RESEARCH ARTICLE

Can bees see at a glance?
Vivek Nityananda1, Peter Skorupski* and Lars Chittka

ABSTRACT
Primates can analyse visual scenes extremely rapidly, making accurate decisions for presentation times of only 20 ms. We asked whether bumblebees, despite having potentially more limited processing power, could similarly detect and discriminate visual patterns presented for durations of 100 ms or less. Bumblebees detected stimuli and discriminated between differently oriented and coloured stimuli when presented as briefly as 25 ms but failed to identify ecologically relevant shapes (predatory spiders on flowers) even when presented for 100 ms. This suggests an important difference between primate and insect visual processing, so that while primates can capture entire visual scenes ‘at a glance’, insects might have to rely on continuous online sampling of the world around them, using a process of active vision, which requires longer integration times.

KEY WORDS: Active vision, Bombus terrestris, Insect vision, Rapid feature extraction, Visual processing

INTRODUCTION
Do bigger brains confer advanced sensory or behavioural capabilities? Larger brains could provide increased representational capacity of objects and greater capabilities for parallel processing (Chittka and Skorupski, 2011). Conversely, animals with smaller brains might rely on continuous, active sampling of their environment. Insect brains are orders of magnitude smaller than human brains. A typical bee brain contains fewer than a million neurons (Menzel and Giurfa, 2001; Wittböfft, 1967) compared with an estimated 85 billion neurons for the human brain (Azevedo et al., 2009; Roth and Dicke, 2005; Williams and Herrup, 1988). Bees are nonetheless capable of remarkable feats of visuo-cognitive behaviour. They can not only learn to associate coloured or black and white patterns with rewards (Menzel and Lieke, 1983; Wehner, 1967; Zhang et al., 1992) but also use visual features to categorise natural scenes, as well as novel visual objects based on shared properties (Zhang et al., 2004). They can learn simple relational ‘rules’ (e.g. above/below-ness) between stimuli regardless of basic stimulus properties (Avargués-Weber et al., 2011). They have also been shown to learn to choose different targets in different contexts (Dale et al., 2005; Lotto and Chittka, 2005) and to use colour cues in different spatial contexts to navigate (Zhang et al., 1996). They can learn sequences of movements in response to visual stimuli (Collett et al., 1993) and their behaviour when navigating along series of identical landmarks conforms to the basic criteria of numerosity (Chittka and Geiger, 1995; Dacke and Srinivasan, 2008). Bees thus display the capability to perform several visual behaviours that are traditionally thought to be the domain of much larger brained animals, including humans.

Much of the research on comparative animal cognition has focused, perhaps too narrowly, on identifying shared capacities between humans and other animals (Shettleworth, 2001; Penn et al., 2008). Undoubtedly, such research has led to remarkable successes in placing human cognition into an evolutionary framework, and also dismissed the myth that large brains automatically convey superior cognition (Emery and Clayton, 2004; Giurfa, 2013). However, an obsession with animal ‘cleverness’ and a focus on human-like capacities of animals might obscure significant differences in cognition between species, and indeed unique cognitive adaptations and constraints (Bolhuis and Wynne, 2009; Chittka et al., 2012; de Waal and Ferrari, 2010).

One important difference between primate and insect visual cognition might relate to visual search. Humans are capable of discriminating between scenes at a glance (Kirchner and Thorpe, 2006) and using parallel search (Wolfe, 2000). Honeybees, by contrast, may be restricted to serial visual search (Spaethe et al., 2006). Target identification is substantially slowed by increasing the number of distractors in a scene, even when target and distractors differ only in one stimulus dimension such as colour (Spaethe et al., 2006). In humans, visual search would be parallel in such a situation, with the target ‘popping out’ rapidly, independent of the number of distractors (Wolfe, 2000). It has therefore been suggested that insects might use ‘active vision’ to compensate for their lack of parallel processing power, actively scanning the scene for key targets rather than using a rapid snapshot (Chittka and Skorupski, 2011; Collett et al., 2013). Indeed, flying bees make systematic side to side scanning movements (‘peering’) during target approach (Boedeker and Hemmi, 2010; Ings et al., 2012), which stabilises translational image flow by cancelling out rotational motion of the retinal image (Dittmar et al., 2010). Such scanning in the translational plane could theoretically increase spatial resolution, if bees correlated self-generated scanning movements with the resulting image translation. This would, however, lead to increased image acquisition time as well as greatly impaired visual discrimination in situations where eye movements (meaning, for a bee, head and whole-body movements) are not possible. In fact, it appears that immobilised bees are visually impaired: although associative olfactory learning has been extensively studied in tethered bees, attempts to condition tethered bees to visual stimuli have only been successful for large-field, coarse colour discrimination (Nigebrügge et al., 2009).

Honeybees can extract at least simple visual features (grating orientation) at presentation times of as little as 2 ms (Srinivasan et al., 1993). In addition, a recent study indicates that bumblebee visual search is not affected by the number of distractors and that they are capable of parallel search (Morawetz and Spaethe, 2012). Simulations of different search mechanisms suggest that these different search strategies might reflect different ecological environments of...
honeybees and bumblebees (Bukovac et al., 2013). Thus bumblebees, at least, might be able to recognize some targets rapidly when distractors are also present in a scene. No study has, however, tested whether bees can recognize complex targets ‘at a glance’ as well as simple visual features. We explored whether bumblebees, Bombus terrestris (Linnaeus 1758), can distinguish both simple visual features and complex, ecologically relevant shapes at a glance, when presented for increasingly brief durations (<100 ms) and therefore without the possibility to scan the visual scene.

RESULTS

Bees foraged in an arena with one wall containing an LCD computer screen (Fig. 1A). Bees were pre-trained to collect droplets of sucrose solution from landing platforms positioned in front of the screen, three on each side. Stimuli were presented on the screen directly behind the platforms.

Bees were trained individually on one of five tasks. Correct choices led to a reward of sucrose solution while incorrect choices were penalised with aversive saturated quinine hemisulphate solution in all tasks. In every task, stimuli were presented continuously in the first condition. In three subsequent conditions, stimuli were presented for durations of 100, 50 and 25 ms. After training on each condition of each task, we tested bees on the same task and condition with distilled water presented across all stimuli behind three randomly chosen landing platforms with no stimulus behind the other platforms.

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Discrimination of stimulus edge orientation

Here, bees had to discriminate between rectangular bars oriented at an angle of 45 deg from otherwise identical bars at an angle of −45 deg (Fig. 1C). All 10 tested bees also learnt to discriminate between differently oriented bars when presented either statically or for 100 ms (Fig. 2A). Nine of the 10 bees successfully distinguished the stimuli when presented for 50 ms and seven of these remaining nine bees (78%) also discriminated the stimuli when presented for 25 ms (Fig. 2A). The mean number of choices taken by the successful bees to learn the task to criterion was near 20 for static and 100 ms presentation but increased slightly to near 22 for very short presentation times (Fig. 3). The number of choices taken to learn the discrimination did not, however, differ across durations of presentation (Friedman test, $\chi^2=3$, d.f.=3, $P=0.39$). Bees chose the correct stimuli significantly above chance in the test bouts for all stimulus durations ($t$-test, all $P<0.05$; the mean ± s.d. proportion of correct choices for static presentation and durations of 100, 50 and 25 ms was 0.73±0.13, 0.68±0.05, 0.61±0.07 and 0.64±0.12, respectively; Fig. 2B). The differences between the proportions of correct choices across durations of presentation were not significant (repeated-measures ANOVA, $F_{3,18}=1.42$, $P=0.27$). Presentation duration thus had no significant effect on either the time taken to learn the task or the accuracy of performance on this task.

Fig. 1. Experimental set-up and stimuli. (A) Bumblebee colony box linked by a Perspex tunnel to the training arena, containing a computer monitor inserted into the wall opposite the arena entrance, shown in black. Expanded view of the monitor depicts the screen and six Perspex feeding platforms. Inset shows a bee feeding on a platform with the rewarding stimulus behind it. (B–F) Representation of the stimuli displayed on the screen during the tasks: (B) task 1: stimulus detection; (C) task 2: discrimination of edge orientation; (D) task 3: colour discrimination: yellow and blue; (E) task 4: colour discrimination: yellow and orange; (F) task 5: complex shape discrimination: spiders and circles.
In theory, bees might have acquired visual information even in a 25 ms window by rapidly scanning the visual stimulus. Visual inspection of the bees’ flight movements revealed that bees typically inspected the screen from a distance of between 2 and 5 cm, and initiated their landing manoeuvre from this range of distance. Given that the length of the stimulus in the first two tasks was 5 cm, this suggests that the bees were not recognising it by actively scanning the entire length but perceived it rapidly while remaining relatively stationary: at the distance at which they made their decisions (typically within 5 cm of the screen), they would need to scan an angle of 38.2 deg or more subtended by the stimulus within the 25 ms presentation time. Using rotational movements, this would require an angular velocity of around 1528 deg s⁻¹, far higher than has previously been observed in bees: 410–480 deg s⁻¹ (Srinivasan et al., 1996). The bees could not therefore have scanned the stimulus with rotational movements. Thus, while they were indeed extracting visual features, they were apparently doing so independently of movement.

**Colour discrimination**

We tested bees on their ability to discriminate between circles of differing colours: blue versus yellow and yellow versus orange (Fig. 1D,E). All 10 bees tested learnt to discriminate between blue and yellow circles across all durations of presentation (Fig. 2A). The mean number of choices taken to learn this task was 20 across all durations of presentation, again indicating that this was a relatively easy task for the bees to learn. Bees also chose correct stimuli significantly above chance only in the tests with stimuli presented statically or for 100 ms (Fig. 2A). When the same stimuli were presented for 50 and 25 ms, the proportion of the bees that learnt to discriminate them successfully was only 0.6 and 0.1, respectively (Fig. 2A). The mean number of choices taken by successful bees to learn this task was 20 for static and 100 ms presentation times, but increased to 23 for the 50 ms presentation time (Fig. 3). This difference was significant across presentation durations (Friedman test, \(\chi^2=6\), d.f.=2, \(P=0.05\)). In this difficult colour discrimination task, bees also chose correct stimuli significantly above chance only in the tests with stimuli presented statically or for 100 ms (\(t\)-test, all \(t>5.5\), \(N=9\), \(P<0.001\)) but not for stimuli presented for 50 ms (\(t\)-test, \(t=1.2\), \(N=9\), \(P=0.27\)). The mean ± s.d. proportion of correct choices for static presentation and presentation durations of 100, 50 and 25 ms was 0.90±0.11, 0.72±0.20, 0.67±0.04 and 0.62±0.11, respectively (Fig. 2B). The proportion of correct choices differed significantly across different durations of presentation (repeated-measures ANOVA, \(F_{3,27}=9.47\), \(P<0.01\))

Thus, while the experience needed to reach criterion did not vary between stimulus durations, accuracy levels deteriorated with shorter presentation times for this simple colour discrimination task.

When tested for discrimination of similar colours, all bees distinguished between yellow and orange circles presented either statically or for 100 ms (Fig. 2A). When the same stimuli were presented for 50 and 25 ms, the proportion of the bees that learnt to discriminate them successfully was only 0.6 and 0.1, respectively (Fig. 2A). The mean number of choices taken by successful bees to learn this task was 20 for static and 100 ms presentation times, but increased to 23 for the 50 ms presentation time (Fig. 3). This difference was significant across presentation durations (Friedman test, \(\chi^2=6\), d.f.=2, \(P=0.05\)). In this difficult colour discrimination task, bees also chose correct stimuli significantly above chance only in the tests with stimuli presented statically or for 100 ms (\(t\)-test, all \(t>5.5\), \(N=9\), \(P<0.001\)) but not for stimuli presented for 50 ms (\(t\)-test, \(t=1.2\), \(N=9\), \(P=0.27\)). The mean ± s.d. proportion of correct choices for static presentation and presentation durations of 100, 50 and 25 ms was 0.90±0.11, 0.72±0.20, 0.67±0.04 and 0.62±0.11, respectively (Fig. 2B). The proportion of correct choices differed significantly across different durations of presentation (repeated-measures ANOVA, \(F_{3,27}=9.47\), \(P<0.01\))

Thus, presentation duration affected both the time taken to learn this task and the accuracy of performance on the task.
Complex pattern detection and discrimination

We tested bees on their ability to integrate information about edges and colour differences by requiring them to discriminate between a biologically relevant stimulus, the silhouette of a yellow crab spider (an ambush predator hunting for pollinators on flowers), and yellow circles, both presented against an orange background. To ensure that the bees learnt this task when stimuli were presented statically, we first pre-trained the bees in a ‘robotic spider’ arena (Ings and Chittka, 2008) where we could simulate predatory attacks if bees approached the spider shapes.

All bees learnt to discriminate yellow spider shapes from yellow circles when presented statically. The mean (±s.d.) number of choices taken to learn the task (27±7.5) was higher than for all the tasks previously described (Fig. 3). All but one bee, however, failed to learn the task when stimuli were presented for 100 ms and none of the bees completed the task with a stimulus presentation duration of 50 ms (Fig. 2A). Bees also chose correct stimuli significantly above chance only in the static presentation condition (t-test, \( t=4.172, N=10, P<0.003; \) mean ± s.d. proportion of correct choices: 0.63±0.10; Fig. 2B). However, for the presentation duration of 100 ms, performance (0.53±0.26 correct choices; Fig. 2B) did not exceed chance levels (t-test, \( t=0.339, N=10, P=0.74 \)). The proportion of correct choices for presentation durations of 50 ms was even lower (0.42; Fig. 2B). Thus, bees could only successfully learn the biologically relevant pattern identification task in the static condition and failed when these complex stimuli were presented for short durations. Control experiments ascertained that bees trained on static stimuli were able to generalise to stimuli presented for 50 ms or above in tests: bees trained on static stimuli chose the correct stimulus significantly above chance in bouts with a presentation duration of 50 ms or above (t-tests, all \( t>2.5, P<0.05 \)) but not for presentation durations of 25 ms (t-test, \( t=0.3, P=0.75 \)). The failure of bees at non-static tasks is thus not explained by their training to static stimuli.

Comparison of performance between tasks

The number of choices taken to learn the tasks in the static condition differed significantly across tasks (Kruskal–Wallis test, \( H_{5}=32.8, P<0.001 \)). Post hoc tests revealed that this difference was entirely due to significant differences between the number of choices taken to learn the pattern discrimination task and all the other tasks (Mann–Whitney U-tests, \( U=10, P<0.001 \)) indicating that this task was more difficult. The number of choices taken to learn the tasks, however, is not an indication of how long bees take to perform the tasks in a given trial and their accuracy should depend on presentation duration of a particular task regardless of task difficulty. Indeed, our results show that bees varied significantly in the proportion of correct choices during the test across tasks and presentation durations (general linear model; task, duration, task×duration; \( F=4.45, 5.64, 2.51; P=0.002, 0.001, 0.009 \)). There was a significant effect of both task (\( P=0.002 \)) and stimulus presentation duration (\( P=0.001 \)) as well as a significant interaction effect between the two (\( P=0.009 \)), which is not explained solely by differing performance on the final task. Interestingly, except for the simple colour discrimination task, bees also took more choices to learn the tasks as the duration of presentation decreased (Fig. 3). Although not all the differences were significant, there was a clear trend for the rate at which learning performance decreased (as measured by the number of choices) being different for each of the tasks (Fig. 3). Thus, the bees had longer learning periods as well as performing worse because of specific combinations of tasks and presentation durations.

DISCUSSION

Our results demonstrate that bumblebees can detect and discriminate between elementary visual features, even when presented as briefly as 25 ms, but not between similar colours and complex patterns. Experiments with humans and monkeys have shown that they are capable of ultra-rapid categorisation of natural versus manmade scenes even when scenes are presented for durations of only 6–20 ms (Bacon-Macé et al., 2007; Girard et al., 2008; Kirchner and Thorpe, 2006; Thorpe et al., 1996).

The fact that bees are capable of extracting simple features at this time scale, but seem to fail to analyse complex scenes, suggests an important difference between primate and bee visual processing; the higher computational power of bigger brains could enable the analysis of whole visual scenes at a glance, whereas insects might require longer integration times for any but the most simple visual identification tasks. Extended integration times might involve continuous ‘online’ sampling of the world around them. Such active vision, where animals sometimes follow repeated paths to memorise contingencies between own movements and object views for target recognition has been observed in a number of insect species (Collett et al., 2013; Collett and Zeil, 1996), and also in birds (Dawkins and Woodington, 2000; Gall and Fernández-Juricic, 2010). Active vision has also been suggested to play a role in colour perception (Skorupski and Chittka, 2011). As ommatidia contain a variety of different sets of colour receptor types (Spaethe and Briscoe, 2005; Wakakuwa et al., 2005), a single-coloured object might be perceived as consisting of multiple pixels each with different colours – unless insects move their eyes over the object to generate a temporal integration (Skorupski and Chittka, 2011). This could explain discrimination of similar colours being limited to presentation durations above 50 ms. Complex pattern discrimination is further limited to durations above 100 ms.

The rapid categorisation of the kind seen in humans and monkeys might rely on pre-attentive feed-forward processing of low level features (Joubert et al., 2009; Walker et al., 2008). Extraction of image components at a glance in primates implies a time course that seems compatible with only a single sweep of sensory information along the known delays of the visual system (VanRullen and Thorpe, 2002). A single sensory snapshot might be less useful for a miniature brain, such as that of an insect, simply because there is less capacity for off-line processing (processing involving significant neural delays). In active perception, the time taken to build up a picture of the world will depend on how much can be sampled at once, and in a miniature brain there may be less capacity to process a single ‘sensory snapshot’ and consequently a greater dependence on continuous online sampling of the scene. It is therefore conceivable that reduced representational capacity may lead to fundamentally different perceptual sampling strategies in large and small brains (Chittka and Skorupski, 2011).

Our hypothesis is that more than a static retinal image (a glance) is required for visual pattern recognition in bees (unlike in humans). We suspect that active scanning is required, which depends upon systematic translations of the retinal image generated by the bee’s own exploratory body movements. The fast photoreceptors of the bee’s visual system would allow for efficient analysis of such image translations (Skorupski and Chittka, 2010), but the time for perceptual analysis would be significantly longer, incorporating motor loops and the actual durations of exploratory movements. This might explain why significantly longer exposure times are required for pattern recognition in bees.

Further evidence for this suggestion comes from the observation that visual learning is severely impeded in tethered bees.
Bees entered a training arena (60×70×40 cm length×width×height) via a 45 cm long Perspex tunnel (Fig. 1A). The entrance to the arena was blocked by a square of cardboard with only a 10 mm gap, approximately equal to the width of a bumblebee’s body. This ensured that the bees were facing the back wall of the arena when they exited from the entrance tunnel into the arena. The stimuli were not visible from within the tunnel but became visible immediately after the bees emerged from the tunnel into the flight arena. At the entry point, stimuli (at their widest dimension; shapes described below) subtended >5.8 deg when viewed from the entrance tunnel into the arena. The stimuli were independently randomised between left and right for each pair of landing positions from the landing balcony, thus experiencing a simulated spider attack (Ings and Chittka, 2008). Four rewarding flowers and four flowers with spiders were presented. Bees were free to revisit flowers but rewards were only replenished if the bee had visited all other correct flowers or after 2 min, whichever was sooner. The positions of the rewarding and unrewarding flowers were changed between bouts according to a previously generated random order. Bees were trained until they had chosen the correct stimulus significantly above chance in the last 20 choices in at least two different bouts. In order to ensure that bees remembered the stimuli across different experimental conditions, the bees were pre-trained on this set-up before every training condition.

Training
During training, each bout contained three possible correct choices and three incorrect choices. Correct stimuli had a 50 μl drop of 50% (v/v) sucrose solution on the feeding posts in front of the stimuli, while posts in front of incorrect stimuli had a 50 μl drop of 0.12% (saturated) quinine hemisulphate solution on them, which bees find aversive (Chittka et al., 2003). The positions of rewarding or unrewarding stimuli were independently randomised between left and right for each pair of landing platforms in the bottom, middle and top rows for every training bout. A training bout lasted 4 min or until the bee returned to the colony, whichever occurred sooner. Each training condition consisted of around five to 12 training bouts (with two to six choices per bout) and lasted until
the bee made significantly more correct choices (14 choices out of 20; binomial probability test, N=20, k=14; exact binomial probability P=0.04) out of the last 20. As our criterion was measured in a window of 20 choices, bees could make several choices before reaching the criterion in this window and the total number of choices made thus served as a measure of how long bees took to learn the task. If the criterion was not achieved after 50 choices had been made, the condition was terminated.

During the non-static training conditions, stimuli were presented multiple times for the specific duration with a blank interval of 500–800 ms in between presentations. The exact duration of the blank interval was chosen by randomly picking a number between 500 and 800 ms. Presenting the stimuli multiple times but with a long enough blank duration in between presentations ensured that the bee would not miss seeing the stimuli but at the same time would be unable to temporally integrate over multiple presentations of the stimuli. The irregularity of the duration of the interval also ensured that the bee would be unable to learn a rhythm of presentation.

Stimuli
Stimulus presence/absence detection
The stimuli in the detection task consisted of three yellow (RGB scale: 255 255 0) rectangular bars (5 mm wide by 50 mm long) at an angle of 45 deg against a black background (Fig. 1B). Table 1 gives the coordinates of the yellow in bee colour space as well as those of the other colours used in the following tasks.

Discrimination of edge orientation
Three bars as described above were presented along with three similar bars oriented at an angle of –45 deg. The bars were interrupted in the centre by a black square (5×5 mm) centred on the feeding platform so that bees would not learn features of only that region during training (Fig. 1C).

Easy colour discrimination task
Bees had to discriminate between three blue (RGB scale: 0 0 255) circles (3.5 cm diameter) and three yellow (RGB scale: 255 255 0) circles of the same dimensions (Fig. 1D). The distance between the colour loci corresponding to these two lights in the bee colour hexagon is 0.67 (where 1 is the distance between the centre of the hexagon and any of its vertices). This is a very large colour distance indicating easy discriminability for bees (Dyer and Chittka, 2004).

Difficult colour discrimination task
Bees had to discriminate between three yellow (RGB scale: 255 255 0) circles (3.5 cm diameter) and three orange (RGB scale: 255 200 0) circles of the same dimensions as in the easy colour discrimination task (Fig. 1E). The colour hexagon distance between the colour loci of the yellow and orange computer-generated lights is 0.07, i.e. one-tenth of the distance between yellow and blue. The colour distance indicates that these colours are distinguishable for bees, but only with some difficulty (Dyer and Chittka, 2004).

Table 1. Colour parameters of computer-generated stimuli

<table>
<thead>
<tr>
<th></th>
<th>Yellow</th>
<th>Orange</th>
<th>Blue</th>
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<tbody>
<tr>
<td>E_x</td>
<td>0.16</td>
<td>0.15</td>
<td>0.2</td>
</tr>
<tr>
<td>E_y</td>
<td>0.36</td>
<td>0.34</td>
<td>0.72</td>
</tr>
<tr>
<td>E_z</td>
<td>0.77</td>
<td>0.69</td>
<td>0.36</td>
</tr>
<tr>
<td>X</td>
<td>0.53</td>
<td>0.47</td>
<td>0.14</td>
</tr>
<tr>
<td>Y</td>
<td>-0.11</td>
<td>-0.08</td>
<td>0.44</td>
</tr>
</tbody>
</table>

Receptor excitations of a bumblebee’s UV (E_x), blue (E_y) and green (E_z) receptors for the three colours used in the experiments, as well as X Y Z coordinates in the bee’s colour space, the colour hexagon. The quantum output of the LCD Samsung SyncMaster 2233RZ monitor for the yellow, orange and blue stimuli was measured from 300 to 700 nm, and converted into receptor excitations, E, using spectral sensitivity functions of UV, blue and green receptors of the bumblebee Bombus terrestris (Skorupski et al., 2007). These were converted into colour loci in the colour hexagon following procedures described elsewhere (Chittka, 1992).

Complex pattern recognition task
Bees were presented with three yellow (RGB scale: 255 255 0) silhouettes of a crab spider set in an orange (RGB scale: 255 200 0) square (side: 3.5 cm) and three yellow (RGB scale: 255 255 0) circles of the same area (diameter: 1.7 cm) also set in an orange (RGB scale: 255 200 0) square (side: 3.5 cm) (Fig. IF).

Testing
At the end of each training condition, the bees were subjected to a test bout. During this bout, all feeding platforms had a 50 µl drop of distilled water on them regardless of the stimulus presented behind them on the screen. The bouts lasted 4 min or until the bee returned to the colony, whichever occurred first. The choices of the bees, including repeated choices, were noted but only the proportion of choices in the first 2 min of the bout was calculated as a measure of the bee performance post-learning to guard against bees potentially choosing randomly in the later part of the bout once they realised that the feeding platforms only had water droplets on them. The proportion of correct choices made during tests for different tasks and presentation durations was tested for normality using a Kolmogorov–Smirnov test and compared with chance values (0.5) using a one-sample t-test.

Control experiment
To ascertain that bees trained on static stimuli could generalise to briefly presented stimuli in a test, we pre-trained 10 bees as above and then trained them to recognise a yellow (RGB scale: 255 255 0) circle of diameter 5.5 cm as a rewarding stimulus. Training procedures were similar to the stimulus detection task above. We then tested the bees with only distilled water presented on the platforms and the stimuli presented behind three feeding platforms for 500, 100, 50 and 25 ms in separate test bouts. Each of the test bouts was followed by three static training bouts so that the bees were re-trained to stimuli in between different tests. The sequence of test bouts with different presentation durations was randomised and the choices of the bees in each test were noted.

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Competing interests
The authors declare no competing financial interests.

Author contributions
V.N., P.S. and L.C. designed the experiments, V.N. conducted the experiments and analysed the data, V.N., L.C. and P.S. wrote the manuscript.

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