Review article

Sucrose responsiveness and behavioral plasticity in honey bees (*Apis mellifera*)

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Abstract – This review will focus on the relationships between sensory responses of bees and behavior. Sensory responsiveness constrains individual foraging plasticity and skews collective foraging decisions of colonies. We will concentrate on pollen, nectar, and water foraging behavior and will show that differences in the sucrose responsiveness of bees correlate with different behavioral roles, which supports the response threshold model of division of labor. We will also show how a colony's "allocation" of foragers into foraging roles results from individual differences in responsiveness to task-related stimuli and discuss hypotheses on the behavioral relevance of these differences.

behavioral plasticity / sucrose responsiveness / foraging behavior / collective decision / response threshold model

1. INTRODUCTION

Individual honey bees respond to stimuli resulting in behavior. Sugar is one of the most important stimuli for honey bees (*Apis mellifera* L.), because it is their main source of carbohydrates, results in foraging and recruitment behavioral responses (see Seeley, 1995 for review), and is a reinforcement stimulus for instrumental and operant associative learning (see Menzel and Müller, 1996 for review). Nectar from a great variety of flowers is collected by foragers and processed into honey in the colony. The main components of nectar are sucrose, glucose and fructose (Beutler, 1935; Seeley, 1995; Corbet, 2003), but bees prefer sucrose to most other naturally occurring sugars (Barker and Lehner, 1974). Sucrose does not only play a key role in nutrition. It serves as reward for foragers when they learn the characteristics of floral sources during foraging and is an important determinant for many foraging-related decisions.

The sucrose concentration of a nectar source correlates with the size of the crop-load of a forager (von Frisch, 1965; Pflumm, 1969; Schmid-Hempel et al., 1985; Núñez and Giurfa, 1996) and affects the speed of nectar intake, the decision to return to a nectar source and the time between foraging bouts (Núñez, 1966; Pflumm, 1969; Greggers et al., 1993). The decision of individual foragers to inform their hive mates about this source by performing a recruitment dance also depends on the sucrose concentration of the floral source (von Frisch, 1965; Raveret-Richter and Waddington, 1993; Seeley, 1995; Waddington, 1997). The sucrose concentration of a feeder also affects the transfer rate of sucrose solution during trophallaxis between a returning forager and a nectar receiver bee (Farina and Núñez, 1991; Roces and Blatt,

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1999; Tezze and Farina, 1999). These examples demonstrate that foragers evaluate the sugar concentration of a food source directly and use this information to "decide" whether to exploit this food source and to recruit more bees to this location. The collective result of these activities based on individual evaluation of the sugar resource is a shift in the allocation of foragers among the different available foraging patches, and changes the quantity and quality of a colony's nectar intake.

Pollen is crucial for colonies as the source of protein for brood rearing. The pollen foraging effort of a colony must constantly be adapted to the requirements of the brood and, like foraging for nectar, must adapt constantly to a rapidly changing foraging environment. Pheromones produced by larvae release pollen foraging behavior (Pankiw et al., 1998) while stored pollen inhibits pollen foraging (Fewell and Winston, 1992; Dreller et al., 1999; Dreller and Tarpy, 2000). The quality of the pollen in the field also affects foraging and recruitment behavior (Waddington et al., 1998; Fewell and Page, 2000). Nectar and pollen foraging are not independent. Bees that collect larger loads of pollen collect smaller loads of nectar (Hunt et al., 1995; Page et al., 2000), and vice versa. Therefore, the total loading capacity of a bee sets a constraint on individual foraging. Shifts in responses to foraging stimuli that affect one resource necessarily affect the responses to the other. Shifts in the colony allocation of foraging effort to one resource necessarily affect the intake rates of the other. The collective response of a colony is therefore constrained by these relationships. In order to better understand the collective behavior of a foraging colony we must understand the relationships between individual worker responses to stimuli and their foraging and recruitment behavior. What are the mechanisms that govern foraging and recruitment decisions? A widely accepted hypothesis regards "threshold models" as the basis for division of labor in social insects (Calderone and Page, 1988; Robinson and Page, 1989; Robinson, 1992; Bonabeau et al., 1996; Theraulaz et al., 1998; Arathi and Spivak, 2001; Beshers and Fewell, 2001). According to this view, the bees of a colony differ in their response thresholds to stimuli associated with certain tasks. Once the inten-

sity of a task-related stimulus exceeds the response threshold of an individual, the bee starts performing the associated task. Subgroups of a honey bee colony which start engaging in a certain task will therefore have a similar response threshold for a certain stimulus associated with that task and will constitute a task group. Sucrose is an important stimulus for honey bee foraging behavior. Variation in responsiveness to sucrose has been found to be related to foraging behavioral decisions and learning. Therefore, this review will focus on responsiveness to sucrose and individual behavior with the understanding that collective foraging responses of colonies are derived from the interactions of the individuals (Page and Mitchell, 1998).

2. MEASURING SUCROSE RESPONSIVENESS

The sucrose responsiveness of honey bees has been measured since the early nineteen twenties by various authors using different paradigms, but how responsiveness to sucrose was measured and defined varies considerably from author to author. Von Frisch (1927) measured the "acceptance threshold" of groups of free-flying bees at feeders whose sucrose concentrations were varied. The acceptance threshold was the lowest concentration which was consumed by at least a few bees. Response thresholds of individuals have been determined by applying different sucrose concentrations to the antennae of restrained bees (Fig. 1, inset). When the antenna of a bee is touched with a droplet of sucrose solution of sufficient concentration, the bee reflexively extends its proboscis – a behavior that is referred to as proboscis extension response (PER). Kunze (1933) and Marshall (1935) regarded the lowest sucrose concentration eliciting proboscis extension as the individual response threshold of a bee. In more recent years, Page et al. (1998) defined the sucrose response threshold of an individual as the lowest sucrose concentration which the bee can distinguish from water. The sucrose response threshold of a group – their "empirical threshold" – is the sucrose concentration at which the group response to sucrose statistically exceeds the group response to water. This
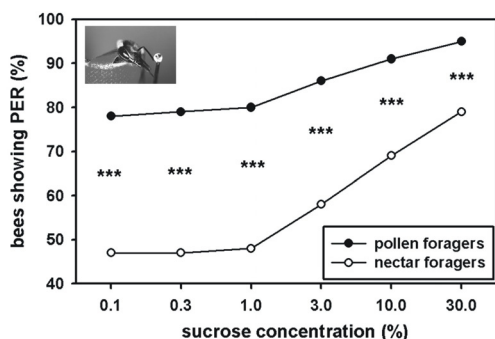
Figure 1. Sucrose-concentration response curves of pollen and nectar foragers tested on their return to the hive. Individual foragers were restrained and tested for their responsiveness to 6 different sucrose concentrations ranging from 0.1% to 30% sucrose on a logarithmic scale. At each antennal stimulation with sucrose (inset) the occurrence of proboscis extension was noted. A significantly greater percentage of pollen foragers responded with proboscis extension at each sucrose stimulation (***: $P = 0.05$, $n_{pollen} = 342$, $n_{nectar} = 353$, two-tailed Fisher Exact Probability Test). Data taken from Scheiner et al. (2003a).

group response threshold depends on the group's average response threshold, the group variance in response thresholds and sample size (Page et al., 1998; Pankiw and Page, 1999, 2000). An alternative measure of sucrose responsiveness which has been used in recent years is the "sucrose response score" (SRS). This score comprises the total number of proboscis responses to a series of sucrose concentrations (Pankiw et al., 2001; Pankiw and Rubink, 2002; Scheiner et al., 2002, 2003a; Pankiw, 2003; Page et al., submitted). The "gustatory response score" (GRS), which has also been used frequently, represents the total number of proboscis responses to water and a series of sucrose concentrations (Scheiner et al., 1999; Pankiw and Page, 2001; Scheiner et al., 2001a, b, c, 2003b). Gustatory and sucrose response scores correlate with individual sucrose response thresholds, because once a bee responds to a certain sucrose concentration, it usually continues to respond to higher sucrose concentrations. Responsiveness to water stimuli which are applied between different sucrose stimuli correlates with sucrose responsiveness (Page et al., 1998).

The variety of terms which have been employed for describing the responses to gustatory stimuli in honey bees is confusing. We have therefore decided to use "sucrose responsiveness" as a general term which describes the responses of bees to sucrose solutions of different concentrations. Bees with a high sucrose responsiveness show proboscis extension to low sucrose concentrations, such as 0.1% (0.003 M) or 1% (0.03 M). Sometimes these bees even respond to water. Individuals with low sucrose responsiveness only respond to high sucrose concentrations, such as 30% (0.9 M) or 50% (1.5 M) sucrose.

3. THE DECISION TO INITIATE FORAGING BEHAVIOR

The colony's need for nectar is great throughout the season, because it serves as a food reserve for the wintertime. Accordingly, nectar collection is high throughout the foraging season, provided the colony has enough space for honey storage. The need for pollen, which is mainly consumed by the brood, changes drastically throughout the year. When the amount of brood is high, particularly in spring and summer, the colony intensifies its pollen collecting behavior. How do potential pollen foragers inform themselves about the amount of brood in a colony and adapt their foraging behavior accordingly?

Honey bees can estimate the amount of brood in a colony by sensing the concentration of an odor produced by the brood (see Pankiw, 2004, this issue). The concentration of this brood pheromone increases with increasing numbers of larvae, which serves as a signal for potential foragers to start pollen foraging (Barker, 1971; Free, 1987; Fewell and Winston, 1992; Eckert et al., 1994; Pankiw et al., 1998; Dreller et al., 1999; Dreller and Tarpy, 2000; Barron et al., 2002). According to the response threshold model, bees with low response thresholds to brood pheromone should decide to start pollen foraging when the intensity of brood odor is low. An increase in the concentration of brood pheromone should soon exceed the response thresholds of other bees and thus result in increased pollen foraging. There is abundant evidence that brood pheromone can trigger pollen foraging

(Barker, 1971; Free, 1987; Fewell and
Winston, 1992; Eckert et al., 1994; Pankiw
et al., 1998; Dreller et al., 1999; Dreller and
Tarpy, 2000; Barron et al., 2002), but individ-
ual response thresholds to brood pheromone
are very difficult to measure. However, it has
been shown that brood pheromone can modu-
late sucrose responsiveness (Pankiw and Page,
2001), and sucrose responsiveness increases
with age (Pankiw and Page, 1999). Newly
emerged bees with higher responsiveness
to sucrose initiate foraging earlier in life
(Pankiw, 2003), suggesting that responsive-
ness to sucrose may correlate with responsive-
ness to brood pheromone. It is interesting to
note that the link between sucrose responsive-
ness and the age of onset of foraging behavior
results in the earlier onset of foraging in pollen
foragers. It is still not known if modulating
sucrose responsiveness by exposure to brood
pheromone results in shifts in individual or
collective foraging behavior.

4. THE DECISION TO COLLECT POLLEN, NECTAR, OR WATER

Sucrose responsiveness correlates with the
decision to collect pollen, nectar, or water.
Pollen foragers of a honey bee colony are on
average more responsive to sucrose than nec-
tar foragers in most weeks of a foraging season
(Scheiner et al., 2003a). Pollen foragers tested
after returning from a foraging trip display a
higher sucrose responsiveness than nectar for-
agers (Fig. 1; Page et al., 1998; Scheiner et al.,
2001b, 2003a). Sucrose responsiveness of
newly emerged bees correlates with their for-
aging behavior that is initiated 2–3 weeks later
(Pankiw and Page, 2000; Pankiw, 2003) Water
foragers are the most responsive followed by
pollen foragers, bees that collect both nectar
and pollen, nectar foragers, and the least
responsive bees are most likely to return
empty (Fig. 2; Pankiw and Page, 2000). Nec-
tar foragers that are more responsive to
sucrose collect nectar with lower sugar con-
centrations than those that are less responsive
(Pankiw and Page, 2000; Pankiw, 2003). It is
assumed that they have such a low sucrose
responsiveness that they do not find an accept-
able food source. The physiological basis for
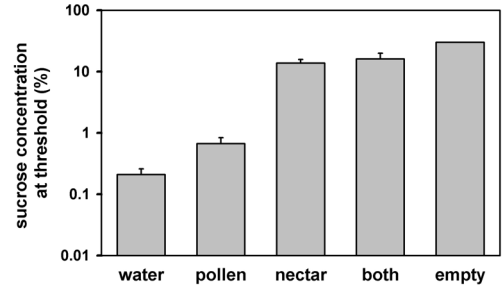the correlation between sucrose response and

Figure 2. Sucrose responsiveness correlates with
foraging tasks. Returning foragers were caught and
restrained to measure their sucrose responsiveness
individually. In that experiment, individual
response thresholds to sucrose were estimated.
High response thresholds correspond to low
sucrose response scores. Low response thresholds
correspond to high sucrose response scores. Water
and pollen foragers were the most responsive bees
and displayed the lowest response thresholds.
Foragers collecting nectar, pollen or nectar, and
bees returning empty from their foraging trips
displayed a low sucrose responsiveness. Their
estimated response threshold was very high. Means
and standard errors are displayed. Figure modified
after Pankiw and Page (2000).

foraging behavior is unclear. It is unlikely that
sucrose responsiveness is causally linked to
foraging decisions. It is more likely that the
correlations of sucrose responsiveness with
the different foraging traits are consequences
of indirect common causal factors affecting
the sensory response system of bees and forag-
ing behavior. Bees with high sucrose respon-
siveness are generally more responsive to
stimuli in other sensory modalities. Bees with
high sucrose responsiveness are also more
responsive to pollen (gustatory; Fig. 3A),
citral (olfactory; Fig. 3B), and to low intensi-
ties of light (visual; Erber, personal observa-
tion) than bees with low sucrose responsive-
ness. These results support the hypothesis
that pollen foragers are also more responsive
than nectar foragers to chemical stimuli like
brood pheromone. So far, there has been no
experimental evidence in the bee that the sen-
sitivities of the sensory systems for different
modalities can be tuned independently. High
sensitivity for one modality is apparently cor-
related with high sensitivity for other modali-
ties. The physiological basis of these findings
is still unclear. We assume that the same neu-
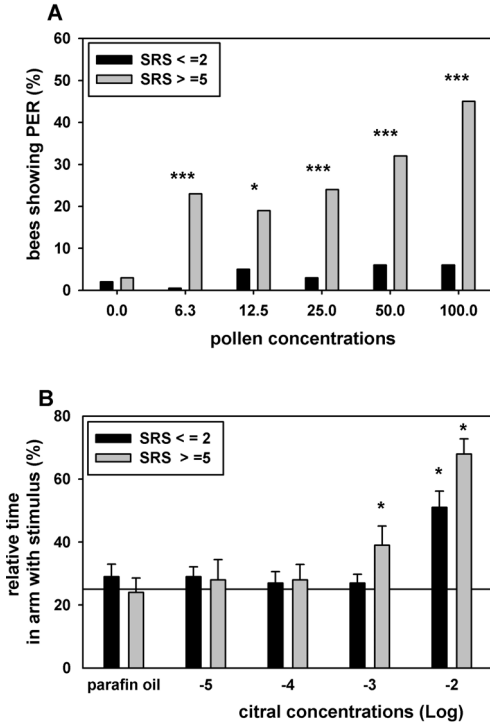romodulators or neurohormones control the

Figure 3. Sucrose responsiveness correlates with responsiveness to pollen and citral. A. Honey bee foragers were restrained in holders and their antennae were stimulated with the same 6 sucrose concentrations as shown in Figure 1. Afterwards, the antennae were stimulated with different concentrations of almond pollen and cellulose of the same grain size. The almond pollen was collected directly from flowers. Bees were separated in groups with low or high sucrose response scores (SRS). At most pollen concentrations the percentage of bees responding with proboscis extension was greater in the group of bees with high sucrose responsiveness (SRS = 5) than in bees with low sucrose responsiveness (SRS = 2; *: $P = 0.05$, ***: $P = 0.001$, $n_{SRS = 2} = 63$. $n_{SRS = 5} = 108$, two-tailed Fisher Exact Probability Test). B. Honey bee foragers were tested in a four-armed olfactometer for their responsiveness to different concentrations of citral. The abscissa shows the different odor concentrations. The ordinate displays the mean percentage of time spent in the arm containing the odor and the standard errors. The reference line indicates the 25% level of erratic choice. Bees are grouped as in A. Only individuals which spent at least half of the time outside the central area and thus displayed average walking activity were analyzed. Individuals with a low sucrose responsiveness (SRS = 2) had a high olfactory response threshold and only recognized the odor at the highest concentration (10^{-2}). Bees with a high sucrose responsiveness (SRS = 5) already spent significantly more time in the arm containing a lower odor concentration (10^{-3}). They displayed a lower olfactory response threshold. The odor concentrations at which bees spent significantly more time in the odor-containing arm are indicated: *: $P = 0.05$, two-tailed T-Test). At the highest odor concentration, when both groups recognized the odor, bees with a SRS = 5 spent significantly more time in the respective arm than the bees with a SRS = 2 ($P = 0.05$, $n_{SRS = 5} = 23$, $n_{SRS = 2} = 26$; two-tailed T-Test).

sensitivities of different sensory systems in the periphery and in the central nervous system. The release of these neuroactive substances probably affects many different subsystems simultaneously.

5. SUCROSE RESPONSIVENESS AND DECISIONS IN ASSOCIATIVE LEARNING

During their foraging trips, bees learn the colors, odors, shapes and structures of floral sources. Foragers have to evaluate the quality of the nectar or pollen and must then decide whether to exploit a food source or not. If they find the food source acceptable, they need to learn the location of it to return for several foraging trips and to possibly recruit other foragers.

In several experiments on olfactory and tactile learning in the laboratory or using free-flying bees it was demonstrated that the sucrose concentration used as reward significantly correlates with associative learning performance (Loo and Bitterman, 1992; Couvillon et al., 1994; Bitterman, 1996; Smith, 1997; Laloi et al., 1999; Scheiner et al., 1999). Bees which received a high-concentrated sucrose solution as reward learned faster than bees receiving a low sucrose concentration. But bees receiving the same sucrose solution as a reward also differed in their learning performance. These differences in associative learning have long
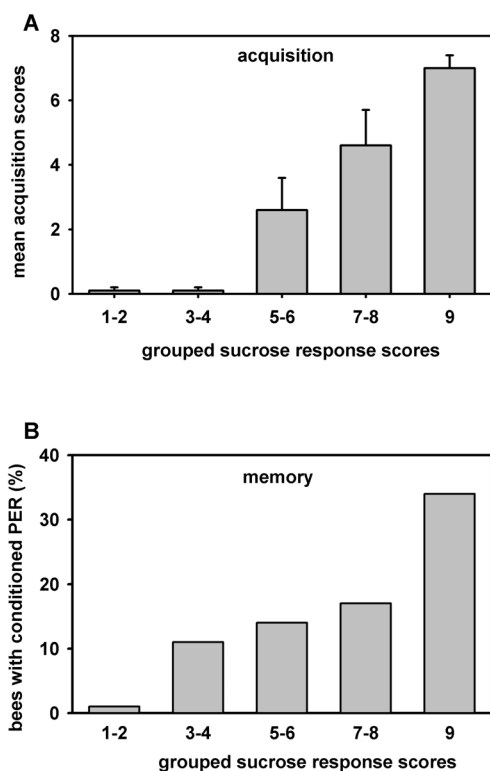
A

B

Figure 4. Tactile acquisition and 24-hour memory correlate with sucrose responsiveness. Honey bees in their second week of life were tested for their responsiveness to 9 sucrose concentrations ranging from 1% to 40% sucrose on a logarithmic scale. Bees were grouped according to their sucrose response scores and conditioned to a tactile object in 10 trials. A. Mean acquisition scores and standard errors are shown. Acquisition scores comprise the total number of conditioned responses during tactile acquisition. Sucrose response scores correlate positively with acquisition scores (r = 0.61, P = 0.001, n = 99). Bees with high sucrose responsiveness reached a higher acquisition score than bees with low sucrose response scores. B. Correlation between sucrose responsiveness and 24-h memory after tactile conditioning in the same bees. The abscissa shows the grouped sucrose response scores. The ordinate shows the percentage of bees displaying the conditioned response 24 hours after conditioning. Data taken from Scheiner et al. (2001a).

been regarded as a form of unavoidable "noise" in the data. Recently, however, the reason for these learning differences was found. Individual differences in sucrose responsiveness correlate with huge differences in associative learning behavior (Scheiner et al., 1999, 2001a, b, c, 2003a). Individuals with high sucrose responsiveness reach a higher level of acquisition and demonstrate stronger memory than bees with low sucrose responsiveness (Fig. 4, Scheiner et al., 1999, 2001a, b, c, 2003a). As discussed in Scheiner et al. (1999) the difference between the individual responsiveness to sucrose and the sucrose concentration of the reward determines the level of acquisition. Bees with high sucrose responsiveness which receive a low-concentrated sucrose solution as reward show the same level of acquisition as bees with a low sucrose responsiveness which receive a high-concentrated sucrose solution as reward (J. Erber, R. Scheiner, personal observation).

6. CONSEQUENCES FOR FORAGING BEHAVIOR

In contrast to nectar foragers, which receive great sucrose rewards at an accepted food source, it is unclear how pollen foragers are rewarded at a foraging site. The latter possibly reward themselves with very small amounts of nectar or even with the dew on the flower petals. Differences in the sucrose responsiveness of pollen and nectar foragers could be related to the different rewards pollen and nectar foragers receive at a floral source. Pollen foragers are very responsive to sucrose and learn a signal characterizing a food source even with low concentrations of a sucrose reward or water. Laboratory experiments indicate that even water can serve as a reward stimulus in highly responsive bees (R. Scheiner, unpublished data). Nectar foragers are less responsive to sucrose and therefore need higher-concentrated sucrose rewards than pollen foragers to reach the same level of acquisition. Further experiments with free-flying bees will show whether pollen itself can act as a reinforcer.

7. MODULATION OF SUCROSE RESPONSIVENESS

Responsiveness to sucrose is not fixed. It varies with season (Scheiner et al., 2003), age (Pankiw and Page, 1999), nutrition, and experience (Pankiw et al., 2001). It is plausible that

the modulation of sucrose responses of bees within colonies could provide "global" information about the current nutritional status of the colony and affect subsequent foraging and recruitment decisions. Seeley (1995) shows how decisions of nectar foragers to perform recruitment dances are related to the quality of the nectar (sugar solution) they collect. In his study, he determined that different bees had different dance thresholds. If dance thresholds themselves are modulated by the quality and quantity of incoming nectar, then collective decisions may be influenced by information shared by most or all colony members, rather than based completely on localized information.

Pankiw et al. (2001) demonstrated that sucrose responsiveness is modulated by food intake and foraging experience. Nectar returned to the hive is distributed throughout the colony. Pankiw et al. (in press) demonstrated that the sucrose responses of non-foraging bees within a colony modulate with the quality of sugar solution collected by the foragers. Therefore, global information about the current nectar intake of a colony is available for collective decision making, however, it has not been demonstrated if this information is used.

8. GENETIC DETERMINANTS OF SUCROSE RESPONSIVENESS

The importance of differences in sucrose responsiveness for collective decision making in the foraging behavior of a colony has been demonstrated. But what determines individual sucrose responsiveness? An important determinant of sucrose responsiveness lies in the genes of a bee. Several quantitative trait loci (QTL) have been found to correlate with sucrose responsiveness and different aspects of foraging behavior. Page and Fondrk (1995) produced genetic strains of honey bees that differed in the amount of surplus pollen they store in the comb and in their pollen foraging behavior. High-strain bees are more likely to collect pollen and are more responsive to sucrose than low-strain bees at all ages (Page et al., 1998; Pankiw and Page, 1999, 2000; Pankiw et al., 2001; Scheiner et al., 2001a, b). Three quantitative trait loci (*pln1*, *pln2* and *pln3*) were found to correlate with different

aspects of foraging behavior in these strains: the probability to collect pollen or nectar (*pln1* and *pln2*: Hunt et al., 1995), the nectar load size (*pln2*: Hunt et al., 1995; *pln3*: Page et al., 2000) and the pollen load size (*pln2*: Hunt et al., 1995; *pln3*: Page et al., 2000). Interestingly, two of these QTL, *pln1* and *pln3*, also correlate with sucrose responsiveness (Chandra et al., unpublished data), suggesting pleiotropic relationships between sucrose responsiveness and foraging behavior (Page and Erber, 2002; Page et al., unpublished data). One of these QTL, *pln3*, correlates with the age of onset of foraging (Rueppell, personal communication).

Collectively, the results from QTL studies and the studies of the correlations of sucrose responsiveness with foraging behavior suggest that pollen foraging behavior consists of a suite of traits that are linked through common causal factors, including some of the mapped QTL. This suite includes a higher response to olfactory, gustatory, and visual stimuli, early onset of foraging behavior, water foraging, collecting nectar with lower concentrations of sugar, and enhanced associative learning performance. It has been hypothesized that these traits vary together, because they share a common physiological signaling pathway involving cyclic AMP (Page and Erber, 2002).

Résumé – Sensibilité de l'Abeille domestique (*Apis mellifera*) au saccharose et plasticité comportementale. La division du travail dans une colonie d'abeilles (*Apis mellifera* L.) est un processus complexe qui nécessite à la fois la persistance d'une activité conduisant à la spécialisation et à une compétence accrue, et aussi une plasticité comportementale dans un environnement toujours changeant. Les modifications dans les activités collectives de butinage, dues aux changements au

sein du nid ou dans les conditions de butinage, res-
semblent aux décisions de groupe, bien que chaque
individu réagisse à un ensemble de stimuli. Les
variations dans les seuils de réponse à des stimuli
qui déclenchent un comportement donné, entraînent
des modifications dans le comportement et la divi-
sion du travail.

Cette synthèse porte sur les relations entre réponses
sensorielles des abeilles et comportement. La sensi-
bilité sensorielle limite la plasticité comporteme-
tale et influence les décisions collectives de la colo-
nie. Nous considérons la récolte de pollen, de nectar
et d'eau et montrons que la différence dans la sensi-
bilité des abeilles au saccharose est corrélée aux
divers types de comportements, ce qui corrobore le
modèle des seuils de réponse pour la division du tra-
vail. Nous montrons également que dans une colo-
nie d'abeilles la répartition des butineuses entre
diverses tâches données peut s'expliquer par une
différence de sensibilité aux stimuli relatifs à la
tâche. Les hypothèses sur la pertinence de ces diffé-
rences de sensibilité pour le comportement sont
discutées.

Les décisions collectives au sein d'une colonie sont
basées sur des différences individuelles de compor-
tement. En analysant les mécanismes de décisions
individuelles nous pouvons peut-être déduire des
règles valables pour l'ensemble du groupe. Mais en
même temps le comportement individuel peut être
contrôlé et modulé par les décisions collectives,
alors que le degré de plasticité collective est lié à la
plasticité individuelle. Nous pensons que l'analyse
des comportements individuels et sa modulation par
les décisions collectives sont un moyen pour
débrouiller les mécanismes complexes de rétroac-
tion entre les comportements des individus, des
sous-groupes d'abeilles et de la colonie.

**sensibilité au saccharose / plasticité comporte-
mentale / décision collective / butinage / seuil de
réaction**

**Zusammenfassung – Zuckerwasserreaktion und
Verhaltensplastizität in Honigbienen (*Apis melli-
fera*).** Die Arbeitsteilung in einer Kolonie von
Honigbienen ist ein komplexer Prozess, der sowohl
das kontinuierliche Ausführen einer Tätigkeit ver-
langt, was zu Spezialisierung und großer Professio-
nalität führt, als auch Plastizität in einer sich ständig
ändernden Umwelt erfordert. Änderungen im kol-
lektiven Sammelverhalten der Bienen wegen sich
ändernder Situationen im Stock oder in den Sam-
melbedingungen ähneln Gruppenentscheidungen,
obwohl jedes Tier individuell auf eine Reihe von
Reizen reagiert. Änderungen in den Reaktions-
schwellen für Reize, die bestimmte Verhaltenswei-
sen auslösen, führen zu Änderungen des Verhaltens
und zu Arbeitsteilung. Die Modulation von Reizen
und/oder von sensorischen Antworten kann zu
scheinbar koordinierten Verhaltensänderungen der
Gruppe führen.

Dieser Übersichtsartikel behandelt die Beziehung
zwischen sensorischen Antworten und dem Verhal-
ten von Bienen. Die sensorische Empfindlichkeit
einer Biene begrenzt deren Plastizität im Sammel-
verhalten und beeinflusst kollektive Entscheidun-
gen der Kolonie. Wir diskutieren das Sammeln von
Pollen, Nektar und Wasser und zeigen, dass Unter-
schiede in der Zuckerwasserempfindlichkeit von
Bienen mit verschiedenen Verhaltensweisen korre-
lieren. Diese Befunde unterstützen das Reaktions-
schwellenmodell der Arbeitsteilung. Wir zeigen
außerdem, dass in einer Honigbienen-Kolonie die
Zuordnung von Sammlerinnen zu bestimmten Sam-
melaufgaben mit unterschiedlichen Empfindlich-
keiten für Stimuli erklärt werden kann, die in Bezug
zu der Sammelaufgabe stehen. Hypothesen zur
Verhaltensrelevanz dieser Unterschiede in der
Empfindlichkeit werden diskutiert.

Kollektive Entscheidungen innerhalb einer Kolonie
basieren auf individuellen Verhaltensentscheidun-
gen. Durch die Analyse der Mechanismen von indi-
viduellen Entscheidungen können wir möglicher-
weise Regeln ableiten, die auch für die gesamte
Gruppe gelten. Individuelles Verhalten wird ande-
rerseits aber auch von kollektiven Entscheidungen
bestimmt werden, während gleichzeitig der Grad
der kollektiven Verhaltensplastizität von der indivi-
duellen Plastizität abhängt. Wir glauben, dass die
Analyse von individuellem Verhalten und seiner
Modulation durch kollektive Entscheidungen ein
Weg ist, die komplexen Rückkopplungsmechanis-
men im Verhalten zwischen Individuen, Untergrup-
pen von Bienen und der Kolonie aufzuklären.

Apis mellifera / **Zuckerwasserreaktion / Arbeits-
teilung / Gruppenentscheidungen**

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