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RESEARCH ARTICLE

Dynamic multimodal interactions in navigating wood ants: what do path details tell us about cue integration?

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ABSTRACT

Ants are expert navigators, using multimodal information to navigate successfully. Here, we present the results of systematic studies of multimodal cue use in navigating wood ants, *Formica rufa*. Ants learnt to navigate to a feeder that was defined by an olfactory cue (O), visual cue (V) and airflow (A) presented together. When the feeder, olfactory cue and airflow were all placed at the centre of the visual cue ($\mathrm{VOA_{Centre}}$), ants did not directly approach the learnt feeder when either the olfactory or visual cue was removed. This confirms that some form of cue binding has taken place. However, in a visually simpler task with the feeder located at the edge of the visual cue ($\mathrm{VOA_{Edge}}$), ants still approached the feeder directly when individual cue components were removed. Hence, cue binding is flexible and depends on the navigational context. In general, cues act additively in determining the ants' path accuracy, i.e. the use of multiple cues increased navigation performance. Moreover, across different training conditions, we saw different motor patterns in response to different sensory cues. For instance, ants had more sinuous paths with more turns when they followed an odour plume but did not have any visual cues. Having visual information together with the odour enhanced performance and therefore positively impacted on plume following. Interestingly, path characteristics of ants from the different multimodal groups ($\mathrm{VOA_{Centre}}$ versus $\mathrm{VOA_{Edge}}$) were different, suggesting that the observed flexibility in cue binding may be a result of ants' movement characteristics.

KEY WORDS: Multimodal navigation, Sensory cues, Cue integration, *Formica rufa*, Vision, Olfaction

INTRODUCTION

Ants are remarkable navigators, with their efficiency coming from the coordinated implementation of a set of navigational strategies (Wehner, 2003; Collett et al., 2013; Knaden and Graham, 2016). Some ant species utilise their social nature and develop pheromone trail networks to recruit ants between the nest and reliable food locations (Czaczkes et al., 2015), while others forage individually and rely on path integration (PI) to explore the environment while being safely connected to the nest (Heinze et al., 2018; Collett, 2019). As these solitary forager ants become familiar with a terrain, visual and olfactory information from the environment is learnt to enable them to navigate along routes (visual: Collett et al., 1992; Kohler and Wehner, 2005; Graham and Collett, 2006; Wystrach et al., 2011; Mangan and Webb, 2012; olfactory: Buehlmann et al., 2015) and locate the nest (visual: Wehner and Räber, 1979; Wehner et al., 1996; Narendra et al., 2007; olfactory: Steck, 2012) or a familiar feeder (visual: Durier et al., 2003; Collett et al., 2014; Buehlmann et al., 2016; olfactory: Huber and Knaden, 2018). We have a relatively good understanding of the behaviour of ants when undertaking visual navigation (Zeil, 2012; Collett et al., 2013; Graham and Philippides, 2017). However, we have only a few behavioural descriptions of olfactory navigation as a personal navigation strategy rather than in a social, pheromone trail context (Steck et al., 2009; Buehlmann et al., 2015; Huber and Knaden, 2018), and we know even less about ant behaviour during multimodal cue use in navigation.

Multiple navigational strategies often provide redundant information in experienced ants, e.g. path integration and visual guidance can influence behaviour simultaneously (Narendra, 2007; Reid et al., 2011; Collett, 2012; Legge et al., 2014), resulting in intermediate headings when directional cues are experimentally set in conflict (reviewed in Wehner et al., 2016). This means that navigational information is processed by separate guidance systems with convergence at the level of the behavioural output (Cruse and Wehner, 2011; Hoinville and Wehner, 2018). Furthermore, detailed path analyses from another set of experiments have shown that PI also interacts with other modalities by generating different movements for home vectors of different lengths, hence facilitating the learning and use of visual or olfactory cues at important locations (Buehlmann et al., 2018).

Another way of studying multimodal navigation is to look at learning rates for ants that are trained to find an important location as defined by multimodal cues. In one such experiment, *Cataglyphis* desert ants were trained to locate their nest using visual cues, olfactory cues or both visual and olfactory cues together (Steck et al., 2011). One result was that these ants learnt bimodal cues (visual and olfactory cues presented together) much faster than a single cue, with another finding being that bimodal landmarks were first learnt as their individual components but later stored as a holistic unit. Hence, although initially the presence of a second sensory cue enhanced the learning performance of a unimodal cue, the components of the bimodal cue were fused together after several training trials and the ants' performance decreased when either of the components was presented alone (Steck et al., 2011).

At the coarse scale, behavioural outputs of multimodal interactions are adaptive and produce ecologically relevant behaviour (e.g. Buehlmann et al., 2011; Cheng et al., 2012). We also know that at a fine motor scale, different sensory modalities require different patterns of movement (Graham and Collett, 2002; Lent et al., 2010; Buehlmann et al., 2014; Wystrach et al., 2014). In recent years, we have gained a good understanding of visual navigational mechanisms by studying path details of wood ants in the lab (Judd and Collett, 1998; Graham and Collett, 2002; Lent et al., 2010, 2013; Buehlmann et al., 2016). Using that well-established system, we here investigated the path details of wood

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ants guided by both multimodal and unimodal cues. Firstly, we asked whether navigation is improved when using multimodal cues. Secondly, we investigated whether ants use different or more complex movement patterns in the presence of multimodal cues. Thirdly, we examined whether the cue binding previously described (Steck et al., 2011) can be explained by the ants' path characteristics and under what circumstances some behavioural flexibility is retained.

MATERIALS AND METHODS

Ants

Experiments were performed with laboratory kept wood ants *Formica rufa* Linnaeus 1761, collected in Broadstone Warren, East Sussex, UK. Ants were kept in the laboratory under a 12 h light:12 h dark cycle and a constant temperature of 25–27°C. They were fed *ad libitum* with sucrose and dead crickets. During the experiments, food was limited to a minimum to increase their foraging motivation, but they had access to water all the time.

Experimental setup

General experimental procedures followed those described previously (Buehlmann et al., 2016). Individually marked ant foragers were taken from the nest and released in the centre of a circular platform (120 cm in diameter) that was surrounded by a cylinder (diameter 3 m, height 1.8 m) with white walls. Ants learnt to find a drop of sucrose on a microscope slide that was located 45 cm away from the centre. The feeder location was defined by multiple cues which varied between the different experiments (Fig. 1). The following cues were used: visual cue (V, black rectangle placed on the edge of the platform, 60 cm wide and 30 cm high, 60 deg wide and 31 deg high from platform centre), airflow [A, constant air flow produced by a Tetra APS 50 aquarium pump, connected to a 62 cm long silicon tube (outer diameter: 7 mm, inner diameter: 5 mm) with its end placed in the platform at a distance from the centre *r*=50 cm and pointing towards the centre] and an odour not innately attractive to the ants [O, drop of miaroma 100% pure essential pine oil pipetted on a small piece of filter paper (~1 cm×1 cm) placed 1 cm in front of the feeder and renewed every 30 min]. For a visualisation of the odour plume, see Fig. S1. These cues were presented individually (V and A) or in combination (VA, OA and VOA). In the VOA condition, the food was either placed in the centre (Fig. 1A, VOA_{Centre}) or at the left edge (Fig. 1B, VOA_{Edge}) of the visual cue. Each group of ants was trained to only one of the six different experimental conditions (VOA_{Centre}, VOA_{Edge}, VA, OA, V or A). To avoid ants relying on cues other than V, O or A, the cues and the feeder were rotated together to a new position within a 120 deg sector after the end of each training round. Ants performed approximately 10 group training runs (i.e. ants were released in groups of approximately 5) before being trained individually. For individual training, ants were put separately into a 6.5 cm diameter, cylindrical holding chamber in the centre of the platform. The ant was released from the holding chamber by remotely lowering the wall. Once the ant had reached the sucrose slide and started to feed, it was transferred into a feeding box and the next ant was released. The ants were recorded using a tracking video camera (Trackit, SciTrackS GmbH) which provided the ant's position on the platform every 20 ms for analysis. All individual training runs were recorded. After approximately 14 training rounds, ants approached the feeder quite directly and once this moment was reached, tests were introduced in the VOA experiments after every 3 or 4 training trials. In these tests, either the olfactory (O) or visual (V) cue was removed from the multimodal cue combination (O removed in VOA, V+O−A+; V removed in VOA, V−O+A+) and the ants' paths were recorded. Furthermore, conflict tests were introduced in some of the experiments. Here, either OA (for VOA_{Centre} ants) or A (for VA ants) was displaced 20 deg to the left of its familiar position and the ants were recorded as described above.

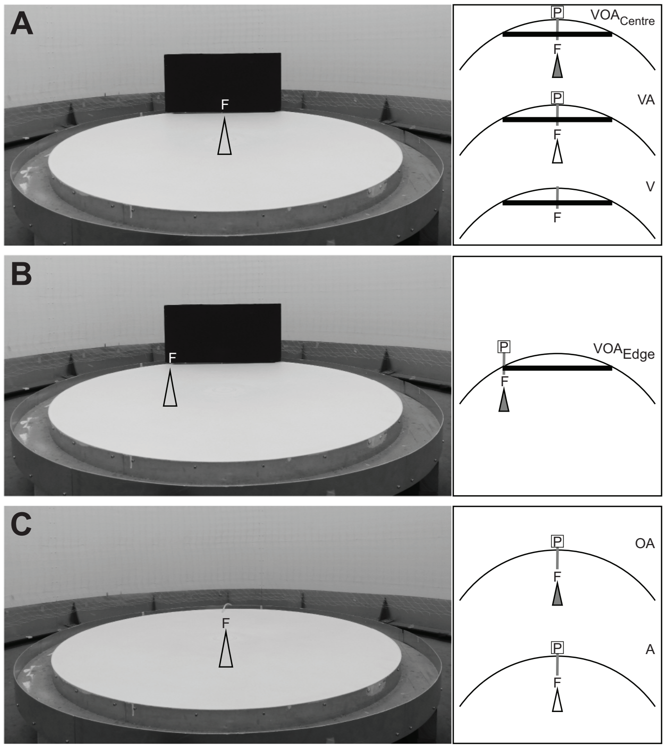

Fig. 1. Experimental configurations. Wood ants, *Formica rufa*, learnt to navigate from the centre of the white platform (120 cm in diameter) to the feeder (F) 45 cm away from the centre in the presence of a visual cue (V, black rectangle), olfactory cue (O, odour plume, filled triangle) and airflow (A, airflow, open triangle) presented either individually (V or A) or together (VOA_{Centre}, VOA_{Edge}, VA or OA). An ant released at the centre of the platform walking towards the edge of the platform reaches the filter paper with the odour at *r*=44 cm from the centre of the platform, the feeder at *r*=45 cm, the centre of the visual cue together with the end of the tube connected to the pump (P) at *r*=50 cm and the edge of the platform at *r*=60 cm. Each group of ants was trained to only one of the six different training conditions. (A) The feeder was placed at the centre of the visual cue with all the cues presented together (VOA_{Centre}), only the visual cue and the airflow (VA) or the visual cue alone (V). (B) The feeder was placed at the left edge of the visual cue where the olfactory cue and airflow were placed (VOA_{Edge}). (C) Feeder location was defined by either the airflow only (A) or the airflow together with the odour (OA).

Data analysis

Training and test paths were analysed from reliable ants that approached the feeder ±10 deg in at least 2/3 of their training trials from training round 14 onwards (at *r*=42 cm).

The performance of naive ants experiencing the cues for the first time and of well-trained ants was determined. In the VOA experiments, tests with either the olfactory (V+O−A+) or visual cue (V−O+A+) removed were also analysed. General walking speed and path straightness (index of straightness=beeline distance/path length) were calculated for paths from *r*=10 cm to *r*=35 cm. Accuracy of path headings were determined at *r*=14, 21, 28, 35 and 42 cm by calculating the difference between the actual heading direction and the beeline to the feeder for each distance. *r*=42 cm had a lower sample size because the tracking system often stopped in the close vicinity of the feeder.

A more detailed path analysis was conducted for all training paths from ants using different cue combinations. Here, paths were taken from the edge of the holding chamber (r=3.25 cm) up to r=35 cm. We took the reliable ants (see above for selection) and focused on their paths when approaching the feeder ±10 deg. Paths were broken into chunks of 15 cm path length, and walking speed and path straightness were calculated for each of these chunks. Means for the first and second halves of the route were calculated for each path and means from all training paths were determined for each ant. Turns along the paths were calculated by finding 1 cm chunks with directions more than ±60 deg away from the target direction. Turns were counted for the first and second half of the route and means over all the training paths were calculated for each ant.

RESULTS

Behaviour of ants during multimodal navigation indicates cue binding

Here, we tested cue binding (as in Steck et al., 2011) in wood ants navigating to a feeder defined by a visual cue (V), olfactory cue (O) and an airflow (A) presented together (VOA training). In the first experiment, the feeder together with the odour and airflow was placed in the centre of the visual cue (see $\mathrm{VOA_{Centre}}$ in Fig. 1A). To accurately approach the feeder location during multimodal navigation, experienced wood ants required all the individual parts of the learnt cue combination. VOA ants that were trained to find a feeder defined by a visual cue (V), olfactory cue (O) and airflow (A) together were subsequently tested with VA or OA only. With either the olfactory (O) or visual (V) cue removed in these tests, well-trained ants were not able to approach the feeder directly (V+O−A+ and V−O+A+ in Fig. 2). Hence, the cues were bound together, and individual parts of the learnt combination alone were no longer sufficient to locate the familiar feeder location directly. The observed decrease in accuracy (Fig. 2D) was coupled with reduced path straightness (Fig. 2F) and walking speed (Fig. 2E). Importantly, both path straightness and walking speed were lower than in ants that were trained with OA or VA only (Mann–Whitney U-tests; index of straightness: V−O+A+ versus OA, $P<0.001$; V+O−A+ versus VA, $P<0.001$; walking speed: V−O+A+ versus OA, $P<0.05$; V+O−A+ versus VA, $P<0.001$).

Apparent cue binding depends on navigational context

We further showed that the apparent cue binding is not a rigid property of multimodal cue learning and depends on the navigational context. Another group of ants was trained with the same set of cues (VOA), but the feeder together with the odour and the airflow were now placed at the edge of the visual cue ($\mathrm{VOA_{Edge}}$; Fig. 1B) to create a simpler navigational task (Harris et al., 2007). In contrast to what we saw before (see Fig. 2), well-trained ants were

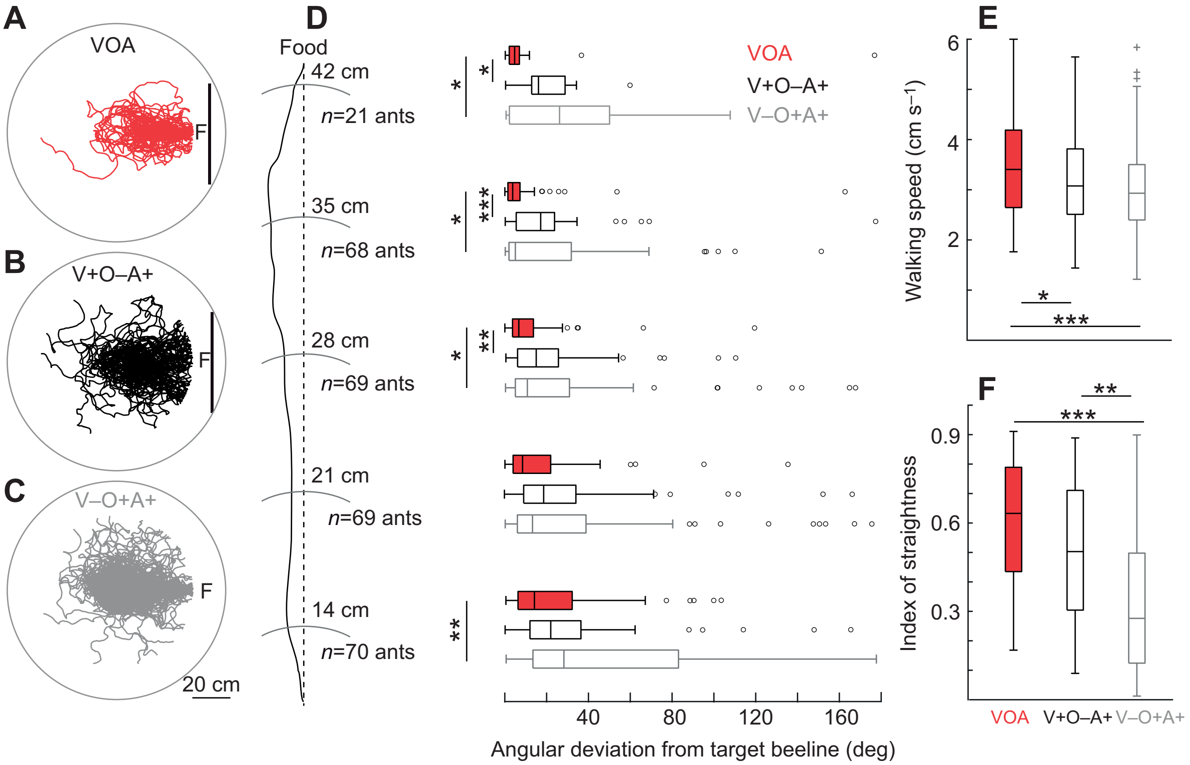

Fig. 2. All individual learnt cues are needed for accurate multimodal navigation. (A) Ants learnt to navigate to a feeder (F) at r=45 cm from the centre of the platform (120 cm in diameter) and defined by a visual cue (V, shown as a black bar), an olfactory cue (O) and an airflow (A). The feeder was placed at the centre of the visual cue ($\mathrm{VOA_{Centre}}$). Trajectories from individual ants are shown as red lines. (B) Ants trained with VOA were tested with the odour removed (V+O−A+). Trajectories from individual ants are shown as black lines. (C) Ants trained with VOA were tested with the visual cue removed (V−O+A+). Trajectories from individual ants are shown as grey lines. (D) Path accuracy was calculated along the paths at r=14, 21, 28, 35 and 42 cm. For each distance, the ants' angular deviation from the beeline to the feeder (shown as a dashed line) is shown as boxplots [median, 25th and 75th percentiles (edges of the boxes) and whiskers for extreme values not considered as outliers (circles)]. The P-values from a Friedman test with Dunn's multiple comparison tests are shown as asterisks for each distance (*$P<0.05$, **$P<0.01$, ***$P<0.001$). For any given distance, ants were only considered if they provided a value for all three conditions. (E) Walking speed for training (VOA) and the two test conditions (V+O−A+ and V−O+A+). n=69 ants. P-values for a Friedman test with Dunn's multiple comparison tests are shown as asterisks. For boxplot and P-value conventions, see D. (F) Path straightness for training and tests. Index of straightness values are between 0 and 1, with 1 indicating a perfectly straight path. n=69 ants. For boxplot and P-value conventions, see D.

still able to accurately approach the learnt feeder location when either the olfactory (O) or visual (V) cue was removed (V+O−A+ and V−O+A+ in Fig. 3). However, when far away, ants were less accurate when the visual cue was removed (Fig. 3D). Furthermore, path straightness was decreased (Fig. 3F) but walking speed was not altered (Fig. 3E).

Cues act additively in determining path accuracy after training

Across the different experimental conditions, we saw some innate attraction to the cues in naive ants (Fig. 4). In all conditions with the visual cue present, ants were directed towards it (Rayleigh test, all $P<0.001$) whilst the odour or the airflow was not attractive to them (Rayleigh test, both $P>0.05$). Training improved the ants' navigational performance and, in general, experienced ants walked more accurately towards the feeder (angular deviation from target beeline at r=35 cm; Wilcoxon matched pairs test, $\mathrm{VOA}_{\mathrm{Centre}}$, $P<0.001$; $\mathrm{VOA}_{\mathrm{Edge}}$, $P<0.001$; VA, $P<0.001$; OA, $P<0.001$; V, $P<0.001$), had straighter paths (index of straightness; Wilcoxon matched pairs test, $\mathrm{VOA}_{\mathrm{Centre}}$, $P>0.05$; $\mathrm{VOA}_{\mathrm{Edge}}$, $P>0.05$; VA, $P<0.001$; OA, $P<0.001$; V, $P<0.001$) and a lower walking speed (walking speed; Wilcoxon matched pairs test, $\mathrm{VOA}_{\mathrm{Centre}}$, $P<0.01$; $\mathrm{VOA}_{\mathrm{Edge}}$, $P<0.01$; VA, $P<0.001$; OA, $P<0.001$; V, $P<0.05$) than naive ants unfamiliar with the experimental environment (for paths and heading direction, see Fig. 4). Comparing the different cue combinations, we found that the proportion of accurate ants increased with the number of navigational cues available (Fig. 5A), i.e. cues act additively in determining path accuracy, although from these results we cannot conclude exactly how each of the cues is weighted.

Different navigational strategies require different path structures

Further path analysis of well-trained ants revealed that the learning of different cues produces differently structured paths. Generally, ants had fewer turns (Fig. 5B), straighter paths (Fig. 5C) and a higher walking speed (Fig. 5D) in the second half of their route to the feeder (Wilcoxon matched-pairs signed-ranked test, all $P<0.001$). When comparing the different conditions, we observed that ants had more sinuous paths and produced more turns when they followed the odour plume but did not have any visual information available (Fig. 5B,C). In contrast, V and $\mathrm{VOA}_{\mathrm{Edge}}$ ants had the straightest paths and the lowest number of turns (see Fig. 5B,C). Interestingly, path characteristics of ants from the two different multimodal groups that had the same set of cues ($\mathrm{VOA}_{\mathrm{Centre}}$ versus $\mathrm{VOA}_{\mathrm{Edge}}$) were different. The $\mathrm{VOA}_{\mathrm{Edge}}$ ants had straight paths and only a few turns, whereas the $\mathrm{VOA}_{\mathrm{Centre}}$ ants had paths somewhere in between those of visually and olfactory guided ants.

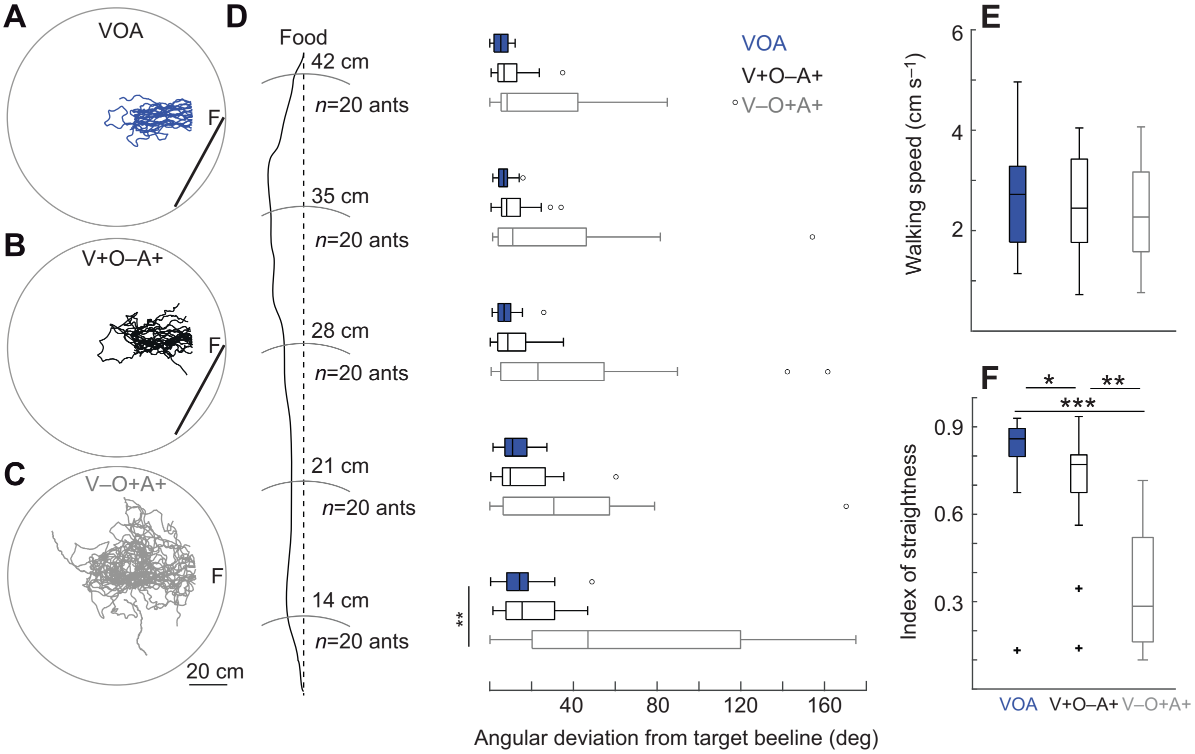

Fig. 3. Multimodal cue binding is flexible. (A) Ants learnt to navigate to a feeder (F) at r=45 cm away from the centre of the platform (120 cm in diameter) and defined by a visual cue (V, shown as a black bar), an olfactory cue (O) and an airflow (A). The feeder was placed at the left edge of the visual cue ($\mathrm{VOA}_{\mathrm{Edge}}$). Trajectories from individual ants are shown as blue lines. (B) Ants trained with VOA were tested with the odour removed (V+O−A+). Trajectories from individual ants are shown as black lines. (C) Ants trained with VOA were tested with the visual cue removed (V−O+A+). Trajectories from individual ants are shown as grey lines. (D) Path accuracy was calculated along the paths at r=14, 21, 28, 35 and 42 cm. For each distance, the ants' angular deviation from the beeline to the feeder (shown as a dashed line) is shown as boxplots [median, 25th and 75th percentiles (edges of the boxes) and whiskers for extreme values not considered as outliers (circles)]. The P-values from a Friedman test with Dunn's multiple comparison tests are shown as asterisks for each distance (*$P<0.05$, **$P<0.01$, ***$P<0.001$). For any given distance, ants were only considered if they provided a value for all three conditions. (E) Walking speed for training (VOA) and the two test conditions (V+O−A+ and V−O+A+). n=20 ants. P-values for a Friedman test with Dunn's multiple comparison tests are shown as asterisks. For boxplot and P-value conventions, see D. (F) Path straightness for training and the tests. Index of straightness values are between 0 and 1, with 1 indicating a perfectly straight path. n=20 ants. For boxplot and P-value conventions, see D.

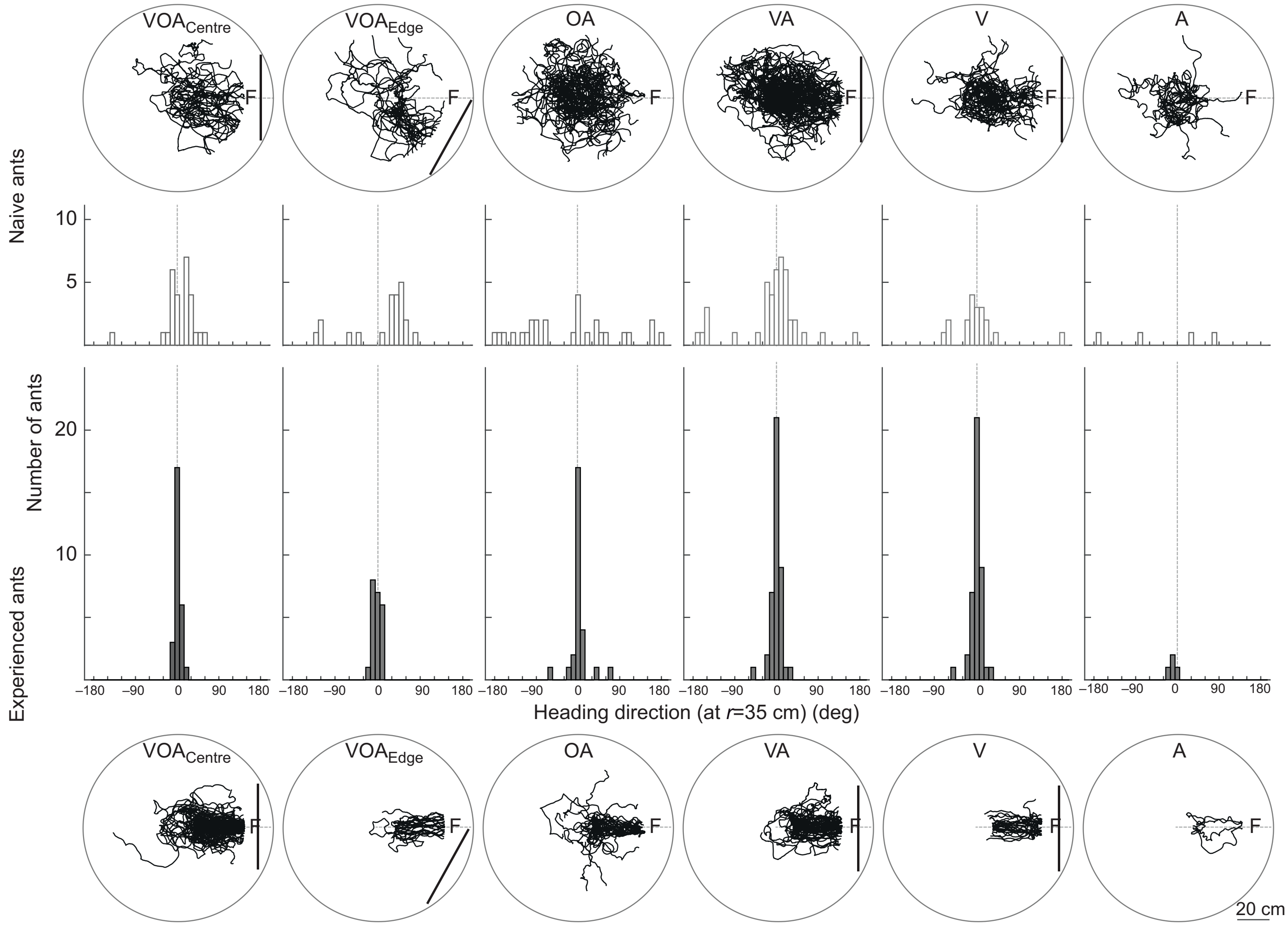

Fig. 4. From innate attraction to stable routes. Naive ants experiencing the cues for the first time (top, $\mathrm{VOA}_{\mathrm{Centre}}$: n=27 ants, $\mathrm{VOA}_{\mathrm{Edge}}$: n=24 ants, OA: n=27 ants, VA: n=44 ants, V: n=20 ants, A: n=5 ants) and well-trained ants after extensive training (bottom, $\mathrm{VOA}_{\mathrm{Centre}}$: n=88 ants, $\mathrm{VOA}_{\mathrm{Edge}}$: n=22 ants, OA: n=32 ants, VA: n=53 ants, V: n=22 ants, A: n=4 ants) are shown for each training condition. Trajectories from individual ants are shown as black lines. The feeder (F) was at r=45 cm from the centre of the platform (120 cm in diameter) and defined by a visual cue (V, shown as a black bar), an olfactory cue (O) and an airflow (A), presented individually or together. Each group of ants was only trained in one of the six conditions. The heading direction at r=35 cm from ants that were recorded in both conditions is shown in the histogram in the middle (bin size: 10 deg). Because naive ants were not recorded for all experimental groups, the sample size for the statistics is lower than in the figure to allow pairwise comparisons. $\mathrm{VOA}_{\mathrm{Centre}}$: n=27 ants, $\mathrm{VOA}_{\mathrm{Edge}}$: n=22 ants, OA: n=27 ants, VA: n=42 ants, V: n=19 ants, A: n=4 ants. For statistics, see Results.

Moreover, $\mathrm{VOA}_{\mathrm{Centre}}$ ants walked significantly faster than most of the other groups while $\mathrm{VOA}_{\mathrm{Edge}}$ ants were in the lower speed range together with the other groups (Fig. 5D).

Functional range of the odour plume is bigger than that of the airflow

In an additional test, ants from the $\mathrm{VOA}_{\mathrm{Centre}}$ training group were tested with the odour and airflow (OA) shifted 20 deg to the left (Fig. 6A,B for the two different conditions). These ants initially headed towards the centre of the visual cue (orange arrow in Fig. 6A,B) and then drifted away from this direction to walk towards the shifted OA (blue arrow in Fig. 6A,B). Hence, visual information was used for navigation when far away and the odour plume became more important further along the route. Ants from the VA training were tested in a similar conflict test, i.e. with airflow (A) displaced by 20 deg, and they also initially walked towards the centre of the visual cue and then shifted away towards the source of the airflow (Fig. 6C). However, the change of direction happened later along the route, suggesting that the spatial scale over which the airflow can be detected, and used as a cue, is smaller than the one for the odour plume.

DISCUSSION

Ants are excellent multimodal navigators (Knaden and Graham, 2016) and here we present information about the details of multimodal cue use in navigating wood ants *Formica rufa*. Controlled lab experiments, with detailed recording of ants' movements, allowed us to investigate a series of questions about the use of unimodal or multimodal cues to find a feeder. We showed that: (i) navigation performance is improved when multiple cues are available; (ii) different navigational strategies require different movement patterns; and (iii) the apparent cue binding previously described by Steck et al. (2011) is flexible and context dependent, with the nature of cue binding potentially being explained by the sensori-motor contingencies of a particular task.

Multimodal sensori-motor integration

Wood ants are excellent navigators, foraging for dead arthropods on the ground and aphid honeydew in trees (Domisch et al., 2016). We know that vision is important for navigation in many ants (Zeil, 2012; Wehner et al., 2014), including wood ants (Rosengren, 1971), but for the detection of food sources an excellent sense of smell is

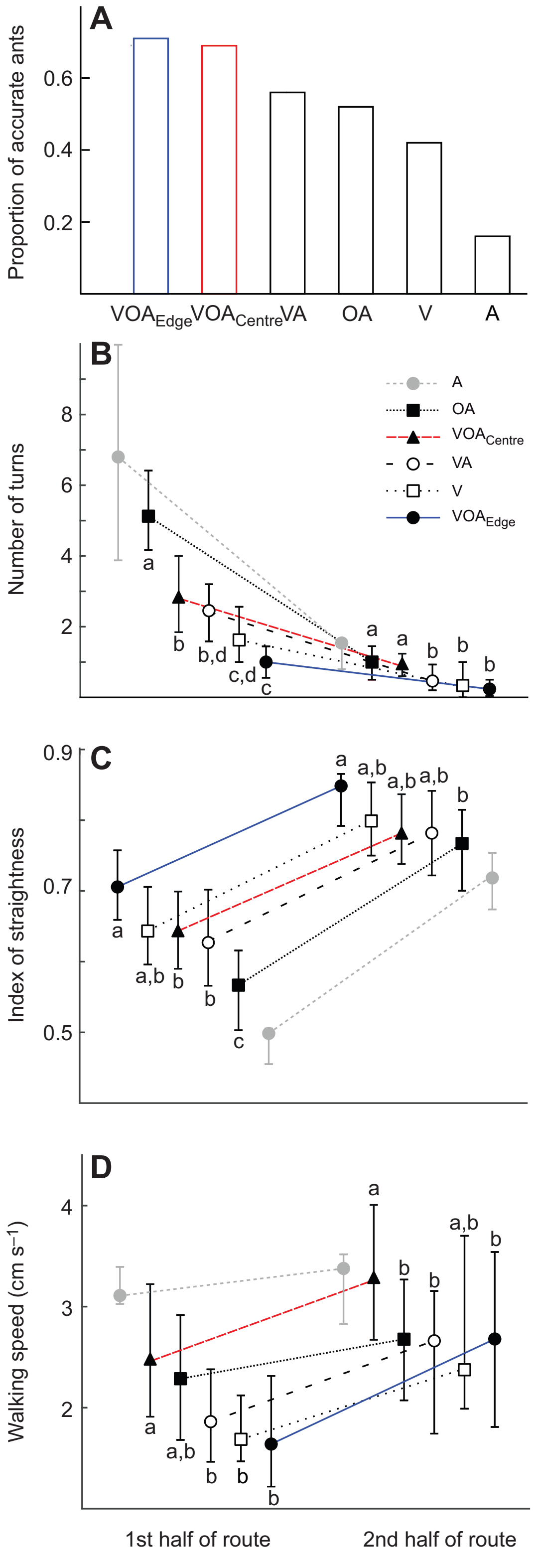

Fig. 5. Path characteristics of ants using different cues for navigation. (A) Proportion of accurate ants for the six different experimental conditions. Accuracy is defined as the proportion of ants that approached the feeder ±10 deg in at least 2/3 of their training trials. VOA_{Edge}: 24 out of 34 ants, VOA_{Centre}: 88 out of 128 ants, VA: 56 out of 100 ants, OA: 32 out of 62 ants, V: 25 out of 60 ants, A: 5 out of 32 ants. (B) Number of turns for the different training conditions for the first and second part of the route to the feeder. Data are plotted as medians with error bars showing the 25th and 75th percentiles. The different training conditions are shown in the key. Lowercase letters indicate significant differences ($P<0.05$) between the different cue combinations (Kruskal–Wallis with Dunn's multiple comparison tests). Groups with the same letters are not significantly different. Ants trained with the airflow (A) are not included in the statistics because of the low sample size. VOA_{Edge}: $n=24$ ants, VOA_{Centre}: $n=88$ ants, VA: $n=56$ ants, OA: $n=32$ ants, V: $n=25$ ants, A: $n=5$ ants. (C) The same as B but for path straightness. (D) The same as B but for walking speed.

also essential (dead arthropods: Buehlmann et al., 2014; aphids: Nault et al., 1976; Lohman et al., 2006; Verheggen et al., 2012). Here, we showed that ants utilised these ecologically relevant sensory modalities to more accurately approach a learnt feeder when multiple cues were available (Fig. 5A) and in general we saw cues acting additively in determining the ants' path accuracy. This demonstration of more efficient paths when multiple cues are available adds to the weight of evidence on the value of multimodal information in a range of behaviours. Multimodal integration has already been shown to enhance performance in perception (van Swinderen and Greenspan, 2003; Goyret et al., 2007; Chow and Frye, 2008; van Breugel and Dickinson, 2014) and learning (Rowe, 2002; Guo and Guo, 2005; Reinhard et al., 2006; Steck et al., 2011) in insects.

We know from fruit flies and other flying insects that visual feedback is needed for stabilizing an upwind flight (Reiser et al., 2004; Budick et al., 2007); thus, plume tracking is enhanced in the presence of visual cues (Fadamiro et al., 1998; Frye et al., 2003) where the cross-modal interaction works because attractive odours enhance the gain of optomotor responses during flight (Chow and Frye, 2008) and with more precise flight, it is easier to track spatial odour gradients (Duistermars and Frye, 2010; Stewart et al., 2010). In a potential similarity, we observed that the use of different cues impacts on the ants' movement patterns (Fig. 5B–D). Across all conditions, experienced ants that accurately approached the learnt feeder always walked slower and straighter than naive ants on their first time experiencing the cues (Fig. 4). This suggests that a lower walking speed is useful for accurate navigation. Indeed, we have seen in a previous study with *Cataglyphis fortis* desert ants that low walking speeds correlate with the learning and use of sensory information (Buehlmann et al., 2018). More detailed path analysis further revealed that navigating wood ants had more sinuous paths with more turns when they followed the odour plume but did not have any visual information available (see OA in Fig. 5B,C) and adding a visual cue to the odour information positively impacted on plume following (see OA versus VOA_{Centre} in Fig. 5B,C) similar to flies (Duistermars and Frye, 2010; Stewart et al., 2010).

Further similarities with flying insects can be highlighted from the conflict tests, where odour and airflow were displaced relative to the visual cue (Fig. 6). When airflow alone was displaced (Fig. 6C), the change of direction happened later along the route than for airflow and odour (Fig. 6A,B), suggesting that the spatial scale over which the airflow can be detected is smaller than for the odour plume. We have learnt from studies in mosquitoes how cues can integrate in a sequential manner. Mosquitoes have developed an elegant mechanism to respond to the multiple cues that indicate a host. The detection of carbon dioxide activates a strong attraction to visual cues which allows mosquitoes to approach a host and then, when closer to the target, they detect thermal cues to pinpoint the host accurately (van Breugel et al., 2015). Hence, different cues can act at different spatial scales.

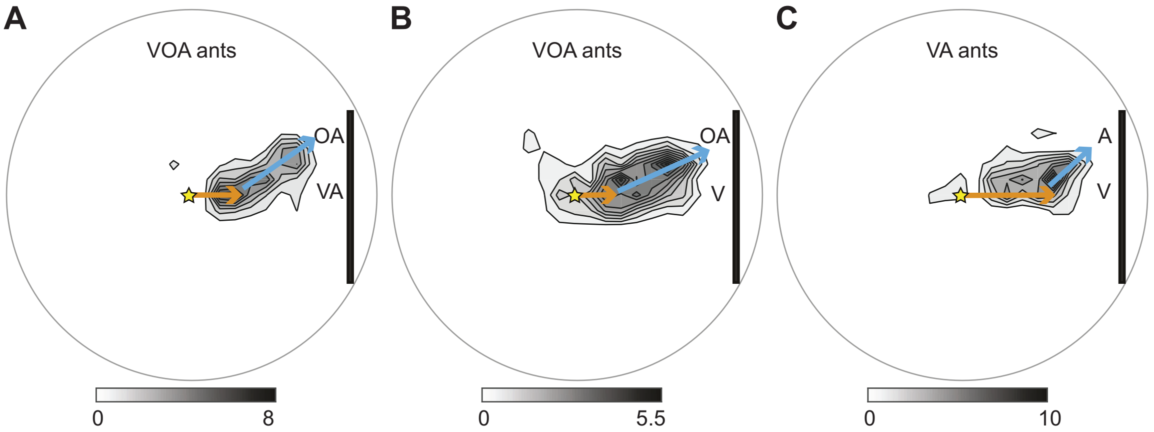

Fig. 6. Routes taken by trained ants in cue conflict tests. Path density plots are shown for three different groups of ants. (A) VOA_{Centre} ants were tested with the olfactory cue and airflow (OA) shifted 20 deg to the left and a clean airflow (A) added to the centre of the visual cue (VA). (B) VOA_{Centre} ants were tested with the OA shifted 20 deg to the left and only the visual information in the centre (V). (C) VA ants were tested with the airflow (A) shifted 20 deg to the left. Yellow star indicates the point of release. Black rectangle indicates the visual cue. Orange arrow indicates the initial walking direction. Blue arrow indicates the change of walking direction.

Is apparent cue binding a cognitive process or can it be explained by sensori-motor motifs?

In the experiments presented here, we challenged ants to learn a feeder location defined by multimodal information. Previously, in a similar experiment, desert ants learnt to use both olfactory and visual cues to navigate back to their nest (Steck et al., 2011) and the bimodal cues were first learnt independently but later stored as a unit, i.e. the search accuracy decreased when either the visual or the olfactory cue was presented alone (Steck et al., 2011). We asked here whether this cue binding can be explained by the ants' path characteristics and whether some behavioural flexibility is retained.

We performed experiments where the feeder location was defined by a visual cue (V), olfactory cue (O) and airflow (A) presented together (VOA experiments). In the first experiment, the feeder was located in the centre of the visual cue (VOA_{Centre}). These ants were no longer able to accurately approach the feeder when either the visual component or the olfactory component was removed; they also walked more slowly and with less straight paths (Fig. 2). Hence, as previously described (Steck et al., 2011), all the learnt cues were required for accurate navigation. However, in our second experiment, ants had the same set of cues (VOA) but the feeder was now located at the edge of the visual cue (VOA_{Edge}). Here, ants in tests with either the olfactory or visual cue missing were not significantly less accurate (Fig. 3). Interestingly, ants from the two groups (VOA_{Centre} and VOA_{Edge}) differed significantly in path straightness, turn frequency and walking speed, even though they experienced the same set of cues (Fig. 5).

In summary, we can conclude that 'binding' is not a cognitive inevitability in multimodal tasks, but depends on the sensori-motor contingencies of the particular task. Furthermore, the interactions between cues may be direct; for instance, when the removal of a familiar cue to an experienced ant is deleterious for path efficiency. Or those interactions could be indirect, such as the fine details of the sensori-motor patterns during learning being important for the ultimate performance of well-trained ants. Navigating to the edge of a large visual cue is a simpler task than navigating to the centre (Harris et al., 2007) and thus the rapid visual learning could also increase the efficiency of olfactory learning.

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Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: C.B., P.G.; Methodology: C.B., P.G.; Formal analysis: C.B.; Investigation: C.B., A.A.; Writing - original draft: C.B.; Writing - review & editing: C.B., P.G.; Visualization: C.B.; Supervision: C.B., P.G.; Project administration: C.B., P.G.; Funding acquisition: C.B., P.G.

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Data availability
Data are available from the University of Sussex research repository: https://doi.org/10.25377/sussex.12018471.

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