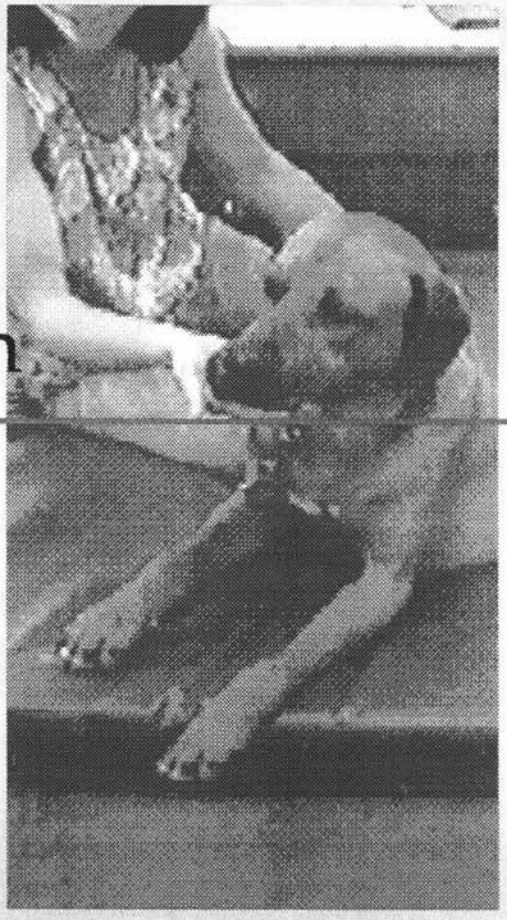
stress from struggling against restraint. Once accepted in dogs, the feasibility of using TI as a form of restraint in other pets and domesticated animals can also be investigated.

Besides its practical application as a form of restraint in dogs, sheep (Holmes 1989), rabbits (Rapson and Jones 1964) or birds (Montevecchi 1978), TI has also been used to assess fear in chickens (Jones and Mills 1983; Jones 1987), index the effects of aversive conditioning (Gallup 1974a), assess the role of early instrumental training in chickens (Gallup and Maser 1977; Sanberg et al 1981) and even to assess rat behaviour in response to chronic zinc deficiency (Hesse et al 1979).

Gallup and Maser (1977) also believed that TI can be used as a model for the study catatonia or other psychotic immobility states in people. In addition to this, TI has the potential to be applied to the study of predator prey defence, innate behaviour, fear or the complex relationship between sensory input and motor output. Its scientific and practical applications aside, tonic immobility in itself is a fascinating phenomenon and deserves more study, considering so little is known about it despite three centuries of investigations.

Chapter seven

Conclusion



Conclusion

This initial study of TI by dogs has shown that dogs exhibit TI. Although the susceptibility to TI was lower than that reported in other species, the characteristics observed during TI, duration of TI and variables affecting TI were remarkably similar to those reported in other species.

While it was possible to conduct various physiological assessments during TI in some dogs, a more thorough evaluation of the effect of individual variables on TI susceptibility and durations is required in order to potentiate TI. More extensive investigations of the characteristics and physiological changes during TI are also required to determine the safety and extent of procedures that may be conducted while dogs are in TI.

The results from this study are however promising as the duration, characteristics and physiological changes observed indicate a potential for using TI as a quick, non-chemical, easily reversible and safe method of restraint in dogs for routine clinical examinations or veterinary procedures.

Chapter eight

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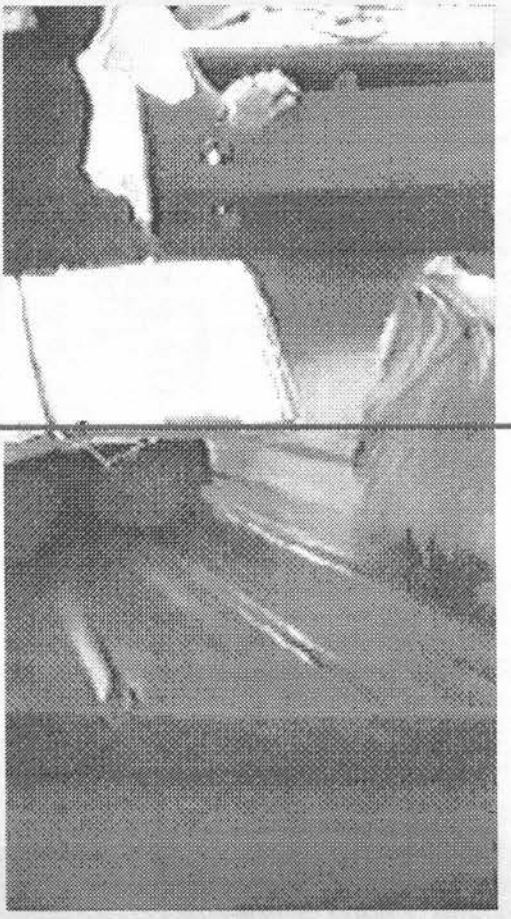
Chapter nine

Appendices



Appendices

Record No._____

TI Record Sheet

Date: __/__/1989

Place:_____

Owner's Name: _____ Time: ____am/pm

Address: _____

_____

Telephone: _____

I am / am not willing to participate in further trials if required.

Dog's Name: _____

Breed / Type: _____

Sex: male (entire / castrated)

female (spayed / pro-oestrus / oestrus / dioestrus / anoestrus)

Age: _____yrs _____mnths

Approximate Weight: _____kg / lbs

Temperament: friendly / timid / aggressive

boisterous / quiet

Amount of Human Contact: house dog / outdoor dog

Previous training: _____

Health Status: good / problems _____

Has this dog been tested for TI before ? Yes / No

Any relevant history eg. age of dog when obtained, upbringing, fearful experiences etc.

Comments or Suggestions

APPENDIX 1 - Record sheets for Preliminary Study II

Record No. _____

Owner's Name: _____ Date: __/__/1989

Dog's Name: _____ Place: _____

Time: ___ am/~~pm~~

State of Dog before Testing: ~~calm~~ quiet / excited

friendly / timid / aggressive

Method Induction:

lateral recumbency 30secs

dorsal recumbency 30secs

dorsal recumbency with stroking 30secs

blanket over head

box over head

cuff around ears

~~pressure~~ on neck scruffing

skin clips

Environmental

noise: _____

light: _____

temperature: ____

other: _____

Duration: _____ secs

Ease of Induction: easy / struggling

Observations during immobility: _____

_____

_____

State after Test: dazed / normal

friendly / timid / aggressive

Comments:

Record No. _____

Owner's Name: _____ Date: 2/11/1989

Dog's Name: _____ (5) Dose X [illegible] X . (24.4kg) Place: J [illegible]

Time: 9.45 am/~~pm~~.

State of Dog before Testing: ~~calm~~ quiet / excited

friendly / timid / aggressive

Temp N

Sex Entire ♀

Method Induction:

(1) lateral recumbency 30secs Ø +stare

(5) dorsal recumbency 30secs Ø

(2) dorsal recumbency with stroking 30secs Ø

(3) blanket over head — Ø struggle — Ø

(4) box over head — Ø struggle

(3) cuff around ears — Ø

(4) ~~pressure on neck~~ scruffing R 30secs, scruff 30secs → Ø

(2) skin clips ½ pc

Environmental

noise: _____

light: _____

temperature: ____

other: _____

Duration: _____ secs

Ease of Induction: easy / struggling

Observations during immobility: _____

_____

_____

State after Test: dazed / normal

friendly / timid / aggressive

Comments:

APPENDIX 2 - Example record sheets for Preliminary Study II

Record No. _____

Owner's Name: _____ Date: 3/11/1989

Dog's Name: (3) Blk Lab x (25.7kg) Place: J'mead

Time: 10 am/~~pm~~

State of Dog before Testing: ~~calm~~ / (excited) (quiet)

(friendly) / timid / aggressive

Temp - N

Sex -

Method Induction:

(1) lateral recumbency 30secs Ø

(3) Lat shaking Ø

(2) dorsal recumbency 30secs Ø

(4) dorsal recumbency with stroking 30secs Ø

(7) blanket over head Ø

box over head —

(6) cuff around ears —lat Ø

scruffing dorsal —

~~pressure on neck~~ —

(5) skin clips Ø

(2) cut nail Ø

Stim Ind

Environmental

noise: _____

light: _____

temperature: ____

other: _____

Duration: _____ secs

Ease of Induction: easy / struggling

Observations during immobility: _____

_____

_____

State after Test: dazed / normal

friendly / timid / aggressive

Comments:

Record No._____

TI Record Sheet

Date: __/__/1989

Place:_____

Owner's Name: _____ Time: ____am/pm

Address: _____

_____

Telephone: _____

I am / am not willing to participate in further trials if required.

Dog's Name: _____

Breed / Type: _____

Sex: male (entire / castrated)

female (spayed / pro-oestrus / oestrus / dioestrus / anoestrus)

Age: _____yrs _____mnths

Approximate Weight: _____kg / lbs

Temperament: friendly / timid / aggressive

boisterous / quiet

Amount of Human Contact: house dog / outdoor dog

Previous training: _____

Health Status: good / problems _____

Has this dog been tested for TI before ? Yes / No

Any relevant history eg. age of dog when obtained, upbringing, fearful experiences etc.

Comments or Suggestions

APPENDIX 3 - Record sheets for Preliminary Study III

Record No. _____

Owner's Name: _____ **Date:** __/__/1989

Dog's Name: _____ **Place:** _____

Time: ___ am/pm

State of Dog before Testing: ~~calm~~ quiet / excited

friendly / timid / aggressive

Control: lateral recumbency / dorsal recumbency

Method Induction:

dorsal recumbency with stroking

blanket over head (lateral / dorsal)

box over head (lateral / dorsal)

cuff around ears (lateral / dorsal)

~~strobe~~ light (lateral / dorsal)

scruffing

skin clips

Environmental

noise: _____

light: _____

temperature: ____

other: _____

Duration: _____ secs

Ease of Induction: easy / struggling

Observations during immobility: _____

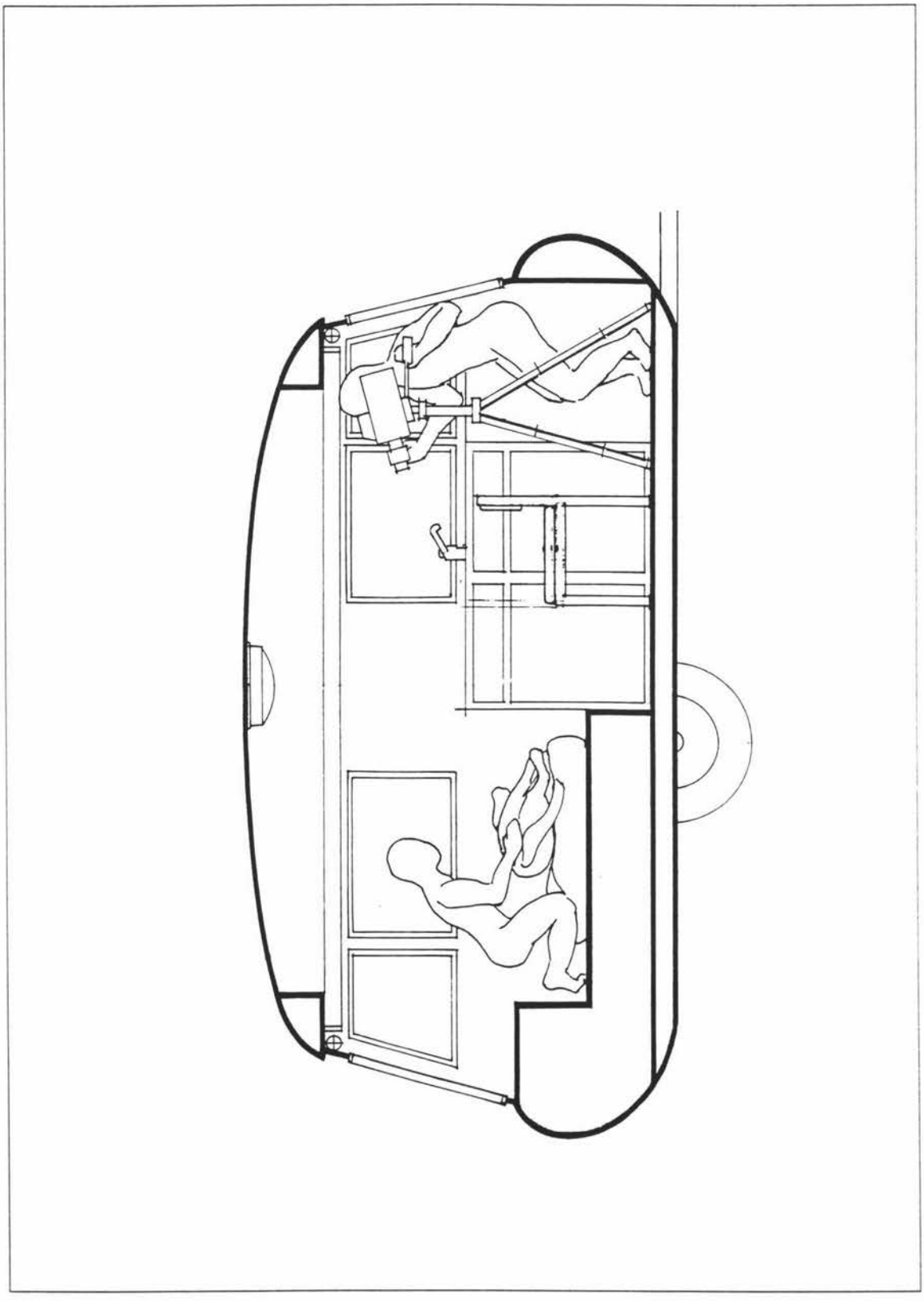
_____

_____

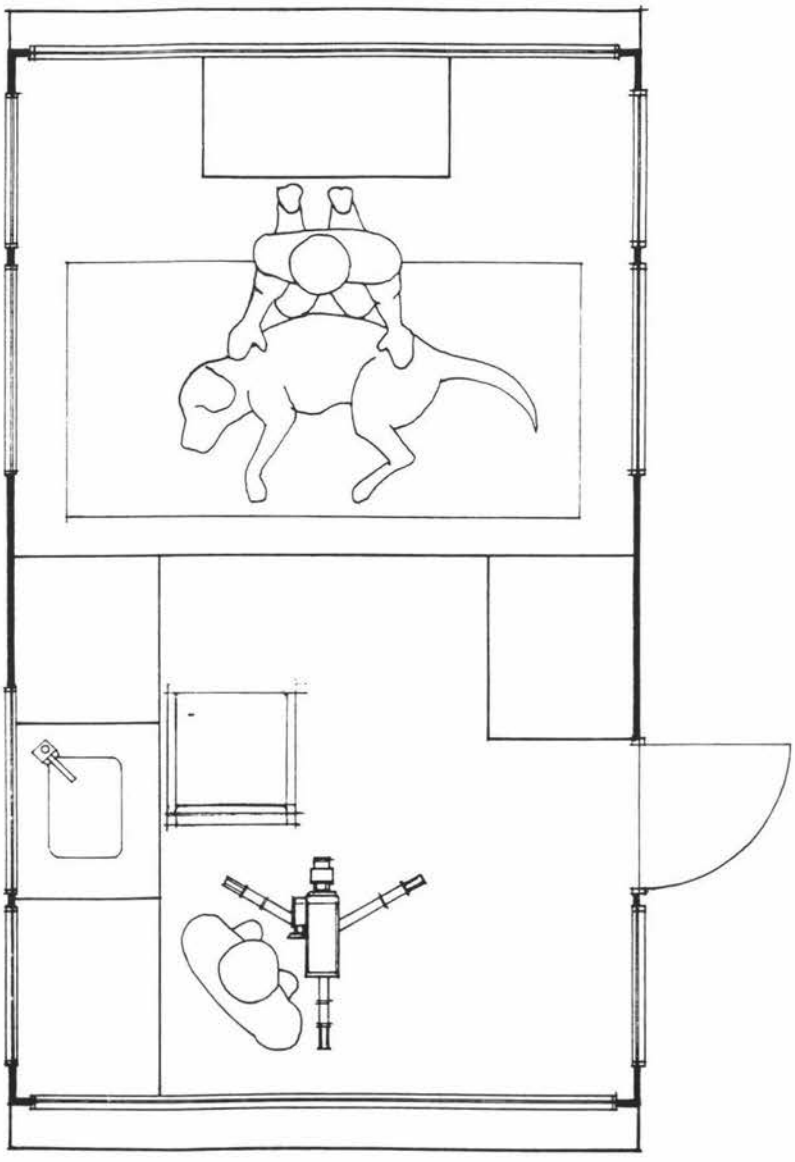
State after Test: dazed / normal

friendly / timid / aggressive

Comments:



APPENDIX 4 - Caravan layout



Record No._____

TI Record Sheet

Date: __/__/1989

Place:_____

Owner's Name: _____ Time: ____am/pm

Address: _____

_____

Telephone: _____

I am / am not willing to participate in further trials if required.

Dog's Name: _____

Breed / Type: _____

Sex: male (entire / castrated)

female (spayed / pro-oestrus / oestrus / dioestrus / anoestrus)

Age: _____yrs _____mnths

Approximate Weight: _____kg / lbs

Temperament: friendly / timid / aggressive

boisterous / quiet

Amount of Human Contact: house dog / outdoor dog

Previous training: _____

Health Status: good / problems _____

Has this dog been tested for TI before ? Yes / No

Any relevant history eg. age of dog when obtained, upbringing, fearful experiences etc.

Comments or Suggestions

APPENDIX 5 - Record sheets for Survey Study

Record No. _____

Owner's Name: _____ **Date:** __/__/1989

Dog's Name: _____ **Place:** _____

Time: ___am/pm

State of Dog before Testing: ~~calm~~ quiet / excited

friendly / timid / aggressive

(1 / 2) Control: lateral recumbency / ~~dorsal recumbency~~

Duration: _____ secs

Ease of Induction: easy / struggling

Observations: _____

_____

_____

(1 / 2) Method Induction:

~~dorsal recumbency with~~ stroking

blanket over head

cuff around ears

light

scruffing

Environmental

noise: _____

light: _____

temperature: ____

other: _____

Duration: _____ secs

Ease of Induction: easy / struggling

Observations: _____

_____

_____

State after Test: dazed / normal

friendly / timid / aggressive

Comments:

Tonic Immobility by Dogs

Department of Veterinary Clinical Sciences,
Massey University.

What is Tonic Immobility ?

Tonic Immobility is a response many animals show where although the animal is conscious, it lies very still and is unresponsive to handling, noise and other stimulation. Because of this, Tonic Immobility is sometimes called **"Animal Hypnosis"**.

How are animals "hypnotised" ?

A wide variety of animals including insects, birds, rabbits, cats, sheep and even monkeys have been "hypnotised". An animal is usually "hypnotised" by holding it on its side or tipping it onto its back. It may then be stroked, have a blanket or box put over its head, have pressure applied to its skin and yes, even stared at !

Why am I interested in Tonic Immobility by Dogs ?

Although Tonic Immobility has been studied in many different animals, very little work has been done on dogs. I am trying to determine if dogs show Tonic Immobility and if so, how responsive they are during it. The technique can then be developed into a simple and humane method of restraining dogs without having to use drugs. It would be useful for veterinary procedures such as taking X-rays, blood samples, skin scrapings or even just clipping nails without having to resort to struggling matches with your dog.

What will I be doing to your dog?

As very little is known about Tonic Immobility by dogs I need to try different methods such as those mentioned above on as many dogs as possible. Nothing painful or harmful will be done to your dog as the aim is to develop a safe and humane method of restraint. Some dogs however, do not appreciate being restrained and so, may struggle a little initially which is why the whole procedure is done on a soft padded surface.

Your participation would be much appreciated and will contribute to a better understanding of dog behaviour and also help improve their care and welfare.

Most sincere Thanks to you and your dog,

Dr. Rae Ming ONG
Department of Veterinary Clinical Sciences,
Massey University.
Palmerston North.
Phone: (063) 63374 ext 8018

APPENDIX 6 - Information sheet

Record No:- _____

Name:- _____

Date:- ___/___/1989

Time:- _____ am/pm

Noise:- _____

Observations on entry Caravan :-

calm / excited

friendly / timid / aggressive

urinated

defaecated

Comments :-

History :-

age when obtained

where from

temperament with . you

. others / at shows etc .

fearful experiences

groomed / handled / trained to lie on side ?

APPENDIX 7 - Record sheets for Characterisation Study

Record No:- _____

Name:- _____ Date:- ___/___/1989

Time:- _____ am/pm

1, 2, 3, 4, 5. CONTROL, STROKE, BLANKET, CLIFF, SCRUFF.

- State Before Test :- Calm / Excited
  Friendly / Timid / Aggressive
  Urinated :- Yes / No
  Defaecated :- Yes / No

  Comments:-

  _____

  _____

  _____

- Heart Rate Before Test :- _____ /15 secs.

- Induction :- Easy / Struggling

  Comments during Restraint:-

  _____

  _____

  _____

1min 30sec Respiration Rate :- _____ /15 secs.
2 minutes Muscle Tone:- Relaxed / Tense
3 minutes Heart Rate:- _____ /15 secs.
4 minutes Withdrawal Reflex :- Strong / Weak / None
5 minutes Rectal Temperature:- _____ °C
* 7 minutes on Termination Heart Rate :- _____ /15 secs.

- Cause of Termination :- _____

- Noise / Other Stimuli During Test :- _____

  _____

- Duration :- _____ mins _____ secs

- Observations During TI :- muscle trembling / limb twitching / paddling / reposition head / limbs swallowing / lip licking / blinking / looking around

  _____

  _____

  _____

- State After Test :- slow / normal
  friendly / timid / aggressive

  Comments:- _____