

# Her odours make him deaf: crossmodal modulation of olfaction and hearing in a male moth

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## Summary

All animals have to cope with sensory conflicts arising from simultaneous input of incongruent data to different sensory modalities. Nocturnal activity in moths includes mate-finding behaviour by odour detection and bat predator avoidance by acoustic detection. We studied male moths that were simultaneously exposed to female sex pheromones indicating the presence of a potential mate, and artificial bat cries simulating a predation risk. We show that stimulation of one sensory modality can modulate the response to information from another, suggesting that behavioural thresholds are dynamic and depend on the behavioural context. The tendency to respond to bat sounds decreased as the quality and/or the

amount of sex pheromone increased. The behavioural threshold for artificial bat cries increased by up to 40 dB when male moths were simultaneously exposed to female sex pheromones. As a consequence, a male moth that has detected the pheromone plume from a female will not try to evade an approaching bat until the bat gets close, hence incurring increased predation risk. Our results suggest that male moths' reaction to sensory conflicts is a trade-off depending on the relative intensity of the input to CNS from the two sensory modalities.

Key words: hearing in moth, moth olfaction, trade-off, sensory conflict, predation risk, crossmodal integration.

## Introduction

Animals receive simultaneous input from several sensory modalities. In some cases, multimodal signals originate from the same sender and serve to enhance communication (e.g. Hölldobler, 1999). Enhancement of communication may even take place through sensory integration of information emanating from distal sources (Partan and Marler, 1999). However, in other cases the signals originate from different sources and the receiver may end in a dilemma because an appropriate reaction to one signal may at the same time be inappropriate to the other signal. In many situations where different sensory cues generate incompatible information forcing animals to choose which one to react to, they do so by focusing attention on selective stimuli (Bernays, 2001). Well-known examples of trade-offs in ecology are those between resource acquisition and predation avoidance (for a review see Dicke and Grostal, 2001). Plasticity and the ability to integrate information from different sensory systems is a fundamental characteristic of the central nervous system (CNS). Recently, crossmodal integration, including chemical senses (Small, 2004), has received some focus in terms of ecological validity (de Gelder and Bertelson, 2003). However, the physiological processes involved in perception of incongruent sensory input are not well known. Studies in humans and other animals have

shown that the amount of information that can be processed simultaneously is limited by the capacity of the brain (e.g. Pashler, 1998; Spence and Driver, 2004). Therefore, behaviour like mating behaviour and anti-predatory behaviour may be constrained by limited attention (Dukas, 2002). The relatively simple system in moths where well-defined signals from the predator and from the mate, respectively, are detected by different sensory channels can serve as a good model system for studying how two incongruent modalities influence each other. Male moths use their antennae to detect and locate females releasing sex pheromone (Farkas and Shorey, 1974; Kennedy et al., 1980; Vickers and Baker, 1997) and their ears to detect and evade echolocating insectivorous bats (Roeder 1962).

At night male moths get aroused by long distance attractant sex pheromones released by conspecific females, and will initiate flight and orient into the pheromone plume (see review by Hansson, 1995). In a zigzagging flight pattern he will locate the calling female, land and together they will initiate mating behaviour. The composition of the pheromone blend as well as the amount is important for the mate finding behaviour in male moths (Linn et al., 1987).

Nocturnal activity of moths is associated with the risk of

predation by echolocating insectivorous bats. Aerial hawking bats detect nocturnal insects on the wing (Neuweiler, 1989), while gleaners catch insects on the substrate (Arlettaz et al., 2001). Gleaning bats may constitute about a third of all insectivorous species and are especially common in tropic regions (Arlettaz et al., 2001). Moths have evolved ears sensitive to bat cries and a repertoire of evasive manoeuvres adapted to evade attacking bats (Roeder, 1967; Miller and Surlykke, 2001). Airborne moths react to bat sound by diving towards the ground or steering away from the bat. Non-aerial moths running on surfaces react by freezing all movement (Werner, 1981; Greenfield and Weber, 2000; Jones et al., 2002), since this will protect them from detection by gleaners. Other defensive responses to gleaners include falling silent in acoustic signalling insect species (Belwood and Moris, 1987; Bailey and Haythornthwaite, 1998; Jones et al., 2002; Greenfield and Baker, 2003). Evasive manoeuvres and other anti-predator tactics, such as 'freezing', involve a cost in the form of reduced mating opportunities. Despite countless studies of either modality (olfaction and hearing) in moths very few studies have focused on how moths deal with simultaneous exposure to sex odours from potential mates and predator sounds, although this often occurs in nature. Exceptions from this are the studies by Baker and Cardé (1977), and Acharya and McNeil (1998), which show that moth sexual behaviours associated with pheromone release, and detection can be disrupted by ultrasound stimulation. However, they (Baker and Cardé, 1977; Acharya and McNeil, 1998) only manipulated predation risk and did not investigate potential trade-off mechanisms, which may occur when a moth receives incompatible sensory input. In this study we manipulated both predation risk and the quality and quantity of the pheromone to examine the hypothesis that moths will make a trade-off between mating and predator avoidance, based on the relative intensity of the two sensory inputs. The alternative hypothesis suggests that a moth should respond to a predator cue every time it exceeds the hearing threshold. As a model species we chose the noctuid moth, *Spodoptera littoralis*, since the sex pheromone compounds are identified (Kehat and Dunkelblum, 1993), and ultrasonic hearing in noctuids in general is well described. Noctuid moths have a pair of tympanic ears located dorsolateral on the thorax. Each ear contains only two sensory cells (Ghiradella, 1971; Surlykke and Miller, 1982). We discuss the ecological relevance of bimodal integration in moths.

## Materials and methods

### Animals

Adult males of *Spodoptera littoralis* Boisduval were obtained from a culture that has been reared for several generations on a semi-synthetic diet (Hinks and Byers, 1976), based on potatoes instead of beans. The culture was maintained at 25°C, 65% r.h. and 16 h:8 h L:D, and has been supplemented with moths collected from the wild in Egypt yearly since 1995.

Pupae were separated according to sex. Emerged males and females were kept separately.

### Neurophysiology

Individual audiograms of male moths were determined by extracellular recording of nervous activity in the tympanic nerve when the moth ears were exposed to sound at different frequencies. The moths were processed 1–2 days after emerging. The tympanic nerve was exposed using a dorsal approach and hooked onto a tungsten electrode. The preparation was placed 40 cm from the loudspeaker. Tympanic nerve activity was bandpass filtered, amplified (custom built equipment) and displayed on an oscilloscope and through an audio monitor. Sound stimuli were 10 ms long pulses with a rise/fall time of 0.5 ms repeated at 1 Hz. Threshold was defined as the sound pressure level (SPL) that evoked at least 1–2 spikes in at least eight out of ten stimulations. The hearing sensitivity was tested randomly in 5–10 kHz steps in the frequency range from 5 to 125 kHz.

The acoustic pulses were generated with an oscillator (Wavetek model 186; San Diego, CA, USA) controlled by a custom-built pulse generator that gave shaped pulses with linear rise and fall times. The stimulus was amplified (Xelex; Stockholm, Sweden) and broadcast through a tweeter (Technics EAS 10 TH400B; Secaucus, NJ, USA). The loudspeaker was calibrated before and after the experiments by means of a  $\frac{1}{4}$  inch microphone (G.R.A.S., Nærum, Denmark) (with grid off) that was calibrated against a G.R.A.S. sound calibrator (type 42AB).

### The walking bioassay

Experiments were conducted in an open arena olfactometer (63 cm × 75 cm) (Schlyter et al., 1995) at 17–18°C. Air was pushed in through a baffle with spaced 2 mm holes. An exhaust at the other end sucked out the odour-contaminated air. The push-exhaust system created laminar airflow above the arena floor as visualised with TiCl<sub>4</sub> smoke. As a stimulus, 10 µl of a pheromone solution was applied to a filter paper and placed upwind at the centre of the arena 2 cm in front of the baffle and close to the table surface. Filter papers were used for a maximum of 20 min. In the walking bioassay the moth moves at relatively slow speed in a narrow path, which facilitates control of the sound intensity at the moth's position. A male released downwind in the olfactometer starts wing fanning upon detection of pheromone and walks toward the pheromone source. [Anderson et al. (2003) compare walking and flying moths, and find that their behavioural response to pheromone is comparable.] Approximately halfway between the odour source and the release site the moth was stimulated with bat-like ultrasound from a loudspeaker. A walking moth responds to ultrasound by 'freezing' and remaining stationary for some time (see also Werner, 1981; Rydell et al., 2000; Greenfield and Weber, 2000). Moths were presented with sound stimuli of different intensities and the behavioural thresholds to sound stimuli were determined at different pheromone qualities and quantities.

### Odour sources

The following chemical stimuli were used. Female extract: glands from 2-day-old virgin females were dissected 2 h into the scotophase and extracted with hexane. One female equivalent (1FE) corresponds to the amount of pheromone from one gland, which was analysed to be approximately 20 ng of the major component. Major component: (Z9, E11)-tetradecadienyl acetate (Z9E11-14:OAc) in 20 ng and 100 ng solutions. Two-component blend [(Z9E11-14:OAc and (Z9, E12)-tetradecadienyl acetate (Z9E12-14:OAc)] in the proportions of 99.5:0.5 ng. This blend was previously shown to be highly attractive to the species in the field (Kehat and Dunkelblum, 1993).

### Sound stimulus

The sound stimulus was a pulse train consisting of 20 pulses (4.7 ms long with a carrier frequency of 30 kHz) with a repetition rate of 23 pulses  $s^{-1}$ . This stimulus elicited a consistent behavioural response. 30 kHz was chosen because it is within the moths' best frequency of hearing (Fig. 1) and since many bats, including gleaners, emit echolocation signals including 30 kHz. The temporal structure of our stimuli corresponds roughly to the search phase of many bats (Faure et al., 1993; Neuweiler, 1990; Waters and Jones, 1995). Furthermore, these stimulus parameters evoke maximum silencing response in the acoustic signalling moth, *A. grisella* (Greenfield and Baker, 2003). The stimulus was produced by multiplying signals from a pulse generator (Berkeley Nucleonics Corporation 555, San Rafael, CA, USA) and a sine wave generator (Agilent 33120A, Palo Alto, CA, USA) in a custom-built trapeze modulator. The signal was attenuated (Kay 865 step attenuator, Lincoln Park, NJ, USA), amplified (UltraSoundAdvice S55A, London, UK) and broadcast through an electrostatic loudspeaker (UltraSoundAdvice S56). The loudspeaker was positioned close to the ground almost perpendicular to the moths' path between release point and pheromone source 25 cm downwind from the pheromone source. The intensity of the sound was measured by a  $\frac{1}{4}$  inch microphone (G.R.A.S., Nærum, Denmark) (with grid off) that was calibrated against a G.R.A.S. sound calibrator (type 42AB). The sound pressure was measured at several points in front of the loudspeaker at the floor level. From these results an area in the middle of the arena was marked in which the sound pressure did not vary by more than  $\pm 3$  dB. Sound pressure levels (SPL) are given in dB relative to 20  $\mu Pa$  rms.

### Experimental protocol

In the behavioural experiments, 1–2 days old naïve male moths were tested 1.5–4 h into the scotophase. For testing, moths in glass cylinders covered with mesh net were introduced in the arena 60 cm downwind from the odour source. The arena was illuminated by red light, 5–10 lux; the temperature was 17–18°C, and relative humidity 30–50%. Pheromone stimulation elicited activation (movement of the antennae), wing-fanning and chemotaxis in this order. Males walked upwind towards the odour source, and when they

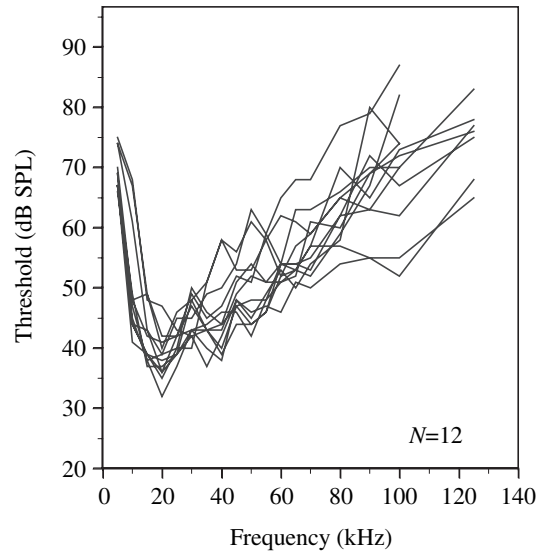


Fig. 1. Hearing threshold for *Spodoptera littoralis* males measured from the tympanic nerve. Lines represent individual audiograms for 12 males.

reached the test zone (approximately half way between release site and odour source) the sound was switched on manually and the behavioural response observed. The responses were only scored as either 'stopped walking' or 'no response' although response to sound seemed to be graded. Cessation of walking was always accompanied by cessation of wing fanning. However, sometimes (especially when exposed to female extract) males would cease wing fanning without cessation of walking as response to the sound. Likewise, at lower sound intensities moths sometimes responded to the sound by turning away from the sound source. We defined a behavioural walking stop response to sound as a complete stop that lasted at least 1 s. We only used responses fulfilling this criterion for threshold determination. The response duration was defined by the time from stimulation until the males started walking again and was only measured for the most intense sound stimuli (102 dB SPL). All reactions lasting two or more minutes were arbitrarily calculated as 120 s. The sound intensity at the position of the moth was varied in 6 dB steps from 72 dB SPL to 102 dB SPL in experiments with odour stimulation, and from 60 to 102 dB SPL in experiments with air. Moths that were exposed to air (i.e. no odour) did not orient in a specific direction, consequently they were introduced in the middle of the arena. After a gentle touch they started walking in a random direction and were stimulated with sound when they entered the pre-defined area. The number of animals that were available for behavioural experiments each day (on average 30) was divided in five treatment groups (Air, 20 ng Z9E11-14:OAc, 100 ng Z9E11-14:OAc, two-component blend and female extract) with equal number in each group. Each day experiments were carried out in the order of increasing pheromone load, thus starting with air and ending with female extract. This order was chosen to minimise potential contamination of the set-up. Experiments from consecutive

days were pooled to minimise possible day effects. All individuals were only tested once (i.e. one walk in the bioassay) and then discarded to avoid habituation effects or pre-exposure effects (see e.g. Anderson et al., 2003). For every treatment we used 20–24 males.

#### Data analyses

The mean difference in sound intensity required for eliciting reaction at 50% level of selected combinations of odour and sound intensities was calculated using a logistic fit (Table 1). Within odour type Spearman rank correlation between sound intensity and reaction frequency were performed using SYSTAT (v7.0, SPSS). Logistic regression fit (Hosmer and Lemeshow, 1989) and pair-wise comparisons using dummy variables were performed using SAS (rel. 8.2, SAS institute Inc.). The non-parametric Kruskal-Wallis test (SAS rel. 8.2) were used for testing differences in odour influence on the response duration, the subsequent multiple comparisons were done by hand following a non-parametric Tukey test (Zar, 1996).

#### Results

Fig. 1 shows individual audiograms for 12 *S. littoralis* males. The best sensitivity is within the range of 15–40 kHz, with a best threshold of  $38.5 \pm 8$  dB SPL at 20 kHz.

The lowest behavioural thresholds were found for moths in clean air. In the absence of pheromone stimulation most male moths ceased walking and froze to stimulus intensities above 66 dB SPL (Fig. 2). In all experiments the proportion of males that responded to sound increased with increasing sound intensity (Fig. 2). Conversely, at constant sound pressure the reaction to sound was successively reduced with increasing pheromone quality and concentration (Fig. 2). The most pronounced disregard to predator sound was found for males

Table 1. Data for pair-wise comparison of treatments

Odour pairs	Difference at 50% reaction probability (dB)*	Significance level
Air vs 1 comp.† 20 ng	12.2±3.0	<0.001
Air vs 1 comp. 100 ng	24.6±3.7	<0.001
Air vs 2 comp. blend‡	26.2±3.9	<0.001
Air vs female extract (IFE)	40.5±5.2	<0.001
1 comp. 20 ng vs 1 comp. 100 ng	12.0±2.6	<0.001
1 comp. 20 ng vs 2 comp. blend	13.8±2.8	<0.001
1 comp. 20 ng vs female extract	27.2±3.5	<0.001
1 comp. 100 ng vs 2 comp. blend	1.3±2.9	<i>P</i> =0.648
2 comp. blend vs female extract	15.6±3.3	<0.001

\*Data are mean values ± S.E.M. †Z9E11-14:Oac. ‡Z9E11-14:Oac (99.5%) and Z9E12-14:Oac (0.5%). Data for pair-wise comparison of treatments. Average pair-wise difference in sound intensity needed for eliciting evasive reaction at 50% level (corresponding to the horizontal dotted line in Fig. 3) for selected odour-pairs. Significant difference (logistic regression with dummy variable) is seen in all the tested pairs except for 1 component (comp.) 100 ng vs 2 components blend.

attracted to female extract, where only about 30% of the males responded to sound at the highest intensity (102 dB SPL) whereas the same sound pressure elicited more than 95% responses when exposed to 20 ng of the one-component odour or no odour at all. By logistic regression, we estimated response probability functions (Fig. 3), which allowed us to test for significant differences between selected pairs of odour treatments (Table 1). At the 50% level (Fig. 3) pair wise comparisons showed that all olfactory stimulations were significantly different (*P*<0.001) except one-component 100 ng vs two-component blend (*P*=0.648) (Table 1). Significantly more moths responded to sound stimuli when

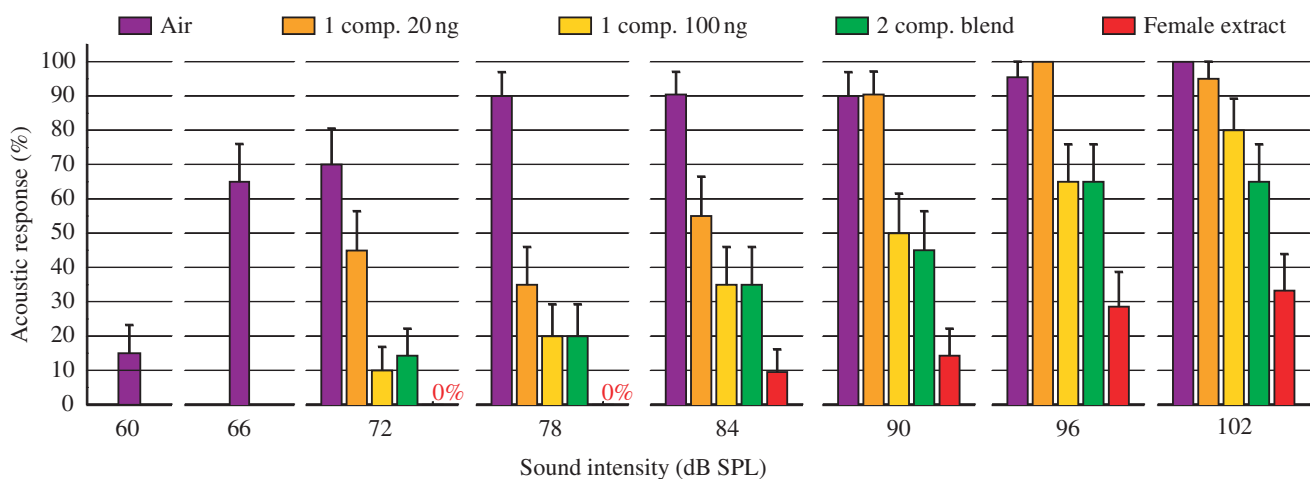


Fig. 2. Response frequencies to varying intensity of sound stimulation in pure air or during attraction to four different pheromone stimuli. The response frequency depended significantly on the sound intensity for all pheromone and none pheromone stimuli (Spearman rank correlation: *P*<0.01, *r*=0.886 for 1 component (comp.) 20 ng; *P*<0.0001, *r*>0.950 for all other odours). Coloured bars illustrate mean percentages of male moths responding by cessation of walking to sound stimulation (20<*N*<25 for all treatments). Values represent data means + S.E.M.

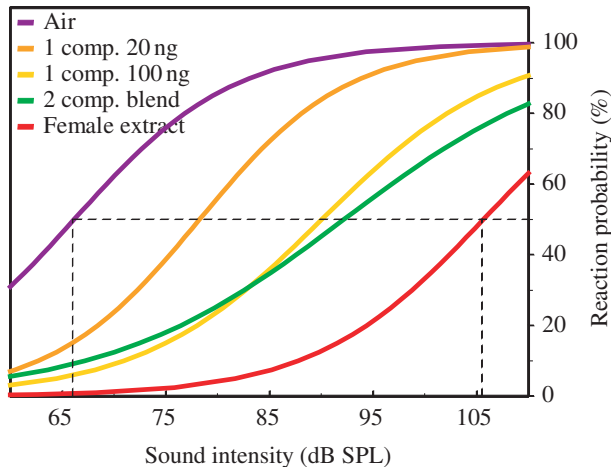


Fig. 3. Sound intensity response curves created by logistic fit of the behavioural data shown in Fig. 2 ( $20 < N < 25$  for all intensity/odour combinations). Significance level and McFadden rho2 are as follows: Air ( $P < 0.001$ ,  $\rho_2 = 0.300$ ), 1 component (comp.) (Z9E11-14:OAc) 20 ng ( $P < 0.001$ ,  $\rho_2 = 0.242$ ), 1 comp. 100 ng ( $P < 0.001$ ,  $\rho_2 = 0.192$ ), 2 comp. blend (Z9E11-14:OAc and Z9E12-14:OAc) ( $P < 0.001$ ,  $\rho_2 = 0.123$ ), Female extract ( $P < 0.01$ ,  $\rho_2 = 0.158$ ). The vertical broken lines indicate the 50% threshold sound intensity for air and female extract.

approaching a low amount of odour (20 ng) than a higher dose (100 ng) (Table 1). At 100 ng the threshold for eliciting walking stop in 50% of the cases was 12 dB higher than at 20 ng pheromone (Fig. 3, Table 1). Also, the pheromone quality (one component < blend of two components < female extract) affected the response to sound significantly (Fig. 3 and Table 1). Female extract increases the threshold for behavioural response compared with stimulation with pure air or synthetic pheromone. At the 50% probability level the increase is approximately 40 dB (Fig. 3). At 102 dB SPL 75% of the moths stopped when stimulated with the two-component blend (Z9E11-14:OAc and Z9E12-14:OAc) while only 40% reacted when the pheromone was female extract (Fig. 2). The difference in acoustic threshold between this blend and the female extract was 16 dB at the 50% reaction probability level.

The time the moth remained motionless following sound stimulation was also affected by pheromone stimulation (Fig. 4). Among the tested odours the median response duration at 102 dB SPL was longest, 16 s, for 20 ng of the major pheromone component. The shortest median response duration, 2 s, was observed for female extract. Without pheromones, the response duration was significantly longer (100 s), than with pheromones (2–16 s) ( $P < 0.01$ , Kruskal-Wallis followed by nonparametric Tukey test).

### Discussion

Here we demonstrate, that olfactory cues can modulate behavioural responses elicited by acoustic cues and acoustic stimuli can modulate olfactory mediated behaviour. Our results indicate that the influence of the two sensory modalities depend

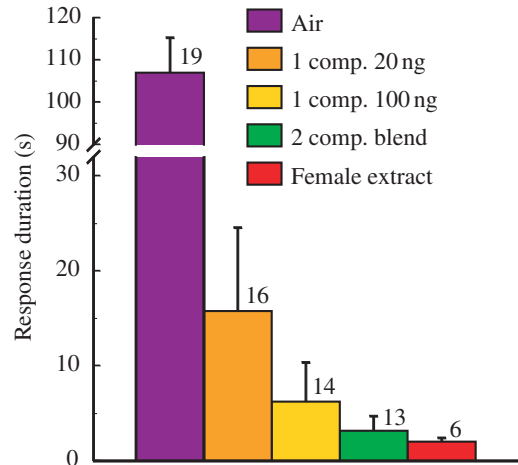


Fig. 4. Response duration at 102 dB SPL. A moth stopped walking after sound stimulus for a significantly longer period of time in air than in pheromone. The differences in response duration between different pheromone stimuli were not significant. The  $N$ -values are given above each bar. Values are expressed as means + S.E.M.

on their relative stimulus intensities, such that higher amount and better quality of pheromone is more likely to block the response to artificial bat sound, and that increased sound pressure is more likely to elicit responses even in the presence of pheromones. Increasing sound pressure corresponds to a bat closing in on the moth and, thus, signalling an increased predation risk. The results showing that the response to acoustic stimuli decreases as the quality or quantity of the pheromone signal increases indicate that the moth accepts a higher predation risk when the chance of a mating is higher. Hence, female sex pheromones can dramatically reduce the attention to predator sounds in male moths to such a degree that the reaction distance to the bat is considerably reduced. Presumably, the higher degree of risk-taking is counteracted by a benefit from a higher reproductive fitness success by increasing the probability of mating (Magnhagen, 1991). In a natural context, this means that moths far away from a pheromone releasing conspecific will pay more attention to the predator signal than if they are close to a mating opportunity. If the bat is close (high sound pressure) the moth's mate-finding behaviour is more likely to be disrupted. Therefore, we suggest that the response to signals from one modality depends on the behavioural context determined by another modality. A moth receiving conflicting sensory input will react based on a cost-benefit analysis including trade-off calculations between the relative importance of the two signals. These results are consistent with the findings by Acharya and McNeil (1998), because at all pheromone concentrations the proportion of male moths responding to sound increased with increasing sound intensity.

We used a walking-stop response as an indicator of an acoustic response. Presumably, this behaviour would protect the moth from predation by gleaning bats (Werner, 1981; Arlettaz et al., 2001; Schnitzler and Kalko, 2001; Greenfield

and Baker, 2003), and may correlate to the last chance manoeuvres of moths hunted on the wing by aerial hawking bats. The advantage of the walking bioassay is that it allows for a precise estimate of response thresholds to acoustic stimuli both with and without odour stimulation, which would be very difficult to obtain for a flying moth. However, a flying moth may be more vulnerable to bats than a walking moth and, therefore, may pay relatively more attention to the predator by exhibiting lower response thresholds to sound. Therefore, it is not straightforward to extrapolate our data obtained from the walking bioassay to flying moths, although several recent experiments indicate similar results for moth in flight tunnels. Svensson et al. (2004) found that both noctuid and pyralid moths respond less to sound when flying towards a high quality or quantity of sex pheromone than when attracted to pheromone of minor quality or quantity. No fundamental differences have been found in the attraction behaviour to pheromones between walking and flying moths (Anderson et al., 2003). In addition, threshold intensities for cessation of walking (Fig. 2) (Werner, 1981) are in the same range as for cessation of flight in moths in tethered flight (Skals and Surlykke, 2000; Zhantiev, 1988) without pheromone exposure. The evidence therefore indicates that the general findings in this study may also apply to flying moths.

The consequence for a male moth ignoring acoustic signals when engaged in mate finding is that his reaction range to the predator signals is reduced considerably. We used acoustic threshold data for the 50% reaction level from Fig. 3 to calculate approximate reaction distances for moths exposed to bats emitting cries at 30 kHz with an intensity of 90 dB peSPL at 1 m and assuming spherical spreading loss and atmospheric attenuation of  $0.7 \text{ dB m}^{-1}$  (Lawrence and Simmons, 1982). These calculations show that a 40 dB reduction in auditory threshold corresponds to reduction in reaction distance from approximately 8 m to  $<0.2$  m, which leaves the moth a very short time in which to react. These calculations represent a best-case scenario for the moths, since we used sound frequencies in the optimal hearing range (30 kHz) to establish the behavioural threshold. The situation for the moth in the field may be worse, if it encounters bats using frequencies outside the moth's best frequency range of hearing and perhaps temporal parameters that are more difficult to detect as they approach their target (Fullard et al., 2003). Thus male moths may appear functionally deaf when they are exposed to a strong pheromone signal. Rydell et al. (2000) found that flying male moths (*Gynaephora groenlandica*) reacted to ultrasound even at close range to the female, which at first sight may seem to contradict our findings. However, these moths were exposed to a very intense stimulus from an electronic dog whistle (110 dB SPL at 1 m corresponding to 20 dB higher than the maximum output of our loudspeaker at 30 cm). Hence if we extrapolate the curve for female extract in Fig. 3 by 20 dB then the expected response probability will be close to 100%. Therefore our results are in good accordance flying moths in the field as

observed by Rydell et al. (2000). The two-component synthetic pheromone blend used in this study, was previously found to attract moths very effectively in the field (Kehat and Dunkelblum, 1993). However, we found that female extract was significantly better than the two-component blend in blocking the acoustic response. Hence, our results strongly indicate that the two-component blend is not optimal, and that female extract contains more hitherto unidentified compounds. In future studies the reaction to ultrasound in an experimental set-up as used here may serve as a sensitive behavioural assay to evaluate pheromone quality in moths.

It is well known from mammalian psychophysics that input from one sensory modality might alter the processing of information in another (e.g. Stein et al., 1993; for review see Calvert et al., 2004). This is especially well studied in humans where many cases have shown how information from various sensory systems (e.g. acoustic, visual, somatosensory and proprioceptive) is integrated (Driver and Spence, 1998). When animals receive concurrent sensory information they may attend to one stimulus by ignoring other stimuli, which is referred to as stimulus-selective attention (Dukas, 2002) or crossmodal selective attention (Spence et al., 2000). The moth model as presented here may be used for studying crossmodal selective attention. However, in our experiments, we cannot tell if the moths actually choose not to react to the sound stimulus when the pheromone stimulus is on (endogenous controlled attention) or whether the acoustic system is turned off by the olfactory system by for example inhibition at higher level, which may be interpreted as exogenous selective attention (see Spence and Driver, 2004).

It has been suggested that acoustic stimuli are dominant over attractive odours (Agee, 1988). However, our results do not support sensory dominance or that the sensory modalities are organised in a hierarchical structure. Instead we suggest that integration of information from different sensory modalities requires complex dynamic comparisons by higher-order neurons, which implies that behavioural thresholds are dynamic and depend on the behavioural context. Therefore behavioural thresholds estimated under unimodal conditions in the lab may be far from the relevant thresholds in the animal's habitat. Studies on the trade-off between acoustic and chemical stimuli in the moth, offers an interesting model for studies on how dynamic integration of bimodal sensory information is processed by the CNS.

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