Motor preparation and sexual action: a psychophysiological perspective on sexual motivation
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Sexual motivation: A psychophiological perspective

Introduction

Motivation is a construct used to understand the generation of actions. This thesis focuses on sexual motivation, more specifically on the generation of sexual desire and sexual action in humans. In clinical practice problems regarding sexual motivation concern sexual desire that is either too low or too high. Hypoactive sexual desire, a chronic lack of sexual desire, sexual fantasies, and sexual initiation, is a common sexual complaint (Simons & Carey, 2001) that is considered to be relatively difficult to treat (Pridal & LoPicollo, 2001). Hypersexuality, described as recurrent, intense sexually arousing fantasies, urges, or behaviors leading to negative personal and psychosocial consequences (Kafka, 2001), may be related to sexually coercive behavior, which is a serious social problem (Prentky, 2003). Insight into the behavioral mechanisms through which sexual action is instigated and regulated is needed to improve the treatment of disorders of sexual motivation.

Sexual motivation can only be inferred from the observation of sexual behavior and, in particular, from behaviors that allow us to infer sexual arousability and the direction and strength of neuronal feedback systems (Pfaus, 1999). Pfaus states that, in this respect, sex is not different from systems that regulate other drives like hunger, thirst, or thermoregulation. It is inferred that an animal is hungry by how much of its attention is spent searching for food, or by the latency to initiate feeding when food is available. The same is true for sexual motivation; high sexual motivation may be derived from greater sexual arousal, or from the thresholds for the initiation of sexual arousal, copulation, and orgasm. In animal
research, sexual motivation is inferred from, for example, how much time an animal spends searching for sex, how willing an animal is to work for sex, or from the latency too initiate sexual contact when a sexual partner is available. Obviously, ethical concerns restrict what we can observe in humans. Consequently, much research on sexual motivation has to rely on data obtained through questionnaires and retrospective reports. The most direct means for the investigation of sexual motivation is to study the process of action generation itself. In humans the focus of such research has been mainly on genital arousability. It may, however, be advantageous to include various measures of appetitive and consummatory responses to obtain a more complete picture of the process of action generation. The purpose of the studies presented in this thesis was to explore an experimental paradigm through which the elicitation of action tendencies and sexual action in response to sexual stimuli\(^1\) can be studied in humans. Such a paradigm may help to specify the behavioral mechanisms underlying sexual actions. Eventually, the understanding of the behavioral mechanisms might add to the development of interventions for problems concerning sexual motivation, such as hypoactive sexual desire or sexual coercive behavior.

To put our view on sexual motivation - which served as the theoretical background of the empirical studies - into context, we will start with a brief discussion of the history of the concept of sexual motivation. We will review the concepts libido, lust and drive that were introduced by psychoanalytic theory. After that, appetitional theories of sexual motivation, and the concept of arousability will be discussed. Incentive motivation theory and the close relationship between emotion and motivation will be elaborated upon. Then, current knowledge about neurobiological mechanisms of emotion and motivation will be discussed; brain systems involved in emotion and motivation, the role of dopamine, and relevant imaging studies in humans are reviewed. Sexual motivation and sexual desire will be considered in the light of that knowledge. A model will be presented in which sexual action and the subjective

\(^1\) As will be discussed in this chapter, stimuli are not intrinsically sexual. However, for reasons of readability we use the term 'sexual stimuli' for stimuli that have the potential to elicit sexual responses. Likewise, we will use the term 'emotional stimuli' for stimuli that have the potential to elicit emotional responses.
experience of sexual desire result from the processing of sexually
competent stimuli that energize emotion and motivation circuits in the
brain, resulting in bodily changes that prepare for sexual action. These
bodily changes are hypothesized to include specific genital responses as
well as more general somatic motor preparation. Subsequently, the
paradigm that is used to study sexual action tendencies and sexual
action will be discussed. In this thesis, Achilles tendon modulation was
explored as a measure for general somatic motor preparation in response
to sexual stimuli. The rationale for the use of Achilles tendon reflex
modulation will be explained, and the studies on sexual arousal, motor
preparation, and sexual action that are brought together in this thesis will
be introduced.

Concepts of sexual motivation: From drive towards incentive
motivation.

Overall, three points of view in motivation theory can be distinguished
(Mook, 1996). From a psychodynamic view urges or impulses are
sources of motivation. In this view actions are driven by psychic energy,
produced by tensions from within our bodies. From a behaviorists view, in
contrast, actions are explained by influences from the outside. Thoughts,
feelings and actions are elicited by environmental events, taking place
outside the organism. Third, from the perspective of cognitive
psychology, thoughts, beliefs, and judgments determine which actions
take place. Across these views runs the biological perspective, with the
focus on how urges, environmental events, or cognitions, are translated
into actions by the physiological processes within the behaving organism.
As we will see, the evolution of the concept of sexual motivation parallels
that of more general concepts of motivation, which developed from
internal drive theory to incentive motivation or information processing
theories.

Sexual motivation as an internal drive
The most influential drive theory on sexual motivation in humans is the
psychoanalytic theory of Freud in which sexual motivation was seen as a
constant force (Everaerd, Laan, Both, & Spiering, 2001). For sexual
desire Freud (1953) preferred the use of the word libido. Libido, according to Freud (1964), is fuelled by the sexual instinct, which arises from a source within the body. Freud explicitly stated that that libido does not arise from an external stimulus. "An instinct, then, is distinguished from a stimulus by the fact that it arises from sources of stimulation within the body, that it operates as a constant force and that the subject can not avoid it by flight, as is possible with an external stimulus" (p. 96). Freud conceived of the instinct as energy that pushes into a certain direction. From that push-factor the German word 'Trieb', drive, is derived. Thus the sexual instinct comes from a source within the body, it operates as a constant force, and the subject can not escape from it as is possible in the case of an external stimulus. In this view libido is the result of an internal bodily tension, and there would be a need to neutralize this state. Elaborating on the drive view, William Reich (1978, in Pfaus, 1999) proposed that sexual tension creates a biological energy that is released during orgasm. Sex is necessary to reduce tension, and pleasure is associated with tension reduction. There is supposed to be a necessity to release the tension; an inability to let go would result in neurotic or in violent behavior.

Whether sexual desire arises from internal states, or whether it arises when attractive stimuli are presented, is a long-standing controversy. In disagreement with the drive view, it was argued that sex is not necessary to survival in the way that food and water are and should be regarded as an appetite rather than a drive (e.g. Beach, 1956). Beach (1956) noted that "no one ever died of a lack of sex" (p. 3), and stated that although sex is indispensable for a species, it is not indispensable for an individual. He concluded that there is no evidence for any adverse effects of sexual abstinence: "No genuine tissue or biological needs are generated by sexual abstinence .... What is commonly confused with a primary drive associated with sexual deprivation is in actuality sexual appetite, and this has little or no relation to biological or physiological needs" (p. 4).

Sex as an appetite

Hardy (1964) proposed an appetitional theory of sexual motivation, which is based on cognitive expectancy and affective theory. In this view, sexual motives are not explicable in terms of biological need or tension, but are based on learned expectations of an affective change. These
expectations are aroused by stimuli that are associated with affective states due to previous learning. The learning is a result of actual experience or imaginal processes. Hardy postulated that stimulation of the genitals and the experience of orgasm are innately pleasurable. The pleasure accompanying genital stimulation and orgasm forms the affective base for motivational development. Stimuli may become associated with it and as a consequence function as cues leading to sexual arousal and desire. As erotic experiences are repeated, the greater the association values of the cues, and the wider the range of cues. On the other hand, habituation processes can occur wherein the repetition of a given activity produces a diminished affective response. Hardy acknowledges that sexual motives are not restricted to the learning of positive expectations (the approach type), but also include the learning of negative expectations (the avoidant type), or a combination of both (the ambivalent type). Hardy’s distinction between sexual motives is similar to Byrne’s conception of erotophilia-erotophobia (Byrne, 1986). Byrne also presumes the existence of an innate mechanism of sexual arousal, and claims that all human beings are born with erotophilic, or positive emotional responses to sex. The acquisition of positive (erotophilic) and negative (erotophobic) emotional responses to sex involves the pairing of sexual cues with emotion-producing reward and punishment (Byrne, 1986).

Sexual motivation and arousability
Whalen (1966) underlined that sexual motivation is controlled by both biological and experiential determinants. Whalen defined six basic components of sexual behavior: (1) Sexual identification, or the gender role of an individual; (2) Object choice, or those persons or objects toward which an individual directs its sexual activities; (3) Sexual gratification, or the reinforcement, reward or sexual pleasure associated with or caused by sexual activities; (4) Sexual arousal, or the momentary level of sexual excitation; (5) Sexual arousability, or an individual’s characteristic rate of approach to maximum arousal as a result of sexual stimulation; and (6) Sexual activity, or the sexual behavior exemplified by reported fantasy and desire as well as by observed or reported behavior. In Whalen’s view, sexual motivation is comprised of sexual arousal and sexual arousability. The sexual motivation of an individual may be represented by a specification of the state of these two components. Arousal is modulated
by the presence and absence of relevant external or internal stimuli. Individuals become conditioned with respect to which stimuli are particularly effective in inducing arousal. Arousability is determined not only by the amount of increment of arousal, but also by the absolute number of stimuli that simultaneously arouse the individual and the number and effectiveness of stimuli that are sexually inhibiting. Like arousal, arousability is determined by learning and by the physiological state of the organism. As the physiological determinants hormonal state and the feedback effect of sexual activity are noticed. Experience influences arousability in the sense that, with experience, sexual arousal will occur through an increasing number of stimuli. Whalen underlined that the choice of the sexual objects toward which an individual directs its sexual activities should be distinguished from sexual motivation. There is no evidence indicating that sexual preference determines sexual motivation, or that motivation determines sexual preference. Whalen characterized his theory as an "energetic" or "arousal" theory in which the direction of motivation is considered independent of the motivational state. We will return to this distinction when we discuss the concepts of wanting and liking that are part of the incentive salience theory of Berridge (1996).

Whalen's concept of arousability is similar to Bancroft's (1989) concept of 'central arousability'. According to Bancroft, sexual arousability, together with cognition and affect, form the three dimensions of sexual appetite. In his view, sexual arousability points to a neurophysiological mechanism that determines the sensitivity of the sexual response system to internal and external stimuli. Both Whalen and Bancroft view hormonal factors as important determinants of sexual arousability. There is ample evidence that androgens influence sexual desire. Increasing levels of androgens in early adolescence are accompanied by increases in self-reported sexual desire (e.g., Halpern, Udry, Campbell, & Suchindran, 1993; McClintock & Herdt, 1996). Studies in hypogonadal men have shown that low levels of testosterone are associated with decreased sexual desire and sexual thoughts, and that sexual desire can be increased by androgen therapy (Bancroft, 1989). Also, in women low levels of androgens are associated with a lack of sexual interest (Sherwin, 1985a,b). In addition, psychophysiological studies in men have shown an effect of low testosterone levels on sexual arousal in response to erotic fantasy, but not on arousal in response to erotic film (Bancroft & Wu,
1983). Similar effects have been found in women (Laan, van Lunsen, & Everaerd, 2001). However, variation in testosterone levels within the normal range is not associated with variation in sexual interest (Bancroft, 1995), indicating that sex hormones do not control human sexual behavior, though act to support, or allow, sexual arousability.

**Incentive motivation**

Incentive motivation theories highlight the interaction of the internal state of the organism with relevant stimuli (Bindra, 1974; Singer & Toates, 1987). According to incentive motivation models sexual motivation is the result of the activation of a sensitive sexual response system by sexual stimuli that are present in the environment (Agmo, 1999; Singer & Toates, 1987). Once the sexual system interacts with the stimulus, the energetic aspect pushes the individual towards the sexual situation, while the stimulus pulls the individual in its direction. In this view, sexual motivation does not emerge through a deficit signaled by the hypothalamus, but through the attractiveness of possible rewards in the environment. Recently, Herbert (2001) proposed that sexual behavior may be thought of as a form of adaptation or response to a perceived deficit. He suggested that the hypothalamus uses the current levels of gonadal steroids to monitor the current levels of sexual interest and behaviour. He underlined, however, that sexual behaviour is a complex activity that relies upon the receipt and analysis of complex social stimuli. In agreement with incentive motivation models he states that changes in hormone levels bring animals and humans towards sexual readiness only when a sexually attractive stimulus is perceived. Thus, sexual motivation is activated through expectations of reward, and the internal state of the organism, for example the hormonal state, influences the sensitivity of the organism for the sexually rewarding stimuli.

Incentive motivation models emphasize that motivational processes are not linked exclusively to organismic-state variables or stimulus properties, but equally to both (Bindra, 1974). According to this emerging view of motivation, the source of motivated behavior is a process that combines state and stimulus properties. Bindra (1974) introduced the basic concept of 'a central motive state', "a hypothetical set of neural processes that promote goal directed actions in relation to particular classes of incentive stimuli, for example, it promotes food seeking and
eating in relation to food, or defensive fighting and escape in relation to a predator." (p. 201). An incentive, it is supposed, guides response selection through the excitatory or priming influence of the central motive state on somatovisceral reactions, consummatory acts, and locomotor and skilled actions. Frijda (1986), in line withBindra, defines motivation as the elicitation of behavior systems by appropriate external stimuli, or thoughts of them. A behavior system is described as a potential action (a program), or a sequence of potential actions.

Pfaus (1999) presented the incentive sequence model of sexual motivation. According to this model, which is based on animal research, sexual motivation is fractionated along appetitive and consummatory responses that are conceived of as sequential and overlapping phases. The appetitive and the consummatory phase consist both of anticipatory and preparatory responses. Anticipatory and preparatory responses are made in response to an incentive, but preparatory responses must be made to obtain the incentive, while anticipatory responses are not necessary to obtain it. Thus, conditioned sexual excitement, reflected by for example motor activation, is considered as anticipatory, while instrumental responses would be considered preparatory. The consummatory phase consists of the species-specific responses made in direct contact with the incentive. In this model, feedback systems operate in both positive and negative feedback loops. Appetitive responses are linked positively to the initiation of consummatory behaviors, while orgasm provides negative feedback on both appetitive and consummatory responses.

According to Pfaus, the arrangement of appetitive and consummatory behaviors is nearly identical in rats and humans, and in male and females, although the acts that constitute the classes of behavior are different. For both human men and women the appetitive phase manifest itself in sexual desire, expressed in fantasy, sexual excitement, and preparatory behaviors. The consummatory phase consists of genital stimulation (masturbation and copulation) and orgasm. In between is the precopulatory phase that comprises appetitive, anticipatory, and preparatory actions that are displayed after contact has been made with the sexual incentive (like solicitation, arousal and foreplay). In this model, sexual excitement (as reflected by psychomotor activation) precedes sexual arousal (as reflected by genital blood flow). In accordance with this
model, Pfaff and Agmo (2001) state that in terms of the temporal order of sexual motivational changes, elevated arousal probably comes first, followed by actual mating behaviors. They underline that since a significant component of motivational mechanisms devolves upon elementary arousal of brain and behavior, influences on arousal components is an important area to study.

**Emotions as motivators**

Interaction with an incentive changes the affective state of an organism; it inflames motivation by producing affect (Singer & Toates, 1987). Bindra (1974) already pointed to the similarity of motivational and emotional states. In his view 'motivational state and emotional state are interchangeable terms' (Bindra, 1974, p. 201). Currently, several emotion theorists view emotion as fundamentally an action disposition, as a tendency to act in relation to the emotional stimulus (Damasio, 2003; Frijda, 1986; Lang, 1993; LeDoux, 2001). In this view, emotions serve the satisfaction of goals and generate relevant action.

According to Lang emotions are driven by two primary motive systems: the appetitive system, prototypically expressed by behavioral approach, and the aversive system, expressed by behavioral escape and avoidance (Lang et al., 1993). Whether a stimulus instigates approach or avoidance behavior depends upon the perceived promotion or obstruction of the subject's concerns (Frijda, 1986). Emotions are not determined by particular stimuli, but by the meaning of the stimulus which is stored in memory. Recently, Damasio (2003) introduced in this context the term 'emotionally competent stimulus', referring to the object or event whose presence, actual or in mental recall, triggers emotion. While there are biologically relevant stimuli that are innately pleasurable or aversive, most stimuli will acquire meaning through classical conditioning. As a consequence, meanings of stimuli depend on the individuals past experience, and may differ from one individual to another. Stimuli may have conveyed several meanings, and meanings relevant for different emotions may be present at the same time. Moreover, the value of a stimulus may differ over time since it will be influenced by the current internal state of the organism. Thus, the rewarding value of a stimulus is
dependent on the current internal state, and on prior experience with that stimulus.

There is an increasing notion that emotional responses often are automatic and precede feelings (Damasio, 2003; LeDoux, 2001). Damasio stresses that all living organisms are born with devices designed to solve automatically, without proper reasoning required, the basic problems of life. He calls this equipment of life governance the "homeostasis machine". At the basis of the organization of that machine are simple responses like approaching or withdrawal of the organism relative to some object, and increases or decreases in activity. Higher up in the organization there are competitive or cooperative responses. The simpler reactions are incorporated as components of the more elaborated and complex ones. Emotion is high in the organization, with more complexity of appraisal and response. According to Damasio, an emotion is a complex collection of chemical and neural responses forming a distinctive pattern. When the brain detects an emotionally competent stimulus, the emotional responses are produced automatically. The result of the responses is a temporary change in the state of the body, and in the brain structures that map the body and support thinking. Damasio (2003) and LeDoux (2001), and a long time before them William James (1884), stress that the conscious experience of emotion, what we call feelings, is the result of the perception of these changes. In this view, feelings are based on the central representation of the emotional bodily and brain responses; they are the end result of the whole 'machinery of emotion'.

Neurobiological mechanisms of emotion and motivation

*Brain systems involved in emotion and motivation*

With increasing knowledge about the neurobiology of motivation, theoretical concepts like 'urge' or 'central motive state' can be described in physiological terms. The view that emotion and motivation mechanisms are closely intertwined is in agreement with current ideas about how the brain may work. For processing of an emotionally competent stimulus to result in goal directed action, sensory information is converted in the brain to set off motor responses in the autonomic and somatic nervous system. Sensory input passes from the sense organs to the sensory cortex and
then from the thalamus to the amygdala. The amygdala is a key element of the neural basis of emotion (e.g., Cardinal, Parkinson, Hall, & Everitt, 2002; LeDoux, 2001). Two subnuclei of the amygdala are particularly implicated in the control of emotional processes: the central nucleus and the basolateral amygdala. The basolateral amygdala has extensive reciprocal projections with the sensory neocortex and the frontal lobes, and projects to the ventral striatum and to the central nucleus of the amygdala. The basolateral amygdala seems to be involved in emotional associative learning; it acts as a site of stimulus association and uses the learned information to control activity of the central nucleus. In turn, the central nucleus projects to the hypothalamus, midbrain reticular formation, and the brainstem, and controls behavioural, autonomic, and neuroendocrine responses.

The motivational effects of emotionally competent stimuli are mediated by the ventral striatum, specifically the nucleus accumbens. The nucleus accumbens receives information from several limbic structures including the amygdala, the hippocampus, and the prefrontal cortex and projects to structures that are involved in behavioural expression. Thus the nucleus accumbens sits at the crossroad of emotion and movement (Mogenson, Jones and Yim, 1980; Kalivas & Nakamura, 1999; LeDoux, 2001). Mogenson et al. (1980) pointed to the nucleus accumbens as the interface between the amygdala and the motor system, and they described the role of the projections from the nucleus accumbens to the ventral pallidum in regulating the initiation of motor activity. The nucleus accumbens receives direct input from the amygdala, and indirect input from the ventral tegmental area (an area in the brain stem). The ventral tegmental area is the source of the dopaminergic connections to the nucleus accumbens. The nucleus accumbens passes information on to the globus pallidus, which in turn is connected to cortical and brainstem areas that control movement.

Related to the proposal of Mogenson et al. (1980) is the concept of the 'emotional-motor system' that is introduced by Holstege (1998). The somatic motor system is controlled by the motor cortex and the brainstem. Through this system voluntary movements are controlled. The emotional motor system is controlled by structures that are part of, or are connected with, the emotional circuit in the brain, the limbic system. The emotional motor system is supposed to consist of two components: the lateral
component through which specific emotional behaviors are initiated, and the medial component, which represents many diffuse pathways through which more general changes that accompany emotion are activated. The specific emotional behaviours include for example defensive postures, cardiovascular changes, but also micturition and mating. The medial component involves gain-setting systems, including triggering mechanisms of rhythmical and other spinal reflexes. This component represents several and diffuse pathways, that originate in the caudal brainstem, and terminate among almost all parts of the spinal gray matter, including the autonomic and somatic motoneuronal cell groups. These diffuse projections are thought to be involved in generalized functions like changes in general sympathetic activity, nociception, and muscle tone.

The role of dopamine in motivation

There is extensive evidence for the involvement of dopamine in the activation of responses to stimuli with incentive-motivational properties (Kalivas & Nakamura, 1999; Robbins & Everitt, 1999). Dopamine systems seem to be involved in the prediction of reward (Schultz, 1998; Schultz, 2001) and in the initiation of behavioral responses to obtain a rewarding stimulus (Kalivas & Nakamura, 1999; Phillips, Stuber, Heien, Wightman, & Carelli, 2003). Dopamine has long been regarded as the transmitter responsible for the experience of satisfaction. However, studies in rats have shown that dopamine is not involved in the valence or appreciation of a stimulus, but in the tendency to approach a stimulus (Berridge, 1996). To date, experimental studies in rodents have shown that dopamine seems to be involved in anticipatory behaviours to a larger degree than in consummatory motivational responses. Berridge & Robinson (1998) suggested that dopamine is not involved in the hedonic pleasure of reinforcers (the affective component or "liking"), but mediates the instigation of goal-directed behaviour and the attraction to an incentive stimulus ("wanting"). They showed in rats that manipulation of the mesolimbic dopaminergic system does not affect the hedonic reactions to food incentives, though it affects the motivation to eat. The difference between wanting and liking is relevant for understanding disorders related to motivation. It explains for example why a person who is addicted to some substance can crave for the drug intensely, whereas subsequent intake of the drug may not be very satisfying. Research on the role of
Dopamine in motivation focused mainly on appetitive motivation, however, dopamine appeared to be not only involved in processes of appetitive conditions but also in aversive conditions (Ikemoto & Panksepp, 1999; Salamone & Correa, 2002). Several studies showed effects of nucleus accumbens dopamine levels on avoidance responses, indicating that nucleus accumbens dopamine is not only involved in approach responses to rewards but also in avoidance responses elicited by aversive stimuli (Ikemoto & Panksepp, 1999).

In sum, for processing of an emotionally competent stimulus to result in goal directed action, the basolateral amygdala has to pass information to the nucleus accumbens. When dopamine is elevated in the accumbens, as a result of activation of dopamine neurons in the ventral tegmentum, the effect of the emotionally competent stimulus on the activity of the accumbens cells is amplified, which results in stronger activation of the ventral pallidum, and in turn in stronger activation of motor systems. Thus, dopamine seems to be involved in the strength of the action tendency that is elicited by an emotionally competent stimulus.

Studies in humans
The available knowledge about the emotional systems in the brain and their connections with motor systems is primarily based on animal research. Imaging studies provide increasing evidence indicating that the findings from animal research may be extrapolated to humans. There is ample evidence for the role of the amygdala in the processing of negative emotional stimuli in humans (Davidson, Jackson, & Kalin, 2000), and there is growing evidence supporting the involvement of the amygdala in positive emotion (Anderson et al. 2003; Baxter & Murray, 2002; Small, et al. 2003; Zald, 2003). Most human neuroimaging studies have found greater amygdala activation to negative stimuli compared to positive. However, this may be explained by differences in intensity. Unpleasant stimuli generally tend to be more arousing than pleasant stimuli, possibly reflecting the greater adaptive importance of avoiding potential harm. Recently, human imaging studies indicated that amygdala activation is associated primarily with emotional arousal intensity, independent of pleasantness, while the orbitofrontal cortex is responsive to hedonic value, independent of intensity (Anderson, et al. 2003; Hamann 2003; Schmell et al. 2003).
Similar to knowledge about the emotional systems in the brain, knowledge about the connected motivational system is primarily based on animal research. However, there is increasing evidence from imaging studies that in humans the same systems are associated with reward (e.g., Aharon, Etcoff, Ariely, Chabris, O'Connor, & Breiter, 2001). For example, Aharon et al (2001) found in heterosexual males that viewing of beautiful female faces activated the nucleus accumbens, the sublenticular extended amygdala, and the ventral tegmentum. Aharon et al. noted that in human neuroimaging studies stimuli leading to signal changes in these regions have included different reward stimuli like drugs, nicotine, pleasant taste, pleasant tactile stimuli, and monetary rewards. They concluded that this points to a common generalized circuitry that processes reward information across stimulus category. A neuroimaging study of Garavan et al. (2000) showed that cocaine and sex stimuli activated largely similar brain regions in cocaine users, indicating that also sexual stimuli are processed by this common reward circuitry.

It may be expected that activation of the mesolimbic dopamine system results in the subjective experience of desire, wanting or craving. However, Berridge (1996) underlines that both wanting and liking can exist without subjective awareness. Subjective feelings of wanting or desire, and of liking or pleasure, may be dissociable from the underlying process that has given rise to the conscious experience. Subjective emotional experience is the product of an active reconstruction by cognitive mechanisms of sensory, affective and memory processes. A feeling can be defined as "the perception of a certain state of the body along with the perception of certain mode of thinking and of thoughts of certain themes" (Damasio, 2003, p. 86). Or as LeDoux (2001) states, emotional experience consists of awareness of bodily responses plus the activation of information from memory. The notion that feelings are based on the perception of the bodily changes plus information from memory offers an explanatory framework for the observed discordance of physiological changes that accompany emotion and subjective experience. For example, in most healthy women exposure to a visual sexual stimulus results in an increase in genital blood flow, while it not necessarily results in feelings of sexual arousal (Laan & Everaerd, 1995a). Apparently, in these women sexual feelings are less determined by their genital responses than by the meaning of the situation (Laan &
Recently, functional imaging studies showed that the subjective experience of various emotions such as anger, disgust, anxiety, and sexual arousal is associated with activation of the insula and the orbitofrontal cortex (Craig, 2002; Critchley, 2004; Morris, 2002; Sumich, Kumari, & Sharma, 2003). It has been suggested that the insula is involved in the representation of peripheral autonomic and somatic arousal that provides input to conscious awareness of emotional states. It appears that the feedback of autonomic and somatic responses are integrated in a so-called meta-representation in the right anterior insula, and this meta-representation seems to provide the basis for ‘the subjective image of the material self as a feeling entity, that is emotional awareness’ (Craig, 2003). It seems reasonably to hypothesize that activity in the mesolimbic dopaminergic system participates in conscious experience. Breiter et al. (1997), for example, studied the relationship between subjective effects of cocaine (which increases dopamine levels in the brain) and brain activity. They found that the activation of the ventral striatum was correlated with subjective experiences of craving. Ikomo and Panksepp (1999) suggested that mild, moderate and high increases in nucleus accumbens dopamine may be associated with, respectively, subjective feelings of curiosity, interest, and urge, and that bursts of dopamine release may be accompanied with feelings of ecstasy.

Recently, Holstege et al. (2003) conducted a PET study on human male orgasm and found orgasm to be associated with primary activation in the ventral tegmental area, an area that is known to be also involved in heroin rush.

To successfully meet the demands of the environment, it is required to decide among alternatives, to judge the consequences of actions, and to control the initiation of actions. The prefrontal cortex appears to be involved in the signalling of rewarding and aversive conditions, and in the regulation and controlling of behaviour (Dolan, 1999). The anterior cingulate cortex receives input from the dopamine neurons in the tegmentum, as well as from the amygdala, the ventral pallidum, the hippocampus, and from other prefrontal areas. It sends outputs to the accumbens and the motor cortex (LeDoux, 2001). Thus, it is in the position to integrate information about emotional arousal, information from memory, and the content of working memory, in the process of controlling
movement. Another prefrontal area, the orbital prefrontal cortex, is known to be involved in decisions making (Fuster, 2001). Damasio (1994) showed that patients with damage to the orbital prefrontal cortex have poor judgement due to insensitivity to changes in incentive value. These patients seem to be unable to use emotional information to guide their actions. Regarding sexual responses, Beauregard, Levesque and Bourgouin (2001) showed the involvement of the prefrontal cortex in the regulation of sexual arousal. They induced sexual arousal by sexual film and imaged brain activity. Subjects were asked to inhibit their emotional responses to the film. The fMRI data showed that confrontation with a sexual stimulus resulted in activation of the emotional circuit in the brain, while inhibition of the response was coupled with activation of prefrontal areas.

**Sexual excitement, sexual desire, and sexual action**

In the dominant model of human sexual response, sexual desire and sexual excitement are distinguished as consecutive phases (DSM-IV, 1994). This model is based on the physiological sexual response model of Masters and Johnson (1966), and on the ideas of Helen Kaplan (1979). Masters and Johnson measured the physiological response of men and women to sexual stimulation in the laboratory and formulated the EPOR model. In this model the build-up and release of sexual excitement is described: a steep increase in sexual excitement during the excitement phase (E), a less steep increase during the plateau phase (P), an abrupt raise during orgasm (O), and finally a period of relaxation known as the resolution phase (R). It should be noted that is unclear whether the changes in sexual response described in the model refer to physiological excitement, psychological excitement, or a combination of both (Levin, 2001). Kaplan, a psychiatrist and sex therapist, criticized the EPOR model for lacking the notion of sexual desire, and introduced the desire phase as the phase preceding sexual excitement, which resulted in the DEOR model. Kaplan was seeing in her clinic many female patients complaining about a lack of desire for sex. Absence of sexual desire, she reasoned, points to a phase in the normal sexual response cycle that activates the wanting to experience sexual excitement. Kaplan
conceptualized sexual desire as an expression of a drive, comparable to hunger and thirst, influenced by sensors that signal changes in the internal environment of the body. In this view on sexual desire psychoanalytic thinking can be heard. The DSM-IV (1994) classification of sexual dysfunctions is based on the DEOR (desire, excitement, orgasm, resolution) model of sexual response. Consequently, hypoactive sexual desire disorder, described as the persistent or recurrent lack or absence of sexual fantasies and desire for sexual activity, is distinguished from sexual arousal disorder that is described as the persistent or recurrent inability to attain or to maintain adequate sexual excitement (APA, 1994).

We assume that the mechanism through which sexual emotional states and sexual feelings appear, will be similar as for other emotions that call for action and which therefore are coupled with relatively strong bodily reactions. Sexual excitement can be construed as an emotion; it has a specific pattern of activity and there is coherence in expression and physiology linked to prototypical situational events (Everaerd, 1988). In addition, sexual excitement serves to satisfy concerns, and it can be expected to generate an action tendency for sexual behavior (to continue, or search for, sexual stimulation and gratification) (Everaerd, Laan, Both, & Spiering, 2001). Sexual desire is the subjective experience of being attracted to, or pushed towards, objects or behaviors with potential rewarding effect. The complexity of the neurobiological mechanisms in emotion and motivation can, applied to sexual emotion and motivation, be summarized as follows. First, there is a sensitivity for sexual stimuli, which results in arousal when confronted with an actually present or imagined sexually competent stimulus. The sensitivity for sexual stimuli is influenced by androgens, and most likely also by other steroids, amines, and peptides (Herbert, 2001). Processing of a sexually competent stimulus results in activation of the emotion systems, which results in preparation of the organism for sexual action. Activation of the emotional systems will go together with dopamine production in the motive circuit, which influences the strength of the action tendency. In animal research the concept of wanting is used to describe this action tendency. Wanting includes the signalling of the availability of the incentive, and the strength of the behavior to get the rewarding stimulus. Wanting may be reflected in the subjective experience of craving or desire for the incentive.
The preparation of the organism for sexual action will include responses that generally are involved in appetitive behavior as well as sex specific bodily responses. When we become aware of these bodily responses, through feedback of these responses to the brain, we experience feelings like sexual excitement and desire. Appetitive behavior includes locomotor responses to the goal, and occurs in parallel with autonomic and endocrine responses that prepare for efficient interaction with the goal (Robbins & Everitt, 1999). The generation of sexual appetitive behavior involves specific genital reactions. However, it can be expected that there will be also changes in the somatic motor system. Signals are sent to the muscles to prepare for action to approach the goal. Eventually, the instigation of action tendency by sexual stimuli may result in actual sexual behavior.

**Modulation of spinal reflexes as a window on the generation of action**

According to Pfaus (1999) arousability, which signals the willingness and ability to engage in behavior, is one of the most direct measures of sexual motivation. Autonomic nervous system efferent activity is the most widely used parameter to monitor the presence and intensity of sexual arousal (Geer & Janssen, 2000). Research using this parameter has shown that sexual stimulation results in changes in nonspecific autonomic arousal (Rosen & Beck, 1988) and in sex-specific responses: relaxation of genital smooth muscles, resulting in an increase of genital blood flow. In women sexual stimuli seem to automatically generate increased genital blood flow, even outside women's awareness (Laan & Everaerd, 1995a). In the studies presented in this thesis, in addition to genital responses, somatic motor system changes in response to sexual stimuli were measured. More specifically, we explored the use of a measure for motor preparation. One way to measure motor preparation is to monitor changes in the amplitude of reflexes. Motor preparation involves heightened activity in the spinal cord, and that activity will be expressed as a stronger reflex (Brunia & Boelhouwer, 1988). To study early motor preparation by sexual arousal we were able to use the expertise on Achilles tendon reflex modulation of Kees Brunia and Geert van Boxtel of the Tilburg University.
psychophysiology group. Achilles tendon reflexes (for short, T reflexes) are not sensitive to the valence of an affective state, but they are augmented in states of preparation for action, and are modified by differences in arousal intensity (Bonnet, Bradley, Lang, & Requin, 1995; Brunia & Boelhouwer, 1988; Brunia & van Boxtel, 2000). Therefore investigation of T reflex modulation offers a window on the generation of action.

T reflexes are elicited by a hammertap at the heel tendon. This hammertap results in a reflexive electromyographic (EMG) response in the soleus muscle of the lower leg. The monosynaptic reflex is a triphasic EMG response whose magnitude reflects the number of motoneurons currently activated in the pool that innervates the soleus muscle. Since the sensitivity of the muscle spindle is controlled by fusimotoneurons, the activity of these neurons is also reflected in the T reflex. When circumstances are held equal, taps of a constant force lead to reflex amplitudes of constant size. Supraspinal excitatory or inhibitory influences on the motoneuron pool or other elements of the reflex arc are reflected in an increase or decrease in reflex amplitude. Thus changes in reflex amplitude are a peripheral manifestation of supraspinal processes influencing spinal excitability (Brunia & van Boxtel, 2000).

The T reflex has been used in studies of cognitive factors and motor preparation (Brunia & Boelhouwer, 1988, Brunia, 1993). Studies investigating the influence of cognitive task demands showed that T reflex amplitudes are augmented when task demands increase (Brunia & Boelhouwer, 1988, Brunia, 1993). This facilitation of reflexes is interpreted as the consequence of a general increase in activation. Studies on motor preparation showed that preparing to make a leg movement results in a diminished T reflex in the limb involved in the action, and an augmented T reflex in the uninvolved limb (Brunia & Boelhouwer, 1988, Requin, Bonnet, & Semjen, 1977). These results are interpreted as reflecting two functions of preparation for action. Responses are facilitated by a generalized increase in arousal, but activity in the involved limb is temporary inhibited until the signal to respond occurs. In a study on the effect of mental simulation of an action on reflex modulation, Bonnet et al. (1997) found that mental simulation of a movement resulted in an increase in spinal reflex excitability, which was only slightly weaker than the reflex facilitation associated with the actual performance of the same movement. Thus,
both intended and imagined actions seem to belong to the same category of neural processes as those involved in preparing actually executed actions. These results support T reflex modulation as a measure for early motor preparation of motivated action.

Bonnet et al. (1995) hypothesized that stimuli that elicit emotional arousal will facilitate T reflex magnitude, relative to neutral, low arousal stimuli. They stated that the T reflex, which functions when the limb is activated for walking, standing, and other activities, is inherently non-directional (one can run either towards or away from stimulation). Since the T reflex is non-directional it would be involved both in actions that are appetitively and defensively motivated. They studied the modulation of T reflexes during the presentation of pictures from 'The International Affective Picture System' designed by Lang, Öhman, and Vaitl (1988). These pictures were designed to induce emotions varying in valence (positive to negative) and in intensity (low to high). T reflexes were significantly augmented when elicited during processing of highly arousing emotional pictures (either negative or positive) as compared with neutral pictures indicating the generation of somatic motor preparation as a component of emotional responding.

Objectives and outline of the thesis

Similar to Bonnet et al. we hypothesized emotional stimuli, including sexual stimuli, to automatically generate action tendencies. These action tendencies were expected to result in increased spinal excitability, reflected in facilitated T reflex magnitude. We conducted, with support of the Tilburg University psychophysiology group, a series of studies in which stimulus valence and stimulus intensity were varied, and genital responses, subjective sexual arousal and subjective action tendencies, and T reflexes were measured. In the first experiment we studied reflex modulation in response to appetitive (sexual), aversive (anxiety and sexual threat), and neutral stimuli. We expected that only the sexual stimuli would result in genital response, but that exposure to a sexual as well as to aversive stimuli would generate a tendency to act that would be reflected in increased T reflexes. It was expected that the 3 emotional stimuli would result in stronger T-reflexes than the neutral film, and that reflexes during
the neutral film would not be higher than during the preceding rest period. In the second study we investigated T reflex modulation by sexual stimuli varying in intensity. It was expected that exposure to sexual stimuli of increasing intensity would result in increased genital responses, increased subjective sexual arousal and approach tendencies, and in increased T reflex magnitudes, while exposure to sexual stimuli of similar intensity would result in stable responses. To demonstrate that confrontation with a sexually competent stimulus leads to action tendencies and, eventually to sexual action, we examined sexual activity after laboratory induced sexual arousal in the third study. In this study we also explored whether induced sexual arousal results, following a feed-forward mechanism, in stronger attention for and stronger responses to subsequent sexual stimuli. Furthermore, based on neurobiological knowledge, we reasoned that measuring somatic motor system activity through means of T reflex modulation might offer a sensitive measure to investigate the effects of dopamine on the instigation of behavioural action in humans. We wanted to find out whether a dopamine agonist, that increases dopamine levels in the brain, would affect sexual response, particularly action tendencies. Therefore, in the fourth study, we investigated the effect of dopamine on the generation of action tendencies in response to sexual incentives. We expected dopamine to facilitate genital response en subjective sexual arousal, and to result in stronger T reflex magnitudes in response to sexual stimulation.

To investigate gender differences in sexual motivation we included both men and women in most of the studies presented in this thesis. Men seem to be stronger motivated sexually compared to women. They masturbate more frequently (Oliver & Hyde, 1993), they report less problems concerning low sexual desire (Baumeister, Catanese, & Vohs, 2001), and problems of hypersexualitity mostly concern men (Kafka, 2001). Baumeister, Catanese, and Vohs (2001) recently reviewed evidence pertaining to the question of whether men and women differ in, what they call, the strength of sex drive. Sex drive is described as referring to intrinsic sexual motivation, ‘usually focused on craving for sexual activity and sexual pleasure’ (Baumeister et al., 2001, p.244). Intrinsic motivation is ‘desire for sex for its own sake’, as opposed to extrinsic sexual motivation, which constitutes of desiring sex for the sake of distal goals like relief from stress or desire to procreate. A person with a higher sex
drive would be one with more intense and/or more frequent desires for sex. Baumeister et al. conclude that across many different studies and measures men have been shown to have more frequent and more intense sexual desires than women, as reflected in thoughts about sex, frequency and variety of sexual fantasies, desired frequency of intercourse, desired number of partners, masturbation frequency, and other measures.

Following an incentive motivation view, sexual motivation requires a sensitive sexual system, and stimuli that can activate that system. The observed gender difference in sexual motivation may be due to a higher arousability of the male sexual system, to a greater availability of competent sexual stimuli for men, or to both. An advantage of T reflex measurement is that it allows for direct comparison of male and female responses. In contrast, directly comparing male and female genital responding is not possible. Changes in vaginal vascular responses cannot be compared with changes in penile responding since they are two different measures on different anatomical structures (Geer & Janssen, 2000). It was hypothesized that if it holds true that men are more sexually ‘arousable’ than women, this should be reflected in a stronger increase in T reflexes in response to sexual stimuli in men than in women.