

**PLAYING WITH PLAY: MOVEMENT AND EXPERIENCE
IN THE DEVELOPMENT OF PLAY FIGHTING IN RATS**

AFRA FOROUD

B.Sc., University of Lethbridge 1998

E.M.A., Université du Québec à Montréal 1998

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ABSTRACT

Playing with Play: Movement and experience in the development of play fighting in rats.

Juvenile rats are more gentle in the way they play fight than are adult rats. I used Laban Movement Analysis (LMA), a form of movement notation used in the theatre arts, to identify and characterize the movements that underlie this age-related difference in 'roughness'. To standardize the behavioural context for comparison, the rats were compared when in the 'pinning' configuration. During a 'pin', the attacker stands over the supine defender.

In the first experiment, male and female rats, from the juvenile phase to early adulthood were videotaped and analyzed using LMA. The results show that with age, rats become more 'forceful' in the way they move. In part, this change in 'forcefulness' seems to be related to the degree of control an individual exercises, over its own body, and that of its partner. I have identified a reliable and objective behavioural marker for such 'control'. This marker, which I call anchoring, can be scored without prior knowledge of LMA. When anchored, the attacker stands with its hind feet on the ground and its fore feet on the supine defender, whereas when unanchored, the attacker stands on the defender with all four feet. With increasing age, the proportion of occasions with the attacker being anchored increases.

One possibility is that younger rats are motorically less competent to gain and maintain an anchored posture. Therefore, in a second experiment, playful pins were analyzed from

around the time of weaning, when play fighting first begins, and onwards. The infant rats were just as able to anchor during pins as were postpubertal rats, and so motoric immaturity cannot account for the reduced levels of anchoring in juveniles. Additional experiments were conducted in an attempt understand what modulates this developmental modulation in anchoring.

Thus, in the third main experiment of this study, rats were reared in isolation from weaning and tested socially once at 30, 60 and 90 days. The results show that the age-related changes in anchoring is not dependent on social experience. Finally, in the fourth experiment, the cortex was removed in neonatal rats, and their play was examined from the juvenile period onwards. Anchoring in decorticates does not show the developmental modulation present in intact rats, rather, anchoring remains at the juvenile typical level at all ages. These data indicate that the developmental changes in anchoring are regulated by cortical mechanisms.

The findings from this thesis suggest that juveniles have an age-modulated change in how strongly the rats control their own movements and those of their partners during play fighting. That is, juveniles exhibit reduced control just when they are the most playful. This reduced control may increase the range and variability of experiences gained during play fighting, and so may have evolved to maximize the benefits to be gained by engaging in play at the juvenile phase of the life cycle.

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In rhythmic waves regularly spreading, the ether trembles, the small, most minute particles of matter tremble. If there were no movement at all, all things would be lying dead in absolute rigidity and complete apathy. No ray of light, no sound would bring messages from one thing to another.

... Movement not only speaks through an object; a living organism owes its final form to it; movement leads to growth and structure ...

That movement speaks that is about to break out of its form: The weighty power of a rock with its visible potential for impact speaks of the tremendous impetus with which it might plunge into the valley as an avalanche. The grace of a plant speaks of the readiness to move which drives a flower out of its stem from which fruit and new seed will sprout ... Animal movement speaks of the fine adaptations with which a particular species has immersed itself into its surroundings to fit increasingly finer, more differentially into the workings of nature.

Rudolf Laban

(Bartenieff & Lewis, 1980, p. 1)

CHAPTER ONE

GENERAL INTRODUCTION

WHAT IS PLAY?

Early observations

One of the first formal accounts of play behaviour is made by Karl Groos (1898). His descriptions suggest play has an “as if” quality. It is a behaviour that is full of “conscious illusion and self deception” (Fagen, 1981, p. 4). In comparing animal play with the arts, Groos gives examples of dancers dashing like deer across a stage, and primates playing with objects in the same way sculptors use their tools to create. At the time of Groos’s observations, many hypotheses of play had appeared in the literature. Preyer (1893), Blow (1894), and Compayre (1902) found play to be important in the learning and development of infants and children. Later, Piaget (1962) and Montessori (1964) applied these theories into schools, using play as a vessel for learning whereby play was assigned the purpose of achieving a learning goal.

Although people have found creative uses for play, researchers have had difficulty with defining play accurately and objectively; however, most agree that play “seems to lack an immediate function or purpose” (Bekoff & Byers, 1981).

The problem of defining play

Because of its elusive and apparently non-functional qualities, the study of animal play is both intriguing and frustrating. As noted by E.O. Wilson, “no behavioral concept has proved more ill-defined, elusive, controversial and even unfashionable” (1975, p.164). The problem,

however, remains. Animals play and there is no obvious biological function for their behaviour. What causes play and what functions does it serve?

Casual observation of play might suggest that play is integrated with the many other behaviours of an animal. Animals play during development, in various social settings, with objects (including prey) in their environment, solitarily, and during other seemingly functional behaviours.

Since play is observed during the course of many other functional behaviours, playfulness can be viewed as a continuum with other non-play behaviours (e.g. Hall, 1998; Pellis, O'Brien, Pellis, Teitelbaum, Wolgin, & Kennedy, 1988). We can think of examples of this in our own lives. Musicians will 'fool around' vocally or with their instruments for fun. This activity is based on what they can do seriously. I remember absent-mindedly walking in a mall as a small girl when I was suddenly in the path of a line of professional football players. My shock must have amused them and they began to laugh, they used a half-full shopping bag as a football and acted as though I was too big and tough to pass through. This playful acting continued until I was laughing whole-heartedly. They were 'playing' with the skills they used in a serious game of football, but this time there was no direct function for the activity.

If playfulness forms a continuum with other non-play behaviours, it could help to explain how play can appear during these other behaviours. For example, a child will play with its food during feeding time. In this case, play may be interpreted as an expression of joy. The benefit of this expression may be that it allows for experimentation. As an animal plays with a playmate, it experiments with a variety of interactions. This process will allow it to

discover and 'play' within the boundaries and possibilities that exist within the context. In turn, its awareness of itself and its relation with its playmate will increase. It is not learning new behaviours, it is facilitating the development of current behaviours.

The contemporary definition

Our understanding of play as a whole is incomplete. Defining play as one would define eating is nearly impossible because there are many variables that pose as exceptions within any concrete definition. Various researchers have provided theories for the causes and functions of play. While something can be learned from such theories, none encompass all forms of play. This is because these causes and functions may differ for different species, types of play, and stages of development. How can we progress to understand play if there is no universal definition?

Bekoff and Byers (1981) offer an all-encompassing definition of play, that it is a motor activity that appears to be purposeless, but is nevertheless borrowed and modified from various behavioural systems (i.e.: sex, aggression, and predation). Unfortunately, arm flapping in autistic children and other stereotypes which may not be playful also fit this profile. Burghardt (1999, 2001) suggests that instead of being purposeless, play is 'not completely functional'. He developed five criteria for identifying play:

1. Play "does not appear completely adaptive in the context in which it is expressed"
2. Play "appears to be spontaneous, voluntary, intentional, pleasurable, rewarding."
3. Play "differs from the 'serious' performance of ethotypic behavior." For example, a child may modify his or her walk home from school (a functional behaviour) to

instead skip, turn, walk backwards, kick the legs up too high, sprint and stop suddenly.

4. Play is “repeatedly observed and not rigidly stereotyped during at least a portion of the animal’s ontogeny”; and
5. Play is noticed when animals are in a low stress “relaxed field” environment.

In summation, Burghardt wrote: “Play is repeated incompletely functional behaviour differing from more functional versions structurally, contextually, or ontogenetically, and occurring voluntarily when the animal is in a relaxed or unstressed setting” (Burghardt, 2001, p. 332).

Although this definition appears to reflect an accurate and consistent description of play, Burghardt himself says that it does not attempt to explain the origin nor evolution of play. In order to do this, the underlying developmental, evolutionary, and neuro-behavioural features of play need to be identified. These features may be identified by making cross-species comparisons.

Often, even closely related species demonstrate different levels of complexity of play (Pellis & Iwaniuk, 1999a; Pellis & Pellis, 1998). Such changes in complexity can be better understood by studying questions related to the content and functions of specific types of play in particular species and at particular ages. In doing so, certain developmental, evolutionary, and neuro-behavioural aspects of play can be pieced together. The problem is that play is not a behaviour one can accurately quantify with simple measures. One objective of this thesis is to offer new measures that will describe sensitive details of play that have not yet been observed.

EVOLUTION OF PLAY

By studying play in a variety of species, we can piece together the possible evolutionary history of play. Object, locomotor and social play are the three major forms of animal play (Burghardt, 1998). Play fighting is the most complex and commonly observed form of social play (Pellis & Pellis, 1998a) and can be broken down into three major categories: 1. chasing, 2. dodging, and 3. wrestling and tumbling. Chasing, when one animal runs after another, is the most complex form of social play in tree shrews (Sorenson, 1970). Once contact is made, or there is a distraction, the chase is over. During play, mice, which have more complex forms of social play than do tree shrews, also chase one another. However, they add another level to their game. Just before potential contact, the chased mouse evades the chaser by dodging (Pellis & Pasztor, 1999).

Dodging, a series of movements performed by an animal to evade another, requires a more complex series of motor skills than chasing, and it provides a stimulus for more chasing. Rats engage in all the play behaviours found in tree shrews and mice, but they further increase the complexity of social play by adding wrestling and tumbling, where once contact is finally made, the chased rat will roll onto its back (Pellis & Pellis, 1987). Tumbling is when animals roll over each other while rolling together on the ground. This is a more complex physical action than dodging and chasing. Rolling over also creates a situation for more playful activity and this is more complex, both physically and socially, than what occurs in the play of mice or tree shrews. As a working model, these different degrees of complexity illustrate how changes in play could have risen, on an evolutionary scale; chasing would come before dodging, and dodging would come before tumbling.

Primary and secondary processes

To answer how play evolved, it is critical to distinguish between the primary and secondary processes that give rise to play (Burghardt, 1999). Primary processes are the organismal and environmental features that make play possible. For example, endothermic, large-brained, large-bodied, omnivores are more likely to engage in play than are ectothermic, small-brained, small-bodied herbivores. Secondary processes are the organismal and environmental features that build on the play made possible by the primary processes to modify that play for some particular function (Burghardt, 2001). For example, in some species of primates, social play is retained into adulthood and is used for various forms of social testing (Pellis & Iwaniuk, 1999b, 2000).

The evolutionary role of play behaviour is unclear. Play could be an adaptation to a specific biological problem, that is, play came into existence to solve some particular problem (Buss, 1999). Alternatively, play could be a byproduct of another adaptation. That is, play did not emerge to solve some adaptive problem; rather, play is coupled with behaviours that serve functional adaptations (Buss, 1999). For example, as animals pass through the juvenile phase and enter the adult phase, there is a gradual development of adult-typical behavioural patterns, as infant-typical behavioural patterns gradually decrease (Coppinger & Smith, 1989). This slow change is often expressed by incomplete behavioural patterns, and Coppinger & Smith, (1989) suggest that these behaviours are play-like. These play-like behaviours can then be co-opted for novel functions.

Pellis suggests that certain behaviours must be added or modified to ensure that these outcomes eventuate. For example, the play fighting of muroid rodents involves the use of functional species-typical precopulatory behaviour patterns (Pellis, 1988, 1993), but the

complexity of such play varies markedly across species (Pellis & Iwaniuk, 1999a; Pellis & Pellis, 1998a).

Some species have a form of play fighting that differs little from the adults' precopulatory behaviour, whereas others play in a way that is not readily mapped onto the adult form even though the same behaviour patterns are involved. Interestingly, some of those species with the most modified forms of play fighting have been shown to have subsequent deficits if deprived of such play as juveniles (Einon, Humphreys, Chivers, Field & Naylor, 1981). The hypothesis here is that starting with a precocial expression of precopulatory behaviour, some species have secondarily evolved new functions for such behaviour and this has involved modification to the behavioural content of the precocial activity (Pellis, 1993). Thus, play emerges as a byproduct which is secondarily modified.

The precocial theory does not describe what functions juvenile or adult play may serve. However, if this theory is correct, then juvenile play behaviour must develop into another behaviour with a separate function in adults. The following chapters support the precocial theory by demonstrating how juvenile and adult play are structurally and functionally different even though they are superficially similar. In addition, this thesis contributes to the characterization of the functions which juvenile play and adult play may serve.

It is important to understand that what may have caused play to emerge historically may not necessarily account for its current function. Origin does not equal current function (Gee, 2000). For this reason, it is difficult to tell how play behaviours have influenced, in an evolutionary sense, other aspects of an organism, especially more abstract ones such as awareness, visualization and mental function. To help get a grasp on play in general, one can

begin by focusing on a specific component of play. Concepts developed within one aspect of play can then be applied towards understanding play behaviour as a whole.

As noted above, play fighting is the most common form of play reported (Pellis & Pellis, 1998a), with chasing, dodging and wrestling being its three major components. Mammals have been found to play fight during infancy and even late into adulthood, but the peak play period in most mammals is found during their juvenile phase (Fagen, 1981). This thesis focuses on one aspect of the wrestling and tumbling in the play fighting of rats.

THEORIES OF THE FUNCTIONS OF PLAY IN JUVENILES

Irrespective of the origins of play, functional theories can be characterized into three major categories: 1. it is practice for functional behaviours, 2. it benefits socialization, and 3. it benefits cognition. Two modern variants of the cognitive theory are 1. that it increases knowledge of self (Thompson, 1998), and 2. that it increases knowledge of the other (Biben, 1998).

Practice theory

One of the oldest and most widely known theories for play fighting is the practice theory, where play fighting is considered practice for serious combat and other life skills such as predation (Groos, 1898). There is little, if any, evidence in support of this hypothesis (Martin & Caro, 1985). Furthermore, there is growing evidence that practicing the performance of particular behaviour patterns is unlikely to be the most important function of play (Aldis, 1975; Byers, 1998; Humphreys & Smith, 1987; Pellis & Pellis, 1998b). In particular, it has been found that when animals play fight, they organize their bodies differently and do not use the same motor patterns as when they are fighting seriously (Pellis & Pellis, 1998b).

Studies have shown that practicing a skill requires the subject to practice the movements without variation; in other words, the mover must move in the same way as it would in a serious context (Stamp, 1995). One of the key aspects of play is that the movement sequence is performed with variations and is a non-functional adaptation of ethotypic behaviours, such as serious combat. Therefore, it is unlikely that play fighting is useful for the practice of behaviour patterns (Biben, 1998; Pellis & Pellis, 1998b).

A second problem with the practice theory is that play in juveniles is often viewed as practice for non-play activities in adults. For example, when young animals play fight, they are thought to be training for the serious fights they will encounter in adulthood. If this is so, then why do some animals continue to play fight during adulthood (Pellis & Iwaniuk, 2000; Burghardt, 1998)?

Socialization Theories

Since most mammalian play is social play, especially play fighting, the socialization theory suggests that animals play in order to gain social skills. However, such a role for play in socialization cannot be critical. For example, in some populations of squirrel monkeys, food is scarce, and the juveniles spend most of their time foraging and so do not play. Yet these populations seem to have comparable degrees of social organization and reproductive success as in other squirrel monkey populations where play is prevalent (Baldwin & Baldwin, 1974).

Cognitive Theories

Cognitive theories for play consider how play may provide animals with information about one's self and one's social and physical environment. In other words, play may be the

process by which animals gain knowledge of their world, and how they exist within it (Allen, & Bekoff, 1997).

KNOWLEDGE OF SELF HYPOTHESIS

The knowledge of self hypothesis suggests that play provides the animal with immediate feedback on its physical capabilities and limitations relative to that of its peers (Thompson, 1998). Animals use play to test their motor and cognitive skills. Furthermore, this increase of self-awareness can prepare the animal on how to handle similar future situations.

INFORMATION GATHERING HYPOTHESIS

This hypothesis suggests that play fighting may function as a means of gathering social and emotional information about others (Biben, 1998). In this way, during play, the animal can test its playmate's capabilities. This information is useful for responding to another's emotional state. For example, in encounters between unfamiliar adult male rats, the context of play fighting differs with the social status of the opponent, suggesting that such play is used to evaluate and test the stranger's capacity to gain dominance (Smith, Fantella, & Pellis, 1999). Behavioural testing appears to occur in the play fighting of sub-adult and adult animals in a variety of species of mammals (Pellis & Iwaniuk, 1999b, 2000; Pellis & Pellis, 1996).

The cognitive theories described above hypothesize an immediate function of play for juveniles. However, since the adults of some species play, it is possible that the enhanced cognitive skills developed during the juvenile phase may also help to prepare the animal for adulthood. For example, play may allow the developing animal to monitor its own and that of its peers' state of maturation, and to use this knowledge to modify its experiences and development. Studying the functions of play in adulthood may offer useful insight into the

functional use of play in the juvenile phase which can later be modified to serve various adult needs (Pellis, 2002b).

THE STUDY OF PLAY

The problem with play

A major difficulty in studying play has to do with the description of the richness and fluidity of the behaviour performed. Hypotheses for the causes and functions of play have arisen from what people 'believe' animals are doing when playing (Pellis & Pellis, 1998b). The problem lies in objectively and accurately identifying what it is animals do during play. In my view, by describing the process of movement during play, we establish a necessary first step to understanding play behaviour. Once the processes of play are understood, we will have the knowledge to develop theories for the causes and functions of play. Placing description before experimentation and theory has been an enduring strength of the ethological perspective in the study of behaviour (Hinde, 1982). In this thesis, a particular aspect of play fighting in rats is described and analyzed in a novel manner. These new descriptions provide new insights into the causes and functions of play.

Play fighting is the most commonly reported form of social play (Burghardt, 1998; Pellis & Pellis, 1998a). The peak frequency of play fighting occurrence is in the juvenile phase and declines with the onset of puberty (Thor & Holloway, 1984). Such age-related changes in frequency of play fighting can be objectively measured. For example, in the study of play fighting in rats, pinning has been the traditional end-point measure (Panksepp, 1981). A pin is when one animal holds its play partner to the ground (Figure 1). This 'on-top/on-bottom' configuration is strongly correlated with the occurrence of play fighting and has a high inter-observer reliability (Panksepp, 1981; Panksepp & Beatty 1980).

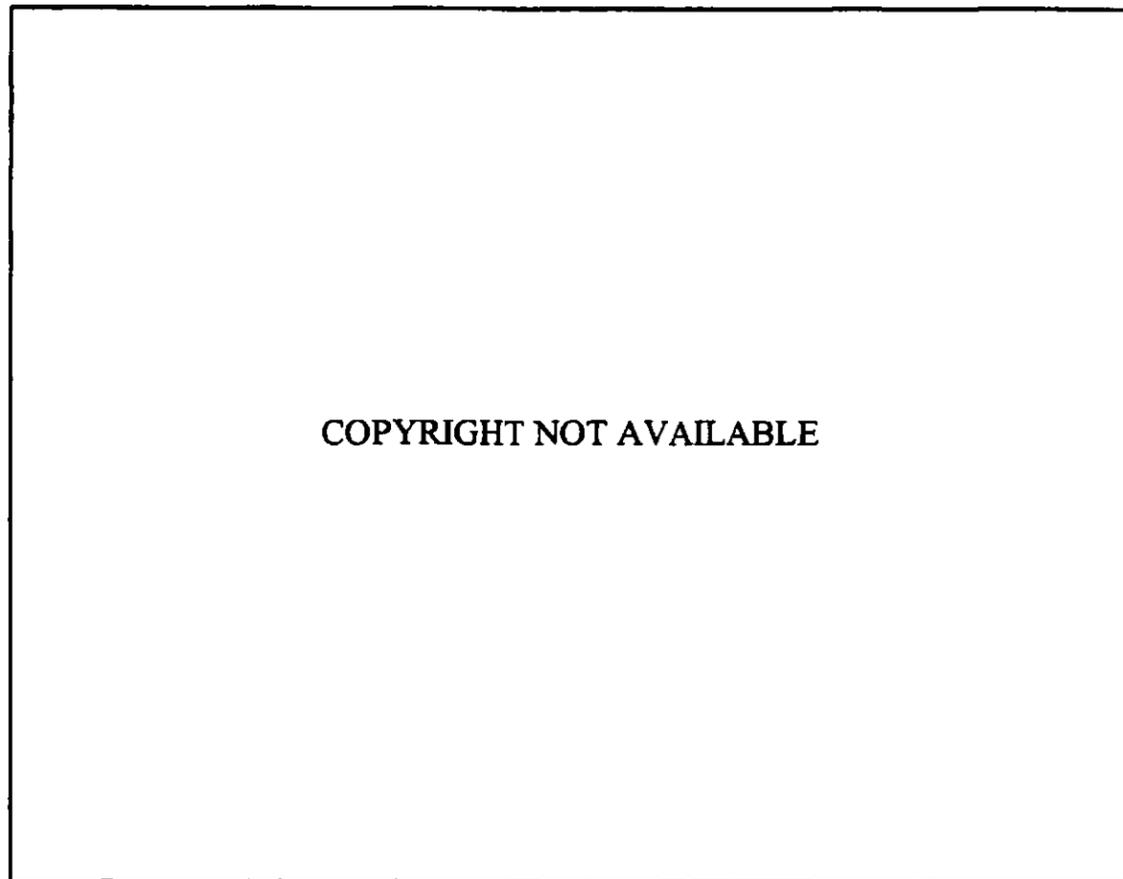


Figure 1. The 'pin' involves one rat standing over its supine partner. Once in a pin, the attacking rat continues to launch attacks at its partner's nape, while the supine rat uses its limbs to block these attacks. Following a successful repulse of the partner's attack, the supine rat may launch its own attack at the partner's nape. (The drawing is from Panksepp, 1998, p. 284).

Such an end-point measure can let the researcher know of changes, in the frequency of play fighting that may take place during development, between different social contexts, and following various experimental procedures. However, there are limitations of using end-point measures.

End-point measures are the outcome, rather than the process of observed behaviour; the process of the behaviour is the series of movements that lead up to the end-point measure. Usually such movements remain undescribed. The absence of such information is important because the components that occur within the behaviour designated as the end-point measure may vary depending on the situation the organism faces. That is, there may be significant differences in how the end-point measure is achieved between and within observed groups. This information is lost when simply recording the result of a given behaviour. Variability of the components within the end-point measure between age groups, species and experimental groups can exist and remain unnoticed. In such cases, researchers may have inadvertently lumped several behavioural processes into one end-point measure and so may not be comparing the same measure between groups. For example, in rats, two different sets of behaviours can lead to the pinning configuration. Play fighting in rats involves attack and defense of the nape, which if contacted, is nuzzled by the snout (Pellis & Pellis, 1987; Siviy & Panksepp, 1987). In response to a nape attack, the recipient may defend itself by rotating around its long axis to a supine position. Alternatively, it may rotate only partially and maintain ground contact with its hind feet, at which point it is pushed over onto its side, and finally onto its back by its partner (Pellis & Pellis, 1987). Thus, in the former, the defender achieves the supine position in one continuous action, whereas in the latter, it is achieved slowly, step-by-step as the partner continues its attack (Pellis & Pellis, 1997). By only

documenting pinning, instead of how the rats get into such a position, the observer loses valuable information by classifying two separate types of behaviours (continuous versus step-by-step rotation) into one (pinning). The problem with relying on end-point measures is further highlighted by an as of yet poorly understood developmental change in play fighting. As the frequency of play fighting wanes with the onset of puberty, the play fighting becomes rougher, especially for males (Biben, 1986; Fagen, 1981). In part, this developmental change in roughness can be accounted for by the different defense tactics used by the age groups (Pellis & Pellis, 1987).

Juvenile rats use more of the continuous rotations described above, called complete rotations, than the step-by-step rotations, which are used more frequently by the adults. Complete rotations do not require that the partner continue to press the attack. In step-by-step rotations, the defending rat resists the actions of its partner. This resistance may even prevent the rat from becoming supine altogether, in which case the rat would only be partially rotated (Pellis & Pellis, 1987). From a partial rotation, the defending rat maintains ground contact with its hindpaws and can push against the attacking rat with its hips, and is thus in a position to launch its own attacks. Such age-related differences in frequency of complete versus partial rotations performed by the defending rat can account for the age-related differences in roughness (Pellis, 2002a). However, this switch in defense tactic does not fully account for the rougher adult-typical play, because even when both juvenile and adult rats perform the same complete rotation tactic, the adults still appear to be rougher. The goals of this thesis were to characterize more fully the difference in roughness between the play fighting present in juveniles and adults, and to identify suitable behavioural markers that can be used to characterize the age-course of such roughness. To achieve these goals, it was necessary to

use alternatives to end-point measures; alternatives which involve techniques that describe the spatio-temporal organization of the movements performed by different parts of the body during behavioural sequences.

Movement analysis

(1) EWMN

Eshkol-Wachman Movement Notation (EWMN) is a form of movement analysis developed by Noa Eshkol and Abraham Wachman (1958). It allows for a detailed description of the mover's limbs in relation to one another, and of the mover's orientation to the surrounding environment, including the ever-changing relationships with other movers. EWMN is designed to score movement in a notated form with such detail that a reader may fully re-enact the sequence without ever having seen it performed. The use of EWMN in the study of animal behaviour has revealed behavioural patterns that have slipped through the cracks of traditional measures (e.g. Eilam & Golani, 1988, 1989; Pellis & Officer, 1987; Whishaw & Pellis, 1990). For example, the age-related differences in complete versus partial rotations described above were first described by EWMN techniques (Pellis & Pellis, 1987). EWMN has proven useful because of the detailed movement score it can provide. Once fully described, valuable aspects of the sequence can then be quantified, tested and analyzed (e.g. Whishaw & Pellis, 1990; Pasztor, Smith, MacDonald, Michener, & Pellis, 2001).

While EWMN can describe the structural differences within an end-point measure, there are qualitative variations within the structure that remain unexamined. For example, two people can grab someone by the shoulders by using the same timing, body limbs, and biomechanics; but one can do it aggressively, and the other can do it romantically. What cues does the

observer use to identify which is aggressive, and which is not? By defining these qualities, researchers can extract out key features of the movement that reflect the *qualitative* components of play.

EWMN has not been successful in identifying a consistent measurable difference which describes the developmental changes in roughness by juvenile and adult rats during play fighting. Thus, there is a need for a descriptive language that reliably focuses on the qualitative differences in behaviour.

Laban Movement Analysis (LMA) focuses on the qualitative aspects which describe *how* a movement is performed. LMA may be an ideal form of analysis and notation to identify the qualitative differences discussed above.

(2) LMA

Rudolf Laban (1879-1958) grew up as the son of an architect in Germany (Figure 2). From an early age, he applied the spatial concepts of architecture to the visual arts and to the study of dance. Laban integrated concepts from everything he studied into his own ideas about the world and, more specifically, into his theories about human movement.

In the 1940's, he established Laban Movement Analysis (LMA), a system of observation and notation for human movement. Laban drew from concepts in biology, physics, and the expressive arts to develop theories on the structure of the human body and the qualities the body accesses to perform the movement. He worked with dancers to explore his

understanding of human movement and developed 'movement scales' and exercises. He was an artist who also studied the humanities and sciences and so was capable of drawing upon their concepts and integrating them into his teachings. His work led to a variety of expressionistic choreographies.

Laban held schools and workshops in outdoor, natural fields. People called on Laban and his expertise to designate factory workers to stations that would suit their individual body structures and 'movement signatures' so that they would be able to work more efficiently and with less injury. He was called on by Hitler to choreograph a dance for the opening ceremonies of the Olympics in 1936. Laban's choreography was found too 'free flowing' and expressive for what Hitler had in mind. Soon after, Laban fled Germany which had banned the expressionistic arts, and established himself in London, England, where he was able to continue his work. This work continues today, long after Laban's death.

LMA is used mostly for recording the great classic ballets and other historically valuable choreographies. Often choreographers today will draw upon Laban's theories to create their own dances and train their performers. LMA is also used in physical therapies. Irmgard Bartenieff, a trained physiotherapist, worked closely with Laban and established a set of movement exercises for the recovery and development of movement called the Bartenieff Fundamentals. She is a recognized pioneer of dance/movement therapy. There are many offshoots of LMA and they are primarily used in the arts and humanities. More recently, Robert Fagen studied various aspects of LMA and began to test their scientific reliability in the study of animal behaviour (Fagen, Conitz, & Kunibe, 2000).

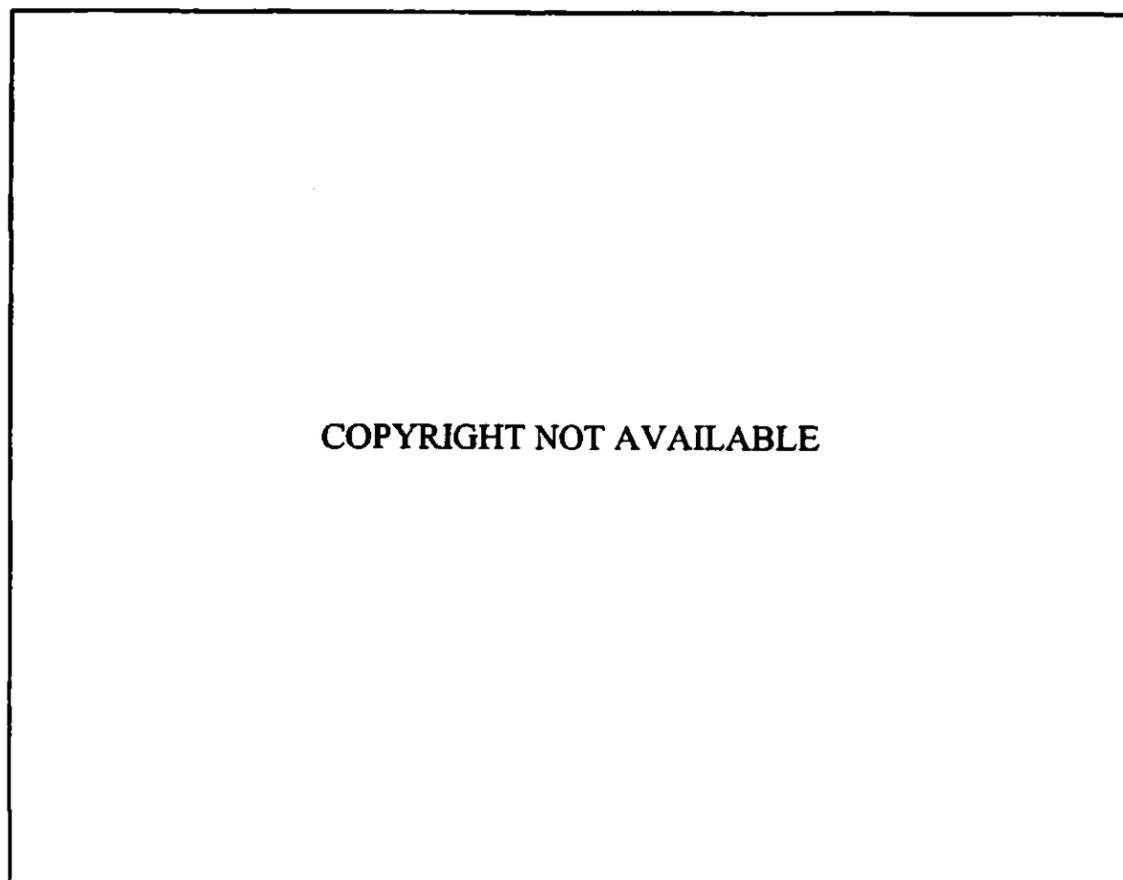


Figure 2. Rudolf von Laban (1879-1958) was known as an artist, scientist and movement educator who "...observed movement process in all aspects of life: from the martial arts to spatial patterns in Sufi rug weaving, factory work tasks, rhythmic patterns in folk dances, crafts and the behaviour of emotionally disturbed people. It was the process itself that compelled his attention, not just the end points or goals of the action, and he, with his colleagues, refined movement observations into an exquisitely precise method of experience, seeing, and recording them so that body movement functional and expressive implications became increasingly apparent." (Barthemieff & Lewis, 1980, p. ix). (The photograph is from Preston-Dunlop, 1989, p. 4).

LMA describes both quantitative and qualitative structures and expressions in human movement (Hutchinson, 1977), with a focal observation on the process of the movement. Descriptions are recorded through notations and have theoretical interpretations.

THE PROBLEM FOR THIS THESIS

The objective of this thesis was to use LMA to describe the pins in juvenile and adult rats to ascertain whether such an analytical approach could reveal the differences in movement that underlie the apparent qualitative differences in roughness between the play of these age-groups. The following chapter uses LMA to describe the qualitative differences in juvenile and adult rat play fighting. These descriptions, in turn, identified an objective difference in movement organization which reflects the qualitative analysis. The difference in movement organization can be easily assessed by a new marker which I call anchoring. Anchoring involves the relationship of an individual's body to that of its partner and to the ground. When anchored, a rat, standing over a supine partner, maintains its hind paws flat on the ground, whereas when unanchored, its hind paws are also on the partner's body. This unanchored position is less stable than the anchored position, as the on-top rat undergoes postural disturbances not only in relation to its own movements, but also to those of its partner.

To establish the developmental pattern of anchoring, I have observed and recorded anchoring in infant (25-29 days), juvenile (30-40 days), pubertal (40-59 days), early post-pubertal (60-79 days), and adult (80-120 days) rats. Details of these experiments and their results are described in Chapters 2 and 3. In brief, the results reveal hitherto, unknown, age-related changes in the content of play fighting.

Once the developmental pattern was established, several experiments were conducted to assess the causes of these developmental changes. Anchoring was measured in rats following altered juvenile experiences, such as the familiarity of the partner and complete social deprivation, and to the removal of the cortex. These experiments are described in Chapters 3 and 4, and suggest that the developmental changes are modulated by cortical mechanisms, and not by social experience.

This thesis not only identifies a new measure for the study of play fighting, it also describes a developmental change in the content of play fighting which to date has not been measurable. Identifying and understanding the regulation of this developmental change has important implications for our understanding of the causes and functions of play fighting, and this is discussed in Chapter 5.

CHAPTER TWO

The development of 'roughness' in the play fighting of rats: A Laban Movement

Analysis perspective.

ABSTRACT

With increasing age, rats, when play fighting, become rougher. In part, this change can be accounted for by the increasing likelihood of using adult-typical fighting tactics. However, even when using the same tactics, adults appear rougher than juveniles in their play. In this study, videotaped sequences of play fighting in rats from the juvenile (30 days) to the post-pubertal (70 days) period were analyzed using Laban Movement Analysis (LMA). Movement qualities called 'Effort Factors' in LMA captured the character of some of these changes. Juveniles tended to use Indulging Efforts, whereas older rats tended to use Condensing Efforts. The latter are related to performing movements that are more controlled. This greater level of control was also evident in the way older rats maintained postural support during play fights. When standing over supine partners, juveniles are more likely to stand on the partner with all four paws, reducing their postural stability, and hence ability to control their partner's movements. Older rats are more likely to place their hind paws on the ground, thus providing a firmer anchor for movements with their upper bodies and forepaws. These age-related changes in behaviour were found for both males and females. The findings lend support to a growing body of evidence that play fighting in the juvenile phase of rats is not just a more frequently occurring version of that present in adults, but rather, it has unique organizational properties.

INTRODUCTION

Many species of mammals engage in various forms of play behaviour (Fagen, 1981), with play fighting, a form of social play, being among the most commonly reported (Burghardt, in press; Pellis & Pellis, 1998). The frequency of play fighting reaches its peak in the juvenile phase and then declines following puberty (Thor & Holloway, 1984), although in many species such play may persist well into adulthood (Pellis & Iwaniuk, 1999b, 2000). As play fighting declines at puberty, it also appears to become 'rougher'; this is especially true for males (Biben, 1986; Fagen, 1981). In part, this rougher play seems to be reflected in the use of more adult-like fighting tactics and the greater likelihood of escalation to serious fighting (Meaney & Stewart 1981; Pellis & Pellis, 1987, 1991; Takahashi & Lore, 1983). This pattern of change during development is well documented in rats.

In rats, play fighting involves attack and defense of the nape, which, if contacted, is gently nuzzled (Pellis & Pellis, 1987; Siviy & Panksepp, 1987). As juveniles, the most frequently used defensive tactic is to rotate to supine when contacted on the nape (Pellis & Pellis, 1990). This results in an on-top/on-bottom orientation referred to as pinning (Panksepp, 1981). When in the pinned position, both partners launch further attacks directed at each others' napes and simultaneously block access to their napes by using their limbs, thus resulting in prolonged ventro-ventral contact (Pellis, 1988). Following puberty, males are more likely to rotate only their forequarters which allows them to keep ground contact with their hind limbs. From this partially rotated position, the rat can block further attempts to contact the nape by pushing the partner with its hip or by rearing and turning to face (Pellis and Pellis, 1987). Furthermore, from the partially rotated position, the defender has a greater chance of

successfully launching counterattacks against the partner's nape (Pellis & Pellis, 1990). That is, from the partially rotated position, contact can be quickly terminated and the partner is forcefully pushed away or over onto its back (Pellis, 1988).

The switch from complete to partial rotation by the defender may account for the difference in the 'roughness' of play fighting apparent between juveniles and adults (Pellis, 2002a). However, this explanation appears insufficient for two reasons. Firstly, females do not show this male-typical switch in the frequency of use of defensive tactics following puberty, continuing instead mainly to use the complete rotation tactic (Pellis & Pellis, 1990; Smith, Forgie & Pellis, 1998). However, their play fighting appears to be rougher in adulthood. Secondly, even if the same tactics and positional configurations between partners are compared between the juvenile and adult phase, in either males or females, there still appears to be a difference in the roughness of the play. That is, a pin between adults looks rougher than a pin between juveniles. Therefore, the increase in roughness with age involves more than merely changes in the fighting tactics used. It must have something to do with the character of the movements performed within the context of any of the tactics that are used. The problem is that of identifying and characterizing those movement qualities. In this study, we used a descriptive technique that offers a systematic language for recording qualitative features of movement.

Laban Movement Analysis (LMA), created by Rudolf Laban, a choreographer and movement educator with an architectural background, is a universal language for human movement that records qualitative features of movement into structured and quantifiable

categories (Bartenieff & Lewis, 1980; Hutchinson, 1977). The reliability of these qualitative measures in LMA has been recently validated for use with non-human animals (Fagen, Conitz & Kunibe, 2000). Fagen trained students to observe and score LMA Effort Factors (see Methods section). They were then individually presented with the same video excerpts of various animal movements and were asked to score the Efforts that they were able to observe. The results showed that the students had a high inter-observer reliability. These findings suggest that non-human animal movement is amenable to being reliably described using LMA.

However, if the regularities in behaviour revealed by LMA were only understandable to readers with knowledge of LMA, then the information would be of limited value. One solution is to identify objective behavioural markers that are correlated with the qualitative patterns revealed by LMA. Once these correlated markers have been identified, the observer can score these without the need to learn LMA. Using this approach, we identified the movement qualities that lead to greater roughness in the play of adults via LMA, and have characterized a non-LMA dependent behavioural marker for the measurement of this change in roughness.

MATERIALS AND METHODS

Subjects

A total of 16 male and 16 female Long Evans rats from four litters were used. At weaning, litters were divided into groups of four, each with two males and two females. Each group was housed in 40 cm x 24 cm x 18 cm hanging wire cage. All animals were maintained on a

12:12 hour light/dark cycle (lights off at 1900 hours) and kept at a constant room temperature of 21-23°C. Water and food (Purina Rodent Chow) were available ad libitum.

Methods

The testing enclosure was a 90 cm x 30 cm x 36 cm terrarium covered with a 2.5 cm layer of processed corncobs. The test sessions lasted for 10 minutes and were videotaped using a Sony 8 mm camcorder. The videotaping was conducted in red light, provided by a 100 watt globe, 20 cm from the testing enclosure. Prior to testing, each group was habituated to the testing enclosure for up to one hour per day for three consecutive days before the day of testing. On the day preceding testing, each rat was housed individually for 24 hours after the habituation session as such isolation has been shown to increase the frequency of play fighting (Panksepp & Beatty, 1980; Pellis & Pellis, 1990). The first day of testing began at age 30 days. After testing, all four members of each group were returned to their home cage for one hour, providing sufficient time for recovery from the effects of isolation (Einon, Morgan, & Kibbler, 1978). They were then isolated again and tested 24 hours later at 31 days. Litters 1 and 2 were tested in same sex pairs on test day one and were tested in mixed sex pairs on test day two. Litters 3 and 4 were tested in the reverse order. Testing was repeated every 10 days until the rats were 70/71 days old. Each test pair, for each group, remained the same throughout the entire testing period (i.e., male 1 and male 2; female 1 and female 2; male 1 and female 1; etc.).

Analysis

In order to ensure that the cross-age comparisons involved comparing subjects engaged in the same behaviour, one particular partner configuration was used for analysis – the pin, where one partner lies on its back (on-bottom rat), and the other stands over the supine partner (on-top rat) (Panksepp, 1981). For reasons noted below, the behaviour of the on-top rat was subjected to detailed analysis to determine whether its behaviour changed with age. The behaviour of the on-bottom rat was simultaneously monitored in case the change in behaviour of the on-top rat arose as a consequence of changes in the behaviour of the on-bottom rat. The analysis involved the use of Laban Movement Analysis (LMA).

LMA was developed for describing the quantitative features of movement, such as the changes in the relation of the body segments, as well as its qualitative features, such as the intensity of specific movements (Bartenieff & Lewis, 1980). LMA emphasizes the processes underlying motor actions, that is, the notation attempts to reveal the motivation, the expression, and the intended function of the mover. Movements described in LMA are fractionated into four components - Body, Effort, Shape and Space (BESS). The notation records how these components are integrated. As detailed descriptions of LMA are available elsewhere (e.g., Bartenieff & Lewis, 1980; Dell, 1977, Hutchinson, 1977; Maletic, 1987), the following is only an abbreviated description.

BESS Components

(1). 'Body'. This is defined by the relationship and interactions between the anatomical segments of the body during postural control and movement.

(2). 'Effort'. This captures the intensity of a movement (see below).

(3). 'Shape'. This is the manner in which the body's structure changes during a movement. There are several ways in which Shape can change. For example, Directional Movement records the type of Shape the body takes along a particular trajectory, and Shapeflow records how the body responds to perturbations.

(4). 'Space'. This is defined as the interactions between the body and its environment, where the environment is conceptualized as a geometric space constructed from the length, width, and depth of the body. These dimensions of the body represent the vertical, horizontal, and longitudinal Directions the body can move through Space. In a movement, some or all of these components of BESS are integrated.

Motif, a simplified version of LMA (Bartenieff & Lewis, 1980), was used in this paper to describe the movements and movement qualities in the pinning of rats when play fighting. Thirty sequences of pinning from two ages - 30 (juvenile) and 70 (post-pubertal) days - were analyzed, with at least one pin from each pair being notated. A pin was defined as beginning at the video frame when the defending rat turned fully to supine, and so released ground contact with all four paws. The pin ended at the frame where one or both rats moved away. As the notation revealed that the movements of the on-top animal were the most reliably observable, it was the on-top rat that was subjected to the most detailed analysis. Furthermore, of all the LMA features recorded, it was the Efforts expressed by the on-top rat that were the most readily comparable with age. Thus the Efforts occurring in each pin were

scored for the on-top rat, and these data were used to assess whether the qualitative changes detected from the Motif notation were quantitatively robust. In any given pin, a rat may express no Effort or multiple Efforts in succession. Therefore, the percentage of each type of Effort was calculated for each rat, at each age and with each partner.

There are four Effort Factors: Weight, Time, Space, and Flow. Each Effort Factor ranges between two types of Effort Qualities - Indulging and Condensing (Table 1). Indulging Efforts can be seen as movements that are gentler and freer flowing than movements described as Condensing Efforts¹ (Bartenieff & Lewis, 1980; Fagen et al., 2000; Laban, 1971).

(1) Weight Effort describes the force of a movement, and can be divided into two extremes: Light Weight and Strong Weight. Light Weight is a release of force during a movement. For example, mothers use Light Weight when brushing their infants' hair. Strong Weight, the opposite of Light Weight, is often used when greater force is required to manipulate heavy objects. Elephants use Strong Weight Effort to bend and push down trees to access the leafy material on tree tops.

(2) Time Effort can involve acceleration (Quick Time), or deceleration (Sustained Time) during an action. In both, the movements undergo a change in velocity. For example, when a cat approaches its prey, it does so in Sustained Time so as to position itself for a sudden attack. Alternatively, when a cat pounces, it does so in Quick Time as it increases its velocity by pouncing.

Table 1. Effort Factors, Qualities, and their placement on the Effort Continuum.*

Effort Factors	Effort Factor Qualities	
	Indulging	Condensing
Weight Effort	<i>Light Weight</i>	<i>Strong Weight</i>
Time Effort	<i>Sustained Time</i>	<i>Quick Time</i>
Space Effort	<i>Indirect Space</i>	<i>Direct Space</i>
Flow Effort	<i>Free Flow</i>	<i>Bound Flow</i>

*Effort Table derived from Bartenieff & Lewis, 1980, p. 51.

(3) Space Effort is how one focuses one's attention on the immediate environment. Indirect Space is a multi-focal attention rather than a lack of focus. For example, lifeguards, when scanning the overall swimming area, use Indirect Space Effort in both gaze and posture, as they must cover all of the activity in a large space. However, when they notice odd movements, such as flailing arms, during their scan, they will pinpoint their focus (again, both in gaze and posture) to that specific location in order to examine the details required to assess the situation.

(4) Flow Effort is the degree of tension used during a movement. One can be in Free Flow or Bound Flow. Free Flow involves the release of physical tensions and restraints. For example, when an adult repeatedly throws a child into the air (and repeatedly catches the child), the child becomes less tense, thus increasing Free Flow. An example of Bound Flow, the opposite of Free Flow, is how people become more tense when walking in the dark so as to avoid bumping into objects.

A behavioural feature, identified in the notated scores, but not measured by LMA qualities – anchoring - was also scored quantitatively. This non-LMA behavioural marker and its measurement is described in the Results.

RESULTS

The Motif scores revealed that there were changes in the pattern of movement of the on-top rat at the juvenile and post-pubertal age. These changes are illustrated in Figure 1. The notation reads from bottom to top and the length of the individual symbols indicate duration.

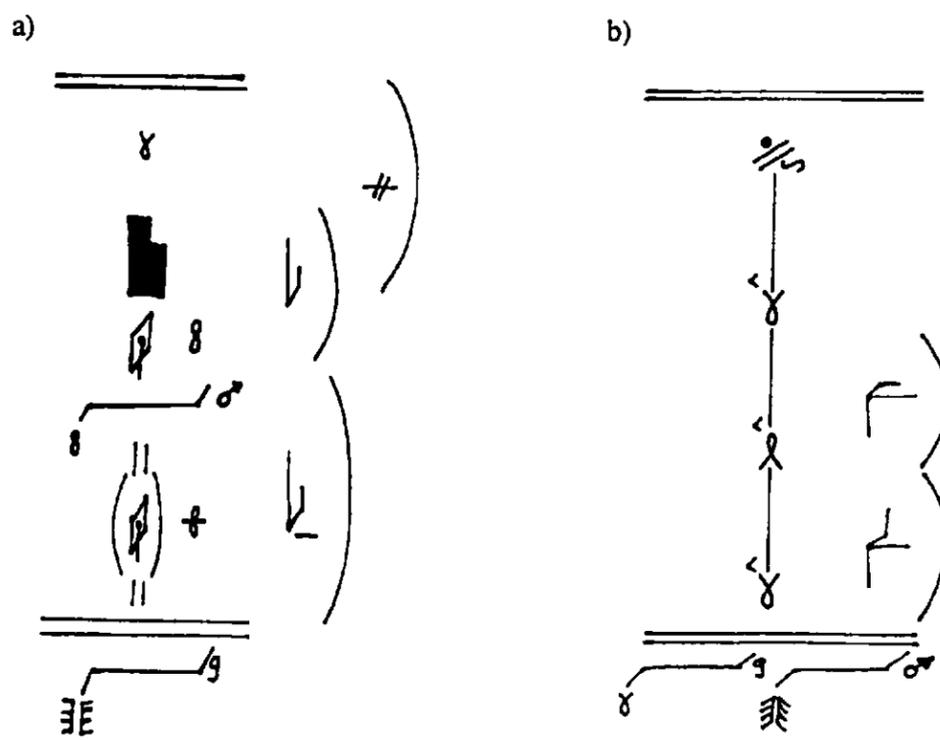


Figure 1. Motif scores for the on-top rat during pins involving the same pair of males as (a) juveniles (30 days old) and (b) young adults (70 days old).

The double horizontal lines near the bottom and at the top indicate the beginning and the end of the movement sequence. The starting posture is shown below the lower double bars. In the Motif score there are three columns: the first describes the structural organization of the body's movements, the second is used to score Efforts, and the third is used to score Shape.

In the score for the juvenile (Figure 1a), the rat begins with both hind paws on the ground. He then jumps. During the jump, he performs a half turn to the right, using Indirect Space, Light Weight and Quick Time Efforts. The turn begins with a lateral rotation of the upper body, which then continues with a recruitment of the lower body. The rat then lands on the partner with all four paws. Using Light Weight and Indirect Space Efforts, the rat's entire body turns simultaneously 90 degrees to the right. While still on top of the partner, the rat moves forward and downward. The rat then pauses, but continues to make small postural adjustments using Shapeflow.

The score for the post-pubertal rat (Figure 1b) begins with the rat having both his hind paws on the ground and his forepaws on the partner. On commencement of the movement, the rat shows Strong Weight, Indirect Space and Bound Flow Efforts in performing a single movement with his lower body, and then with Strong Weight, Direct Space, and Bound Flow Efforts, makes a single movement with his upper body. This is followed by another single movement with the lower body, and then another by the upper body. These sequential movements by the rat's upper and lower body are then repeated several times over.

At 30 days, the rat uses many movements and many Efforts, and these Efforts are mostly Indulging. Also, many of the movements performed simultaneously involve several parts of

Table 2. Consistent differences identified by Motif scores of 30 and 70 day old rats.

Juvenile (30 days)	Adult (70 days)
<ul style="list-style-type: none"> Moves different body parts simultaneously 	<ul style="list-style-type: none"> Moves different body parts sequentially
<ul style="list-style-type: none"> Uses more jumping and twisting components 	<ul style="list-style-type: none"> Maintains a relationship between itself, its partner, and the rest of the environment
<ul style="list-style-type: none"> Has random sequence of movements 	<ul style="list-style-type: none"> Has consistent pattern of movement sequences
<ul style="list-style-type: none"> Changes its base of support 	<ul style="list-style-type: none"> Maintains its base of support
<ul style="list-style-type: none"> Uses more Indulging Efforts 	<ul style="list-style-type: none"> Uses more Condensing Efforts
<ul style="list-style-type: none"> Moves between Single Efforts, Effort States, and Effort Drives 	<ul style="list-style-type: none"> Consistently uses Effort Drives
<ul style="list-style-type: none"> Has high use of Efforts 	<ul style="list-style-type: none"> Has less use of Efforts
<ul style="list-style-type: none"> Uses Shape 	<ul style="list-style-type: none"> Has no visible use of Shape

the body. In contrast, at 70 days, there are fewer movements, and those performed involve only a few body parts, and there are fewer Efforts used, and those used tend to be Condensing. While individual Motif scores could vary in duration and amount of movement, a comparison of all the notated scores revealed that these types of differences between 30 and 70 day old rats were consistent (Table 2). To evaluate statistically at least some of these changes, the Efforts used at all ages were quantified. This feature of LMA was chosen for two reasons. Firstly, based on the Motif scores, the use of Efforts differed consistently across the two ages, and secondly, the study by Fagen et al. (2000) provides independent validation that Efforts can be scored objectively.

There was a significant difference in the Effort Factors most often used ($F_{3,51}=121.93$, $p<0.0001$), with Weight and Space Effort Factors used most often and Time and Flow Effort Factors used less often. There was also a significant age by Effort Factors interaction ($F_{12,204}=2.70$, $p<0.01$), but no significant sex of performer, sex of partner, or other interaction effects ($p>0.05$) (Table 3). The qualities in both Weight and Space Factors were divided into Indulging and Condensing categories and tallied. There was a significant age effect ($F_{4,64}=4.92$, $p<0.01$) and age by Effort category effect ($F_{4,64}=13.96$, $p<0.0001$). That is, in the juvenile phase, Indulging Efforts were more commonly used, whereas with increasing age, Condensing Efforts were more likely to be used (Figure 2). There was also a significant sex of performer effect ($F_{1,16}=6.70$, $p<0.05$), a significant sex of performer by sex of partner interaction ($F_{1,16}=5.51$, $p<0.05$), and a significant sex of performer by category of Effort interaction ($F_{1,16}=7.80$, $p<0.05$). The switch from using Indulging

Table 3. The use of Weight, Space, Time and Flow Efforts during pinning at all ages tested.

Subject Groups	Effort Factors	Age (days) *				
		30	40	50	60	70
Male with male	Weight	95.15	83.43	68.26	90.23	74.10
	Space	89.27	90.63	82.89	89.96	71.70
	Time	15.45	24.76	16.31	9.55	16.47
	Flow	13.05	21.27	19.57	27.04	50.01
Female with female	Weight	86.05	88.40	63.75	86.60	66.25
	Space	93.03	88.10	88.75	92.25	53.75
	Time	34.48	38.68	26.68	30.65	37.50
	Flow	31.25	12.50	18.75	15.55	29.58
Male with female	Weight	78.03	78.03	65.85	72.49	69.06
	Space	77.59	77.59	91.55	94.38	82.85
	Time	30.38	30.38	14.15	12.61	15.82
	Flow	21.50	21.50	8.38	12.50	22.23
Female with male	Weight	74.83	100.00	70.00	75.00	79.18
	Space	80.50	76.68	88.00	100.00	83.35
	Time	25.10	41.68	30.00	25.00	33.33
	Flow	27.30	17.50	0.00	12.50	20.85

*At each age, the average percentage of pins containing different types of Effort Factors is shown.

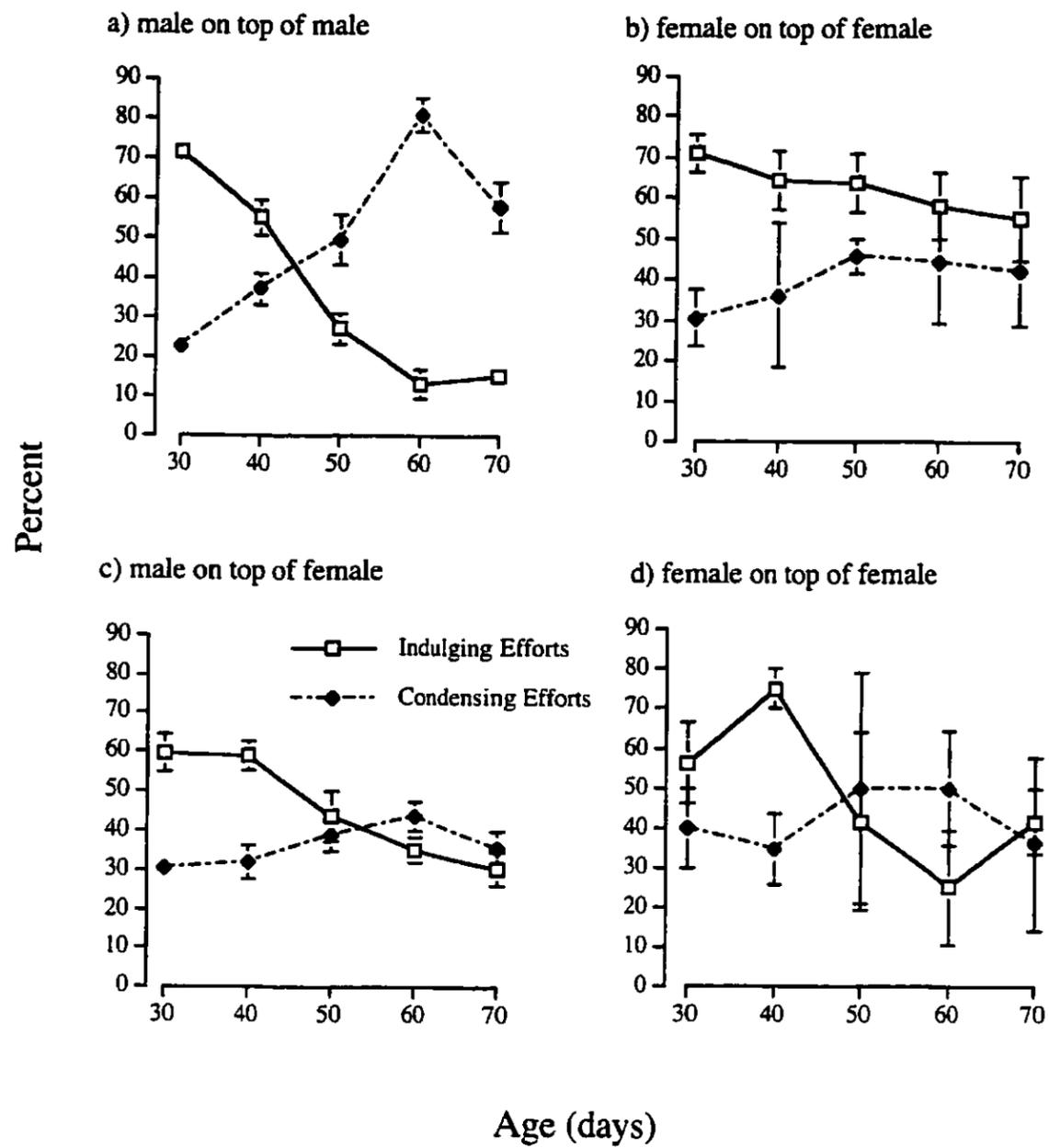


Figure 2. The change in the percent ($\bar{X} \pm SE$) of Indulging and Condensing Efforts used by the on-top rats during pins from the juvenile stage (30 days) to after puberty (70 days).

Efforts at younger ages and Condensing Efforts at older ages was greatest when males were on top of males (Figure 2).

There was also a consistent difference in how the on-top rat organized its base of support. While in the on-top position, the rat typically placed its forepaws on the on-bottom partner. However, the placement of the hind paws could vary - the rat either stood on the ground or on the partner. To quantify this, the base of support was recorded as an end-point measure during each pin. If at least one of the rat's hind paws maintained ground contact and was weight bearing, the rat was scored as being 'anchored' (Figure 3a). If the rat's hind paws maintained weight bearing contact on the partner during the pin, the rat was scored as not being anchored (Figure 3b). Rats received a score of 1 for being anchored and a score of 0 for not being anchored during a pin. If a rat was anchored during the first part of the pin, and not anchored during the second part of the pin, or vice versa, the rat was scored as a 0.5.

Results revealed a significant age-related change in anchoring ($F(1,4)=21.09, p<0.0001$), with it being less frequent at 30 days than at older ages (Figure 4). There was also a significant sex of performer effect ($F(1,29)=9.53, p<0.01$), but no significant differences for sex of partner, or sex by age interactions ($p > 0.05$). The greatest change in anchoring occurred between the ages of 30 and 40 days. After 40 days, there was a consistent, but smaller, increase in anchoring until it leveled off at 60 days. With regard to sex differences, males on top of males showed the largest and most consistent age-related change (Figure 4).

a)



b)

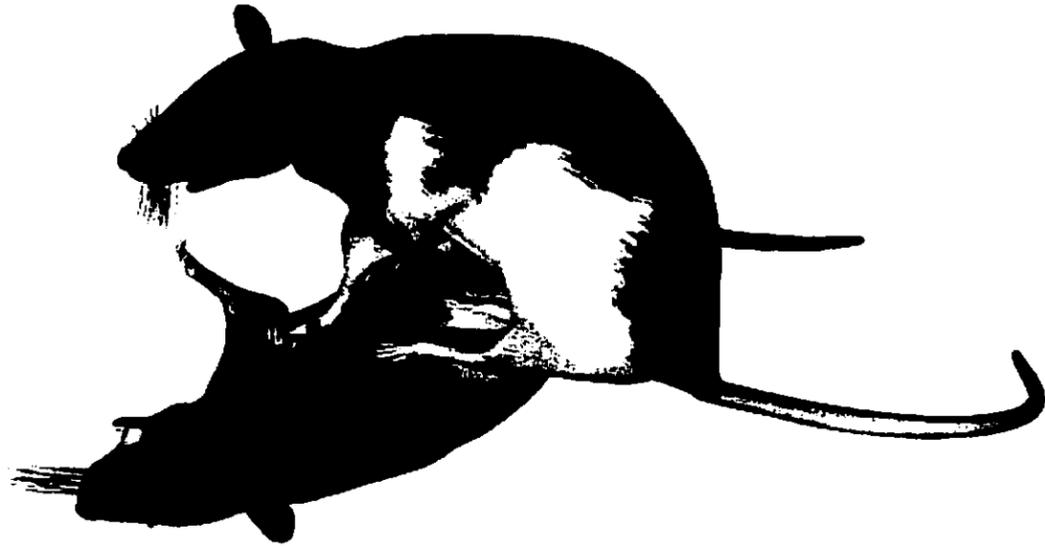


Figure 3. A pair of rats during pinning with the on-top partner (a) anchored and (b) unanchored.

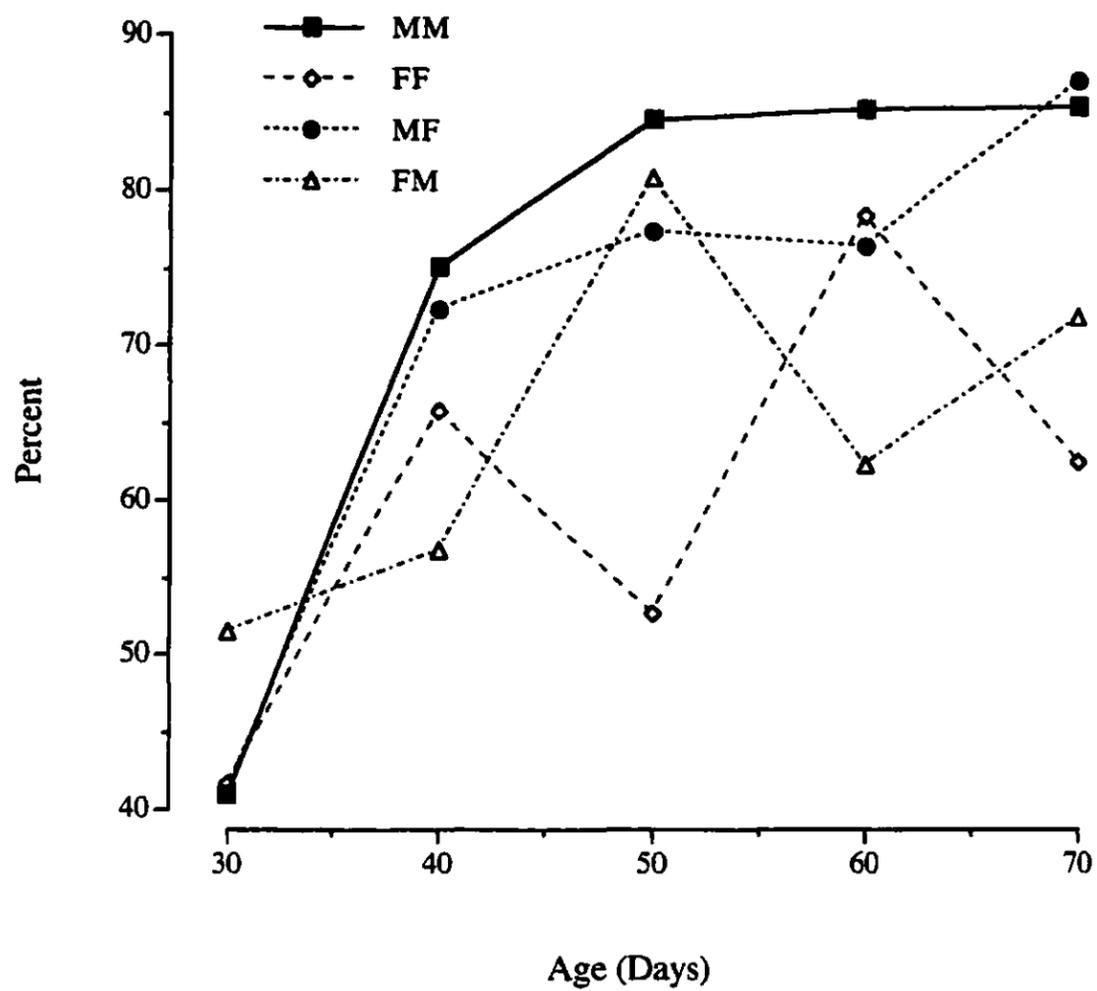


Figure 4. The changes in mean percent of pins in which the on-top rat is anchored is shown from the juvenile stage (30 days) to after puberty (70 days). MM= male on top of male, MF= male on top of female, FF= female on top of female, FM= female on top of male (for standard errors see Appendix 1, p. 126).

DISCUSSION

Play fighting is most frequent in the juvenile phase, which for rats occurs between 30-40 days post-natally. Play fighting then decreases with the onset of puberty (Thor & Holloway, 1984). Even so, play fighting in rats can persist, albeit at a much reduced frequency, well into adulthood (Pellis & Pellis, 1990, 1991). As noted in the Introduction, there is a change, especially in males, in the use of some fighting tactics with age, that leads to them engaging in a rougher form of play (Pellis, 2002a). In this study, we found that even when juveniles and adults use the same tactics, the adults have a rougher form of play.

Results from an LMA analysis of the development of this rougher play show that, with increasing age, the rats switch from mainly using Indulging Efforts - that is, ones that are more gentle - to mainly using Condensing Efforts - that is, ones that are rougher. This suggests that the rats go from being more affiliative, where their movements may facilitate reciprocal contact, to being more aggressive, where their movements may be more likely to block reciprocal contact. These differences in behaviour may also be viewed in terms of the degree of control that the on-top animal exerts over its own movements and those of its supine partner. When using Indulging Efforts, the subject performs many body movements, many of which are not related to the defensive actions of the partner (see Table 2). This lack of coordination of its own movements with those of its on-bottom partner leads to postural instability and a failure to respond effectively to the partner's tactics. Indeed, counterattacks during pinning, where the supine defender lunges at the on-top rat's nape, are both more frequent and more likely to be successful in the juvenile stage (Pellis & Pellis, 1990; Pellis, Pellis & Dewsbury, 1989). Overall, the lack of control during pinning creates an

unpredictable physical environment to which the rat must continuously adapt itself. In contrast, maintaining control provides the rat with the opportunity to evaluate how its playmate adapts to the situation. Anchoring appears to be a good measure of such control during pinning (see Figure 3).

When the on-top rat places all four paws on its supine partner, its postural stability is affected by both its own movements and by those of its partner. However, when the on-top rat has its hind paws anchored on the ground, it can easily maintain its base of support while using its forepaws to feel, hold and restrain its partner. That is, when standing on its partner with all four paws, the on-top rat's forepaws are primarily engaged in a postural support role, as none of the four paws are free from responding to postural disturbances. In contrast, when its hind paws are on the ground, they can be used to support the body, freeing its forepaws for use in attack and defense. Thus, when placing all four paws on the partner, the on-top rat has less control over the situation. Therefore, the increase in the likelihood of anchoring following the peak period of play in the juvenile phase lends objective support for the post-pubertal shift in roughness that was identified using LMA notation and Effort scores. Furthermore, these findings based on anchoring provide support for the conclusion that this shift relates to the degree of control exerted by the on-top rat during play fighting.

The present findings also reveal that while males and females differ in the frequency of play (Thor & Holloway, 1985), in the age-related changes in the fighting tactics used during play fighting (Meaney & Stewart, 1981; Pellis & Pellis, 1990), and in the likelihood that their play fights will escalate into serious fights (Smith et al., 1998; Takahashi & Lore, 1983), both

sexes become rougher in their play with age. These results are not consistent with the view that following puberty, females find male playmates less appealing because they play too roughly (e.g., Fagen, 1981; Biben, 1986; Meaney & Stewart, 1981; Smith et al., 1998). Rather, play partner preferences of the sexes may have more to do with the social functions of post-pubertal play (Pellis & Iwaniuk, 2000; Pellis & Pellis, 1996) than with the aversiveness of some partners. Even so, our data suggest that the change in roughness, measured in terms of LMA Efforts or in anchoring, is greater for males than for females. Therefore, some of our data do support the idea that with age males become rougher in play than do females. Clearly, while more refined analyses are needed to resolve this issue, our data suggest that the view that a male increase in play roughness, in the absence of a comparable change in females, mainly influences post-pubertal play partner preferences, is an assumption that needs to be more fully tested.

In the juvenile phase, play fighting in rats is characterized by three features: (1) it is at its most frequent (Thor & Holloway, 1984), (2) subjects are most likely to rotate to a supine position when defending against a nape attack (Panksepp, 1981; Pellis & Pellis, 1990), and (3) subjects exhibit less control over their own movements and those of their partners' (this study). This leads to the hypothesis that these features are part of an adaptation that ensures that animals gain the maximum opportunity for skill acquisition during play fighting. That is, it is unlikely that such a combination of features arose by chance (Williams, 1966). However, before this age-structured pattern of developmental change can be used to support any particular adaptive hypothesis (Fagen, 1974), a simpler alternative needs to be tested. The lower level of anchoring and the higher level of Indulging Efforts in juveniles may simply

reflect a lower level of motoric competence. That is, the peculiar pattern of gentle play fighting in juveniles maybe the byproduct of the level of sensorimotor maturation at this age. Support for this possibility is shown by the steady increase in the likelihood of anchoring with age, reaching an asymptote between 80-90% at around day 60. The switch from Indulging to Condensing Efforts exhibits a similar age pattern. There is, however, some indirect evidence against this maturation hypothesis. As noted earlier, when play fighting, juvenile rats are more likely to rotate around their long axis to a fully supine position than are male post-pubescents (Pellis & Pellis, 1990). Post-pubertally, males are more likely to rotate only partially, maintaining hind paw contact with the ground – a motorically more sophisticated manoeuvre. However, post-weaning, pre-juvenile rats, of both sexes, are more likely to rotate partially than to turn to supine (Pellis & Pellis, 1997). This preference for the partial rotation tactic exists even though the young pups are unstable in this posture and are likely to fall over – that is, they use this tactic even though they are not motorically mature enough to use it effectively (Pellis & Pellis, 1997). These findings suggest that a seemingly poorer motor performance in juveniles as compared to adults cannot be uncritically taken as evidence for motor incompetence in the younger animal. The use of anchoring and Effort Factors need to be empirically evaluated for a wider range of ages than conducted in this study in order to properly test the two hypotheses.

ⁱ Condensing Efforts are sometimes called Fighting Efforts (Bartenieff & Lewis, 1980; Fagen et al., 2000).

CHAPTER THREE

The development of 'anchoring' in the play fighting of rats: Evidence for an adaptive age-reversal in the juvenile phase.

ABSTRACT

During play fighting, rats often assume a pinning configuration, where one animal stands over its supine partner. The on-top partner can stand on the ground or on its supine partner with its hind paws. When standing on the ground, the rat is more stable and is better able to respond to its partner's actions. The frequency of this more stable pattern of standing during pinning (here referred to as 'anchoring') is higher following puberty than during the juvenile phase. Three hypotheses explaining this developmental change in anchoring were tested. Firstly, that the lower level of anchoring in juvenile rats reflects an immature sensorimotor capability. If so, pre-juvenile peri-weaning infants should have levels of anchoring as low as, or lower than juveniles. Therefore, in this study, changes in anchoring were compared between pre-juvenile and juvenile rats. Secondly, the low level of anchoring in the juvenile phase may be one of many fluctuations present at many ages. Therefore, anchoring was evaluated in rats well into adulthood. Thirdly, changes in anchoring levels may not be age-related at all, but instead, only occur within the context of play fighting between littermates. Therefore, the developmental pattern of anchoring was compared when rats were playing with a littermate versus a stranger. Results showed that infants have similar anchoring levels to post-pubertal rats, and that once the adult-typical level of anchoring is achieved, no further fluctuations occur. Also, the results show that the developmental change in anchoring occurs irrespective of the identity of the partner. Therefore, anchoring appears to have a robust pattern of change during development, with its occurrence being lowest at the juvenile phase,

when the frequency of play fighting is at its highest frequency. These findings support the view that play fighting in the juvenile phase is organized in a manner that increases the benefits derived from engaging in this activity.

INTRODUCTION

Play fighting in rats, as in other mammals and birds (Fagen, 1981), is most frequent in the juvenile stage of development (Thor & Holloway, 1984). However, play fighting also changes in content with age (Biben, 1986; Meaney & Stewart, 1981). In rats, play fighting involves attack and defense of the nape, which if contacted, is gently nuzzled (Pellis & Pellis, 1987; Siviy & Panksepp, 1987), whereas during serious fighting, bites are directed to the rump and face (Blanchard & Blanchard, 1994; Pellis, 1997). While the target of attack remains the same for play fighting at all ages, what changes are the tactics most likely used for defense (Pellis & Pellis, 1990). Juveniles more frequently rotate around the long axis of their body to a fully supine position when contacted on the nape (Pellis & Pellis, 1990). With the onset of puberty, male rats are more likely to rotate only their forequarters, thus keeping ground contact with one or both hind paws (Pellis and Pellis, 1987). During the juvenile period, then, when play fighting is most frequent, the rats are also more likely to roll over and wrestle. That is, they are more likely to exhibit the on-bottom/on-top pinning configuration (Panksepp, 1981).

In a previous study using Laban Movement Analysis (LMA) to evaluate the apparent increase in roughness in play fighting with age (Pellis, 2002a), it was found that during pins, juvenile rats are more likely to stand on their supine partner with all four paws (Chapter 2), rather than maintaining ground contact with their hind paws (i.e., anchored). By doing so, juvenile rats are in a less stable position and so are more likely to fall over as they and their partners move (Chapter 2). A major question arising from this finding is whether this reflects the juveniles' sensory, motor or integrative immaturity, or whether this reduction of

anchoring in the juvenile phase is a design feature of play at this age. If the latter is the case, then the lower levels of anchoring may be part of the age-related changes that increase the occurrence of particular kinds of experiences that may function to develop particular cognitive and physical skills (Biben, 1998; Pellis & Pellis, 1998a, b; Thompson, 1998).

In this study, two possible influences on the levels of anchoring are evaluated. Firstly, in Chapter 2, changes in play fighting were assessed from 30-70 days. This covers the peak juvenile play period, 30-40 days, and the pubertal to early post-pubertal period, 50-70 days. The increase in the frequency of anchoring over this time may simply reflect an age-related maturation of the sensorimotor system. Alternatively, the lower level of anchoring in juveniles may be one of many fluctuations in levels of anchoring that may occur sporadically at any age. That is, there may be fluctuations in anchoring at many ages, not only in the juvenile phase; this reduces the likelihood that the attenuation of anchoring in the juvenile phase represents an age-specific adaptation. Therefore, one study was done to evaluate whether post-weaning, pre-juvenile infants have levels of anchoring as low or lower than juveniles, and another was done to evaluate whether once rats reach the asymptote value of around 80-90% at 60 days, they remain at this level well into adulthood.

Secondly, in the Chapter 2 study, play fighting was videotaped when subjects were interacting with their littermates. However, the behaviour patterns used during play fighting may be modified when interacting with unfamiliar rats (Kahana, Rozin & Weller 1997; Smith, Forgie & Pellis, 1998; Takahashi, 1986). That is, the pattern of change in the frequency of anchoring may not be a rigidly determined age-related feature of play, but

rather, one that emerges only in particular environmental contexts. Therefore, in the present study, the developmental changes in anchoring were compared for rats interacting with familiar and unfamiliar pair mates.

Together, these studies provide an assessment of whether the lower frequency of anchoring in juvenile rats is an age-related adaptive feature of play, whether it arises indirectly due to an underlying lag in the rate of sensorimotor maturation, or appears only in specific environmental contexts.

MATERIALS AND METHODS

Subjects

A total of 50 male and 21 female Long Evans rats, born and reared in an animal colony of the Department of Psychology and Neuroscience at the University of Lethbridge, were used. All animals were maintained on a 12:12 hour light/dark cycle (lights off at 1900 hours) and kept at a constant room temperature of 21-23°C. Water and food (Purina Rodent Chow) were available ad libitum.

Methods

Animals were housed either in pairs or in larger groups depending on the experiment. Each group was habituated to the testing enclosure for up to 20 minutes per day for three consecutive days prior to the day of testing. The floor of the testing enclosure was covered with a 2.5 cm layer of processed corncobs. On the day preceding testing, each rat was housed individually for 24 hours after the habituation session, as such isolation has been

shown to increase the frequency of play fighting (Panksepp & Beatty, 1980; Pellis & Pellis, 1990). All testing sessions were videotaped in the dark using the 'Night Shot' feature of a Sony 8 mm camcorder. To ensure a clear view of all body parts and partner orientations, subjects were videotaped from a lateral view with the camera pointing down at an angle of 45 degrees. A mirror at the back of the test enclosure further facilitated observation of the otherwise hidden parts of the rats' bodies. The animals were returned to their home cages following testing.

Data collection and analysis

In order to ensure that the present study collected data comparable to the previous one (Chapter 2), pinning, where one partner lies on its back (on-bottom rat) and the other stands over the supine partner (on-top rat) (Panksepp, 1981), was used for analysis. Anchoring refers to the placement of the hind paws by the on-top partner. While in the on-top position, the rat typically places its forepaws on the on-bottom partner. However, the placement of the hind paws can vary – the rat either stands on the ground or on the partner. To quantify this, the base of support was recorded as an end-point measure during each pin. If at least one of the rat's hind paws maintained ground contact and was weight bearing, the rat was scored as being anchored. If at least one of the rat's hind paws maintained weight bearing contact on the partner during the pin, the rat was scored as not being anchored. Rats received a score of 1 for being anchored and a score of 0 for not being anchored during a pin. If a rat alternated between anchoring and not anchoring over the course of one pin, it was given a score of a 0.5 (see Figure 3a & b in Chapter 2).

EXPERIMENT 1: Anchoring in the pre-juvenile phase.

This study was designed to evaluate any changes in the frequency of anchoring in the play fighting from immediately before and during weaning (19-24 days), to the onset of the juvenile period (25-30 days).

Subjects

A total of 37 Long Evans hooded rats from three litters were used. Litter 1 had six males and five females, Litter 2 had seven males and six females, Litter 3 had seven males and six females. Subjects were housed with their mothers until weaning at 22-24 days in 46 cm x 25 cm x 20 cm polyethylene tubs with a 2.5 cm layer of processed corn cob for bedding. At weaning, mothers were removed and the litters remained in their home tubs. Once litters outgrew their home tubs, they were moved into similar, but larger, tubs (46 cm x 42 cm x 20 cm).

Methods

Preceding testing, each litter was habituated to the test enclosure for 15-20 minutes a day for three days. Two methods were then used for videotaping play fights. In the first method, at 24, 29, 34, and 39 days, each animal was isolated for 24 hours. Following isolation, same sex pairs of rats were tested, for 10 minutes as described above. The same pair mates were used at each age. The extra female from litter 1 and one extra male from each of the other two litters were not videotaped. This short-term isolation procedure increases the level of play fighting in the rats when they are reunited (Panksepp, 1981; Pellis & Pellis, 1990), and these paired encounters provided data comparable to that used in the previous study (Chapter 2). In

the second method, litters were subdivided into male and female groups. At 19, 20, 21, 22, 23, and 24 days, each same sex group from each litter was placed in the testing enclosure, a glass terrarium (50 cm x 26 cm x 36 cm) with a 2.5 cm layer of processed corncobs, and was videotaped for 10-15 minutes. Such group testing is important for the youngest ages, as the pups may otherwise be inhibited by the novelty of the situation combined with the separation from their littermates (Pellis & Pellis, 1997).

Experiment 2: Anchoring in adulthood.

This study examined the frequency of anchoring well past puberty to determine whether the high rate of anchoring at around puberty remains high in adulthood; that is, whether or not there are sporadic fluctuations in that frequency when an extended age range is compared.

Subjects

Twelve male rats were pair housed at the onset of puberty. Each pair was housed in a 46 cm x 25 cm x 20 cm polyethylene tub with a 2.5 cm layer of processed corncobs for bedding.

Methods

Each pair was habituated for 10 minutes daily for a period of three days, in the testing enclosure, which was a 50 cm x 50 cm x 50 cm terrarium with two wooden sides, a Plexiglass front, a mirrored back wall and a 2.5 cm layer of corn cob bedding on the floor. Immediately following habituation on the third day, subjects were isolated for 24 hours. On the fourth day, each pair was videotaped in the testing enclosure for 10 minutes at ages 80, 90, 110, and 120 days.

Experiment 3: Anchoring and partner familiarity.

This experiment was designed to evaluate whether the pattern of developmental change in anchoring is partner-specific or whether it shows the age-related reduced frequency at the juvenile phase irrespective of the familiarity of the partner.

Subjects

Fourteen male rats were pair housed when weaned at 22 days. Each pair was housed in a 46 cm x 25 cm x 20 cm polyethylene tub with a 2.5 cm layer of processed corncobs for bedding.

Methods

The same habituation procedure and test enclosure as described in Experiment 2 was used for this experiment. Testing began at 32 days of age, after the rats were isolated for 24 hours. Subjects were then housed in their pairs for 24 hours, and then, following another 24 hours of isolation, they were tested at 34 days. On one day of testing, the subject was paired with its littermate and on the other day, it was paired with a stranger. Three pairs were tested with their littermate first and a stranger second, whereas the other four pairs were tested with a stranger first. The testing procedure was repeated at 60 and at 120 days.

Data Collection and Analysis

For Experiment 1, in the paired condition, pins were scored for each pair mate, and the percentage of these in which the on-top animal was anchored was calculated. For the grouped tests, all pins in which the hind paws could be observed were scored for anchoring; this was converted to a percentage for each sex for each litter. For experiments 2 and 3, the percentage

of pins when each subject was anchored was scored. Repeated measures ANOVAs were used for age and partner comparisons, and Scheffe's post hoc tests were used for pair-wise comparisons.

RESULTS

Analysis of the paired infant data for Experiment 1 revealed a significant age effect ($F(3,123) = 5.163, p < 0.05$) (Figure 1). Pair-wise comparisons showed a significant difference between day 30 and day 25 ($p < 0.05$), and day 30 and day 40 ($p < 0.05$), but not between day 25 and day 40 ($p > 0.05$). That is, the juvenile rats (day 30) had a lower frequency of anchoring than they did shortly after weaning. That young infants can have a high frequency of anchoring was supported by the group data collected between 19 and 24 days. Too few pins occurred over these days to score individual days, so these pins were summed for each litter. Over the three litters, males scored an average of 74% and females an average of 67%. In Experiment 2, the adults achieved a frequency of anchoring of over 80%, and retained this high frequency across all ages (range: 81.8-94.9%). There was no significant age effect ($p > 0.05$). There was no significant difference in anchoring between being paired with a littermate or a stranger ($p > 0.05$), but there was a significant age effect ($F(2,32) = 27.94, p < 0.0001$) with 30 day old rats showing the lowest frequency (Figure 2). Therefore, the identity of the partner did not affect the age-related modulation in the frequency of anchoring.

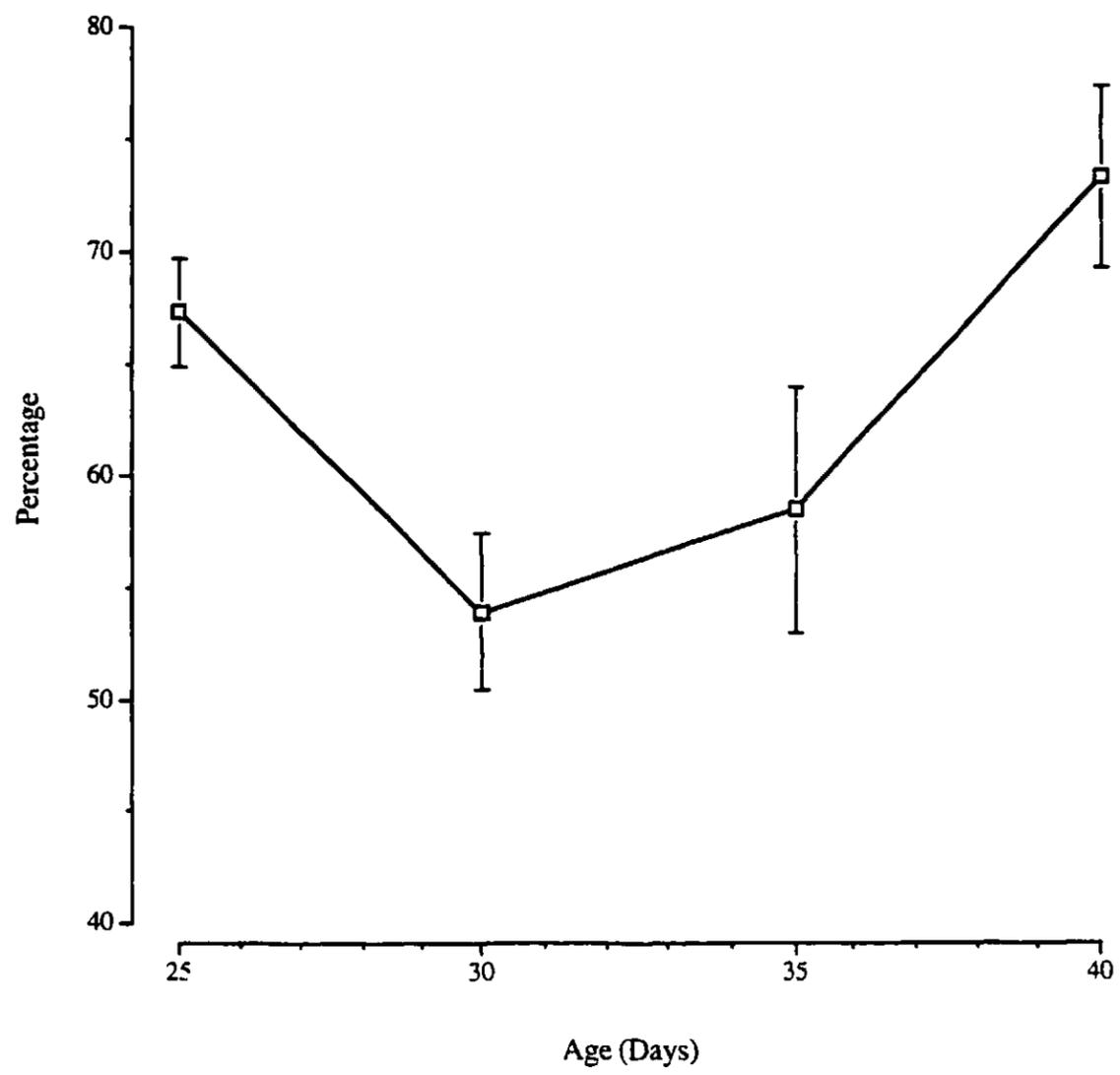


Figure 1. The change in the percent ($\bar{X} \pm SE$) of pins in which the on-top rat is anchored is shown from shortly after weaning (25 days) to the juvenile phase (30-40 days).

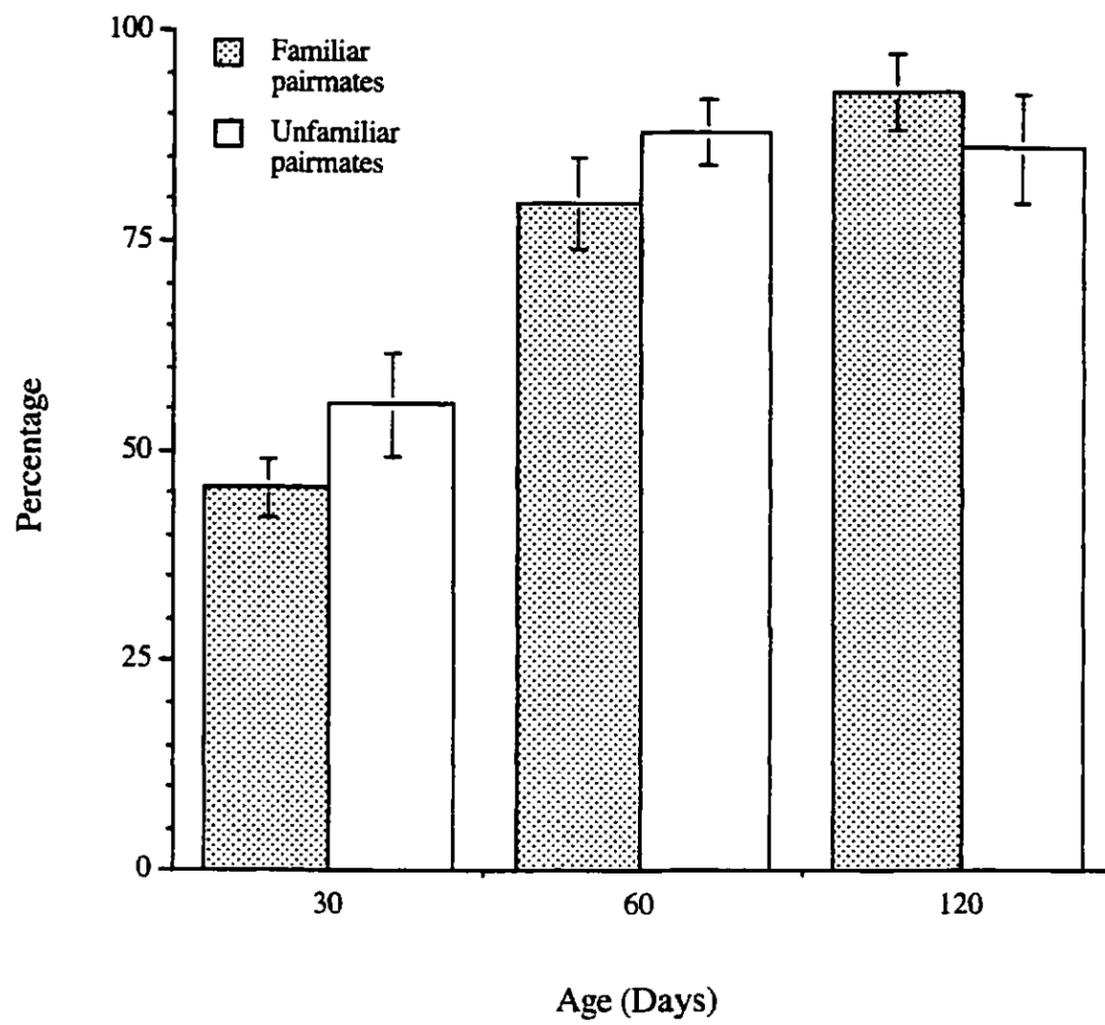


Figure 2. The change in the percent ($\bar{X} \pm SE$) of pins in which the on-top rat is anchored is shown when paired with a littermate or an unfamiliar partner from the juvenile phase (30 days) to shortly after puberty (60 days), and then well into adulthood (120 days).

DISCUSSION

When play fighting, rats attack and defend the nape (Pellis & Pellis, 1987), and many, if not most, of the movements performed by the participants are explainable in terms of the tactics used to gain or block access to the nape (Pellis, 1988). At any given age, rats seem to be attacking and defending as best as they can (Pellis & Pellis, 1990, 1997). That is, they use the capabilities that they have to the best effect. In the pinning position, the on-top partner uses its limbs to hold and block counterattacks by the on-bottom partner, and then uses moments of advantage to press its own further attacks to its partner's nape (Pellis, 1988). Standing on top of the supine partner with all four paws compromises the ability of the on-top rat to gain and make use of such advantages. While standing on top of the partner with all four paws, the on-top rat has to use its paws to maintain its postural stability in response to the movements made by its partner, and those made by itself (Chapter 2). Yet, in the juvenile phase, the rats stand on their partner with all four paws more often than is the case with the approach of puberty (Chapter 2).

One possible explanation for this seemingly poor manoeuvring by the juvenile rats is that they lack the sensorimotor skills to position themselves effectively with their hind paws on the ground. In this way, the lower frequency of anchoring may be accounted for by incomplete development of the requisite skills. In the present study, the incidence of anchoring was examined in infant rats during the periweaning period, when play fighting first emerges (Bolles & Wood, 1964; Pellis & Pellis, 1997). The data show that as infants, rats anchor as frequently as do pubescent and adult rats. In fact, the lower level of anchoring in the juvenile period, between 30-40 days, actually involves a decline from the level present in

weanlings. Therefore, the lower level of anchoring in the juvenile period cannot be explained as being due to the incomplete maturation of the sensorimotor system, as younger animals are as capable of exhibiting anchoring as are older ones. The level of anchoring increases at around 40 days and reaches adult-typical levels by about 60 days (Chapter 2). The present study showed that this high level of anchoring remains consistently high well into adulthood. That is, there are no significant fluctuations in the levels of anchoring from 60-120 days, and certainly none are as pronounced as that seen in juveniles.

The dip in anchoring in the juvenile phase appears to be a robust and programmed developmental change. There are two other such programmed developmental changes in the play fighting of rats. One is the frequency of play fighting, which peaks in the 30-40 day period (Meaney & Stewart, 1981; Panksepp, 1981; Panksepp & Beatty, 1980). When attack and defense during play fighting are scored separately, the changes in the frequency of play fighting have been shown to arise from changes in attack, not defense (Pellis & Pellis, 1990, 1997; Thor & Holloway, 1986). While the height of the peak in frequency of play fighting in the juvenile phase is sensitive to the organizational effects of gonadal hormones in the perinatal period (Meaney, 1988), that the frequency of launching playful attacks peaks in the juvenile period, is not (Pellis, 2002a). This peak in play fighting frequency is expressed in a wide range of rearing and testing paradigms (Thor & Holloway, 1984), and is expressed whether rats are paired with a same sex or opposite sex partner (Pellis & Pellis, 1990; Thor & Holloway, 1985, 1986), or with a familiar or unfamiliar partner (Smith et al., 1998).

The other programmed change in development involves the defensive tactics used during play fighting. In the juvenile phase, the most likely defense to be used is to rotate completely to supine (Pellis & Pellis, 1987; 1990), and so end in the pinned position (Panksepp, 1981). However, at puberty, males switch mostly to using the partial rotation tactic (Pellis & Pellis, 1987), while females continue mostly to use the complete rotation tactic (Pellis & Pellis, 1990). In the periweaning period, young rats of both sexes mostly use the partial rotation tactic (Pellis & Pellis, 1997). That is, the infant rats are capable of using the motorically more difficult tactic. Furthermore, the findings show that infant females are also capable of using the partial tactic more frequently than they do as either juveniles or adults. Indeed, the failure of females to switch at puberty mostly to using the partial rotation tactic, has been shown to be due to the inhibitory effects of female gonadal hormones (Smith et al., 1998). In the absence of circulating gonadal hormones, females at the chronological age of puberty switch to the use of partial rotation (Pellis, 2002a). Neither the actions of male or female gonadal hormones can explain the switch from partial to complete rotation at the onset of the juvenile phase. As is the case for the frequency of launching playful attacks, the switch to complete rotation in the juvenile phase is not dependent on the sex or familiarity of the partner (Pellis & Pellis, 1990, 1997; Smith et al., 1998).

Anchoring resembles the age-related modulation in play frequency and switch in playful defensive tactics, in that its modulation in the juvenile phase occurs whether play fighting with a partner of either sex (Chapter 2), or whether the partner is a familiar animal or a stranger (this study). Therefore, anchoring appears to have a robust pattern of waxing and waning, occurring at its lowest level in the juvenile phase.

Play fighting in juvenile rats cannot simply be considered as an exaggerated performance of the species-typical behaviour patterns present in adult sex and aggression, as may be the case for many other rodents (Pellis & Pellis, 1998b). Instead, play fighting in rats exhibits preprogrammed modulations in its organization that suggests that it may be designed to promote the acquisition of particular experiences. When play is at its most frequent, juveniles are most likely to roll over and wrestle, thus prolonging the play fights and increasing the degree of body-to-body contact (Pellis & Pellis, 1987, 1990, 1997). We have now shown that at this same age, the rat standing on top of the supine partner places itself in such a way as to increase its postural instability, making it more likely that the partner can successfully defend itself and even counterattack (Chapter 2). The confluence of these design features in the juvenile phase makes it unlikely that they arose by chance – instead, they appear to have the structured organization to be expected for an adaptation (Williams, 1966). The question is, an adaptation for what?

CONCLUSION

There have been proposed some thirty or so functions for play (Baldwin, 1986). While it is not clear which of the extant theories (Bekoff & Byers, 1998; Burghardt, 1998) may be supported by the present findings, the greater knowledge that is emerging of the organization and developmental changes occurring in play fighting can be used to test many of these theories. For example, Thompson (1998) posits that play fighting is used to assess one's own prowess relative to others. A prediction that emerges from this hypothesis is that an individual should do its best to win the play fight. After all, the proposed function of play in this hypothesis is to assess its relative skill level against that of its peers (Thompson, 1998).

Our data on anchoring seems to be evidence against this hypothesis. By not anchoring itself, the juvenile rat is making it less likely that it will be able to win the contest. However, this conclusion must be viewed as tentative, as it is still not clear what constitutes winning and losing in such contests. Perhaps, instead of competing, the animal is gaining information about itself, for example, how far can it be pushed and how far it is willing to go (Biben, 1998; Pellis & Pellis, 1998b). A fuller understanding of the actions performed during play fighting, and how they are modified with age, context and experience, provides a data base which can be more effectively used to develop decisive tests of specific functional theories.

CHAPTER FOUR

Experience and cortical control over the pubertal transition to rougher play fighting in rats.

ABSTRACT

With the onset of puberty, play fighting in rats decreases in frequency and the tactics of attack and defense that are used are rougher. Previous studies have shown that the changes in the frequency of play and in the use of defensive tactics arise independently of social experience. Furthermore while the former involves subcortical regulation, the latter depends on cortical mechanisms. In this study, the possible mechanisms regulating the developmental changes in the tactics of attack were examined. Two experiments were conducted using male rats. In the first study, rats reared in isolation from weaning were compared to rats reared in pairs, and were tested in the juvenile and early post-pubertal phases (30 and 60 days post-natally). In the second experiment, rats with the cortex removed shortly after birth were compared to sham-treated controls, and were tested in pairs at both the juvenile and early adult phases (30 and 90 days). Two measures of roughness, derived from previous studies, were measured. Results showed that isolation-reared rats had the typical age-related changes in roughness of attack, whereas decorticated rats failed to show this age-related modulation, maintaining, or even exaggerating, the juvenile-typical pattern of attack. These findings suggest that social experience is not needed for this developmental change to occur, and that an intact cortex is needed to regulate this change in behaviour.

INTRODUCTION

Play fighting, as is typical of play in general, exhibits an age-related waxing and waning, with the juvenile stage being the most playful in the vast majority of species for which play has been reported (Burghardt, 1998; Fagen, 1981). Rats are no exception. Regardless of rearing conditions and methods of measurement, rats engage in play fighting more frequently as juveniles (Thor & Holloway, 1984). As the frequency of play fighting declines with the onset of puberty, another change occurs in many species, especially for the males; the play becomes rougher (Biben, 1986; Fagen, 1981). In rats, two types of changes in behaviour contribute to this age-related change in roughness.

In rats, play fighting involves attack and defense of the nape, which if contacted is gently nuzzled with the snout (Pellis & Pellis, 1987; Siviy & Panksepp, 1987). As juveniles, the most likely response to a nape attack is to rotate around the longitudinal axis of the body to a fully supine position. From this position, the defender can ward off further attacks by pushing and grabbing with all four paws (Pellis & Pellis, 1987). With the onset of puberty, males are more likely only to rotate partially, maintaining ground contact with one or both hind paws (Pellis & Pellis, 1990). From the partially rotated position, the defender can grab and push the partner with its forepaws, push against the partner with its hip, or rear and turn to face the partner (Pellis & Pellis, 1987). Therefore, one change in roughness is that of switching to the more frequent use of a defensive tactic that allows for more effective defense and counterattack (Pellis, 2002). However, whether adopting the partial or the complete rotation tactic, post-pubertal male rats are more likely to escalate to serious fighting (Pellis & Pellis, 1991; Smith, Fantella & Pellis, 1999;

Takahashi & Lore, 1983), suggesting that irrespective of the tactic being used, the rats are behaving differently.

When adopting the complete rotation tactic, the performer lies on its back and the partner stands on top, producing a readily identifiable pinning configuration (Panksepp, 1981). Detailed analysis of the movements by the on-top rat during pin using Laban Movement Analysis (LMA, see Methods), revealed that developmentally at puberty, the rats switch to the use of movements that increase their control over the actions performed by the on-bottom partner (Chapter 2). Quantification of two measures confirmed the robustness of this transition. The first is an LMA measure of movement intensity called Effort (see Methods). Post-pubertal rats use more Condensing Efforts, which reflect more controlled movements and are sometimes called 'Fighting Efforts' (Bartenieff & Lewis, 1980). In contrast, juvenile rats are more likely to use Indulging Efforts. Such Efforts reflect more relaxed movements, and their use appears to be coupled to the greater likelihood of successful counterattacks during the juvenile phase (Chapter 2). That is, as juveniles, the rats are more likely to organize their movements in a way that leads to the on-bottom rat gaining the advantages. This leads to a role reversal in which the on-bottom rat gains the on-top position.

This shift in relative advantage is supported by the second measure. When the on-top rat maintains weight bearing ground contact with its hind paws, it is free to use its forepaws to grasp and hold the partner. Also, irrespective of the partner's movements, the on-top rat can maintain its balance. In contrast, if the rat stands with all four paws on its partner,

then the forepaws, along with the hind paws, have to be used to maintain postural support, and the movements by the on-bottom partner are more likely to result in the unbalancing of the on-top animal (Chapter 2). In the former case, the on-top rat's weight, and hence postural support, is anchored on the ground, whereas in the latter, by standing on the partner, the on-top rat is placing its postural support on a spontaneously moving platform. The added stability from the anchored configuration leads to the on-top rat having more control over the partner's movements. Juveniles are less likely to anchor themselves than are post-pubertal rats (Chapter 2 & 3).

A major developmental question concerning these age-related changes in play fighting is with regard to the mechanisms that produce them. The waxing and waning of the frequency of play fighting appears to be dependent on the frequency with which rats launch playful attacks (Pellis & Pellis, 1990; Thor & Holloway, 1985, 1986). That is, playful attacks increase in the juvenile phase and then decrease with the onset of puberty, even though the probability of defense against an attack remains unchanged with age (Pellis, Field, Smith & Pellis, 1997). Furthermore, the age-related waxing and waning of playful attack occurs whether the cortex is present or has been removed at birth (Panksepp, Normansell, Cox, & Siviy, 1994; Pellis, Pellis & Wishaw, 1992). It appears that the age-related change in the frequency of play fighting is dependent on the maturation of a subcortical system (Spear & Brake, 1983; Siviy, 1998).

The waxing and waning of use of the complete rotation defense tactic is dependent on the presence of an intact cortex. If the cortex is removed at birth, juveniles will use the partial

rotation tactic at an adult-typical frequency (Pellis et al., 1992). Therefore, for the normal expression of this age-related change in play fighting, an appropriately functioning cortical mechanism is needed. However, even though the age-related changes in playful attack and in the use of the complete rotation tactic are dependent on different neural mechanisms, neither appears to be dependent on actual play experience.

For rats, it has been found that isolation during the juvenile phase leads to a variety of social and non-social deficits as adults (Einon, Humphreys, Chivers, Field, & Naylor, 1981; Hol, van den Berg, van Ree, & Spruijt, 1999; van den Berg, Hol, van Ree, Spruijt, Everts, & Koolhaas, 1999a; van den Berg, van Ree, & Spruijt, 1999b). One hour of play experience daily with a partner is sufficient to overcome these negative effects of social isolation, but less is not (Einon, Morgan, & Kibbler, 1978). When rats are isolated at weaning and then given play trials lasting only five minutes, they exhibit the typical waxing and waning of both playful attacks and complete rotations (Panksepp, 1981). Similarly, when isolated at weaning and tested at 60 days of age or later, rats show the age-typical lower frequency of playful attacks and complete rotations (Pellis, unpublished observations). Rats reared continually in sex-mixed or sex-segregated pairs or larger groups all show the age-related increase and decrease in playful attack and complete rotation (Pellis & Pellis, 1990; Pellis, Pellis & McKenna, 1993; Smith, Forgie & Pellis, 1998). That is, irrespective of the social experience during the juvenile and early post-pubertal phases, these features of play fighting exhibit the typical age-related pattern of change. This is not to imply that the magnitude of these changes may not be affected by experiential factors, but only that the pattern of change seems not to be.

In this study, we asked whether the age-related changes in 'control' over the partner, as measured by anchoring and LMA Efforts (Chapter 2 & 3), is dependent on social experience or not, and whether the control for this age-related change is dependent on cortical or subcortical mechanisms.

METHODS AND MATERIALS

Both experiments in this study used Long Evans male rats that were born and raised in the animal facility of the Department of Psychology and Neuroscience at the University of Lethbridge. All animals were maintained on a 12/12 hour light/dark cycle (light off at 1900 hours), and kept at a constant room temperature of 21-23°C. Water and food (Purina Rodent Chow) were available at libitum.

Experiment 1: The effects of isolation on play fighting

This experiment was designed to identify if social experience during development is necessary to achieve the age-related patterns of anchoring and Effort Qualities during play fighting.

Subjects

Twenty four Long Evans male rats were weaned at 20 days and divided into two groups of twelve. Rats for the control group were housed as pairs in 18 cm x 63.5 cm x 25 cm hanging stainless steel mesh cages, whereas the rats for the experimental group were individually housed in 18 cm x 25 cm x 21 cm hanging stainless steel mesh cages.

Procedure

At around 27 days of age, each subject was individually placed in a testing enclosure (50 cm x 50 cm x 50 cm) for a habituation period of 10 minutes for 3 consecutive days prior to testing. Immediately after habituation on the third day, subjects from the control group were isolated for 24 hours. After the 24 hour isolation period, subjects were videotaped in the testing enclosure with their pair mates for 10 minutes; they were then placed in their home cages. Subjects from the isolation group were also videotaped in pairs, using two isolates to form each pair. After testing, the pairmates were returned to their respective isolated homes. This procedure was repeated with habituation commencing at 57 days and testing at 60 days. All test trials were videotaped in the dark with a Sony 8 mm camcorder using the "Night Shot" feature.

Even though the isolates had 10 minutes of social experience at 30 days of age, earlier studies have shown that such a brief period of social exposure is insufficient to offset the deficits arising from being reared in isolation (Einon, Morgan, & Kibbler, 1978). Also, given that studies have reported significant social deficits by the age of 60 days as a result of lack of social experience in the juvenile phase (Byrd & Briner, 1999; Potegal & Einon, 1989; van den Berg et al., 1999a), we tested rats at 60 days for the post-pubertal trial instead of an older age (e.g. Pellis & Pellis, 1991), so as to avoid the greater likelihood of adult isolates escalating to serious fighting (Pellis, unpublished data). Also, previous data suggest that by 60 days, group housed rats are at or nearly at the adult typical frequency for anchoring and Condensing Efforts (Chapter 2 & 3).

Experiment 2: The effects of decortication on play fighting

This experiment was designed to identify if the cortex is needed to develop the age-related patterns of anchoring and Efforts during play fighting.

Subjects

This study examined the videotapes from a previous study done by Pellis, Pellis, & Whishaw (1992) in which six groups of four Long Evans male rats were used. Each group was composed of two intact and two decorticated rats, with the decortications performed in the first four days postnatally (see Whishaw & Kolb, 1985). Prior to the surgery, the rat pups were placed in a cooling chamber set at 0°C until they were anesthetized (which was determined by a failure to respond to the pinching of the tail or foot). The cortex above the rhinal fissure, including the medial frontal and cingulate cortex, was then removed by suction. Some tissue in the medial frontal lobe was spared and unintentional damage to the hippocampus occurred in some rats. However the caudate-putamen and thalamus were not injured (see Pellis et al., 1992, for details). Housing conditions were similar to those of Experiment 1 (see Pellis et al., 1992, for details).

Procedure

Each group was habituated in the testing enclosure (90 cm x 30 cm x 36 cm) with a 2.5 cm layer floor cover of processed corn cob for one hour the day before each testing day. Test day one (videotaping) started after an isolation period of 24 hours, a procedure which is known to increase the frequency of play fighting (Panksepp & Beatty 1980). All

rats were tested immediately after isolation. After testing, they were housed in their groups for 24 hours. They were then isolated again and tested a second time 24 hours later. Groups 1 and 2 were tested in intact-intact/decorticate-decorticate pairs on test day one and were tested in mixed group pairs, intact-decorticate, on test day two. Groups 3 and 4 were tested in the reverse order for counterbalancing. This procedure occurred at ages 30-40 and 80-90 days. Testing between 80-90 days occurred with the same pair mates at 30-40 days (i.e. rat 1 – rat 2; rat 3 - rat 4, etc...). Testing periods lasted 10 minutes and were videotaped under a red light by a 100 watt globe kept at a 20 cm distance from the testing enclosure. For further details see Pellis et al. (1992).

Data Collection and Analysis

Anchoring and Efforts were measured for the on-top partner when the pairs were in the pin configuration during play fights. The proportion of pins in which the on-top rat was anchored and used either Condensing or Indulging Efforts was recorded for each subject from each pair. These data were then used to compare across age classes and between experimental groups using Repeated Measures ANOVAs with follow-up comparisons using Scheffe's post hoc tests.

Anchoring

While in the on-top position during a pin, the rat typically places its forepaws on the on-bottom partner, whereas the hind paws can be placed in one of two locations – either standing on the ground or on the partner. To quantify this, if at least one of the hind paws maintained ground contact that was weight bearing, the rat was recorded as being

anchored. If the hind paws maintained weight bearing contact on the partner, the rat was recorded as not being anchored. If, at the end of the pin, the rat had maintained contact with the ground, it was given a score of 1, whereas if it maintained contact on the partner, it was given a score of 0. If, over the course of the pin, the on-top rat alternated between the two positions, it was given a score of 0.5 (Chapter 2).

LMA Effort Analysis

Laban Movement Analysis (LMA) is a movement notation system that describes both quantitative and qualitative aspects of human movement (Bartenieff & Lewis, 1980). LMA describes four categories of movement, Body, Effort, Shape, and Space (BESS) (Bartenieff & Lewis, 1980; Dell, 1977; Hutchinson, 1977). In this study, Efforts (see below) were scored, as these have been shown to be applicable for the description of movements by non-human animals (Fagen, Conitz, & Kunibe, 2000), and have been previously used to characterize the age-related change in the roughness of play fighting in rats (Chapter 2).

Efforts describe such features as intensity and velocity of the movement during an action. There are four Effort Factors: Weight, Time, Space, and Flow. Each Effort Factor ranges between two types of Effort Qualities - Indulging and Condensing (Chapter 2). Indulging Efforts can be seen as movements that are gentler and freer flowing than movements described as Condensing Efforts (Bartenieff & Lewis, 1980; Fagen et al., 2000; Laban, 1971). During a pin, the on-top rat could show no Efforts or several in succession.

Therefore, Efforts from each Factor (Weight, Time, Space, and Flow) were recorded from each pin and tallied up to provide Indulging and Condensing scores.

RESULTS

For the isolation experiment, there was no significant group difference in the use of Indulging and Condensing Efforts ($p < 0.05$), but there was a significant interaction between Indulging/Condensing Efforts and age ($F(1,6) = 17.76$, $p = 0.0056$). That is, for isolated and control rats, there was an age-related decrease in the use of Indulging Efforts and an age-related increase in the use of Condensing Efforts (Figure 1). With regard to anchoring, there were no significant group ($p > 0.05$) or age by group effects ($p > 0.05$), but there was a significant age effect ($F(1,15) = 11.76$, $p < 0.01$). That is, both isolates and controls increased the likelihood of anchoring with age (Figure 2). Therefore, there appeared to be no differences between isolation reared and pair reared rats for either of the two measures used.

For the decorticate experiment, there was a significant difference in the use of the Indulging and Condensing Efforts ($F(1, 11) = 5.69$, $p < 0.05$), a significant Effort category by experimental group interaction ($F(1, 11) = 9.98$, $p < 0.01$), and a significant age by group by Effort category interaction ($F(1, 11) = 5.52$, $p < 0.05$). That is, while the intact rats showed the typical age-related increase in Condensing Efforts and decrease in Indulging Efforts, the decorticate rats did not change, or even tended to exaggerate the juvenile pattern as adults (Figure 3). With regard to anchoring, there was a significant difference between groups ($F(1,12) = 35.42$, $p < 0.0001$). The intact rats showed the typical age-

related increase in anchoring, whereas the decorticate rats did not. If anything, the decorticate rats tended to show a decrease in anchoring with age (Figure 4). Indeed, the interaction between age and group approached significance ($F(1,12)=4.52, p=0.0551$). Therefore, for both measures used, decorticate rats differed from the intact controls by not showing the age-related changes typical of normal rats during play fighting.

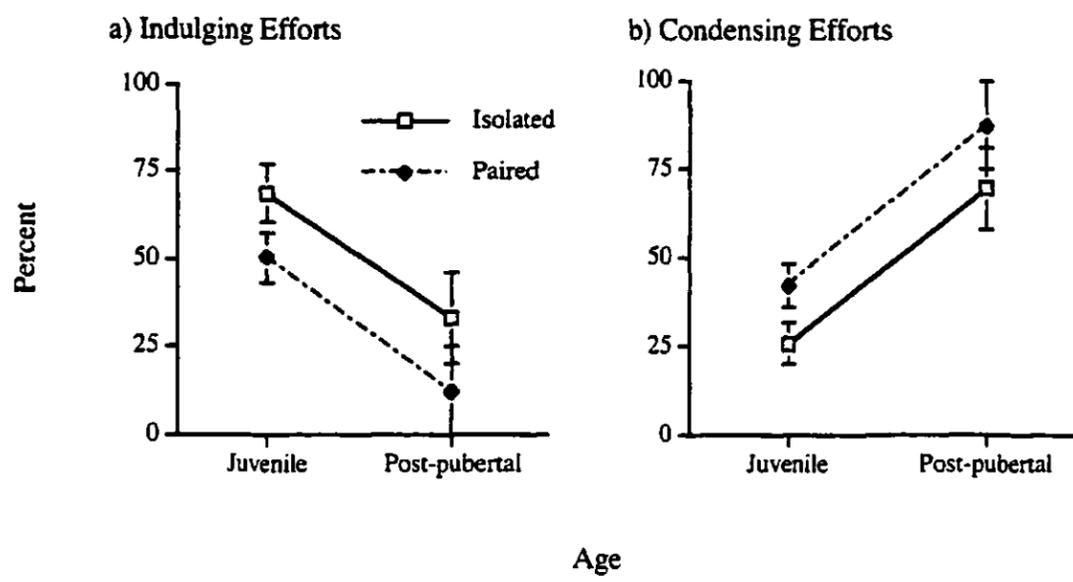


Figure 1. The change in the percent ($\bar{X} \pm SE$) of Indulging and Condensing Efforts used by the on-top rats during pins for isolation-reared and pair-reared rats as juveniles (30 days) and shortly after puberty (60 days).

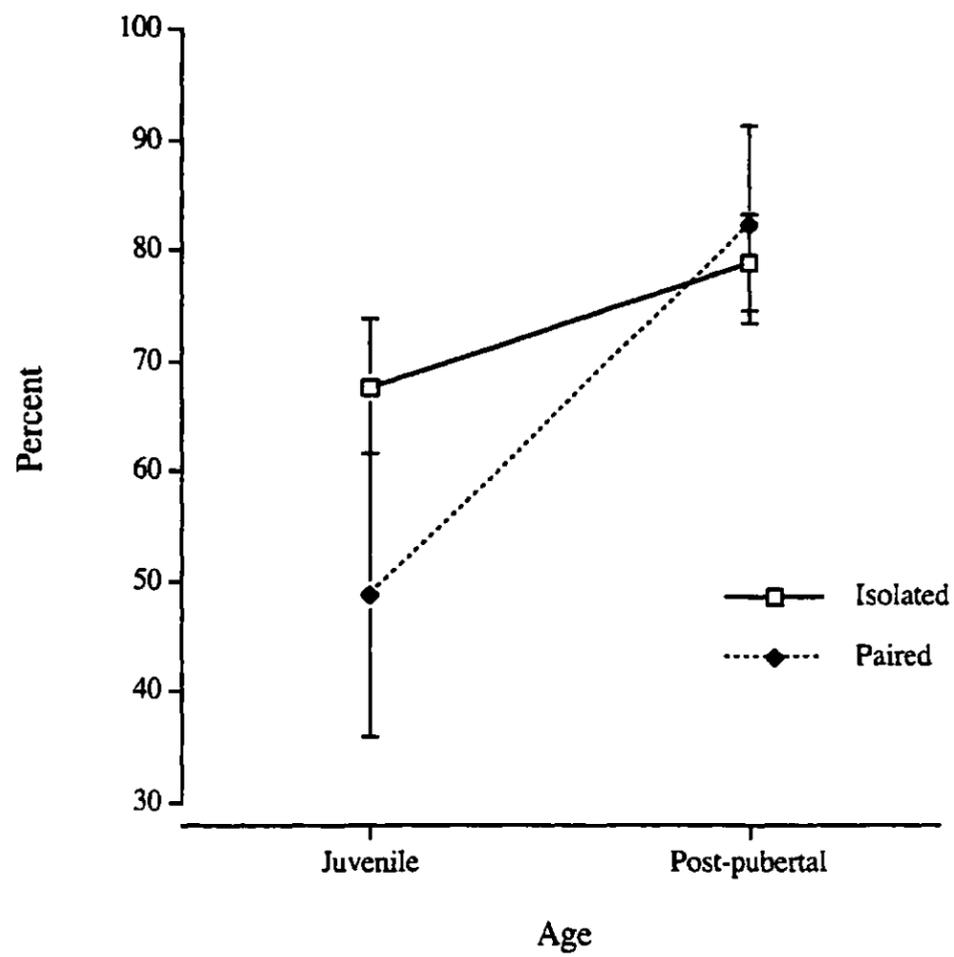


Figure 2. The change in the percent ($\bar{X} \pm SE$) of pins in which the on-top rat is anchored is shown for the isolation-reared and pair-reared rats in as juveniles (30 days) and shortly after puberty (60 days).

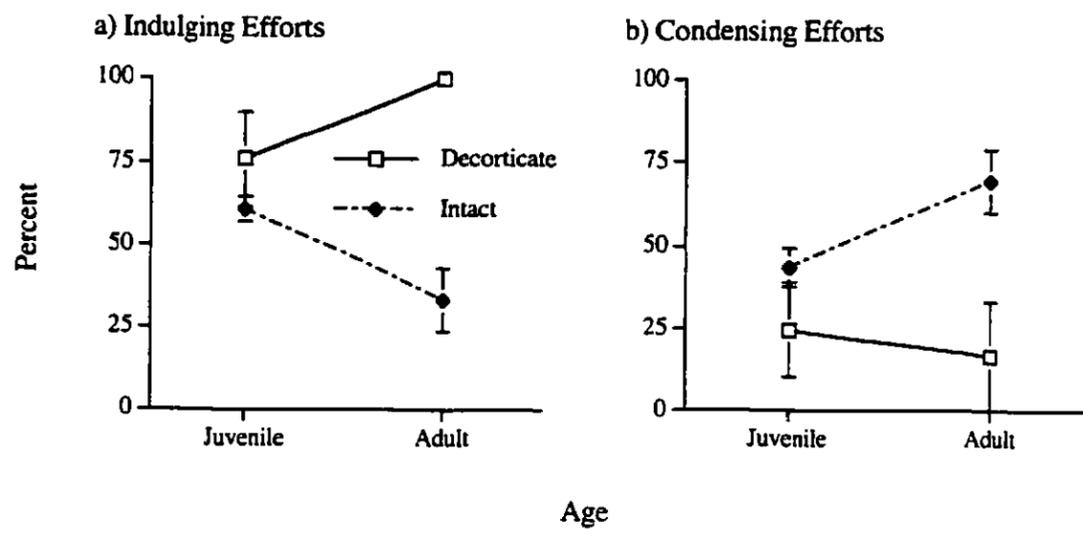


Figure 3. The change in the percent ($\bar{X} \pm SE$) of Indulging and Condensing Efforts used by the on-top rats during pins for decorticate and intact rats as juveniles (30-40 days) and adults (90-100 days).

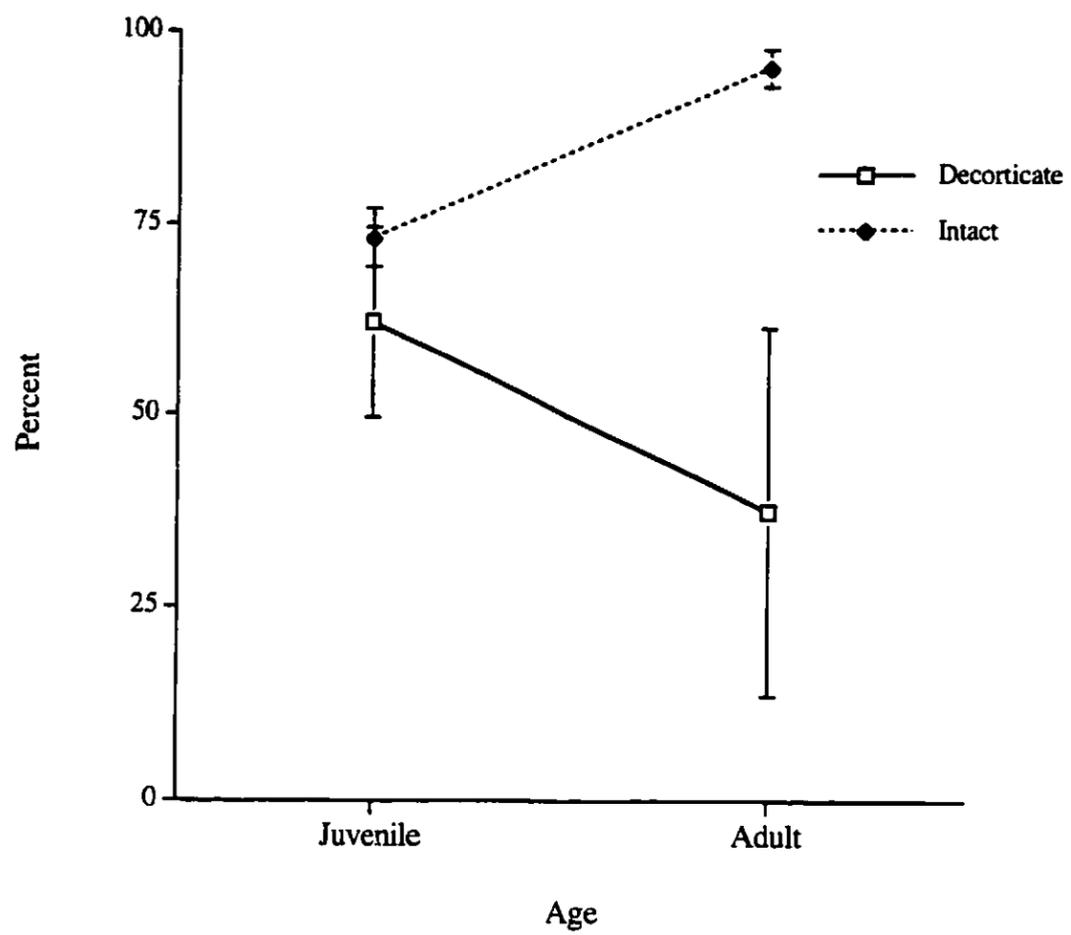


Figure 4. The change in the percent ($\bar{X} \pm SE$) of pins in which the on-top rat is anchored is shown for decorticate and intact rats as juveniles (30-40 days) and adults (90-100 days).

DISCUSSION

With the onset of puberty, rats begin to exert more control over their partners during play fighting. They do this by increasing the use of defensive tactics that can more effectively prevent the partner from gaining access to the nape and are more able to extricate themselves from such contact if it is attained by the partner (Pellis, 2002). In addition, irrespective of the tactic used, during the execution of the tactic, they position themselves, and use movements that are more effective in preventing the partner from gaining the advantage (Chapter 2 & 3). That is, with increasing age, rats use manoeuvres that can more effectively control the movements of the partner. In this study, we found that social experience, which includes play fighting, is not necessary for rats to exhibit this age-related change in control. That is, rats reared in social isolation showed the same age-related changes as rats that are reared with a same-age, same-sex companion. Therefore, neither general social experiences nor those specifically derived from play fighting, are necessary.

Rats decorticated as neonates, however, fail to show these age-related changes. The present data suggest that decorticate rats retain, or even exaggerate, the juvenile-typical pattern of control over the partner. These findings indicate that although the cortex is not needed to generate play fighting, or the various defensive (Pellis et al., 1992) and controlling tactics during play (this study), it is needed to switch the frequency of use of these movements with the onset of puberty.

The present findings add to the list of age-related modulations in several aspects of play fighting that are experience-independent. One such modulation is the subcortically regulated juvenile peak in the frequency of play fighting (Spear & Brake, 1983; Siviy, 1998) that results from an age-related increase and decrease in playful attacking (Pellis & Pellis, 1990, 1997; Thor & Holloway, 1985, 1986). The other two involve cortical mechanisms. There is a juvenile increase in the likelihood of using the complete rotation tactic to avoid or remove the nape from being contacted by the partner (Pellis & Pellis, 1987). The likelihood of using this tactic is lower in the early post-weaning phase for both males and females (Pellis & Pellis, 1997), and following puberty in males (Pellis & Pellis, 1990). In the absence of the cortex, use of the complete rotation tactic remains at a low frequency at all ages (Pellis et al., 1992).

The present study shows that in the absence of the cortex, the third age-related change, the level of control over the partner which is at its lowest in the juvenile phase (Chapter 2 & 3), remains at that low level following puberty. Therefore, while both the age-related modulation in complete rotation and in control are seemingly regulated by cortical mechanisms, they are regulated in different ways. In the juvenile phase, the cortex increases the use of the complete rotation tactic and decreases the level of control exerted during play fighting. Two possible hypotheses may account for this seeming difference in neural regulation. The first is that one mechanism may regulate both changes, as both lead to more prolonged play fights. By rotating to supine, a wrestling contest is promoted that leads to an extended interaction with lots of physical contact (Pellis & Pellis, 1987). By lessening control over the partner, the on-top rat allows for the increased likelihood

for the supine rat to counterattack successfully, overthrow the on-top animal, and gain the on-top position (Chapter 2). Indeed, counterattacks by the supine partner are both more common and more often successful in the juvenile phase (Pellis & Pellis, 1990). Thus, both increasing the use of the complete rotation tactic and reducing control over the supine partner, may act to increase the duration of play fights and the degree of body contact involved. In this way, a single signal from the cortex to subcortical mechanisms may regulate both changes in behaviour at the juvenile phase.

The second hypothesis is that while these two age-related changes may promote longer-lasting play fights with more bodily contact, their neural regulation may involve two distinct cortical circuits that are in turn synchronized by some as yet to be identified endocrinological signal. At present, there are no compelling data to support one hypothesis over the other. However, there are some data that suggest that while the hypothesis involving two separate circuits may be less parsimonious, it is possible. For example, there is another modulation in play fighting that is regulated by the cortex. Adult subordinate males use a different combination of defensive tactics when play fighting with a dominant versus when play fighting with another subordinate male (Hastings, Shimizu, Forgie, Kolb, & Pellis, in preparation; Pellis & Pellis, 1991; Pellis et al., 1992) or a female (Pellis & Pellis, 1990). Such partner-related modulation of play fighting is absent in decorticate rats, which play the same with all partners (Pellis et al., 1992). Thus, the cortex is necessary for regulating both the age-related and the partner-related modulation in the use of the complete rotation tactic. It has been recently shown that while damage limited to the prefrontal cortex abolishes the partner-related

modulation, it does not interfere with the age-related modulation (Hastings, et al., in preparation). That is, there are two separate cortical mechanisms for the regulation of the age-related and the partner-related modulation in playful defense.

CONCLUSION

A full wiring diagram for the regulation of play fighting requires not only the characterization of the subcortical mechanisms that motivate playfulness (Panksepp, 1998), but also that which enables different types of responses to predominate at different ages. Along with the age-related increase in the use of the complete rotation tactic by the defender at the juvenile phase (Panksepp, 1981; Pellis & Pellis, 1990), there is also a concurrent decrease in the level of control exerted by the attacker (Chapter 2 & 3). The present study shows that the age-related modulation in the level of control is experience-independent, and that like the modulation in the use of complete rotation (Pellis et al., 1992), is regulated by cortical mechanisms. How the different cortical and subcortical mechanisms that are involved in regulating play fighting interact with one another remain to be determined.

CHAPTER FIVE

GENERAL DISCUSSION

The study of play offers a challenge in that the functions of this behaviour remain obscure. This poses a problem because, unlike the case for many other behaviours, we cannot use the functions of play as a guide for research into how play behaviour produces those functions. For example, pre-copulatory behaviour can be analyzed and interpreted with regard to how it leads to copulation. Pre-copulatory behaviour, when used in play, especially in juveniles, has no clear fitness enhancing outcome, and hence cannot be analyzed and interpreted in terms of a specific outcome (Pellis, 1993). It is because of this, that it is difficult to know where to begin in the study of play. Given this problem, a useful first step is to describe how the animal moves during play in objective and accurate ways. In describing these movements, along with their possible neural substrates and developmental trajectories, we can develop an empirical data base to aid in the construction of theories about its functions.

For this thesis, Laban Movement Analysis (LMA) was used to describe how rats move during pinning when play fighting. As described in Chapter 2, LMA defined two new measures: Condensing Efforts and anchoring. These new measures have quantified the age-related differences in pinning, thus suggesting a developmental change in the way rats pin. The difference is that juvenile rats play more gently, that is, they use less Condensing Efforts and anchoring, than infant and adult rats (Chapter 2, Figures 2 & 4; Chapter 3 Figure 1). This contrasts with previous data which show that juvenile rats play more often than do both infant and adult rats (Thor & Holloway, 1984). The opposing

relationship between increased frequency and decreased roughness (see Figure 1 this Chapter), outlines a unique period of play fighting during the juvenile phase. In attempting to understand how the developmental changes occur, experiments in Chapters 3 and 4 measured the developmental changes in anchoring in rats with altered social context and environment. Results showed that in spite of partner unfamiliarity (Chapter 3, Figure 2) and social isolation (Chapter 4, Figures 1 & 2), the developmental changes in anchoring were not disturbed. This suggests that such changes are not experience dependant. However, as described in Chapter 4, it appears the cortex modulates this change. Rats which have been decorticated and still play as frequently as those who have remained intact, do not show a developmental change in roughness, if anything, there is a trend in the opposite direction. This suggests that decorticated adults may be even less rough than when they were juveniles (Chapter 4, Figures 3 & 4). More studies need to be done to establish which cortical systems are involved.

Before discussing the implications of the findings described above, their limitations need to be considered. Firstly, different pairs of rats often demonstrate different frequencies of pinning. For example, one pair of juvenile rats may perform 15 pins within 10 minutes, whereas another age-matched pair may perform 30 pins. The problem may be even worse when as adults the absolute number of pins decreases markedly, say between 5 and 10 pins per 10 minutes. Since anchoring could only be scored when the rats were pinned, the absolute occurrence of anchoring could not be compared between pairs and ages. To control for this problem, I compared the percentage of pins that involved anchoring. Unfortunately, in cases where few pins occur, a percentage score may grossly over or

underestimate the actual value just by chance. This may account for the large differences found between the different experiments of this thesis. In future studies, a more reliable way to control for such differences is by only scoring a standard number of pins, with that standard number set by the pair showing the least number of pins. That is, if all pairs perform at least 10 pins, one should only measure anchoring in the first 10 pins of all pairs. This will provide comparable numbers between pairs, and statistics applied to the absolute number of anchored pins performed. Despite these statistical concerns, however, all the experiments in this thesis showed that juveniles have lower levels of anchoring than at any other age, and so suggest that the developmental pattern shown here is robust.

Another limitation in using anchoring as a measure of the age-related differences in control characterized by LMA notation, is that it can only be scored during pinning. The problem is that while many species of animals play fight, not all animals pin during play fighting. In the absence of the pin, anchoring is lost as a useful measure. In order to capture what anchoring measures in rats, the study of play fighting in other species may require more complete LMA notation to identify other species-specific postural configurations that can be used to evaluate differences in stability during play fighting. That is, by observing how subjects position their bodies relative to one another, new markers for stability and the exertion of control within a play bout may be characterized. Certainly, anchoring is not the only way to increase stability, so as to enable more control, and perhaps different species express stability and control during play fighting in different ways. Nonetheless, for rats, anchoring is a robust behavioural marker for

stability and control that can be used as a meaningful substitute for processes captured by LMA scores.

PLAY: MOVEMENT, EXPERIENCE, AND DEVELOPMENT

Previous studies of play have described age-related changes in the behaviour of the defending rat (Pellis & Pellis, 1987, 1990, 1997). As the attacker approaches the nape of the partner, the defending rat can avoid nape contact by rotating its forequarters away from the attacking rat. As the rat does this, its nape moves further out of reach from the attacking rat. At this point, the rat can push the attacking rat away with its hips. This type of nape evasion is called a partial rotation because the defending rat only partially rotates its body, maintaining ground contact with its hindpaws. A complete rotation is when the defending rat rotates its body completely to a supine position. At this point, the defending rat is 'on the bottom' of the attacker. This on-top/on-bottom configuration, called pinning, has been used widely as an end-point measure for the study of play fighting (Panksepp, et al. 1984). From the supine position, the on-bottom rat can block further attempts to the nape with its forelimbs. The partial rotation tactic is rougher than the complete rotation because from the partial rotation, the defending rat can more effectively launch its own attacks (Pellis, 2002a).

Pre-juvenile and post-pubertal rats have higher frequencies of partial rotations during play fighting than do juvenile rats, which use complete rotations more often. Since pre-juvenile rats use adult-typical rotations (Pellis & Pellis, 1997), the increase in partial rotations from the juvenile to the adult phase is not due to maturation of the motor system

or to learning. Furthermore, as this developmental change in defense tactics is dependent on an intact cortex (Pellis, Pellis & Whishaw, 1992), this change in play fighting is somehow coupled with functions of an intact cortex during ontogeny. Naturally, these findings lead to more questions. Firstly, why does this age-related increase in roughness occur as play frequency decreases? Secondly, why is the cortex important for regulating this developmental change found in play fighting? In this thesis, I analyzed the behaviour of the partner standing on top of the supine defender. The analysis showed that with increasing age, the attacker used 'rougher' tactics in controlling the actions of its supine partner. That is, when both juvenile and adult rats perform complete rotations, adult rats still appear rougher than juveniles. Thus switching from mostly using complete to mostly using partial rotations cannot fully account for the age-related change in roughness in rat play. What does? Once this last question is better understood, speculations can be made about the first two questions.

A form of notation from Laban Movement Analysis (LMA, see Chapters 1 and 2), called Motif, was used to describe differences in roughness between the complete rotations performed by juvenile and by adult rats. The analysis revealed two previously undescribed differences between juvenile and adult pinning that contribute to the perceived change in roughness: 1. LMA Efforts, and 2. anchoring.

LMA Efforts

Juvenile rats use different Efforts (see Chapters 2 and 4) than do adult rats during play fighting. As youngsters, rats use more Indulging rather than Condensing Efforts and this

is reversed as adults. Indulging Efforts are a more relaxed and gentle form of movement and oppose Condensing Efforts, which are sometimes called 'Fighting Efforts' as they are more restrictive and forceful (Bartenieff & Lewis, 1980). That is, juveniles organize their movements in a gentler form when play fighting than do adults. When I interpreted this to be a play-specific feature, some other observations that I made during the course of this thesis raises a different interpretation.

Efforts were not observable from the video of infant rats, that is, rats in the prejuvenile phase. However, when observing infant rats play fighting in their home cages with the naked eye, I noticed many Effort-like movements. These Efforts were not as crystallized, or as intense, as the ones observed in juvenile or adult rats. Furthermore, the Efforts were integrated with Shape qualities (see Chapter 2). Some LMA theorists call Efforts that are not crystallized pre-Efforts. Pre-Efforts are found mostly in infants and the elderly, and are often coupled with Shapeflow. Shapeflow is sometimes viewed as a precursor to Effort Flow in human infants (for further readings on pre-Efforts and Shapeflow, see Kestenberg, 1982). Like Efforts, pre-Efforts have an Indulging and Condensing continuum, though it is not as intense as in Efforts. It would be interesting to identify which side of the Effort continuum infant rats lean towards. This would pose several challenges, the first being the difficulty in comparing integrated pre-Effort/Shapeflow qualities with the Effort qualities found in juveniles and adults. However, understanding the switch from the combination of Effort-like/Shapeflow movements in infants, to Effort qualities that are combined with Body and Space by juveniles and adults, may further our understanding of the development of play in rats.

The notated scores of juvenile and adult rats revealed that Efforts are used in conjunction with Body and Space, which are the structural components of movement and are often viewed as building an awareness of self and the environment. In contrast, there is very little Shape present in the juvenile scores, and none in the adult ones. Shape, particularly Shapeflow, is sometimes described as connecting the environment to the mover's inner drives (Bolster & Studd, personal communication, 1998)ⁱ. My preliminary observations indicate that Shapeflow is performed with pre-Efforts in infant rats, thus suggesting that the organization of movements in the periweaning period is different from later stages of development. If so, the age-related changes that I have described in terms of Efforts may reflect some general reorganization of movement, rather than one that is specific to play fighting. That is, as pre-Efforts and Shapeflow wane from infancy onwards, and Efforts along with Body and Space increase, then the use of Indulging qualities in the juvenile phase may arise as a byproduct. In this view, the pattern of Efforts used by juveniles reflects a transitional state, and should be expressed in many behavioural contexts, not just play. A more detailed developmental analysis, beyond the scope of the present study, is required to evaluate this possibility.

Anchoring

Anchoring, when the on-top rat maintains weight bearing ground contact during a pin (Chapter 2), is a new measure for the observed roughness described above. By anchoring, the on-top rat is best positioned for controlling the movements of its partner. Increasing control over another is more rough than relinquishing it. As with partial rotations,

juvenile rats have lower levels of anchoring than both infant and adult rats. During the juvenile phase, rats tend to be mostly unanchored when play fighting. Since infant rats have higher levels of anchoring than juvenile rats (Chapter 3), thus showing the adult-typical pattern, it is unlikely that anchoring increases from the juvenile to the postpubertal phases because of maturation of the motor system or because of learning. Furthermore, lack of social experience does not appear to alter age-related changes in anchoring (Chapter 4). Therefore, unlike the case for Efforts, the juvenile-typical reduction in the use of anchoring must reflect a play-specific modification of behavioural organization at this age.

Taken together, the changes in Efforts and in anchoring from the juvenile to the adult stage in the play fighting of rats both describe and quantify the increase in roughness. Furthermore, such changes coupled with the developmental changes in complete versus partial rotations and the frequency of play fighting illustrates the unique pattern of play fighting during the juvenile phase. Play frequency is low in both infant and adult rats, and high in juvenile rats (Thor & Holloway, 1984). In contrast, roughness and control, as measured by partial rotations, anchoring (and perhaps Efforts), is high in infants and adults, and low in juveniles (Figure 1). That is, play fighting in rats is rough, but during the juvenile phase, when play fighting is at its most frequent, it becomes gentler. Perhaps it is during such time that a window of opportunity opens and the benefits that play fighting may reap are enhanced. What are such benefits and why should they occur at the juvenile age?

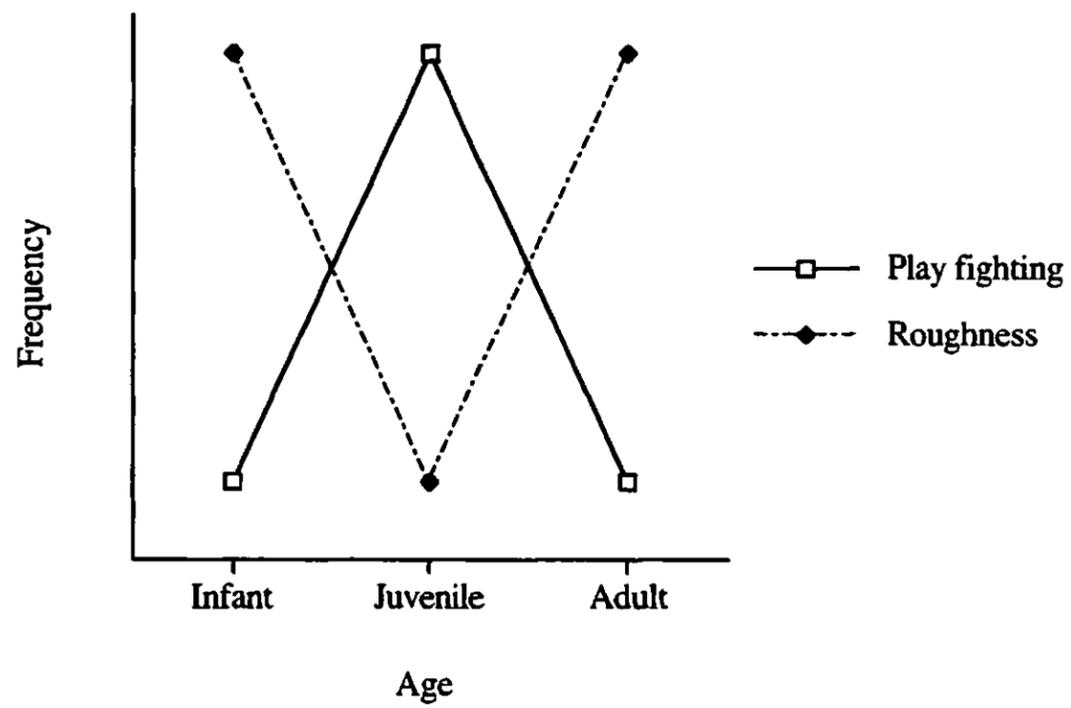


Figure 1. The developmental changes in roughness, as measured by partial rotations and anchoring, are contrasted to the developmental changes in frequency of play fighting in rats. During the infantile and adult phases, when the frequency of play fighting is low, play is rougher. In contrast, during the juvenile phase, when the frequency of play fighting is at its highest, play is less rough.

PLAY: BRAIN AND BEHAVIOUR

There are three known age-related modulations in play fighting, which appear to involve distinctive neural mechanisms. The increase and decrease in the frequency of play fighting seems to be regulated subcortically (Spear & Brake 1983; Siviy, 1998). The decrease and increase in the frequency of partial rotations and anchoring levels both appear to be cortically regulated (Pellis et al., 1992; Chapter 4). These age-related modulations in the content of play fighting are not experience-dependent, but rather, appear to depend on maturational changes of the brain. In addition, by play fighting being most gentle at the time that play is most frequent raises the possibility that it may provide valuable feedback for the maturing brain. The beneficial effects of juvenile play fighting may be either to facilitate the maturation of the nervous system, or to provide the experiences needed to acquire particular skills. An example of the first possibility is illustrated by the finding that play in mice, rats and cats has its peak frequency of occurrence at the same age as when the cerebellum is maturing (Byers & Walker, 1995). The implication of this correlation is that play provides valuable feedback to the developing cerebellum (Burghardt, 2001).

An example of the second possibility is illustrated by the finding that the behavioural deficits in the sexual behaviour of male rats following juvenile social deprivation (Larsson, 1978) are comparable to those of rats that were decorticated at birth (Whishaw & Kolb, 1985). The same behavioural abnormalities, in coordinating one's own movements with those of the partner, are seen in the play of juvenile rats that are decorticated at birth (Pellis et al., 1992). The implication here is that the lessons learned

from play fighting require an intact cortex to be encoded (Pellis et al., 1992). Another example further illustrates how play experience may influence the development of neural systems and the cognitive ability associated with those systems. Postpubertally, male rats establish dominance relationships (Adams & Boice, 1989; Lore & Stipo-Flaherty, 1984). Dominant males exhibit the typical age-related change in using complete rotations, whereas subordinate males do so only when play fighting with other subordinates or females (Pellis & Pellis, 1991; Pellis, Pellis & McKenna, 1993; Smith, Forgie & Pellis, 1998). When playing with a dominant, the subordinate responds in the juvenile-typical manner (Pellis & Pellis, 1992).

Decorticate rats lack the ability to modulate their play fighting with the identity of their partner (Hastings, Shimizu, Forgie, Kolb & Pellis, in preparation; Pellis et al., 1992). Again, lack of social experience in the juvenile phase disrupts this ability to modulate play with partner identity (Pellis, unpublished observations). The enhanced opportunity for playful experiences, along with the ability to process such experiences during the juvenile phase may contribute to the ability of reading the 'intentions' of the partner and identifying its social status. This possibility is supported by the finding that the content of play can be modulated with strangers of differing status (Smith et al., 1999), and that the identification of the strangers' status need not involve physical contact (Pellis, 2002b). Therefore, the modulation in play may require modifications that are dependent on interpreting subtle differences in movement by the partner. The increased frequency of play fighting and increased contact afforded by its greater gentleness may provide juveniles with a suitable context to learn about such subtle social information.

The experience-independent, age-related modulations in frequency and content of play fighting may provide an experience-expectant environment for brain development. That is, the developing system is designed to develop in an environmental context in which particular experiences are normally encountered (Greenough, Black & Wallace, 1987). Therefore, the environment can provide reliable feedback for the development of particular neural systems. For example, experiences in early development are thought to affect the development of the pituitary-adrenal axis which modulates stress-response sensitivity in adulthood (Bateson & Martin, 2000). Later, during the juvenile phase, experience may similarly be important for the development of 'social- and self-assessment'; mechanisms which appear to involve cortical systems (Hastings et al., in preparation). Such playful experiences have also been argued to be important for fine-tuning cerebellar motor systems (Byers & Walker, 1995). It must be remembered, however, that the opportunity for play may not be critical for normal development. As already noted in the General Introduction, some populations of squirrel monkeys play during the juvenile phase, while others, where food is scarce, do not. Monkeys from both types of populations have seemingly normal functioning social behaviour (Baldwin & Baldwin, 1974). Therefore, while it is possible that play fighting may provide experiences for fine-tuning several neural systems, play experience cannot be essential. Such fine-tuning may be achieved via several developmental trajectories, with play being but one of several sources of relevant experiences (Martin & Caro, 1985).

FUNCTIONS OF PLAY

The issue remains, however, that for rats, unlike many other rodents, the play fighting of juveniles has unique organizational features (Pellis, 1993; Pellis & Pellis, 1998a), such as the juvenile-typical gentle play reported in this thesis. These findings suggest that play fighting in rats is not just immature sexual behaviour, but rather, has been shaped by natural selection to enhance the occurrence of particular experiences. Given the subtle nature of these experiences, the loss of ability to fine-tune social responses in play, and in other social contexts, following a lack of social experience in the juvenile phase, or cortical damage after birth, it seems highly likely that if the juvenile play of rats does serve a function, it is likely to be to enhance cognitive skills.

ⁱ Bolster, G. and Studd, K. were my two supervisors for my program of studies in Laban Movement Analysis and the Bartenieff Fundamentals at the Université du Québec à Montréal.

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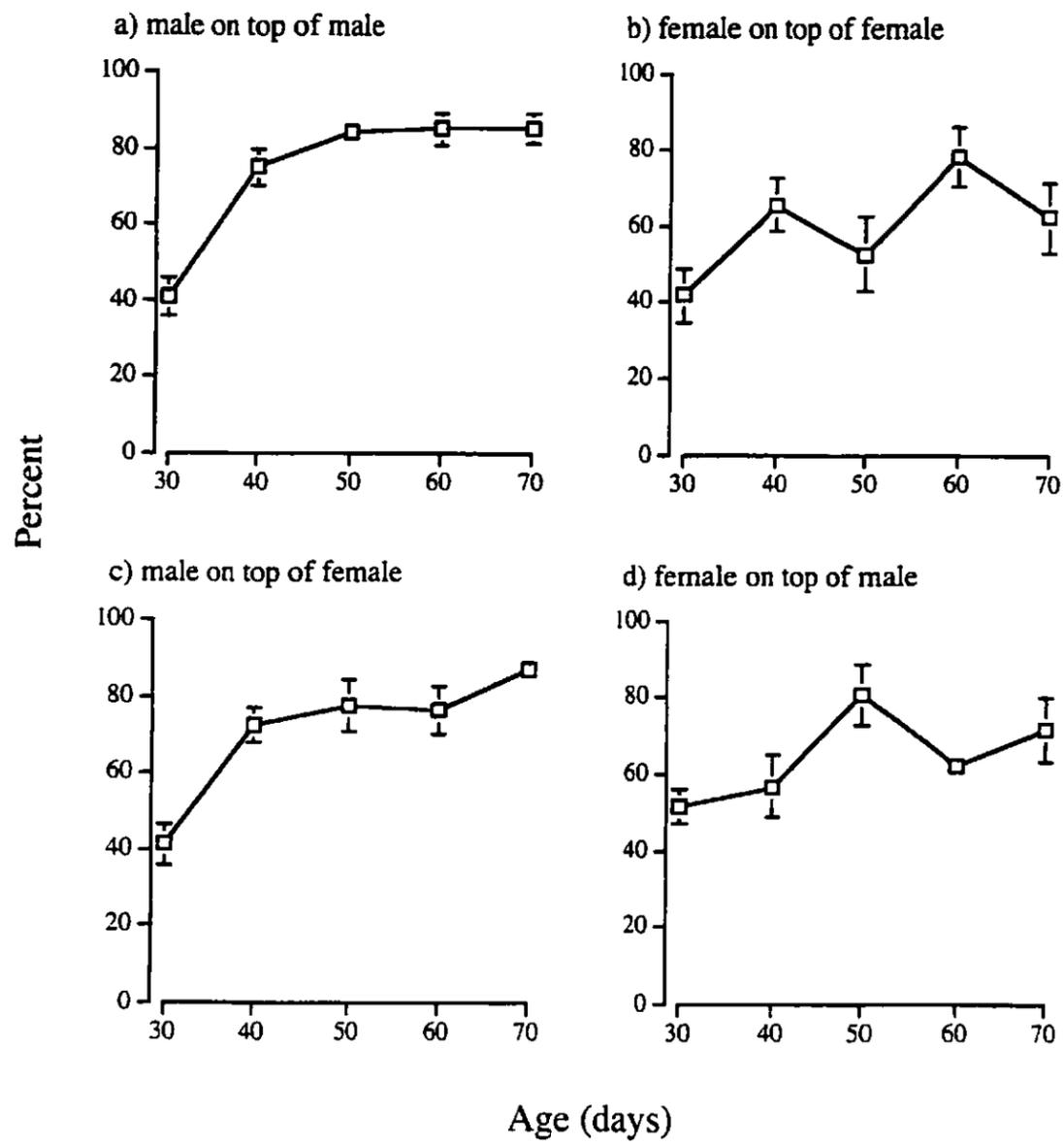
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Appendix 1. Changes in the percent of pins in which the on-top rat is anchored: $\bar{X} \pm SE$.

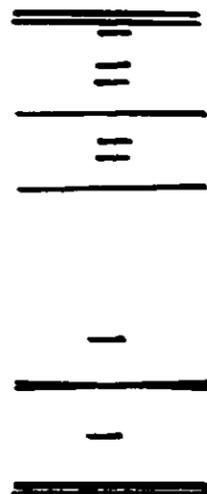


Appendix 2. Reference Legend of Most Commonly Used Symbols in Laban Movement Analysis.

NOTATION STAFF

		<u>Double Bar</u> lines indicate the beginning and ending of a movement sequence.
		A <u>Single Bar</u> line signifies phrasing and can be used to describe timing.
		<u>Horizontal Staff:</u> is read from left to right captures order of movement actions does not capture time duration of movements
		<u>Vertical Staff:</u> is read from the bottom up captures order, time duration, and simultaneous movements
		A <u>Tic</u> indicates rhythmic beats

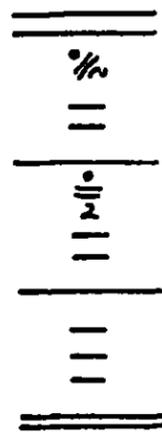
Examples:



REPEAT & CONNECTION SYMBOLS

	<p>All movements from the previous bar line until the repeat symbol are repeated.</p>
	<p>All movements from the beginning of the notation staff until the repeat symbol are repeated.</p>
	<p># indicates number of repeats performed.</p>
	<p><u>Ad libitum</u> symbol</p>
	<p><u>Caret</u> is used to connect two symbols</p>

Examples:



ACTIONS, PAUSES, & RELATIONSHIPS



Generic Action Stroke signifying that an action has occurred.
Length of the action stroke indicates time duration.



Gestural Action Stroke



Postural Action Stroke



Pause in the movement; mover hold the current position



'Active stillness'
The mover becomes still, however the position is not static.
The qualitative expression is active even in the absence of the movement.



Near



Contact



Grasp



Release

BODY

 Generic symbol for the whole body

Body Divisions & Actions

 Breath

 Centre of Support

 Naval Radiation

 Head-Tail Connection

 Head

 Tail

 Upper-Lower Division

 Upper Body

 Lower Body

 Body Half

 Left Body Half

 Right Body Half

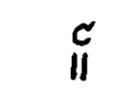
 Contralateral Movement

 Upper left to lower right

 Upper right to lower left

Body Areas

 Head

 Neck

 Shoulder Area

 Chest

 Waist

 Pelvis

 Torso

 Upper Torso

 Lower Torso

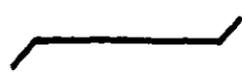
LIMBS & LIMB SECTIONS

	Generic symbol for a limb		
	Both Arms		Both Legs
	Left Arm		Left Leg
	Right Arm		Right Leg
	Upper Arms		Upper Legs
	Left Upper Arm		Left Upper Leg
	Right Upper Arm		Right Upper Leg
	Lower Arms		Lower Legs
	Left Lower Arms		Left Lower Leg
	Right Lower Arms		Right Lower Leg

ARTICULATIONS

↑↑	Both Shoulders	↵↵	Both Hips
↑	Left Shoulder	↵	Left Hip
↑	Right Shoulder	↵	Right Hip
↵↵	Both Elbows	⊕	Both Knees
↵	Left Elbow	⊕	Left Knee
↵	Right Elbow	⊕	Right Knee
↵↵	Both Wrists	⊕	Both Ankles
↵	Left Wrist	⊕	Left Ankle
↵	Right Wrist	⊕	Right Ankle
↵↵	Both Hands	⊕	Both Feet
↵	Left Hand	⊕	Left Foot
↵	Right Hand	⊕	Right Foot
↵↵	Both Sets of Fingers	⊕	Both Sets of Toes
↵	Left Set of Fingers	⊕	Left Set of Toes
↵	Right Set of Fingers	⊕	Right Set of Toes
↵	Left Index Finger	⊕	Left Big Toe
↵	Right Index Finger	⊕	Right Big Toe

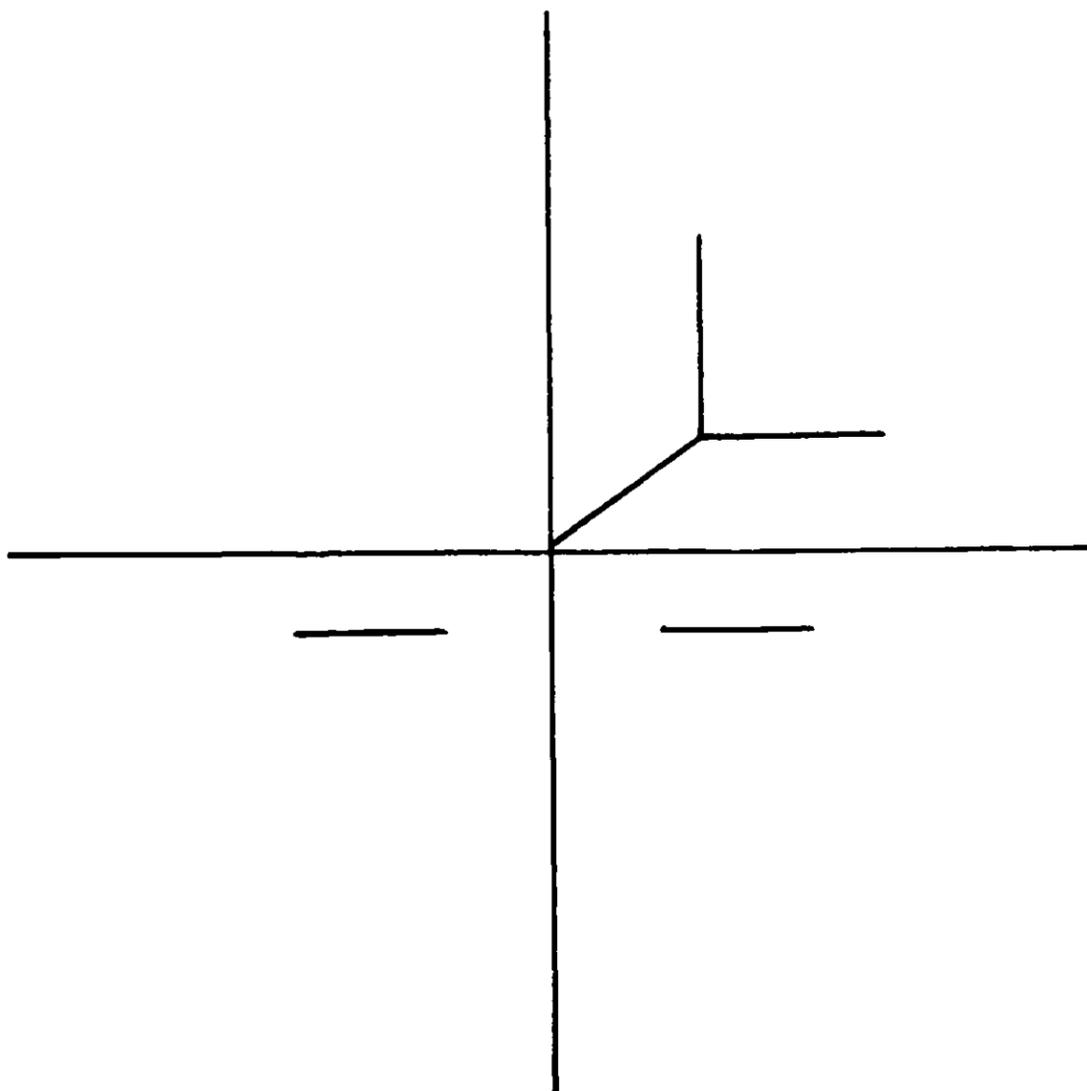
BODY ACTIONS

	Extension; Major Extension; Ad lib size of Extension
	Flexion; Major Flexion; Ad lib size of Flexion
	Generic Rotation
	Counterclockwise Rotation; Clockwise Rotation
	Support Symbol
	A = the object or the body part being supported B = the supporting object or body part
	Change in the body's centre of gravity
	Loss of Balance
	Jump Action
	Jump: take off and land on two limbs
	Jump: take off on two limbs and land on one limb

EFFORT

	Generic Effort Action Stroke
	Various bows used for describing Effort Rhythms

Effort Graph



EFFORT FACTORS & ELEMENTS

Effort Factors		Single Effort Elements			
		Indulging Efforts		Condensing Efforts	
	Weight Effort		Light Weight		Strong Weight
	Time Effort		Sustained Time		Quick Time
	Space Effort		Indirect Space		Direct Space
	Flow Effort		Free Flow		Bound Flow

EFFORT COMBINATIONS (STATES & DRIVES)

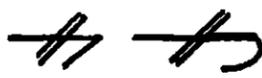
Effort States: combination of two Effort Elements

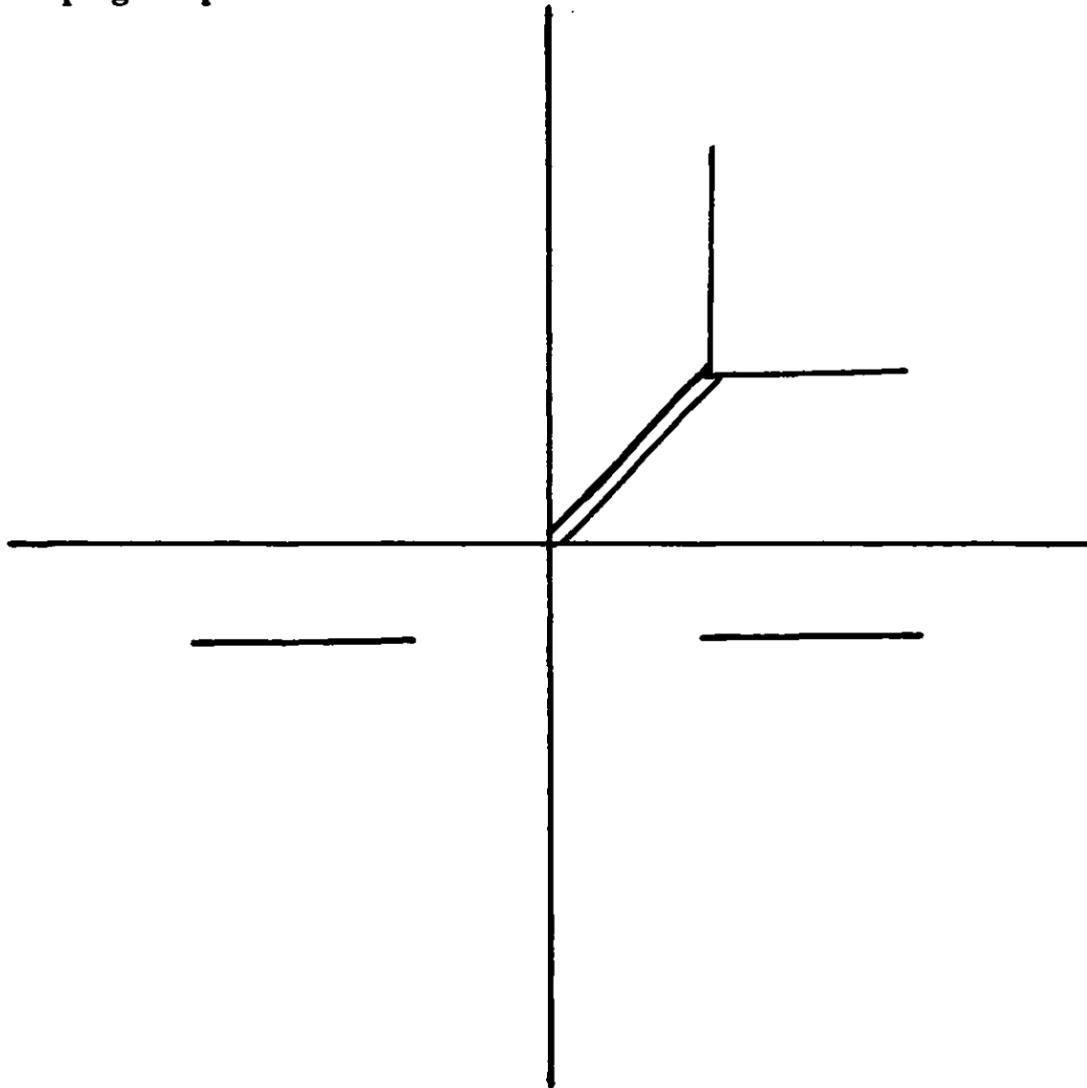
Effort States		Paired Factors		Element Combinations	
	Stable		Weight		
			Space		
	Mobile		Flow		
			Time		
	Rhythm		Weight		
			Time		
	Remote		Flow		
			Space		
	Awake		Space		
			Time		
	Dream		Flow		
			Weight		

Effort Drives: combination of three Effort Elements

Effort Drives		Paired Factors		Element Combinations
	Action (Flowless)		Weight	
			Time	
			Space	
	Passion (Spaceless)		Weight	
			Time	
			Flow	
	Spell (Timeless)		Weight	
			Space	
			Flow	
	Vision (Weightless)		Space	
			Flow	
			Time	

SHAPE

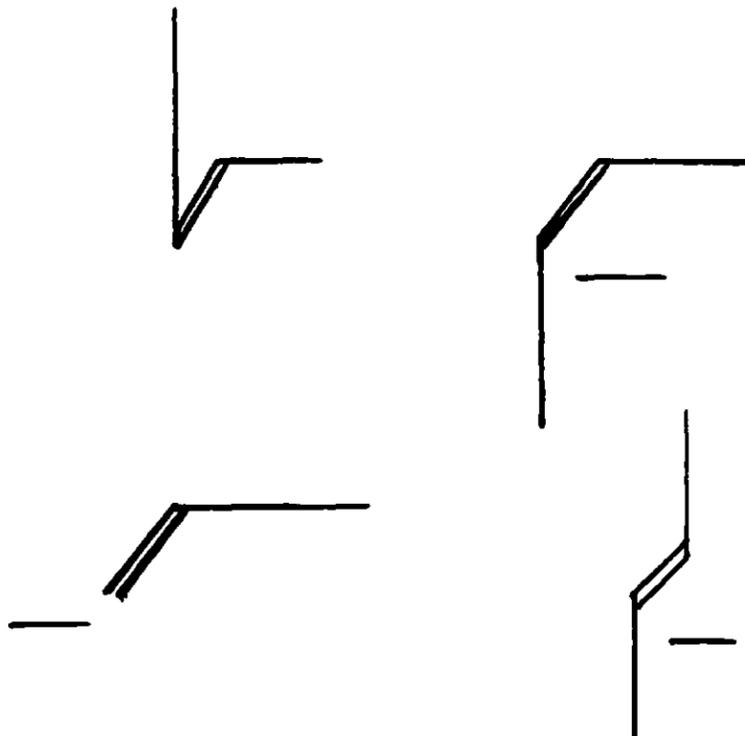
	Generic Shape Action Stroke
	Shaping
	Shapeflow
	Directional Shape: Spokelike, Arclike

Shaping Graph

Single Shaping Elements

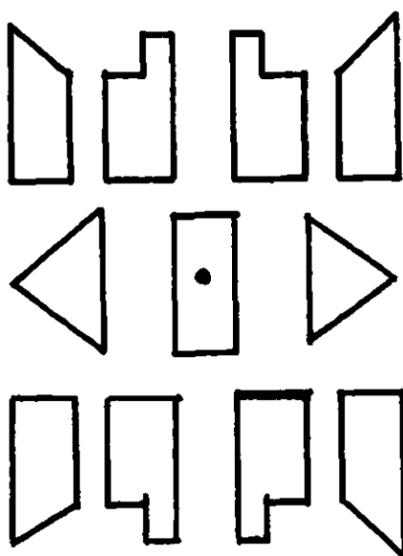
	Rising
	Sinking
	Advancing
	Retreating
	Spreading
	Enclosing

Examples of Shaping Elements Combinations:



SPACE

	Generic symbol for traveling
	Moving towards
	Moving away
	Generic spatial direction
	Ad lib spatial direction
	High
	Middle
	Low

Spatial Directions Graph



Forward



Simultaneously Forward & High



Simultaneously Forward & Low



Backward



Simultaneously Backward & High



Simultaneously Backward & Low

	Sideward Left
	Simultaneously Sideward Left & High
	Simultaneously Sideward Left & Low
<hr/>	
	Sideward Right
	Simultaneously Sideward Right & High
	Simultaneously Sideward Right & Low



Simultaneously Sideward Left & Forward



Simultaneously Sideward Left, Forward & High



Simultaneously Sideward Left, Forward & Low



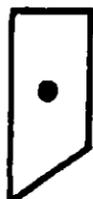
Simultaneously Sideward Right & Forward



Simultaneously Sideward Right, Forward & High



Simultaneously Sideward Right, Forward & Low



Simultaneously Sideward Left & Backward



Simultaneously Sideward Left, Backward & High



Simultaneously Sideward Left, Backward & Low



Simultaneously Sideward Right & Backward



Simultaneously Sideward Right, Backward & High

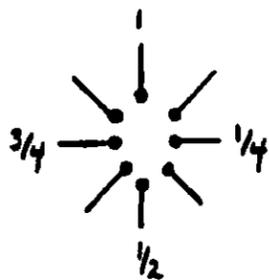


Simultaneously Sideward Right, Backward & Low

Spatial Pins

	<p>Various styles of Pins</p>
	<p>Location: box represents space (i.e.; room) Pin designates location within the space</p>
	<p>Facing: box represents space (i.e.; room) Pin indicates direction mover is facing</p>
	<p>Surface of body part or object, Pin designates which area on the surface.</p>
	<p>i.e.: symbol for head (see Body section p.109)</p>
	<p>Pin indicates which surface area of the head: top of the head, face, chin, back of the head</p>

Number of rotations



$\downarrow^2 = 2$ full rotations

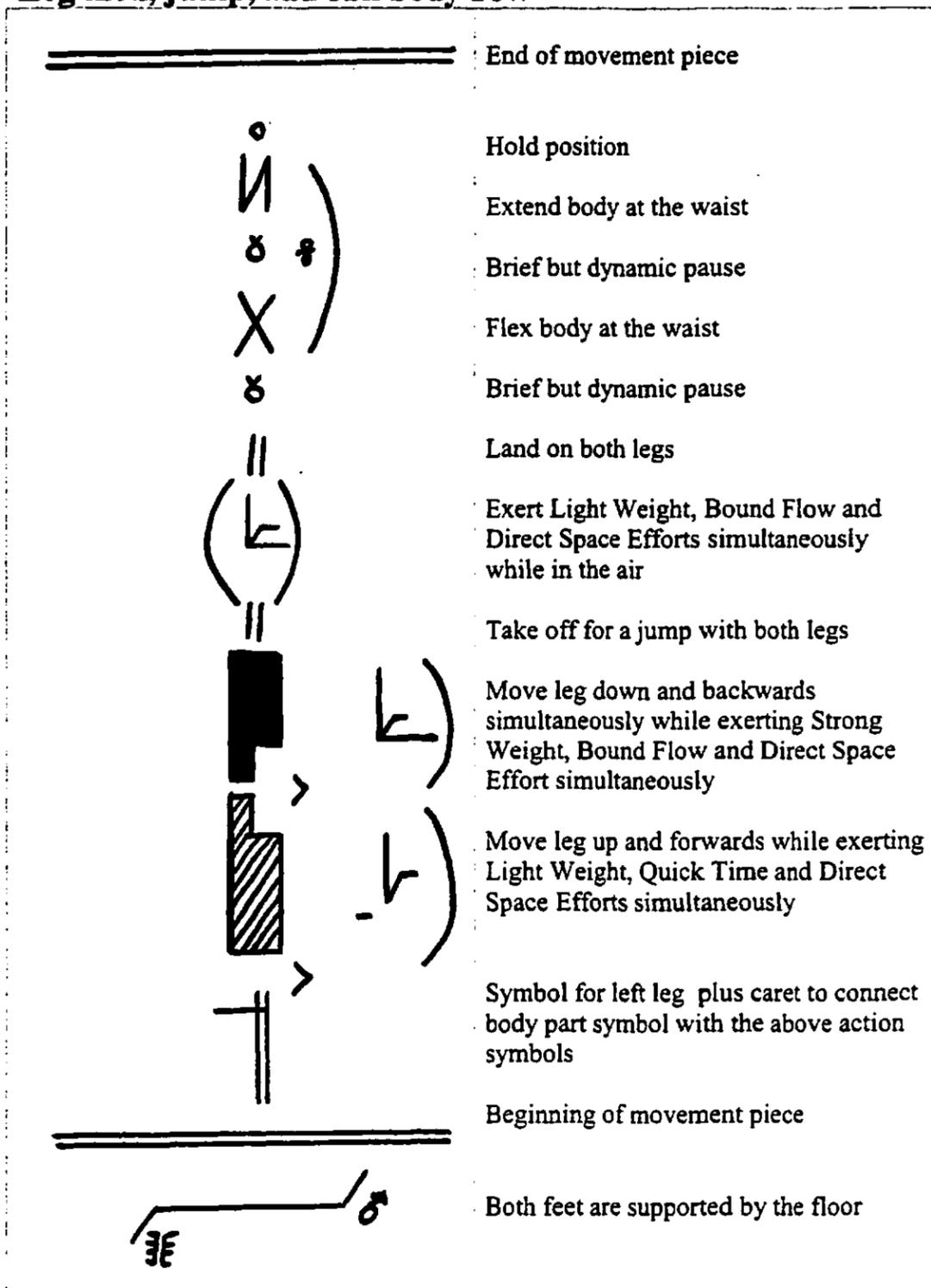
Examples:

= 3/4 clockwise rotation

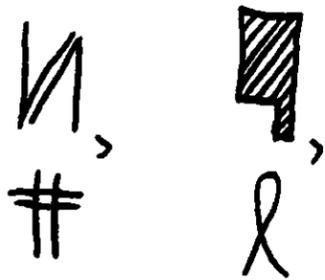
= 3 full counterclockwise rotations

Appendix 3. Some examples of Motif

Leg kick, jump, and full body bow

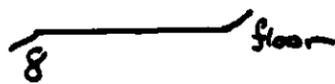


Moving from sitting on a chair to standing position



End of movement piece

Both knees extend as the upper body simultaneously moves up and backwards

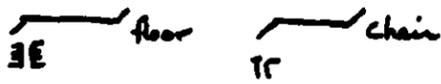


The whole body is now being supported by the floor



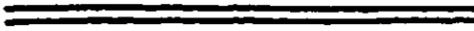
The upper body simultaneously moves down and forwards as both hips simultaneously move up and backwards

Beginning of movement piece



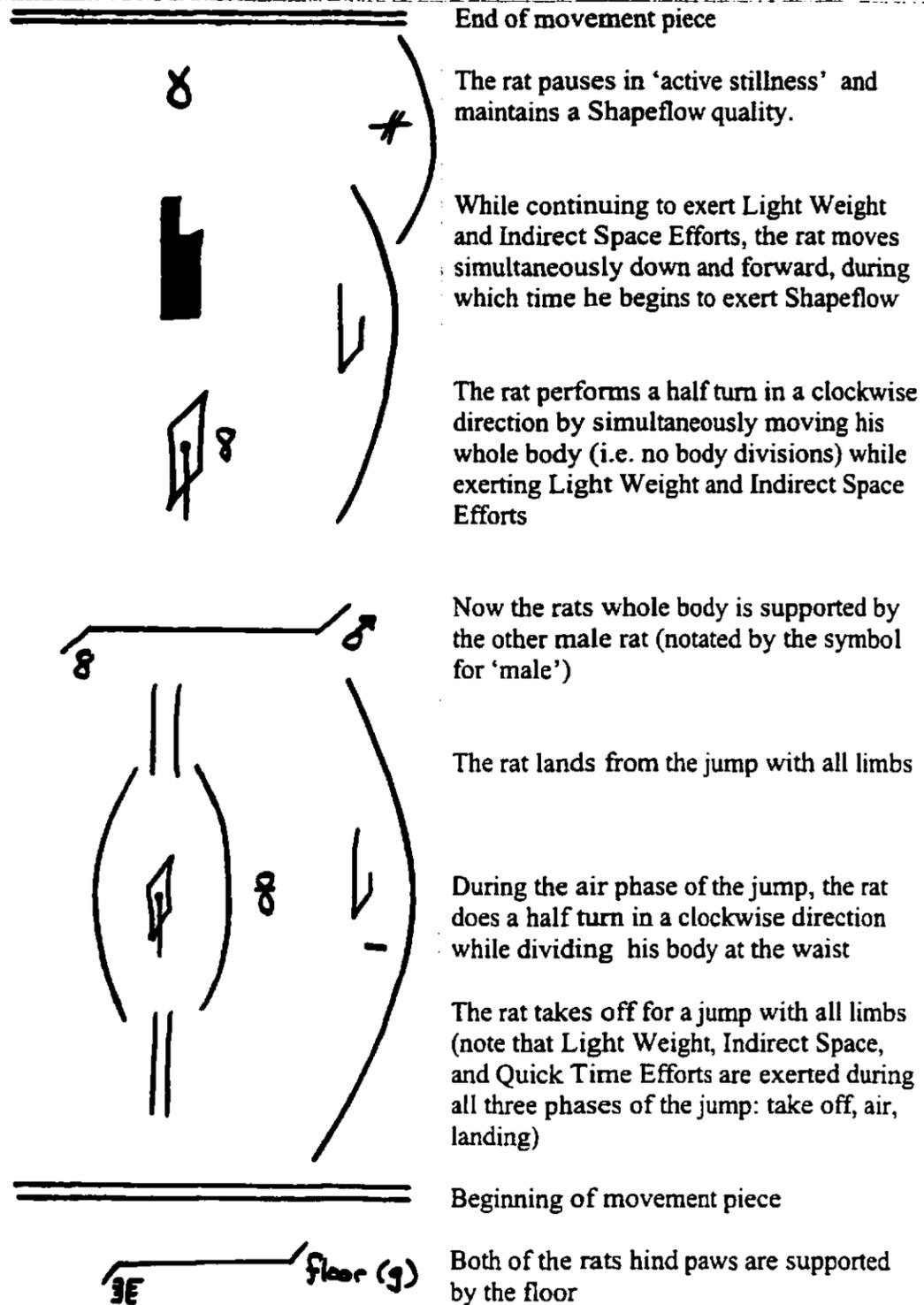
Both feet are supported by the floor and both hips are supported by a chair

Clapping of the hands

	End of movement piece
	Left hand and right hand make contact
	Left hand and right hand break contact
	Rhythmic beat, accent
	Left hand and right hand make contact
	Left hand and right hand break contact
	Left hand and right hand make contact
<hr style="border: 1px solid black;"/>	Single bar line
	Left hand and right hand break contact
	Left hand and right hand make contact
	Left hand and right hand break contact
	Rhythmic beat, accent
	Left hand and right hand make contact
	Left hand and right hand break contact
	Left hand and right hand make contact
	Beginning of movement piece

Appendix 4. Detailed description of the Motif Scores describing the on-top rat during a pin at 30 and 70 days (Chapter 2 Figure 1).

Juvenile (on-top rat)



Adult (on-top rat)



End of movement piece



Ad lib number of times to repeat movement piece from the beginning of the notation



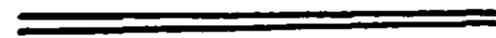
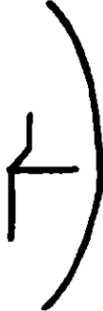
Lower body does one action



Upper body does one action while exerting Strong Weight, Bound Flow and Direct Space Efforts



Lower body does one action (symbol for lower body connected to general action stroke with a caret) while exerting Strong Weight, Bound Flow and Indirect Space Efforts



Beginning of movement piece



The rats lower body is supported by the ground while his hands are being supported by the other male rat (notated by the symbol for 'male')