THE CALMING PROPERTIES OF THE HONEYBEE QUEEN, YOUNG BROOD AND OLDER BEES

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Received 07 March 2006; accepted 12 April 2006

S u m m a r y

The aim of this study is to present the psychobiological manner in which the calming properties of the queen substance (QS) influence worker bee behaviour and behavioural development. The author examines the mechanism of control of bee emotions by QS via suppression of juvenile hormone production already at the level of mushroom bodies (MBs). The calming, slightly tranquillizing (ataractic) effect of QS on especially nest worker bees is usually enforced by similarly acting pheromones of the young brood and older workers. The article also puts forward a hypothesis of the possible role of QS in the control of some bee stereotypies and primary emotional affects type of anxious and fear.

Keywords: *Apis mellifera*, honeybees, emotions, queen substance, opioid system, behavioural development, juvenile hormone, anxious, fear.

INTRODUCTION

Considering that excitatory stimuli, which can exert anxiety and/or fear, repel the bees or cause alarm effects it is obvious, that non-excessive doses of slight tranquillizers (attractants) must calm and attract the bees (Lipiński 2001). The most potent stimulus of this kind is the bouquet of all queen pheromones described today as queen substance (QS). This blend consists mostly of heavy pheromones from mandibular glands (nQMP) and highly volatile abdominal pheromones originating mainly from the tergite glands (Free 1987).

THE CALMING PROPERTIES OF THE QUEEN SUBSTANCE IN VIEW OF SEPARATION DISTRESS IN WORKERS

In honey bee colony a queen first has to be recognized as a queen before other activities such as queen court formation and feeding with royal jelly commence (Snodgrass 1956). The worker bee is able to discriminate its own queen only through composition of pheromonal bouquet of tergite glands (Moritz et al. 1988).

This calming smell of QS resembles the fragrance of *melissa officinalis* and is so attractive to young, especially stress sensitive bees (Lipiński 2001) that "during intensive egg laying of the queen, workers from the royal court "becomes excited" (Gary 1999). These last words indicate two important things: first, emotional nature of the perception of QS by bees, and second, that neuronal circuits of emotional system (NCES) of the worker bee (Lipiński 2006 in press) are influenced by QS.

This assumption finds support in the well known fact that the rapid withdrawal of the queen from the honey bee colony causes enormous emotional agitation due to some kind separation distress manifested by apparent "…nervousness" and "aggressiveness" (Winston 1987). There is increased walking throughout colony connected with emission of a roaring sound at a frequency of 300 – 400 Hz (Vancata 1995) due to significantly "…increased scenting behaviour" (Winston 1987). In

meanwhile all of these behaviours serve the motoric and pheromonal abreaction of a surplus of emotional agitation due to rapid enhancement of perception or, as it is often called – a decrease in response thresholds. Of course, this emotional enhancement of perception fascilitates queen finding.

It is noteworthy that phenomenon of emotional affect of the bonding of an offspring to its mother is well known in other animal species (Panksepp 2005a). Remarkably the orphaned bees retain their ability to differentiate between their own queen mother and a strange queen for about 24 hours after her loss (Morse and Hooper 1985) despite the relatively fast decay the 9-ODA from the nest environment (Neumann et al. 1991, Seeley 1979).

THE CALMING PROPERTIES OF QS AT THE LEVEL OF A WORKER'S BRAIN-CA AXIS

If we consider that: 1. – significantly different levels of octopamine, dopamine and serotonine were detected among workers in colonies that contained unrelated queens compare to normal colonies (Harris and Woodring 1992), 2 – in queenright colonies young workers have significantly lower levels of all three main biogenic amines (Wagener-Hulme et al. 1999) and JH titres (Fahrbach & Robinson 1996) than did foragers, and lower JH titres compared to: (a) queenless colonies (Huang et al. 1998 after Robinson unpubl. date, Kaatz et al. 1992) and compared (b) synthetic queen mandibular pheromone (sQMP) treated bees (Pankiw et al. 1998), 3 – the application of sQMP, to workers suppressed their JH hemolymph titers (Kaatz et al. 1992, Pankiw et al. 1998, Pankiw and Page 2003) and elevated their response thresholds (Pankiw et al. 1998). The suggestion arises that QS (in fact nQMP) suppresses the bee perception (manifested by lower levels of neurotransmitters) when interfere with arousal of it NCES (Lipiński 2006 in press), which is finally connected with decreasing JH production and release. Most probably via decreased excitation of corpora allata via vegetative nervous system (VNS). Apart of neurohormonal regulations of these bodies (allostatins etc).

Thus, nQMP (in fact QS) acts as typical minor tranquillizer (Panksepp 2005a, Delay 2004) which slightly suppresses perception and stabilizes emotional agitation of especially young worker bees. This phenomenon confirms the observation of Pankiw and Page (2003) who found that bees reared with sQMP were less sucrose responsiveness than controls. Moreover, because ataractans have an anti-anxiety effect (Delay 2004), it could suggest that QS suppresses the anxiety in worker bees.

The best practical example of suppression of bee emotional affects by QS is fact that: "… a tap on a queenright colony is immediately followed by a hiss which can be heard without any aid to hearing. It lasts for about one quarter of a second with fundamental amplitude of about 3000 Hz. A queenless colony, when tapped, replies with a hiss of a much smaller amplitude but continuing for three or four seconds" (Morse and Hooper after Woods 1959). Significantly, this calming is so efficient that even some qeenlike pheromones from queen cells (Free 1987) "are able to encourage this phenomenon". Woods reported that hiss (stereotypy-auth) duration, length and the amplitude decrease during the production of queen cells by a colony" (Morse and Hooper 1985).

Considering that: 1 – mild stress (mild emotional agitation – auth) speed up behavioral development of young bees (reviewed by Winston 1999), through emotional enhancement (extension) of their perception (Lipiński 2006 in press) it become clear that ataractic properties of QS

which calm them down must slightly supress and emotionally stabilize their perception, so far that must "... delay the behavioural development" (Pankiv et al. 1998, Zeng et al. 2005) of young bees, when working as a "modulator for the division of labour" (Pankiv et al. 1998).

A similar calming effect is possessed by young brood pheromones BP which slow down the behavioral development of worker bees (Le Conte et al. 2001) and modulate sucrose response thresholds in a dose dependent manner (Pankiw 2004) to the point that bees reared in colonies with high doses of BP foraged at significantly older ages than bees reared with low doses (Pankiw 2004). The interesting fact that decreased responsiveness of young bees to social inhibition by older bees in queenright colonies (Barron and Schulz 2002) seems to suggest that emotional reaction of bees can also be supressed by mandibular pheromones (10-HAD) of older workers (Pankiw 2004, Huang et al. 1998). Moreover, they are also able to inhibit JH-3 production in younger bees (Huang and Robinson 1992, Huang et al. 1998) because 10-HDA shows structural similarity to the major component of QMP, known as 9-ODA (Huang et al. 1998).

So in colonies lacking foragers, some more emotionally agitated bees (lack of inhibitory effects of older bees), initiate foraging, when they are as young as 5 days of age, > 2 weeks earlier than under more typical conditions (Huang and Robinson 1992). As result of that, "if the foragers are too many the transition to foraging may be delayed, if the foragers are too few, some hive workers mature into foragers sooner" (Beshers et al. 2001, Fahrbach and Robinson 1996, Robinson 1992).

THE STRUCTURAL AND MOLECULAR CORRELATES OF EMOTIONAL REACTIONS OF WORKER BEES

In view of this tranquillizing and anti-anxiety phenomenon the recent findings of Grozinger et al. (2003) suggest that nQMP is able to regulate bee behaviour through the activation of "nursing genes" and repression "foraging genes," encoding sets of signalling substances needed for expression of these stereotypical behaviours through activated transcription factors seems to be very significant. Especially in view of fact that "... an ortholog of the *Drosophila* transcription factor kruppel homolo I, was strongly regulated by QMP, especially in the MBs of the bee brain".

It seems to suggest, that QMP interferes with regulation of the expression of these genes at the molecular level of NCES of honeybee MBs. This is because expression of rigid patterns of behaviour is impossible without their orchestration, with physiological reactions, which in turn requires activation of the respective sets of genes (Ben-Shahar et al. 2003, Robinson 1999) also via JH –3 hormone production (Kaatz et al. 1992) which influences DNA synthesis (Schmidt Capella and Hartfelder 1998).

The remarkable decrease in the sensitivity of worker bees to QMP during the summer (Skirkyavichus and Skirkyavichene 1979) and the increasing number of some stereotypies (DVA-V) before swarming (Allen 1959a) indicates that under potent pressure of stress factors (overheating, overcrowding, lack of forage, old queen, etc.), queens (specially older one), and the queen substance (in fact nQMP) loses its calming potency.

Stricking evidence of this phenomenon is fact that "approximately 50 minutes after removing the queen, the bees remained indifferent to the traces of the nestmate queen

pheromone on the wall of experimental cage (Skirkevicius 2004). The other symptom of loss of queen dominance over more and more emotionally agitated workers due to chronic (consistent) pressure of stress factors (Lipiński 2001), is the frequency of sounds emitted by them in social stress preceding swarming (reviwed by Lipiński 2001). At the beginning of this period (early spring) worker bees abreact emotional agitation on worker combs (ventilation) at the level slightly below 130--160 Hz (Morse and Hooper 1985). Drone combs (as result of weaker supression of perception by QS – auth) are built at the level of 240 Hz. When queen cells are constructed this frequency rises to the level of almost 270 Hz (Vancata 1995).

In this context a fact that: 1 – the construction of queen cells is connected with increase of JH titres (Zeng et al. 2005). 2 – elevated JH titres are characteristic for workers in stress (Lin et al. 2004), strongly supports the notion that appearance of queen cells is a result of swarming (social) stress (Lipiński 2001) which hinder workers' sensitivity to calming pheromones of the queen and extend their perception of nest stimuli so far that enable construction of these cells. Finally when swarming, the frequency of emitted sounds achieves a level of about 300 Hz (Vancata 1995).

Remarkably for the emotional, affective nature of bee perception and behaviour, in the case of queen loss the frequency of stereotypical sounds emitted by the colony increases for a period of 0.5 – 4.5 hours up to the level of 300 – 400 Hz (Vancata 1995).

In this context the fact that: 1 – stereotypies, understood as repetitive and stereotyped behaviours (Broom and Johnson 2000) are connected with disturbances in the metabolism of dopamine in the in the functioning of the opioid system (Dantzer and Mormede 1983), 2 – honeybee dances possesses all features of animal streotypies (Lipiński 2001, 2005, 2006 in press), 3 – one of constituents of nQMP (Simon et al. 2001) is homovanillyl alcohol (HVA) which possesses a chemical structure similar to dopamine (Winston and Slessor 1993), 4 – dopamine receptors are involved in anxiety phenomenon (Vaas 2004), 5 – dopamine receptors are involved in the processing of different sensory modalities (Blenau et al. 1998), I hypothesize that QS – mostly nQMP protects the bee against excessive emotional agitation and emotional affects as well – usually connected with production of endogenic opioids and insufficiency of dopamine.

Especially because the stereotypes in insects can be experimentally produced by morphine administration (Hentzhel and Penzlin 1982, Friederich et al. 1987). It is noteworthy that Núñez et al. (1998) found evidence to suggest that in the honeybee an endogenic opioid system is responsible for modulation of perception for noniceptive stimuli.

SOME PRACTICAL EVIDENCES OF THE CALMING EFFECT OF THE QS ON WORKER BEES

Thus, a young well egg-laying queen is the best producer of tranquillizing blend of queen substance (QS) and consequently the open brood (BP) pheromones "... may impose a labour schedule that promotes efficiency in task performance by physiologically delaying the onset of foraging" because "... inhibiting the shift from within--nest work to foraging tasks" (Pankiw et al. 1998, Giray and Robinson 1996).

Considering that emotional agitation of bees in swarm stress (Lipiński 2001) due to over-stimulation by social and environmental stress stimuli diminishes their normal sensitivity to QS, it subsequently ruins the cognitive expression of nest behaviours (depends on lower levels of agitation) on favour of reproductory behaviors – which

require higher emotional agitation (Lipiński 2001).

Thus, application of sQMP, or exchange of the queen in advanced swarm stress, usually do not re-establish the working mood in a colony (Lipiński 2001). This explains for instance, why in general, highly agitated bees in queenless colonies of European (Winston 1987) and African (Neumann et al. 2000) bees do not build combs. Hovewer queen cells at certain level of this agitation are constructed. For the same reason queen cells with artificial wholes are repaired in colonies with caged queens (insufficiency of QS) and rapidly destroyed in queenright colonies (Caron and Greve 1979). Remarkably in queenless colonies of *A. capensis* where pseudoqueens start to lay eggs and release rich queen-like calming signals, worker cells are built (Neumann et al. 2000).

Due to above emotional and affective psychophysiological mechanisms, adding sQMP with weak tranquillizing properties into honey bee colonies earlier that 24 h after queen loss resulted in an inhibition of queen-rearing, but not when added after 4 days (Melathopolous et al. 1996) when emotional agitation of queenless bees is much higher. This is a reason why application of sQMP or exchange of the queen in advanced swarm stress usually do not re--establish the working mood in a colony. (Lipiński 2001). It is nothworthy that word mood means "a pervasive and sustained emotional state" (Dorland's 1994).

Of course, this suppression of bee perception and simultaneous stabilization of bee emotions through calming properties of the queen is commercially used for many reasons. For instance, one of the most popular tricks used by beekeepers to regain the working mood, prevent swarming, diminish defensiveness (reviewed by Lipiński 2001) and even restore sick larvae rejection (Gliński and Rzedzicki 1987) is the exchange of the old queen for a younger one (especially at the moment of intensive trophallaxis). This regains the emotional perception at the level required for the stable performance of nest tasks.

What is more the calming properties of sQMP lures can be used to substitute for queens during shipment of package bees. This make bees noticably calm and prevent their agitation and overheating while in transit (Winston and Slessor 1993). Similarily the attracting in fact calming effect of sQMP lures over foragers can also be used for pollination (Winston and Slessor 1993).

CONCLUSIONS

The behaviuoral dominance of the queen over workers is maintained through the ataractic and anti-anxiety effect of a blend her calming pheromones (mainly QMP) enforced by similarly acting pheromones of young brood and old bees. The subsequent emotional stabilization of the worker bees connected with slight suppression of it perception, fascilitate expression of nest behaviors and slow down their behavioral development. In general, it enhances colony fitness when coping with the stress pressure of social and environmental factors.

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USPOKAJAJĄCE WŁAŚCIWOŚCI MATKI PSZCZELEJ, MŁODEGO CZERWIU ORAZ STARSZYCH PSZCZÓŁ

Lipiński Z.

S t r e s z e n i e

Celem tej teoretycznej pracy jest prezentacja psychobiologicznego sposobu, który pozwala uspokajającym właściwościom substancji matecznej (SM) wpływać na behawior oraz rozwój behawioralny robotnicy. Autor przedstawia również mechanizm kontroli emocji szczególnie młodych pszczół przez SM na drodze tłumienia produkcji ich hormonu juwenilnego już na poziomie ciał grzybkowatych. Uspokajający, nieznacznie trankwilizujący (ataraktywny) wpływ SM, szczególnie na młode pszczoły robotnice, jest zwykle wzmacniany podobnie działającymi feromonami młodego czerwiu i starszych robotnic. Praca zawiera hipotezę możliwej roli SM w kontroli niektórych stereotypii (tańców) oraz pierwotnych doznań emocjonalnych u pszczół robotnic, typu niepokój oraz strach.

Słowa kluczowe: *Apis mellifera*, pszczoły miodne, emocje, substancja mateczna, układ opioidowy, rozwój behawioralny, hormon juwenilny, lęk, strach.