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Multimodal signals enhance decision making in foraging bumble-bees

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Multimodal signals are common in nature and have recently attracted considerable attention. Despite this interest, their function is not well understood. We test the hypothesis that multimodal signals improve decision making in receivers by influencing the speed and the accuracy of their decisions. We trained bumble-bees (*Bombus impatiens*) to discriminate between artificial flowers that differed either in one modality, visual (specifically, shape) or olfactory, or in two modalities, visual plus olfactory. Bees trained on multimodal flowers learned the rewarding flowers faster than those trained on flowers that differed only in the visual modality and, in extinction trials, visited the previously rewarded flowers at a higher rate than bees trained on unimodal flowers. Overall, bees showed a speed–accuracy trade-off; bees that made slower decisions achieved higher accuracy levels. Foraging on multimodal flowers did not affect the slope of the speed–accuracy relationship, but resulted in a higher intercept, indicating that multimodal signals were associated with consistently higher accuracy across range of decision speeds. Our results suggest that bees make more effective decisions when flowers signal in more than one modality, and confirm the importance of studying signal components together rather than separately.

Keywords: *Bombus*; bumble-bees; decision making; multimodal signals; plant–pollinator interactions; speed–accuracy trade-off

1. INTRODUCTION

Many signals in nature are multimodal, consisting of components from two or more sensory modalities (Guilford & Dawkins 1991; Rowe & Guilford 1999). Yet the evolutionary advantages of multimodal signals are not well understood. Adding another signal component, especially from another modality, may be costly for a sender due to increased energetic constraints (Partan & Marler 2005), or may be disadvantageous in situations where the signal attracts an unintended receiver or a predator (Roberts *et al.* 2007). Given these possible costs, the question of why organisms use multimodal signals remains largely unanswered. We explore the decision-making benefits of multimodal signals to the signal receivers, with particular attention on how multimodality affects the speed–accuracy trade-off experienced by receivers.

From a receiver's point of view, both the accuracy of choices and the time taken to reach a decision have fitness consequences. However, in many cases, animals cannot maximize the accuracy and the speed of their decisions simultaneously. A negative correlation between accuracy and speed of decisions, known as the speed–accuracy trade-off, was first shown in humans (Garrett 1922). Recently, several studies have documented that animals, including bumble-bees (Chittka *et al.* 2003), honeybees (Passino & Seeley 2006), ants (Franks *et al.* 2003), rats (Uchida & Mainen 2003; Uchida *et al.* 2006) and mice (Abraham *et al.* 2004; Rinberg *et al.* 2006; Slotnick 2007), experience the same trade-off. For example, when forced to make swift decisions between similar odours, mice become less accurate (Uchida & Mainen 2003).

The speed–accuracy trade-off is affected by the difficulty of a decision, therefore, any influence of multimodal signals on decision making would be reflected in the speed and the accuracy of decisions. Difficult tasks, such as discriminating between two very similar stimuli, result in slower and relatively less accurate decisions (Roitman & Shadlen 2002; Kiani *et al.* 2006; Palmer *et al.* 2006), while easy decisions may not even result in a trade-off (Dyer & Chittka 2004). In many cases, animals can change the amount of time they allocate to making a decision depending on context, thus also changing their accuracy and their position on the speed–accuracy trade-off line. For example, if accuracy is favoured over speed, ants reduce the speed of their decisions (Franks *et al.* 2003), and if errors are costly, bumble-bees invest more time in making a decision (Chittka *et al.* 2003). This dependence on context and task difficulty makes it crucial to analyse both the speed and the accuracy of decisions when addressing whether adding another modality to a signal improves signal detection and/or processing.

In this study, we investigate how multimodal signals influence both the speed and the accuracy of decision making. Because signal properties have a direct influence on how well signals can be detected, processed and learned, sending information in multiple modalities may aid in signal receivers decision making (Rowe 1999; Hebets & Papaj 2005; Partan & Marler 2005). An appropriate system for addressing this issue is the plant–pollinator interaction. Flowers attract pollinators with visual, olfactory and somatosensory modalities. While several studies have investigated how the presence of a second modality influences foraging behaviour of bumble-bees (Odell *et al.* 1999; Kunze & Gumbert 2001), butterflies (Omura & Honda 2005) and hawkmoths (Raguso & Willis 2005;
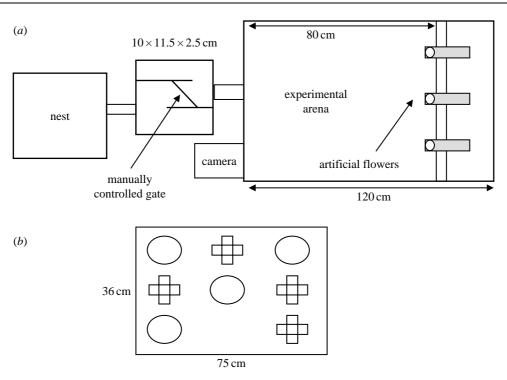
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Figure 1. (*a*) View of the nest, manual gate, experimental arena and the array from above. (*b*) Example experimental array with the differently shaped flowers.

Balkenius *et al.* 2006), the role of multimodal signals in the speed and the accuracy of foraging decisions has not been considered.

We studied the speed–accuracy trade-off in bumble-bees (*Bombus impatiens*) by training them on artificial flowers that differed in shape and/or odour. Bumble-bees experience speed–accuracy trade-off while foraging for nectar under laboratory conditions (Chittka *et al.* 2003; Dyer & Chittka 2004). If the multimodal signals provide decision-making benefits, we expect that bees foraging on flowers that differ in two modalities will make faster and/or more accurate decisions than bees foraging on flowers that differ in one modality. We also addressed how the speed and the accuracy of decisions influences foraging success by estimating the rate at which bumble-bees visit rewarding flowers when the flowers differ in two modalities versus one modality.

2. MATERIAL AND METHODS

(a) *Experimental set-up*
Bombus impatiens colonies were obtained from Koppert Biological Systems, MI, USA. Colony nest-boxes were connected to a Plexiglas 'buffer box' ($10 \times 11.5 \times 2.5$ cm) featuring a manual gate that allowed bees to be released individually into the experimental arena. The plywood $120 \times 75 \times 36$ cm arena (figure 1) had transparent acrylic panels on top. Except during training and testing, bees foraged on 'Beehappy' solution (Koppert Biological Systems) and were provided with frozen pollen daily. We used three colonies.

We constructed artificial flowers by drilling 200 µl circular wells into clear acrylic rods (US Plastic) inserted into a poster board (75×36 cm) placed vertically in the experimental arena, 80 cm from the entrance. We covered the poster board with green paper (54N) from the HKS-N paper series (Hostmann–Steinberg K+E Druckfarben, H. Schmincke & Co., Erkrath, Germany). In the pre-training phase, bees

visited the 30% sucrose solution filled wells ad libitum. Bees making regular visits were individually marked with enamel paints on their thorax.

During training, flowers that were cut in circles or crosses (6 cm in diameter, HKS-N yellow (3N) paper) were used. These shapes were fit around the acrylic rods, placed behind transparent sheets of acetate and inserted in the poster board. The acetate sheets were cleaned regularly with 30% alcohol to eliminate olfactory cues left by foraging bees. We used a vertical flower array because bees can discriminate between shapes presented on a vertical plane but not on a horizontal plane (Lehrer & Campan 2005). In treatments with odours, we used 2 µl of peppermint or clove essential oils (Aura Cacia, Frontier Natural Products, Norway) diluted in 1 : 100 pentane and located the odours in Eppendorf centrifuge tubes (1.5 ml) placed behind each flower. Placing the odours behind the flowers that were perforated with small holes decreased the risk of odours filling the whole arena. We ventilated the arena by removing the acrylic panels between the trials. Since odour cues brought into the nest by returning foragers can affect responses of other bees (Dornhaus & Chittka 1999), this design also reduced the possibility of foragers carrying odours back to the hive after contacting odour solutions.

(b) *Training*
Bees were trained on one of the following discrimination learning tasks: (i) shapes (cross and circle), (ii) odours (peppermint and clove), and (iii) shapes + odours (peppermint and cross plus clove and circle). The flower array included four rewarding and four non-rewarding flowers. In all trials, only one type of flower (e.g. circle) was rewarding with 30% sucrose, and the other (e.g. cross) was non-rewarding with water. At least 10 bees were trained in each experiment, and no bee was used in more than one experiment. We switched the rewarding and non-rewarding stimuli after training five bees in each category.

Marked bees were released individually into the arena. A trial began when a bee entered the arena and continued until the bee returned to the nest. During training, bees visited flowers freely as we recorded their visits. If the bee in the arena did not visit flowers within 10 min, the trial was terminated and it was returned to the nest until its next trial. We cleaned and rearranged the flowers between the trials so that not more than two rewarding flowers were in the same location in consecutive trials for each bee. To proceed to the testing phase, a bee had to complete a minimum of three trials and achieve 80% correct choices in their last 10 visits.

(c) Testing
Bees were tested immediately after achieving 80% accuracy. During testing, all flowers were non-rewarding. We video-taped testing sessions with a Sony DCR-HC48 Mini DV Camcorder stationed outside the arena. If a bee did not immediately visit the arena after the last training trial, we tested the bee the following day. In those cases, the tests were preceded by a training trial, since bumble-bee foraging skills may decline overnight (Keasar *et al.* 1996; but see Chittka 1998).

Video recordings were made at 30 frames s^{-1} and analysed frame by frame. We quantified the following variables: (i) time of landing, defined as first contact with the flower, (ii) time of take-off, defined by the last leg leaving the flower, (iii) whether 'searching', defined by facing the flower array between visits to subsequent flowers, and (iv) whether visits were 'correct' (to cues rewarded in training) or 'wrong' (to cues not rewarded in training). Decision time for each visit was estimated as the time difference between leaving a flower and landing on another flower.

(d) Data analysis
The effect of flower treatment on the number of visits to reach the 80% criterion was analysed by ANOVA. We also used ANOVA to test whether modality influenced flower visitation rate, calculated per bee as the number of correct visits divided by the total amount of time spent searching for flowers during test trials. The effect of treatment on speed and accuracy was analysed by ANCOVA in which the percentage of correct choices (accuracy) was regressed against average decision time (inverse of speed). Although this method allows us to analyse the trade-off across individuals in a group, the trade-off exists within individuals (Chittka *et al.* 2003) as well. We used *post hoc* Tukey's analysis to construct contrasts between treatments, and all analyses were carried out with JMP Statistical Software (JMP v. 6. SAS Institute, Inc., Cary, NC, 1989–2005).

3. RESULTS
(a) Learning
We trained 44 bees, of which 33 ($n=10$, 12 and 11 for visual, olfactory and multimodal, respectively) met our learning criterion (80% correct choices in the last 10 visits). Figure 2 shows a typical learning curve estimated by logistic regression. The mean number of visits required to meet the learning criterion did not depend on whether crosses or circles were rewarding (ANOVA, $R^2=0.001$, $F_{1,29}=0.04$, $p=0.85$). Although not quite statistically significant ($R^2=0.18$, $F_{1,29}=4.20$, $p=0.054$), bumble-bees learned clove more slowly than peppermint (mean$\pm$s.d.: 23 ± 10
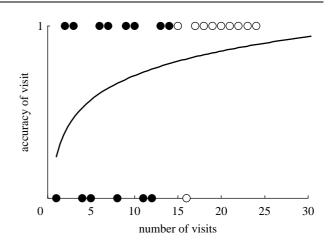
Figure 2. Example of learning curves. Each data point in the graphs represents a visit, and the last 10 visits are shown with open circles. Accuracy is represented in the *y*-axis by either 0 (incorrect) or 1 (correct) visit.
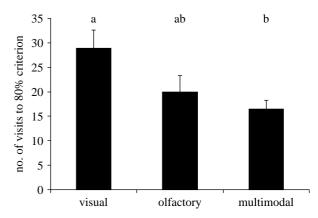

Figure 3. Mean number of visits ($\pm$s.e.) required to learn flowers in each treatment group. Values with the same letter are not statistically different from each other. Sample size areas are as follows: $n=10$, 12 and 11 for visual, olfactory and multimodal, respectively.

and 14 ± 2 visits, respectively). The number of visits to reach learning criterion differed across treatments ($R^2=0.24$, $F_{2,28}=4.52$, $p=0.019$; figure 3). A *post hoc* Tukey test revealed a significant difference between visual and multimodal treatments (mean$\pm$s.d.: 28.9 ± 11 and 16 ± 5.4 for visual and multimodal treatments, respectively). The olfactory treatment (mean$\pm$s.d.: 20 ± 10.8) was not statistically different from either of the other treatments.

(b) Flower visitation rate
Out of the 33 bees that met our learning criterion, we tested 31 ($n=8$, 12 and 11 for visual, olfactory and multimodal treatments, respectively) in extinction trials during which no flowers were rewarding. In those trials, modality treatment had a significant effect on flower visitation rate, calculated per bee as the number of correct visits divided by the total amount of time spent searching (ANCOVA, $R^2=0.42$, $F_{2,26}=9.46$, $p=0.0008$; figure 4). Multimodal flowers were visited at significantly higher rates than unimodal flowers (Tukey $p<0.05$). There was no statistical difference in flower visitation rates between visual and olfactory treatments (Tukey $p>0.05$).
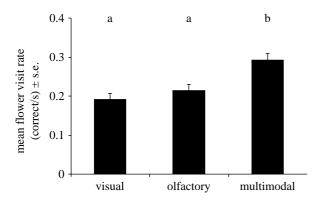
Figure 4. Mean flower visit rates (visits per second$\pm$s.e.), defined as the correct visits/total decision time. Values with the same letter are not statistically different from each other.
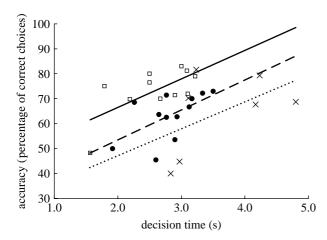

Figure 5. Decision speed and accuracy during testing. Decision time correlates with the accuracy. Crosses and the dotted line represent the visual treatment. Filled circles and the dashed line represent the olfactory treatment. Open squares and the solid line represent the multimodal treatment. Sample sizes are as follows: $n=8$, 12 and 11 for visual, olfactory and multimodal, respectively.

(c) *Speed and accuracy*

Across all testing trials, the mean percentage of correct choices was 67.26%$\pm$11.58 (mean$\pm$s.d.), while mean decision time was 2.93 s$\pm$0.67 (mean$\pm$s.d.).

Accuracy (percentage of correct visits) and mean decision time for each bee were entered into an ANCOVA model. There was no heterogeneity among slopes for different treatments ($R^2=0.43$, $F_{5,25}=0.10$, $p=0.90$), so the interaction term (treatment$\times$decision speed) was removed from the model and the ANCOVA was performed again. There was a strong treatment effect as reflected in a difference among y-intercepts ($R^2=0.42$, $F_{3,27}=6.56$, $p=0.001$; figure 5), suggesting statistical differences in accuracy of choices across treatments ($F_{2,27}=7.79$, $p=0.002$; figure 6a). Bees trained on multimodal flowers had the highest mean accuracy (73%$\pm$10), measured by percentage of choices on correct flowers, followed by bees trained on shape (64%$\pm$15) and odours (64%$\pm$9). The multimodal treatment yielded the highest y-intercept (44%), followed by olfactory (33%) and visual (29%) treatments. A Tukey test showed no significant differences between y-intercepts of the visual and olfactory groups, whereas the y-intercept of the
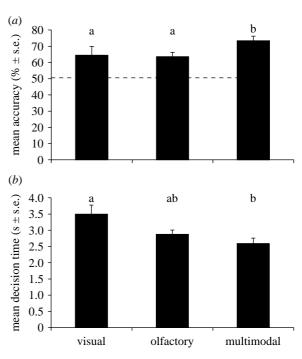
Figure 6. (a) Mean accuracy (%$\pm$s.e.) of bees during testing trials. Dashed line at 50% indicates random choice. (b) Mean decision times during testing trials (s$\pm$s.e.). Sample sizes are as follows: $n=8$, 12 and 11 for visual, olfactory and multimodal, respectively. Values with the same letter are not statistically different from each other.

multimodal treatment differed both from the visual and the olfactory treatments (Tukey $p<0.05$).

Speed of decisions was also influenced by treatment ($R^2=0.29$, $F_{2,28}=5.62$, $p=0.008$; figure 6b). Bees trained on shapes made slower decisions (3.49 s$\pm$0.79, mean$\pm$s.d.) than that on multimodal flowers (2.59 s$\pm$0.55). However, there were no statistically significant differences between decision times for olfactory (2.87 s$\pm$0.45) versus multimodal flowers, or for visual versus olfactory flowers (Tukey $p>0.05$).

In the olfactory and the multimodal treatments, the accuracy of choices was significantly positively correlated with the decision times (Pearson's correlation $r=0.6$, $t=2.37$, $p=0.04$ and $r=0.66$, $t=2.66$, $p=0.03$ for olfactory and multimodal treatments, respectively). However, the correlation between accuracy and decision time in the shape group, though also positive, was not significant ($r=0.48$, $t=1.32$, $p=0.23$).

4. DISCUSSION

Bees visited the correct flowers at a higher rate when flowers differed both in the visual and the olfactory modalities, suggesting that multimodal signalling by flowers is of potential fitness benefit to one or both members of the plant–pollinator interaction. Overall, a speed–accuracy trade-off between individuals in the same treatment was observed: bees that spent more time making decisions were more accurate. Bees in the multimodal treatment had higher accuracy than those in the visual- or olfactory-only treatment. However, the relative increase in accuracy on the multimodal flowers was not accompanied by a decrease in decision speed, suggesting that although choosing between multimodal flowers was still challenging

enough to produce a trade-off, it was easier than choosing between flowers that differ only in visual or olfactory cues.

Although multimodal cues were not advantageous over olfactory cues during the learning phase, multimodal flowers resulted in more accurate decisions than olfactory flowers once they were learned, suggesting that one way multimodal signals may benefit signal receivers is by increasing the accuracy of their response at a given decision speed. Even if adding a second modality to a signal is costly (Partan & Marler 2005), enhanced detection and/or discrimination by receivers may benefit the senders, if the fitness of the sender is influenced by the receiver's response. Both the decision speed and the accuracy influence foraging behaviour of bees (Chittka & Spaethe 2007), and multimodal signals may provide fitness benefits for flowers if faster visits and more accurate choices result in higher likelihood of pollen transfer.

How does a signal with two components improve accuracy at any given decision time? There are a number of possible mechanisms, some depending on how signals are transmitted and some relating to how effectively signals are processed. In terms of signal transmission, one modality may be effective at a distance while the other may be effective at close range, an explanation known as the efficacy trade-off hypothesis (Hebets & Papaj 2005). For example, olfactory cues might be detected from a longer distance than visual cues (Kunze & Gumbert 2001; but see Odell *et al.* 1999), while visual cues may be more reliable for pinpointing signal senders (Raguso 2001). Alternatively, signal components from different modalities may be interacting with each other, first to alert, and then to orient the receiver to a target. This mechanism has been shown in courtship displays in wolf spiders (Hebets 2005). Although our results are consistent with the notion of inter-signal interactions (Hebets 2005; Hebets & Papaj 2005), carefully designed future studies are needed to distinguish between the efficacy and inter-signal explanations.

Another possible mechanism occurs strictly at the level of signal processing, after both types of stimuli have been detected. Reaction time to a stimulus is routinely used to study signal processing (Abraham *et al.* 2004). If two components of a signal are processed separately (serial processing), the expected decision times would correspond to the sum of the processing times required for two signals, because the animals would need to process the components sequentially. If the two components are processed simultaneously (parallel processing), the expected decision times would correspond to the maximum of the processing times required for either stimulus (Thomas 1996). Although our knowledge of multimodal signal processing and integration in invertebrates is scant (Hölldobler 1999), there is some evidence of parallel processing of multimodal signals in insects (Müller *et al.* 2002). If accuracy is a function of the rate at which sensory information is processed (cf. Abraham *et al.* 2004), multimodal signals may benefit receivers if overall processing rate is improved by parallel processing.

An important implication of a parallel processing explanation for multimodal signals is that the same benefit to the receiver cannot be achieved equally well within a single sensory modality. We lack the information necessary to address this implication. Several authors have noted that multimodal signals are processed fundamentally differently than unimodal signals due to multisensory integration, in which input from one modality influences processing of others (Stein 1998; Calvert 2001; Small 2004); therefore, it would be useful to conduct a follow-up study to ours, in which bees are presented either with multimodal flowers or with flowers that differ in shape and another visual dimension (e.g. colour or pattern). If the provision of information in multiple modalities, rather than the mere provision of more information, is key for decision-making benefits, then unimodal complex signals would not be expected to result in decisions that are as accurate and/or as rapid as multimodal signals.

This work demonstrates that complex signals consisting of stimuli in multiple sensory modalities can improve the accuracy of a receiver's response. If such effects are widespread, then constraints on receiver cognitive abilities may be one of the driving forces behind the evolution of multimodal signals. It would therefore be interesting to know whether the benefit of multimodal signalling reported here pertains to other interactions where multimodal signalling is common, including predator–prey (in particular, aposematic displays), male–male and male–female interactions. In all cases, the assessment of the function of multimodal signals may benefit from consideration of speed–accuracy trade-offs experienced by signal receivers.

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