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Sex differences in movement organization : a kinematic analysis of evasive dodging movements used during food protection in the rat : influence of partner's sex, neonatal and pubertal exposure to androgens

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SEX DIFFERENCES IN MOVEMENT ORGANIZATION

A Kinematic Analysis of Evasive Dodging Movements Used During Food
Protection in the Rat: Influence of Partner's Sex, Neonatal and Pubertal
Exposure to Androgens

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DEDICATION

This thesis is dedicated to my husband Rodger, and to my uncle Martin who made me realize that the past is exactly that.

ABSTRACT

The role of sex in the organization of movement is not commonly addressed in the literature. The objective of this thesis was to determine whether differences exist between males and females in the way they organize their movements during dodging to protect a food item. Detailed kinematic analysis of these movements in adult rats shows that females move their snout through a greater spatial curvature, relative to the pelvis, than males. The sex of the robbing animal did not alter the sex-typical movement patterns exhibited. Manipulation of neonatal androgens altered the sex-typical dodge patterns of both males and females. Removal of androgens at weaning however, did not affect the male-typical pattern. The existence of sex differences in the organization of movement provides a new level of analysis for the study of sexual dimorphism in behavior.

ACKNOWLEDGEMENTS

Twists of fate have always intrigued me and the genesis of the ideas for this thesis is one of those twists of fate that has come full circle.

I began the work that has led to this thesis in the fall of 1991 (although at the time I didn't know it would lead to this) by doing a project for a senior level undergraduate course with Ian Whishaw, who with Jo-Anne Tomie, taught me how to train rats in the dodging and robbing task. Subsequently, I spent a year deciding whether I wanted to continue in university; Ian convinced me that a cooking diploma was not the same as a university degree.

It was at the point when I decided to return to university that I met Sergio Pellis and began to work on play behavior. Sergio provided me with the "permission" to think and explore some of the fledgling ideas that I had about how play behavior may differ for males and females; this was the fall of 1993. The knowledge I had gained in Ian's lab, coupled with what I had gained from Sergio, became the basis I needed to begin a two year attempt to answer the question of how males and females may differ in their movement organization during dodging to protect a food item.

This project, however, could not be completed without the help of a number of other people within the university and without. The first person I must acknowledge is my husband Rodger who keeps telling me to do “whatever makes you happy”.

Others I could not have done this without are:

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To everyone else who works within the Neuroscience division of the Psychology department: Lori, Bogdan, Grazyna, Karen, Robbin, Tanya, Elena & Bryan, for always answering my questions and for being willing to help me out when I needed a hand.

Pam Sureman for listening to me talk *ad nauseum* about my work. It is not quite the same as training at DQU, but in other ways it almost is.

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The circle is complete.

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There are no absolute truths.

Levi-Strauss

The last thing to be discovered in any science is what that science is all about.

Whitehead

CHAPTER 1

GENERAL INTRODUCTION

“There are two major classes of living organisms - male and female. In many cases, they are so different in form and habit that one might well be excused the thought that males and females are different species.”

(Kelley, 1986; p.499)

During the last two centuries, our understanding of the effects of hormones on the developing nervous system has developed from the realization that there is “something different” between males and females, to the study of how the sexes differ, using complex behavioral, physiological and biochemical analyses. Beach (1975) referred to the field of behavioral endocrinology as an emerging discipline and even fifteen years ago noted that the amount of research on the role of hormones in the control and development of behavior had increased ten- to twenty-fold during the previous few decades (Beach, 1981).

The roots of behavioral endocrinology can be traced back almost two centuries. Understanding the history of this discipline can aid in our

understanding of the relationship between hormones and the brain, and how these relationships influence the development of behavior in the two sexes. It can also provide insights into why behavioral endocrinology has evolved in the manner it has and how this development has created the present state of the discipline. The following sections will summarize the salient events in the development of the field of endocrinology; in particular, behavioral endocrinology. Finally, I will then briefly discuss how these developments have led to our present state of knowledge.

Historical Background

Turner and Bagnara (1976) have divided the development of endocrinology into three main periods: (i) the early history starting with the ancient Greeks, (ii) the birth of the discipline as a "real science" with the discovery of secretin by Bayliss and Starling in the first decade of this century (Nelson, 1995), and (iii) the present era, which is defined by the exponential growth of the discipline in both techniques and knowledge.

The study of the relationship of hormones and behavior (i.e., behavioral endocrinology) has followed a similar pattern of development as its parent discipline, endocrinology, and can also be divided into three phases (Beach, 1981). First, the predisciplinary era, that began in 1849 and continued

until the end of the 1800's. These years comprise the time prior to the acceptance of endocrinology as a "real science". The second phase of the development in the study of hormones and behavior has been called the formative years, and lasted from the beginning of this century until about the mid 1950's. It was during this time that the study of the influences of hormones on behavior became a separate identifiable area of research. Finally, the modern era, which is marked by the development of true specialists in the field of behavioral endocrinology. The advent of specialists has led to an increase in the empirical evidence delineating sex differences in behavior and on the role of hormones in generating those differences. Specialization has also led to increasingly sophisticated techniques for the study of hormone action at a neural level and their correlation with behavior. The following section will examine a number of the major discoveries during these three periods in the area of behavioral endocrinology, with special focus on the study of sex glands and their secretions.

Predisciplinary Era

In 1849, A. A. Berthold performed what has become known as "the first proof of endocrine function as we know it" (Forbes, 1949). Berthold castrated

Figure 1. Adults that were castrated at birth (Group 1) were smaller than normal roosters and failed to engage in rooster-typical behaviors. The birds that were castrated and received either an implant of one of their own testes (Group 2), or a testis from another bird (Group 3) into the abdominal cavity, looked and acted like normal roosters as adults. Subsequent dissection of these birds showed that the reimplanted and transplanted testes had developed vascular connections and had produced sperm. (Taken from Nelson, 1995; After Berthold, 1849).

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six pre-adult roosters and then, in three of them, re-implanted one of their removed testicles into each of their abdomens, where it could establish new connections with the circulatory system. Berthold's description of the behavior of the three roosters with the reimplanted testicles became the first evidence showing that a substance secreted from a discrete organ could modify the behavior of an animal (Fig. 1). He describes the behavior of the roosters with the implanted testis as follows:

“So far as voice, sexual urge, belligerence, and growth of comb and wattles are concerned, such birds remained true cockerels. Since, however, transplanted testes are no longer connected with their original innervation, and since...no specific secretory nerves are present, it follows that the results in question are determined by the productive functions of the testes. i. e., by their action on the blood stream, and then by the corresponding reaction of the blood on the entire organism... of which... the nervous system represents a considerable part.”

(Beach, 1981 pp.328-9)

Following this discovery by Berthold, a number of studies were conducted in France, Germany, Italy and Russia to determine the effects of the

removal or addition of the sex glands on the behavior of animals. At this time, there was agreement, although no evidence existed, that the influence of the action of the secretions of these glands must be on the central nervous system, but what the exact mechanism of action was, remained a subject of continued debate (Beach, 1981)

During this time, the question of the effects of glandular secretions on the behavior of humans was also being scrutinized. Research was not confined to the secretions of the sex glands and their effects on behavior, but also focused on the behavioral effects of secretions by the thyroid, liver and adrenal glands. It was Claude Bernard, the eminent French physiologist studying the secretions of sugar into the blood from the liver, who first coined the term "internal secretion" to refer to the release of substances into the blood from internal organs (Beach 1981). He also stressed that the maintenance of this internal environment is necessary to maintain an organism in good health.

With regards to the potential effects of sex gland secretions on human well being, the first experiments were done by Claude Bernard's successor, Charles Edward Brown-Sequard. In 1889, when he was 72 years old, Brown-Sequard conducted an experiment to determine whether the secretions of gonadal hormones could have a rejuvenating influence (no doubt his age

was a significant factor in the carrying out of this experiment!). He injected himself, intramuscularly, for ten days with a mixture of blood, semen and fluid from crushed testis. After these ten injections, he reported that he felt improvement in bladder tonus and bowel regularity as well as increased mental alertness and resistance to fatigue. His observations, however, were scorned by fellow scientists, and when he suggested to older colleagues that they repeat his experiment on themselves, he was ridiculed (Beach, 1981).

One further interesting historical note from the predisciplinary era on the effects of secretions by the sex glands is worth mentioning here. During the late 1800's experiments were carried out by Eugen Steinach on very old rats, dogs and horses. In these experiments, Steinach ligated the vas deferens to prevent the expulsion of sperm by the testis. He reported that within weeks the coats of these animals showed heightened gloss, and they displayed increased activity and a "reawakened virility" when placed with females. These changes in appearance and behavior were coupled with microscopic changes in the gonads. However, before these claims could be debunked, experiments conducted on humans produced "amazing" results. So much so that thousands of men were "Steinachized" (Beach, 1981).

Brown-Sequard and Steinach were honest investigators with excellent reputations who misinterpreted their own results. Due to these errors in

interpretation there was a subsequent suspicion about the possibility of correlating the action of hormones with behavior. The belief that behavior would be difficult to correlate with the hormonal effects on the nervous system colored the subsequent research that was done during the formative years, and it was not until the beginning of the modern era with the work of Phoenix, Goy, Gerall and Young (1959) that scientists once again focused on the relationship between hormones and behavior (Beach, 1981).

The Formative Years

During this period, attempts to correlate hormones with behavior became infrequent and the emphasis switched to the application of new biochemical techniques. Research increasingly emphasized the physiology of endocrine glands and the composition of the secretions produced by these glands. The following quote by Frank Beach (1981), succinctly summarizes the climate at this time:

“Any bright young endocrinologist receiving his training around that time could clearly see where his professional future lay so that he would scarcely waste time in experiments on behavior when there was so much to be learned about

biochemistry and cellular biology.” (p.336)

Samuels (1958) states that it was this new area of biochemical research that took endocrinology from the realm of theory to real science. During this time however, while the potential relationship of hormones and behavior was considered unimportant, it was not forgotten, and there were a few, in diverse areas of research, that still attempted to investigate this relationship.

The first hormone-behavior relationship described during this time was between ovarian hormones and the estrous cycle. This was described by Stockard and Papanicolaou in guinea pigs in 1917, and by Long and Evans in rats in 1922. Shortly after these descriptions appeared in the literature Allen and Doisy, (1923) published a paper showing that injections of the gonadal hormone estrogen influenced the behavior of spayed female mice and rats. They described the behavior in the following way:

“While these spayed animals are in a condition of artificially induced estrus, they can be mated with normal vigorous males. They experience typical mating instincts, the spayed females taking the initiative in the courtship and showing no aversion to advances by the male. Successful copulation occurs, followed as in normal animals, by the formation of typical vaginal plugs. Since these animals will

copulate only when in estrus, the conclusion seems justified that this follicular hormone is the cause of estrual or mating instincts." (pp. 821)

During these years, one person who was influential in the study of behavior and endocrine function was Frank R. Lillie (Beach, 1981). In 1917 Lillie published a paper on freemartins (the female twin of a normal male calf) (Fig. 2). Lillie concluded that the substance secreted by the testis of the male fetus must contribute to the differentiation of male and female characteristics because the female twin of a male calf is masculinized and is subsequently sterile. In 1923, Lillie proposed that the study of sexual development should be more than a catalogue of subjects:

"It should be directed specifically towards the fundamental problems which are these:

(1) How is sex determined? Can sex determination be controlled? How?

(2) What are the factors active in the development of sexual characteristics, whether anatomical, physiological, or psychological? Can sex development be quantitatively controlled?

(3) The problems of sex relationships; their nature, their

Figure 2. A freemartin is the sterile female twin of a male. They are found in cattle, sheep, goats and pigs. It was hypothesized by Lillie (1917) that masculinizing factors travel from the male to the female through the vascular connections in the placenta (arrow) which affect the development of the internal anatomy of the female. The phenomenon of freemartinism, however, has not been replicated by the administration of androgens in pregnant cows and the mechanism underlying its genesis is still unknown. (Taken from Nelson, 1995; After Lillie, 1917)

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control.

Practically all problems concerning sex come under these three. The specific problems are innumerable..." (Aberle & Corner, 1953; pp. 17)

Even though the problems stated by Lillie laid the foundation for subsequent work on the role of hormones in the development of the sexes and in controlling behavior, for the next thirty years, little attention was paid to behavior in hormonal research. The reason for this lack of attention to behavior can be summed up in a statement by Moore, a student of Lillie's, regarding the role of hormones after puberty.

"After the stage of puberty, or masculine maturity, the loss of the hormone is less evident. It is clear in many specific cases, but less clear in others, that the instinct of mating is conditioned by male hormones, either directly or indirectly. To mention only two cases in which hormonal control is in doubt: We have often employed male guinea pigs, castrated at 30 days of age (prepubertal), as a means of detecting females in heat when actual mating is undesired; the mating instinct persists and male behavior persists for many months despite early castration."

(Beach, 1981 p.335-36)

The skepticism regarding the role of hormones in controlling behavior coupled with the growing emphasis on determining the chemical properties of hormones and the physiological response to these substances left the study of behavioral endocrinology on the sidelines of endocrine research for another half a century.

The Modern Era

In 1959, Phoenix, Goy, Gerall and Young demonstrated that the potential for either masculine or feminine sexual behavior in female guinea pigs is dependent on early exposure to gonadal hormones. Males undergo masculinization of male-typical characteristics and defeminization of female-typical characteristics due to the action of gonadal hormones in early development. Post-pubertally, hormones activate the expression of these sex differences. Since this early work, a number of studies using different species have replicated these findings (Baum, 1979; 1990), supporting the idea that gonadal hormones have an organizing effect early in development and an activating effect in adulthood. In addition, the development of sex differences between males and females has been extended beyond reproductive behavior patterns to include sexual orientation (Adkins-Regan,

1988), spatial behavior (Williams, Barnett, & Meck, 1990; Williams & Meck, 1991), spontaneous/exploratory activity (Stewart & Cygan, 1980; Mead, Hargreaves, & Galea, 1996), rotational behavior (Carlson & Glick, 1996), micturition in dogs (Beach, 1974) and play (Meaney & Stewart, 1981; Meaney, 1988; 1989; Pellis, Pellis & McKenna, 1994).

Even though sex differences in mammals have been shown to exist in both reproductive (Ward, 1992) and non-reproductive behaviors (Beatty, 1992), most sexually dimorphic behaviors have been shown to be dimorphic only in the sense that one sex is more likely to perform a particular behavior than is the other sex (Aron, Chateau, Schaeffer, & Roos, 1991; Goy & Roy, 1991). Sexually dimorphic behavior patterns may therefore occur in both sexes, but have a lower threshold for elicitation in one sex versus the other (Money, 1988). Males differ from females not in what they do, but in how likely they are to perform particular behavior patterns. For these reasons, most studies of sex-typical behavior patterns (see Beatty, 1992, for a review) have focused on differences in the relative frequency of occurrence of a specific behavior pattern for each sex.

Introduction to the Research Question

In this thesis I will show that it cannot be assumed that when males and females are performing what appears to be the same behavior pattern,

that they are in fact using the same combination of movements. One example where this has been documented is during micturition in dogs. After puberty, while females squat, males raise one hindleg; prior to puberty, however, males squat like females (Fig. 3). This difference in micturition pattern is modifiable by neonatal androgen exposure (Beach, 1974). I will also demonstrate, in this thesis, that the composition of the movements comprising a functionally similar behavior is different in males and females.

The remainder of this introduction will first briefly describe play fighting in rats, a behavior where sexual differences have been studied extensively (see Beatty, 1992, for a review). A brief discussion of sex differences in play fighting will serve to highlight the research question of this thesis. Following this discussion, I will briefly describe how the question of whether males and females use a different composition of movements to complete the same functional task, of dodging to protect a food item, was addressed. Finally, the specific experiments that were conducted to answer this question will be addressed.

Play fighting in juvenile rats is one area of behavior where the role of sex differences has been examined. Play fighting or rough and tumble play is an activity common to juveniles of many species of mammals and some

Figure 3. The urinary postures of domestic dogs is sexually dimorphic after puberty. Adult females and puppies of both sexes assume a squatting posture (A). During the onset of puberty however, males switch to the adult male form where one leg is raised (B). (Taken from Nelson, 1995; After Beach 1974)

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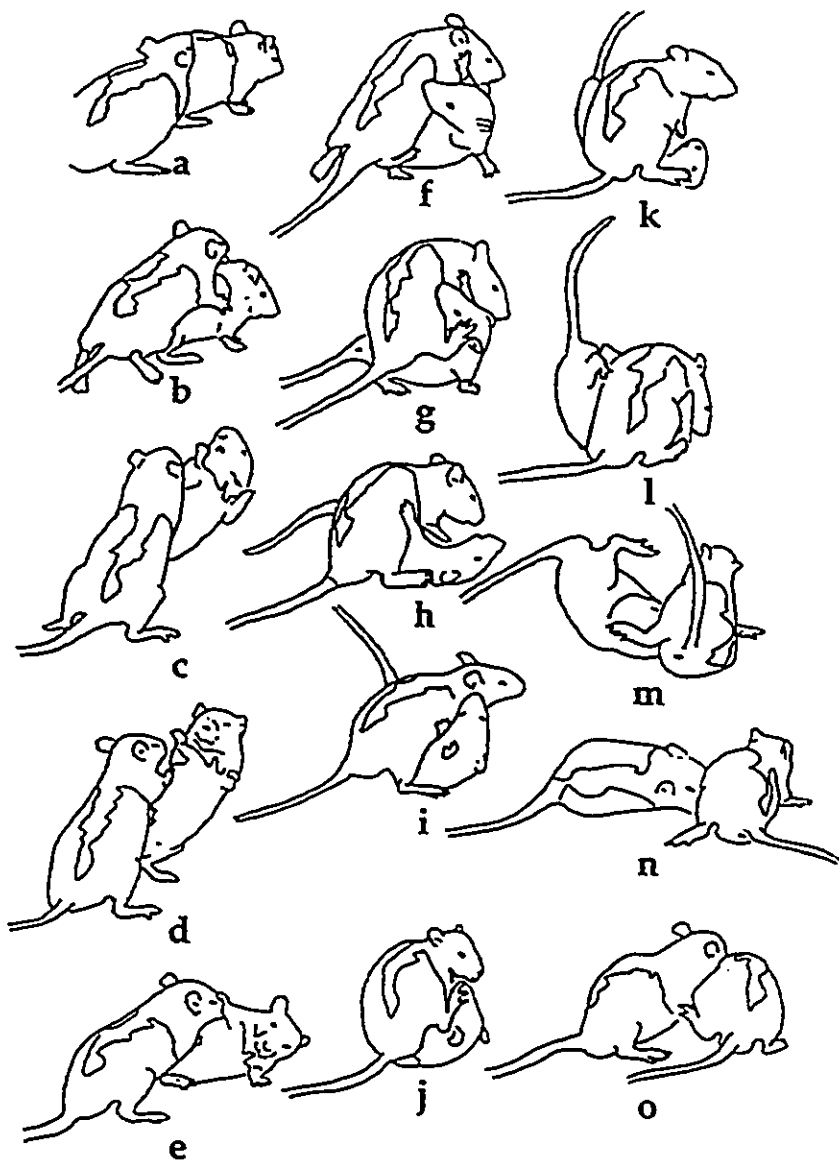
birds (Fagen, 1981). It is commonly believed to involve species-typical behavior patterns of agonistic attack and defense that are used in a non-serious manner (Meaney, Stewart, & Beatty, 1985). In rats, males typically engage in play fighting more frequently than females (Beatty, 1992; Meaney, 1988; 1989). Indeed, it is commonly believed that "(s)ex differences in social play are quantitative and not qualitative, referring to the frequency and not the forms of behaviors" (Meaney, 1989, p, 247). This quantitative difference in play fighting has been shown to be dependent upon the action of steroid sex hormones in the perinatal period. Castration at birth reduces the frequency of play fighting to female-typical levels, whereas androgenization of females perinatally raises play fighting to near male levels (Meaney, Stewart & Beatty, 1985). The evidence strongly supports the role of gonadal hormones in the organization of male-typical levels of play fighting (Beatty, 1992; Meaney, 1988).

Play fighting in rats involves attack and defense of the nape (Pellis & Pellis, 1987), where attacks involve the initiator attempting to rub its snout into the back of the neck of the partner. About 90% of such attempted nape contacts are resisted by the recipient, who adopts several defensive tactics so as to protect the nape from being contacted. In addition, the defender will also

launch counterattacks of its own in order to contact the partner's nape. An example of this is illustrated in Figure 4. The attacker approaches from the rear and reaches for the nape. The defender then rotates cephalocaudally around its longitudinal axis to lie supine. From this supine position, the defender can use its paws to hold off the attacker who is standing above and making lunges at the nape. The supine defender can also launch its own attacks to its partner's nape; these counterattacks can often be blocked by the attacker. Such an interaction can proceed for several seconds before stopping and then starting again.

Males and females differ in their likelihood of using particular behavior patterns to defend their napes from playful attack (Meaney & Stewart, 1981, Pellis & Pellis, 1990). This difference is magnified with the approach of puberty as male rats switch to a more adult form of defense when playfully attacked (Meaney & Stewart, 1981). This change includes a switch from using evasion or rolling over to supine to only partially rotating to supine. From this partially rotated position, they can either rise to an upright posture or push against their partner with their flank (Pellis, 1989; Pellis & Pellis, 1987). In contrast, females do not exhibit this age related change in defensive tactics (Pellis & Pellis, 1990). The male-typical change in defense tactics at puberty is contingent on the identity of the partner. Females use the

Figure 4. Play fights in juvenile rats involve attack and defense of the nape. In the example shown, the play fight is initiated by an approach (a) and an attack to the nape (b). Prior to the nape contact, the attacked rat rotates along the longitudinal axis and faces the attacker (c). The defender, however, while standing on his hindfeet is unstable and is pushed over by the attacking animal into a supine position (d-f). The attacker then positions himself over the defender perpendicular to the longitudinal axis of the body where both the attacking animal and the defending animal attempt to make contact with the nape area of the other (g-l). Once the animal that was initially attacked has extricated itself from under the attacking animal by kicking him off (m-n), the roles are reversed and the defending animal becomes the attacking animal (o). Play fighting in rodents consists of repeated attempts to attack and defend the nape as depicted in this sequence of play fighting. (Taken from Pellis & Pellis, 1987)

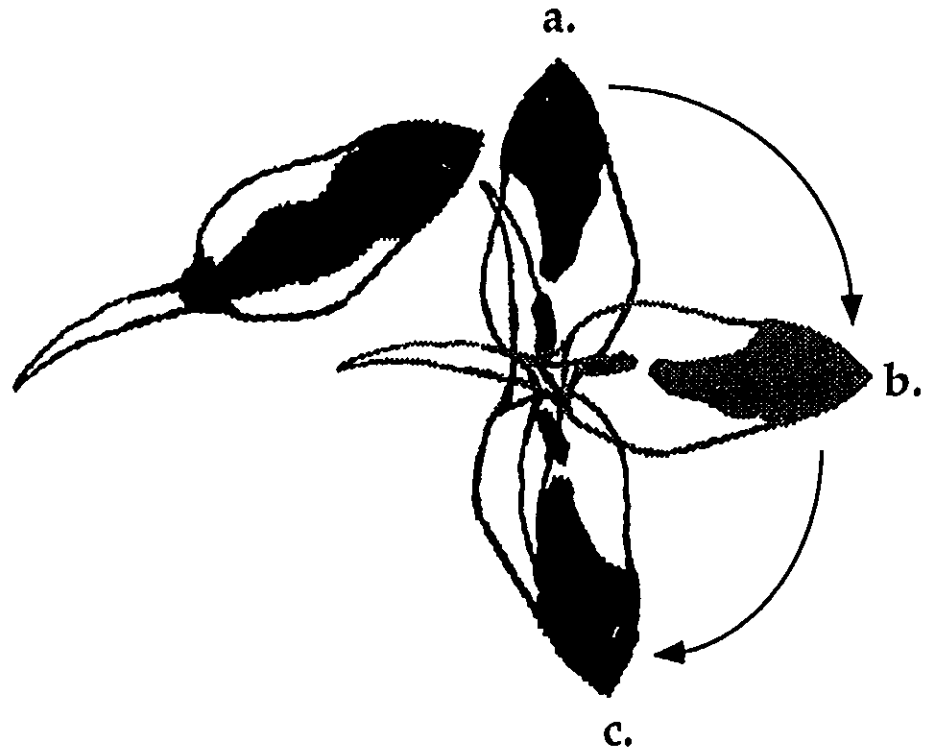


same pattern of defense as adults whether interacting with a male or a female. Males however, show the age related change in their defensive behavior when interacting with females or subordinate males, but maintain a more juvenile pattern of defense when interacting with a dominant male (Pellis & Pellis, 1990; Pellis, Pellis & McKenna, 1993). This age related change in the defensive tactic used is dependent on the presence of androgens neonatally (Smith, Forgie & Pellis, work in progress) but not at puberty (Smith, Field, Forgie, & Pellis, 1996; Pellis, Field, Smith, & Pellis, in press). These are sex-typical changes in that both males and females can perform all defensive tactics, but only differ in the likelihood of their use.

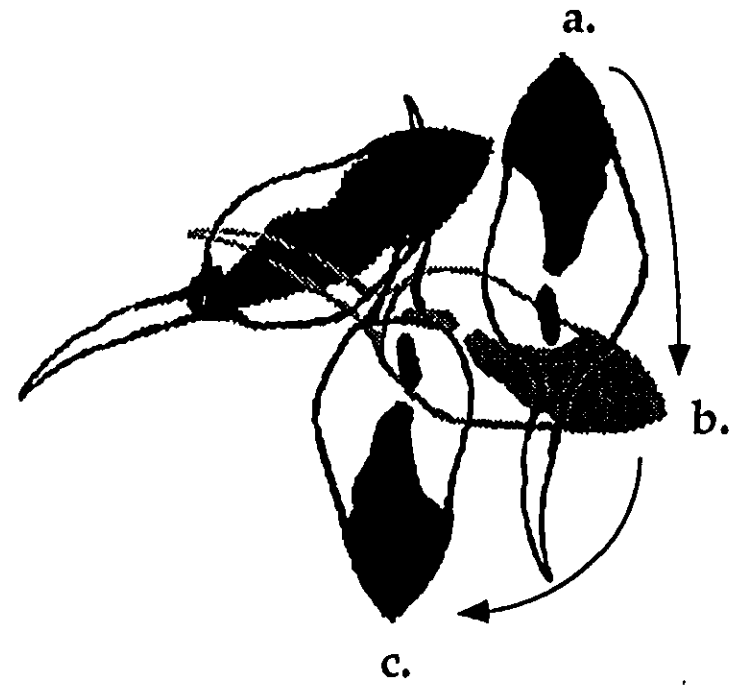
Close examination of one defensive behavior pattern, however, that of swerving away laterally from an approaching partner, has revealed that even though the tactic is functionally similar in males and females, they use a different combination of movements to execute an evasive defense. Females swerve so that their bodies move unidirectionally, in a cephalocaudal manner, away from the opponent (Fig. 5A). In contrast, males are more likely to couple this evasion with a movement of the pelvis towards the opponent (Fig. 5B) (Pellis & Pellis, 1987; Pellis, 1989). That is, not only do males move the nape away from the attacker, but they also use the lower body to block the

Figure 5. A consequence of the sex-typical evasive maneuvers during play fighting is that the female, by pivoting on her pelvis and moving forward, increases her distance from the opponent (left). In contrast, the male, by pivoting around the midbody and moving backwards, closes the gap with the opponent, often making contact with its rump (right). The numbers represent three successive stages of movement during dodges, so that number 1 represents the initial position and number 3 represents the final position. The intermediate position, number 2, is represented by the grey drawing. (Taken from Pellis, Field, Smith & Pellis, in press)

A . FEMALE



B . MALE



approach of the opponent.

Given that males are more likely to counterattack than are females (Pellis & Pellis, 1990), it is possible that the males may be organizing their evasive maneuver to functionally enhance their ability to counterattack. Another possibility however, is that there are intrinsic differences in the way that females and males organize their movements. The possibility that males and females differ in motor organization has been alluded to occasionally (e.g. Dittman, 1992), but has not been experimentally evaluated. The aim of this thesis was to evaluate whether there are sex differences in the organization of movement patterns.

The Research Question

During play fighting, as already noted, rats, especially males, may counterattack a conspecific immediately after making an evasive movement (Pellis & Pellis, 1990). In addition, evasive maneuvers during play fighting often involve a combination of vertical, rotatory and horizontal movements around the longitudinal axis (Pellis, Field, Smith & Pellis, in press). Due to the complexity of these movements, a different behavioral paradigm was chosen for analysis where evasive dodging movements are limited to the

horizontal plane and counterattacks following a dodge do not occur. A feeding rat will protect a food item by swerving laterally away from an approaching conspecific or robber. Dodging to protect a food item involves a lateral turn of about 180° (Whishaw, 1988; Whishaw & Gorny, 1994; Whishaw & Tomie, 1987; 1988).

My work has shown that when dodging from a same-sex conspecific, females typically pivot away by moving around a point located near the pelvis, whereas males typically pivot away from a same-sex robber by moving around a point located near the midbody. Thus, while the excursion of the female's pelvis is small, the excursion of the male pelvis is large. This difference in the movement of the pelvis is accompanied by differences in the associated velocity and number of steps taken by the hindpaws. A detailed examination of these differences is the focus of chapter two.

The third chapter focuses on whether there are differences in the composition of the dodge pattern due to the sex of the conspecific attempting to rob the food item. Given that in the first experiment, chapter two, only dodges with a same-sex partner were tested, it is possible that the sex of the robber may influence the organization of dodging movements.

It has been shown that during aggression male rats are both more likely to engage in aggressive encounters with one another and to attack male

intruders (Blanchard & Blanchard, 1977) than are females. During offensive attacks, males often use a "lateral attack" in an attempt to bite the flank area of the intruder (Blanchard & Blanchard, 1977); a movement that is similar in composition to evasion seen during play and dodging to protect a food item. Furthermore, females inhibit their bites when attacking a male conspecific (Blanchard, Kleinschmidt, Fukunaga-Stinson & Blanchard, 1980). Given the higher likelihood of aggression between males, it is possible that males are more likely to use a lateral tactic or mid-body pivot when placed with another male during a food wrenching and dodging paradigm than are females.

I found that the dodge composition remained sexually dimorphic regardless of the sex of the robber. Males still moved their hindquarters larger distances relative to the snout than did females, regardless of the sex of the robber. In addition, the approach of the robber was analyzed to determine whether aspects of this behavior were different between males and females. No differences were found between the robbing behavior of males and females. Thus, it is unlikely that the sex differences in the movement composition of dodges are due to the presence of extrinsic contingencies. Rather, it appears that there are intrinsic sex differences in motor organization.

The final experiment, chapter four, focuses on whether the differences

that have been described in the organization of dodging are dependent upon the presence of gonadal hormones in early development or during puberty. Goy, Phoenix, Gerrall and Young (1959) proposed that gonadal hormones acting during the perinatal period have an organizational influence on the development of sex-typical behavior and that post-pubertally they are necessary for the activation or expression of sex-typical behavior. It has subsequently been demonstrated that gonadal hormones perinatally influence the development of sex differences in both reproductive (Ward, 1992) and non-reproductive behavior (Beatty, 1992). In most studies of sex differences in behavior however, males have simply been shown to exhibit a higher or lower frequency of response than females on a selected behavioral index. Whether the composition of the movements used by males and females on a specific behavioral index can be modified by androgen exposure, has not been addressed.

To test whether the sex differences in movement composition are influenced by androgen exposure, males were either gonadectomized on the day of birth, after weaning and prior to puberty or were left intact. Females were either injected with 200 μ m of testosterone propionate or 200 μ m of the oil vehicle on the day of birth and the following day. My work has shown

that neonatal castration makes males more female-like in their dodging, whereas castration of males at weaning does not. Females treated with testosterone neonatally perform dodges that are more male-like in their organization. Therefore, the development of these sex-typical movement patterns are dependent on the organizational effect of gonadal hormones directly after birth, but do not require the activational effect of gonadal androgens after puberty.

The purpose of this thesis is to describe the specific patterns of movement exhibited preferentially by males and females during dodging, and to determine whether these differences in movement composition are due to extrinsic characteristics of the robbing animal or are dependent on intrinsic events such as gonadal hormone exposure during development. In the final chapter I will consider the the implications of these findings with respect to the development of sex differences in peripheral anatomy and in the central nervous system. The evolution of differences in the organization of movement by males and females will also be discussed.

CHAPTER 2*

A Kinematic Analysis of Evasive Dodging Movements Used During Food Protection in the Rat: Evidence for Sex Differences in Movement

ABSTRACT

Food deprived rats will protect their food by dodging away from a conspecific. A detailed kinematic analysis of these movements in adult rats shows that each sex uses sex-typical movements. Females move their snout through a greater spatial curvature, and their snout achieves a greater velocity, relative to the pelvis, than males. Males make more hindpaw steps than females and achieve a more simultaneous movement of the fore- and hindquarters. This suggests that females pivot around a point more posterior on the body than males. The finding that functionally similar patterns of movement have a sex specific organization provides a new dimension for the study of sex differences. These differences are discussed in relation to sex differences in sex-typical behaviors, associated body structure and neural control.

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INTRODUCTION

Sex differences in mammals exist in both reproductive (Ward, 1992) and non-reproductive behaviors (Beatty, 1992). Most sexually dimorphic behaviors however, are dimorphic only in the sense that one sex is more likely to perform them than the other (Aron, Chateau, Schaeffer, & Roos, 1991; Goy & Roy, 1991). Thus, except for some behavioral patterns associated with parturition, most sexually dimorphic behavior patterns are described as sex-typical not sex-exclusive (Money, 1988). The sex-typical behavior patterns that are described in the literature (see Beatty 1992, for a review) have focused on sex differences in the frequency of occurrence of a selected behavior. The possibility that sex differences may also exist in the form or composition of movements that appear functionally similar in males and females, and not just in the frequency of the occurrence of a selected behavior, has not been addressed previously.

Lateral evasive movements are commonly seen in both females and males. They are exhibited in a number of behavioral contexts such as play (Pellis, Pellis & Whishaw, 1992), aggression (Blanchard, Blanchard, Takahashi & Kelly, 1977; Pellis & Pellis, 1987), sex (Whishaw and Kolb, 1985) and in the protection of a food item (Whishaw, 1988; Whishaw & Gorny, 1994; Whishaw

& Tomie, 1988, 1987). This suggests that a lateral evasive maneuver or 'dodging' is a motor pattern which has characteristics that are relevant across species-typical behaviors (Whishaw, 1988).

The purpose of this chapter is to examine sex differences in the composition of the movements that constitute a dodge during a food protection task. Both females and males eating a piece of food held in the forepaws will dodge away laterally to prevent the approaching partner, or robber, from stealing the food (Whishaw, 1988; Whishaw & Gorny, 1994; Whishaw & Tomie, 1988, 1987). Dodging is a movement pattern which features clearly identifiable elements such as the head, trunk and paw movements, kinematic profile and endpoint. In addition, dodging can be videotaped and analyzed both from a ventral and a lateral view to provide both a horizontal and vertical perspective of the behavior. An in-depth analysis of the elements that constitute a dodge is used here to determine whether sex differences exist at the level of motoric organization in a behavior that is commonly used by both females and males.

GENERAL METHODS

Subjects:

Eighteen adult female and 18 adult male adult Long-Evans hooded rats

raised in the animal colony of the Department of Psychology at the University of Lethbridge were used. The animals were housed, as isosexual pairs, in wire mesh cages (17 x 25 x 20 cm), from weaning at 21 days postnatally. They were maintained in the main colony room (~23°C) on a 12:12 hour light/dark cycle (lights on at 1930h). When the experiment began, the adult males weighed between 350 and 450g, and the females weighed between 200 and 300g. The rats were maintained on a limited feeding schedule in order to maintain their body weight at about 80-85% of their initial free feeding weight (Whishaw & Tomie, 1987), by providing them with a limited supply of rat pellets (Purina Rodent Chow). Water was provided *ad libitum*.

Training and Testing:

Trials were conducted between 1400 and 1600 hrs. Two same sex pairmates were placed in a thin plexiglass cylinder, 40 cm in diameter and 45 cm high. The cylinder was placed on a table with a clear glass top. The animals could then be filmed either from a lateral view through the plexiglass cylinder or from the ventral view off a mirror mounted under the glass table top that was inclined at 45 degrees (see Fig. 1 in Pinel, Jones & Whishaw, 1992).

Prior to videotaping, the pairs were habituated to the testing apparatus.

For both habituation and testing, a single food pellet, weighing approximately 2.5g, was placed in the testing apparatus with the two subjects. Habituation was complete when shortly after being placed in the cylinder, one of the animals began to eat and the other attempted to steal the food. Once one of the animals had performed at least ten dodges the food was removed and a new piece was introduced to the testing arena. The new piece of food was given to the animal that had previously been attempting to rob the food pellet. The trial continued until at least ten dodges were obtained from this animal also. The testing was terminated after at least ten dodges of 135° were obtained for each rat.

Video Recording:

Video records were obtained using a Sony Hi-8 Camcorder at a shutter speed of 250 of a second. Additional light was provided by two 150 watt spotlights on the ceiling 125 cm above the testing apparatus. The Hi-8 video was subsequently transferred to a Sony VHS tape and a digital time code was added using a TRG-50 Horita Micro Window. The VHS tape was then analyzed using an AG-7300 Panasonic Video Cassette Recorder connected to a Sony Trinitron monitor and a computerized measurement system (Peak

Performance Technologies Inc., Englewood, CO).

Analysis of Horizontal Movement:

To determine whether there were differences in the organization of horizontal movements during dodges the dodges by twelve females and twelve males were videotaped and analyzed from the ventral view.

Behavioral Analysis: Ten videotaped dodges of at least 135° were analyzed for each rat. A computerized measurement system (Peak Performance) was used to digitize selected points on the animals' bodies. A frame grabber was used to capture the individual frames; this allowed for an analysis at 60 frames/s (Whishaw, Pellis & Gorny 1992). The tip of the snout, a mid point along the longitudinal axis of the body and the base of the tail were digitized. Analysis began on the frame of the first movement of the snout and continued until the rat realigned its fore- and hindquarters and had resumed eating. In addition, the tip of the robber's snout was digitized. The movement of all digitized points were graphically displayed using the Peak Performance movement analysis system. This computerized digitizing system provides a re-integration of the sequences of dodges so that the trajectories, traced by the points digitized, can be followed and examined.

Using this system, the distance travelled, and the resultant velocities of the snout, torso and pelvis can be displayed over the course of each dodging sequence. To quantitatively compare the dodges of the males with those of the females, comparisons of the relative distance travelled and the relative velocity attained were used to reduce the complex temporal sequences into summary values. These values were then analysed using a one-way analysis of variance to determine whether significant differences were obtained on the measures described in the following sections.

Distance Travelled by the Pelvis and the Snout: The relative distance travelled by the base of the tail (pelvis) (y) was subtracted from that of the snout (x). The resulting value was then divided by the distance travelled by the snout. This score was then multiplied by 100 in order to obtain the percentage difference in distance travelled by the snout relative to the pelvis ($(x-y)/x*100$). During a dodge, the food held in the mouth by the defender is moved away from the robber. Thus the movement of the snout represents a swerve away from the robber. A large movement of the pelvis represents additional body movement during the dodge. A large score (%) meant that only the snout moved with little other body movement. A small score (%) meant that not only the front of the rat moved, but that a large movement

was also made by the pelvis.

Velocity of the Pelvis and Snout: A similar procedure to that used for comparing the distances travelled by the digitized points was used to make two comparisons of the differences in velocity by the snout and the pelvis. (1) The maximum velocity obtained for the snout relative to the pelvis was determined following the same formula used to calculate the relative difference in the distance moved by the pelvis compared to the snout. A large score (%) meant that the velocity of the snout was greater than that of the pelvis. A small score (%) meant that the pelvis of the rat attained a maximum velocity closer to the velocity attained by the snout. This corresponds to a large rapid movement of the pelvis. (2) The relative temporal relationship of the occurrence of the first peak in velocity by the snout and by the pelvis was measured by converting the frame at which the initial peak occurred (x) into a percentage of the total number of frames of the dodge (y) ($x/y=z$). The value obtained for the pelvis was then subtracted from the value obtained for the snout. This provided a difference in the amount of time elapsed between the two peaks which could then be compared across trials. A large difference in the time elapsed between the initial peak in velocity for the pelvis as compared to the snout corresponds to a small

amount of movement of the pelvis during the initial part of the dodge, whereas a small difference in the time elapsed indicates that the pelvis began to move shortly after the dodge was initiated.

Comparison of Torso to Pelvis: In addition to the quantification of the relative displacement and velocity of the snout to the pelvis, comparisons were also made between the torso and the pelvis. The point digitized for the torso was determined by following the midline of the body and selecting a point that was approximately halfway between the shoulders and the pelvis. More movement of the pelvis relative to the torso would suggest that the point of pivot is closer to the torso; conversely, more movement by the torso than the pelvis would suggest that the point of pivot is closer to the pelvis. Two measurements were calculated comparing the pelvis(x) and torso(y) (i.e., $x-y/x*100$); the relative distance travelled and the maximum velocity obtained. A large positive score corresponds to a large movement or velocity obtained for the pelvis relative to the torso. A small positive score or a negative score represents a small movement or velocity of the pelvis compared to the torso.

Analysis of Stepping by the Hindlimbs: The amount of stepping with the hindlimbs was analyzed using frame-by-frame inspection of the videotaped dodges. Hindlimb stepping was summarized by scoring the number of steps taken by the hindlimbs during each dodge.

Calculation of Group Means: The scores for the ten dodges of each rat were used to calculate individual means for all the quantitative measurements. These were then used to calculate group means. In addition, one example for each dodging animal where the animal was away from the walls of the test enclosure and the robber was approaching at a perpendicular angle to the food, was analyzed separately and was termed an unconstrained dodge (see Fig. 1). These unconstrained dodges minimized the influence of confounding environmental factors, and therefore provided a more precise comparison of male and female dodges. Group means for the unconstrained dodges were calculated from the individual value obtained for each rat.

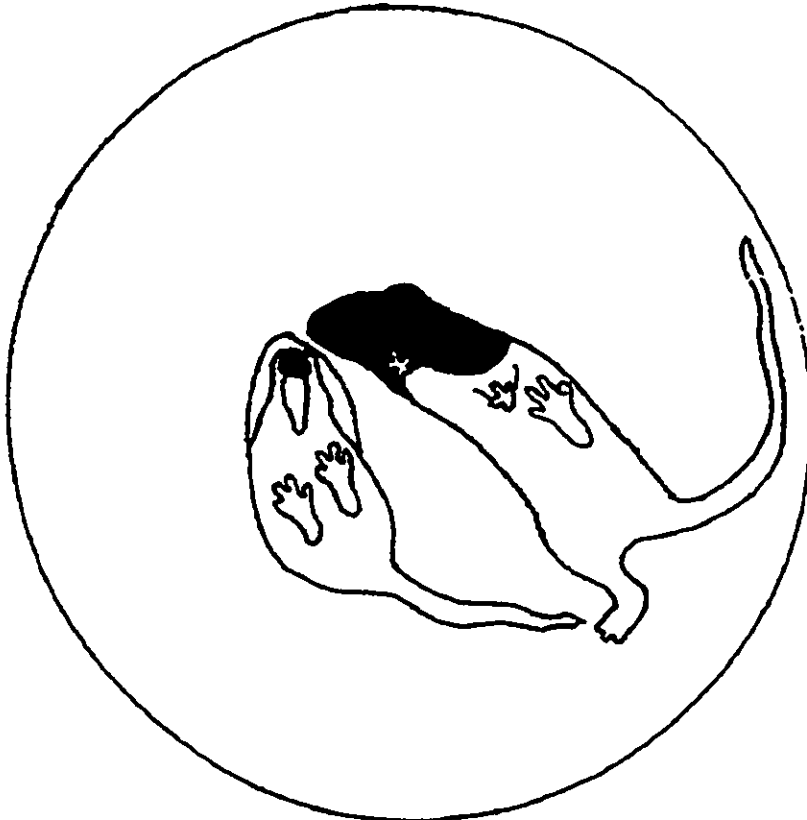
Analysis of Vertical Movement: The degree to which sex differences in the movement patterns of females and males in the horizontal plane may be due to differences in the amount of vertical movement was analyzed. The dodges by six females and six males were videotaped and analyzed from the lateral

Figure 1. An example of a constrained (A) and unconstrained (B) dodge are shown. During a constrained dodge both the circular testing arena and the position of the robber can influence the movements of the defender. The unconstrained situation permits greater freedom of movement for the defender and hence allows comparisons of dodges with minimal influence of the testing enclosure or the robber's position.

A. CONSTRAINED



B. UNCONSTRAINED



view.

One dodge was chosen for each animal where the distance of the snout from the plexiglass floor could be measured. The maximum amount of vertical displacement by the snout was calculated by subtracting the initial distance of the dodging animal's snout above the floor from the maximum height reached by the snout above the floor during the trial. The initial and maximum height were calculated by copying the position of the snout and the floor from the video monitor onto transparencies and measuring the distance between the two points. The resulting difference in vertical distance was then compared using a one-way analysis of variance.

Analysis of the Movement of the Robber: Three measurements were taken of the robber's behavior during the unconstrained trials. These were: (1) the number of video frames in which the robber followed the dodging animal, (2) the video frame, following the initiation of the dodge, where the first peak in velocity of the robbing animal occurred, and (3) the maximum velocity obtained by the robber during that first peak in velocity.

RESULTS

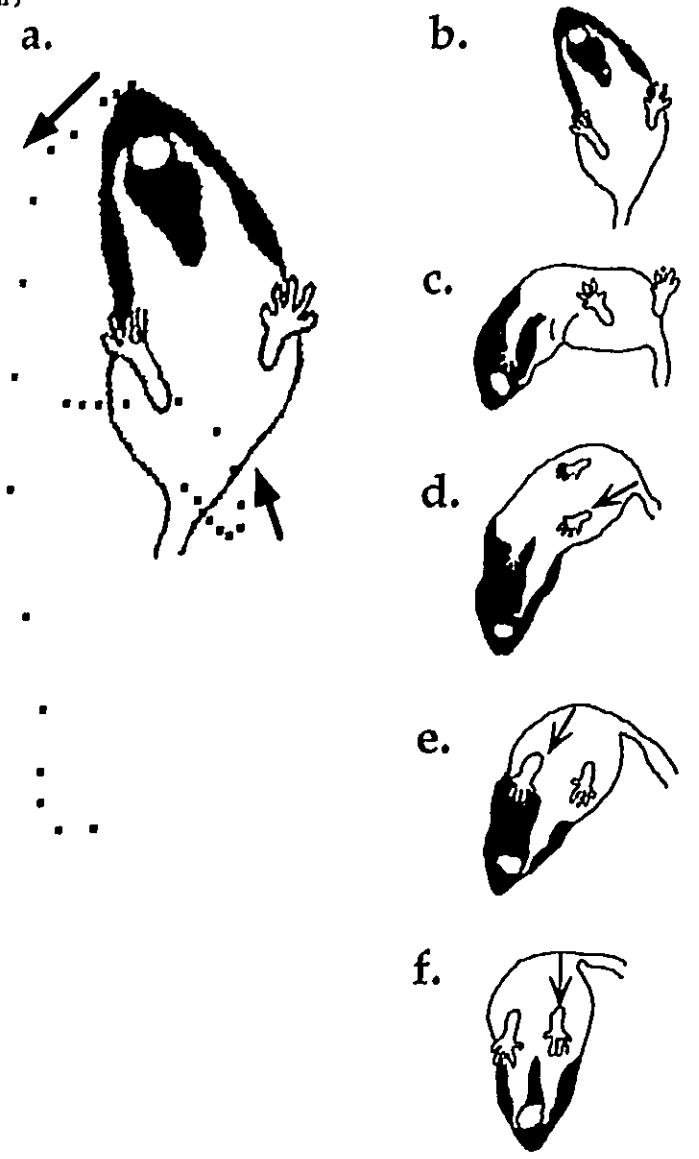
Trajectories of Horizontal Movement for the Snout and the Pelvis: The trajectories of the snout and the pelvis during the unconstrained dodges revealed differences between males and females (Fig. 2). Females moved away from the robber using a large movement of the snout and a small movement of the pelvis (Fig. 2Aa). In contrast, males combined large movements of the snout with large pelvic movements (Fig. 2Ba). Both sexes thus produced similar trajectories for the snout but different ones for the pelvis. Whereas the movement of the females' pelvis was small and generally in a forward direction, the movement of the males' pelvis was large and involved both an initial backward component and a large forward component.

Hindpaw Stepping Sequences: The stepping sequences that accompanied the dodges described above were also different for females and males. Females made their initial step sideways with the paw ipsilateral to the direction of the dodge (Fig. 2Ad), this was then followed by a forward step of the paw contralateral to the direction of the dodge (Fig. 2Ae). A final step forward by the hindpaw ipsilateral to the direction of the dodge (Fig. 2Af) realigned the fore and hindquarters.

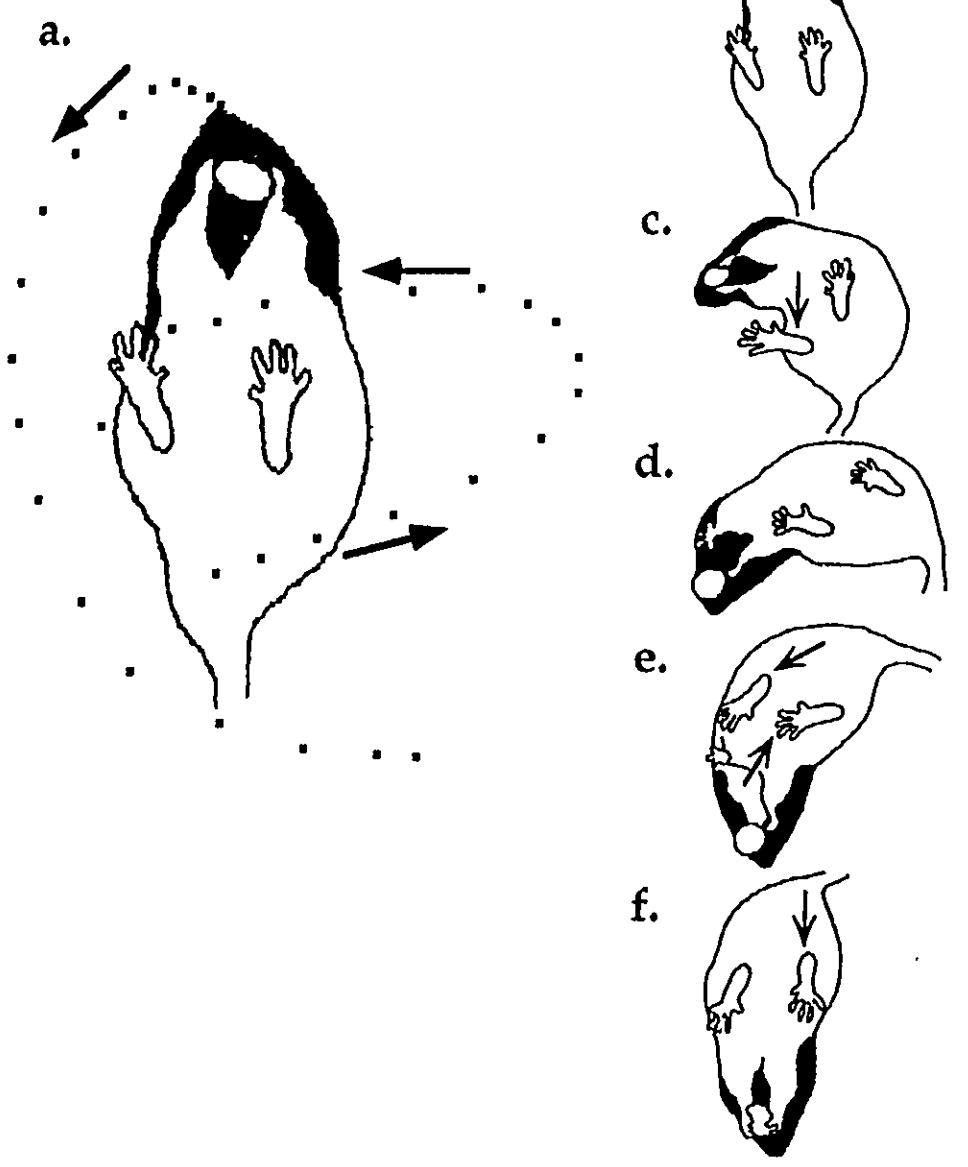
The stepping sequence for males began with an initial step backwards

Figure 2. The trajectories of the snout and pelvis are shown for an unconstrained female dodge (Aa) and an unconstrained male dodge (Ba). Each solid round dot represents two video frames with the arrows with closed heads indicating the direction of the movement. Note that unlike the female, the male makes a large outward swing of the pelvis. The number and direction of steps taken by the hindpaws are also indicated by the open-headed arrows. After turning the laterally (Ab-c), the female makes an initial sideways step with the paw ipsilateral to the direction of the dodge (Ad). This step is followed by a forward step with the paw contralateral to the direction of the dodge (Ae) and a final step forward by the hindpaw ipsilateral to the direction of the dodge (Af). The male in contrast has less lateral movement of the upper body (Bb) before taking a step backwards by the hindpaw ipsilateral to the direction of the dodge (Bc). This was followed by a second backwards step with the ipsilateral hindpaw, that is followed shortly after with a forward step with the contralateral hindpaw (Be). The ipsilateral hindpaw then made a final forward step (Bf) Note: The animals represented in this figure are scaled to represent the actual size of female and male adult rats.

A . FEMALE



B . MALE



by the hindpaw ipsilateral to the direction of the dodge (Fig. 2Bc). This was followed by a second backwards step with the ipsilateral hindpaw and a forward step with the contralateral hindpaw (Fig. 2Be) shortly after. The ipsilateral hindpaw then made a final forward step (Fig. 2Bf) to realign the body and complete the dodge.

Horizontal Distance Travelled by the Pelvis Relative to the Snout: In females, there was a large lateral displacement of the snout, with only a minor displacement of the pelvis, and it was only after the snout reached its asymptote that the pelvis made its biggest movement (Fig. 3A). However, in males, the pelvis began to move shortly after a small movement of the head (Fig. 3B). For most of the dodge the movements of the pelvis and the snout were parallel. Furthermore, unlike females, as the male's snout reached its asymptote, the pelvis moved towards its point of origin. Thus the curve for the pelvis turned downward.

Comparison of the relative difference between females and males in the distance travelled between the snout and the pelvis showed a significant difference for both the overall sample ($F(1,22)=12.53$, $p=0.0018$; Fig. 4A) and the unconstrained examples ($F(1,22)=50.93$, $p=.0001$; Fig. 4B). These data show

Figure 3. The distance travelled by the snout and the pelvis is shown graphically for the dodges illustrated in Figure 2. Note that the distance travelled by the pelvis is less in the female (A) than in the male (B). Also note that in the male, the snout and the base of the tail are initially moving together; whereas in the female, the snout moves independently of the base of the tail.

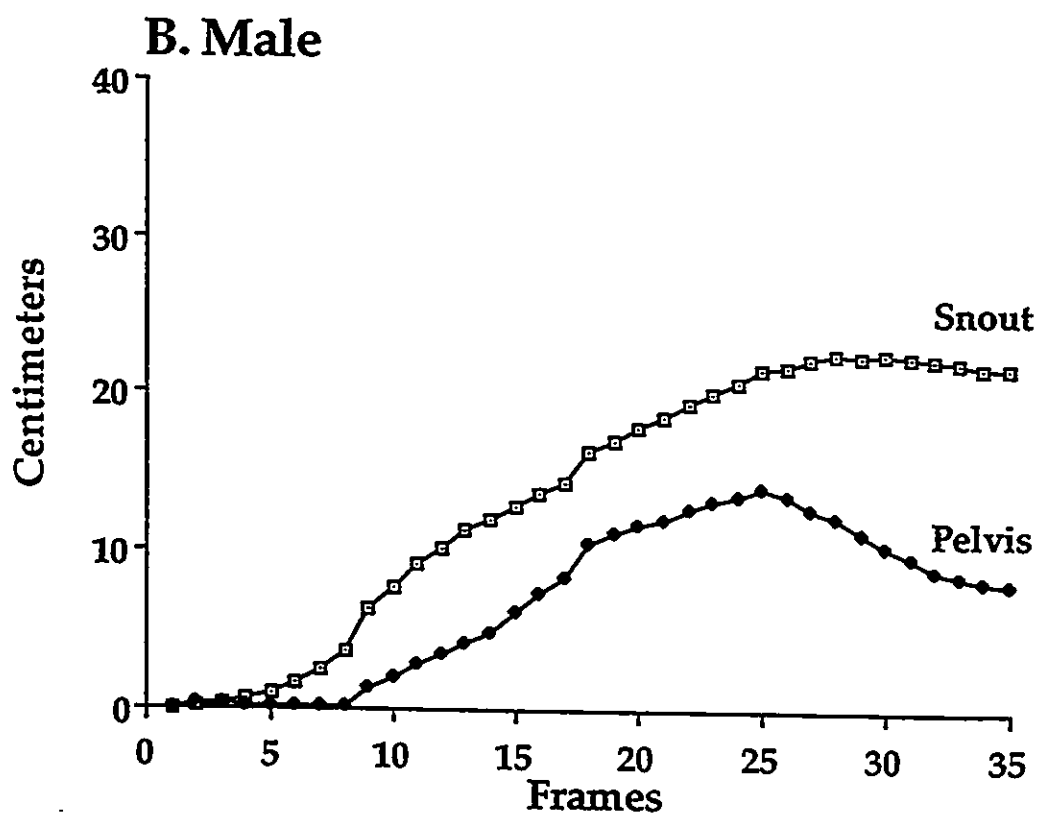
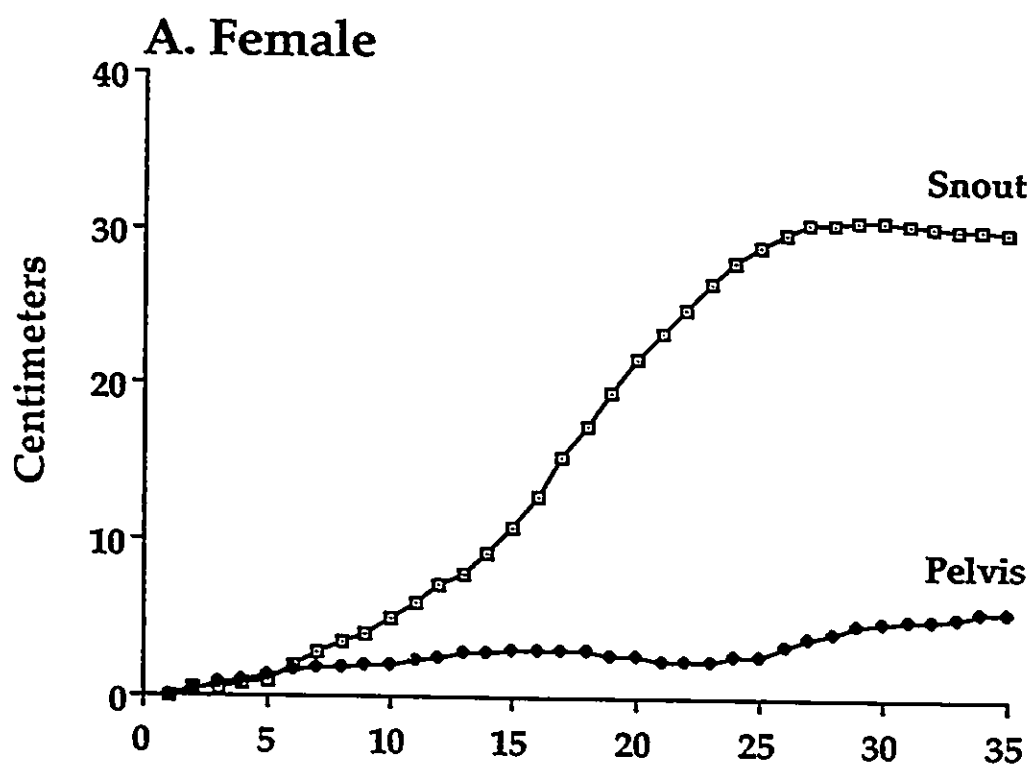
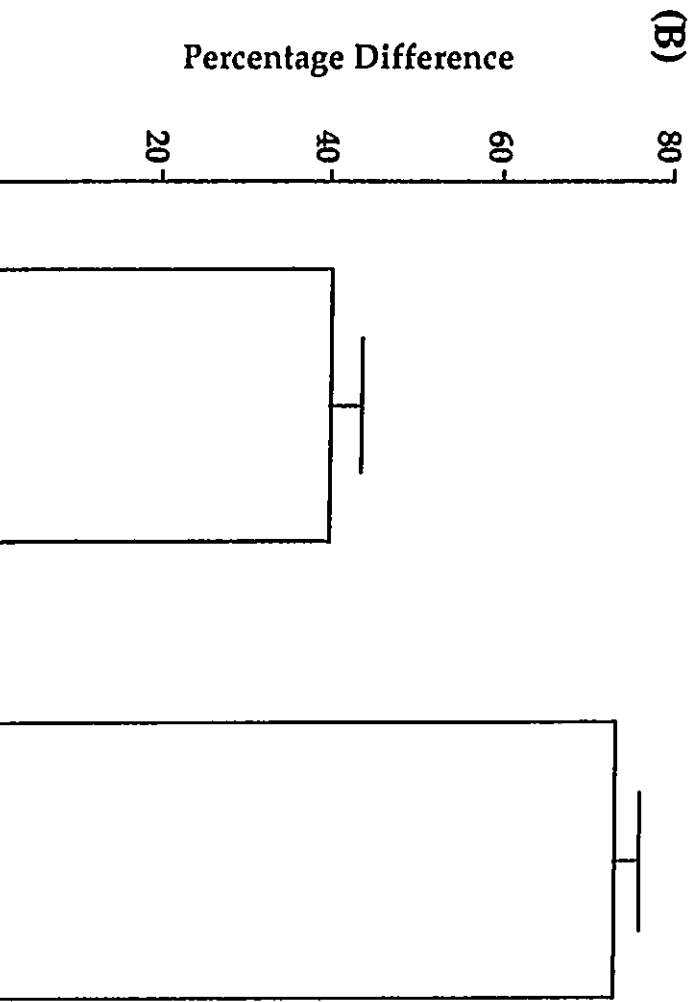
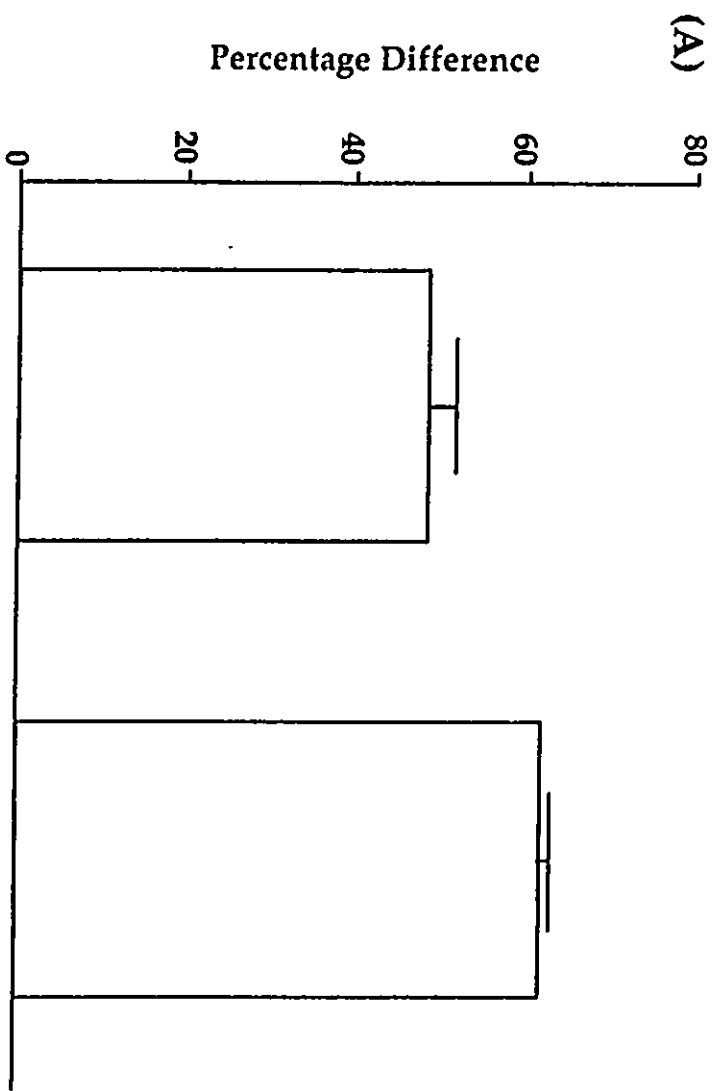


Figure 4. The differences in percentage of distance travelled by the snout relative to the pelvis are shown for males and females. The data obtained from all the digitized sequences are shown in A. The data for the unconstrained sequences for each rat are shown in B.



that the females' snouts moved more, relative to the pelvis, than was the case for the males.

Velocity of the Pelvis Relative to the Snout in the Horizontal Plane: The differences in the distance travelled by the pelvis for males and females (see Fig. 2) were also revealed by the differences in the associated velocities for the snout and the pelvis throughout the dodge (Fig. 5). For females' snouts, there was a peak about halfway through the dodge, and another for the pelvis near the end (Fig. 5A). In contrast, for males, the peak for the snout was followed closely by the peak for the pelvis, with both occurring in the first half of the dodge. There was also a second peak for the pelvis in males which occurred near the end of the dodge (Fig. 5B).

There were significant sex differences for the overall sample ($F(1,22)=4.79$, $p=.0396$) and the unconstrained examples ($F(1,22)=5.45$, $p=.0291$) in the maximum velocities achieved by the snout relative to the pelvis. The relative difference in the time elapsed prior to the initial peak in velocity by the snout as compared to the pelvis was also significantly different between the sexes for both the overall sample ($F(1,22)=5.47$, $p=.0288$; Fig. 6A) and the unconstrained examples ($F(1,22)=8.58$, $p=.0078$; Fig. 6B). The males had a

Figure 5. The velocities for the snout and the pelvis are shown graphically for the dodges illustrated in Figure 2. About halfway through the dodge, the female reaches the peak of velocity of its snout. The peak of velocity for the pelvis occurs near the end of the dodge (A). In contrast, the male's pelvis peaks in velocity shortly after the peak in velocity of the snout. Both of these peaks occur shortly after the dodge begins (B). In addition, the difference in peak velocity reached by the snout relative to the pelvis is much greater in the female than in the male.

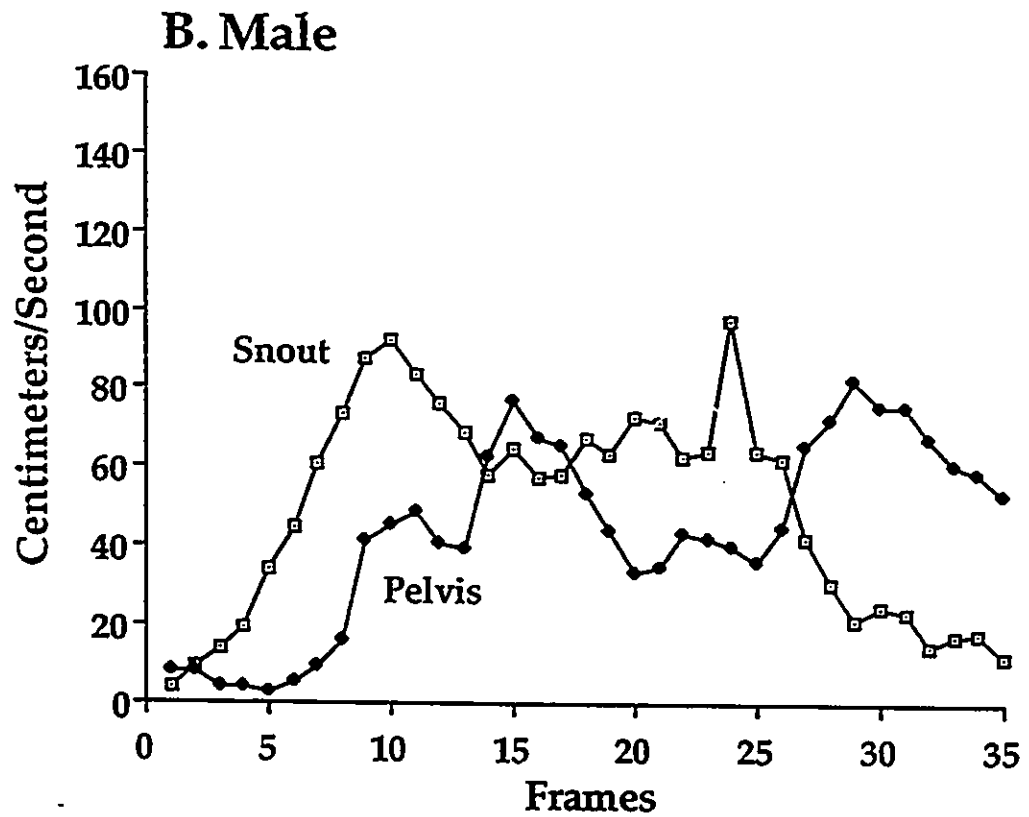
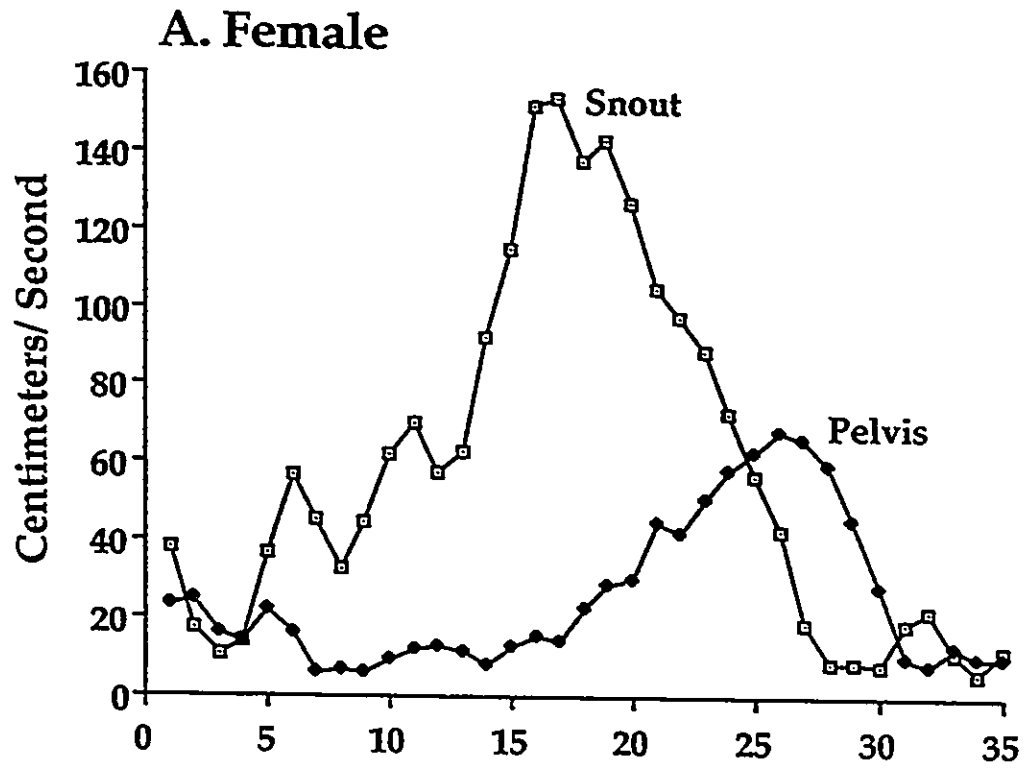
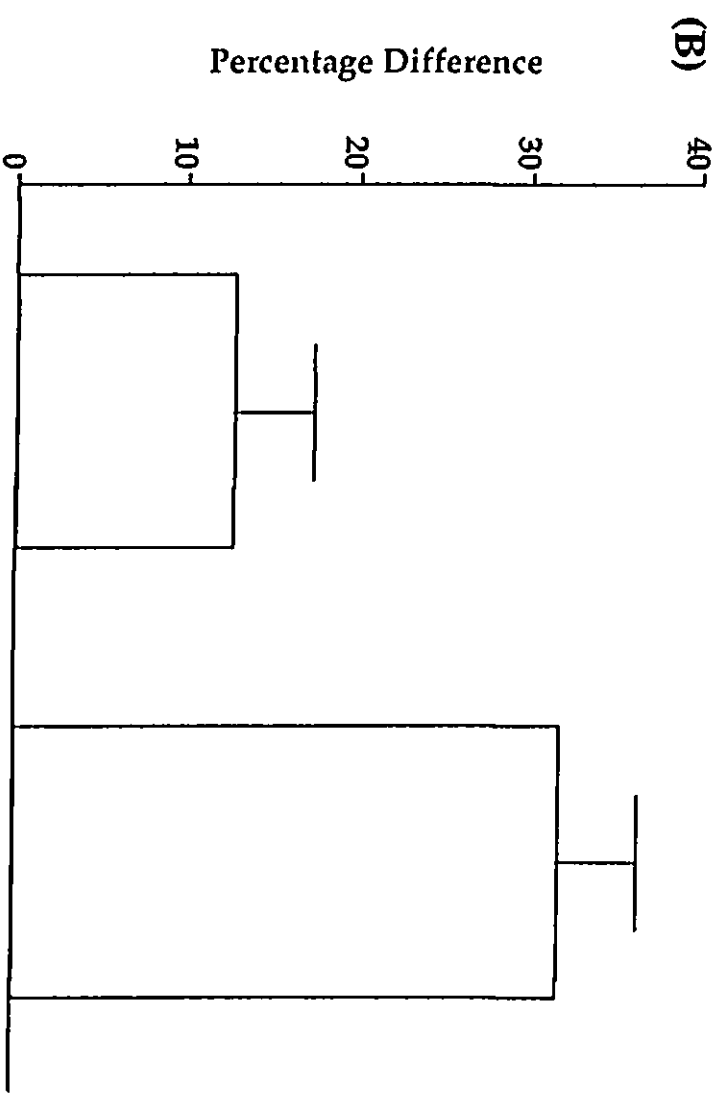
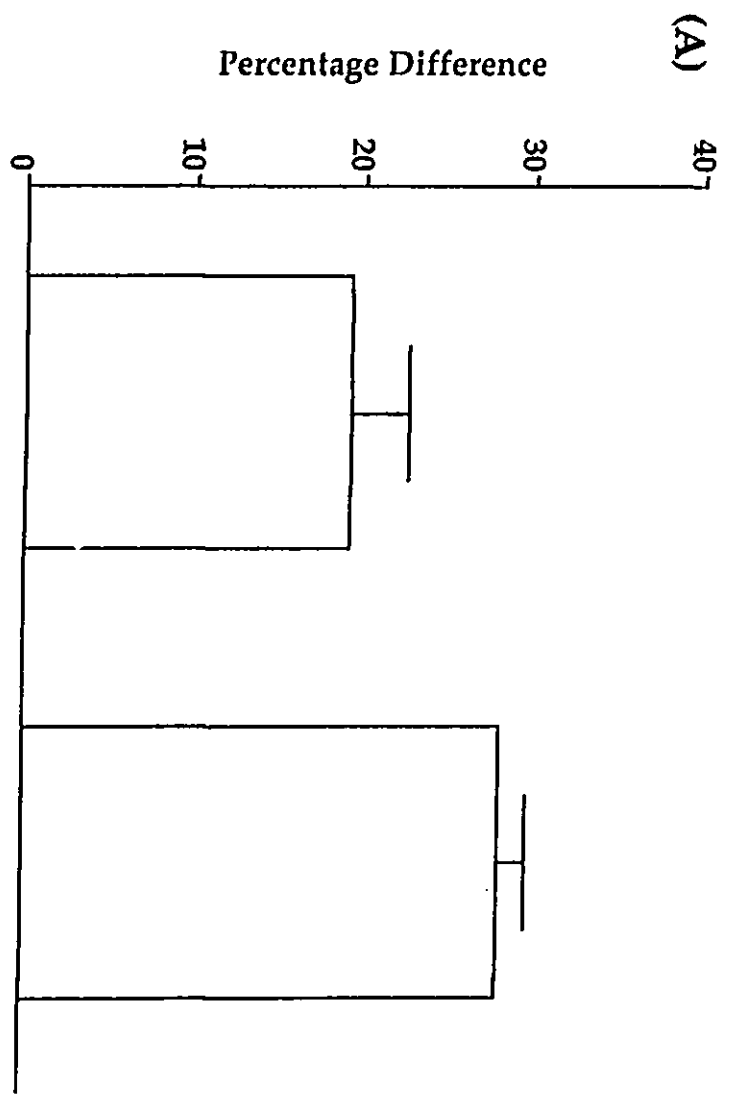


Figure 6. The percentage difference in the temporal location of the initial peak in velocity are shown for males and females. The data obtained from all the digitized sequences are shown in A. The data for the unconstrained sequences for each rat are shown in B. A negative value means that the pelvis reached its initial peak in velocity before the snout, a positive value means the snout has reached its initial peak in velocity before the pelvis. The larger the positive value the greater the time elapsed between the initial peak of velocity of the tip of the snout as compared to the pelvis.

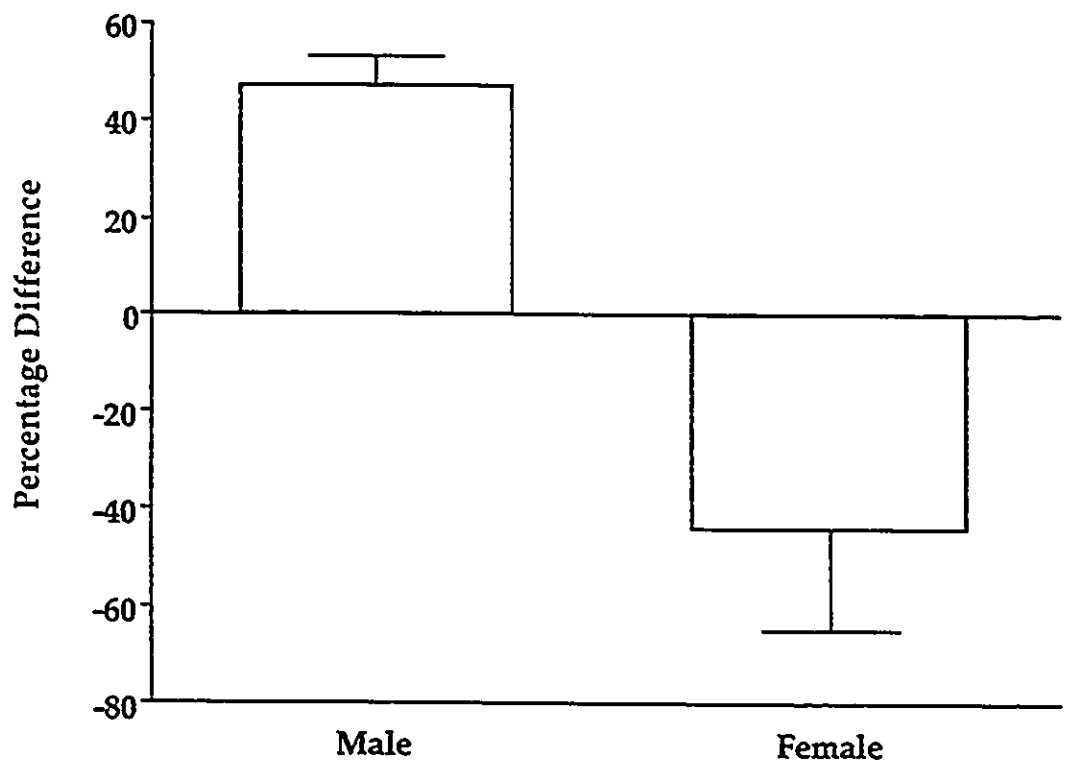


smaller difference in the maximum velocity obtained for the snout relative to the pelvis, and the initial peaks in the velocity of the snout and the pelvis were closer together than those of the females.

Horizontal Movement of the Torso Relative to the Pelvis: The above results suggest that the females were pivoting around a point more posterior than the males. To test this hypothesis, another point between the snout and the pelvis (designated "torso"), was analyzed. It was predicted that if the males were moving around a vertical axis closer to the middle of the body, the total distance travelled and the maximum velocity obtained for the pelvis should be greater than that of the torso in males as compared to such measures for females. The first unconstrained trial of each rat was used for comparison.

The difference in the distance travelled by the torso as compared to the pelvis was significantly different between the sexes ($F(1,22)=45.054$, $p=.0001$; Fig. 7). The relative difference in maximum velocities was also significantly different ($F(1,22)=15.52$, $p=.0007$). These data support the hypothesis that males pivot around a point closer to the midbody, whereas females pivot around a point nearer the pelvis.

Figure 7. The relative distance travelled by the torso compared to the pelvis is shown for males and females during the unconstrained trials. Note that negative percentages signify that the pelvis has travelled less than the torso, the positive values indicate that the torso has moved more than the pelvis.



Hindlimb Stepping: The average number of steps made by the hindpaws were significantly different for both the overall sample ($F(1,22)=12.58$, $p=.0018$; Fig. 8A) and the unconstrained examples ($F(1,22)=38.30$, $p=.0001$; Fig. 8B). The males made more steps with their hindpaws than females. This was consistent with the males' more complex pattern of movement and stepping.

Analysis of Vertical Movement: Quantitative comparison of the maximum amount of vertical movement during dodges was not significantly different between females ($X\pm S.E.:4.67\pm 0.99\text{mm}$) and males ($4.33\pm 1.52\text{mm}$). Both females and males show minimal vertical movement throughout the dodge (Fig. 9).

Analysis of the Robber: It is possible that the sex differences in the movements used during dodging were an indirect by-product of the actions of the robbing animal. As all the dodges for the males were initiated by a male robber, and all those for females were initiated by a female robber, the actions of the robbing animal may have influenced the type of dodge exhibited. To test this hypothesis, the robber's snout was digitized during its approach. On all three measures, no significant differences were found (Table 1).

Figure 8. The average number of steps taken for females and males for both overall (A) and unconstrained dodges (B).

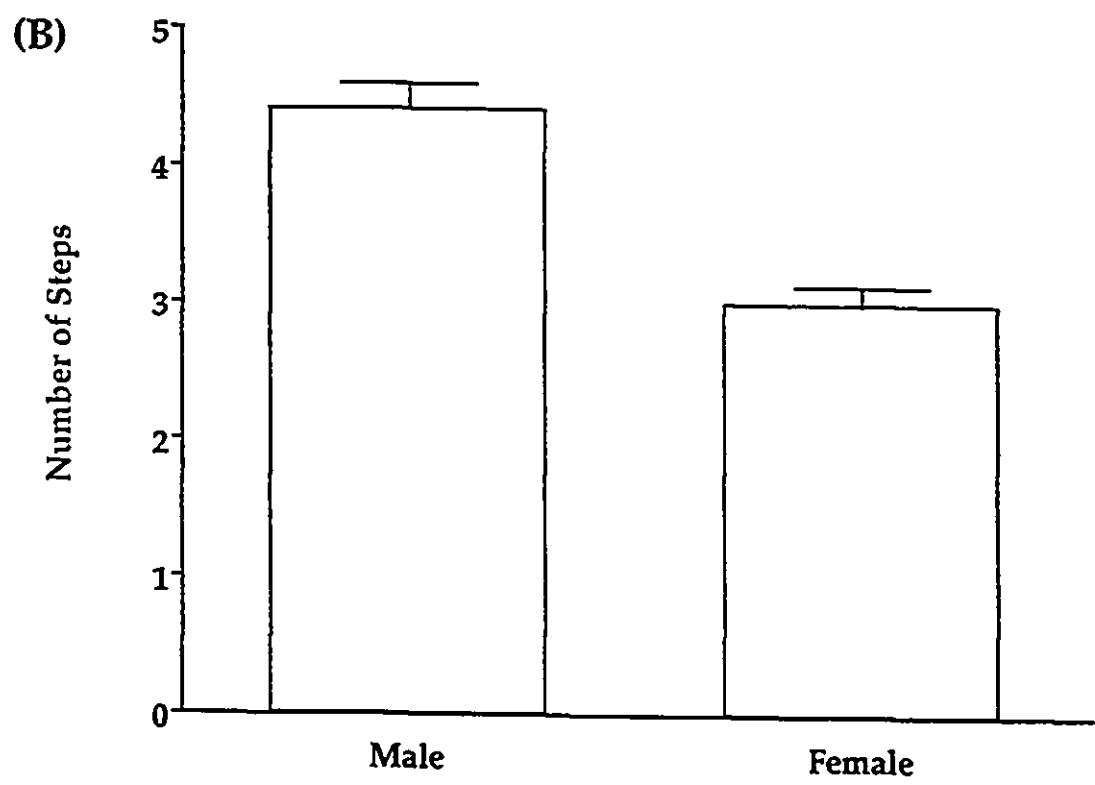
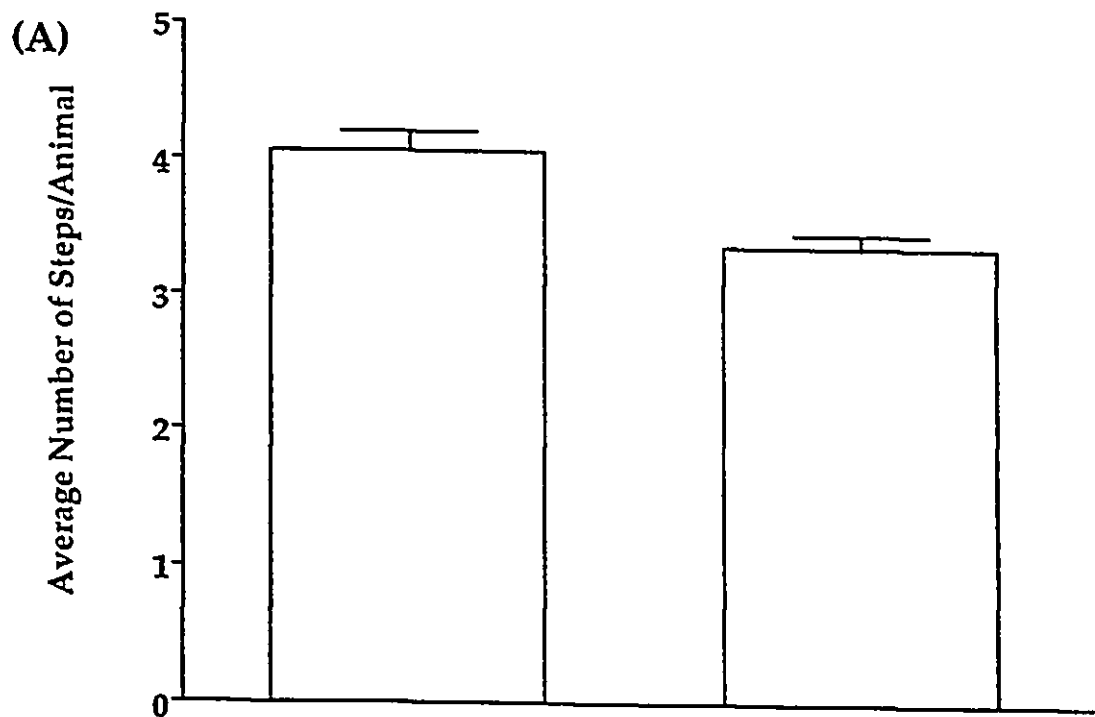


Figure 9. A dodging sequence is depicted for both females (A) and males (B) from a lateral view showing the initial position (a) three positions during the dodge (b, c, & d) and the final position (e). Note that throughout the dodging sequence the distance from the floor to the tip of snout does not change markedly in either sex.

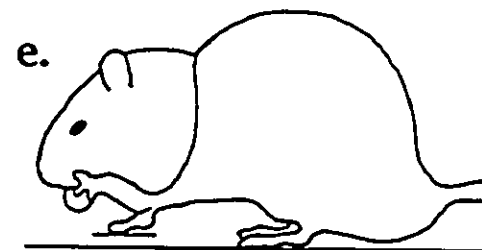
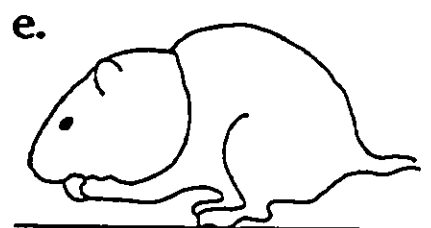
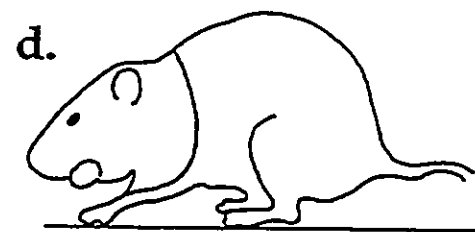
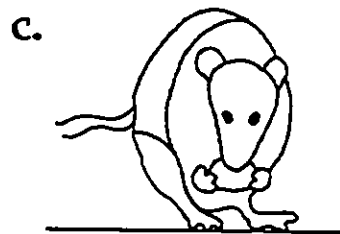
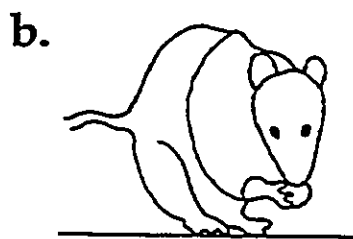
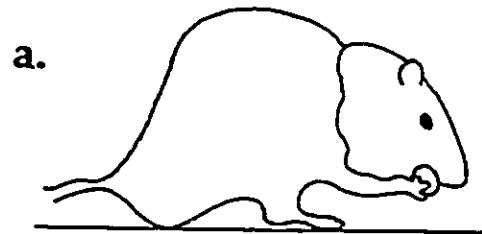
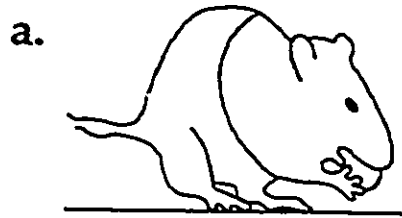
A . FEMALE**B . MALE**

TABLE 1

COMPARISON OF THREE ASPECTS OF ROBBING BEHAVIOR

	Variables Measured*		
	1	2	3
Males (X ± SE)	42.97 ±6.46	18.06 ±3.01	40.63 ±5.25
Females (X ± SE)	36.86 ±2.92	19.24 ±3.57	51.49 ±11.46
F-Test	0.74, ns**	0.06, ns	0.74, ns

*1 = the number of frames in which the robber followed the dodging animal.

2 = the frame, following the initiation of the dodge, where the first peak in velocity of the robbing animal occurred.

3 = the maximum velocity that was obtained during the first peak in velocity.

**ns = not significant at $p < 0.05$.

DISCUSSION

When dodging, females show a greater amount of movement of the snout relative to the pelvis than do males. In order to produce the larger amount of hindquarter movement, it is necessary for the males to take more steps with the hindlimbs. The maximum velocity attained by the snout relative to the pelvis was also greater for females than for males. This was coupled with a larger temporal separation of the initial peaks in velocity of the snout and the pelvis for the females as compared to the males. Furthermore, analysis of the movement of the torso relative to the pelvis showed that for females, the torso travelled a greater distance and attained a greater velocity than the pelvis. The opposite was true for the males. The difference in movement composition was not due to differences in vertical movement during the dodge.

The lack of sex differences in the robbers' movements showed that the sex differences in dodging could not be accounted for by the behavior of the robber. The unconstrained dodges were particularly revealing, because in the absence of obstacles that could affect the movement of the dodging rat, there was no overlap in the score of relative distance travelled of the snout to the pelvis between the females and males. In all cases, females pivoted around a

point more posterior on their bodies than the males. Both sexes appeared to conserve their sex typical movement pattern even when the rats were constrained, and the movement was modified.

Even though male and female robbers do not move differently, it is possible that the sex of a robber in itself, could influence the dodging pattern performed. That such a judgement may be possible is suggested by the finding that the magnitude of a dodge can be influenced by the time it takes for a piece of food to be consumed (Whishaw & Gorny, 1994). In a study using quadrads, composed of two males and two females, each rat was tested with a same sex partner and an opposite sex partner. Preliminary data show that irrespective of the sex of the robbing animal, both the males and females continued to employ their sex typical pattern of pivoting during the dodge (Pellis, Field, Smith & Pellis, 1995). This suggests that the sex of the robbing animal does not determine the pattern of dodging.

Since the different patterns of dodging are not functionally related to the behavior of the robber, and appear to be equally successful, the question is raised as to why a sex difference in the composition of dodges should occur. One possibility is that anatomical differences in the skeleto-musculature and/or body proportions of adult male and female rats produce corresponding differences in movement. However, preliminary data suggests

that this sex difference in movement is present early after weaning, at a time when the size differences between males and females are minimal (Field, Whishaw & Pellis, work in progress). While only tentative, these findings support the possibility that this difference in movement cannot be explained solely by a difference in body morphology.

That sex differences in movement may be due to neural differences rather than peripheral anatomical differences is further suggested by work done on both rats and humans. Low levels of estrogen in female rats can increase the number of footfall errors made when they traverse a narrow beam. The number of these errors are decreased on the day of estrus or by 17beta-estradiol treatment (Becker, Snyder, Miller, Westgate & Jenuwine, 1987). The performance of normal women on several sexually dimorphic motor tests fluctuates during the menstrual cycle, with changes in performance being associated with changes in the levels of estrogen and progesterone (Hampson and Kimura, 1988). Girls with congenital adrenal hyperplasia (CAH) are prenatally androgenized and may exhibit more male-like movement patterns than their unaffected sisters (Dittman, 1992). Two forms of this condition occur, the simple-virilizing and the salt-wasting variant. Based on a questionnaire study of the afflicted subjects, their unaffected sisters and their respective mothers, Dittman (1992) reported that

the CAH variant with the most strongly masculinized body morphology (i.e., the simple-virilizing variant) was reported to be the least male-like in movement, whereas the salt-wasting variant that was reported to be the most female-like in body morphology was the most masculine in movement. These studies suggest that motoric sex differences may be influenced by the effects of gonadal hormones at a neural level.

Another non-reproductive behavior pattern that serves the same function but differs in motor organization between the sexes is the post-pubertal urinary position of dogs (Beach, 1974). Until puberty, both sexes squat to urinate, and it is only after puberty that males switch to raising one hindleg in the air. In contrast, the sex difference in dodging by rats appears to be present prior to puberty (Field, Whishaw & Pellis, work in progress), and unlike the urinary position in dogs, it may not be restricted to a specific functional context. It is possible that this sex difference is not task-specific, but rather is a sex-typical difference in the topography of similar movements that occur in such diverse contexts as play (Pellis, Pellis & McKenna, 1994), aggression (Blanchard et al, 1977, Pellis & Pellis, 1987), sex (Whishaw & Kolb, 1985) and spontaneous turning (Eilam & Golani, 1988). Further research on possible sex differences in the movement organization of these behaviors

will help determine whether the differences described in this paper are, or are not task specific.

Studies on non-reproductive sex differences have indicated that “(t)hese differences are typically small in magnitude, and tend to vary with the genotype and prior behavioral history of the individual” (Beatty, 1992, p. 115). However, most studies have not investigated the organization of the movements performed, and as shown here, even behavior patterns that appear to be the same in both sexes can differ markedly in motoric organization. The possible role of hormones, neural maturation and behavioral experience during development all need to be addressed in future research to determine both how these differences arise and why they exist. That similar non-reproductive behavior patterns differ in form, and not only in the likelihood of occurrence, suggests there must be some fundamental differences in the environmental milieu faced by each sex. What these might be is uncertain, but the existence of the robust difference in the pattern of lateral dodging provides an opportunity for further analysis. Clues may be sought from the development of this motoric difference, the presence, or not, of similar differences in other behavioral contexts, and in the comparative distribution of such differences in mammals and other vertebrates.

CHAPTER 3***The Organization of Sex-Typical Patterns of Defense During Food Protection
in the Rat: The Role of the Opponent's Sex****ABSTRACT**

Feeding rats defend a food item from an approaching conspecific by turning away about 180° in the horizontal plane. Females and males use a different composition of movements and stepping patterns to perform these evasive dodges. This study was designed to examine the role of the robber's sex on the execution of sex-typical patterns of dodging. All subjects were tested with a partner of each sex. During dodging, females used the female-typical pattern of pivoting around the pelvis and males used the male-typical midbody pivot, irrespective of the robber's sex. Females and males however, differed in how they were oriented towards a same sex robber at the end of the dodge. Males aligned their pelvis with the head of a male robber at the completion of the dodge, whereas females aligned their pelvis with the mid-body of a female robber. When dodging from an opposite sex partner, both males and females were equally likely to oppose the head or the midbody. These findings show that the sex-typical patterns of dodging are not determined by

the sex of the partner. However, feeding rats do make subtle changes in their orientation to the approaching partner by modification of the sex-typical dodge patterns. This suggests that while male and female robbers must pose different defensive problems, these differences are dealt with by a modification of the sex-typical pattern of dodging rather than by switching to the dodge pattern of the opposite sex. This further suggests that the differences in the composition of the dodge pattern in males and females are not due to extrinsic contingencies, but rather, are due to intrinsic differences in the sex-typical organization of defensive motor patterns.

*This chapter is modified from a paper that has been submitted to Aggressive Behavior

INTRODUCTION

In colonies of wild rats, conspecifics will often attempt to steal food from one another (Whishaw & Whishaw, 1996; Barnett, 1975). Whishaw & Whishaw (1996) have documented that rats returning to their home territory with food are often investigated by other rats and that attempts to steal the food from a returning rat are common. A robber will attempt to gain access to the food item by approaching the feeding rat from either the rear or the side and try to wrench the food away. To protect a food item, the victim generally dodges away from an approaching conspecific in a manner similar to that described for laboratory rats (Whishaw, 1988; Whishaw & Gorny, 1994; Whishaw & Tomie, 1987, 1988).

In laboratory rats, a feeding animal will dodge to protect a food item by rotating their fore- and hindquarters away in a turn of about 180°. This dodging movement, while functionally similar in both sexes, is organized differently by males and females (Field, Whishaw & Pellis, in press). Females initially pull their forequarters away approximately 90° from an approaching conspecific using minimal hindquarter movement. Continued forequarter movement is then accompanied by hindquarter movement in the same direction, which realigns their fore- and hindquarters. In contrast, males, at

the beginning of a dodge, make large hindquarter movements in a direction opposite to the movement of their forequarters. This is followed by a change in the direction of the movement of their hindquarters, or pelvis, from backward to forward, which realigns their fore- and hindquarters (Field, Whishaw & Pellis, in press). This difference in movement organization is not due to differences in the amount of vertical movement that occurs during a dodge (Field, Whishaw & Pellis, in press). What is unclear however, is whether the sex differences in the composition of defensive dodging arise from different functional contingencies presented by the sex of the robber, or from an underlying intrinsic difference in motor organization.

Evasive or lateral movements, which are similar to dodging, are commonly displayed in a number of other behavioral contexts, including play fighting (Pellis, Pellis & McKenna, 1994; Pellis & Pellis, 1990), serious fighting, (Blanchard, Blanchard, Takahashi, & Kelly, 1977; Pellis & Pellis, 1987) and sex (Whishaw & Kolb, 1985). During play fighting, both males and females attack and defend the nape (Pellis & Pellis, 1987). Close examination of evasion, however, has shown that males and females use a different composition of movements (Pellis, Field, Smith & Pellis, in press). While females turn away from an approaching partner by pivoting around the pelvis, males are more likely to pivot around the mid-body, thus moving their pelvis towards the

partner while moving their head away (Pellis & Pellis, 1987; Pellis, 1989). Males however, are more likely to initiate counterattacks following a defensive maneuver than are females (Pellis & Pellis, 1990). Therefore, it is possible that males are using a different combination of movements in order to facilitate counterattacks.

Males also differ from females in their use of combat tactics during aggressive encounters. They are more likely both to engage in aggressive encounters with one another than are females (Blanchard, Flannelly, & Blanchard, 1988), and to attack intruders than are females (Blanchard & Blanchard, 1977). During these aggressive encounters, males often use a "lateral attack", a dodging-like movement which they use as a tactic to bite the flank of the intruder (Blanchard & Blanchard, 1977). Females, on the other hand, actively inhibit their bites when attacking a male intruder (Blanchard, Kleinschmidt, Fukunaga-Stinson & Blanchard, 1980). This suggests that females react differently than males, to a male intruder.

When in proximity to food, feral rats exhibit heightened aggression (Whishaw & Whishaw, 1996). Furthermore, males on a food restricted diet are more likely to display lateral threats, and for longer durations, in response to a male intruder than are male rats fed a standard laboratory diet (Lore, Gottdiener and Delahunty, 1986). These findings suggest that males may be

more likely to use lateral displays in response to an approaching male than are females. Therefore, the sex differences present in the organization of dodging tactics may be due to the differences that are contingent on male-male encounters and not due to sex differences in the organization of defensive movements. To test this possibility, same sex and opposite sex pairs were tested in the food wrenching and dodging paradigm.

In a previous experiment using the dodging paradigm (Field, Whishaw & Pellis, in press), only isosexual adult pairs were tested. In this experiment, the organization of movement during dodging by males and females, defending against either a male or a female robber, were compared. In addition, the approach of the robber was analyzed to determine whether sex differences in robbing strategies exist that influence the sex-typical organization of the dodges. With regards to the outcome of the dodges, the relative position and distance of the dodging and robbing rats were analyzed. These analyses provided a framework for determining whether the motor differences in dodges between the sexes were due to extrinsic contingencies or to inherent differences in motor organization.

METHODS

Subjects:

Twelve adult female and 12 adult male Long-Evans hooded rats raised in the animal colony of the Department of Psychology at the University of Lethbridge were used. The animals were housed in six quadrads, each composed of two males and two females. The animals were housed in an air-conditioned room (21-23°C) on a 12:12 light:dark cycle (lights off at 1930 hours). They were weaned at 21 days of age and housed as quadrads of siblings. Food and water were provided *ad libitum* until testing began at which time all animals were placed on a food restricted schedule. At the start of the experiment, the adult males weighed between 350 and 450g, and the females weighed between 200 and 300g. The rats were then placed on a limited feeding schedule, with each rat being given approximately 20 grams of Purina Rodent Chow, per day, in order to maintain their body weight at about 80-85% of their initial free feeding weight (Whishaw & Tomie, 1987). All animals were ear punched for individual identification.

When 50 days old, the males (n=12) were vasectomized, to prevent pregnancy in the female cagemates. The animals were anesthetized using isoflurane (AErrane, Anaquest, Mississauga, Ontario). Once anesthetized, the scrotum was shaved and cleaned with antiseptic soap. A single, vertical, midline incision was made through the scrotum, followed by a second

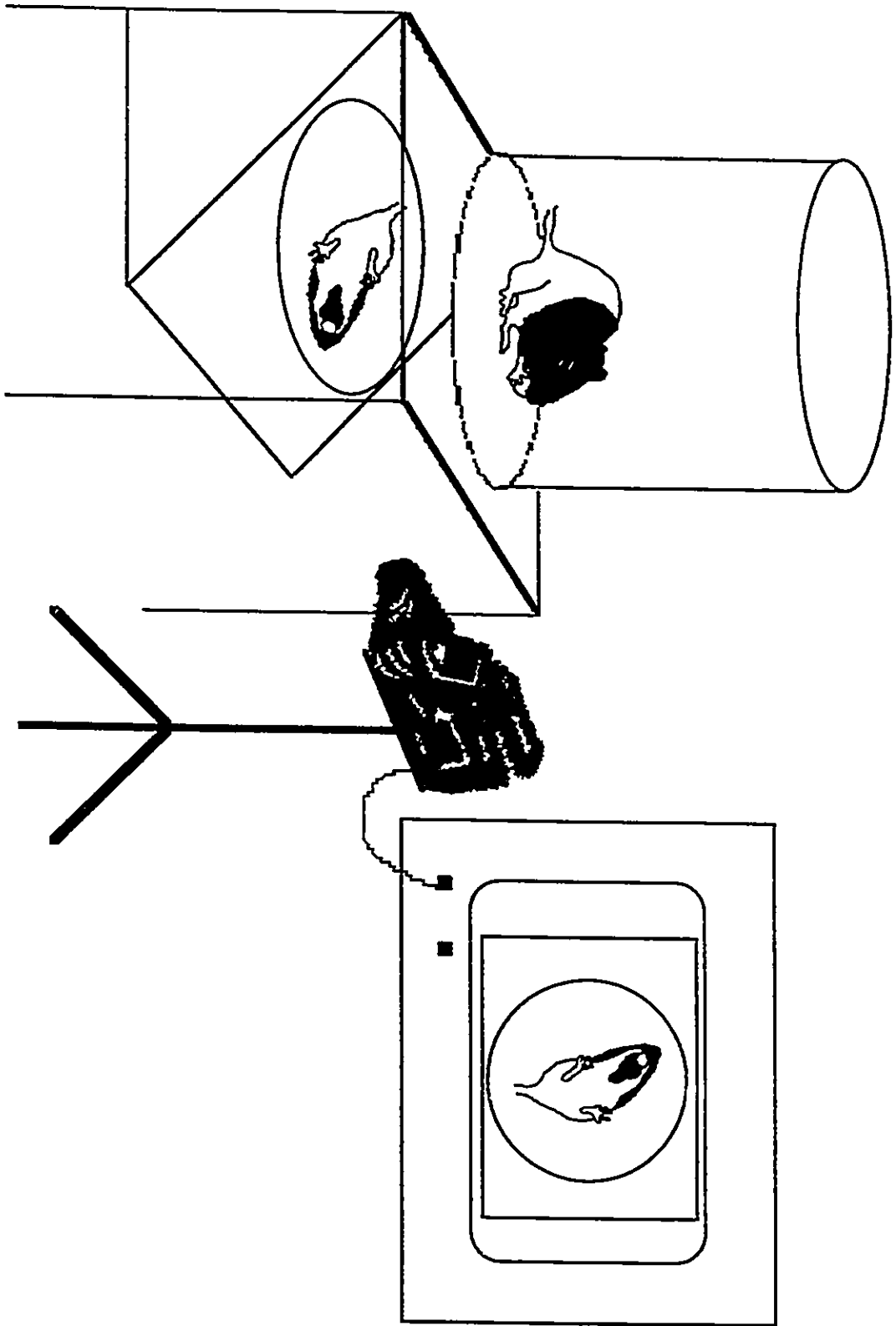
incision through the tunic to expose the vas deferens. Two ligatures, one centimeter apart, were tied around the vas deferens. The vas deferens was then severed between the two ligatures and the procedure was repeated on the other side. The tunica was closed with single interrupted absorbable sutures and a series of interrupted, single, silk sutures was used to close the scrotal incision. Following surgery, the animals were given an intramuscular injection of 15,000 units of penicillin (Penlong XL; Rogar/STB, Inc., London Ontario).

Training and Testing:

Testing began when the animals were between 100 and 110 days. Trials were conducted between 1400 and 1600 hrs. Two same sex or opposite sex cagemates (the same male and female were always tested together) were placed in a thin plexiglass cylinder, 40 cm in diameter and 45 cm high. The cylinder was placed on a table with a clear glass surface. The rats could then be filmed either from a lateral view through the plexiglass cylinder or from the ventral view off a mirror mounted under the glass table top at 45° (Fig. 1) (Pinel, Jones & Whishaw, 1992).

The pairs were habituated to the testing apparatus prior to videotaping. For both habituation and testing, a single food pellet, weighing approximately

Figure 1: The testing apparatus and filming setup are depicted here. The rats are placed, in pairs of two (for clarity only one rat is depicted here), in a plexiglass cylinder on a clear table top. An incline mirror is positioned at a 45° angle beneath the table top. The ventral view of the rats is then videotaped, from the mirror. The video camera is connected to a monitor to ensure the quality of the videorecording. Tapes of the behavioral sequences are then later analyzed frame-by-frame.



2.5g, was placed in the testing apparatus with the two subjects. Habituation was complete when shortly after being placed in the cylinder, one of the animals would begin to eat and the other would attempt to steal its food. The same sex and opposite sex pairs were trained and tested on alternate days. Once one of the animals had performed at least five dodges, the food was removed and a new piece was introduced to the testing arena. The new piece of food was given to the animal that had previously attempted to rob the other rat of the food pellet. The trial continued until at least five dodges each, of 135°, were obtained from each pairmate.

Video Recording:

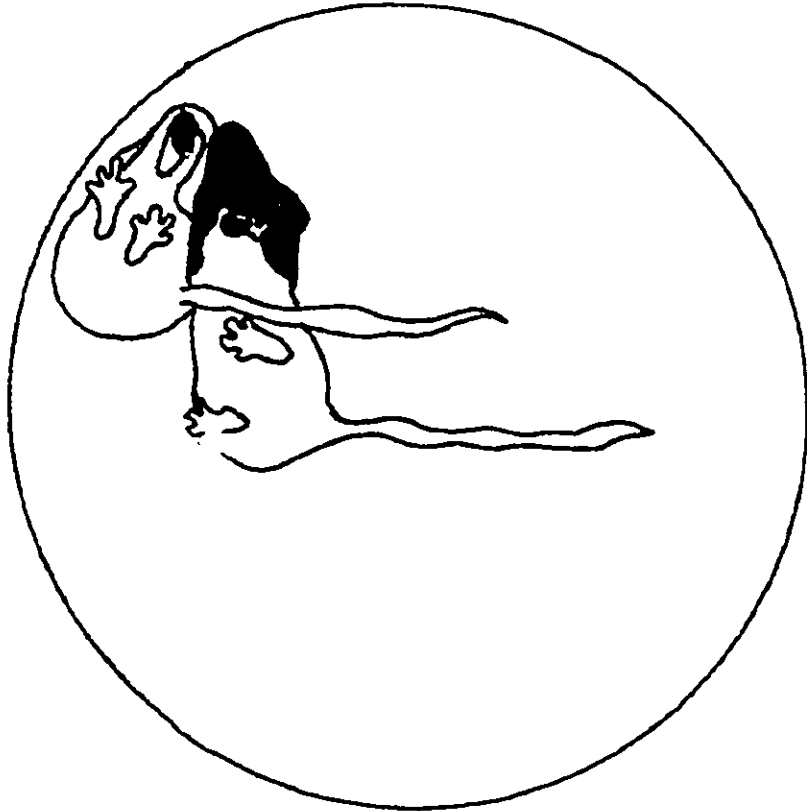
Video records were obtained using a Sony Hi-8 Camcorder at a shutter speed of 250 of a second. Additional light was provided by two 150 watt spotlights on the ceiling 125 cm above the testing apparatus. The Hi-8 video was subsequently transferred to a Sony VHS tape and a digital time code was added using a TRG-50 Horita Micro Window. The VHS tape was then analyzed using an AG-7300 Panasonic Video Cassette Recorder connected to a Sony Trinitron monitor and a computerized digitizing system (Peak Performance Technologies Inc., Englewood, CO).

Behavioral Analysis Based on Digitized Computer Generated Data:

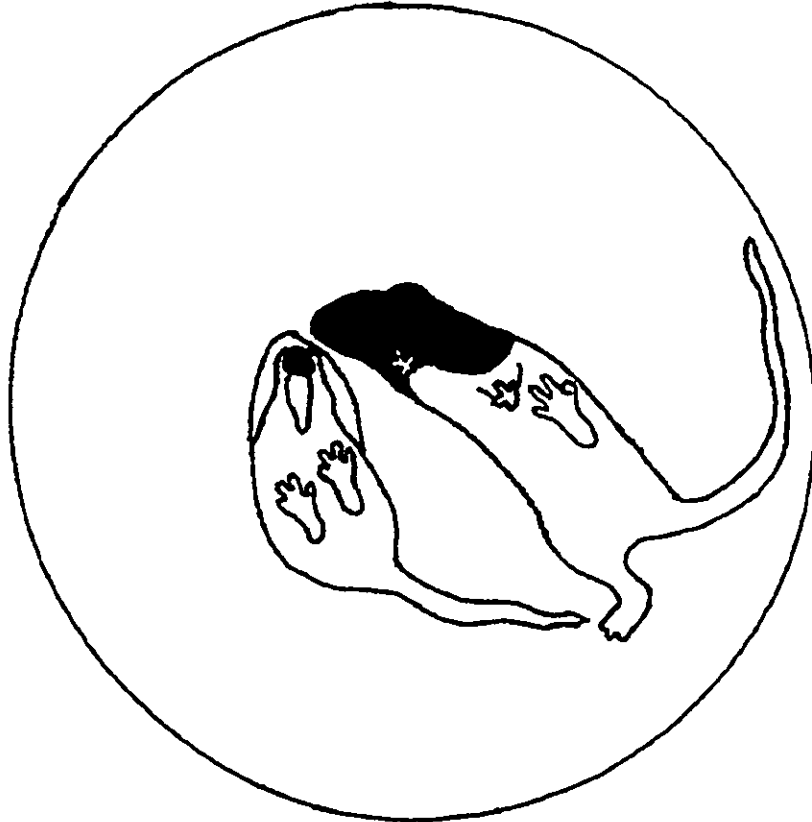
Previous research has shown that the organization of the movements used by males and females during dodging are sex-typical, irrespective of where the dodge occurs in the testing enclosure. It was also shown, however, that by examining dodges that were not constrained by either the walls of the test enclosure or the body of the robber, a more accurate view of the organization of the dodge can be obtained (Fig. 2) (Field, Whishaw & Pellis, in press). For all rats then, the first unconstrained videotaped dodge of at least 135° was analyzed. A movement analysis computer system (Peak Performance) was used to digitize selected points on the animals' bodies. A frame grabber was used to capture the individual frames; this allowed for an analysis at 60 frames/s (Whishaw, Pellis & Gorny 1992). The tip of the snout, a mid-point along the longitudinal axis of the body and the base of the tail were digitized. Analysis began on the frame of the first movement of the snout and continued until the rat realigned its fore- and hindquarters and had resumed eating. In addition, the tip of the robber's snout was digitized. The movement of all digitized points were graphically displayed using the Peak Performance movement analysis system. This computerized digitizing system provides a re-integration of the sequences of dodges so that the

Figure 2: Examples of a constrained (A) and unconstrained (B) dodge are shown. During a constrained dodge, both the circular testing arena and the position of the robber can influence the movements of the defender. The unconstrained situation permits greater freedom of movement for the defender and allows comparisons of dodges with minimal influence of the testing enclosure or the robber's position. (From Field, Whishaw & Pellis, in press)

A. CONSTRAINED



B. UNCONSTRAINED



trajectories, traced by the points digitized, could be followed and examined. Using this system, the distance travelled, and the resultant velocities of the snout, torso and pelvis can be displayed over the course of each dodging sequence. To compare quantitatively, the dodges of the males with those of the females, comparisons of the relative distance travelled and the relative velocity attained were used to reduce the complex temporal sequences into summary values. The summary values were then analyzed using a one-way analysis of variance. Significant differences between groups were determined using post hoc analysis (Fisher PLSD, $p < 0.05$).

(a) Distance Travelled by the Pelvis Relative to the Snout: The distance travelled by the base of the tail (pelvis) (y) was subtracted from that of the snout (x). The resulting value was then divided by the distance travelled by the snout. This score was then multiplied by 100 in order to obtain the percentage difference in distance travelled by the snout relative to the pelvis ($(x-y)/x*100$). During a dodge, the food held in the mouth by the defender is moved away from the robber. Thus the movement of the snout represents a swerve away from the robber. A large movement of the pelvis represents additional body movement during the dodge. A large score (%) meant that

only the snout moved with little other body movement. A small score (%) meant that not only the front of the rat moved, but that a large movement was also made by the pelvis.

(b) Distance Travelled by the Torso Relative to the Pelvis: In addition to the quantification of the relative displacement and velocity of the snout to the pelvis, comparisons were also made between the torso and the pelvis. The point digitized for the torso was determined by following the midline of the body and selecting a point that was approximately halfway between the shoulders and the pelvis. More movement of the pelvis relative to the torso would suggest that the point of pivot is closer to the torso; conversely, more movement by the torso relative to the pelvis would suggest that the point of pivot is closer to the pelvis. The relative distance travelled was calculated comparing the pelvis(x) and torso(y) (i.e., $x-y/x*100$). A large positive score corresponds to a large movement of the pelvis relative to the torso. A small positive score or a negative score represents a small movement of the pelvis relative to the torso.

(c) Temporal Relationship of the Initial Peak in Velocity of the Pelvis Relative to the Snout: A similar procedure to that used to compare the

distances travelled by the digitized points was used to compare the differences in velocity of the snout and the pelvis. The relative temporal relationship of the occurrence of the first peak in velocity by the snout and by the pelvis was measured by converting the frame at which the initial peak occurred (x) into a percentage of the total number of frames of the dodge (y) ($x/y=z$). The value obtained for the pelvis was then subtracted from the value obtained for the snout. This provided a difference in the amount of time elapsed between the two peaks that could then be compared across trials. A large difference in the time elapsed between the initial peak in velocity for the pelvis as compared to the snout corresponds to a small amount of movement of the pelvis during the initial part of the dodge, whereas a small difference in the time elapsed indicates that the pelvis began to move shortly after the dodge was initiated.

(d) Analysis of the Movement of the Robber: Two measurements were taken of the robber's behavior during the digitized unconstrained trial. This analysis was done in order to determine whether differences in the robber's behavior could account for the differences in the pattern of movement of dodging males and females. These were: (1) the video frame, following the initiation of the dodge, where the first peak in velocity of the robbing animal occurred, and (2) the maximum velocity obtained by the robber during that

first peak in velocity.

Behavioral Analyses Based on Frame-by-Frame Videotape Inspection:

Five dodges were analyzed for each rat, regardless of environmental constraints, to determine whether the differences found in the digitized trials were consistent with their behavior in constrained contexts. Also, measurements of other aspects of dodging behavior were analyzed to determine whether aspects of the behavior that were not addressed by our initial analysis were affected by the sex of the robber. For each of these measurements, group means were calculated from the individual value obtained for each rat. The individual scores obtained were then analysed using a one-way analysis of variance. Significant differences between groups were determined using post hoc analysis (Fisher PLSD, $p < 0.05$).

(a) Categorization of Dodge Patterns: To determine whether male or female typical dodges were performed, the sequence of steps during the dodge was analyzed. The differences between the sexes in the trajectories of the pelvis were due to the males generally making both more hindlimb steps and initiating the dodging movement by stepping backward towards the pelvis.

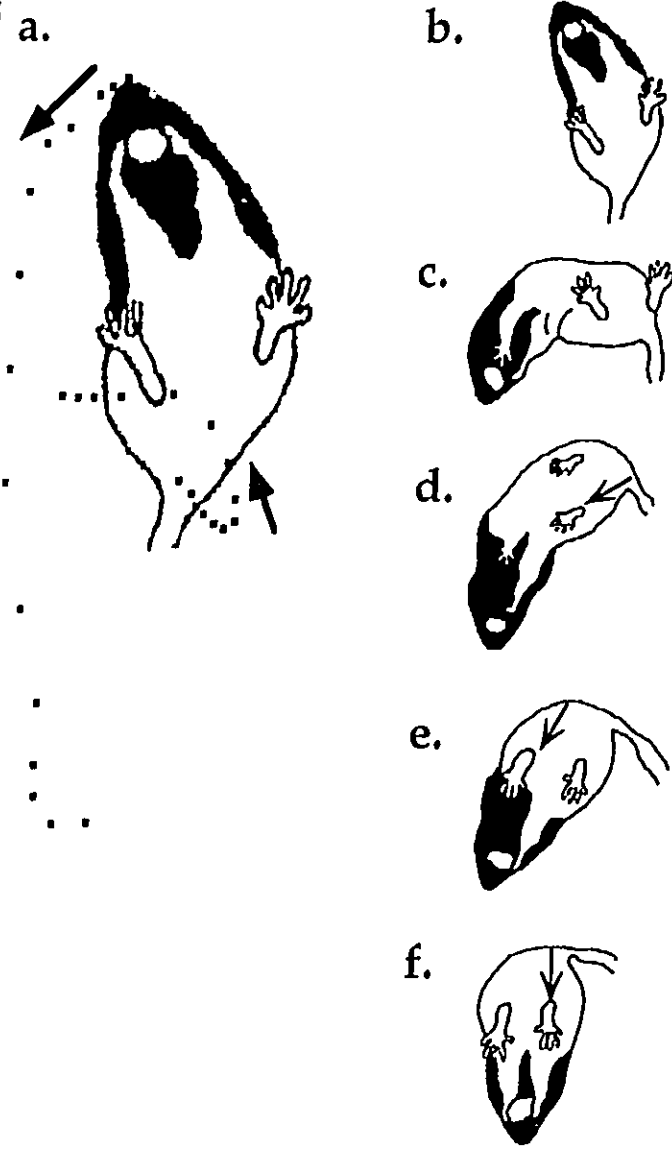
In contrast, females made fewer hindlimb steps and generally initiated the dodging movement with a step either out to the side or forward. (Fig. 3) (Field, Whishaw & Pellis, in press; Chapter 4). Based on these differences in stepping, dodges were assigned to either a female- or male-typical category. Dodges that did not fit either category were assigned to a third, or other category.

(b) Analysis of the Number of Steps by the Hindlimbs: The number of steps taken by the hindlimbs for a dodge were scored for the first five dodges for each rat.

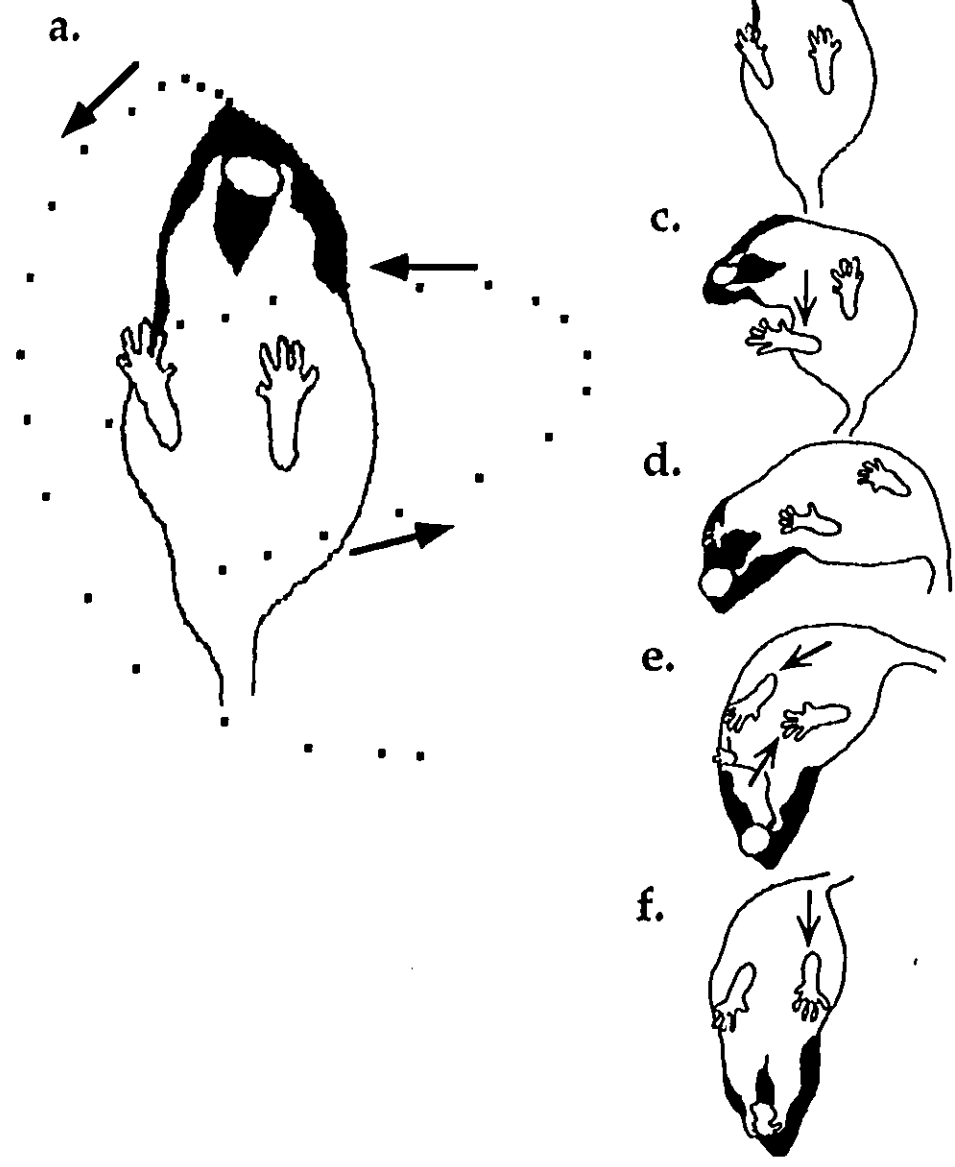
(c) Analysis of the Hindquarter Position of the Dodging Animal in Relation to the Robber's Head: As males may possibly be using a midbody pivot to avoid aggressive encounters, and hence bites, it was predicted that males paired with males may align themselves in order to minimize this possibility. The body of the robber was divided into three segments with which the dodging animal could align itself: (1) the head-the area from the shoulders to the tip of the snout; (2) the midbody-the area from the shoulders to the sacrum; (3) the pelvis-the sacrum to the base of the tail.

Figure 3: The trajectories of the snout and pelvis are shown for an unconstrained female dodge (Aa) and for an unconstrained male dodge (Ba). Each solid round dot represents two video frames with the arrows with closed heads indicating the direction of the movement. Note that unlike the female, the male makes a large outward swing of the pelvis. The number and direction of steps taken by the hindpaws are also indicated by the open-headed arrows. After turning laterally (Ab-c), the female makes an initial step with the hindpaw ipsilateral to the direction of the dodge (Ad). This step is followed by a forward step with the hindpaw contralateral to the direction of the dodge (Ae) and a final step forward by the hindpaw ipsilateral to the direction of the dodge (Af). In contrast the male, has less lateral movement of the upper body (Bb) before taking a step backwards by the hindpaw ipsilateral to the direction of the dodge (Bc). This is followed by a second step backwards with the ipsilateral hindpaw, and shortly after, with a forward step of the contralateral hindpaw (Be). The ipsilateral hindpaw then makes a final forward step (Bf) Note: The animals represented in this figure are scaled to represent the actual size of female and male adult rats. (From Field, Whishaw & Pellis, in press)

A . FEMALE



B . MALE



(d) Comparisons of the Distance Between the Snout of the Robber and the Snout or Base of the Tail of the Dodging Animal: At the end of each dodge, both the distance between the snout of the robber and the snout and pelvis of the dodging rat was measured. To score these measurements, a XL-100 (RCA) monitor attached to a videorecorder (GE) with frame-by-frame capabilities was used. The frame at which the dodge was completed was selected. An overhead transparency was then placed on the screen of the monitor, and the snout of the robber and the snout and base of the tail of the dodging rat were marked. The distance between the marked points was then measured.

RESULTS

Distance Travelled by the Snout Relative to the Pelvis: In females, regardless of the sex of the robber, there was a large lateral displacement of the snout with only a small displacement of the pelvis. It was only after the snout reached its asymptote that the pelvis made its biggest movement (Fig. 3A). In males, however, the pelvis began to move shortly after a small movement of the head (Fig 3B), and for most of the dodging movement the pelvis and snout were parallel. Furthermore, as the male's snout reached its asymptote, the movement of the pelvis changed and moved back towards its point of

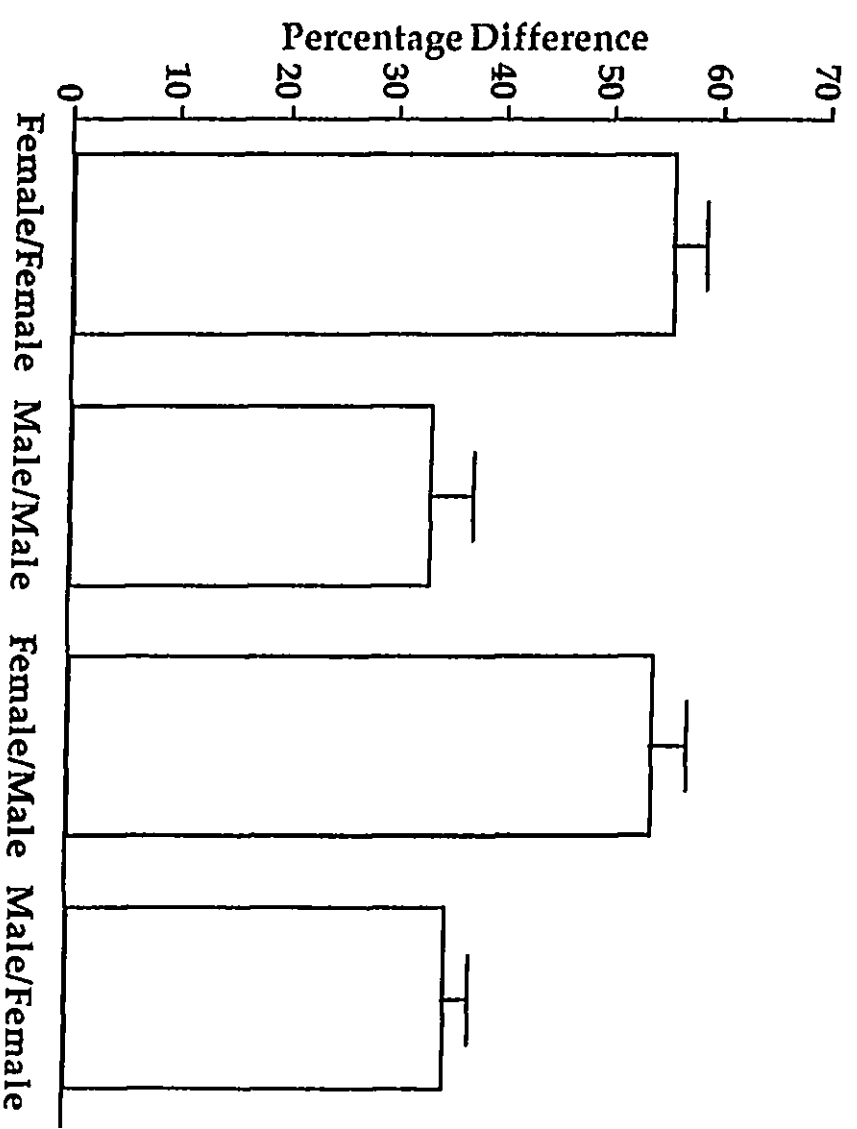
origin.

Comparison of the relative difference of the movement of the snout and pelvis between males and females paired with a same sex robber or a opposite sex robber revealed significant differences ($F(3/44)=13.012$, $p<.0001$). Post hoc analysis showed that males and females were significantly different from one another whether paired with same sex partners or opposite sex partners. Neither females nor males differed across trials from themselves when tested with robbers of either sex (Fig. 4).

Distance Travelled by the Torso Relative to the Pelvis: The above results suggest that, regardless of the robber's sex, males are pivoting around a point closer to the midbody than are females. To test this hypothesis, a point between the snout and the pelvis (designated "torso") was analyzed. It was predicted that if the males were moving around a point closer to the middle of the body, the total distance travelled by the pelvis should be greater in males than in females.

Comparison of the relative difference between males and females paired with a same sex robber or a opposite sex robber revealed significant differences ($F(3/44)=15.837$, $p<.0001$). Post hoc analysis showed that males and females were significantly different from one another whether paired with

Figure 4: The difference, as a percentage, in the distance travelled by the snout relative to the pelvis is depicted. For each column, the first sex listed is the dodging rat and the second is the robber. The mean difference for dodging males was significantly less than that for dodging females, irrespective of the robber's sex.



same sex or opposite sex partners. Females nor males differed across trials from themselves when tested with robbers of either sex (Fig. 5).

Temporal Relationship of the Initial Peak in Velocity of the Dodging Animal in Relation to the Initial Peak in Velocity of the Snout: In conjunction with the differences found in the distances travelled for the nose and the pelvis, the initial peaks in velocity for these two points were analyzed. Previous work (Field, Whishaw & Pellis, in press) has shown that the initial peaks in velocity for males are temporally closer together than they are for females.

Analysis of the relationship between the occurrence of the initial peak in velocity of the snout as compared to the pelvis revealed significant group differences ($F(3/44)=3.275$, $p=.0298$). Post hoc analysis showed that males and females paired with opposite sex partners were significantly different. While males and females paired with a same sex partner were not significantly different, they did show a trend in the direction predicted. Neither females nor males differed from their sex-typical pattern when tested with robbers of either sex (Fig. 6).

Movements of the Robber: It is possible that the differences in the dodge

Figure 5: The difference, as a percentage, between the distance travelled for the pelvis relative to the torso is depicted. For each column, the sex first listed is the dodging rat and the second is the robber. The mean difference for dodging females was significantly less than that for dodging males, irrespective of the robber's sex.

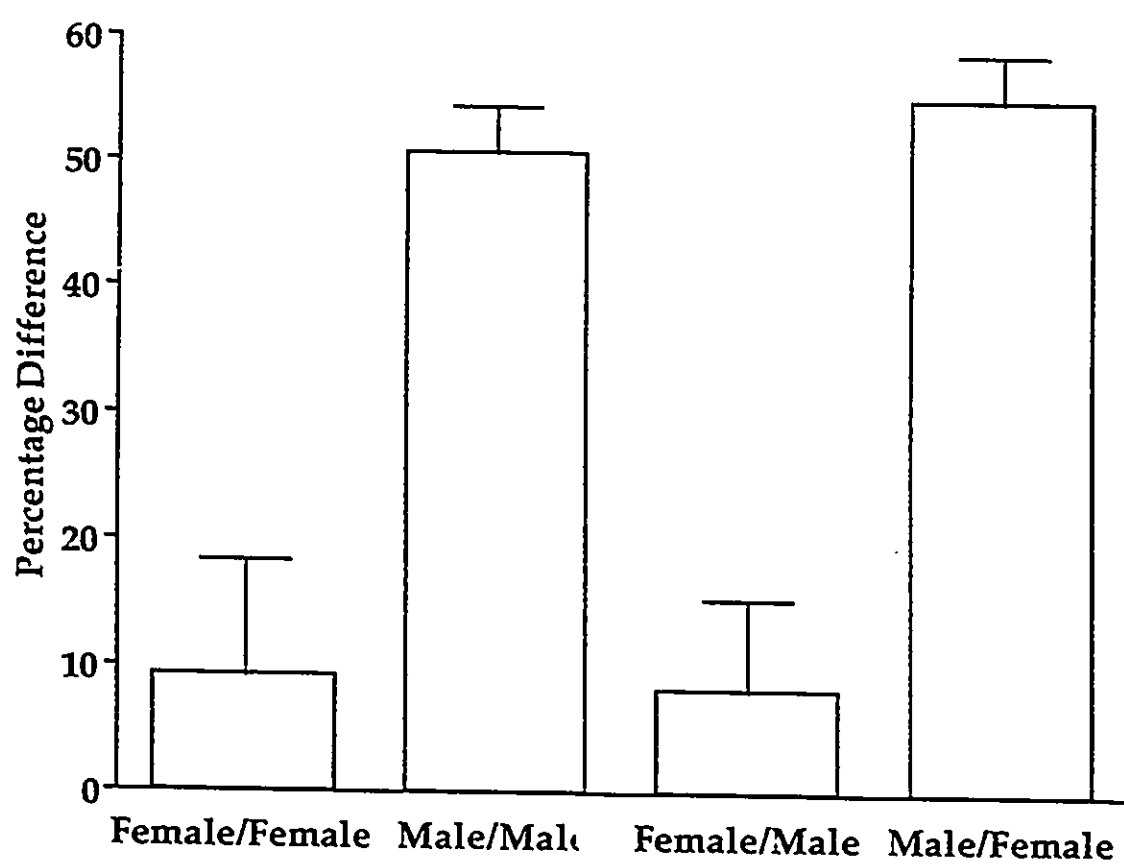
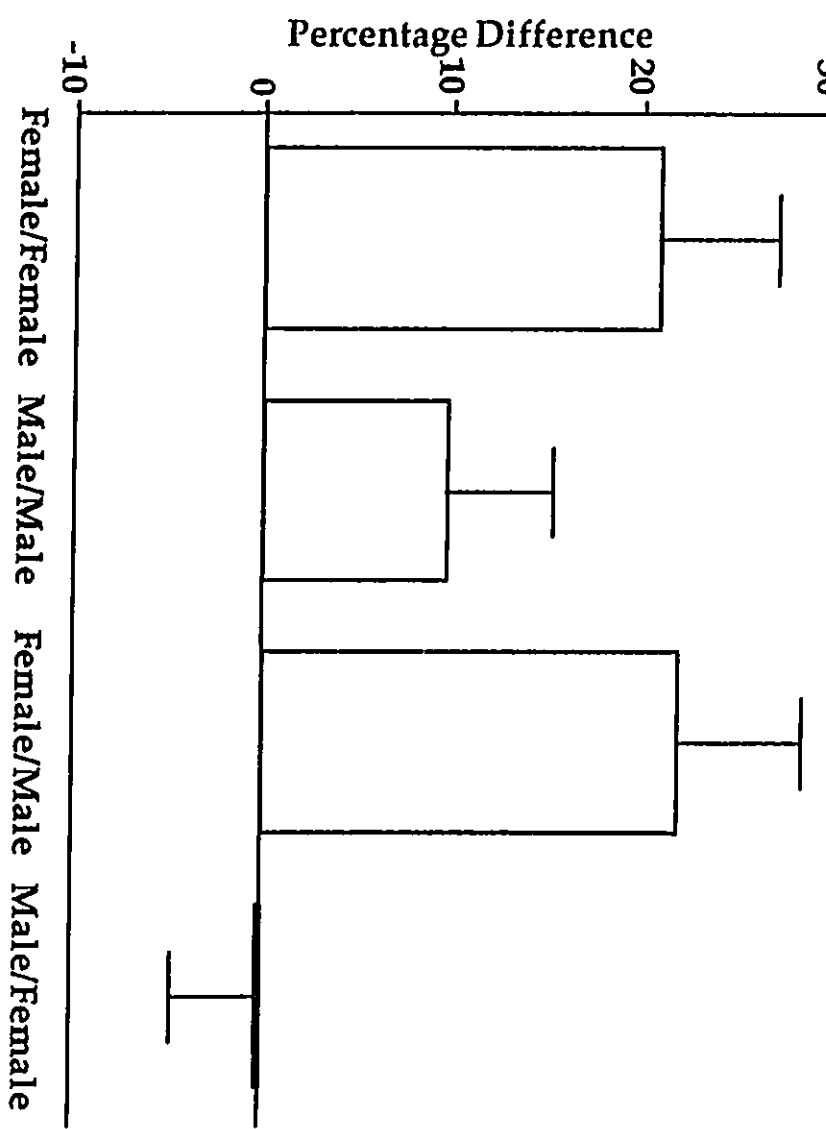


Figure 6: The percentage difference in the temporal location of the initial peak of velocity for the snout as compared to the pelvis is depicted. A value close to zero indicates that the initial peaks in velocity for the snout and the pelvis occurred almost simultaneously. The larger the positive value, the greater the time elapsed between the initial peaks of velocity. For each column, the first sex listed is the dodging rat and the second sex the robber. Males dodging from females were significantly different from females dodging from an opposite sex partner. Males and females dodging from a same sex partner were not significantly different, but showed a trend in the same direction as opposite sex pairs.



patterns between males and females may be due to differences in the robber's behavior. To determine whether there were significant differences in the behavior of male and female robbers, two measurements were scored (see Methods). On both measures, no significant differences were found between the robbers, irrespective of the sex of the dodging animal (Table 1). Therefore, it is unlikely that the sex differences that exist between male and female dodges are influenced by the robber's behavior.

Categorization of the Dodge Patterns: The frequency of male- and female-typical dodges was analyzed for the first five dodges of each animal, with either a same or opposite sex partner (see Methods). There were significant group differences for the likelihood of a female-typical dodge ($F(3/44)=39.276$, $p<.0001$). Post hoc analysis showed that females performed significantly more female-typical dodges than males irrespective of the sex of the robber. Similar results were found for the likelihood of male-typical dodges ($F(3/44)=39.213$, $p<.0001$). Post hoc analysis showed that males performed significantly more male-typical dodges than females, irrespective of the sex of the robber. The differences in the likelihood of dodges not fitting either the female- or male-typical categories were not significant (Fig. 7).

TABLE 1

COMPARISON OF TWO ASPECTS OF ROBBING BEHAVIOR

	Variables Measured*	
	1	2
Female/Female† (X±SE)	21.5 ±3.3	41.7 ±2.6
Male/Male (X±SE)	21.2 ±2.9	33.7 ±2.5
Female/Male (X±SE)	17.6 ±1.7	43.1 ±5.7
Male/Female (X±SE)	16.4 ±2.3	44.5 ±6.0
F-Test	0.96, ns**	1.11, ns
p-value	0.42	0.35

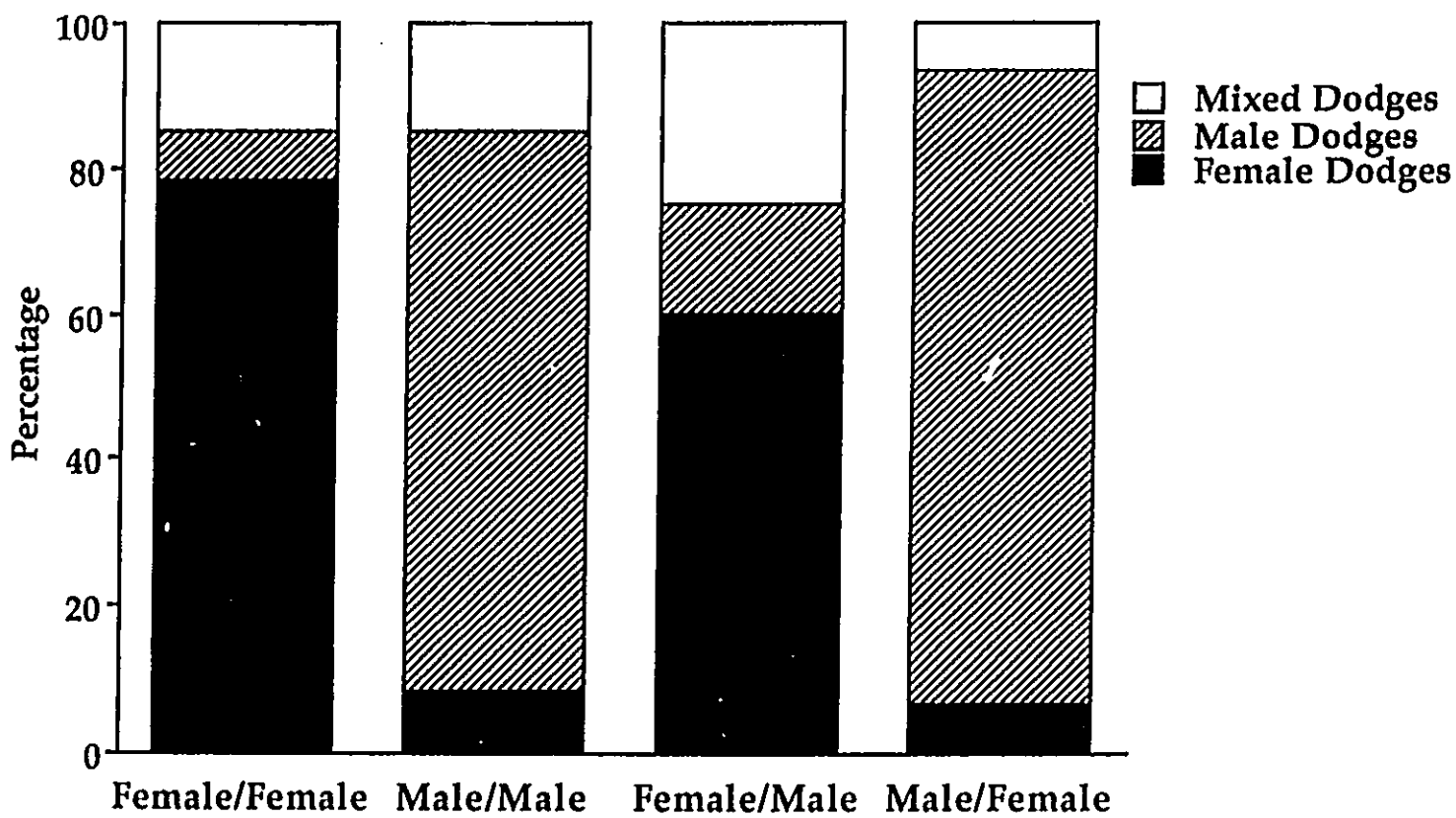
* 1= the frame, following the initiation of the dodge, where the first peak in velocity of the robbing animal occurred

2= the maximum velocity obtained during the first peak in velocity

**ns = not-significant at $p < 0.05$

†=for each comparison, the first sex listed is the dodging rat, the second the robber

Figure 7: The occurrence, as a percentage, of the different dodge types is depicted here. Females showed significantly more female-typical dodges, irrespective of the robber's sex. In contrast, males showed significantly more male-typical dodges, irrespective of the robber's sex. No significant differences in the occurrence of mixed dodges were found between males and females (see text for definitions of dodge types)



Analysis of the Number of Steps by the Hindlimbs: Males generally make more hindlimb steps in order to complete a dodge than do females. There were significant group differences in the number of hindlimb steps made ($F(3/44)=4.145$, $p=.0113$). Females, paired with females, made significantly fewer steps than males paired with robbers of either sex. Females paired with male robbers also tended to make fewer hindlimb steps than males, but the difference was not significant.

Analysis of the Hindquarter Position of the Dodging Animal in Relation to the Robber: I predicted that if males are using a different dodge tactic to prevent possible aggressive attacks, they would position their pelvis away from the snout of a male robber. For alignment of the dodger's body to either the head ($F(3/44)=6.403$, $p=.0011$) or midbody area ($F(3/44)=9.963$, $p<.0001$), significant group effects were found. No effect was found between the groups for alignment of the pelvis of the dodger with the pelvis of the robber. Males (63.3%) were significantly more likely to align their pelvis with the head of a same sex robber than were females (18.3%) . In contrast, females (76.7%) were more likely to align their pelvis with the midbody of a same sex partner than

were males (25.0%). When paired with an opposite sex partner however, this sex difference disappeared (Fig. 8).

The Distance Between the Snout of the Robber and the Snout or Base of the Tail of the Dodging Animal: In the laboratory males and females both successfully defend food items in about 93% of robbing attempts for equally matched partners (Whishaw & Tomie, 1987). Nonetheless, the male or female-typical dodges may have other more subtle advantages. For example, the relative distance between pairmates may differ, thus changing the behavioral options of the robber (Pellis, Field, Smith & Pellis, in press).

There were no significant group differences for the distance between the snouts of the dodging rat and the snout of the robber at the end of the dodge (Table 2). At the end of the dodge, the distance between the snout of the robber and the final position of the dodger's pelvis was significantly different, but only for males paired with males (Table 2). This suggests that while males and females are using different patterns of movement, these different patterns do not confer an advantage on one sex versus the other with respect to the distance of the food item from the robber.

Figure 8: The final position of the dodger in respect to the position of the robber and the frequency of the occurrence of these alignments are depicted here. In SA, the final position of the dodging rat is shown with its pelvis aligned to the head of the robber (arrow). In SB, the final position of the dodging rat is shown with its pelvis aligned to the midbody of the robber (arrow). A third possible alignment of the pelvis of the dodging rat is with the pelvis of the robber (not shown). Dodging females aligned their pelvis with the midbody of a same sex robber (8C). Males were significantly more likely to align their pelvis with the head of a same sex robber. In contrast, both males and females aligned their pelvis equally with either the head or the midbody of an opposite sex robber. There were no significant differences between any of the groups with regards to the alignment of the dodger's pelvis with the pelvis of the robber.

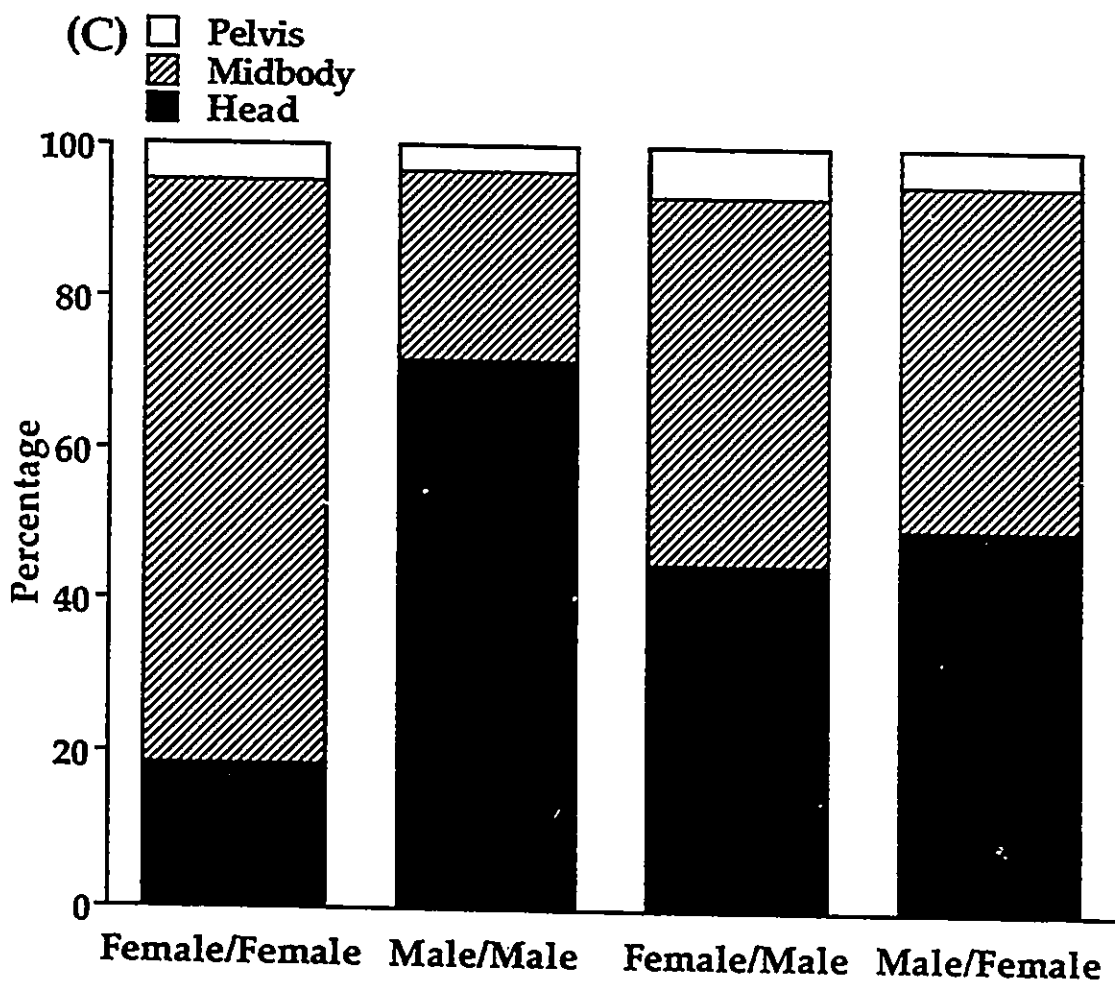
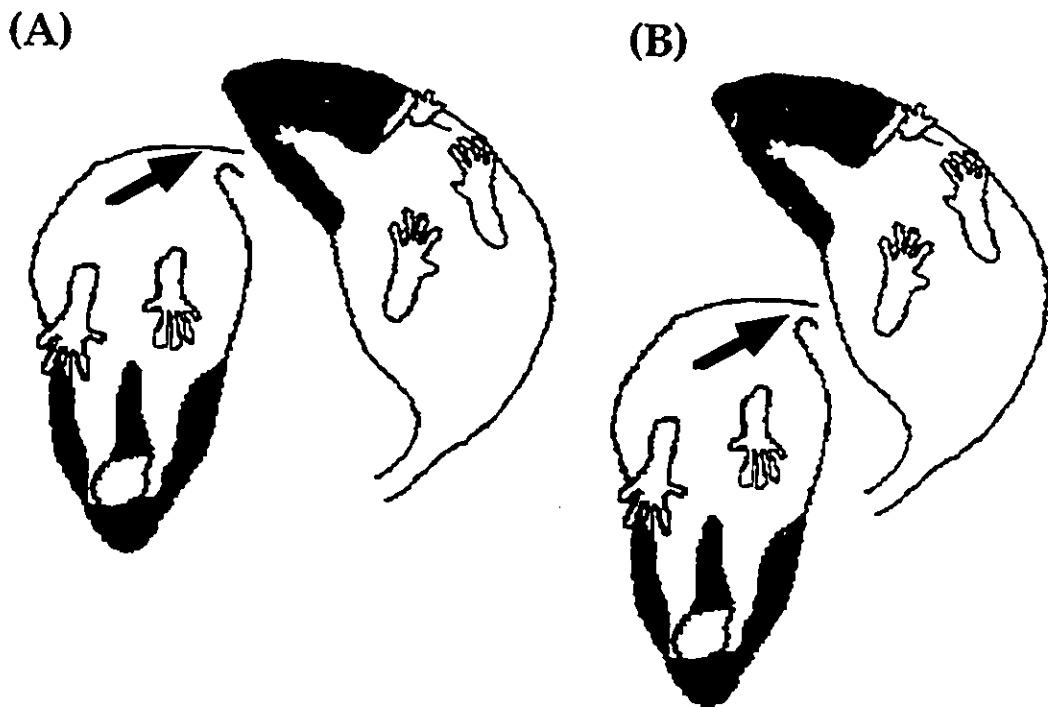


TABLE 2

THE DISTANCE AT THE END OF THE DODGE, BETWEEN THE SNOUT AND PELVIS OF THE DODGING RAT AS COMPARED TO THE SNOUT OF THE ROBBER

	Relative Distance (cm)*	
	1	2
Female/Female† ($\bar{X} \pm SE$)	12.0 ± 47	5.9 ± 26
Male/Male ($\bar{X} \pm SE$)	11.2 ± 42	4.6 ± 4
Female/Male ($\bar{X} \pm SE$)	12.0 ± 61	5.8 ± 41
Male/Female ($\bar{X} \pm SE$)	12.4 ± 44	5.6 ± 34
F-Test	1.13, ns**	2.97
p-value	0.35	0.04***

* 1= the distance between the dodger's snout and the robber's snout

2= the distance between the dodger's pelvis and robber's snout

**ns = not-significant at $p < 0.05$

***= post hoc analysis revealed a significant difference between female/female and male/male groups

†=for each comparison, the first sex listed is the dodging rat, the second the robber

DISCUSSION

The results of the present experiment demonstrate that during dodging, males and females use sex-typical patterns of movement organization to protect a food item, irrespective of the robber's sex. I have also shown that on the behavioral measures that were analyzed, the behavior of male or female robbers does not change with the sex of the dodging animal. Therefore, one can conclude that sex differences in the organization of dodging are likely to arise from intrinsic differences in motor organization rather than different extrinsic contingencies.

It is possible that by using a midbody pivot, males obtain an advantage in the prevention of aggressive attacks in the male/male combination. The finding that males still maintain their sex-typical pattern of dodging when placed with females suggests that this may not be true. It is possible however, that if the male tactic evolved to deal with potential male-male aggression, it would be more efficient to use the same tactic in all encounters irrespective of the robber's sex. In colonies of feral rats, it is unlikely that a feeding rat would be approached by only one conspecific (Whishaw & Whishaw, 1996). Further, it is also likely that the sex of potential robbers would be variable and so, in order to prevent potential aggressive encounters, males would likely have to

treat all potential robbers as male.

If, in fact, the male dodge pattern is designed to prevent male/male aggression, one would expect that the final position of the dodging animal would minimize potential aggressive attacks and bites. While it has been shown that the target for aggression in rats is primarily the rump area (Blanchard & Blanchard, 1977; Pellis & Pellis, 1987), a male dodging from a male robber will align its pelvis with the head of the robber at the end of a dodge, thus placing its rump closer to the robber's mouth. Furthermore, males, when dodging from males, have a smaller distance between their pelvis and the snout of the robber than do female/female or male/female combinations. This would be functionally counterproductive if male-typical dodges were used in order to prevent potential aggressive attacks. By aligning their pelvis and placing it in closer proximity to the snout of the robber, males would actually be facilitating an attack on the rump by the robber.

Aggression in male rats becomes more prevalent after puberty (Takahashi & Lore, 1983). It would be expected then, that if the male-typical pattern of dodging is associated with aggressive behavior, it would appear around puberty. I have found, however, that the sex-typical differences in dodging are already present at around 35 days, prior to puberty (Field, Whishaw & Pellis, work in progress). Furthermore, it has also been shown

that aggressive behavior in males is dependent on the presence of circulating testosterone in adult rats (Brain & Haug, 1992). The male-typical pattern of dodging, however, is not influenced by castration of male rats at weaning (Chapter 4), suggesting that this behavior pattern develops independently of the behavioral changes associated with aggression and dominance.

There are, however, modifications of the sex-typical dodging movements that are dependent on the sex of the robbing rat. It is possible that while sex-typical patterns of dodging are not affected by the robber's behavior, there are aspects of dodging behavior that are modified by the identity of the robber. I have found that, at the end of the dodge, males are more likely to align their pelvis with the head of a same-sex robber than are females. In contrast, females are more likely to align their pelvis with the midbody of a female robber. Males and females that are placed with an opposite sex partner are equally likely to align their pelvis with the head or the midbody.

Whishaw & Gorny (1994) have shown that rats make judgements regarding the size of the dodging movement based on the time it takes to consume a food item. The modifications seen in these sex-typical patterns of dodging may therefore give an advantage to one sex over the other with respect to possible eating time. One way to determine whether this is likely is

to measure how far away the food or snout of the dodging animal is in relation to the snout of the robber. If the food item is farther away from the robber when using one sex-typical dodging tactic versus the other, the potential eating time would be influenced, since the robber would have to traverse a greater distance in order to reach the food item. When measurements of the snout to snout distance were compared however, it was found that, irrespective of the sex of either rat, the distance between the dodging rat and robber was not significantly different. This suggests that the difference in dodging tactics is not likely translated into a gain of additional time to eat.

A final possibility is that the modifications of the dodge pattern as seen in males and females is a defensive tactic that is composed specifically for the task at hand; that is, to protect a food item. Aligning the rump with the opponent's head is functionally useful as a tactic to protect the anterior of the body; in this case, the food item which is held in the mouth (Pellis & Pellis, 1992; Pellis, MacDonald & Michener, 1996). By aligning its rump with the head of a male robber, a male would make it more difficult for the robber to re-orientate to the food and re-approach. In order to facilitate another approach, the robber would either have to pull back, turn and realign with

the dodging animal to approach on the side of the dodger closest to its own position, or would have to walk around the rump of the animal so as to realign itself with the position of the dodging animal (Fig. 8A). In contrast, a female, by aligning its rump with the midbody of a female robber, does not make the subsequent approach of the robber as difficult. In this situation, the robber has only to circle the rump and re-approach (Fig. 8B). It is possible then, that a male is perceived as more of a threat as a robber than is a female. The data from the mixed-sex pairs supports this possibility. Females, when dodging from males, show a higher frequency of aligning their pelvis with the head of the robber, whereas males, when paired with a female robber, exhibit a higher frequency of alignment of the pelvis with the midbody than do either sex when paired with a same-sex robber. Thus females have switched to a more male-typical alignment and males have switched to a more female-typical alignment. This suggests then, that even though the sex-typical pattern of dodging is maintained, aspects of the dodging behavior are modified based on the sex of the robber.

The results of the present study suggest that there are intrinsic differences in how males and females organize their defensive dodging movements in order to protect a food item, and thus confirms previous results (Field, Whishaw & Pellis, in press). Furthermore, I have shown that

these differences are not due to differences in the robbing behavior of the sexes. Lateral movements such as those in dodging (Field, Whishaw & Pellis, in press; Whishaw, 1988; Whishaw & Gorny, 1994; Whishaw & Tomie, 1987; 1988), are also present in a number of other social interactions, such as play (Pellis, Pellis & Whishaw, 1992), sex (Pellis & Pellis, 1988, Whishaw & Kolb, 1985) and aggression (Blanchard & Blanchard, 1977, Pellis, MacDonald & Michener, 1996; Pellis, 1988).

That differences may exist in how male and female rats organize dodging movements suggests that differences may also exist in how males and females organize their movements during lateral maneuvers in other behaviors. Pellis, Field, Smith & Pellis (in press) have shown that when evading a conspecific during play, males and females organize their movements in a similar way to that used in dodging. Furthermore, preliminary investigation of spontaneous turning has shown that there are sex-typical differences in their associated stepping patterns (Pellis, Pellis & Field, 1995; Field, Pellis & Pellis, in preparation). Further research into the prevalence of sex differences in the motor organization of different behaviors will help to determine whether these sex differences are task or sex specific. The existence of these differences suggests that the environmental milieu in which each sex has evolved must contain fundamental differences that lead

to sex differences in the organization of movement. Comparative analyses of such sex differences, in a variety of defensive behaviors, are necessary in order to determine both the factors influencing their development and the reason for their presence.

CHAPTER 4***A Kinematic Analysis of Sex-Typical Movement Patterns Used During Evasive Dodging to Protect a Food Item: The Role of Gonadal Androgens****ABSTRACT**

Feeding rats will dodge laterally away from a conspecific who attempts to steal their food. The defensive dodges of females and males are similar in their direction and magnitude. However, the composition of the movements used differ. Females pivot around a point more posterior on the longitudinal axis than do males; which produces a greater amount of movement of the snout as compared to the pelvis. The difference in this pivotal point is further illustrated by an analysis of the movement of the torso compared to the pelvis. Females show less pelvic movement relative to the torso than do males. Neonatal androgen manipulation alters these sex-typical patterns. Castration neonatally makes males more female-like. Castration just after weaning and prior to puberty, however, does not affect the male-typical pattern. Injections of testosterone propionate neonatally alters females so that they perform more male-like dodges. These findings suggest that a functionally similar motor pattern can differ in motor organization between

the sexes, and that this difference in organization involves the action of gonadal hormones perinatally. These results are discussed in relation to anatomy, neural structure and the role of gonadal hormones during development.

*This chapter has been modified from a paper that has been submitted to Behavioral Neuroscience

INTRODUCTION

In 1849, A. A. Berthold demonstrated “the first proof of endocrine function as we know it” (Forbes, 1949). He showed that if young roosters were castrated and their testes reimplanted into either the abdomen of the same animal or into another castrated rooster, they would develop the proper sexual urge and physical characteristics of true cockerels. Castrated roosters that did not receive a testes implant however, did not develop the typical characteristics of adult roosters (Nelson, 1995; Forbes, 1949). This was the first demonstration that a substance secreted from a discrete organ could modify the behavior of an animal. Subsequent work undertaken in France, Germany, Italy and Russia attempted to determine further the effects of the removal or addition of the sex glands on the behavior of various animals. While there was no agreement or evidence at this time for a site of action for the secretions of these glands, it was assumed that the site of action must be in the central nervous system (Beach, 1981).

In 1959, Phoenix, Goy, Gerall and Young demonstrated that the potential for either masculine or feminine sexual behavior in guinea pigs is dependent on early exposure to gonadal hormones. Consequently, they suggested that the exposure to gonadal hormones around birth has an

organizing effect on the nervous system and the subsequent behaviors that are displayed. Males undergo masculinization of male-typical characteristics and defeminization of female-typical characteristics due to the organizing action of gonadal hormones. Post-pubertally, hormones are often necessary to activate the expression of these sex differences. Since these early works, a number of studies using different species have replicated these findings (Baum, 1979; 1990), supporting the idea that gonadal hormones have an organizing effect early in development and an activating effect in adulthood (although this dichotomy may not be rigid in all cases (Arnold & Breedlove, 1985)). In addition, the development of sex differences has been extended beyond reproductive behavior patterns to include sexual orientation (Adkins-Regan, 1988), spatial behavior (Williams, Barnett, & Meck, 1990; Williams & Meck, 1991), spontaneous/exploratory activity (Stewart & Cygan, 1980; Mead, Hargreaves, & Galea, 1996), rotational behavior (Carlson & Glick, 1996), micturition in dogs (Beach, 1974) and play (Meaney & Stewart, 1981; Meaney, 1988; 1989; Pellis, Pellis & McKenna, 1994).

Even though sex differences in mammals exist in both reproductive (Ward, 1992) and non-reproductive behaviors (Beatty, 1992), most sexually dimorphic behaviors are dimorphic only in the sense that one sex is more likely to perform them than the other (Aron, Chateau, Schaeffer, & Roos,

1991; Goy & Roy, 1991). Except for some behavioral patterns that are associated with parturition, most sexually dimorphic behavior patterns are described as sex-typical not sex-exclusive. Sexually dimorphic behavior patterns may therefore occur in both sexes, but have a lower threshold for elicitation in one sex versus the other (Money, 1988). Males differ from females not in what they do, but in how likely they are to perform a particular behavior pattern. A question that is not commonly addressed, however, is whether males and females organize their movements differently during a functionally similar behavior and whether these differences are dependent on exposure to hormones early in development.

A rat eating a piece of food held in its forepaws will dodge laterally away from an approaching conspecific in order to prevent the theft of the food (Whishaw & Tomie, 1987; Whishaw, 1988). Even though the lateral movement away from an approaching conspecific is functionally similar for both females and males, the composition of the underlying movements that make up this lateral evasive maneuver is not (Field, Whishaw & Pellis; in press). The purpose of the present study was to determine whether the sexually dimorphic composition of movements by a dodging animal was modifiable by neonatal and pubertal androgen exposure. An in-depth analysis was also done on the hindlimb stepping that occurs during dodging

in order to determine whether these differences in stepping pattern were also modifiable by androgen exposure. In addition, the behavior of the robbing animal was analyzed in order to determine whether there was an effect of the hormonal manipulations on this behavior that could subsequently affect the dodge pattern present in the partner.

METHODS

Subjects:

Twenty-four female and 36 male Long-Evans hooded rats raised in the animal colony of the Department of Psychology at the University of Lethbridge were used. The pups were removed from the breeding cage, on the day of birth (P0) and sexed. Twenty-four males were either gonadectomized under hypothermic anesthesia (12), or were subjected to only the anesthesia during the first 24 hours (12); the rest of the males were gonadectomized between 22-26 days of age. Females received a subcutaneous injection of either 200 μ g testosterone propionate or the peanut oil vehicle on both P0 and 24 hours later. The rats were housed, in same condition, littermate pairs, in wire mesh cages (17x25x20 cm) from weaning at 21 days of age. They were maintained in the main colony room on a 12:12 hour

light/dark cycle until adulthood, when they were tested between 100 and 110 days of age. Subjects were maintained on a limited feeding schedule of approximately 20 grams per day (Purina Rodent Chow), in order to maintain their body weight at about 80-85% of their free feeding weight.

Neonatal and Pre-Pubertal Castration: Within three to four hours after birth, 12 males were castrated. They were anaesthetized with hypothermic anaesthesia and a two to three mm midline abdominal incision was made. The testes were identified and bluntly dissected. The abdominal wall was closed with a single, interrupted, silk suture. A series of single, interrupted sutures were then used to close the abdominal incision.

A second group of 12 males were castrated between 22-26 days of age. The animals were anaesthetized using isoflurane anesthesia (AErrane; Anaquest, Mississauga, Ontario). Once the animal was anaesthetized, the scrotum was cleaned with antiseptic soap and then a single, vertical, midline incision was made through the scrotum. The testes were bluntly dissected from the tunica, the spermatic cord was ligated and transected, and the testes and the fat pad along the cord were removed. The tunica on either side were closed with a single, interrupted, absorbable suture. A series of single, interrupted, sutures were then used to close the scrotal incision. Following

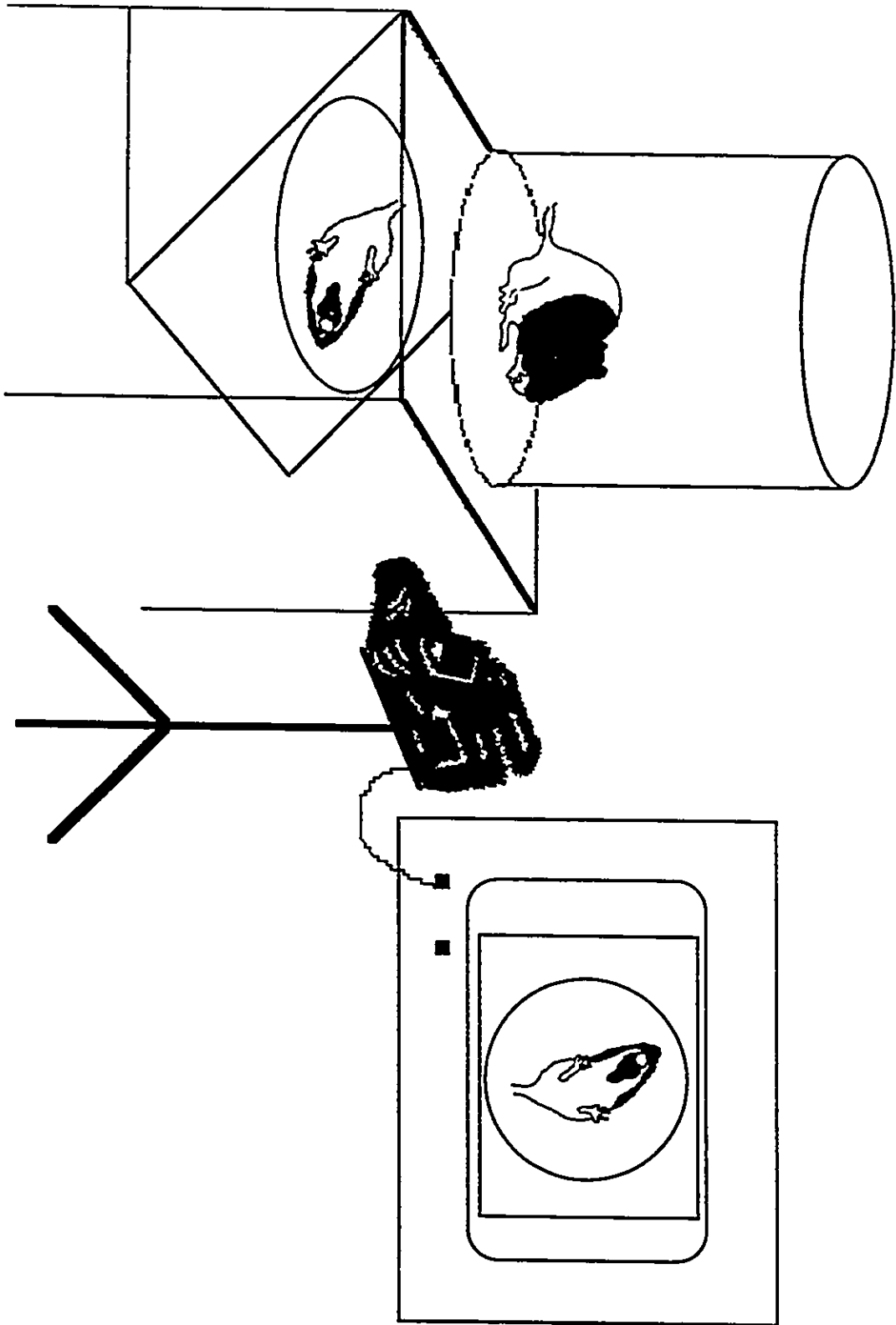
surgery, each animal was given an intramuscular injection of 15,000 units of penicillin (Penlong XL; Rogar/STB, Inc. London, Ontario).

Testing and Videorecording:

Trials were conducted between 1400 and 1600 hours. Each pair was placed in a thin plexiglass cylinder, 40cm in diameter and 45cm high. The cylinder was placed on a table with a clear glass top. Under the table was a mirror inclined at 45° from which the ventral side of the animals could be viewed and videotaped (Fig. 1) (Pinel, Jones & Whishaw, 1992).

The animals were habituated to the testing apparatus, prior to videotaping, by placing each pair in the testing apparatus with a 2.5g pellet. Habituation was complete and filming began when shortly after being placed in the cylinder one animal would commence eating. Dodges of greater than 135° were filmed for each animal. Video records were obtained using a Sony Hi-8 Camcorder with a shutter speed of 250 of a second. Additional light was provided by two 150 Watt spotlights on the ceiling 125 cm above the glass table. The Hi-8 video was subsequently transferred to a Sony VHS tape and a digital time code was added using a TRG-50 Horita Micro Window. The tapes were then analyzed using a computerized measurement system (Peak Performance Technologies Inc., Englewood, CO).

Figure 1: The testing apparatus and filming setup are depicted here. The rats are placed, in pairs of two (only one rat is depicted here for clarity), in a plexiglass cylinder on a clear table top. An incline mirror is positioned at a 45° angle beneath the table top. The ventral view of the rats is then videotaped from the mirror. The video camera is connected to a monitor to ensure the quality of the videorecording. Tapes of the behavioral sequences are then analyzed using frame-by-frame analysis.

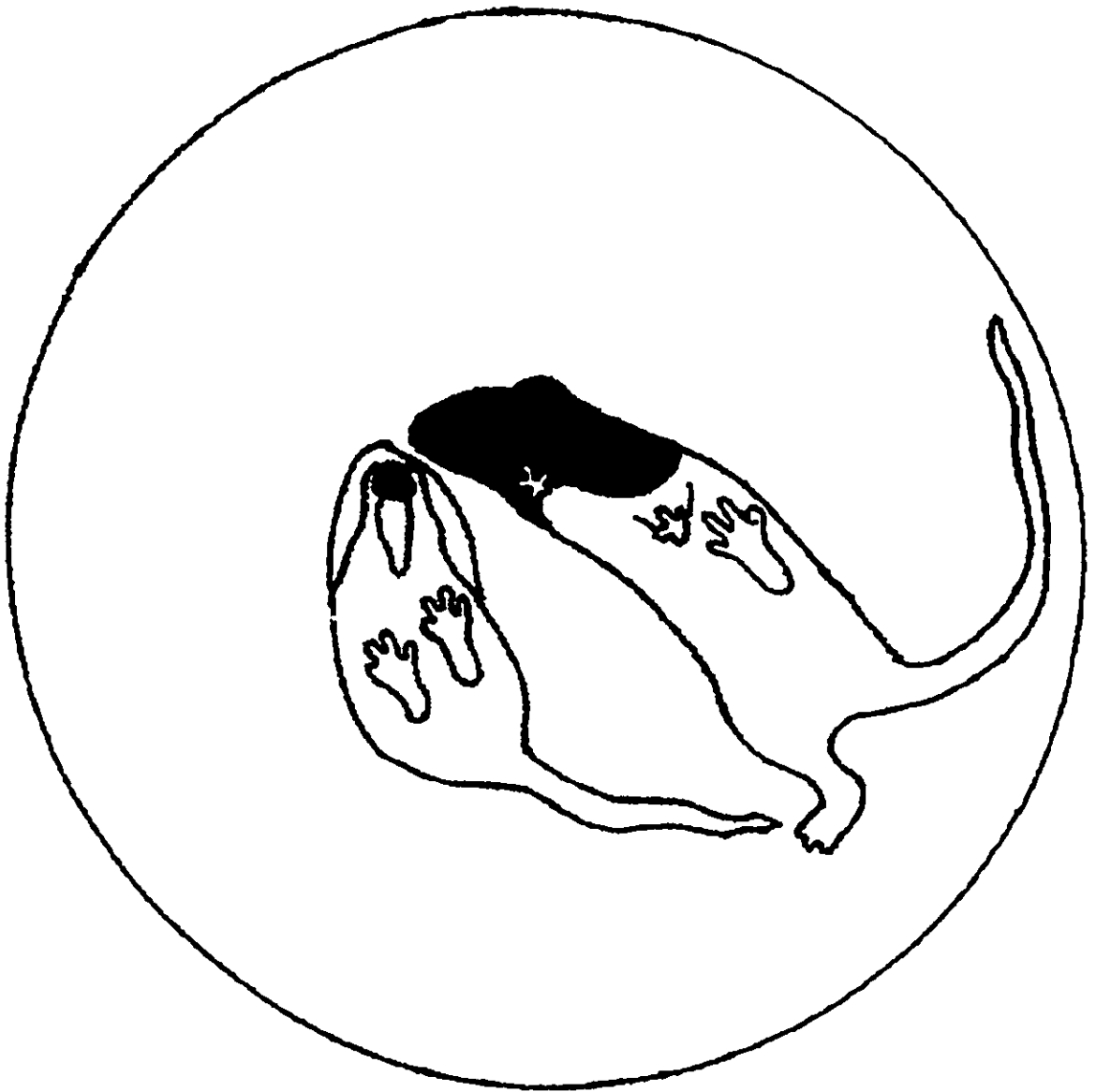


Behavioral Analysis:

Previous research has shown that the organization of the movements used by males and females during dodging are sex-typical, irrespective of where the dodge occurs in the testing enclosure. It was also shown, however, that by examining dodges that are not constrained by either the walls of the test enclosure or by the body of the robber, a more accurate comparison of the organization of the dodge could be made (Fig. 2) (Field, Whishaw & Pellis, in press). The first unconstrained dodge of at least 135° was analyzed for each rat. A computerized measurement system was used to digitize selected points on the animals' bodies, and a frame grabber was used to capture the individual frames; this allowed for an analysis at 60 frames/s (Whishaw, Pellis & Gorny 1992). The tip of the snout, a mid point along the longitudinal axis of the body and the base of the tail were digitized for the dodging animal. The tip of the robber's snout was also digitized.

Analysis began on the frame where the first movement of the snout occurred and continued until the rat had realigned its fore and hindquarters and resumed eating. The movement of all digitized points were graphically displayed using the Peak Performance movement analysis system. This

Figure 2: An example of an unconstrained dodge is shown. During a constrained dodge, both the circular testing arena and the position of the robber can influence the movements of the defender. The unconstrained situation permits greater freedom of movement for the defender and allows comparisons of dodges with minimal influence of the testing enclosure or the robber's position. Note here that the dodging animal is away from the sides of the enclosure and that there is no contact between the bodies of the two rats (Adapted from Field, Whishaw & Pellis, in press)



computerized digitizing system provides a re-integration of the sequences of dodges so that the trajectories, traced by the points digitized, can be followed and examined. Using this system, the distance travelled, and the resultant velocities of the snout, torso and pelvis can be displayed over the course of each dodging sequence. To compare quantitatively the dodges of the males with those of females, comparisons of the relative distance travelled and the relative velocity attained were used to reduce the complex temporal sequences into summary values.

Two other aspects of the dodging behavior were also analyzed. These were: (1) The hindpaw stepping patterns of each dodge which were notated from the videotaped sequences. Using a modified version of the Eshkol-Wachmann Movement Notation (EWMN) system (Eilam & Golani, 1988) the direction of the hindpaw steps was analyzed in relation to the position of the body. (2) The initial maximum velocity attained by the robber (a) and the frame at which this occurred were recorded. This was used to determine whether the behavior of the robber was different between the various conditions and could thus influence the dodging pattern of the same condition partner. The following sections describe how the values were calculated for each measure.

Distance Travelled by the Pelvis Relative to the Snout: The distance travelled by the base of the tail (pelvis) (y) was subtracted from that of the snout (x). The resulting value was then divided by the distance travelled by the snout. This score was then multiplied by 100 in order to obtain the percentage difference in distance travelled by the snout relative to the pelvis $(x-y/x*100)$. During a dodge, the food held in the mouth by the defender is moved away from the robber. Thus the movement of the snout represents a swerve away from the robber. A large movement of the pelvis represents additional body movement during the dodge. A large score (%) meant that only the snout moved with little other body movement. A small score (%) meant that not only did the front of the rat move, but that a large movement was also made by its pelvis.

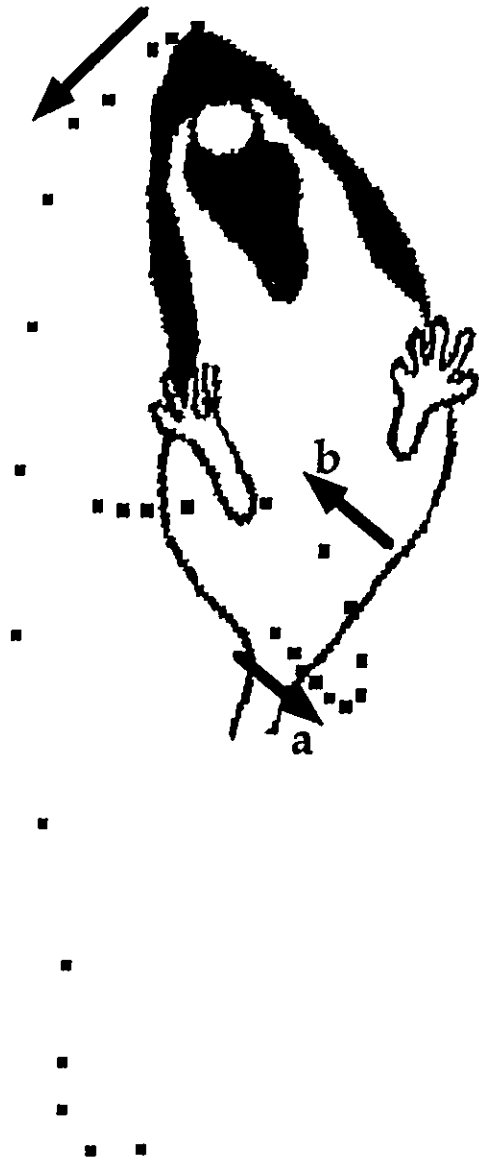
The distance travelled by the pelvis as compared to the snout was then broken down further to compare both the backward and the forward movement of the pelvis relative to the movement of the snout. The amount of backward pelvic movement was calculated by determining the distance travelled by the pelvis in the opposite direction of the snout at the initiation of the dodge; this distance was then compared to the overall distance travelled by the snout. The amount of forward pelvic movement was

calculated by measuring the distance moved by the pelvis when it was moving in the same direction as the snout in order to realign its body in a posture from which eating could resume (Fig. 3). These values were then compared to the distance travelled by the snout in the same manner that the comparison of the overall distance travelled by the pelvis relative to the snout was analyzed (see above section for details).

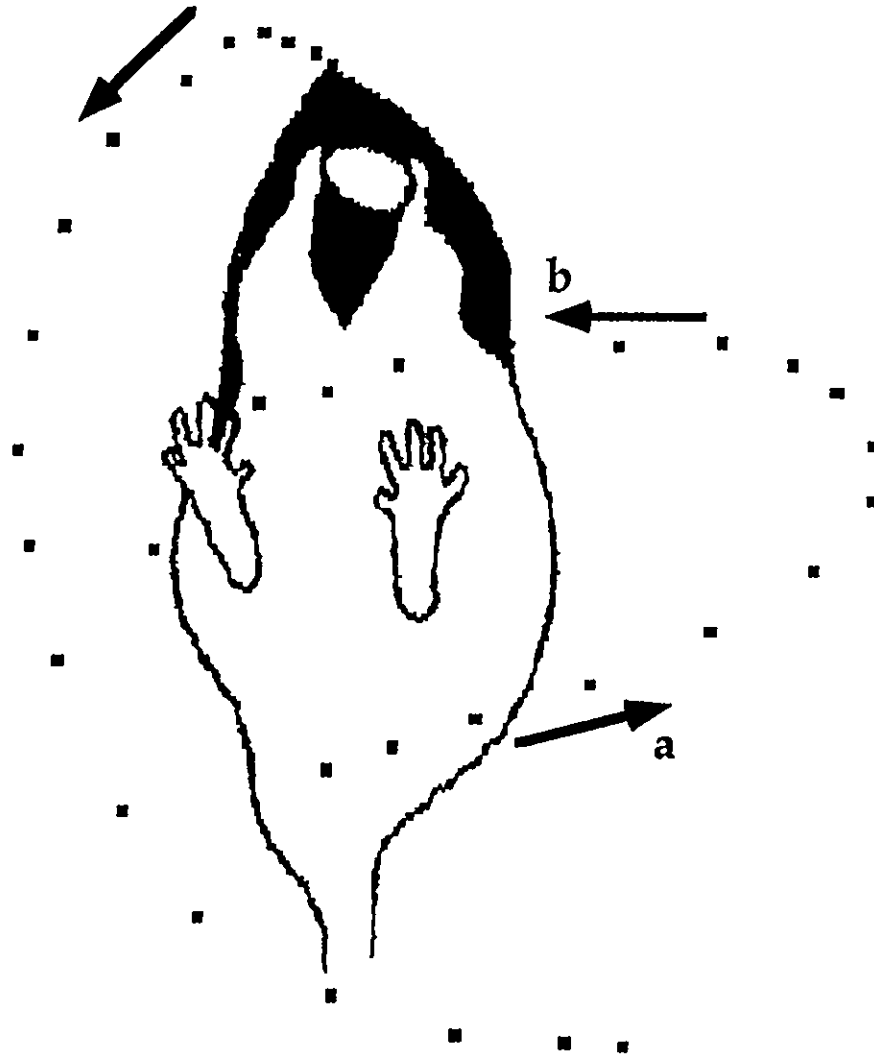
Distance Travelled by the Torso Relative to the Pelvis: In addition to the quantification of the relative displacement and velocity of the snout to the pelvis, comparisons were also made between the torso and the pelvis. The point digitized for the torso was determined by following the midline of the body and selecting a point that was approximately halfway between the shoulders and the pelvis. More movement of the pelvis relative to the torso would suggest that the pivotal point is closer to the torso; conversely, more movement by the torso than the pelvis would suggest that the pivotal point is closer to the pelvis. The relative distance travelled was calculated, comparing the pelvis(x) and torso(y) (i.e., $x-y/x*100$). A large positive score corresponds to a large movement of the pelvis relative to the torso. A small positive score or a negative score represents a small movement or velocity of the pelvis compared to the torso.

Figure 3: The trajectories of the snout and pelvis are shown for an unconstrained female dodge (A) and an unconstrained male dodge (B). Each solid round dot represents two video frames with the arrows with closed heads indicating the direction of the movement. Note that unlike the female, the male makes a large outward swing of the pelvis. The backwards movement of the pelvis for both the female and male example are designated with an arrow (a). The forward movement of the pelvis is also designated by an arrow (b) (Adapted from Field, Whishaw & Pellis, in press).

A . FEMALE



B . MALE



Temporal Relationship of the Initial Peak in Velocity of the Pelvis Relative to the Initial Peak in Velocity of the Snout: A similar procedure to that used for comparing the distances travelled by the digitized points was used to make comparisons of the differences in velocity of the snout and the pelvis. The relative temporal relationship of the occurrence of the first peak in velocity by the snout and by the pelvis was measured by converting the frame at which the initial peak occurred (x) into a percentage of the total number of frames of the dodge (y) ($x/y=z$). The value obtained for the pelvis was then subtracted from the value obtained for the snout. This provided a difference in the amount of time elapsed between the two peaks that could then be compared across trials. A large difference in the time elapsed between the initial peak in velocity for the pelvis as compared to the snout corresponds to a small amount of movement of the pelvis during the initial part of the dodge, whereas a small difference in the time elapsed indicates that the pelvis began to move shortly after the dodge was initiated.

Analysis of Number of Steps made by the Hindpaws and the Associated Stepping Patterns: The number of hindpaw steps as well as the pattern of

stepping was notated during the dodging sequences. To describe the pattern of hindlimb stepping a simplified version of the EWMN system (Eshkol & Wachmann, 1958) was used. This system enables the observer to label numerically the direction of the hindpaw steps in relation to the position of the body at the time of the step. The numerical values were then compared to determine whether differences existed in the direction of the locomotor steps by the hindpaws. The details of this analysis is described in association with the results of this analysis.

Analysis of the Movement of the Robber: Two measurements were taken of the robber's behavior during the digitized unconstrained trial. This analysis was done in order to determine whether differences in the robber's behavior could account for the differences in the movement pattern. These measurements were: (a) the video frame, following the initiation of the dodge, where the first peak in velocity of the robbing animal occurred, and (b) the maximum velocity obtained by the robber during that first peak in velocity.

Calculation of Group Means:

Group means and standard errors were calculated from the individual

values obtained for each rat. The data were analysed using a one-way analysis of variance followed by Fisher PLSD post hoc analysis ($p < 0.05$).

RESULTS

Distance Travelled by the Snout Relative to the Pelvis: Females, when dodging, have a large lateral displacement of the snout with only a small displacement of the pelvis (Fig 3A). In contrast, males have a displacement of the snout that is not much larger than that for the pelvis (Fig 3B). Comparison of the relative distance travelled by the pelvis as compared to the snout revealed significant group differences ($F(4/55)=4.810$, $p=.0021$). Post hoc analysis showed that the difference between males and females was significant, replicating my previous findings (Field, Whishaw & Pellis, in press; Chapter 3). Females treated neonatally with testosterone propionate (TP) and males gonadectomized at birth were also significantly different from males, whereas males that were gonadectomized prior to puberty were not significantly different from control males but were significantly different from all other conditions (Fig 4A).

Distance Travelled by the Snout Relative to the Backward Movement of the

Pelvis: From the initial comparisons between the groups of the overall distance travelled by the pelvis relative to the snout, it appeared that neonatal gonadectomy prevented males from developing a male-typical pattern but that TP treatment of females had no effect on this measure. It is possible, however, that only certain aspects of the behavior are modified by the hormone treatment. The initial backward movement of the pelvis appears to be a sex-typical characteristic that is predominantly seen in males (Field, Whishaw & Pellis, in press). To determine whether this aspect of the male pattern is present in TP treated females, the backwards movement of the pelvis was compared to the movement by the snout.

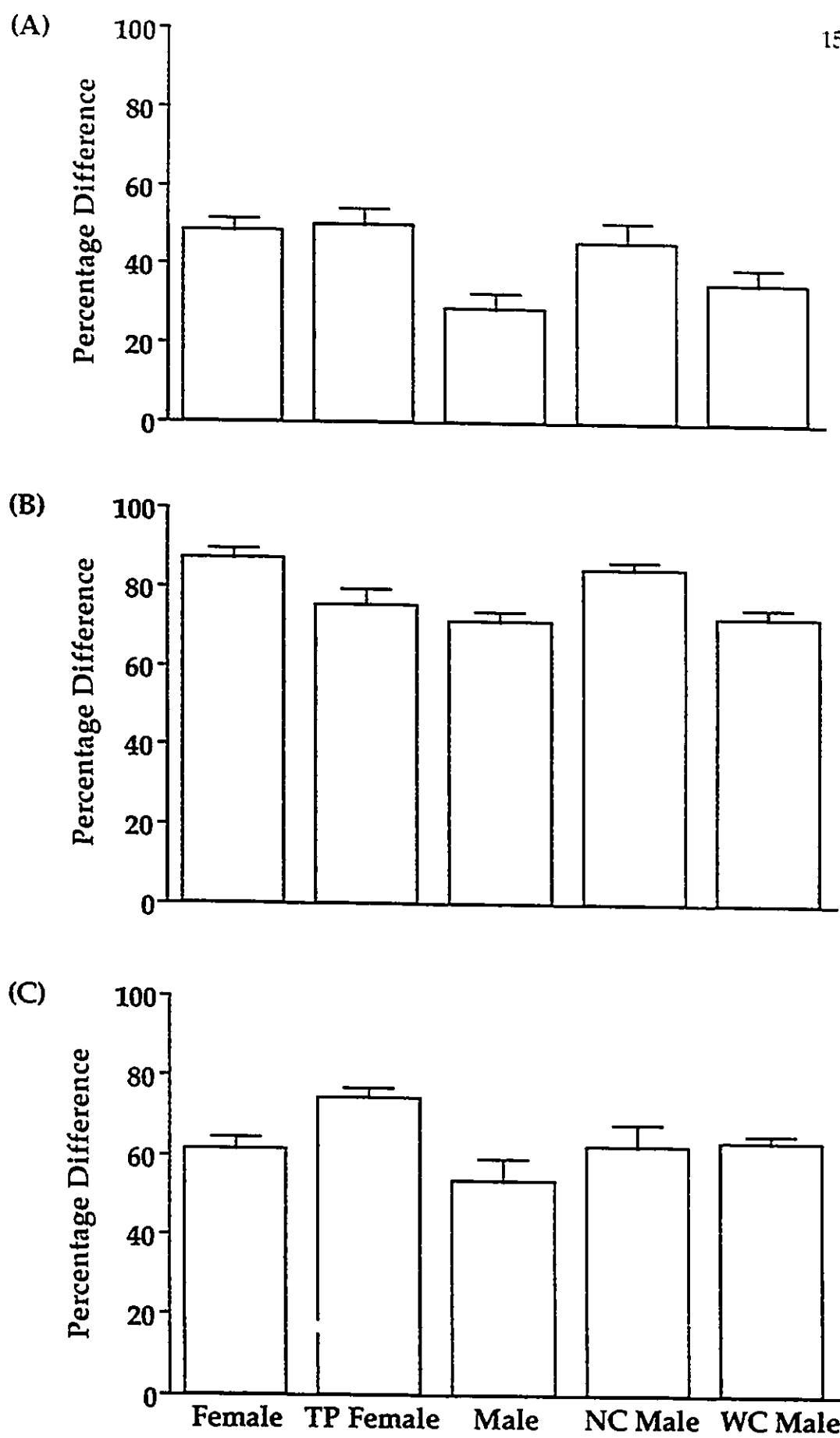
There were significant group differences for this measure ($F(4/55)=6.499$, $p=.0002$), with post hoc analysis showing that females were significantly different from males, TP treated females and males castrated at weaning. TP treated females were not significantly different, however, from control males or males castrated at weaning. Males castrated at birth were not significantly different from females but were significantly different from control males, males castrated at weaning and TP treated females. Males castrated at weaning, unlike males castrated at birth, were not different from control males. These findings suggest that the backward movement in

dodging is dependent on neonatal, but not pubertal, androgen exposure (Fig. 4B)

Distance Travelled by the Snout Relative to the Forward Movement of the Pelvis: One possible conclusion from the above results is that TP treated females must not be making as large a forward movement as control females. Analysis of the amount of forward movement of the pelvis as compared to the snout revealed significant group differences ($F(4/55)=3.291, p=.0173$). Post hoc analysis showed that not only did TP treated females make less forward movement of the pelvis than did control females, but that they also made less forward pelvic movement than did control and neonatally castrated males. There were no other significant differences between the groups (Fig. 4C). These results suggest that while the backward component of the male-typical dodge is present in TP treated females, the forward component that is typically present in all other conditions is not. The testosterone propionate treatment in females affected both the backward (see above) and forward movement of the pelvis.

Distance Travelled by the Torso Relative to the Pelvis: Previous work has shown that in conjunction with the differences in the amount of distance

Figure 4: The overall distance travelled by the pelvis relative to the snout is depicted (A). Intact males and males castrated at weaning (WC) showed significantly more overall movement of the pelvis relative to the snout than did intact females, testosterone propionate (TP) treated females and neonatally castrated (NC). The backward movement of the pelvis relative to the snout was compared (B). In this comparison intact males, WC males and TP treated females showed significantly more backward movement of the pelvis relative to the snout than did intact females and NC males. The forward movement of the snout as compared to the snout was also calculated (C). TP treated females showed significantly less forward movement of the pelvis than did intact males, females and NC males.



travelled by the snout relative to the pelvis, females also make more midbody (torso) movement than do males (Field, Whishaw & Pellis, in press). Less movement of the torso relative to the pelvis suggests that the point around which the body pivots is closer to the torso; conversely, more movement of the torso relative to the pelvis suggests that the point around which the body pivots is closer to the pelvis. A large positive score corresponds to a large movement of the pelvis relative to the torso, whereas a small positive score or negative score represents a small movement of the pelvis relative to the torso. It was predicted that if TP treated females are using a more male-typical pivotal point, then they should have a large positive score on this measure. In contrast, males castrated at birth should have a relatively low score if they are pivoting around a point similar to females.

There were significant group differences ($F(4/55)=4.313$, $p=.0042$). Post hoc analysis showed that control and TP treated females had significantly lower scores than both control males and males castrated at weaning. They were not, however, significantly different from males castrated at birth. Conversely, males castrated at birth were significantly different from control males and males castrated at weaning. These results suggest that while

androgens present neonatally are necessary for the masculinization of this aspect of dodging, such hormones are not sufficient to change this aspect of dodging from a female- to a male-typical pattern (Fig. 5).

Temporal Relationship of the Initial Peak in Velocity of the Dodging Animal in Relation to the Initial Peak in Velocity for the Snout: Males initially make a large backward movement of the pelvis simultaneously with a movement of the snout away from the robber. Analysis of the corresponding velocity curves shows peaks in the initial velocity of these two points to be temporally closer together than in females (Field, Whishaw & Pellis, in press). It was predicted that males castrated at birth would be different from control males, whereas males castrated at weaning and females injected with TP neonatally should not.

There were significant group differences ($F(4/55)=5.561, p=.0008$). Post hoc analysis showed that males castrated at birth and control females were significantly different from all other groups. Females treated with TP at birth were similar to intact males and males castrated at weaning (Fig. 6).

Analysis of Number of Steps made by the Hindpaws and the Associated Stepping Patterns: It was previously shown that the number of steps taken by

Figure 5: The difference, as a percentage, between the distance travelled for the pelvis relative to the torso is depicted. Intact females, TP treated females and NC males showed significantly more movement of the torso as compared to the pelvis than did intact and WC males.

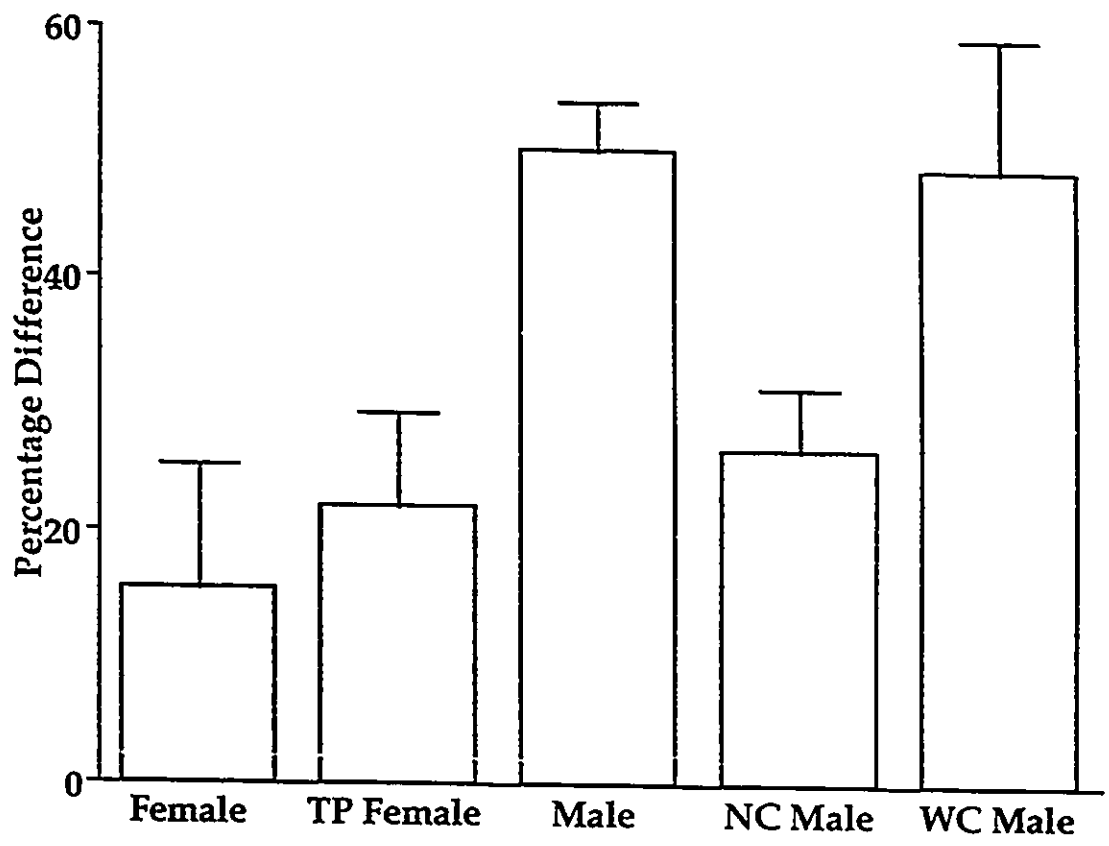
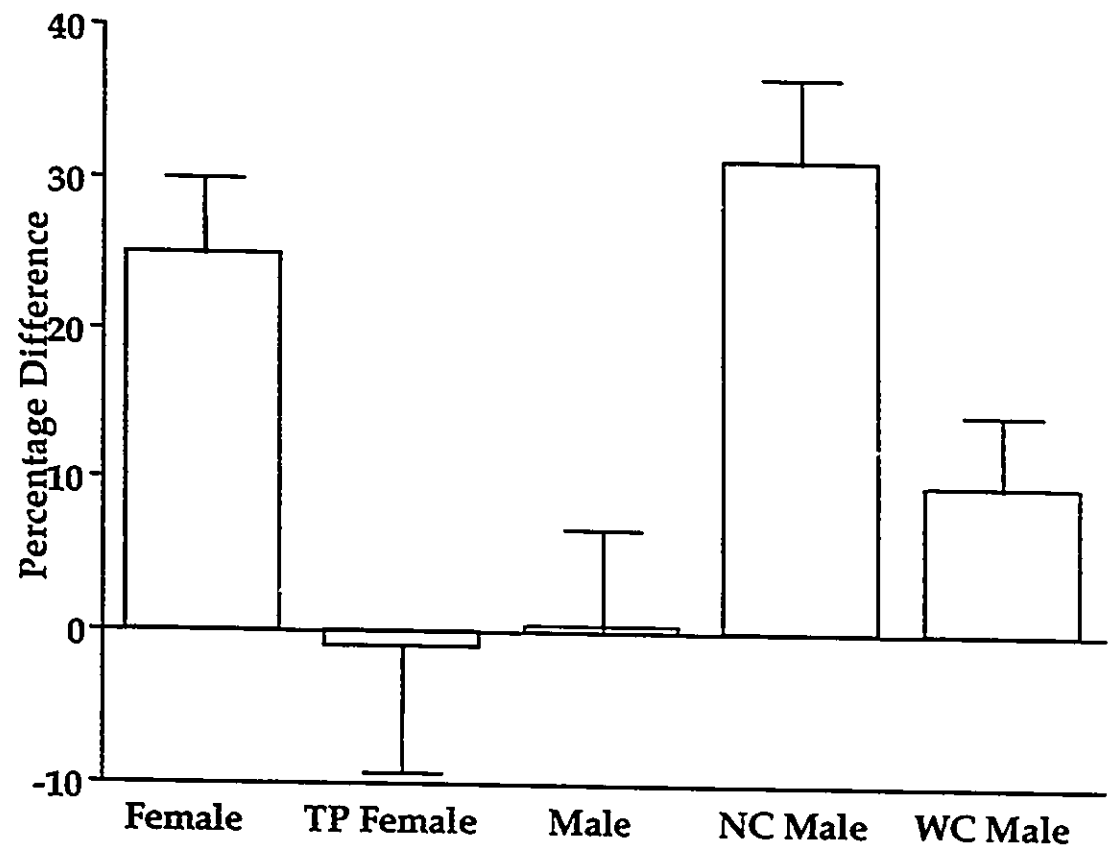


Figure 6: The difference, as a percentage, in the temporal location of the initial peak of velocity for the snout as compared to the pelvis is depicted. A value close to zero indicates that the initial peaks in velocity for the snout and the pelvis occurred almost simultaneously. The larger the positive value the greater the time elapsed between the initial peaks of velocity. Intact females and NC males showed a longer latency between the initial peak of velocity of the snout as compared to the pelvis than did TP treated females, intact and WC males.



the hindpaws during dodging differs significantly between males and females (Field, Whishaw & Pellis, in press; Chapter 3). Based on these past findings, it was predicted that females and males castrated at birth should perform fewer hindpaw steps than the other groups. While the differences were not significant, the trend was in the predicted direction. The average number of steps per dodge was 3.6 (S.E. \pm .336) for intact males, 3.3 (\pm .256) for weaning castrated males, 2.9 (\pm .229) for neonatally castrated males, 3.4 (\pm .149) for TP treated females and 3.0 (\pm .213) for females.

It was previously reported that males and females not only differ in the number of hindpaw steps performed, but also in the pattern of stepping (Field, Whishaw & Pellis, in press). The difference is illustrated in Figure 7A and B. Females make their initial step with the hindpaw ipsilateral to the direction of the dodge (Fig. 7Ac); this is then followed by a forward step of the hindpaw contralateral to the direction of the dodge (Fig. 7Ad). A final step forward by the hindpaw ipsilateral to the direction of the dodge (Fig. 7Ae) realigns the fore and hindquarters. The stepping sequence for males, on the other hand, begins with an initial step backwards by the hindpaw ipsilateral to the direction of the dodge (Fig. 7Bb). This is followed by a second backward step with the ipsilateral hindpaw and a forward step with the contralateral

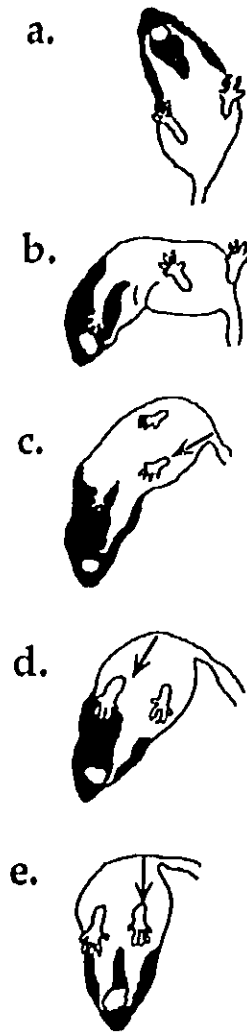
hindpaw (Fig. 7Bd) shortly after. The ipsilateral hindpaw then makes a final forward step (Fig. 7Be), which realigns the body and completes the dodge.

To determine whether the stepping sequences made by males and females were modifiable by androgen exposure, the sequence that accompanied each dodge was notated. Each step during the dodge was described as either forward, backward, sideways or to a point 45° in between these three. This was achieved by adapting aspects of the EWMN system. Steps were described numerically in relation to the body at the time of the step. The direction of each hindpaw step was recorded in the horizontal plane with intervals of 45° on the circumference. The intervals are read in a clockwise direction from 0,1,2,3,4,5,6,7 and back to 0. The circle is placed so that 0 is always aligned with the snout and 4 with the pelvis (Fig. 7Ca). As the rat moves the circle maintains the same orientation to the body (Fig. 7Cb). The direction of the hind paw steps were then scored by notating the number that corresponds to the direction of the step; for example, a step backwards towards the pelvis is notated as a 4. For numerical comparison, dodges to the right and left were all converted to the right. Therefore, a step directly to the left of the body (i.e., 6) was converted to the right side of the body (i.e., 2). Similarly a step to 7 was converted to 1, and a step to 5 to a 3 (Eilam & Golani, 1988).

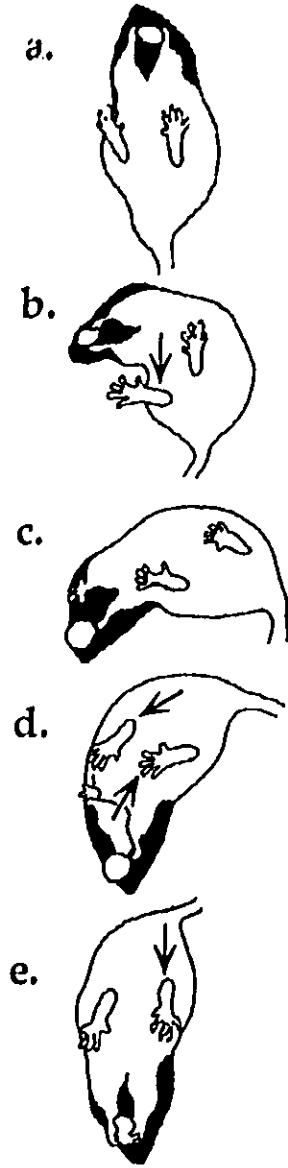
Figure 7: The stepping sequences for each dodge were analyzed. The number and direction of steps taken by the hindpaws for females and males are indicated by the open-headed arrows in (A and B). After turning laterally (Aa-b), the female makes an initial step ipsilateral to the direction of the dodge (Ac). This step is followed by a forward step contralateral to the direction of the dodge (Ad) and a final step forward ipsilateral to the direction of the dodge (Ae). In contrast, the male has less lateral movement of the upper body (Ba) before taking a step backwards ipsilateral to the direction of the dodge (Bb). This is followed by a second backward step with the ipsilateral hindpaw and then shortly after with a forward step of the contralateral hindpaw (Bd). The ipsilateral hindpaw then makes a final forward step (Be).

To analyze and compare the direction of the steps a simplified version of the EWMN system was used (Fig. 7C) (See Results for a description of this analysis).

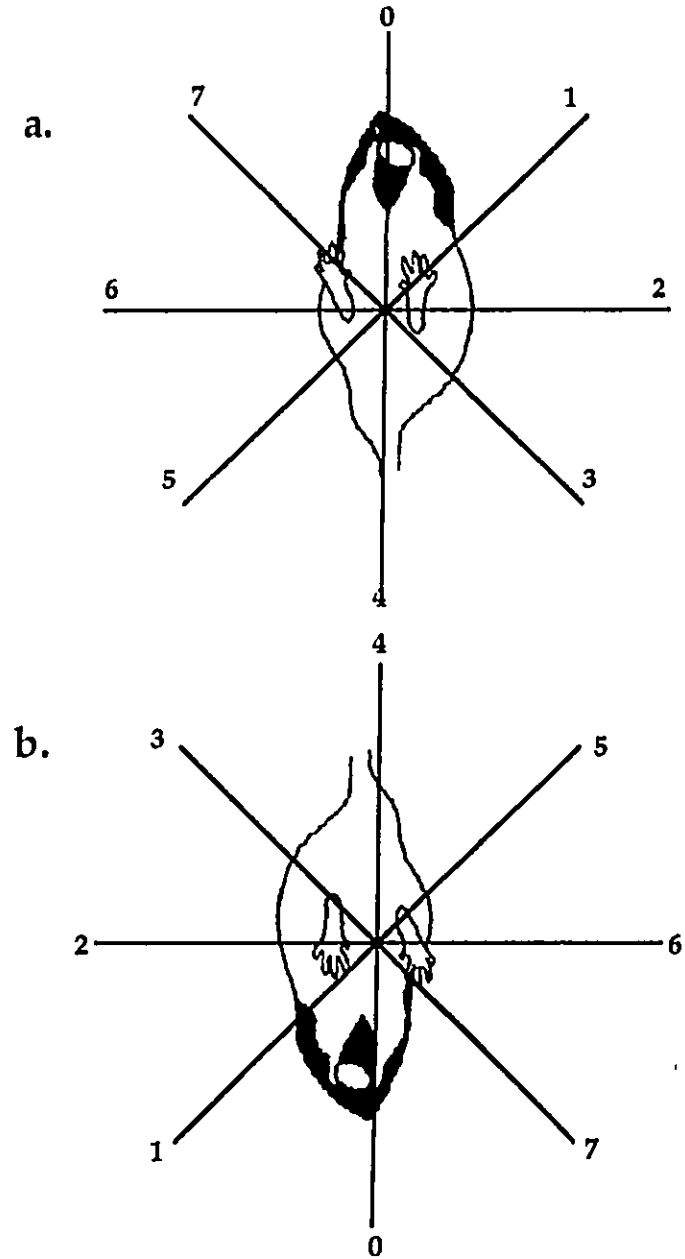
A. FEMALE



B. MALE



C.



Steps were compared so that they were equivalent across trials (i.e., for comparison of the placement of the initial step only steps made by the hindpaw ipsilateral to the direction of the turn were compared). Comparisons of the direction of stepping were made for three of the steps that frequently occur during a dodge sequence. These were: (1) the initial step made by the hindpaw ipsilateral to the direction of the turn (see fig. 7Ac & Bb), (2) the forward step made by the hindpaw contralateral to the direction of the dodge (see Fig. 7Ad & Bd), and (3) the forward adjusting step that is made at the end of the dodge (see Fig. 7Ae & Be). The fourth step shown (Fig. 7Bd) was not included in the comparison because it did not often occur in control females and neonatally castrated males.

There were significant group differences on the first ($F(4/55)=9.378$, $p<.0001$) and second step ($F(4/55)=9.140$, $p<.0001$), but not on the third step. Post hoc analysis for the first step showed that females were more likely to step sideways away from the body than any other condition. Males castrated at birth were different from both males and females, and while more likely to step away from the body, they did so by stepping obliquely. TP treated females were similar to both intact males and males castrated at weaning in that they were more likely to make a step backwards towards the pelvis (Fig 8A).

Post hoc analysis of the second step showed that females and males were significantly different in the placement of the hindpaw. Females were more likely to step forward with the hindpaw contralateral to the direction of the dodge and to place their hindpaw directly in line with the snout. In contrast, males were more likely to step and place their hindpaw outward at approximately a 45° angle to the snout (see Fig. 7C for details). Females were also significantly different from both gonadectomized male conditions, but not from females treated with TP neonatally. Females treated neonatally with TP were significantly different from all male conditions (Fig 8B). On the third step, rats from all groups were most likely to step forward with the hindpaw ipsilateral to the direction of the turn, in line with the snout (Fig 8C). These results suggest that while aspects of the stepping sequence are modifiable by neonatal androgen exposure (step 1), other aspects are not (step 2 and 3) (Fig. 8)

Analysis of the Movement of the Robber: It is possible that the differences in the dodge patterns between the five conditions are due to differences in the robber's behavior. To determine whether there were differences between the behavior of the robbers in the various treatment conditions, two measurements were scored (see Methods). On both measures, no significant

differences were found in the robbers regardless of the treatment condition (Table 1). Therefore, it is unlikely that the robbers' behavior influenced the differences in dodging behavior that were found between the five conditions.

Figure 8: This figure depicts the average direction of the hindpaw steps on the three steps that were analyzed as described in the caption for Figure 7. For the first step by the hindpaw ipsilateral to the direction of the dodge intact females generally step out sideways from the body to 2 or 6 (see Fig. 7C). In contrast, TP treated females step backward towards the pelvis to 4 and were similar to intact and WC males. NC males were different from all other groups and generally step out sideways from the body and also backwards at an oblique angle to 3 or 5 (8A). The second hindpaw step analyzed was made contralateral to the direction of the dodge. Intact and TP treated females generally step forward toward the snout or zero. In contrast, intact, NC and WC males, while still stepping forward, also step outwards at approximately a 45° angle to the snout or to 1 or 7 (8B). For the final step made by the hindpaw ipsilateral to the direction of the dodge, the rats in all conditions generally step forward towards the snout and no significant differences were found (8C).

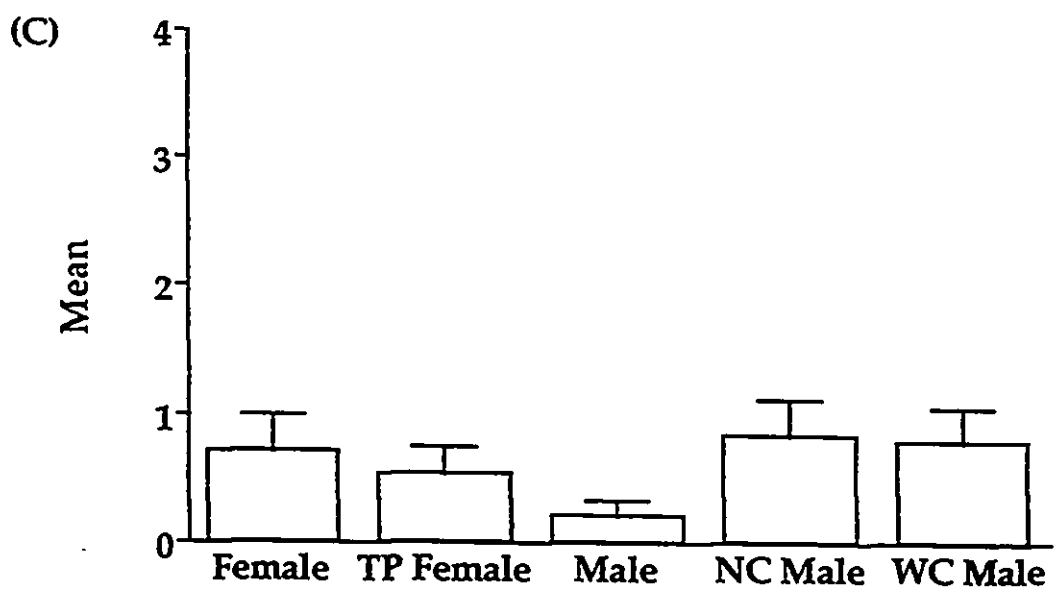
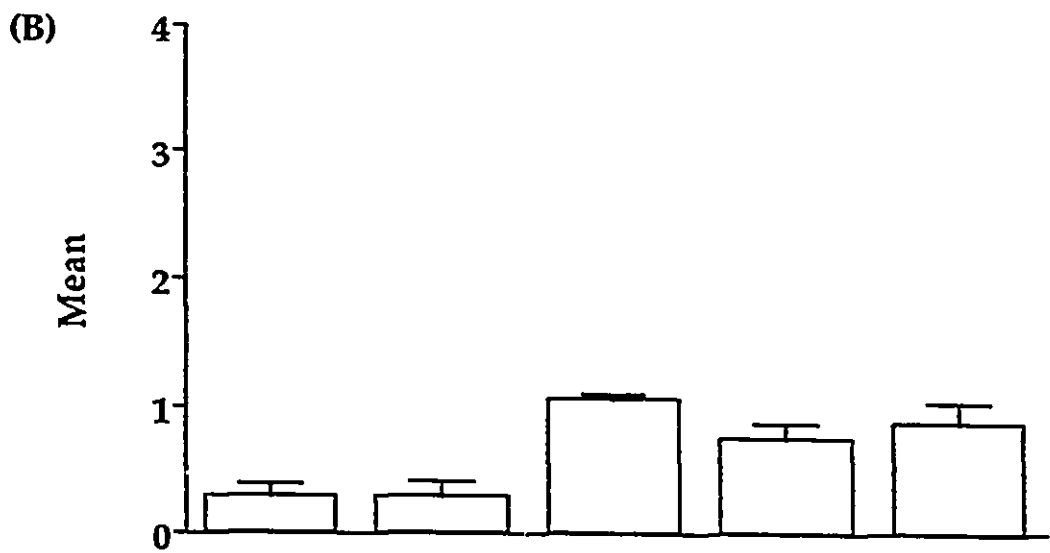
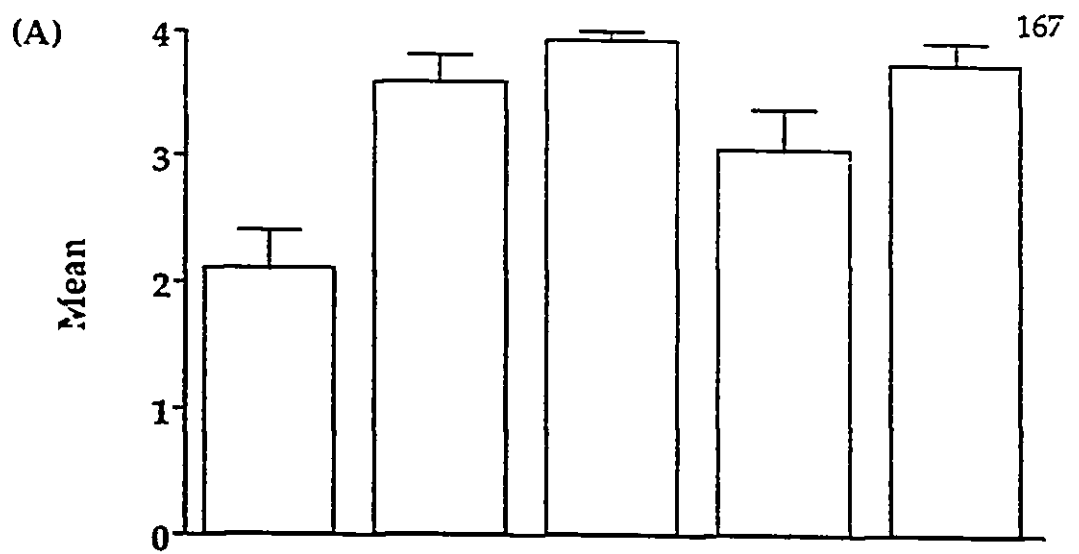


TABLE 1

COMPARISON OF TWO ASPECTS OF ROBBING BEHAVIOR

	Variables Measured*	
	1	2
Control Females ($\bar{X} \pm \text{SE}$)	20.3 ± 2.5	33.8 ± 5.4
Neonatally Treated TP Females ($\bar{X} \pm \text{SE}$)	25.2 ± 1.9	38.1 ± 3.5
Control Males ($\bar{X} \pm \text{SE}$)	15.9 ± 3.9	42.2 ± 5.7
Neonatally Castrated Males ($\bar{X} \pm \text{SE}$)	20.0 ± 2.7	34.1 ± 2.5
Weaning Castrated Males ($\bar{X} \pm \text{SE}$)	18.9 ± 2.4	37.8 ± 3.0
F-Test	1.5, ns**	0.66, ns
p-value	0.21	0.62

* 1= the frame, following the initiation of the dodge, where the first peak in velocity of the robbing animal occurred

2= the maximum velocity obtained during the first peak in velocity

**ns = not-significant at $p < 0.05$

DISCUSSION

The data reported in this paper confirm previous findings showing that males and females use different tactics when dodging to protect a food item (Field, Whishaw & Pellis, in press; Chapter 3). Males make significantly more movement with the pelvis relative to the snout than do females. This difference is due to more movement by the pelvis both backwards in the opposite direction to the dodge, and forwards in the same direction as the movement of the snout. Furthermore, this difference is accompanied by differences in the movement of the torso relative to the pelvis, the temporal separation between the initial peaks in velocity for the snout and the pelvis, and differences in hindpaw stepping patterns. Given that the differences in dodging tactics do not appear to be due to differences in the behavior of the robber, it seems likely that there are intrinsic sex differences in the organization of the movements themselves.

Males castrated on the day of birth are more female-typical in aspects of their behavior than are intact males. When compared to intact males, they make less movement of the pelvis in comparison to the snout. Qualitative analysis of the trajectories of these males shows that they are similar to the dodge trajectories of females. During hindpaw stepping however, subtle

differences were found between neonatally castrated males and females. This suggests that while postnatal androgens are necessary for the masculinization of most aspects of the male-typical dodge pattern, some of the components of dodging, such as the direction of the locomotor steps used, may be masculinized by gonadal hormone exposure prior to birth. While neonatal castration changed the male-typical pattern of dodging to a more female-typical pattern, castration of males at weaning had no effect. On all measures, males castrated at weaning were not significantly different from intact males suggesting that exposure to circulating gonadal androgens is not necessary to perform the male-typical pattern of dodging.

Females treated neonatally with testosterone propionate (TP) differed substantially from control females. While the overall distance travelled by the pelvis relative to the snout was not significantly different from control females, the composition of this movement was. TP treated females showed significantly more backward pelvic movement as compared to the snout. Unlike control females however, this backward movement by the TP treated females was not coupled with a large forward movement. It appears that TP females, while moving the pelvis initially backwards, pivot around a point on the longitudinal axis in a manner similar to that of control females.

Even though females treated with testosterone propionate neonatally

demonstrated aspects of the male-typical dodging pattern, and males castrated at birth were more female-typical, both still retained aspects of the movement patterns typical of their sex. This suggests that exposure to both the prenatal and the postnatal androgen surge may be necessary for the complete masculinization of this behavior. A complete reversal to the dodge pattern of the opposite sex may require manipulation of prenatal androgens for both males and females.

Weisz & Ward (1980) have shown that the testosterone surge in males is greatest at embryonic (E) day 18, and have suggested that the high level of exposure to androgens on E18 is necessary to sensitize the central nervous system to the subsequent lower doses of androgens that are present in males after birth. The data presented in this paper supports the hypothesis that both prenatal and postnatal exposure to testosterone is necessary for the complete masculinization of dodging patterns. This is consistent with work showing that prenatal hormonal exposure can affect adult behavior (Clark, Tucker & Galef, 1992; Clark & Galef, 1994; 1995; vom Saal, 1989), and the degree to which the male rat's brain is masculinized (Perakis & Stylianopoulou, 1986). It is possible however, that at least some of the sex differences in dodging patterns are due to differences in peripheral skeleto-muscular morphology rather than to differences in the central nervous system.

Sex differences in the composition of the pelvis have been reported for mice (Shimizu & Awata, 1984), rats (Bernstein & Crelin, 1967) and humans (Coleman, 1969). Further sex differences have also been described in the size of the muscles and innervating motoneuron nuclei of the bulbocavernosus (BC) and levator ani (LA) muscle in rats (Breedlove, 1992). Masculinization of peripheral skeleto-muscular morphology is dependent on the direct effects of testosterone (Bardin & Catterall, 1981; Breedlove, 1992), whereas masculinization of the central nervous system is dependent on estrogen that is converted from testosterone (Toran-Allerand, 1984). Vega Matuszyk & Larsson (1995) have shown that treatment of male rats prenatally with an antiandrogen did not significantly alter their sexual behavior as adults even though they had a poorly developed penis and a blind-ending vagina. In contrast, males treated with an antiestrogen had a decrease in male-typical sexual behavior and an increase in feminine sexual behavior. These findings support the possibility that sex differences in movement and behavior are not due solely to peripheral anatomical differences, but rather, may be neurally generated.

Some human pathologies also suggest that movement differences are not due solely to sex differences in body morphology. For example, girls with

congenital adrenal hyperplasia (CAH), who are prenatally androgenized, appear to exhibit more masculine behavior (Collaer & Hines, 1995). Indeed, based on a questionnaire study of afflicted subjects, their unaffected sisters and their respective mothers, Dittman (1992) reported that the CAH variant with the most strongly masculinized body morphology (i.e., the simple-virilizing variant) was reported to be the least male-like in movement, whereas the variant that was reported to be the most female-like in body morphology was the most masculine in movement. While the development of sex-typical movement patterns and the role of gonadal hormones in their development has not been studied extensively, there is evidence that movement patterns are modifiable by exposure to circulating gonadal hormones in adulthood. This further suggests that gonadal hormones play a role in the organization of movement.

Several studies have shown that motor output can be influenced by differences in gonadal hormone levels. Low levels of estrogen in female rats can increase the number of footfall errors made when they traverse a narrow beam. The number of these errors are decreased on the day of estrus or by 17 beta-estradiol treatment (Becker, Snyder, Miller, Westgate, & Jenuwine, 1987). The performance of normal women on several sexually dimorphic motor tests fluctuates during the menstrual cycle, with changes in performance

being associated with changes in the levels of estrogen and progesterone (Hampson & Kimura, 1988, Hampson, 1990). Gonadal hormones have also been implicated in movement disorders (Van Hartesveldt & Joyce, 1986; Di Paolo, 1994). Neuroleptic induced parkinsonian symptoms are more common in women than men and estrogen treatment increases the severity of these symptoms (Van Hartesveldt & Joyce, 1986). Another movement disorder that appears to be linked to the levels of circulating estrogen is the finding that in patients with a previous history of choreatic movements, both pregnancy and oral contraceptives, which correlate to elevated levels of circulating estrogens, are associated with choreatic episodes. Once the pregnancy ends or oral contraceptive use is discontinued, the symptoms slowly disappear (Van Hartesveldt & Joyce, 1986).

It is likely that at least some of the differences in movement composition by males and females are due to differences in neural wiring, and that these neural differences are influenced by gonadal hormones. Nonetheless, to determine the precise origins and development of sex differences in movement composition, the interaction of peripheral skeletal-muscular anatomy, central nervous system and gonadal hormones need to be further analyzed.

CHAPTER 5

GENERAL DISCUSSION

I have demonstrated, in this thesis that males and females, when eating a food item, use a different composition of movements to dodge away from an approaching robber. This difference is not due to differences either in the robbing behavior of males and females, nor in the sex of the robber. Furthermore, the sex differences in the organization of dodging movements are dependent upon the action of androgens early in development.

During a dodge, females typically pivot away from the robber by moving around a point located near the pelvis, whereas males typically pivot away from the robber by moving around a point located near the midbody. Both sexes thus produce a large trajectory with the snout. However, while the excursion travelled by the female's pelvis is small, that traced by the male's pelvis is large. By pivoting around the midbody, the male moves its snout and pelvis simultaneously.

These two types of lateral dodges, while superficially similar, and functionally designed to move the head away from the robber, arise from a different combination of stepping patterns and shifts of body weight (Field, Whishaw, & Pellis, 1994; Field, Whishaw, & Pellis, in press). Dodging to

protect a food item first appears at around weaning (Bolles & Woods, 1964; Coles & Whishaw, work in progress), and the sex-based differences in pivot patterns are detectable shortly thereafter (Field, Whishaw & Pellis, work in progress).

Given that both male and female robbers stop moving towards the defender shortly after the dodge has commenced, the difference in the type of dodge pattern used cannot be accounted for by differences in the behavior of male and female robbers (Chapter 2, Field, Whishaw, & Pellis, in press). Rats, however, can modulate the magnitude of the dodge based on the properties of the food pellet. With increasing size or hardness of a food item the eating time is increased; this leads to a dodge of a larger magnitude (Whishaw & Gorny, 1994). These findings suggest that rats are capable of modifying their dodges in a manner sensitive to subtle contextual features beyond the immediate movements of the partner. For example, when play fighting, males and females alter their defensive responses depending on the sex of the attacking play partner, even though the form of the attack does not appear to differ (Pellis & Pellis, 1990). Therefore, the sex-specific dodging patterns may be a byproduct of the fact that I had used isosexual pairs in my first experiment (Chapter 2, Field, Whishaw, & Pellis, in press). Thus it is possible that the sex-typical composition of the dodge is influenced by the sex of the

robber.

The evidence presented in Chapter 3, however, shows that the composition of the dodge performed by males and females is not determined by the sex of the robber (Pellis, Field, Smith, & Pellis, in press; Chapter 3). There are subtle variations in the response of males and females to a same or opposite sex partner; that is they are making adjustments of their final position based on the robber's sex. The sex-typical patterns of dodging, however, are maintained irrespective of the robber's sex.

One aspect of sex differences in behavior frequently considered in the literature is whether these differences are due to exposure to gonadal hormones (Beatty, 1992). In Chapter 4, the role of gonadal hormone exposure on the development of sex-typical dodge composition was examined. Females injected with testosterone propionate on both the day of birth and the day after exhibited male-typical characteristics during dodging. In contrast, males castrated on the day of birth use a more female-typical combination of movements during dodging. Males that were castrated at weaning after the neonatal, but prior to the pubertal surge in testosterone were not different from control males.

Prior to this thesis, most studies on sex differences in movement have focused on the difference in the frequency of performance of specific

behaviors (Beatty, 1992; Ward, 1992). The research conducted for my thesis has shown that the composition of movements that comprise a specific behavior pattern can also be sexually dimorphic and under the control of neonatal androgen exposure. This research highlights the possibility that males and females may differ at the level of organization of the motor system and hence the manner in which the behavior is subsequently composed. This possibility is not without precedent. Kimura (1993) has shown that aphasia is more likely to occur in women, after damage to the anterior portion of the left hemisphere, in contrast, males are more likely to be aphasic after damage to the posterior of the left-hemisphere. Thus differences in movement organization have implications for both our understanding of how male and female behavioral and neural phenotypes are constructed, and for the consequences of disease states that compromise these phenotypes.

Sex differences in movement composition during solitary behaviors:

The defensive lateral evasive maneuvers used during dodging to protect a food item occur in a socially competitive situation, where subtle contextual factors may trigger a more formidable defensive tactic by males. Given that males engage in more combat (Blanchard, Flannelly, & Blanchard,

1988), they may have a lower threshold for the use of the midbody pivot which maximizes defense of the head by interposing the rump between the opponent and the defender's head (Pellis & Pellis, 1992a; Pellis, MacDonald, & Michener, 1996). During exploratory locomotion, an animal's movements, unlike those in dodging, are unconstrained by a partner. Therefore, sex differences during exploratory locomotion would support the possibility that males and females differ in their motor organization. Current work on the composition of spontaneous turning in an open field and during forward locomotion suggests that the differences I have found in the movement composition of dodges are not due to the presence of a conspecific, but rather, are intrinsic to each sex (Pellis, Pellis & Field, 1995).

Turning in an open field by adult animals can be defined as a transitional act occurring between bouts of forward locomotion (Eilam, 1994). Turning is one of the first behaviors exhibited by neonate rats (Eilam & Golani, 1988; Golani, Bronchti, Moualem, & Teitelbaum, 1981), and continues to be exhibited through development and into adulthood. Previous work has shown that the motor composition of turning can be influenced by body morphology (Eilam, 1994), dopaminergic agonists and antagonists (Cools, Scheenen, Eilam, & Golani, 1989; Zeigler & Szechtman, 1988) and neural manipulations (Miklyeva, Martens, Whishaw, 1995; Zeigler & Szechtman,

1988).

Sex differences in turning behavior are usually documented in terms of the frequency of rotations in the horizontal plane (Carlson & Glick, 1996). These studies, however, have not looked at whether the composition of the behavior exhibited is different between males and females. A study was conducted to determine whether males and females use different movement patterns when turning laterally in an open field (Pellis, Pellis, & Field, 1995; Field & Pellis, in preparation). Turning was defined as a cessation of forward movement and a change in the horizontal position of the head and upper body by 90 degrees or greater (Eilam, 1994). Turns that were immediately preceded by another behavior such as rearing or grooming, or turns that were constrained by the plexiglass cylinder and involved vertical movements, were not included. For each example chosen, the fore and hindpaw stepping patterns were notated in their order of occurrence.

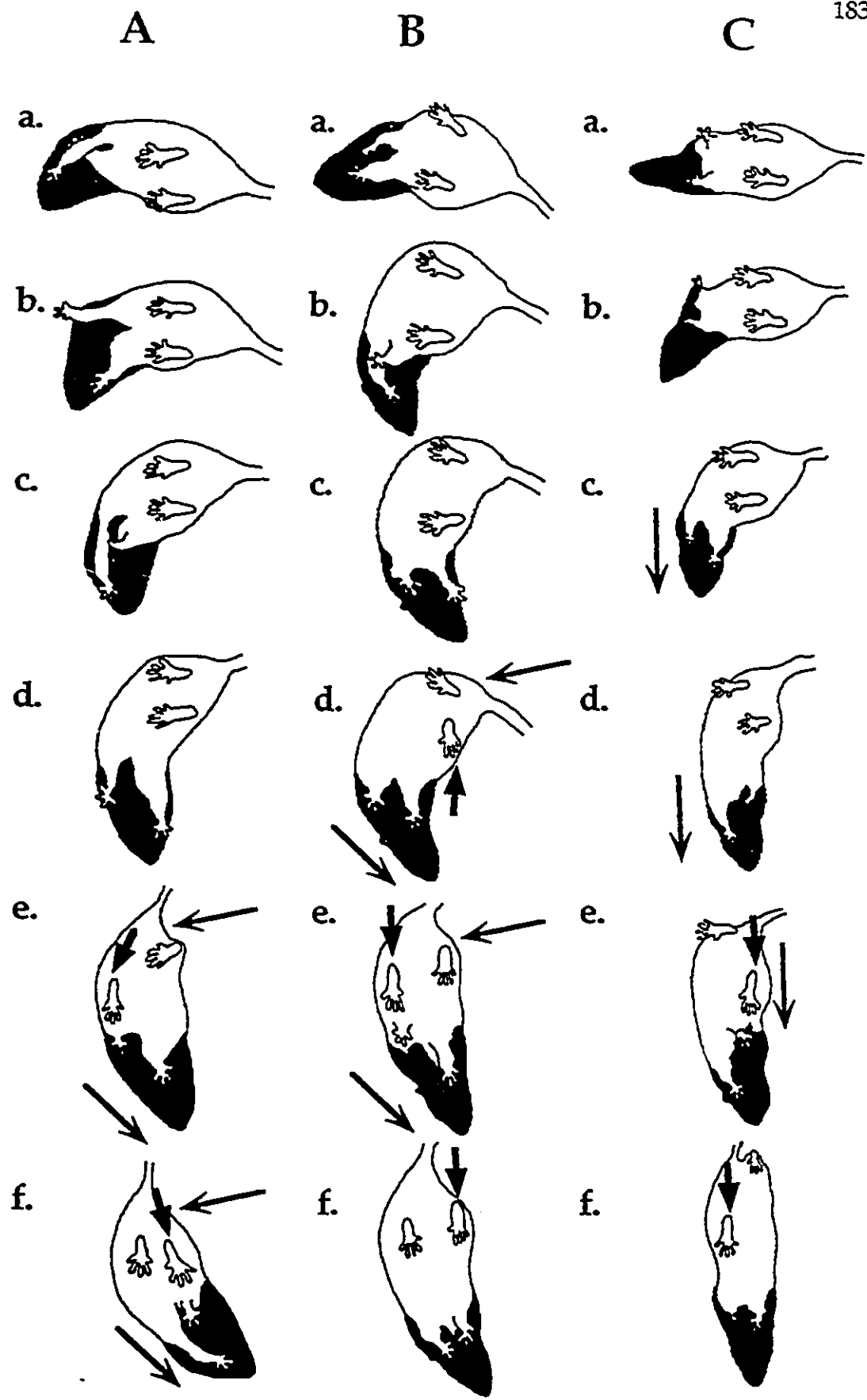
There were three sequences of hindpaw stepping patterns exhibited during spontaneous turns; in all cases, hindpaw stepping was preceded by forepaw stepping. In (A), the hindpaw contralateral to the direction of the turn steps first, moving the pelvis into alignment with the forequarters which have already turned. This first step is then followed by a forward step of the ipsilateral hindpaw (Fig. 1A). In (B), the hindpaw ipsilateral to the turn

makes an initial step backwards, towards the midline of the body. This step is followed by a forward step of the contralateral hindpaw. A third forward step is then made by the ipsilateral hindpaw (Fig. 1B). Finally, in (C), the initial hindpaw step is made in a forward direction by the ipsilateral hindpaw. This is followed by a forward step of the contralateral hindpaw (Fig. 1C).

When turning, males appear to move their pelvis more, producing a different pattern of stepping than that seen in females. In about 70% of cases, females turn their forequarters towards the direction of the turn and follow this with the sequence of steps as described in (C); this produces a small amount of horizontal displacement of the pelvis. In contrast, males are significantly different from females in that they use hindlimb stepping patterns which produce a greater amount of pelvic movement. Therefore, after the initial movement of the forequarters in the direction of the turn, males step in the manner described in (A) and (B) in about 89% of cases.

Preliminary findings suggest that these sex differences in spontaneous turning are present shortly after birth (Field, Pellis, & Pellis, work in progress). It is likely, therefore, that the sex differences in dodging patterns are not simply differences in the selection of sex-typical behavior patterns, but rather, reflect underlying differences in how the movements are generated. This possibility is further supported by the presence of sex differences in

Figure 1: The stepping patterns for the three types of 90° turns used commonly by adult rats are depicted. The male-typical patterns (A and B) result in movement of the pelvis in the direction opposite to that of the turn (d-f open arrows). In contrast, the female-typical pattern (C) shows unidirectional movement as indicated by the open arrows (d-f). In conjunction with the differences in pelvic movement there are differences in the stepping patterns that accompany the three types of turns. All three types of hindfoot stepping patterns are preceded by forelimb stepping. The closed arrows show the hindpaw that is stepping and the direction of the step. The direction of movement of the body is depicted by the larger arrow. (Taken from Field & Pellis, in preparation)



stepping and pelvic movements during forward locomotion.

The term locomotion has been defined as any forward progression that involves rhythmic limb movements (Gambaryan, 1974). In this experiment (Pellis, Field, & Pellis, 1995; Field, Pellis & Pellis, work in progress), only slow walking, where at least three paws are in contact with the plexiglass surface at all times, was analyzed (Gambaryan, 1974). Whereas sex differences in general locomotor activity and open field behavior have been documented (Stewart & Cygan, 1980; Beatty, 1992), differences in the pattern of movements during rhythmic forward locomotion have not been described in detail. Parker and Clarke (1990) showed that there is a difference in stride width for male and female Wistar rats. Even though this measure increased with increased body size, the sex difference remained present. Therefore, the difference in step parameters cannot be accounted for by the size differences between males and females. Further sex differences have been characterized in locomotion.

The amount of sway by the pelvis during a hindpaw step was calculated. Each step was chosen from within a sequence of steps so that they were not involved in the initiation or cessation of walking. In replicating the results of Parker & Clarke (1990), it was found that males had significantly

more displacement of the pelvis than females (Pellis, Field, Smith, & Pellis, in press). In part, the increased 'swagger' of the males' pelvis was produced by the way in which the hind paws were placed. To measure this, in ten steps for each rat, the angle of the long axis of the placed hind paw was scored relative to the direction of movement. On average, in the initial step placed, the males turned their hindpaws inward in reference to the midline of the body, whereas the females placed their hindpaws outward in reference to the midline of the body (Pellis, Field, Smith, & Pellis, in press). Thus even simple forward locomotion involves kinematic differences between the sexes (Pellis, Field, & Pellis, 1995; Field, Pellis & Pellis, work in progress). These findings further support the hypothesis that there are major sex differences in the organization of motor patterns.

For both of these behaviors, spontaneous turning and forward locomotion, the role of neonatal androgen exposure was studied. Females injected with testosterone propionate on the day of birth and the day after show a preference for the male-typical stepping sequences during spontaneous turning (82.5%). Males castrated at birth, however, show a preference for the more female-typical pattern of stepping (65%) (Pellis, Pellis, & Field, 1995; Field & Pellis, in preparation). Neonatal androgen exposure also modifies aspects of forward locomotion. The amount of 'swagger'

exhibited by males castrated at birth is significantly less than control males. Females treated with testosterone propionate however, are also significantly different from males. With regards to hindpaw placement however, they are significantly different from both males and females in that they place their hindpaws parallel to the midline of the body. Males castrated at birth are also significantly different from intact males but not from control females (Pellis, Field, & Pellis, 1995; Field, Pellis & Pellis, in preparation). These findings support the hypothesis that there are major sex differences in the organization of motor patterns and that these differences are influenced by gonadal hormone exposure.

Sex differences in movement and posture:

I have provided evidence, throughout this thesis for sex differences in the composition of movement patterns having the same endpoint: evasion during play (Pellis, Field, Smith & Pellis, in press), dodging to protect a food item (Chapters 2, 3 & 4), spontaneous turning (Pellis, Pellis, & Field, 1995; Field & Pellis, in preparation) and forward locomotion (Pellis, Field, & Pellis, 1995; Field, Pellis & Pellis, in preparation). In all cases, it appears that the underlying difference between males and females is in their coordination of fore and hindquarter movements. Females use patterns of movement where

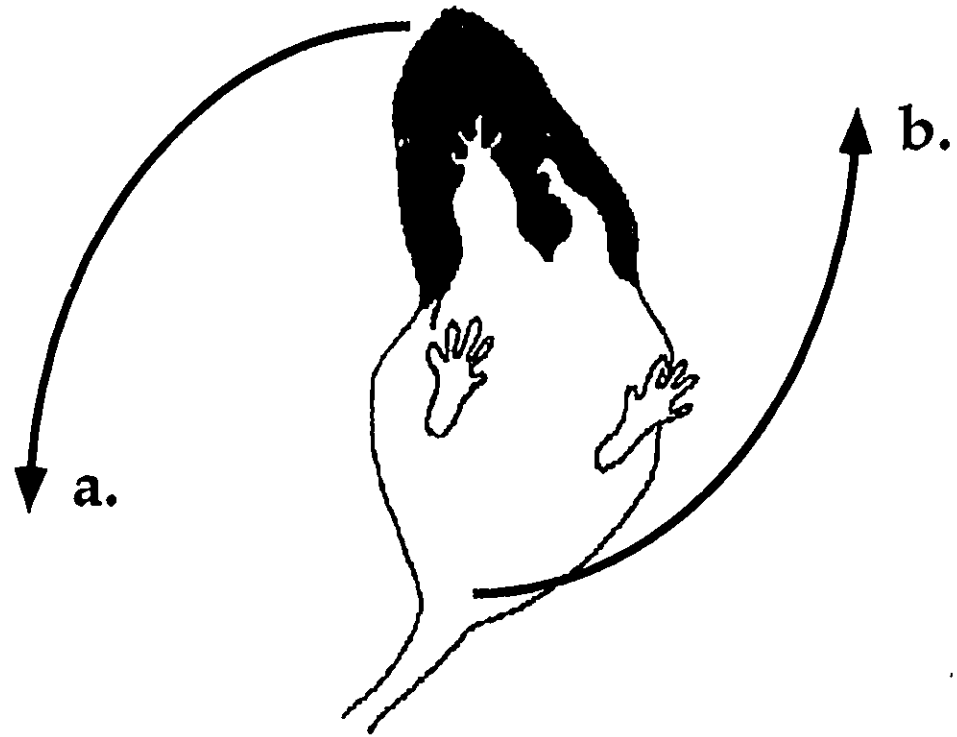
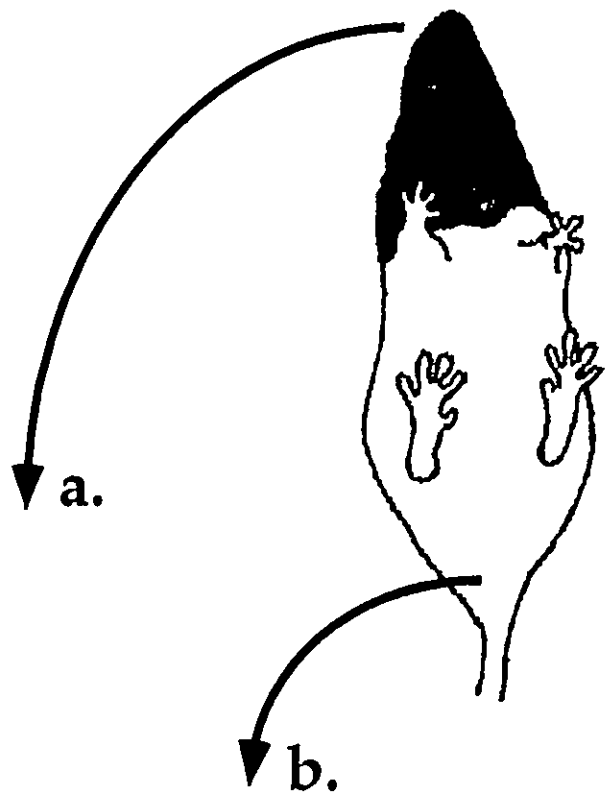
the hindquarters generally follow the direction of the forequarters. This results in minimal hindquarter movement. In contrast, males use simultaneous movements of the fore and hindquarters, often with the hindquarters moving in the direction opposite to that of the forequarters (Fig. 2). That the underlying factor generating the sex differences in movement patterns around the horizontal plane is a difference in the coordination of movement of the fore and hindquarters, is supported by sex differences in other planes of movement.

In rats, the ability to turn from a supine position on the ground to prone, is present from birth. At first, the rats use varying combinations of limb and body movements to rotate the longitudinal axis of the body to prone. Eventually, by about three weeks of age, they use the adult-typical pattern of cephalocaudal axial rotation to right to prone (Pellis, Pellis, & Teitelbaum, 1991). Males and females appear to use a different combination of limb and body movements to achieve the prone position, and these differences become evident within the first few days after birth. At two days after birth, males right the hindquarters following rotation of the forequarters to prone in about half the time that it takes females. This appears to be due to a difference in the coordination of the movements of the forequarters with

Figure 2: No matter what the behavioral context, when turning laterally, females (A) generally move in a unidirectional manner where their hindquarters (Ab) follow the movement of the forequarters (Aa). In contrast, males generally move their hindquarters (Bb) in the direction opposite to that of the forequarters (Ba). (Taken from Pellis, Field, Smith & Pellis, in press)

A . FEMALE

B . MALE



those of the hindquarters (Field, Martens, Pellis, & Pellis, work in progress). Therefore, this suggests that, in part, the differences in the composition of the behavior patterns of righting may arise from a sex difference in the coordination of the anterior and posterior parts of the body. Some evidence suggests that a separate, postural difference may also be involved.

Preliminary observations suggest that while males tend to rear away from the walls of a testing container, females tend to rear while placing their forepaws against the vertical surface of the enclosure. Following the method devised by Clarke & Williams (1994) to determine where an animal is placing its weight on its paws, it was found that when rearing, males place most of their weight on the posterior part of the hindpaw. In contrast, females appear to maintain most of their weight on the anterior part of the hindpaw (Field & Pellis, unpublished observations). This differential weight placement on the hindpaws is likely to be a contributing factor in determining the differences between males and females when rearing. This conclusion has been supported by similar sex differences in another behavioral context.

Sex differences in postural support:

When facing downward on an inclined plane, rats respond to the

resultant downward force by turning around to face upward (Crozier & Pincus, 1926). The eliciting stimulus for this response appears to be the pressure exerted on the limbs, which brace against the incline by pushing backwards (Morrissey, Pellis, Pellis & Teitelbaum, 1989). Preliminary observations have shown that females turn at a lower angle than do males (Field, Whishaw & Pellis, in preparation). This is consistent with the hypothesis that females, by differentially placing their body weight on the anterior portions of their paws, are more likely to overbalance in response to the downward force. An alternative explanation, however, is that females may have a lower threshold to initiate a locomotor response to the incline of the board. That is, the difference may be locomotor, not postural. To test this alternative possibility, another approach was used.

Rats that are made cataleptic by the blockade or depletion of ascending dopamine systems no longer initiate movement (Mason, 1984). However, these rats have intact postural support reflexes and are able to maintain and regain a stable equilibrium (Teitelbaum, Schallert, DeRyck, Whishaw & Golani, 1980). Therefore, when pushed, they will brace against the applied force (Schallert, DeRyck, Whishaw, Ramirez & Teitelbaum, 1979; Pellis, Chen & Teitelbaum, 1985). Once stability has been regained, the rats resume an immobile state. When placed on a sloping board, rats treated with a

cataleptogenic agent such as haloperidol will initially brace against the downward force. However, when the angle of the board is increased and the downward force becomes greater, the rats begin to slip and subsequently leap forward (Morrissey, Pellis, Pellis & Teitelbaum, 1989); yet upon landing, they will once again resume an immobile state. Therefore, cataleptic postural mechanisms can be studied in isolation from movement (Teitelbaum, 1982).

Female rats treated with 5 mg/kg of haloperidol jumped off a sloping board at a shallower angle than did males. Frame-by-frame inspection of these jumps revealed that the females, even when bracing, continued to place more of their weight on the anterior portion of their paws. This resulted in the females sliding downward on the inclined board sooner than did the males (Field, Whishaw & Pellis, in preparation). Therefore, this experiment shows that when posture is tested independently from locomotion, females differ posturally from males in their relative distribution of body weight.

This suggests that the sex differences present in the composition of movements during various experimental paradigms arise from a combination of differences in both the anterior-posterior coordination of the body and in the postural support mechanisms. How sex differences in these two factors interact will likely depend on the task performed, and will require detailed analyses of movements by males and females in a variety of

behavioral tasks. However, two major questions arise from these motoric differences between males and females: How do these sex differences in motor organization develop, and why are they there?

Sex differences and the role of peripheral anatomy:

Sex differences in movement and posture may arise from peripheral differences in skeleto-muscular morphology, especially of the pelvic area, given the functional requirements of gestation and parturition of female mammals. Sex differences in the composition of the pelvis have been reported for humans (Coleman, 1969), rats (Bernstein & Crelin, 1967), mice (Shimizu & Awata, 1984) and rabbits (Lowrance, 1968). While it is obvious that differences in peripheral anatomy are likely to be involved in differential patterns of movement, there are several reasons to believe that this does not explain all the differences in movement described in this thesis.

Preliminary observations have shown that the differences in lateral movements between male and female rats are similar to the sex differences present in mice (Field, Pellis & Whishaw, work in progress), hamsters and domestic cats (Field & Pellis, unpublished observations). Even though male and female rats are more similar to each other in body morphology than are

rats to hamsters, in terms of the organization of lateral movements, male rats are more like male hamsters than like female rats. Furthermore, sex differences in movement patterns of rats are present in infancy (Field, Pellis & Pellis, work in progress; Field, Martens, Pellis & Pellis, work in progress), and thus before the onset of changes in body form (Bernstein & Crelin, 1967). That is, the differences in movement appear when physical differences in the morphology of the bony pelvis are minimal.

Some human pathologies also suggest that movement differences are not solely due to sex differences in body morphology. For example, it has been suggested that girls with congenital adrenal hyperplasia (CAH), who are prenatally androgenized, appear to exhibit more masculine behavior (Collaer & Hines, 1995). Indeed, based on a questionnaire study of afflicted subjects, their unaffected sisters and their respective mothers, Dittman (1992) reported that the CAH variant with the most strongly masculinized body morphology (i.e., the simple-virilizing type) was reported to be the least male-like in movement, whereas the variant that was reported to be the most female-like in body morphology (i.e., the salt-wasting type) was the most masculine in movement. Also consistent with these data are a number of experimental findings.

In males, it appears that the masculinization of the central nervous

system is due to the conversion of testosterone to estrogen within the central nervous system (Toran-Allerand, 1984). In contrast, the masculinization of the peripheral skeletal muscles, (Bardin & Catterall, 1981) and of the motoneuron nuclei that innervate the muscles controlling penile reflexes are due to the direct effects of testosterone (Fishman & Breedlove, 1988; Breedlove, 1992). Vega Matuszyk & Larsson (1995) have shown that treatment of male rats prenatally with an antiandrogen did not significantly alter their sexual behavior, when injected with testosterone as adults, even though anatomically they had a poorly developed penis and a blind-ending vagina. In contrast, males exposed to an antiestrogen prenatally showed a decrease in the level of female-oriented behaviors and an increase in the likelihood of exhibiting feminine sexual behavior even though anatomically they appeared to be normal. These results demonstrate that even with incomplete development of male genitalia, male sexual behavior is still present. This suggests that the behavior is not solely due to peripheral anatomical development. These findings support the idea that sex differences in movement and behavior in the rat are not solely due to differences in skeleto-muscular morphology, but rather, are likely due to the masculinization of the central nervous system.

Again, given that many of the movement differences emerge before

the differences in skeletal anatomy, it is unlikely that this is an adequate explanation for sex differences in the organization of movement. In fact, it has been shown that neural sex differences may precede peripheral anatomical ones. Kelley & Dennison (1990) have shown that a sex difference exists in the number of motoneurons that innervate the larynx of male clawed frogs (*Xenopus laevis*) prior to the development of sex differences within the larynx. Indeed, structural differences in the development of males and females may occur prior to hormonal exposure. Recent findings have demonstrated that XY embryos grow faster than XX embryos prior to the differentiation of the gonads. This has been demonstrated in mice, rats, cattle and humans (Mittwoch, 1993). It has also been suggested that differences in neuron structure are present in male and female rats prior to the presence of gonadal hormones (Reisert & Pilgrim, 1991). In vitro sex differences have also been found in mesencephalic dopaminergic neurons, (Engele, Pilgrim & Reisert, 1989) their projections (Ovtscharoff, Eusterschulte, Zienecker, Reisert & Pilgrim, 1992) and in hypothalamic prolactin cells (Beyer, Kolbinger, Froehlich, Pilgrim & Reisert, 1992). Therefore, as Reisert & Pilgrim (1991) have suggested, small, neurally based differences between males and females may be genetically determined and these differences may be further exaggerated by exposure to gonadal hormones.

An alternative possibility, however, is that differences in peripheral anatomy generate neural differences (Balaban, 1994). This process has been described for the differential size of muscles and innervating motoneuron nuclei of the bulbocavernosus (BC) and levator ani (LA) muscles that control penile reflexes, which in females atrophy shortly after birth (Cihak, Gutmann & Hanzlikova, 1970). This difference is determined by the effects of testosterone directly on the muscles (BC/LA) to prevent their atrophy; this in turn spares the motoneurons innervating them (Breedlove, 1992). Therefore, for some systems, peripheral differences may influence the development of neural differences. In contrast, for other systems, neural differences may influence the development of peripheral differences. The challenge for future research is to identify how these processes emerge and interact to produce the differences in movement that are generated by sexually dimorphic behavioral phenotypes.

Sex differences in movement and the role of gonadal hormones:

It has so far been shown that the differences between males and females during forward locomotion, spontaneous lateral turns, evasive movements during play and dodging to protect a food item, have patterns of

movement that are modifiable by androgens immediately after birth (Pellis, Field, & Pellis, 1995; Pellis, Pellis, & Field, 1995; Field, Whishaw, & Pellis, 1995). Males can be made female-like by depriving them of postnatal gonadal hormones, and females can be made male-like when such hormones are added. This suggests that gonadal hormones have an organizational role in the development of sex differences in movement patterns and that these differences are partly independent of differences in peripheral anatomy.

Jost (1960) showed that the testes are necessary to produce the external genitalia typical of genetic males. In contrast, the ovaries are not needed to produce the female-typical external genitalia. In the absence of testicular hormones, the genetic male develops into the female phenotype (Voutilainen, 1992). Thus, the presence of the testes and their hormones are necessary for the development of the male form and in their absence males would not differentiate from females. Subsequent work has shown that male rats have significantly higher mean testosterone levels from embryonic day 18 to postnatal day 5 (Wiesz & Ward, 1980). From the early work by Jost (1960) on the development of the external genitalia, a model for the differentiation of the central nervous system has been established. MacLusky & Naftolin, (1981) have stated this model in the following way:

“The intrinsic pattern of CNS development is assumed to

be organized along lines that are appropriate for the homogametic sex. In the heterogametic sex, differentiation away from this pattern occurs as a result of hormones produced by the gonads. Thus, in mammals the intrinsic pattern is female, with differentiation toward masculine patterns of gonadotropin secretion and behavior occurring in the male as a result of exposure to testicular hormones during development." (pp. 1294)

Since this early work, a number of studies using different species have shown that exposure to gonadal hormones perinatally affects the subsequent development of both behavioral (Beatty, 1992; Ward, 1992) and neuroanatomical (MacLusky & Naftolin, 1981; Gorski, 1985) sex differences, thus supporting the idea that gonadal hormones have an organizing effect early in development. Furthermore, studies have shown that movement organization can be influenced by gonadal hormones (Becker, Snyder, Miller, Westgate, & Jenuwine, 1987; Di Paolo, 1994; Hampson & Kimura, 1988, Hampson, 1990; Van Hartesveldt & Joyce, 1986; see Chapter 4). Therefore, it is likely that at least some of the differences in movement composition by males and females are due to differences in neural wiring, and that these neural differences are influenced by gonadal hormones.

Possible reasons for the existence of sex differences in movement:

As pointed out by David Buss (1994):

“Men and women have evolved powerful desires for particular characteristics in a mate. These desires are not arbitrary, but are highly patterned and universal. The patterns correspond closely to the specific adaptive problems that men and women have faced during the course of human evolutionary history.” (pp. 249)

That is, sex differences should be looked for in areas where males and females have had to adapt to, and solve, different problems. The question is, then, what are the different adaptive problems that ancestral male and female mammals have had to face that could lead to differences in the organization of movement? There are three behavioral possibilities that will be considered in this section - sex, aggression and internal gestation.

During mating and copulation males and females have to deal with different adaptive problems. Female rats, like female mammals generally, have a higher degree of investment in the development and maturation of the young and thus are more selective with whom they mate (Trivers, 1985,

Buss, 1994). Work by McClintock (1984), has shown that when tested in a large arena with a number of potential mates, female rats will orchestrate their movements in such a way as to differentially initiate contact and copulations with specific males. Male rats during the initial stages of copulation use a snout-to-nape contact with the female to orient themselves in order to mount. Once the nape is contacted, and the forepaws have grasped the female's upper back behind the shoulders, the male will then shift his hindquarters in line with the female's pelvis and attempt intromission. In the case of the male's failure to orient successfully to the female, the female will swerve laterally, maintaining her rump orientation to the male (Whishaw & Kolb, 1985). In this context, the movements by the male and the female appear similar to those that are seen during the dodging paradigm. The movements in the male however, while similar, are not identical. During sex, the male maintains a fixation of the snout to the nape of the female and thus pivots around the snout in contrast to the midbody pivot that is present during dodging. Furthermore, studies on the sexual behavior of other rodent species suggest that pivoting around either an anterior or midbody axis is not necessary for copulations to occur.

If receptive, a female hamster will adopt the lordosis posture in the presence of a male (Beach, 1976), and will pivot around her pelvis in order to

maintain the orientation of her pelvis towards the male (Pellis & Pellis, 1988). Male hamsters, unlike male rats, do not pivot around a snout-to-nape contact (S. Pellis, personal communication). Male mice, after smelling the anogenital area of the female, will mount the female by leaping on her back (Pellis, Pellis, Manning & Dewsbury, 1991). Field observations of feral rats also suggest that while a pivot around the anterior of the body may be present in male rats during laboratory tests, it may not be present in the wild. Whishaw & Whishaw (1996) report that males, usually in a large group, chase a receptive female and will mount her from the rear in an attempt to gain intromission. Therefore, while males of the species listed above appear to use a midbody pivot during dodging or spontaneous turning, this maneuver appears to be rare or absent during copulatory behavior.

A second possibility is that male and female rats have faced different selective pressures due to differences in their involvement in aggressive encounters. As already stated, female rats appear to be selective in their choice of a mate. Such selectivity by the female favors high levels of male-male competition for access to females or for the acquisition and retention of territories that then attract females (Trivers, 1985). In rats, the dominant male engages in most of the aggression directed towards intruding males and other colony males (Blanchard & Blanchard, 1977). In contrast, female

aggression is usually for the defense of the nest and pups (Blanchard & Blanchard, 1977), but is otherwise rare. Lateral combat movements involving midbody pivoting are common during male-male aggression (Blanchard, Blanchard, Takahashi & Kelly, 1977), but rare in females (Parmigiani, Palanza, Mainardi & Mainardi, 1990). A movement organization suited to facilitating such lateral maneuvers may be advantageous to male rats. The comparative evidence however, again suggests that this is not the sole explanation. In hamsters both males and females defend territories (Murphy, 1985) with females being more aggressive (Payne & Swanson, 1970). During aggressive encounters, both males and females use lateral combat movements involving midbody pivoting (Pellis & Pellis, 1988). If the differences in the movement organization of males and females were based solely on the tactics used during aggression one would predict then that female hamsters should be male-like in their motor organization. However, preliminary investigations show that while female hamsters use a midbody pivot during aggression that is similar to that performed by males, when they turn spontaneously in an open field they do so in a female-typical manner (Field & Pellis, unpublished observations). Therefore, while female hamsters may use a male-typical behavior pattern during aggression, this pattern of movement does not extend to other behavioral contexts as it does in males. This suggests

that the female-typical pattern of movement may exist primarily as an adaptive behavioral organization for some activity specific to females.

Sex differences in peripheral pelvic anatomy (Coleman, 1969; Crelin & Bernstein, 1967) have evolved due to the demands of the birthing process. It is possible then that there are differences in the organization of movement and associated neural structures, that are designed to deal with the demands of gestation and nursing from the teats located on the ventral surface (L. Smith, personal communication, 1995). A bias towards forward movement may deal with the extra weight and abdominal girth of pregnancy by providing clearance of the abdomen from the ground and by inducing a posture that facilitates quicker initiation of forward movement and hence escape from potential threats. If true, this would suggest that a sex difference in motor organization should be widespread in mammals.

Marsupials give birth to very immature young, which make their way to the abdominal area where they attach themselves to a teat and then complete their development (Renfree, 1994). Whether gestation is completed internally, as in placental mammals, or externally as in marsupials, both these types of mammals carry their developing young ventrally in the abdomen. The problem this poses is strikingly illustrated by the short tailed

gray opossum (*Monodelphis domestica*) carrying her young (Fig. 3); note the high arch of the back, and the forward and upward push of the hindpaws. Preliminary observations of walking and nursing by gravid female rats show similar postural adjustments (Field, unpublished observations)

Preliminary observations of the spontaneous lateral turns by neonatal male and female marsupial cats (*Dasyurus hallucatus*) from Australia, indicate that the males move in a male-typical manner and the females move in a female-typical manner (C. Kingham, personal communication, 1995). This supports the possibility that these sex-typical postural and movement biases are intrinsic to the motor system. Given that marsupials and placental mammals diverged approximately 100 million years ago (Clemens, 1977), these observations suggest that sex differences in movement organization may be a widespread mammalian characteristic. Whether this difference in movement organization extends to other vertebrates such as birds and reptiles has yet to be determined.

Given that gestation and lactation are universal in female mammals, I would suggest that the demands of these behaviors act as constraints on the evolution of the female form and corresponding motor organization. Therefore, this suggests that males and females have conserved sex differences in movement patterns that are best suited to solve a variety of

Figure 3: A female *Monodelphis domestica* carrying an 18-day old litter. Note the typical female posture of the mother which elevates the pups from the underlying surface and reduces the likelihood of trauma as a consequence of activity by the dam. (Taken from VandeBerg, 1990)

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functional problems such as those present in sex, play, aggression, dodging and maternal behaviors.

Conclusion:

Studies on non-reproductive sex differences have indicated that “(t)hese differences are typically small in magnitude, and tend to vary with the genotype and prior behavioral history of the individual” (Beatty, 1992, p. 115). However, most studies have not investigated the organization of the movements performed. As shown here, even behavior patterns that appear to be the same in both sexes can differ markedly in motoric organization. This suggests that the measurement of the frequency of occurrence of a behavior at its endpoint may not adequately describe the behavioral differences between males and females. To understand how sex differences develop and their relationship to anatomical differences, one needs also to consider the structure of a particular behavior and whether this structure is sexually dimorphic. In this way, one may gain a greater understanding of the relationship between anatomy and behavior. Furthermore, the differences in the organization of movement between males and females are not task-specific, but rather, are sex-typical differences in the composition of similar

movements that occur in such diverse contexts as play (Pellis, Pellis, & McKenna, 1994; Pellis & Pellis, 1990), aggression (Blanchard, Blanchard, Takahashi, & Kelly, 1977; Pellis & Pellis, 1987), sex (Whishaw & Kolb, 1985) and spontaneous turning (Eilam & Golani, 1988).

That similar non-reproductive behavior patterns differ in form, and not only in the likelihood of occurrence, suggest there are some fundamental differences in the environmental milieu faced by each sex. What these functional contingencies may be is uncertain, but the existence of robust sex differences in the organization of movement provides an opportunity for further analysis. Clues may be sought from the development of these motoric differences and the comparative analysis and distribution of such differences in a diversity of mammals and other vertebrates that vary in body morphology and ecological niche. In conjunction with this, the possible role of hormones, neural maturation and behavioral experience during development need to be addressed in future research in order to determine both how sex differences in movement composition arise and the reason for their presence.

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