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Ethological needs in Humans

Motivation in Humans for social behaviour, autonomy, compentence, exploration and occupation

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Review of existing literature on Ethological needs in Animals and in Humans. The review focuses on the question to what extend humans have ethological needs and the overlap in current knowledge concerning this subject with animals.

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The thesis as it is right now took a lot longer than expected. 12 Months ago I went to Marie-Jose Duchateau a little frustrated because I did not know what to do for my literature study. She came up with the question whether humans like animals have ethological needs. It made sense to me that humans did, especially in the course of evolution, yet it is one of those questions where you think you know the answer to but have never really red anything about it. That's what the question very interesting to me, the assumption that you already know, but really you don't. Come to think about it, this question and its possible answers are very much implemented in our daily lives. Televisions shows evolve around the question: what happens if we put 12 people in one house for several months without the possibility of other social contacts. And what about the news? A lot of attention goes to young people being abducted and held prisoner making it impossible to execute their own behavioural needs. In an attempt to answer this question I researched literature in several scientific fields like neurobiology, psychology and ethology. To make sense of this huge amount of information, I was guided by assistant professor Marie-Jose Duchateau. Many thanks go out to her; she helped me when I didn't know what to do next or where to look when I got stuck. I might not have asked a lot for feedback but I very much appreciated the fact I could always call or mail and get a very fast response. I know how busy Ms Duchateau is, but she always took a lot of time to see me.
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Chapter one

Introduction

In this society animals have been given several roles: to serve as food, lab animals, recreation, pets, company, help for the disabled and government and many more. In 1965 Brambell's Report stated five freedoms for farm animals: to have the freedom to stand up, lie down, turn around, groom them selves and stretch their limbs (Committee, 1965). Over the course of time, no matter what role has been assigned to these animals, animal welfare has been an upcoming concern in all fields, including laboratories and farms. Traditionally a way of determining the welfare of animals was to assess their biological functioning. In other words, do they show normal growth, development and are they healthy (Fraser & Weary, 2004). There are more ways to determine the quality of life of animals; one can make sure there is no such thing as cruelty or harm, or simply look at the quality itself. To ensure the quality of life of farm animals the Farm Animal Welfare Council (FAWC, 1979) determined in 1979 that the freedoms as specified by Thorpe in Brambell's report needed revision and came up with the following list: 1) Freedom from Hunger and thirst, 2) Freedom from discomfort, 3) Freedom from pain, injury or disease, 4) Freedom to express normal behaviour by providing sufficient space, proper facilities and company of the animal's own kind 5) Freedom from fear and distress by ensuring treatments and conditions which avoid mental suffering (FAWC, 1979). This thesis will show that there is a link between the last two freedoms. Especially freedom 4 can complicate the housing of animals in some situations. In farming situations the farmer wants to get the most profit out of his company. Not considering the animal's needs, that would mean that you would place as much animals as possible in a small space, providing them with sufficient food, water and shelter and process them as fast as possible. From the animals point of view this method can compromise freedom 4. In order to assess whether or not freedom 4 is compromised it is necessary to define normal behaviour, several scientist have tried answering this question. Scientists have agreed on the definition of normal behaviour as behaviour that promotes wellbeing in the animal (Poole, 1988). Facilitating normal behaviour can be achieved in two ways. One can create an environment promoting as much behaviours as possible; by doing so no distinction is made between behavioural patterns in terms of importance. Unfortunately this solution is not adequate for everyone. Pet owners, farmers, zookeepers, or laboratories may not have the space or money to facilitate this. The second option is to accommodate only specific behaviours viewed upon as essential, so called ethological needs (Gonyou, 1995). Jensen and Toates defined these needs as: "*The need to perform a specific behaviour pattern whatever the environment is like and even if the physiological needs which the behaviour serves are fulfilled*" (cited from (Jensen & Toates, 1993)). However I feel this definition is somewhat bluntly put. Behaviour falls into two categories: 1) appetitive and 2) consummatory behaviour. Appetitive behaviour is behaviour that leads up to need fulfilment. So if the individual is hungry it will start to move around and forage in order to obtain food. The actual food ingestion will satisfy the need to forage for food and is called a consummatory behaviour. In ethological needs the emphasis is on appetitive behaviour. Appetitive behaviour patterns do not necessarily have to lead to a direct outcome, to refer back to the food example: foraging does not have to lead to consuming food if for instance the environment does not contain any. If however foraging in itself would not be satisfactory to the individual it could result in a negative feedback in behaviour compromising the survival of the individual. This means that a need to perform behaviours without a direct reward must be **rewarding in itself**. What would happen if for some reason the execution of the behaviour is thwarted? **Thwarting behaviour** that is rewarding can be **stressful** for animals. Prolonged stress has been known to induce stereotypies (Schouten & Wiegant, 1997), making stereotypies an indicator of possible undermined execution of ethological needs. Animals deprived of expression of certain behaviour patterns that are suddenly given the opportunity to do so, sometimes exhibit increased performance of some of these activities (Duncan, 1998), and this is called: a **rebound effect**. Taking these parameters all together, my definition of ethological needs as used in this thesis is:

> *"The need to perform a behaviour that is rewarding in itself. The need for performance of this behaviour, even if appropriate substrate is absent, is so strong that thwarting it too long leads to stress and stereotypies. If a possibility is offered to perform the behaviour after extensive periods of deprivation a rebound effect occurs."*

The fact that ethological needs for animals are included in the law system, stresses their importance. But it also raises the question if perhaps we humans also have ethological needs. This question I hope to answer by studying existing literature. By linking theories in the ethological, neurobiological and psychological field I hope to find an answer. I have my own thoughts on the subject.
My **hypothesis** is that humans do have ethological needs, but they might be **less pronounced** compared to animals. It makes sense to me than in the course of evolution certain behaviours that can promote one's wellbeing are self-satisfying such as behaviours related to foraging for food. Thousands of years ago we did not have supermarkets so hunting for food was a necessity. But this can be time consuming in times of scarceness, so if an individual would enjoy foraging, it would start this behaviour long before the sensation of hunger sets in. This way there is little risk of dying of starvation if food is not readily available. Since certain behaviours such as foraging can be observed across species (Taylor, Main, Mendl, & Edwards, 2010) (Cooper & Albentosa, 2005) (Clegg, Buckley, Friend, & McGreevy, 2008) (Huber-Eicher & Wechsler, 1997), it is not unthinkable we still have these needs as well even if we no longer need them. Something that complicates the matter is the fact that according to my definition, the ethological need should be found across species. But one thing that is very unique to our species is culture. Culture is found in other species like orang-utans (van Schaik, et al., 2003) but unlike great apes, we are able to shape culture across generations (Enquist, Ghirlanda, Jarrick, & Wachtmeister, 2008), this ensures a vast diversity of culture across the world. Economic and technological inventions shape these cultures. If there is something as foraging behaviour among western human populations this must be extremely different from foraging behaviours in some parts of Africa where supermarkets are not on every corner.
In order to answer the research question I am going to look in to animal ethological needs as well, but of course it is impossible to include all needs of all animal species. Therefore in this thesis I will focus mainly on our close related species the non-human primate and well researched farm and/or pet species, such as horses and pigs.

Chapter two
Ethological needs defined

2.1 Ethological needs: the theories

Performed behaviour that is rewarding in itself and therefore does not serve a direct function is called a ethological need. These needs are motivated by both external and internal stimuli, and when an individual is unable to perform the desired behaviour, welfare is affected (Jensen & Toates, 1993). An interesting question is when and which of these stimuli trigger the performance of the behaviour. The internal stimuli of an empty stomach could induce the need to eat, but if food is not close by the individual could feel motivated to forage in order to acquire food. This is a simple example however individuals are far more complex, giving rise to the question why individuals choose to employ certain behaviours at specific times. This is a question that many scientists have tried to answer for many years. Lorenz was one of the first to design a possible model. According to his psycho-hydraulic model animals portray fixed action patterns in response to stimuli. This can be visioned as a fluid reservoir in which pressure builds up till enough action specific energy (motivation) causes it to burst. Internal drive is like an incoming stream in the reservoir, filling it up. An external stimulus then triggers an outflow valve that in turn will lead to FAPs (Hogan, Chapter 3 motivation, 2005). The higher the drive the smaller the strength of a stimulus needs to be to exhibit certain behaviour. In fact sometimes behaviours are performed without a stimulus. This is said to happen when the drive is so high, a spontaneous burst occurs, this is called a vacuum reaction (Berridge, Motivation concepts in Behavioral neuroscience, 2004). This model is rigid, meaning there are no learning processes or feedback involved (Perez, Martinez, & Garcia, 2000). The Lorenzian model also does not have an explanation for priming. Priming occurs when in the presence of a stimulus the original motivation to perform a specific behaviour(such as aggression, or maternal behaviour) is low, but when given a free reward the motivation rises and the behaviour is performed anyway (Hogan, Chapter 3 motivation, 2005). This behavioural model is now considered out of date (Jensen & Toates, 1993), and ethologists have started to use homeostatic models fuelled by homeostatic drive. An organism has a set point for a physiological state and an error detection mechanism that will constantly check the current value with the set point. If the current state deviates from the set point then appropriate actions will be taken. When the body temperature of a human increases too much for instance, the body will start to sweat to loose excessive heat. With these mechanisms organisms are capable of maintaining steady physiological states; which is called homeostasis (Berridge, 2004). Originally it was thought that when the motivational drive was reduced the following behaviour would stop. So, if you are hungry you eat, when you are tired you sleep and so on, But this is too simplistic as can be demonstrated with electrodes on specific brain regions. If drive reduction works then that would mean that stimulation of the brain region that causes individuals to feel satisfied can be considered rewarding since apparently the need is satisfied. However, feeling hungry by stimulating the brain region controlling appetite can be considered as punishment. Several studies however showed the opposite effect, meaning stimulation of the feeding centres in the lateral hypothalamus causes self-stimulating rewarding rates (Margules & Olds, 1962). In other words the sense of reward is not due to drive reduction. Instead the sense of reward should be seen as a separate motivational mechanism, in a way that behaviour itself can be rewarding. Having established that behaviour itself can be rewarding, this makes the explanation for ethological needs much easier. The definition for this being: “The need to perform a behaviour that is rewarding in itself. The need for performance of this behaviour, even if appropriate substrate is absent, is so strong that thwarting it too long it leads to stress and stereotypies. If a possibility is offered to perform the behaviour after extensive periods of deprivation a rebound effect occurs”. When deprived of the opportunity to perform such behaviour, welfare is in jeopardy resulting in stress. The critical question remains when highly motivated behaviour is thwarted. Initially preference tests

were used to determine if motivation for certain behaviours were stronger than for others. This kind of testing was later replaced by testing the strength of motivation in so called consumer demand approaches. According to this theory, first formulated by Dawkins (1988) the strength of a motivation can be tested by imposing an increasing cost of access to perform the particular behavioural pattern. By measuring the motivation of individuals for behaviours, ranking of motivation of behavioural patterns is possible. Hughes and Duncan (1988) agreed with Dawkins that needs can be ranked. They proposed needs can be qualified from "no need" to "critical need" and only critical needs determine the welfare of an individual and can contribute to welfare assessment. The strength of motivation can be tested by enabling an individual to perform a particular behaviour by paying a cost in the form of an operant task. If the need is critical then the performance of the individual will remain heightened in spite of an increased price. This behavioural demand function can be derived from the level of performance as a function of the cost imposed. It has been questioned whether this method is valid to determine the strength of motivation (Jensen & Pedersen, 2008). Sensitivity to the cost of the performance of the tested behaviour can be obtained from the slope of the demand function if it is log-log scaled (Jensen & Pedersen, 2008). The area under the demand function (consumer plus) and the maximum price paid are also ways to determine the strength of motivation (Houston, 1997). This way of determination is meaningful if the test is only interpretable for the tested behaviour, in other words the response should only reflect the motivation for the particular behaviour pattern (Jensen & Pedersen, 2008).

2.2 The reward system

For behavioural patterns to emerge or persist, motivation is required. Motivation to perform these patterns can originate from two processes; this is best explained with an example in this case we will use eating. An individual who eats has two means for eating: the urge to eat (wanting) and the sensory pleasure of eating (liking). The distinction between these two was made clear by Berridge (1996) and is of great importance since the urge to eat is a motivational process and the sensory pleasure that (might) accompany this act is merely an affect. It is important to realise that 'wanting' does not necessarily equals 'liking' but these can be intertwined. Going back to the food example it makes sense that wanting is based on experiences. When walking on the beach on a hot summer day, seeing an ice truck does not have the same value to someone who never had an ice-cream before and someone who has. In other words the ice-cream does not have an incentive until value is attached to it by previous experiences. It has been suggested that in order to get from the ice truck to a "wanting" sensation to eat ice-cream it is necessary to enhance its hedonic value. But as I explained before "liking" and "wanting" are two different processes, so to go from liking to wanting more is needed. Berridge (1996) suggested this is accomplished by a separate system to achieve full reward, as depicted in Figure 1B. The active attribution of incentive salience by the brain confers upon a representation, the ability to capture attention, to direct elicit orientation and approach to instigate instrumental and cognitive strategies directed towards the goal and potentially to become manifested in subjective awareness as an object of desire. In other words on a hot summer day (unconditioned stimulus) we see an ice truck (conditioned stimulus) and our memory tells us that we had an ice cream from an ice truck on an equally hot summer day last year (memory comparison). Because of associative learning our attention is drawn to the truck, redirecting our goal towards it (due to the incentive salience attributor). By now we "want" the ice-cream. Whatever the outcome of this motivation (actual consumption or subjective consumption) the motivational representation has come about at least in part by activation of the neurotransmitter dopamine.

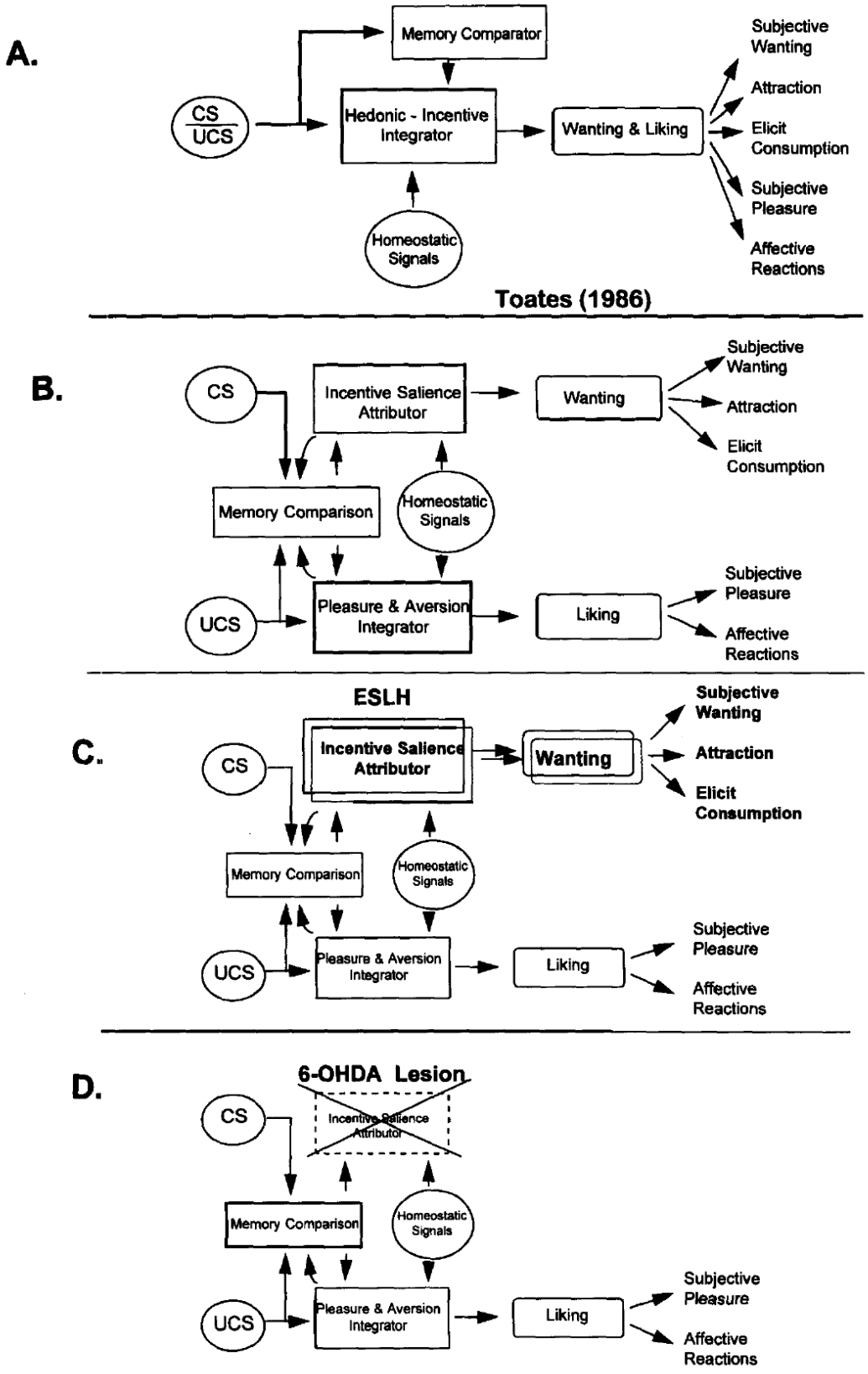

Figure 1Models of incentive motivation A) contemporary Bindra/Toates model in which wanting and liking are identical (B) Incentive salience model in which liking and wanting are processed separately. (C) Hypothesized food reward during selective activation of wanting without liking by electrical stimulation of the lateral hypothalamus. Food becomes an attractive incentive and elicits consumption, but liking is not enhanced (D) Hypothesized food reward after selective loss of incentive salience produced by high doses of neuroleptics or by 6-OHDA lesions of mesotelencephalic dopamine systems. All wanting aspects are eliminated, but liking remains intact. (Borrowed from Berridge, 1996)

At first one behavioural measure was used to determine whether a subject wanted a reward. In the case of food, the researcher would determine the facial expression made by the subject when encountering food. But as you can image this is not a proper measure to determine if the subject really wants food, it is more a measure for hedonic sensations. Reward reactions in a behavioural measure are best assessed in a traditional manner: with active approach constructs. To exclude other factors that influence the individual's responses several paradigms have been developed (Berridge, 1996).

Another method that has been applied more and more to assess differences between neural substrates for liking and wanting is neural imaging. A recent study (Born, Lemmense, Martens, Formisano, Goebel, & Westerterp-Plantenga, 2011) scanned the brains of 15 normal female subjects in two conditions: satiated and fasted. In both these conditions the participants were shown pictures of food they were asked to rate in terms of how much they liked the food or how much they wanted the food. The results are depicted in Figure 2; the scans show that more activity is present in the anterior insula for liking and more activation in the caudate for wanting. The results (not depicted) also indicated that the state where the participant is in, determines the reward-related signalling of the brain. When the women were on this dietary restraint, they were more rewarded by the brain when visually stimulated with pictures of food than non-fasted women (Born, Lemmense, Martens, Formisano, Goebel, & Westerterp-Plantenga, 2011). This could indicate a change in sensitivity to food reward when satiated. Unfortunately the technique used in fMRI has some disadvantages: it is precise but slow imaging. This could be the reason why some studies show a bit different results. Pelchat et al (2004) found that wanting is indeed a desire emanating from the caudate, but liking is associated with activation in the amygdala (among other areas). It seems that determining the areas involved in liking are more difficult to determine.

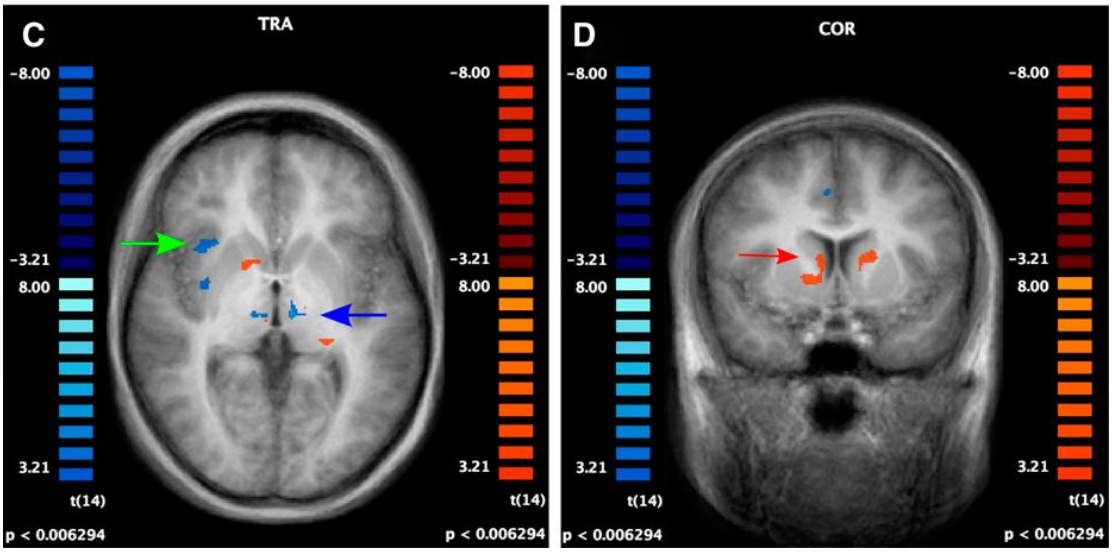

Figure 2 Brain activation images of C) Contrasting premeal versus postmeal liking, D) contrasting imagery of premeal versus postmeal wanting. The green arrow indicates the anterior insula, the blue arrow shows the thalamus, and the red arrow indicates the caudate. Picture A and B are not depicted (borrowed from Born et al 2011).

Despite the variation of results in literature on brain regions responsible for liking and wanting researchers do agree on what neurotransmitter dopamine is the main component in motivation and a sense of reward (Wise, 2004) (Ridley, 1994) (Park, et al., 2005) (Naranjo, Tremblay, & Busto, 2001) (Harst, 2003) (Di Chiara, 2002). Dopamine is produced in the substantia nigra and the ventral tegmental area (see figure 3) and accounts for different pathways there (Marsden, 2006). Only one pathway is associated with the sense of reward, it works its ways from the Ventral Tegmental Area to the accumbens, central striatum and amygdala: the limbic areas of the brain. As will be explained later in section 2.4 this pathway is also involved in addiction (Marsden, 2006).

There is a lot of research that states that dopamine is involved in the sense of reward. The dopamine pathway responsible for the sense of reward originates from the substantia nigra and then eventuates from the Ventral Tegmental Area to the accumbens, central striatum and amygdala: the limbic areas of the brain. As will be explained later in section 2.4 this pathway is also involved in addiction (Marsden, 2006).

However serotonin (5HT) has also been suggested to play a role in reward sensation but as an opponent partner of dopamine. Serotonin targets several anatomic agents, one being the dorsal raphe nuclei. These nuclei connect to some areas that are also innervated by dopamine systems such as the amygdala and the striatum. Recall that we have identified these limbic areas as highly important for reward sense. There are different types and subtypes of serotonin receptors making it difficult to pinpoint what serotonin does. A model has been proposed by Daw et al., (2002) as to how the opponent responses of serotonin and dopamine look in response to aversive or appetitive stimuli (see Figure 2).

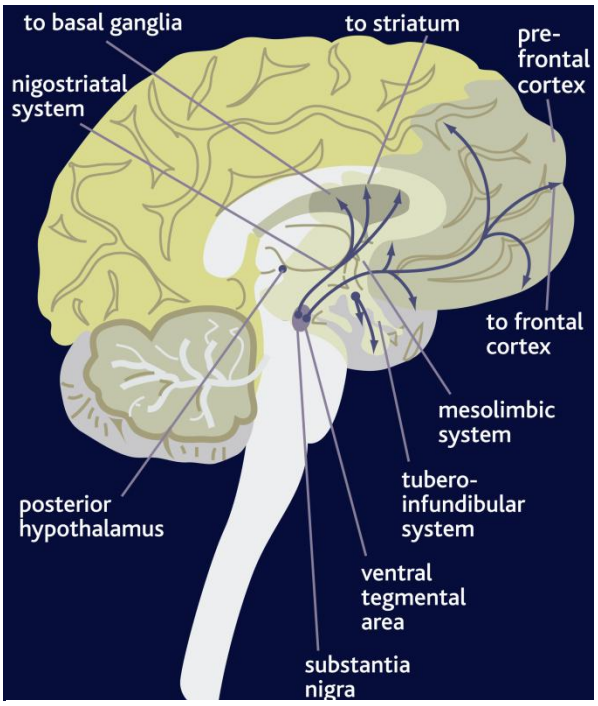

Figure 3 The three major pathways of dopamine in the (human) brain, the pathway affecting the sense of reward goes from the VTA to the mesolimbic areas (picture from http://www.cnsforum.com/

The model shows that in case of reward when dopamine is activated, serotonin acts as an opponent. At first when reward is expected or signalled, dopamine exclusively regulates responses, when the reward fails to arrive the opponent is activated. The model as depicted takes in account the degree to which both components are blended in a signal; this is caused by the value of α. When activity of dopamine cells go extinct they show a phasic depression at the time an expected reward is not delivered, as is shown in the right panel when α = 0,8 (Daw, Kakade, & Dayan, 2002). Bear in mind this is only one model and very likely to be a simplification of the true process.

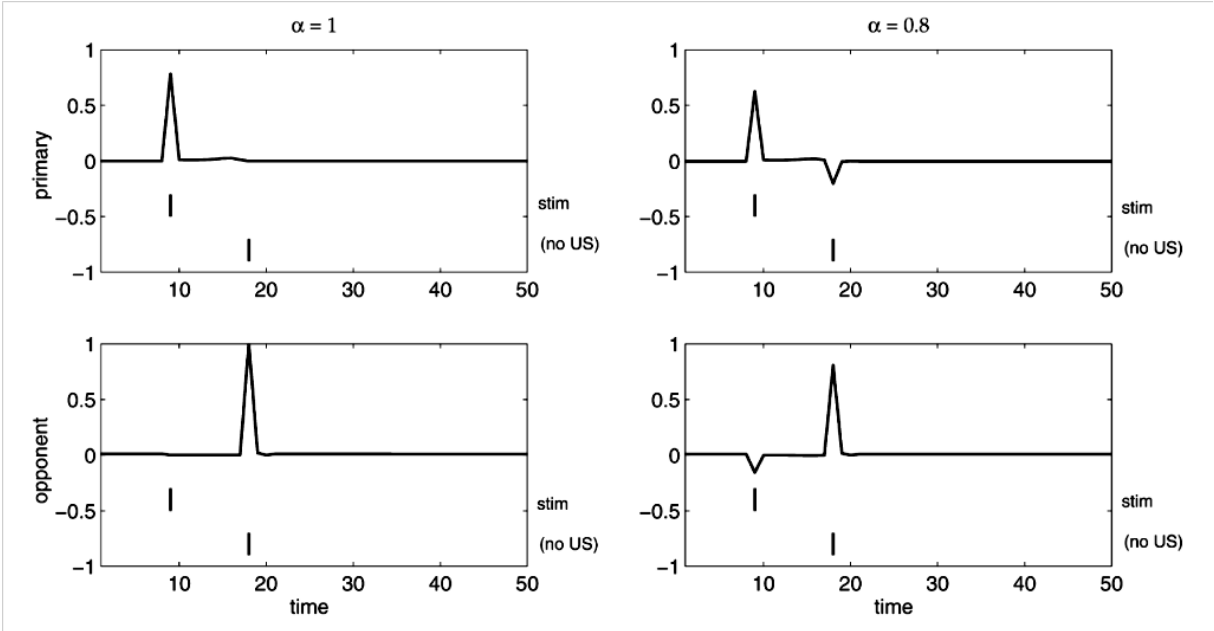

Figure 2 Model of dopamine and serotonin responses of a conditioned stimulus when the unconditioned stimulus is omitted. Primary represents dopamine when looking at appetitive conditioning, opponent would be serotonin, aversive conditioning would reverse these roles but it is expected that results are the same (borrowed from Daw *et al*., 2002).

This is only a model but several studies have shown that serotonin is involved in reward responses. Rats that have been trained to associate a stimulus with water delivery. When experiments started they were confronted with a lever that would either work and deliver the stimulus they were previously trained for (Conditioned Reward) or an inactive lever that yield no consequences when pressed. Response to the lever was greater when it worked than when inactive, an effect that increased when the nucleus accumbens (the reward centre) was injected with *d*-amphetamine. Injecting the nucleus accumbens with a non-selective serotonin agonist (such as 5-CT) reduces this effect, processes (Fletcher & Korth, 1999) indicating that serotonin has an important role in reward. A statement that is endorsed by other studies such as those that used so called SSRI's. SSRI's are selective serotonin reuptake inhibitors, they prevent the reuptake of serotonin thereby increasing the amount of serotonin the synaptic cleft. They are mostly used to treat anti-depression (McCabe, Mishor, Cowen, & Harmer, 2010). When considering the model proposed by Daw et al (2002) it makes sense that people treated with SSRI's due to depression feel 'emotionally blunt'. The

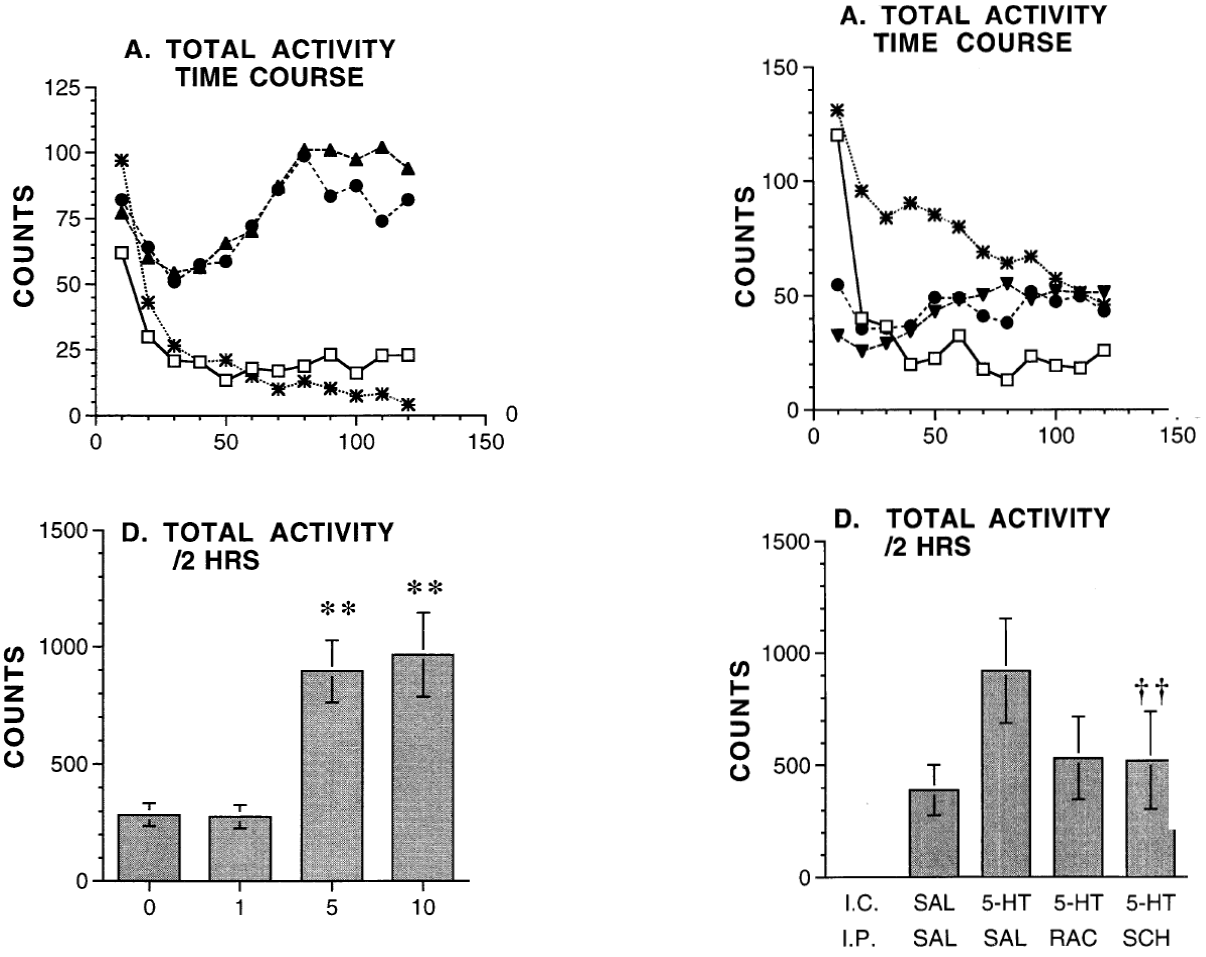

Figure 3 Influence of Serotonin on activity. Left panel:Serotonin injection in the nucleus accumbens increases overall activity that increases over time, when administering doses of 5 or 10µg. Right panel: Influence of serotonin on overall activity after a pre-treatment of dopamine, borrowed from **(Sasaki-Adams & Kelley, 2001)**.

serotonin track has been inhibited but rewarding feelings mainly caused by production of dopamine has not been increased. Serotonin is also the most important neurotransmitter driving responses after an aversive stimulus. Indeed research shows: individuals treated with an SSRI display a diminished neural processing of rewarding stimuli. Likewise SSRI's also diminish the neural processing of aversive stimuli (McCabe, Mishor, Cowen, & Harmer, 2010). Another study showed an interaction between dopamine and serotonin, but they came to a slightly different conclusion. With a similar set up they reinforced the behaviour of rats to press a lever that they knew through training

would yield a reward. When injecting serotonin into the nucleus accumbens overall activity was greatly increased. Lever pressing was also increased in general but did not reinforce specific lever pressing, something that did happen with dopamine injected rats. They significantly pressed the conditioned reward lever more often than the inactive lever (Sasaki-Adams & Kelley, 2001). So far this only shows that dopamine increases the need for reward, thus stimulating "wanting sensations" and serotonin does not selectively induce these feelings but does increase overall motor activity. However when rats are pre-treated with dopamine antagonist and are then submitted to an intra-accumbens serotonin treatment overall activity is decreasing (see Figure 5). These findings suggest that an increased serotonic level in the reward centre of the brain somehow influences dopaminergic functioning and consequently behaviour (Sasaki-Adams & Kelley, 2001). This underlines the interaction of both neurotransmitters for feelings of reward or lack thereof.

We have now established which neurotransmitters are necessary for the sense of reward and what pathways and neural substrates account for this *wanting* feeling. That liking and wanting are two different systems makes sense when we consider where these two arise. Liking can be measured in several ways, which method is most effective depends on the species. When working with humans, rating can be sufficient but simply asking a rat how he would rate how much he liked the sugar offered to him will not provide any results. Instead testing for liking in animals can be done by measuring hedonic and aversive reactions. When receiving a taste reward, the taste reactivity shows the immediate *liking* reaction (such as tongue manipulations, paw licks), whether or not the reward is wanted. Berridge and Robinson (1998) showed that liking is independent of wanting. When depleting dopamine neurons in the nucleus accumbens and neostriatum by means of neurotoxins, rats do not respond differently from other rats concerning liking. But these rats that have been given these neurotoxins sometimes starve to death because they fail to eat food even when it is right in front of them. This impaired behaviour is not due to motor deficits because the rats are able to make other movements such as forelimb and mouth movements. So if liking is still intact but the drive to eat has diminished, dopamine responses in the Nucleus accumbens and neostriatum account for wanting or incentive salience (Berridge & Robinson, 1998). If starvation is mediated by depleted dopamine, then this neurotransmitter may also mediate overeating when present in larger amounts. When mice are genetically mutated to increase levels of dopamine in synapses by knocking out transporters they are more motivated to acquire sweet rewards. These mice are more goal orientated, but do not increase their number of hedonic responses compared to other mice. This behaviour is not due to enhanced motor skills since these mice do not run any faster than a normal mouse does (Peciňa, Cagniard, Berridge, Aldridge, & Zhuang, 2003). These findings suggest that wanting mediates a neural representation of reward-related stimuli (Berridge & Robinson, 1998).

To understand the nature of ethological needs it is important to understand that there is a difference between "wanting" and "liking" and dissociation of "liking" and "wanting" does not occur only due to addiction but also on current states. A simple research with uses of chocolate milk, orange juice and water showed that being acutely deprived of food, influences motivation because it increases the reinforcing value of food. But there are no differences found in hedonic reactions, either objectively (behavioural responses) or subjectively (ratings of the participants) (Epstein, Truesdale, Wojcik, Paluch, & Raynor, 2003) so "liking" is unchanged. Similarly Finlayson et al. (2007) showed that when people are given a choice between low and high fat and savoury or sweet tasting foods, their desire for certain food depends on the state of the participant. If people were hungry they choose high-fat savoury over low-fat savoury, showed no difference in *"liking"*, but liked the high-fat sweet food over low-fat sweet without "wanting" one more than the other. When satiated and asked which of the food items on the shown photograph they would most like to eat right now, participants wanted low-fat sweet food more than high-fat sweet tasting food. When asked to rate them according to pleasantness the wanted items were not liked more than the lesser wanted food items (Finlayson, King, & Blundell, 2007). Stress also interferes with the "liking" and "wanting" system. Participants were trained to perform for two instrumental tasks which were both coupled to specific food

outcomes. Candidates were then saturated with the rewards and send back to perform the same instrumental tasks. Because of satiation rewards are devaluated but under stress; subjects tend to engage in the instrumental task anyway (Schwabe & Wolf, 2009). So under stress people are still motivated to get a reward independent of the value of the reward. These studies shows that the choices we make are based on the state we are in which in turn changes our motivation. Liking and wanting often have a strong relationship, but this does not always apply. The most direct evidence for this is found in addiction, to enhance further understanding on this matter I will briefly discuss this subject later.
The studies reviewed above underline the difference between "liking" and "wanting" for food rewards but not for other behaviours. Despite the theory of Berridge (1996) being based on food rewards it can also be applied to behavioural rewards. Incentive salience can be a behaviour wanted in the sense that the animal or human will work to obtain the possibility to execute the behaviour itself even in the absence of an actual reward.

2.3 Stress and stereotypies

The welfare of animals has gotten significant attention lately, especially in the farm industry where animals often live in barren environments. Poor welfare is thought to be the main reason to perform misdirected activity: complex functionless behaviours that are repeated often, also called stereotypies. Sometimes misdirected activity can become destructive or aggressive and animals may harm pen mates or themselves (Poole, 1988). Confirming a relationship between stereotypies and retained welfare is difficult but the development of such behaviour does suggest a relation. Stereotypies are believed to arise in different phases. This is mostly described in the animal world. Initially the animal experiences stress when confronted with a stressor or when it is not able to perform motor patterns. It establishes motor patterns to cope with its environment which are context specific at first. If the aversive stimulus persists, is presented several times, or the desire to perform specific motor patterns is unfulfilled stereotypic behaviour can become fully established (Keeling & Jensen, 2009). If this happens the behaviour can be seen even after the individual is placed in a new environment, because of this it is difficult to say if the stereotypic motor patterns employed mean the welfare of the individual is currently affected or has been in the past (Keeling & Jensen, 2009) (Mason, 1991). But it appears that misdirected activity can be categorized: grazing and omnivorous species are prone to oral stereotypies and predators are more likely to develop locomotory stereotypies. Animal models are frequently used to examine human stereotypies. The repetitive movements documented by scientists are usually found in people suffering from a developmental, psychiatric or neurological disorder, examples being mental retardation, autism, Rett syndrome and Fragile X syndrome. To my knowledge no research has been done on humans concerning stereotypies arising from living in barren or restrictive environments in which they do not have the ability to perform certain behavioural patterns. Nonetheless stereotypies from animals can help shed light on the rewarding aspects of the observed behaviour (Bauman, Toscana, Babineau, Mason, & Amaral, 2008).
We have identified the brain regions responsible for reward. And according to our definition thwarting behavioural needs that are rewarding can lead to stereotypies. This means it may very well be possible that the same brain regions that account for reward sensation are also responsible for stereotypic development. As it turns out neonatal amygdala and hippocampus lesions in non-human primates result in stereotypies in the second year of development. This is interesting because in the first year, no signs of stereotypies are present, in other words subjects initially develop normally (Bauman, Toscana, Babineau, Mason, & Amaral, 2008). It has been shown that damage to the medial temporal lobe structures alters the regulation of the prefrontal cortex. Subjects with a lesion in this area show a reduction in dopamine overflow (Saunders, Kolachana, & Bachevalier, 1998). As we have seen before this structure is in charge of subcortical dopamine functioning: the structure involved in the sense of reward. Lesions or removal of the medial temporal lobe causes a drop in the metabolite

N-acetyl-asapartate (NAA) in the prefrontal cortex. It is not entirely clear what the function of this metabolite is, but it is believed to serve as an initiator of neuronal protein synthesis and serve as a donor of an acetyl group for myelination during brain development. Neurons in the brain are in constant communication with each other by hormonal growth factors, neurotransmitters and neuronal electrical activity. These mechanisms ensure survival of the neurons. The lesions caused might affect other anatomically connected brain areas because the mentioned feedback processes are no longer present (Bertilono, Saunders, Mattay, Bachevalier, Frank, & Weinberger, 1997). So we know that lesions in the MTL can affect the development of the frontal cortex which in turn can affect stereotyped behaviour.
We have established which neural substrates are related to the rise of stereotypies and that these structures are in charge of the reward system. This indicates that stress and reward are involved in the same neurological tract. That one influences the other has been shown in many studies involving opioids. Opioids are chemicals produced in the brain and can be considered drugs produced by one's own body. A well-known opioid is morphine, morphine can induce oral stereotypies in rats. These behaviour patterns however can be blocked when the rat is administered a dopamine receptor antagonist. The interesting thing about this finding is that morphine can cause sensitization to these oral stereotypies. This means that once a stereotypy has set, its rewarding properties become less apparent to the individual. This means that the rat needs to perform a particular stereotypy longer or more frequent to be able to maintain the same rewarding sensation (Knapp, Jha, & Kornetsky, 2004).

Long-term stress can trigger activation of the Hypothalamic Pituitary adrenal axis, also known as the HPA axis. When under stress the body starts to secrete a number of hormones including (but not exclusively), the corticotrophin releasing hormone (CRF from the hypothalamus), affecting the release of adrenocorticortropic hormone (ACTH from the anterior pituitary) which causes the production of glucocorticoids such as cortisol (from the adrenal cortex) (Pruessner, et al., 2008). Cortisol is also known as the stress hormone because of its release during stressful moments, and the effect it has on the body: it causes the individual to exert maximum alertness when in a state of enhanced arousal. In the case of acute stress the activation of the HPA axis should at some point be inhibited. This negative feedback comes from the glucocorticoid receptors in the hippocampus. However, exposure to chronic stress and an elongated exposure to glucocorticoids changes the morphology of the hippocampus. The neurotransmitter dopamine, responsible for *wanting* sensation in individuals, is regulated by the neuro-peptide cortisol a glucocorticoid in humans (Erickson, Drevets, & Schulkin, 2003). When experiencing acute, psychological stress the right ventral striatum responds by releasing dopamine. In contrast severe, uncontrollable or chronic stress leads to decreased dopamine utilization causing the pleasant effects of drugs to be softened (Oswald, et al., 2007). The influence of glucocorticoids on dopamine becomes most clear when adrenalectomy is performed. This is de removal of one or two adrenal glands. These glands are responsible for the production of corticosterone (and) or cortisol depending on the species. Without these glands the amount of extracellular dopamine concentrations in the nucleus accumbens both during and without stressful conditions is decreased. The concentrations can rise again if corticosterone is replaced, indicating the relationship between the two (Marinelli & Piazza, 2002). As indicated earlier the nucleus accumbens is responsible for dopamine associated wanting and many goal seeking behaviours (Berridge & Robinson, 1998);release of glucocorticoids can increase the extracellular dopamine concentrations in this structure (Marinelli & Piazza, 2002);chronic stress can alter the morphology of the hippocampus responsible for the negative feedback on the stress response (Erickson, Drevets, & Schulkin, 2003) and lesions in the hippocampus of primates lead to stereotypies in the second year of their lives (Bauman, Toscana, Babineau, Mason, & Amaral, 2008).Combining this information might be the answer to the origin of stereotypies or drug abuse in chronic stressful circumstances. The exact mechanism and interaction between dopamine and the stress response in relation to stereotypies is not yet clear but it is likely that a relationship is present.

2.4 Addiction

As mentioned before the mesolimbic pathway is associated with the sense of reward. It is this pathway that is involved in addiction such as drugs and alcohol. Drug abuse is thought to induce increased *wanting* for a specific drug but does not have to increase *liking*. Drugs such as cocaine or the less addictive morphine decrease dopamine release in the central striatum, and as a result of this, subjects are less likely to "like" natural rewards (Volkow, Fowler, Wang, & Swanson, 2004). In 1996 (Berridge) a concept for addiction was proposed that focused on sensitization of a *wanting* feeling.
Till that point it was believed that addicts continue their destructive behaviour for pleasure seeking, but the reality is that they do so even to, and beyond a point where drugs of any kind are pleasurable. Drug addiction has four major components. The first is that drug seeking results from progressive and persistent hypersensitivity of neural systems. When someone uses drugs, it can more than double the original effect on the neurobehavioral systems. These systems account for the '*wanting*' feeling. Bear in mind that wanting something does not always equal liking it. The wanting sensation lacks pleasurable emotion and is usually not consciously perceived (Berridge, Food reward: Brain substrates of wanting and Liking, 1996). *Liking* is the impact of a pleasurable reward triggering senses on the brain, wanting is the motivational value of this reward (such as the rush of getting high). Drugs only hyper sensitise the *wanting* system, causing addicts to want drugs more and more. Desensitisation to *liking* occurs but *wanting* persists, a drug addict just wants drugs but might not experience the same pleasure as someone who has never used before (Volkow, Fowler, Wang, & Swanson, 2004). Drug abuse also results in the decrease of dopamine D_2 Receptors in the striatum leading to a decreased activity in the orbitofrontal cortex. This cortex is responsible for motivation and might be involved in the origin of compulsive disorders (Volkow, Fowler, Wang, & Swanson, 2004). So the difference between *liking* and *wanting* is the presence or absence of a sensory pleasure (Berridge, Motivation concepts in Behavioral neuroscience, 2004). Consequently the sensitivity increase of the wanting but not liking system causes dissociation between the two. But as mentioned before, *wanting* is not associated with conscious awareness, so in order for people to seek out what they want, it has to be perceived as a desire. Lastly, the wanting or liking neural substrates have to result in awareness (Berridge, Food reward: Brain substrates of wanting and Liking, 1996).
The mesolimbic system is involved in addiction but also in the pleasure experiences of normal stimuli. Under normal circumstances, it operates as a reinforcer to increase frequencies of behavioural patterns that result in the gain of a specific reward: "wanting". Drugs desensitise people for natural reward experience, like people suffering from depression, drug addicts, suffer from a reduced ability to experience pleasure and a lack of motivation (Volkow, Fowler, Wang, & Swanson, 2004)

Chapter three:
Needs in Animals

As mentioned before in other chapters, the five freedoms proposed by the FAWC (1992) ensure the welfare of farm animals. Whereas the first four freedoms ensure an absence of negative symptoms of welfare the last freedom, promotes positive signs of welfare (Bracke & Hopster, 2006). Assessing the fourth freedom (freedom to express normal behaviour) can be a challenge. Because what constitutes natural behaviour in an artificial environment? Defining natural behaviour as simply being species-specific is not correct because some behaviour is widespread across species but is nonetheless important for welfare. Also certain behaviours such as tail biting in piglets are species-specific but can be harmful and are therefore used as an indicator of poor welfare (Bracke & Hopster, 2006)

The term natural also implies that the behaviour has to be seen in natural environment, and if not it would be classified as abnormal. However certain behaviours employed in artificial environments may even contribute to welfare, whereas other behaviours that would be appropriate in natural environments can be viewed as abnormal or unwanted in an artificial environment, and even be an indicator of negative wellbeing such as territorial aggression (Bracke & Hopster, 2006) (Poole, 1988).

The third requirement in defining natural behaviour is to define it as being internally motivated. However I have explained in the second chapter that most behaviour is not only internally motivated but external stimuli also contribute to the onset of behavioural patterns. When we assume natural behaviour in itself to be pleasurable, it makes sense that individuals strive to perform this behaviour, these are ethological needs (Defined in chapter one). Ethological needs take up an important part of the welfare aspect because of the pleasure required for behaviour to occur. Taking the mentioned three requirements together Natural behaviour in artificial settings can be defined as: "*Behaviour that animals tend to perform under natural conditions, because it is pleasurable and promotes biological functioning*." (Cited by (Bracke & Hopster, 2006). In this chapter I will show the importance of ethological needs in the welfare of animals. This is best illustrated for domesticated animals.

3.1 Nesting needs

A lot of research has been done concerning pigs and piglets in the farm industry. In order to keep production at the highest possible level, e.g. pigs should grow as fast as possible and sows should produce as many piglets as possible and the entire litter should survive. High profit for the farmer means in the ideal setting as many animals as possible should live on the least possible amount of space. In these high production farms it is common to use farrowing crates that restrain the sow's movement during parturition and lactation to keep the sow from crushing her litter. When a sow is kept in a crate it still shows signs of the need to build a nest despite the absence of external stimuli to promote this behaviour. In the wild, sows tend to separate them selves from the group one to three days prior to giving birth and may travel a great distance before starting to build a nest. By rooting and pawing in the ground the sow digs a shallow hole, then the sow collects nesting materials and places these on the edges of the nest (Wischner, Kemper, & Krieter, 2009). These nest materials are usually gathered within a small radius of the nest. In crates sows try to employ such behaviours as well by biting and rooting at the rails: a behaviour that compares to the natural gathering behaviour. These sows are also very active and frequently try to stand up and move position. Whereas their wild counterparts have the space to turn around in circles during nest building in an attempt to elevate the edges of the nest, the crated sows are restricted in their movements (Wischner, Kemper, & Krieter, 2009). When the sow is allowed to farrow in an ellipsoid crate, she can perform this circular movement. Not only the sow's need to perform this behaviour is fulfilled, the number of stillbirths is also decreased. This could be because the sow is less stressed but probably

the overall health and strength of the sow is increased due to physical fitness. Strangely enough the birth process is also much shorter in the ellipsoid farrowing crates then in the normal ones (Lou & Hurnik, 1994). However, pen soiling is increased, and in general free farrowing pens are more difficult to keep clean, presenting the farmer with another problem.
So despite the unnatural environment it is clear that elements of natural behaviour are still expressed, sometimes to an excessive degree. It is hard to classify the constant repetitive motion of pressing a head against the bar as a stereotypy since this behaviour is part of the natural repertoire (Wischner, Kemper, & Krieter, 2009). But stress is involved when these behaviours cannot be expressed; this is clear when comparing this farrowing situation to another (artificial) one: farrowing in pens. The most commonly used is the *Schmid farrowing pen.* These pens differ from a normal crate because they contain a nest and a non-rest compartment which is about twice as large as a regular crate. In these pens a certain amount of straw is usually present. This allows the sow to perform more nest-building behaviour. Sows in these pens show a greater variety of related behaviour during their nest-building period (Damm, Lisborg, Vestergaard, & Vanicek, 2003) and do this to full completion in contradiction to crated sows (Boulton, Wickens, Brown, Goode, & Gilbert, 1997). The overall time spent on nest building behaviour is about 2 hours shorter but providing cover in pens can lengthen this behaviour. This probably mirrors the natural environment better because sows create a cover of the nest by making edges around the nest and cover it with grasses. Providing straw does not increase nest building, but it does decrease the number of crushes or near-crushes of piglets (Damm, Heiskanen, Pedersen, Jorgensen, & Forkman, 2010).
Increased heart rate can be an indication of stress. This occurs more in sows farrowing in crates. Perhaps the lack of feedback from the nest for the crated sows is the stressor that leads to the increase in heart rate. Sows farrowing in crates take significantly more time to do so compared to sows farrowing in pens (Olivero, Heinonen, Valros, Halli, & Peltoniemi, 2008).
The importance of a sow to be able to build a nest extends to her offspring. At a certain point the piglets need weaning. This is a natural process, but the condition at which the sow is allowed to farrow affects this process. Outdoor-reared piglets are bound to show less unwanted and injurious behaviour such as belly-nosing and ear and tail biting then indoor-reared piglets. In outdoor systems sows are allowed to build their own nests unlike indoor sows, which are singly-housed (Cox & Cooper, 2001).
Pigs are not the only farm animals that value nest building, hens also require a site to nest when laying eggs. The nest can provide the eggs with extra warmth and some form of shelter. To test if having a nest site is truly that important obstacles can be placed in order to measure the effort an individual puts in to achieving the reward a concept called the consumer demand theory first described by Dawkins (1983). Hens do consistently prefer certain nests to lay eggs even if the costs to go to these sites is increased (Cooper & Appleby, Demand for nest boxes in laying hens, 1996), for most hens this is a sheltered nest box while for others this is litter tray (Kruschwitz, Zupan, Buchwalder, & Huber-Eicher, 2008). Sows have the need to build a nest, and for hens having a nest is important as well, but do they feel the need to build one? When presenting a hen with different sites to lay an egg (so without restraints to access them) they still show nest building behaviour. If there is no need to show nest building behaviour the time spent on it would be shortest if the hen is already presented a preformed nest. And perhaps would be absent if in this preformed nest an egg is already present. But on the contrary: nest building behaviour is shortest when presented a flat surface and longest when presented a self-made preformed nest with an egg (Hughes, Duncan, & Brown, 1989). In modern western farms some form of a nest box is present so no eggs are lost, however these industries usually face bigger problems as discussed in Chapter 3.3.

3.2 Social Behaviour

Unlike pigs, (most) horses in the Netherlands are kept for other reasons than meat production. But like pigs they evolved under natural conditions and solely for our purpose they have been

domesticated. It is no wonder that most behavioural patterns between feral and domesticated horses are similar. Feral horses are very social animals, and a group is usually made up out of family members or bachelors. Social interactions are expressed by means of play and allogrooming. What is interesting is that all animals do have another individual they prefer above others, a 'friend' they rather groom or are groomed by and a playmate. Play makes up such an important part of the behavioural patterns of feral horses that foals do it, but also sub adults and even elder geldings (Dierendock, 2006a). In modern husbandry however horses are usually kept confined and solitary and play and allogrooming is not possible (Dierendonck, 2006b). According to chapter two this likely leads to frustration and stress. Horses previously placed in a social setting and are then housed in a solitary situation show a negative response to this change. Their health deteriorates tremendously. Even with the same feeding regimes, horses forced to live solitary with little contact gain very little weight compared to others who are allowed contact. The heart rate of these horses is higher; they spent less time feeding, and show more stress related behaviours such as neighing, nibbling and snorting (Visser, Ellis, & van Reenen, 2008). This stress and frustration is also clear when assessing behavioural patterns, unlike socially housed horses, individually housed horses show far more stereotypies, one that has been related the most with motivation for social contact is weaving. One known measure to reduce this behaviour is to provide solitary horses with mirrors, so it can mimic social behaviour (McAfee, Mills, & Cooper, 2002). A second method is to provide the horses with an outdoor view (Cooper, McDonald, & Mills, 2000). Or providing horses with a view of other horses with an internal grill within their stalls will decrease the weaving behaviour significantly (Cooper & Albentosa, 2005). By having equines perform test to gain access to another companion horse the need for sociality can be determined. If the need is high a horse will be willing to put more effort in performing the operant task for the following reward, in this case social contact. And to no surprise horses are willing to work more if this means they gain contact with a conspecific. This is especially true for young female horses that in normal conditions only see, smell or hear other horses, When provided with some contact with others on a weekly basis, there seems to be no difference in reluctance or motivation to perform a task when the reward is full social contact compared to head or muzzle contact (Søndergaard, Jensen, & Nicol, 2011). When there is no contact what so ever during test phases stallions who come in contact with other horses seem to display a sort of rebound effect, they tend to allogroom and play significantly more than horses not deprived of social contact (Christensen, Ladewig, Søndergaard, & Malmkvist, 2002). These findings suggest that social contact is an essential need for horses to fulfil since it is worth working for and when deprived of such, stereotypies may arise, and a rebound effect can be found when introduced to a new horse.

Social bonding is important for horses later in life, therefore it makes sense that this is important early on in life. When a foal is born its main contact is its mother, the bond between them is vital for survival, especially in feral horses. At some point in the development of the foal the weaning period starts in which the interaction with its mother is decreased but interaction with peers is increased. In domesticated horses several methods for weaning are be used. The foal can be either group weaned or individually, abrupt or gradually (Waran, Clarke, & Famworth, 2008). When foals are weaned individually they spend significantly more time engaging in abnormal behaviours such as licking or chewing the stall and kicking the stall walls then when they can here see and smell others through paddocks (Heleski, Shelle, Nielsen, & Zanella, 2002)(abstract of Waters, Nicol & French, 2002). Weaning can be considered extra stressful in domestic situations due to nutritional challenges and more intense human intervention. But that social bonding with peers is an ethological need is illustrated by the fact that individual weaning increases stereotypical behaviour. Abnormal behaviours are even more increased when the weaning takes place in a barn instead of grass (abstract of Waters, Nicol & French, 2002). Horses displaying some sort of abnormal behaviour prior to weaning are prone to other stereotypies as well after the weaning period. But they also influence other horses with this. Individuals sensitive to restlessness of other horses may also start to employ stereotypic behaviour (Nagy, Schrott, & Kabai, 2008) even when their ethological needs are not compromised.

Social behaviour is found across many species and thus far I have only discussed farm animals. However in terms of evolutions these are not by far our closest relatives. Macaques are a lot closer in the family tree and in the sixties a few controversial social experiments with this species were executed. These were later on viewed as being immoral and cruel. Nowadays we would never condone this kind of research, but I would like to stress the scientific importance of it. Harlow *et al*. (1965) raised monkeys in partial or total isolation, causing the monkeys to employ compulsive non-nutritive sucking, repetitive stereotyped movements, detachment from the environment, hostility directed themselves, abnormal sexual behaviour and aggression toward others when social interaction was allowed. These monkeys were exposed to severe stressful circumstances, but however extreme; they have showed us the importance of sociality for non-human primates. These experiments did contribute to the awareness of the importance for sociality to ensure welfare in these to us much related species.

In their experiment of total isolation, Harlow *et al* (1965) used Rhesus Macaques who were completely visually isolated hours after being born. After a test period they are allowed to enter a play room to interact with conspecifics. Present at that time is a control group who has not been isolated before. Macaques that are released from isolation after three months usually go in a shock state where they clutch themselves and rock from side to side. But some of the effects can be reversed after a period of time of social contact. This in contrast to macaques that were isolated for six months: they did not engage in any play form four weeks after they were released from isolation. After four weeks they only played with monkeys who had been isolated as well. Over the course of time social contact between isolated and not isolated monkeys did increase but only when the not isolated macaques directed aggression toward the other group. Monkeys who are isolated for a year after birth do not play, show no aggression, and show no sexual behaviour like normal monkeys do. In fact they become so helpless the social part of the experiment had to be ceased due to severe aggressive interactions with controls (Harlow, Dodsworth, & Harlow, Total social isolation in monkeys, 1965). When Rhesus Macaques are isolated for a long period in their early life several complications arise: one being the disability to establish normal sexual behaviour. When impregnating females who never experienced maternal care, they become very indifferent to their offspring. Some even abuse their children. These infants are so eager for maternal contact they keep clinging to their mothers even if this causes the mother to become more abusive (Harlow & Suomi, 1971). After (sometimes) killing several of their offspring some of these motherless mothers learn to become proper mothers, but most do not.

So isolation in primates' leads to social impairment and stereotypy's such as rocking. According to our definition of an ethological need, thwarting the behavioural pattern would result in frustration and stress. In primates this can be done my measuring cortisol levels. When marmosets are isolated for a short period of time (30 to 120 minutes) from their mothers and the rest of the family they exhibit a higher basal level of cortisol, and have reduced glucocorticoid receptor expressions (Pryce, Aubert, Maier, Pearce, & Fuchs, 2011) (Arabadzisz, et al., 2010). The importance of sociality is not only observed in the laboratory or other captive primates, but also in their wild counterparts. Wild baboons that are considered isolated (who have little agonistic or affiliative interactions and are not in close proximity to others very often) have increased cortisol levels. Not only that, they also show increased dexamethasone resistance (Sapolsky, Alberts, & Atlmann, 1997) (dexamethasone is a synthetic corticosteroid). Isolation stress can down regulate glucocorticoid receptor numbers like in the marmosets. These receptors in the hippocampus are involved in a negative feedback loop for more glucocorticoid secretion. However, lesser receptors increases resistance to the feedback mechanism, resulting in elevated cortisol levels (Sapolsky, Alberts, & Atlmann, 1997).

That sociality is not only important for infants but throughout the entire lifecycle of primates comes to show when monkeys are isolated later in life. These monkeys also develop stereotypies like self-biting (Novak, 2003) (Tiefenbacher, Lee, Meyer, & Spealman, 2003). Subsequent stress in individually housed monkeys elicits self-biting, suggesting that this stereotypy functions as a coping mechanism. The fact that heart rates go down after a biting sessions confirms this suspicion (Novak, 2003).

In Chapter one it has been explained that stress can alter the dopamine response. If being social is a need for primates it is expected that functioning of the dopamine receptors has been altered. When testing rhesus macaques that were totally isolated for nine months after birth it becomes clear that their sensitivity to dopamine has changed compared to socially reared conspecifics. Isolated reared macaques respond more strongly to the administration of the dopamine agonist apomorphine by increasing intensity and occurrence of whole-body stereotypy's (Lewis, Gluck, Beauchamp, Keresztury, & Mailman, 1990).
In order for an ethological need to be a need, it has to be fulfilling in itself. In other words having social contact can be a reward in itself. Like Dawkins proposed (1988) you can measure the need by having the subject pay a price in order to acquire the reward. Unfortunately no consumer demand approaches have been done to test the motivation of any primate species to engage in social contact with others. But the fact that mere images or pictures of other conspecifics are preferred over other pictures indicated that visual social cues have high values. Several Macaques species will press a lever longer to view pictures of their own species, then pictures of others species (Fujita, 1987), and depending on the genotype macaques are also willing to pay (in the form of fruit juices) to view upon other Macaques (Watson, Ghodasra, & Platt, 2009). When taught so, macaques even employ unnatural behaviours such as pulling ropes to acquire access to conspecifics. The latter mentioned experiment was done with both feral and socially deprived Rhesus macaques. Socially deprived monkeys choose mirror images of themselves significantly over real life conspecific views but the overall interest in social contact is about the same as the feral Macaques. If the animals did not want to see others they did have to pull the rope, or one would expect the count to be much lower. Instead, the macaques pull the lever to engage in social contact (in any form) as much as 56 to 97 counts per day (Gallup & McClure, 1971). Marmosets are even prepared to jump over a wired grid to see a conspecific (Forster, 1995). Even though no records are to be found of dopamine involvement or specific wanting or social behaviour, these results indicate a need for sociality in non-human primates.

3.3 Exploration and Foraging

Pigs are known to root in the ground in an attempt to find food. In farms food is offered to the pigs making the rooting behaviour superfluous, however in pigs rooting is the most predominant behaviour even in artificial environments. The need to perform the behaviour even in the presence of enough food is so great that in poor enriched environments pigs start to perform other oral activities such as belly nosing (Bench & Gonyou, 2006) (Beattie, Sneddon, Walker, & Weatherup, 2001) (Olsen, 2001). Belly nosing first occurs about 14 days after weaning and can potentially be injurious. Providing enrichment such as mushroom compost and roughage significantly helps to reduce this behaviour (Olsen, 2001) (Beattie, Sneddon, Walker, & Weatherup, 2001). Providing a pen wall as enrichment shortly after the behaviour starts to occur is the best strategy to reduce the harmful consequences when the behaviour is performed on pen mates (Bench & Gonyou, 2006).
For the farmer it is most useful to remove the sow from the piglets as fast as he can so she can be impregnated as fast as possible. In early weaned pigs a behaviour called tail biting is present. This behaviour can be divided into three categories (two-stage tail-biting, sudden-forceful tail-biting and obsessive tail biting) whereas most of the categories represent a form of establishing dominance among a group, two-stage tail-biting seems to arise from unfulfilled needs (Taylor, Main, Mendl, & Edwards, 2010) (Schrøder-Petersen & Simonsen, 2001). The origin of this behaviour is still under investigation but it could be related to either early weaning so the pigs still have the need or urge to suckle on a teat (Schrøder-Petersen & Simonsen, 2001), (even if enough nutrients are provided for them) or, more likely, to not being able to satisfy explorative or foraging behaviour (Taylor, Main, Mendl, & Edwards, 2010). This need is so strong that they will suckle or nibble on the tails of others and can harm other pen mates by inflicting minor wounds or even amputations. Eliminating this behaviour in farms as they are now might not be possible but providing enrichment to satisfy

foraging, explorative or suckling behaviour by means of straw bedding or compost does reduce tail biting significantly. The best results can be found when enough straw is given (Zonderland, et al., 2008) implicating that foraging or exploring is the reason for pigs to bite another's tail.
A big problem found in the poultry industry is feather pecking, and it can lead to heavy injuries including death. This can be stopped by clipping the beaks of the birds (Huber-Eicher & Wechsler, 1997), but this is regarded to be animal unfriendly. Another method is to prevent the behaviour. Feather pecking is believed to be the result of redirected ground pecking. So when offered more foraging opportunities the fowls reduce their feather pecking activities towards others (Huber-Eicher & Wechsler, 1997). This behaviour is considered an ethological need. When giving chickens a choice between long-cut straw, which is nutritious, and polystyrene blocks, that contain no nutrients at all, foraging behaviour is equal and feather pecking behaviour is reduced. If the quality of the offered foraging substrate is increased the feather pecking is consequently decreased (Huber-Eicher & Wechsler, 1997). Having no access to foraging material such as straw, results in stress. Higher Heterophil/Lympocyte ratios indicate stress in chickens; these ratios are elevated in chickens that are unable to express foraging behaviour due to absence of appropriate material (El-Lethey, Aerni, Jungi, & Wechsler, 2000). Stress can also inhibit the immune response when it is chronic (Padgett & Glaser, 2003); no access to foraging materials such as straw inhibits the immune response of chickens (El-Lethey, Aerni, Jungi, & Wechsler, 2000). These results confirm the statement that foraging is an ethological need because the behaviour is performed regardless of any nutritional value and results in stress and redirected (abnormal behaviour) when inhibited.
Another behaviour that chickens employ is dust bathing. It has been thought that performing this behavioural pattern is of such importance that it causes severe stress when chickens are deprived of it. The fact that dust bathing is rewarding and thus an ethological need in itself is supported by several studies. The upkeep of feathers is useless if you have no feathers to clean, yet featherless chickens show the behavioural patterns nonetheless (Vestergaard, Damm, Abbott, & Bildso, 1999). When chickens cannot dust bathe due to an inappropriate environment they experience stress. Births raised on a wire floor (and so are never able to perform this behaviour) employ more stereotypic behaviours such as pecking and a higher level of stretching then birds who are reared on sandy floors. When they are given access to sand so they can clean their feathers, they still employ these stereotypic behaviours but pecking at other birds and threats toward them decreased. When you would measure stress levels in corticosterone you would find no difference in stress levels prior to access to sand. Contrarily chickens reared on sand have heightened levels of corticosterone when they are deprived of sand, but this does not result in any sudden stereotypic feather pecking later on (Vestergaard, Skadhauge, & Lawson, 1997). This indicates that dust bathing is important even if there are no feathers to clean and having no access to it results in stress. Stereotypies only arise if deprivation starts early in the development of the chick.
The equivalent of rooting in pigs and pecking for seeds in chickens is grazing in calves. This behaviour is so important it must be maintained even if there is no milk to drink. If the sucking behaviour (nutritive or not) is deprived during a meal this motivates the calf to perform more suckling behaviour on its next meal (Rushen & de Pasillé, 1995). Suckling might seem harmless but like tail biting in pigs, suckling in calves can lead to damage in pen mates, e.g. due to cross-sucking, suckling on body parts of other calves with injurious results (de Pasillé, 2001). Because suckling is an oral behaviour necessary to obtain milk it may seem that this behaviour is an indication of hunger. But suckling is seen more after a meal then before (de Pasillé, 2001) (Rushen & de Pasillé, 1995). If calves get a taste of milk they want some more and can engage in non-nutritive sucking. This behaviour does not occur when other cues for feeding time are present. Milk is important and works as a reinforcer so maybe it is not an ethological need at all but more a reaction to stimuli? When providing 2 groups of calves with milk of which only one receives a dry rubber teat as well, that group will stop suckling faster in the second meal, when both groups receive a dry teat (Rushen & de Pasillé, 1995). In other words when deprived of performing this behaviour, the behaviour is reinforced in the next meal. Though under debate I consider this behaviour still an ethological need even though it needs an onset. According to my definition in chapter one, a need is only a need if it is performed no

matter what the environment is like even if the physical needs are met. Calves that are either fed on an artificial teat or from a bucket and a rubber dry teat next to it, show different sucking behaviour after feeding time. Teat-fed calves perform only a minute of sucking per day, but bucket-fed calves perform this behaviour for 13 minutes on a daily basis (Hammell, Metz, & Mekking, 1988). For non-nutritive suckling in calves a taste of milk is necessary to start the motivation, however, once motivated the behaviour is strongly reinforced whatever the environment. This motivation is so strong calves start to suckle on other calves or their housing, if this is for some reason not possible the calves become frustrated. Calves strongly rely on their mothers for food and protection. In modern husbandry many calves are separated early from the mother and reared alone or in a group with other calves. Separate housing has clear advantages because disease transmission after cross-sucking is prevented. On the other hand the calf cannot perform social behaviour, so rearing in a group can help, yet cross-sucking is the downside. One option is to restrain the calves with special feeders so they are not disturbed when sucking on the teat. With this method cross-sucking is significantly reduced (Weber & Wechsler, 2001), but the underlying problem is not resolved by this. The motivations for suckling may be different for different age groups. At all ages the placement of an artificial teat instead of a bucket helps reduce the cross sucking. When the calves reach the age of 76 days, the motivation to suckle can also be reduced when given the possibility to exercise (Ude & Schwalm, 2011).

Heifers show a lot of oral stereotypies, which are usually food related. Cows are known to graze for large portions of the day but in farms they are not always allowed to do so. Especially in winters when it is considered too cold for the cattle to graze outside the food regime is restricted indoors. The need to eat constantly results in oral stereotypies like inner and outer tongue rolling, bar-biting, chain-chewing and biting other objects. Several studies have found this behaviour to be reduced when providing food *ad libitum* instead of in restricted feeding regimes (Redo & Nordblad, 1997; abstract from Redbo, Emanuelsson, Lundberg, & Oredsson, 1996). Especially if heifers were previously allowed to forage and are then tethered (tied up so they are restricted in free movement and foraging opportunities) their cortisol levels and levels of stereotypies are increased (Redbo, 1992) (Redbo, 1993). These stereotypies reduce the nervousness of the cow in the sense that food-related tongue rolling decreases the heart rate significantly when performed (Seo, Sato, Kosaka, Sakamoto, & Tokumoto, 1998).

Feral horses spend about 16 hours a day foraging, in stables however concentrated food is usually present, which contains the necessary nutrients in concentrated doses, restricting foraging behaviour. To mimic the horses' natural behaviours several types of enrichment can be introduced, a commonly used enrichment in stables is the provision of hay. Foraging does not only satisfy the need to forage itself but also has a positive influence on the social behaviour of individuals allowed to do this. Mares provided with *ad libitum* hay are spending more time on feeding but also had more social interactions and bonding between other mares (Benhajali, Richard-Yris, Ezzaouia, Charfi, & Hausberger, 2009). This can be explained in terms of stress. Not being able to forage (even though the nutrients provided in your food are sufficient) might lead to stress behaviour such as alert standing and increased locomotion leaving less time to interact socially. Allogrooming is rarely seen in horses that do not have the opportunity to forage (Benhajali, Richard-Yris, Ezzaouia, Charfi, & Hausberger, 2009). This makes sense because this behaviour is only seen among preferred partners. Being a preferred partner means you have established a bond, but as mentioned before this is easier if the horses are allowed foraging behaviour. So increased foraging opportunities have a positive effect on the welfare and behaviour of horses. Simply increasing meal frequency from concentrated meals to prolong feeding naturally can reduce oral stereotypies like sham chewing, tongue rolling, biting or grasping stable fittings or repeated licking of stable fittings significantly (Cooper & Albentosa, 2005). But if this is an ethological need then being deprived of this would lead to frustration and ultimately stereotypies. It has been found that crib biting in horses is a behaviour that is found two hours after a meal is provided suggesting that it is food related behaviour (Cooper & Albentosa, 2005) (Clegg, Buckley, Friend, & McGreevy, 2008). Horses employing this stereotypic behaviour take more time to consume their food. It would make sense that crib biting is a result of stress and therefore

horses that show this compulsive behaviour have elevated levels of cortisol, or increased heart rate, but this is only the case during the biting itself. Also crib biters have a lower serotonin threshold then horses that don't (from abstract Lebelt, Zanella, & Unshelm, 1998).
Foraging behaviour is not only important in the previously mentioned species but also to a more closely relative of ours: the primate. One commonly used solution to reduce abnormal behaviours brought about by the thwarting of activity or foraging needs in individually or socially housed primates are foraging devices (Vignes, Newman, & Roberts, 2001) (Borges, Byk, & Del-Claro, 2011) (Roberts, Roytburd, & Newman, 1999) (Bayne, 2005). Using these devices abnormal behaviours such as pacing and inactivity are reduced and more species specific behaviour are observed. In the wild, monkeys spend significantly large amounts of time foraging, varying per species (Honess & Marin, 2006). In captivity most food is readily offered, so foraging is no longer necessary and this leaves the animals with a lot of spare time. Especially when housed alone this leads to inactivity or stereotypic pacing. In other words, not being able to occupy your day with meaningful activities will lead to frustration. But weather this reflects an ethological need? I would say there is lack of evidence to support that statement. Most foraging tasks and devices are rewarded by means of food. Though the task makes the obtaining of food much more interesting it does not provide evidence that the task itself is interesting. To my knowledge no research has been done to find out what the role of dopamine in foraging itself is. Nonetheless considering the stereotypies that manifest itself when monkeys lack stimulation, I would think either foraging or exploration (or perhaps both) might be a ethological need in non-human primates, which is not surprising considering food related ethological needs in other species (see paragraph one 2.1 to 2.4). But this does require intense research.

Chapter four:
Needs in Humans

The last word has not been said regarding theories of ethological needs in animals, but the consensus seems to be that the proposed theories cannot completely be extrapolated to human beings. Humans show highly intelligent and flexible behaviour, but this is not the only reason why internal motivation and needs in humans is hard to describe. All over the world people act and behave differently because of culture and individual intelligence. In other words, something that might be innate could be (mildly) suppressed due to culture. The self-determination theory tries to explain some needs in humans. According to this theory all human needs can be categorized into the need for competence, the need for relatedness and the need for autonomy. These needs are essential for human growth, wellbeing and social development (Deci & Ryan, 2000a) (Deci & Ryan, 2000b).
According to the researchers who came up with this theory, humans have innate psychological needs that are the basis for self-motivation and personality integration. Quite similar to our definition of ethological needs Ryan and Deci describe the humans psychological needs as: "*A basic need, whether it be a physiological need or a psychological need, is an energizing state that if satisfied, conduces toward health and well-being but, if not satisfied contributes to pathology and ill-being*" (Ryan & Deci, 2000b). They concluded that in nature, humans are growth oriented and have a natural drive to find a unified sense of self. It is important to realise that there is a great difference between a need fulfilment and a drive. The need fulfilment as used in this theory means that behaviour patterns that are driven by a motivation do not necessarily arise from a deficit (Deci & Ryan, 2000b). Note this definition is very similar to our stated definition in chapter one: in order to perform appetitive behaviours a motivation for consummatory behaviour is not essential. What is essential is the motivation for autonomy and competence, according to the authors this is innate but has to be intrinsically motivated. Extrinsically motivation can undermine one's motivation to achieve a particular need satisfaction. Figure 4 shows how the theory works. Need satisfaction as a whole is composed of three components: the need for autonomy, the need for relatedness and the need for competence. If the needs are met this will influence the individual's general self-esteem. Conversely when the needs are thwarted or not met anxiety will occur.

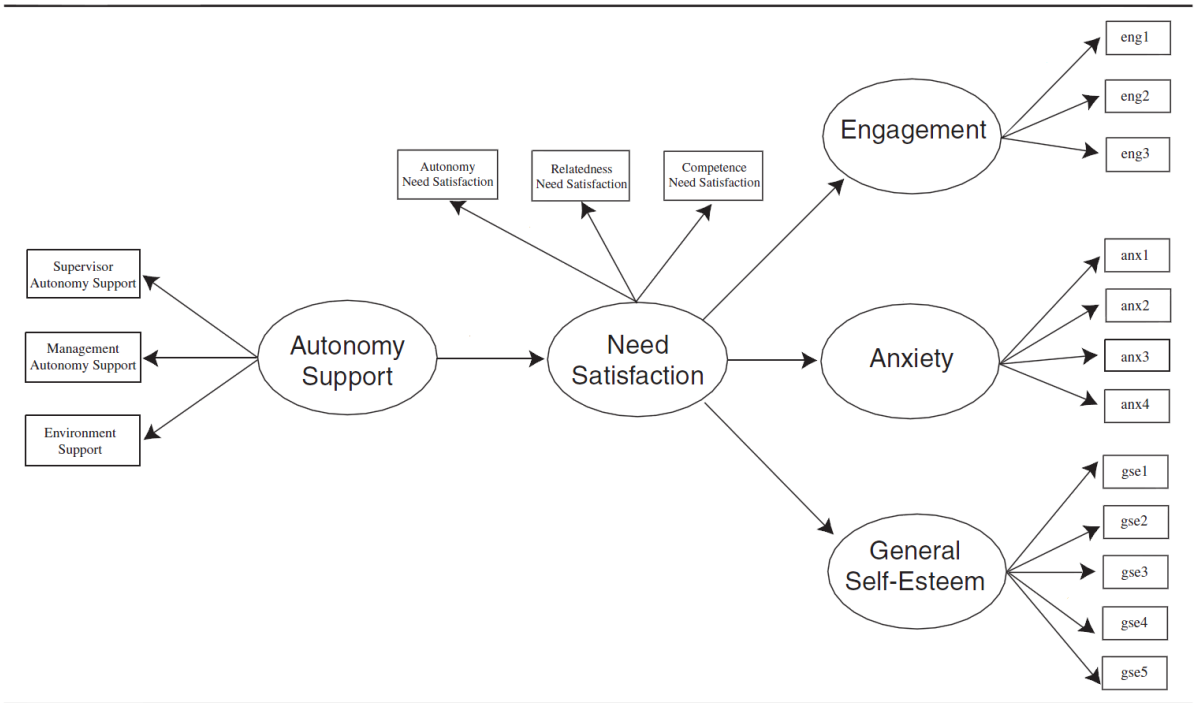

Figure 4 Self-determination model. Model revised from **(Deci, Ryan, Gagné, Leone, Usunov, & Kornazheva, 2001)**

This can explained by a model specifically designed for work motivation (see figure 6). The model also states that perceived autonomy support can facilitate the satisfaction of different need components. This in turn will promote task engagement. In other words: when an individual feels that the work environment stimulates autonomy, satisfaction of needs goes up resulting in a positive feedback by promoting the will to engage in the task.
In order for this model to have worth it is important that it can be applied to every individual, meaning it should not be culture-dependant. When applied to the work environment this seems to hold true (Deci, Ryan, Gagné, Leone, Usunov, & Kornazheva, 2001). To what degree employers feel supported in self-sufficient predicts to what degree they feel their needs are satisfied. This goes for employers across cultures, as does the effect this has on the individual's well-being: so it seems the model is valid. However the study does show that there are some slight differences across cultures, Bulgarian employees for instance are more prone to anxiety related behaviours when needs are not met, whereas for United States employees need satisfaction is reached more easily when they feel support from management in terms of self-sufficiency (Deci, Ryan, Gagné, Leone, Usunov, & Kornazheva, 2001).

4.1 Social contact and solitude

Like animals, humans have needs too. Initially this goes as far as hunger, thirst, safety, rest, thermoregulation and other basic needs. But when these needs are met other needs arise. This was first acknowledged by Freud (1930) who believed that men can suffer from three different factors: one being our own body which decays over time, a process one cannot stop and is preceded by pain, anxiety and warning signals, the second being the external world, merciless and full of destruction, and thirdly our relationship with other men. Freud claims that the basis of civilisation lies in the ability to love. When genital satisfaction was a need that needed fulfilment more often, it was useful for a man to keep his woman close. Because the woman's interest lies with her offspring it was useful to stay with her man for care. Family bonds became more and more important. Moreover when trying to overpower their fathers, sons realized that a group is stronger than one individual. As a result, larger and larger amount of people were able to live together in a community. In his book, Freud (1930) makes a distinction between sensual love and aim-inhibited love. These kinds of affection both extend beyond the family but sensual love, genital love leads to the formation of new families and aim-inhibited love to friendships. A lot of researchers have adjusted this theory over the course of time, but most of them trace the need for sociality back to the familial bond, as Freud did (found in (Baumeister & Leary, 1995)). The need to interact with others is so great that it might be a foundation for other needs, such as the need to enquire power, the need to achieve, the need for approval and the need to affiliation. Much of these needs can be explained by the need to belong. This need to belong as a basis for social behaviour will be addressed further as the belongingness theory. This theory states that human culture is at least partly adapted for people to be able to live together, thus satisfying the need to be social (Baumeister & Leary, 1995). Unlike the Freudian belief that sociality and the establishment of bonds is sexuality driven, this theory assumes that this is an innate feeling. For this to be true, social bonds should be able to be traced back to all humans' cultures to different degrees. That living in groups offers several advantages is well known. Whilst living in a group, individuals are able to split hunt for larger prey, defend against more of bigger predators, the ability to compete better for limited resources and share food. But also in terms of reproduction, living in a group can be advantageous, one does not have to find a mate, and once mated, rearing offspring can be a mutual effort (Pusey, 2008). Long-term relationships also increase the chances that offspring reaches maturity and so the ability to rear offspring themselves, increasing fitness of the original couple. Though offering benefits, living in a group also has its costs. You have to share food even when it is scarce, diseases can spread easily and one may have to compete for mates. However there is no doubt when faced with the choice to face another group alone or with a group of yourself, the outcome will be more positive when cooperating with others too (Baumeister & Leary, 1995). Forming and establishing bonds is beneficial when others do so as well. Viewing this,

sociality has an evolutionary basis; a likely result would be if certain human properties would be selected to maintain social bonds. In other words it would be useful if an individual would experience positive emotions when in proximity to other humans, and experience negative ones when deprived of social contact. This resembles what we see in other social animals such as primates (REF).Even though being single in this time of age is considered a modern life style, research suggests single people that do not regularly engage in social contact are less happy then others. Individuals having close relationships like in an active social life in religious terms are much happier than previously mentioned singletons. Being married and or having children also increases happiness (Haller & Hadler, 2006). These positive emotions can be a mechanism to reinforce the behaviour to make positive social contact and avoid deprivation (Baumeister & Leary, 1995). The term social contact is somewhat incorrect, since not every form of social contact has to be positive. And even when positive it does not have to be satisfying. When interacting in a non-hostile manner with strangers or people someone really dislikes, the need for belonging is probably not met. This need to belong infers that relationships are desired and should be perused. This means that long term contacts are more fulfilling and short term contacts are only a way to form a potential long term bond (Baumeister & Leary, 1995). For this to be true, common ground and fast social bonds have to be able to be formed. Several studies back this theory up. Most of them work by the same method; randomly assigning subjects to a group and have them assess or evaluate another group (also randomly assigned). While there is no predisposed difference between the groups, groups do rate their own group more positive then the out-group and even discriminate against the other group (Tajfel, Billig, Bundy, & Flament, 1971) (Ahmed, 2007). This behaviour is visible as early at the age of 6 (Bigler & Jones, 1997) (Bigler, Brown, & Markell, 2001). It would make sense that if people try to create bonds between strangers as fast as possible, dissolving relationships may also be hard, however little research has been done backing up or contradict this statement (Baumeister & Leary, 1995). That positive emotions are associated with social bonds is clear, but that the intensity of the happiness is also correlated with the strength of the relationship is illustrated by marriage. Getting married in western developed countries does not mean that one gains a new social relationship, since the couple usually knows each other for a long time. But couples getting married are happier then when they just live together, this finding goes for both men and women, and is true for several nations (Stack & Eshleman, 1998). If having strong bonds means you are happier, lacking these bonds should have the reversed effect: being deprived of or having relatively little social contacts results in negative emotions and symptoms in normal individuals. Studies show that when women are maltreated in any way (such as physical or emotional neglect or sexual abuse) this has great impact on their later life. It is argued that the aversive arousal with all of these kinds of neglect is common, and the following copying mechanisms are similar, as are the negative psychological outcomes (Vranceanu, Hobfoll, & Johnson, 2007). When confronted with any of this kind of abuse, such as social neglect, stress later in life can increase depression vulnerability. When social support is lacking was well, these women may also suffer from Post-traumatic stress disorder as a result of early childhood maltreatment. Even though the original onset for depression was the maltreatment, stress does seem to play a crucial role in this process (Vranceanu, Hobfoll, & Johnson, 2007). Social neglect by parents can be a large stressor later in life but, the feeling of loneliness may also come from peers. In fact peer contact may even become more important to the individual then contact with parents, since the contacts made in developmental period are usually in the early middle childhood and adolescence. At this time most frequent social contacts are between peers and not between child and parent. When feeling lonely for more than four consecutive years increased the chance that depression at later age occurs (Qualter, Rotenberg, Brown, & Munn, 2010). That loneliness or neglect leads to negative emotions such as depressions is clear but feelings of loneliness do not have to have an external cause. People themselves also have different ways or strategies to attach to others; categorization can make results more clear. Three categories arise when individuals bond or attach to their parents or peers. According to the attachment theory, the first pattern is the so called “secure attachment” category; these people tend to see their caregiver or others as a source of comfort when confronted with stressful stimuli or situations. The second category tends to avoid or

ignore others in stressful situations or stimuli and is therefore named the “avoidant attachment”. The third category, the “ambivalent attachment” seeks attention of others sometimes in a clingy manner but this does can be in a rejective or angry way (Muris & Meesters, 2002). Children at ages between 11 and 15 that show forms of social phobias, panic disorders, separation anxiety and other anxiety disorders usually attach themselves to their parents and others in an ambivalent and avoidant way. And more interestingly the attachment style and different disorders both account for a unique proportion of the variance of anxiety disorders (Muris & Meesters, 2002). Feelings of loneliness and different attachment styles also play a role later in life. Though most researchers focus on signs of depression at early middle childhood, large changes in social contacts also occur later in life. When going to college people are forced to go to new surroundings and establish new bonds with strangers. Again, dealing with new people can be categorized according to the patterns of the attachment theory. Freshman’s who have a rejecting attitude towards social contacts with others tend to feel lonelier and subsequently more depressive then others. Some freshman’s prefer not to express emotions or distress towards others, but it is this information that is an important factor in developing new friendships (Wei, Russel, & Robyn, 2005). This behaviour is typical for students who rely on avoidance attachment. On the other hand we have the ambivalent attachment strategy, resulting in attachment anxiety and depression. Freshman University Students who employ this behaviour do not all experience discomfort when expressing emotions, in fact they tend to exaggerate their feelings in hopes of getting special attention, in a clingy yet rejective manner (Wei, Russel, & Robyn, 2005). While we use different methods to establish positive social contact, sometimes this is out of our hands. In some countries such as the US it is a normal procedure for sentenced criminals to initially be placed in solitary confinement. In the US system inmates, solitary confinement is used to control and punish difficult or dangerous prisoners. Sometimes these prisoners did not commit a serious crime but have violated prison rules and are therefore placed in super maximum prisons (Metzer & Fellner, 2010) (Rhodes, 1971). In these prisons it is not uncommon for prisoners to spend about 23 to 24 hours per day in their typically small cells. They eat alone and rarely see other inmates, the only contact with other humans is with the guards who take back their eating tray and shackle them for exercise or some other activity. Apart from not being able to socialize in any form for many years these prisoners are usually under constant surveillance and denied from any educational programs (Metzer & Fellner, 2010) (Haney, 2003). It makes sense that being confined in a prison is a stressor itself since 15 per cent of the inmates who are not in solitary confinement show some kind of psychiatric disorder. This is small percentage compared to inmates who are forced to live solitary and who of which 28 per cent show psychiatric disorders. The most common disorders inmates show are adjustment disorders, followed by depression and anxiety (Andersen, Sestoft, Lillebaek, Gabrielsen, Hemmingsen, & Kramp, 2000). Though suffering from depression has a devastating effect on your life, this can be medicated. Studies among individuals outside prison show that loneliness also increases mortality rates. When taken into account age and gender the chances of dying when often feeling lonely compared to never feeling are increased by about 40 per cent. This increase in risk of dying due to loneliness is independent of age. Death by loneliness according to Patterson and Veenstra (2010) is usually caused by cardiovascular diseases such as stroke and cardiac arrest. It comes to show that the need for social contact is so great that it likely decreases the lifespan of an individual when this need is not satisfied.

4.2 Autonomy and competence

The difficulty of humans is that no one is the same; this is also true for most mammals but no to the same extend. Humans are able to shape their environment much more then animals do, even when they are feral. There are some indications that certain animal species (chimpanzees and Orang-utans) like us have cultures (van Schaik, et al., 2003). Due to our intelligence and culture we are able to shape our surroundings to whatever way we want. The need for competence is closely related to the need for cognition. Though we all seek some form of fulfilment for the latter, some people are more

motivated to do so than others. The need for autonomy and competence are closely intertwined and are therefore discussed simultaneously in this paragraph.

According to the Self Determination theory motivation is a balance between external rewards and internal or intrinsic motivation. Intrinsic motivation drives us to explore, learn and seek out novelty and other challenges (Ryan & Deci, Intrinsic and Extrinsic Motivations: Classic Definitions and directions, 2000a). In other words in order for this theory to work we need to have an innate desire for knowledge fuelled by curiosity. Unfortunately, little research has been done to link curiosity with a pleasurable sensation. But when presenting a group of people with questionnaires to test for pleasure and reading for knowledge a positive correlation arises. This explorative study shows that acquiring knowledge is a behaviour experienced as positive (Perlovsky, 2010) and can thus be viewed as an ethological need. This is further illustrated when readers are asked how much enjoyment they get out of reading a passage of a book. The crime fictional novels with medium difficulty level was much more enjoyable then the easy novels. Interestingly enough high levels of difficulty are not so enjoyable either (Knobloch-Westerwick & Keplinger, 2008). Making sense of the world around you is a need closely related to the need for knowledge, this so called need for cognition can lead to frustration, tension and deprivation when not fulfilled (Thompson, Chaiken, & Hazlewood, 1993).

Sometimes this need is in contradiction with another need, the need for autonomy. In the pursuit of understanding the world, we are influenced by external factors that can have an effect on our sense of free choice. As much as we want to understand and learn, the sense of control is taken away. It therefore makes sense that when people are rewarded for a performance task the need to perform the task is decreased. When analysing several studies this statement is confirmed: in most cases having a reward diminishes the internal motivation (Deci, Koestner, & Ryan, 1999). This is true when the reward is being provided with so called contingent rewards (such as money or candy) and as long as if it was known that the subject would receive this particular reward (Deci, Koestner, & Ryan, 1999). At a preschool age children are less likely to be sensitive to rewards and intrinsic motivation is clearest. About 50 per cent of the children prefer no reward system at all when employing playful active behaviour (Heal & Hanley, 2007). This pattern is still visible in adulthood. According to the need for cognition hypothesis there are two categories: people with low need for cognition and people with a high need for cognition. Especially in the latter group extrinsic rewards result a less enjoyable feeling in the task (Thompson, Chaiken, & Hazlewood, 1993) (Cameron & Pierce, 1994). When aging, some forms of reward do have a positive effect. In college students, positive feedback increases internal motivation (Deci, Koestner, & Ryan, 1999).

There are several theories about the early human; one hypothesis states that early humans were hunters and gatherers in order to survive. Since meat and berries do not coming running to you, you must find or hunt them yourself. Being physically fit to gather up your meal was essential. But nowadays we have supermarkets and being fit is no longer necessary to acquire food, yet people try to stay fit. You would expect that staying in shape is rewarding but the advantages this might bring in the battle for the other sex cannot be disregarded either. However when reviewing questionnaires of female students who started exercising in an anonymous and relatively autonomous manner it has been found that intrinsic motivation for exercise was positively correlated with sport competence and a task orientation for exercise. When trying to correlate the positive perception with body attractiveness no correlation can be found (Boyd, Weinmann, & Yin, 2002). When these women had a positive self-image regarding physical competence they were also motivated to exercise. When they were given a task involving exercise, physical activity was not only increased but results also suggest that tension and pressure are reduced (Boyd, Weinmann, & Yin, 2002). Again a social environment seems important for the increase or decrease in internal motivation. If the purpose of the task is simply self-improvement, effort or mastery: motivation is maintained. This in contrast to women who had an ego orientation towards the exercise, and solely worked out to outcompete others (Boyd, Weinmann, & Yin, 2002). These findings also apply to men. In a mixed sex setting people who were internally motivated to exercise were more likely to enjoy physical activity. In fact, those who were externally motivated were less likely to attend and maintain long-term adherence (Ryan, Frederick, Lepes, Rubio, & Sheldon, 1997) (Markland, 1999). The link between these concepts

is not so peculiar. When someone starts to work out for the purpose of improving self-perception, the motivation is external. In order to maintain the motivation results have to be apparent fast, so low self-determined people need a high competence level to maintain motivation. If people feel that engaging in a physical activity is a choice of their own it does not matter if they are good at this, in other words: high self-determined people are motivated regardless of their level of competence (Markland, 1999).

The study mentioned before in 4.1 of stereotypies found in infants (Thelen, 1979), also found a relationship between frequency of stereotypic motor patterns and restricted movements. This pattern was found across several ages. The researcher suggests that infant seats are designed to restrict movements of the torso and head, therefore restricting goal directing movements and facilitating stereotypic behaviour. I would translate the finding as followed: even as infants some ethological needs have to be expressed such as the need to move and explore. When restricted in a seat, this need is impaired leading to stress and frustration, which, if frequent or chronic will result in stereotypies. While this study does not show whether exploration or the need to move is the driving force, the latter seems to be closely linked to the need to exercise later in life.

One very well-known disease that results from autonomy impairment is anorexia nervosa. Patients suffering from this disease often say that their self-esteem is low, and they feel a certain loss of control. It is believed that the basis of anorexia nervosa lies in a low self-esteem. Due to the inability to become independent a person can resort to a maladaptive way to regain a sense of autonomy. When individuals are requested to place other people's needs above others, autonomy is affected in a negative way. Usually the cause is twofold, not only is the sense of autonomy thwarted but the family situation plays part as well (Espíndola & Blay, 2009) (Wechselblatt, Gurnick, & Simon, 2000). An important component for need satisfaction relies in parental support. Parents who support autonomy in their children by means of offering choices, supporting those choices and not pressuring their offspring will facilitate need satisfaction of intrinsic motivated goals. These goals are not so much related to health goals, but to goals in general (Thøgersen-Ntoumani, Ntoumanis, & Nikitaras, 2010). So feeling in control of your life is essential but having parents early in life that support you in those choices is crucial as well. It is suggested that restricting food intake is initially rewarding (Södersten, Nergårdh, Bergh, Zandian, & Scheurink, 2008) but as the individual maintains the behaviour it will alter the rewarding system by desensitizing it. Recall that reward processing happens in the limbic areas of the brain, with the ventral striatum as a key player. In a study done in healthy controls and women with anorexia nervosa, the latter group shows more activity in the ventral striatum when presented with stimuli of underweight women. An activity pattern that is absent in healthy subjects, who show increased brain activity in that area when confronted with stimuli of normal women. This increased activation of brain areas associated with reward of women with anorexia nervosa in response to underweight female bodies, endorses the crucial role of reward in this illness (Fladung, et al., 2010).

Somewhat comparable to stereotypies in animals might be Obsessive Compulsive Disorders (OCD) in humans. It would be unfair to attribute the cause of this psychological disorder entirely on the need for competence. OCD's usually arise if someone has a certain genetic profile combined with experiences. About sixty per cent of our personality and consequent behaviour is genetically determined (Bouchard, 1994) meaning the rest is due to environmental cues and experiences. Szechtman and Woody (2004) argue that OCD's arise because the sense of knowing a goal is achieved is impaired. A lot of OCD patients say that when they feel the urge to perform a ritual behaviour pattern they experience this as being overpowering, or "impairment of will power" (Szechtman & Woody, 2004). Although the authors do not use this term I believe this sounds much like the impairment of autonomy. This impairment may not have its cause in external cues but the impairment of it does lead to ritualistic obsessive behaviour patterns. The key word in fulfilment is satiation. A need becomes frustrated when impaired, and the need becomes less vivid when satiated. OCD patients lack this sense of fulfilment. To me this sounds equal to stereotypy's found in animals. When their needs are thwarted they develop stereotypy's that are very hard to stop due to changes in the brain causing the wanting threshold to be elevated. The motivation to stop also diminishes

because satiety is not achieved till the behavioural pattern is completed. The answer lies again in dopamine. OCD patients have decreased dopamine D_2 receptor binding in the left caudate nucleus (Denys, van der Wee, Janssen, de Geus, & Westenberg, 2004). And as we recall this is the place where motor plans are initiated or inhibited depending on the receptor it binds to. Combining this with a genetic inherited polymorphism in the D3 receptor in some forms of OCD, this can account for the rewarding sensation when engaging in the repetitive behaviour patterns (Light, et al., 2006).

4.3 The need to explore and be occupied

Recall that in our definition of an ethological need thwarting results in the rise of stereotypies. In primary literature very little information is found for adult stereotypies in normal and healthy individuals. More information is found when we look at children of infants. Stereotypies in humans are generally described in psychology as rhythmical body movements that seem to be: "*Involuntary, patterned, coordinated, repetitive, often rhythmic, non-reflexive movements that are goal directed and occur in the same fashion with each repetition*" (Singer, Mink, Gilbert, & Jankovic, 2010). In order for these stereotypic movements to be classified as such they must be present for at least 4 weeks and disrupt the life of individual in a injurious way or be a impede normal activities. There is great variety among human motor stereotypies (hand waving, skin picking, body rocking, hand nodding) and the explanations for underlying pathophysiologic mechanisms is unknown (Singer, Mink, Gilbert, & Jankovic, 2010). Some scientist believe mechanisms lie predominantly in genetics while others state that there are some indications that certain stereotyped behaviours can be connected to boredom, lack of stimulation (Troster, 1994), or social contributors (Thelen, 1979). Caregivers say that in almost 50 per cent of the case children tend to exhibit some form of stereotypy when they are bored or when they do not know what to do to occupy them selves. Despite this finding being very convincing, this study was done with children living in residential homes, meaning they most likely have experienced negative social influences before participating. This means that the influence of another human need, sociality, cannot totally be excluded (Thelen, 1979).
It was found that stereotyped rhythmical behaviour was inversely correlated by the amount of vestibular stimulation given by the caregiver (Thelen, 1979). In this particular study, stereotyped behaviour was categorized from onset but every rhythmic repeating behaviour pattern was recorded. There is a large diversity in these behaviour patterns, not only in form but also in frequency. Where some infants repeated particular motor patterns 17 times per hour taking up 2 per cent of the time awake, other engaged an astonishing 70 times per hour in the stereotyped behaviour pattern, spending 11 per cent of their time in this. Infants who showed so many bouts of stereotypic movements were less likely to be sleepy or drowsy at the time of assessment. The lack of vestibular stimulation by the caregiver (e.g. rocking or bouncing) was thought to be a factor in the maintenance of stereotypies in infants (Thelen, 1979).
Stereotypic movements as a result of stress or inoccupation are not only found in infants but in undergraduates as well. Not only is this seen by observers but students report these themselves. Nail biting as a result of boredom is observed twice as much compared to a frustration condition. This referred condition means that subjects were imposed a difficult math task. Strangely enough social interaction results in very little nail biting, as explained by the authors the presence of another individual would signal a form of negative reinforcement (Williams, Rose, & Chisholm, 2007). In my view the social interaction state could also reflect a baseline condition, meaning when social interaction is absent stress levels rise and the person starts to bite nails. Subjects self however indicate that boredom is biggest motivator for nail biting and consequently provides a sense of relieve. Nail biting as a result of boredom has been found in Preschool children as well (Foster, 1998). This tells us that these kind of deviating behavioural motor patterns can be persistent through live and are most likely caused by thwarting the ethological need for occupation. The latter I must emphasize is speculation from me. Unfortunately most studies only reflect stereotypies in their

current state, meaning the trigger to perform such stereotypies at that time may not be related to what situation gave rise to them in the first place.

Linking novelty seeking to reward systems in humans has only recently been made possible by new techniques such as fMRI. Subjects in the scanner would be shown a clue, this clue was either predictive of a familiar scene or of a novel scene. This clue was accurate in only 75 per cent of the time, meaning in 25 per cent of the cases it would show the opposite scene than predicted. When subjects were informed they would soon see a novel scene the reward system (substantial nigra and ventral tegmental areas) would be activated on those cues. Interestingly the reward system also showed signs of activation when novel scenes were shown whereas (false) familiar cues were provided (Wittmann, Bunzeck, Dolan, & Duzel, 2007). The results are indicative of a rewarding sensation when an individual encounters something new or anticipates that he will.

Chapter five

Discussion

This thesis is written in an attempt to answer the question if humans like animals have ethological needs. And if the answer is yes, what are those needs? The answer is not so straight forward but I plead for a confirmatory response. That being said, much more research is needed to get a better understanding of what these specific behavioural patterns are and the possible negative consequences when they are thwarted.

5.1 Human ethological needs

In my thesis I have tried to provide examples of ethological needs according to the following definition: *The need to perform a behaviour that is rewarding in itself. The need for performance of this behaviour, even if appropriate substrate is absent, is so strong that thwarting it too long leads to stress and stereotypies. If a possibility is offered to perform the behaviour after extensive periods of deprivation a rebound effect occurs*. These examples are found for both animals and humans alike, so even though these ethological needs may not be similar it does show that **humans have ethological needs**. As it might be expected one major ethological need of humans as a social species is to be social. Like other non-human social species, not being around conspecifics leads to frustration and subsequently stereotypies or depression. But being able to interact with others contributes to wellbeing as social bonding like friendship and marriage lead to happiness and positive emotions. According to Deci and Ryan (2000), being social is part of a psychological need. Their theory called the Self-Determination theory sheds light on the psychological needs as a foundation of ethological needs. **In order to fulfil psychological needs such as relatedness, competence and autonomy ethological needs have to be met**. An example might be reading. This is a behavioural pattern that can be fulfilling in itself. Reading a fictional crime novel does not have a direct goal but when the difficulty level is high enough but not too high it is pleasurable in itself, because it fulfils the need for cognition or competence. The suspicion that this behaviour like others is rewarding in itself is confirmed when groups are rewarded for their behaviours. Extrinsic rewards diminish self-motivation. When individuals work out because they enjoy working out, they will likely sustain this behaviour longer then when they are extrinsically motivated (e.g. they want to look good). For animals there are specific behavioural patterns that can be labelled as ethological needs like: suckling on teats (artificial or not) for calves and piglets, and picking the ground to forage in chicks. For humans in literature there is no such thing found, at least not one a wide scale. That can mean two things either: we do not have ethological needs or it has not been researched yet, I believe the latter is the case. In order to survive nest feeders are very dependent on their mothers (or fathers in some species). Humans are like pigs and calves such a species and because they have such a strong need to suckle perhaps so do we. Infants do like to suck on things such as their own thumb and that is why they are given pacifiers. It has been found that premature human babies benefit from nutritive sucking so that they can leave hospital care faster (Harding, 2009) (Pinelli & Symington, 2009). Sucking seems to have a direct beneficial effect as well; babies who are breastfed have lower heart rates after doing so. This is not just due to the food they just received. Babies like to suck on a pacifier although there is no reward. New-borns have the lowest heart rates when suckling and 6 week old infants have the highest, though still reduced compared to normal (Lappi, et al., 2007). Non-nutritive sucking in babies is present even before birth. While in the womb and provided with nutrients through the umbilical cord, most foetuses suck on their thumb as early as 15 weeks old (Hepper, Shahidullah, & White, 1991). The fact that this behaviour is present so early in life where it seems to have no function in an appetitive sense could indicate a need. If we assume that the heart rate decrease is experienced as a decrease in stress then non-nutritive sucking can be labelled as an ethological need in humans. Unfortunately there is a lot of evidence lacking to confirm this. Babies like animals can be difficult to

communicate with; especially new-borns can only express what they want and do not want by crying. Giving them a pacifier sometimes helps to sooth them, implicating either the need is satisfied or the option to suck is rewarding enough that the initial desire is pushed to the background. There is no evidence of cortisol level increase if the infant is denied of non-nutritive sucking and subsequent decrease when they are provided this opportunity. To my knowledge no research has been done examining the rewarding role of dopamine in non-nutritive sucking in infants. I believe that the results of this kind of research will confirm my statement that non-nutritive sucking is an ethological need in human infants.

I have argued that exercise is rewarding for humans in chapter 4.2. Most of the studies done with regard to exercise and rewarding feelings in humans are done with surveys, making it difficult to determine the exact mechanism that lays the groundwork for this relationship. But more extensive research has been done with rats that might explain what happens in the brain when employing activity willingly. Rats that are given a running wheel are frequently found near it. After six week of being exposed to the wheel and being able to use it, the mesolimbic reward system has altered. Less dopamine receptors are found in the nucleus accumbens, more specific opioid receptors are located in the nucleus accumbens shell and gene transcription has changed (Greenwood, et al., 2011). In order for this plasticity chance to occur the exercise must be over a longer period of time since rats with access to the wheel for 2 weeks did not show this plasticity. The chance in the reward system might be a useful tool for addicts who are no longer able to experience rewarding sensations from natural rewards.

I have found few ethological needs in humans that resemble ethological needs in animals, but Wittmann et al (2007) suggested that novelty seeking in humans was rewarding. Unfortunately very little evidence is found in actual studies on humans but they base their statement on fMRI scans of humans that show increased activation in reward systems when novel scenes were anticipated or seen. Rats that are given the choice to explore novel environments show an increase of dopamine in the nucleus accumbens, specifically the shell (Rebec, Christensen, Guerra, & Bardo, 1997). There is a large difference in autonomy between humans and rats but I do think novelty seeking is rewarding humans and the results of the Wittmann study are promising.

Another expression of behaviour that I believe is an ethological need is creativity. Unfortunately little no research has been done linking the reward system to this personality trait. It must be noted though that this is very wide spread and can take many forms. Early man already decorated tools and made jewellery. In order for this behaviour to persist it must be rewarding and perhaps valued by others. In modern day we can see that expression of creativity can be seen in a spectrum: some people just feel more need to be creative than others. When creativity somehow is impaired people will experience negative effects. These negative consequences can be more elevated in highly creative people. Creativity has been frequently linked to psychopathology (Carson, 2011) (Flaherty, 2011). The fact that creativity is also associated with negative emotions strengthens my belief that expression of creativity is an outlet of the need to be creative.

Like I said creativity can be seen in a spectrum, I think this goes for multiple ethological needs such as sociality and exercise. These differences between people in my view can be the result of social, economical factors but also innate differences. Findings support the idea that there are differences between people. So much even, that this might be gender biased. While the same structures are activated in both men and women in anticipation of a reward, men seem to value monetary rewards more than women do. Not only do men respond faster when anticipating a larger reward in general, they also respond faster when this reward is cued as monetary. This difference is not seen in women responding to cued rewards, but what is suggested is that women are more sensitive to social rewards. The neural networks responsive to monetary reward and social rewards overlap in women, but the larger the expected social reward, the more responsive the social reward-network (Spreckelmeyer, et al., 2009).

5.2 Human ethological needs can be traced back to primitive human behaviour

For an organism to survive it is useful if behaviours leading up to increased fitness are promoted. This is possible in two ways, the outcome of the behaviour is rewarding or the behaviour itself is rewarding. I believe behaviours that had its function in the primitive humans are still present in the modern human even if they no longer serve a function. But as I stated earlier I think most human ethological needs are harder to detect due to our increased cognitive abilities developed over the years. Most ethological needs I think are still present in children who have not yet developed the ability to predict and control their environment. However the ethological needs that are universal and clear such as the need to be social and the need to be active are fundamental behaviours the primitive human needed to survive. I am thoroughly aware of the risky statement I just made. There is much debate about the origin of man, where we came from and what we behaved like. There are several theories regarding the behaviour of men, the later upper Pleistocene model states that man did not hunt, fish or tried to capture any type of animal, they simply scavenged. Other models like the Middle Stone Age model state that primitive man behaviour is similar to modern day hunter-gatherer behaviours: plant resources are exploited and also animals are hunted (Henshilwood & Marean, 2003). To confirm or reject my hypothesis it would be helpful (but not necessary) if it was clear what model was correct. For all models being social is a trend. According to Alexander (1974) social behaviour is a byproduct of living in groups. Groups can be advantageous on several levels: decreased predation risk, increased chances of finding a mate or food and so forth. Once groups are formed they are maintained by social behaviours that in turn can evolve under the affect of other factors. For instance competition evolves under social behaviours: a dominant individual will learn when to use aggression and display his strength in group conditions. Whereas subordinate behaviour will evolve when the individual is informed by interactions within the group regarding his own display of aggression (Alexander, 1974). Of course evolution of behaviour within groups can be applied to many behaviours such as reproductive and foraging behaviour. The common denominator is the social behaviour to keep groups together. In the Middle Stone Age model being social serves a purpose since hunting for animals together means you can hunt more and greater wild, with more complex strategies. Also both models require a certain amount of activity for this behaviour to occur. Whether or not the early human scavenged or hunted both entail travelling from one place to the next if resources are scarce. In fact some researchers believe physical exercise played a significant role in human evolution, physical exercise is believed to result in a Calcium turnover. This neural stimulant could have played a role in the evolution of the brain (Bortz, 1984). No matter what model is closer to the truth it is a fact that at some point in time man started to use tools to improve on food acquirements, cultural legacies, improving lifestyles in general. It leaves no doubt that this increased knowledge led to increased survivability. If tool use and crafting was the driving factor in the need for cognition or if the need for cognition has led to tool use and crafting is the well-known chicken or egg question, but the will to learn and create has contributed to modern day lifestyle. **So many ethological needs can be traced back in behavioural patterns in early man**.

Chapter six

Conclusions

Humans like animals have ethological needs which can be traced back to behavioural patterns seen in primitive man. The reason why the needs are hard to identify in humans is because we are able to predict and control our environments. If we can predict that our needs are (temporarily) thwarted then this will exert a less stressful response then we cannot. The same goes for controlling our environment, if we are able to control the timing of employing our ethological needs this will be experienced as less stressful. If needs are thwarted despite our cognitive abilities this can lead to depression, mental illnesses and even shortened lifespan. Ethological needs in humans that are known to cause frustration when not fulfilled are sociality, need for cognition and need to be active. Another need that needs more research concerning rewarding properties is the need to suckle in infants.

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