THE EMOTIONAL NATURE OF THE WORKER HONEYBEE (*Apis mellifera* L.)

Zbigniew Lipiński

10 – 736 Olsztyn, Janina Wengris str 8. Poland. E-mail: Lipinski@sprint.com.pl

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Summary

This psychobiological analysis of the manner of the expression of some stress honeybee behaviours has revealed that the arousal of it emotional brain structures and subsequent changes in perception is the *modus vivendi* for all it stereotypical activities and behavioural development as well. The author presents different aspects of objective and subjective symptoms of the emotional nature of bee behaviours. In the analysis, there is new psychobiological interpretation of the nature of bee dances, classified as stereotypies***. This neurotic, psychogenic behaviour serves as a motoric abreaction of surplus of emotional agitation.

This paper contains a short description of the hypothesized structural and molecular background of the emotional reaction of bees. The author presents juvenile hormone (JH-3) as the modulator of all emotional reactions in honeybees, considering its sensitizing effect on mushroom bodies (MBs). The author also presents behavioural evidences that emotional affects can influence senso-perceptual consciousness of the worker honeybee.

Keywords: *Apis mellifera*, honeybees, emotions, cognition, perception, emotional affects, juvenile hormone, anxious, fear.

INTRODUCTION

The significance of emotions for human and animal behaviour was already known to Darwin (1872). Nowadays, the neuropsychophysiological foundations of emotions (understood as arousal of emotional neuronal circuits) are the object of increasing interest among scientists (reviewed by Panksepp 2005a). However, the notion that the expression of animal behaviour requires a respective level of emotional excitation is widely accepted (Załucki 1998), especially in view of the fact that: 1 – the cognitive abilities of animals have co-evolved with affective processes (Panksepp 2003), 2 – affective/emotional processes provide intrinsic values-organic "pressures" and "drives" to guide animal behaviour (Panksepp 2002).

Thus, it is possible that, a honeybee can "extract the logical structure of its world" (Giurfa 2003) without any affective/emotional response to its excitatory or calming stimulations, indicating that the bee colony "…may be calm or excitable, peaceful or eager to sting" (Frisch 1993).

Trying to answer this fundamental question, I put forward the hypothesis, that the honeybee possess neuronal circuits (structures) of an emotional system (NCES) (Lipiński 2005) which orchestrate its behaviour and physiology when it reacts with different "cognitive structures and physiology regulatory centers" of it's mini-brain (Giurfa 2003) in a similar way as it occurs in reptiles, birds, mammals and humans (Panksepp 2005a). For instance, "bees that are annoyed or hurt elevate their abdomen, open the sting chamber and protrude the stinging apparatus and usually fan the wings (behavioral response – auth.) with the occasionally release a poison drop at the top of the sting" (physiological reaction – auth). (Frisch 1993).

From a practical point of view, arousal of NCES and the appearance of the symptoms of emotional agitation of animals occur when the acting energy of external and internal stimuli is transducted in their sensory organs into bioelectric impulsations that activate the process of cognition*. This process (based on mechanisms of learning and memory), passes through steps involving sensation, impression and perception (Sadowski and Chmurzyński 1989).

Considering that symptoms of emotions appear in higher animals and man during the process of perception based on consolidation of impressions – derivated from comparing patterns of impulsations reflecting features of usually complex stimuli (colour + odour + taste + visual, etc.) with their patterns from genetic (signals) and acquired memories (cues) (Sadowski and Chmurzyński 1989, Sadowski 2001), - an assumption arises that, a similar mechanism is also present in the bee brain. The more so that many specific stimuli called "signals", which clearly promote stereotyped behaviours, are usually accompanied by a respective level of emotional agitation (reviewed by Lipiński 2001). These in turn allow them for instance to concentrate attention during cognitive appraisal on task related stimuli etc. It is worth mentioning that during this process the stimuli called "cues" serve for cognitive fitting of these innate behaviours in to their actual social and environmental context (Lipiński 2001). For instance, "bees that forage on alfalfa eventually learn how to enter the flower without "tripping" it and getting hit by the flower structure" (Gary 1999).

Interesting observations that: 1 – "sucrose responsiveness strongly correlate with tactile and olfactory learning performance in pollen and non-pollen foragers throughout the season" , 2 – "learning performance was significantly better when sucrose responsiveness was high" (Schneider et al. 2003) indicates that level of emotional agitation of the bee, due to excitatory/calming stimulations and changing environmental/social conditions, in terms of given physiological status and genetic make up, finally influences it perceptive and per se learning abilities.

Considering that: 1 – emotions influences bee learning abilities, 2 – this learning "occurs only within the context of innate behavioral patterns" (Gary 1999), the cognitive abilities of the worker bees are very limited compared to highly conceptual human thinking. In consequence the potent over-stimulation often leads to surplus of emotional agitation. The best example of such an over-stimulation is the emotional agitation of scout bees, which appears while visiting (break dance) and after visiting (waggle dance) a new good dwelling site, when they perceive potent excitatory signals (appropriate: smell, capacity, humidity, etc).

The observation of Free (1968, 1987) that "…bees usually do not scent until after the first visits to a source of sugar syrup" , indicates that the emotional memory of experiences can culminate in NCES and persist over the period required for one behavioral event, whereas such a observation that dry sugar, contrary to sugar solutions, causes no visible excitement and does not call attention of robbers (Morse and Hooper 1985) confirms innate control of such an emotional experiences. Furthermore, bees differ genetically, this can be seen by considering their sensitivity to social and environmental stimulations. For example "…some bees not scenting at all during numerous consecutive trips, and some consistently doing so more readily than others" (Free 1987).

While searching in world literature for evidence of bee emotionality, I found quite a rich collection of symptoms of bee emotional agitation similar to that in "higher animals" and in man. In the case of objective symptoms (Sadowski 2001), they are as follows:

1 – specific postures.
2 – moves (runs).
3 – excitations of the Vegetative Nervous System (VNS).
4 – specific pheromone release.
5 – stereotypies (dances).
6 – freezing behavior.
7 – clustering.
8 – specific sounds release.
9 – engorgement with honey.
10 – warm ups.

Whereas in the case of subjective symptoms, the so called emotional affects can include behavioural symptoms of anxious, fear, panic, rage, etc (Sadowski 2001) often connected with disturbance of expression of innate behaviour (Lipiński 2001).

OBJECTIVE SYMPTOMS OF BEE EMOTIONS

1 – specific postures. Let us start from the well known specific defensive warning postures of guard bees, when they "stand on their middle and hind legs with their forelegs uplifted and antennae outstretched" and in case of "greater excitement, they open their mandibles (mimic ?) and spread their wings as if ready to attack" (Gary 1999). It is significant that guard bees assume these startling postures and open mandibles even when they perceive iso-pentyl acetate from an evaporate lure (Moorse and Hooper 1985).

2 – moves (runs). To these emotional movements we can add for example jostling runs of highly agitated foragers in the hive (Frisch 1993) or buzzing runs (stereotypy) which encourage the swarm to lift off (Frisch 1993, Winston 1987). It is significant at that emotional moment, that the buzzing bees "force their ways with great excitement and nervousness through the other bees standing about; running in a random zigzag they butt them energetically aside, vibrating the abdomen violently and letting a readily perceptible buzzing of the wings be heard" (Lindauer 1955a) after Frisch (1993).

3 – excitations of Vegetative Nervous System (VNS). What is more, such symptoms as shedding the faeces by queens when put on cold iron plate (Czekońska and Teofilski 2001) before starting to fight each other (Tarpy and Fletcher 2003) or when they are attacked by workers just before swarming (revised by Tarpy et al. 2004) strongly resemble gastric perturbances in mammals suffering from emotional excitation of VNS due to potent stress.

4 – specyfic pheromone release. Pheromonal symptoms of bee emotions are also well pronounced. For instance, workers expose the Nasonov gland, when they perceive new sources of honey, pollen, propolis, water, live queens or even 9-HDA (Ferguson and Free 1981). The fact that, release of these attractant pheromones by bees increases after entering the hive entrance is temporarily denied (Fergusson and Free 1981) or when bees are emotionally "frustrated" from a lack of food which they have learned as a result of previous training (Bittermann 1988, 1996) indicates that bee emotions arise not only in response to over-stimulation by real potent stimuli, but also due to psychogenic stress caused by the lack of possibility to express behaviour in response to real or expected stimuli.

5 – stereotypical dances (streotypies**)**. Considering that 1. – bees expose the Nasonov gland while approaching a dish with water or sucrose syrup or when they begin to feed (but without fanning their wings) (Morse and Hooper 1985), 2. – the presence of an odour (peppermint, clover oils) at a food source encourages dancing (Morse and Hooper 1985), 3. – both scenting and dancing are stimulated by an increase in the attractiveness of the forage (Free 1987), 4 – waggle dances appear after a visit to good forage or an impressive nest cavity (Frisch 1993), 5 – followers vibrate the comb at 380 Hz and get a droplet of nectar from a waggle dancer (Michelsen et al. 1986), 6. – vibrations (tremble dance) of a forager appear when she is not unloded within 40 sec, in the case of nectar. (Seeley 1992) and water (Lindauer 1954). I deduced, that foragers can abreact surplus of emotional agitation called earlier "excitement" not only in a pheromonal way, but also in a motoric way in the shape of mentioned dances most probably because learning abilities limited to a set of stereotypical behaviors do not allow abreaction of such a excessive agitations other way.

The best known are waggle dances performed by nectar foragers or the previously mentioned scout bees. Lessser known are the dances of water foragers (Lindauer 1954), and propolis foragers (Meyer 1954). Significantly for their emotionality, longer waiting periods for unloading cause habituation and degrade performance of these dances, e.g. by water foragers (Lindauer 1954, 1955b).

Because these dances, including "…jostling run, spasmodic dance, buzzing run" (Frisch 1993) etc., consist of repeated invariant sequence of movements of the whole body and/or some of its parts with no obvious function, I classified them as stereotypies (Lipiński 2001). This psychogenic, neurotic behaviour serves (in higher animals and man) for motor abreaction of a surplus of emotional agitation. Stereotypies are usually expressed when an "individual has some difficulty in coping with the conditions" (Broom and Johnson 2000).

Considering that, in general, the emotional nature of stereotypes reflect a poor social and/or environmental conditions, the tremble dance, for instance, appears "under the most varied circumstances whenever the bees are exposed to a harsh disturbance or are in poor state of health" when "foragers are handled roughly, while they are being marked at the feeding dish or visit Asclepias flowers with their sticking organs" (rewieved by Frisch 1993). Similar emotional roots also seem to be found in the "tremblings" of the queen between the fingers of inseminator (Jasinski 1998). It is noteworthy that tremble dance as responses to adverse circumstances and experiences were first noticed by (Florey 1954) who described them as neurosis (after Frisch 1993).

The jerking** dances towards workers (Allen 1959b) which occur at night or in bad weather (overcrowding – auth annot.) Hammann (1957) are also performed on a queen or queen cells before swarming (Allen 1959a) due to increasing social stress (Lipiński 2001) and on virgin queens before they fly out (Allen 1958a). These dances also occur in queenless colonies or in colonies close to starvation (Gary 1999). Thus, all of them occur in stress conditions. In this context, the observation of the Gahl (1975) that 96% of jerking dances were performed on worker bees that were older than the shaker is significant, indicate that young bees, as with other animals, are more sensitive to stress than older ones.

6 – freezing behaviuor. Interestingly, the opposite of stereotypy, is freezing behaviour. It is common when animals suffer from so called somatic (physiological) stress, especially when they are unable to find a solution to avoiding stress factors (Broom and Johnston 2000), e.g. pre-swarming bees suffer somatic stress in festoons under the frames (Lipiński 2001) or are placed in circumstances "where they have previously been frightened" (Panksepp 2005a). Such behaviour was most probably observed by Moritz et al. (2000) when young bees were moved to a foreign nest.

7 – clustering. In the above context, some forms of stress clustering of bees (Lipiński 2001) seem to be also an objective symptom of their emotional agitation. Consider the similar behaviour of other young animals, e.g. nestlings (Broom and Johnston 2000).

8 – specific sounds release. Significantly for the emotional nature of bee stereotypies, they are often connected with issue of specific sounds. Apart from the continuous "hum" issued by the colony with the background of sounds at about 40 dB depending mostly upon fanning activity with the main peaks of power at about 200 – 500 Hz, bees abreact emotional agitation through different methods: hissings (3000 Hz), pipings (300 – 600 Hz), quackings (1000 Hz), tootings (1200 Hz) squeakings (300 Hz) etc., (Morse and Hooper 1985, Frisch 1963).

The most spectacular form of this acoustic emotional behaviour is a loud "hissing" issued by a colony after a rapid knock on the hive (Morse and Hooper 1985). This is strongly reminiscent of the emotional sound of startled response described by Broom and Johnston (2000) in birds. In general, workers "pipe" producing short bursts of sound at about 500 – 600 Hz for many excitatory reasons (reviewed by Lipiński 2001). Interestingly, this piping, appears to calm the colony (Morse and Hooper 1985).

9 – engorgement with honey. Another, very significant objective symptom of bee emotions is engorgement with honey or nectar for different stress factors (reviewed by Lipiński 2001). For instance, due to swarm stress (Lipiński 2001) or even shaking or/and smoking (Morse and Hooper 1985). Significantly, the amount of this engorgement is related to the level of agitation, because "...worker engorgement occurred gradually during the 10 days prior to swarm issue (Combs 1972) and "…when foraging bees fly out the content of the honey stomach varies according to the distance to be flown" (Frisch 1993 after Istomina-Tsvetkova 1960).

10 – warm ups. The interesting non-visible physiological symptom of bee emotionality appears to be the warm up of foragers before flight out (Frisch 1993) or swarming bees preparing for lift off (Seeley and Tautz 2001) due to potent emotional activation of brain neurosecretory centres by NCES which orchestrate their metabolism with mentioned behaviors. This mechanim was already known to Kosmin et al. in 1932, who found that the intensity of bee metabolism depends on the type of performed activity. What is more this warm up is emotionally enhanced by the piping of the queen and energized by scout bees in a whir dance. A special form of this emotional warm up seems to be the "baking" of hornets by the high temperature produced by soldier workers of *A. cerana* (Ono et al. 1993).

SUBJECTIVE SYMPTOMS OF BEE EMOTIONS

The fact that workers: 1. – expose Nasonov gland and release attracting pheromones when perceiving new sources of honey, pollen, propolis, water, live queens or even 9-HDA (Ferguson and Free 1981), 2. – release deterrent pheromones when visiting unprofitable flowers (revised by Free 1987), 3. – release alarm pheromones (in queenless swarms), when recognizing a strange queen, but when viewing their own queen, release attraction pheromones (Blum 1999) not only confirms that the arousal of NCES orchestrates bee behaviour with physiology, but also suggests that worker bees can release attractive, repellent or alarming pheromones in response to specific types of emotional affects generated by the perception of respective stimuli.

This hypothesis finds strong support in the observation that, bees can react differently to the same excitatory stimulus when the intensity changes. They can be calm, anxious, fearful or even eager for pollen hording in response to respective attractant, alarming, repellent doses of 2 – heptanone. For instance, at low concentrations, 2-heptanone can act as an attractant, whereas increasing doses act as alarm or even powerful reppellent with some topical irritant properties (reviewed by Blum 1999). Interestingly, emotional perception of alarm pheromones by other bees can cause their silent pipings (Lefebvre and Beattie 1991).

Also, the fact that the expression of a line of specific partial defence behaviours (Collins et al. 1980) is orchestrated with respective amounts of alarm pheromone (2-heptanone) released (Kerr et al. 1974) suggests that the increasing arousal of NCES abreacted through increasing wing movements with emission of characteristic sound tones is supported by primordial affects – a type of fear. The affective, emotional nature of bee defensive behaviour seems to also confirm the observation of Frisch (1993) that "…when bees were seized whose stinging apparatus had been excised half an hour previously, they run in agitation, fanning their wings, into the hive".

Thus, in the bee the type of emotion - anxiety, fear, rage, etc. reflects the accumulated memories of emotional "negative" or "positive" experiences. Significantly, this is the basic manner of the rise of emotional effects in animals and humans (Vaas 2004).

As a result of this emotionally supported affective mechanism, other excitatory stimuli: high humidity and temperature, overcrowding, tremblings due to colony manipulation, lack of nectar, smoke of poor quality, crushed bees and combs, high amounts of empty combs or even moving dark objects in the hive vinicity, etc are able to enhance this anxiety so far, that stressed bees become more eager to sting. It is noteworthy, that fear can cause both the release of attack or escape behaviours in response to known threats, while anxiety emerges in response to unknown threats (Vaas 2004).

The best example of bee emotional affect type of fear seems to be the terminal emotional agitation of swarming bees during nest abandonment (Lipiński 2001) in a characteristic "frenzy" (Winston 1987). At that moment, their emotional bonding to the nest is broken down by the stronger terminal fear arising due to poor nest and social stress conditions. This is additionally enhanced by the excitatory effect of queen piping and the stressful whir dance of scout bees (reviewed by Lipiński 2001). Significantly, when the whir dance occurs "...one can hear a very loud humming inside the cluster and bees start running to and fro, creating the tumult". What is more, "..when the excited (emotionally agitated – auth.) running reaches it's highest point the whole cluster disbands" (Gary 1999). A similar fear seems to be responsible for escape of the honeybee queen and workers "...to the corner of the hive" (Morse and Hooper 1985) due to excessive colony examination.

The above mentioned symptoms of emotions take a clearer affective dimension if we consider that in the intensive electro-stimulation of subcortical mammaliam brain, the fear system leads animals to run away as if they are intensively scared (Panksepp 2005a). However, due to weak stimulation, these animals exhibit just the opposite motor tendency – a freezing response (Panksepp 2005a).

Significantly for the emotional-affective nature of bee behaviors, nest abandonment in swarms occurs more often under high power electrical line, whereas a weak disturbing electrical field makes bees very aggressive to the point that venom can be collected. It was also found that, an electromagnetic field of 7.4 kV will produce a rise in hive temperature followed by evacuation of the colony, however, at 50 kV/m bees of the same colony will fight and sting each other (reviewed by Morse and Hooper 1985).

The role of emotional affects in type of anxiety or fear for bee behaviour is also confirmed by the fact that propolisation as one specific defence behaviour can occur for many different threatening reasons. For instance, cold (own observations) and hot air (Woyke 1993), the smell of a dead mouse (Winston 1987) or live *Ethina tumida* (Ellis et al. 2004) etc. The affective nature of the simple bee emotions is also confirm by the fact that, propolisation can also appear under the high pressure of electromagnetic fields (Warnke 1976, Greenberg et al. 1981).

Furthermore, the fact that workers balling the queen "issue a distinctive hissing sound" (due to perception of false (stress) bouquet of her pheromones - auth) whereas facing the cage with a new queen they engage in "biting the wires for up to 18 hours" (Morse and Hooper 1985) (due to perception of strange bouquet of her pheromones – auth) indicates that both behaviours can be support by emotional affect type of primordial rage often expressed by higher animals in similar stress conditions (Panksepp 2005a). Hence, when agitated workers attack or sting an intruder bees or foreign queen, "they may grip them with their mandibles and possibly mark the spot with alarm (2-heptanone) pheromone" (Morse and Hooper 1985).

Of course the emotional affects of the bee, due to the primordal nature of its consciousness and lack of cortex, thalamus or other such mammalian neuroanatomy (Swinderen and Andretic 2003) are not comparable to highly subjective human emotional feelings. However even in human emotions and related feelings are mostly subcortical in nature (Panksepp 2005a).

THE PRIMARY CONSCIOUSNESS OF THE HONEYBEE

The "arousal" in honeybee (Schulz et al. 2002) or "arousal" in fruit fly (*Drosophila melanogaster*) viewed in terms of the general capacity of the nervous system to perceive and respond to environmental stimuli, changes from periods of high vigilance or responsiveness (attention) to periods of very low responsiveness (sleep or resting) (Swinderen and Andretic 2003) can be defined by the level of sensory alertness, motor activity and reactivity (reviewed by Schulz et al. 2002).

Considering that "...if the pollen pellets are gently removed from the hind legs of the forager as she is entering the hive, she will unload non-existent pollen pellets into the comb cell through a set of characteristic stereotypical motions" (McDonald 1968), and that "…foragers can collect chewing gum from the streets in situations of a lack of resin" (Gulmahamad 2003), I deduced that bees are very limited in cognitive awareness about their own experiences when express their innate behaviours. .

Such an ability (Panksepp 2005b) is possessed by more evolutionarily advanced animals with secondary forms of consciousness which operate, for example, on some kind of perceptual/metaphorical non-linguistic images. However, there is also some evidence, that bees can also store sequences of eidetic images or snapshots of landmarks in their memory (Seeley 1993). What is more, Eskov (1972) has shown that the bees of the colony are conscious of the background sound, because they shift the frequency of the dance sounds to avoid confusion with the peak frequencies of the background hum. It is noteworthy, that there is a tertiary form of human perceptual consciousness based on thoughts about thoughts and awareness about awareness" (Panksepp 2005b).

Thus honeybees seems to possess no more than primary consciousness. This kind of animal consciousness, lastly discussed for invertebrates by Edelman et al. (2005) may reflect raw sensory/perceptual and emotional/motivational experiences (Panksepp 2005b). The limitations of this kind of consciousness is possible to observe when „grooming and offering food for the queen can be induced by exposing bees to queen odour placed on of cork" (Gary 1999).

Considering that bees can be calm, anxious or fearful in response to respective attractant, alarming, repellent doses of the same stimulus. For instance 2 – heptanone,. assumption arise that, this kind of conscious may be connected with accumulation of respective emotional affects. This can explain numerous emotional disturbances of expression of their innate behaviours due to constant stress (reviewed by Lipiński 2001). For instance, Warnke (1976) observed that in small queenright mating colonies exposed to increasing electromagnetic fields, starting from 7 kV/m, bees reacted after 10 minutes with a 10°C increase in temperature and more noise. Next they strengthened their wings on alighting boards (typical for alert – auth. annot.) and become aggressive towards each other and balled around the queen. Later they destroyed the brood and removed honey stores. Significantly for anxiety and/or fear evoking nature of electromagnetic field it intensity at a level of 7.4 kV/m produced a rise in hive temperature followed by evacuation of the colony (Morse and Hooper 1985).

The emotional/affective roots of bee consciousness especially confirm the temporary decay of consciousness due to high emotional agitation (fear ?), when soldier bees jump into the open fire of a smoker or loose their lives when stinging (Lipiński 2001). The most terminal case of this phenomenon seems to be the rapid coma of queens when kept between the fingers of beekeeepers, as described by Moosbeckkhofer (2001).

It is worth mentioning, that bee resting behaviour (connected with the lowering of the antennas, muscle relaxation, etc) (Kaiser 1984, Kaiser-Steiner 1987, Kaiser 1988) is similar to some extent to human sleep, which is described by psychiatrists as a transient step of a decay in consciousness (Kaiser-Steiner 1987).

STRUCTURAL AND MOLECULAR BASIS OF BEE EMOTIONS

Changes in bee arousal supported by cognitive perception of acting stimuli are mediated and modulated by different signalling substances (reviewed by Lipiński 2001). This is mainly through biogenic amines which control neuronal excitability (Sigg et al. 1997). This includes octopamine which can enhance sensory perception (Schulz et al. 2002) and dopamine which can promote motor arousal (Menzel and Müller 1996). Serotonine (SE) – usually reduces the responsiveness of neuronal components (Erber et al. 1991, 1993). This signalling effect is supported by the sensitizing and energizing effect of juvenile hormone (JH-3) on neuronal circuits of mushroom bodies (Mbs) which enhances emotional background of bee perception and per se it cognitive abilities. This is because MBs are involved in learning and memory (Menzel and Müller 1996).

Interestingly at the same moment the perception of acting stimuli mediated and modulated by biogenic amines influence the release of JH-3 (Rachinsky 1993). So

JH-3 and for instance octopamine are commonly involved in emotional expression of different bee activities, e.g. foraging (Schultz et al. 2002). Furthermore, because JH-3 strongly influences the structures of MBs (Withers et al. 1995) it indicates that emotional agitation due to cognitive perception of different social and environmental factors will stimulate these bodies also via VNS which in line "…innervate corpora allata" (Gałuszka 1998). As a result of that, JH-3 does not activate foraging (and most probably other activities – auth.) but rather somehow is involved in controlling the (emotional – auth) pace at which bees develop into foragers (Schulz et al. 2002). What is more, because JH affects response thresholds in honey bees (Schneider et al. 2004) and per se their perceptive abilities, incresed titers elicited by the different excitatory stimulations (e.g. vibraion signals) may allow these stimuli to influence the variety of behaviors.

The emotional nature of above phenomenon as a whole is well pronounced in potent stress situations, when levels of octopamine (Harris and Woodring 1992) and juvenile hormone (Jasim et al. 2000, Lin et al. 2004) sharply increases to enhance both the perception and speed up metabolism of sources of energy to fight or flee, as result of the excitatory effect of perception of stress stimuli. For the same reason due to social stress before swarming (Lipiński 2001) the JH-3 titres are significantly higher in queen cell colonies compared to normal colonies (Zhijang et al. 2005).

The leading role of MBs in emotional affects apart of multimodal integration of olfactory, visual, gustatory and mechanosensory pathways, also suggests a high concetration of GABA receptors (Grünewald 1999) typical of the emotional system of more evolutionarily advanced animals (Panksepp 2005a). Especially in view of the fact that MBs: 1 – separates stimuli based on temporal structure, 2 – it weights these stimuli with respect to the unconditioned stimulus (predictor or context), 3 – grades stimuli during retention according to their predictive value (Menzel and Giurfa 1999).

Considering that hydroxyurea can selectively damage MBs and disturb emotional control over self-behaviour when given to larvae (Malun et al. 2001) and that a similar molecule called urethane can evoke jerking movements (DVA-V) which usually occurs in (emotional – auth.) stress conditions (Frisch 1993) I deduced that NCES are present in MBs. Significantly, for metabolic dimension of discussed emotionality, the brain neurosecretory cells which influences its physiology centers (e.g. corpora allata), lie in close vinicity to the MBs (Cymborowski 1992).

THE EMOTIONAL MODUS VIVENDI OF BEE BEHAVIOUR AND IT BEHAVIOURAL DEVELOPMENT

Because the emotional arousal of the bee and respective perceptive abilities (apart from age-related and genetically controlled sensitivity) depends on a wide range of excitatory and calming nest and outside-nest stimulations, modulated in line by the potent influence of calming social factors (pheromones of the queen, the young brood and older workers) "at any given age a worker will be doing a number of jobs" (Winston 1987).

However, due to the mentioned limitations of learning in the framework of the highly stereotypical nature of its behaviours (Gary 1999), the over-stimulation of NCES often occurs. The excitatory effect of these over-stimulation is additionally enhanced by fact that in insecte there is maintenance of neurotransmitters over the period required for expression of given stereotypical behaviour (Harrris and Woodring 1992, Madrell 1974).

As result of that, worker bees tire easily and the recovery period to return the emotional equilibrium is relatively long (Lindauer 1953). It also seems that this is the main reason why "long periods of inactivity are interspaced with frantic (emotional – author annot) activity sessions during which individual workers perform many different tasks in a short period before resting again" (Winston 1987).

Significantly for the emotional and affective nature of bee behaviour "mildly stressed colonies may first respond by (emotional – auth annot) changing the frequency but not the age of task performance, while workers in more heavily stressed colonies respond by changing the ages of task performance" (reviewed by Winston 1999). For instance, due to sudden deprivation of combs, emotionally agitated bees can start to produce more wax (physiological reaction – auth) and build more combs (behavioural response – auth) or even begin foraging at younger ages (speed up behavioral development – auth) (Fergusson and Winston 1988).

Thus emotional agitation supported, most probably by anxiety not only speeds up the expression of a some behaviours but also speeds up the behavioural development of bees. This concerns the earlier mentioned mechanism of emotional production of different signalling substances and their influence on the extension of bee perception. In this context is obvious that potent calming stimulations – especially queen and young brood pheromones must slow behavioural development of young bees and limit their perceptive abilities. (Lipiński 2006 in press).

Considering the extreme complexity of conditioning of this psychophysiological process, in terms of nest and social stimulations we can only artificially speed up the transformation of nest bees into foragers and vice versa through manipulation of colony demography (Robinson 1992), but not evoke expression of particular nest behaviours. Nevertheless, natural changes in colony demography, state of food resources etc., influence the level of the emotional excitation of individual bees to the the point that it can promote respective changes in their behaviour. This is especially so because the vivid emotional behavioural responses of bees to these changes, are able to sensitize their nestmates, which can cause an extension of their perception to other stimuli. However, rapid over-stimulation often leads to contrary behaviors. For instance, DVA-V dances inhibit certain activities of workers and queens (Fletcher 1975).

Thus emotionally supported, exchange of excitatory or calming stimulations between bees depends on abreaction of surplus of emotional agitations in the form of different sounds, dances, pheromones etc. It resembles some kind of primordial language, which facilitates colony coordination and integration.

CONCLUSIONS

Honeybee perception is highly emotional. This emotionality is manifested by characteristic subjective and objective symptoms. Due to this emotionality the primary form of bee consciousness may reflect different primordial affects type of anxious, fear, rage etc. The JH-3 appears as the modulator of all emotional reactions in honeybees. As result of this, the phenomenon emotional nature of bee perception strongly influences its behaviour and behavioural development.

It seems that presented above new psychophysiological approach to bee behaviour can become a powerful tool for better understanding the manner of the social organization of the honeybee colony and other insect societies.

* The term cognition, derrivate latin words cognoscere (to learn) and gnoscere (to know) (Dorland's 1994) means process through which information is obtained, transformed, stored, retrieved and used

** Jerking movements – dorsoventral abdominal vibrations (DVA-V) (Frisch 1993).

*** Stereotypies – repetitive and stereotyped behaviours (Broom and Johnson 2000).

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EMOCJONALNA NATURA ROBOTNICY PSZCZOŁY MIODNEJ

Lipiński Z.

Streszczenie

Psychobiologiczna analiza ekspresji niektórych stresowych zachowań się pszczoły miodnej ujawnia, że wzbudzenie emocjonalnych struktur jej mózgu i powstałe w wyniku tego zmiany w percepcji, są siłą sprawczą jej stereotypowego behavioru oraz behawioralnego dojrzewania.

Autor przedstawia różne aspekty objektywnych oraz subjektywnych objawów emocjonalnej oraz doznaniowej natury behawioru pszczół. Pośród nich nową psychobiologiczną interpretację emocyjnej natury tańców pszczół sklasyfikowanych jako stereotypie. To neurotyczne, psychogenne zachowanie służy motorycznemu odreagowaniu nadmiaru emocjonalnego pobudzenia.

Praca zawiera krótki opis przypuszczalnego strukturalnego oraz molekularnego podłoża emocjonalnych reakcji pszczół. Autor przedstawia hormon juwenilny (JH-3) jako modulator wszystkich emocjonalnych reakcji pszczół, mając na uwadze jego zdolność do uwrażliwiania ciał grzybkowatych na bodźce. Praca zawiera również behawioralne dowody na doznaniową naturę czuciowo-percepcyjnej świadomości robotnicy pszczoły miodnej.

Słowa kluczowe: *Apis mellifera*, pszczoły miodne, emocje, poznanie, percepcja, doznania emocjonalne, hormon juwenilny, lęk, strach.