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Paper wasps form abstract concept of 'same and different'

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Concept formation requires animals to learn and use abstract rules that transcend the characteristics of specific stimuli. Abstract concepts are often associated with high levels of cognitive sophistication, so there has been much interest in which species can form and use concepts. A key abstract concept is that of sameness and difference, where stimuli are classified as either *the same as* or *different than* an original stimulus. Here, we used a simultaneous two-item same-different task to test whether paper wasps (*Polistes fuscatus)* can learn and apply a same-different concept. We trained wasps by simultaneously presenting pairs of *same* or *different* stimuli (e.g. colours). Then, we tested whether wasps could apply the concept to new stimuli of the same type (e.g. new colours) and to new stimulus types (e.g. odours). We show that wasps learned a general concept of *sameness* or *difference* and applied it to new samples and types of stimuli. Notably, wasps were able to transfer the learned rules to new stimuli in a different sensory modality. Therefore, *P. fuscatus* can classify stimuli based on their relationships and apply abstract concepts to novel stimulus types. These results indicate that abstract concept learning may be more widespread than previously thought.

1. Introduction

Many behaviours rely on categorizing relationships between stimuli [1]. Animals must distinguish safe from poisonous food, sounds of conspecifics from heterospecifics and threatening from non-threatening individuals [2]. Categorization often relies on learning specific physical features shared by items in a category (e.g. colour, odour, shape). Abstract concept formation differs from simple categorization because it requires the ability to learn abstract rules that transcend specific stimuli. Same-different concept learning is a form of abstract concept learning where stimuli are classified as either *the same as* or *different than* an original stimulus [1]. Relational concepts like same-different concepts are thought to be cognitively challenging [1]. Therefore, there has been long-standing interest in which species can form and use same-different concepts [3].

The ability to form same-different concepts is far from universal [1,3–5]. Historically, only primates were thought to be capable of same-different concept learning, but subsequent research found evidence of same-different concepts in many taxa, including corvids, pigeons, parrots, dolphins, ducklings and even honeybees [1,4–7]. However, other species appear unable to learn same-different relationships [2]. For example, there is no evidence that Malawi cichlids can learn concepts [2]. The lack of same-different concept learning in some groups may be owing to differences in social behaviour, cognitive capacity or experimental methods used to test same-different concepts [1,8].

The oddity task and relational matching-to-sample tasks are two methods commonly used to test same-different learning [1,3,7,9,10]. The oddity task requires test subjects to respond to a stimulus that is *different from* the original stimulus, while the relational matching-to-sample task requires test subjects to respond to a stimulus that represents the same relationship as the original sample stimulus set [1]. Test particulars, like how an animal demonstrates its choice for 'same' or 'different' must be carefully adjusted to ensure taxonomic differences do not interfere with testing accuracy [10]. Some argue that the oddity task may not test same-different concept learning because subjects may succeed by choosing the familiar stimulus instead of learning the concept of sameness [1]. However, studies typically add a final test using novel stimulus types (termed a 'transfer test') to ensure that the subjects use abstract concept learning rather than relying on simpler cognitive mechanisms [6].

Another method for testing same-different concepts is the simultaneous two-item same-different task. The two-item tasks may provide a more effective method for testing same-different concepts than matching or oddity tasks [9]. During simultaneous two-item tasks, subjects are exposed to two stimuli *concurrently* that are either identical (AA) or non-identical (BC) [9]. Subjects must select a novel stimulus set representing the same relationship (same or different) between stimuli as the trained stimulus pair [1]. For example, an animal trained to select a pair of different stimuli would be asked to choose between (DD) and (EF) with (EF) being the correct choice [1]. In this method, subjects must learn the relationship between stimuli, rather than a representation of a perceived stimulus. Primates [9], pigeons [5], parrots [10] and corvids [1] have solved such problems [8], but no invertebrates have been shown to form same-different concepts using the simultaneous two-item task.

Although simultaneous two-item tasks are fundamentally similar to matching and oddity tasks, the tasks test slightly different cognitive processes [1,4]. Specifically, the matching and oddity tasks assess whether the subject can identify a previously observed stimulus, whereas the simultaneous two-item task assesses whether the subject can determine if pairs of stimuli represent the same *relationship* to one another as an original pair of stimuli [1]. Therefore, a simultaneous two-item task requires that the subject learns the relationships *between relationships* (the relationship between AA compared to the relationship between BC) [1].

Thus far, the scope of same-different concept learning research has primarily been dominated by animals considered to have 'complex cognition', such as primates, mammals, and birds [3–5,9]. One exception is the honeybee (*Apis mellifera)*. Remarkably, honeybees were able to learn and apply same-different concepts when tested on matching and oddity tasks [6]. Further, bees transferred the concept to new types of stimuli both within and across sensory modalities. For example, bees trained to match a colour were able to match to an odour without additional training, indicating that bees learned the relational same-different concept rather than merely learning physical characteristics of the stimulus [6,8]. Thus far, to our knowledge, honeybees are the only non-vertebrate that has been tested for same-different learning [6,11].

Here, we test whether paper wasps (*Polistes fuscatus*) are capable of learning same-different concepts. *Polistes fuscatus* exhibit a range of complex social behaviour that may involve same-different concepts [8,12]. *Polistes fuscatus* have variable facial patterns that are used for individual recognition [13]. Conspecifics learn and remember the unique facial patterns of conspecifics during social interactions, then recall specific individuals during subsequent encounters [13]. Paper wasps also differentiate nest-mates from non-nest-mates using cuticular hydrocarbon chemical profiles [14]. Wasps from the same nest have similar chemical profiles and wasps with non-nest-mate cuticular hydrocarbon profiles are attacked if they land on a nest [14]. Finally, paper wasps are pollinators and may use both abstract and concrete concept formation to make flower choices [15].

We trained *P. fuscatus* on two-item same-different stimulus pairs and tested their capacity to transfer this knowledge to new types of stimuli. Wasps were trained using four different sets of stimuli of the same type (e.g. four pairs of same colours and four pairs of different colours). After training, wasps were tested on novel stimulus pairs of the same type. For example, wasps would be tested on new colours never encountered during training. Finally, wasps were given a transfer test on entirely different types of stimuli. For example, a wasp trained and tested using colours would be tested using face pictures or odours. While some argue that success on transfer tests within the same sensory modality could be explained by stimulus generalization, success on transfer tests across modalities demonstrates that wasps can learn the abstract concept of sameness and difference [3].

2. Methods

(a) Subjects

Polistes fuscatus foundresses were collected on their nests in June and July of 2020 in the areas surrounding Ann Arbor, Michigan. Wasps and their nests were housed in the laboratory and given ad libitum water, sugar and waxworms.

(b) Procedures

(i) Training

Wasps were trained using negative reinforcement to associate one set of stimuli with an unpleasant shock, and another set of stimuli with no shock (figure 1*a*). Our previous work has used the same training method to show how factors like social experience, sex, population of origin and type of stimulus influence *Polistes* learning performance [16–18]. For example, *P. fuscatus* are 'specialized' for conspecific face learning, as wasps with normal experience excel at learning conspecific face images [19] but cannot learn wasp faces without antennae [20]. Further, socially isolated *P. fuscatus* and other *Polistes* species [17,21] are unable to learn *P. fuscatus* faces, as they choose the correct stimulus at chance levels. Therefore, our previous work indicates that this training method provides consistent and relevant information about learning.

During training, wasps were placed in a 3.8 cm width × 3.8 cm length × 0.48 cm height wood and plexiglass chamber with eight stimuli on the inside walls (two stimuli per wall). In the 'same' trials, a pair of identical stimuli were on each wall. In the 'different' trials, each wall of the chamber had a pair of two different stimuli. The chambers were placed on an electrified pad made of anti-static conductive foam electrified by two copper wires connected to a Variac transformer, providing continuous 0.4 volt AC current. The chambers were shallow so that wasps could not escape the shock by flying or climbing the walls. The mild electric shock is aversive but not harmful to the wasp. Each round of training in a cycle consisted of 2 min exposure to either 'same' or 'different' stimulus pairs in a chamber placed on the electrified portion of training pad, and then a 2 min exposure to the remaining stimulus set on the non-electrified portion of the training pad (figure 1*a*). Wasps rested for 1 min between stimulus exposures. In half of the exposures, the wasps were placed in chambers with stimulus pairs representing the incorrect relationship (CS+) while receiving a mild electric shock. In the other half of the exposures, wasps were placed in chambers with only the correct stimulus pairs

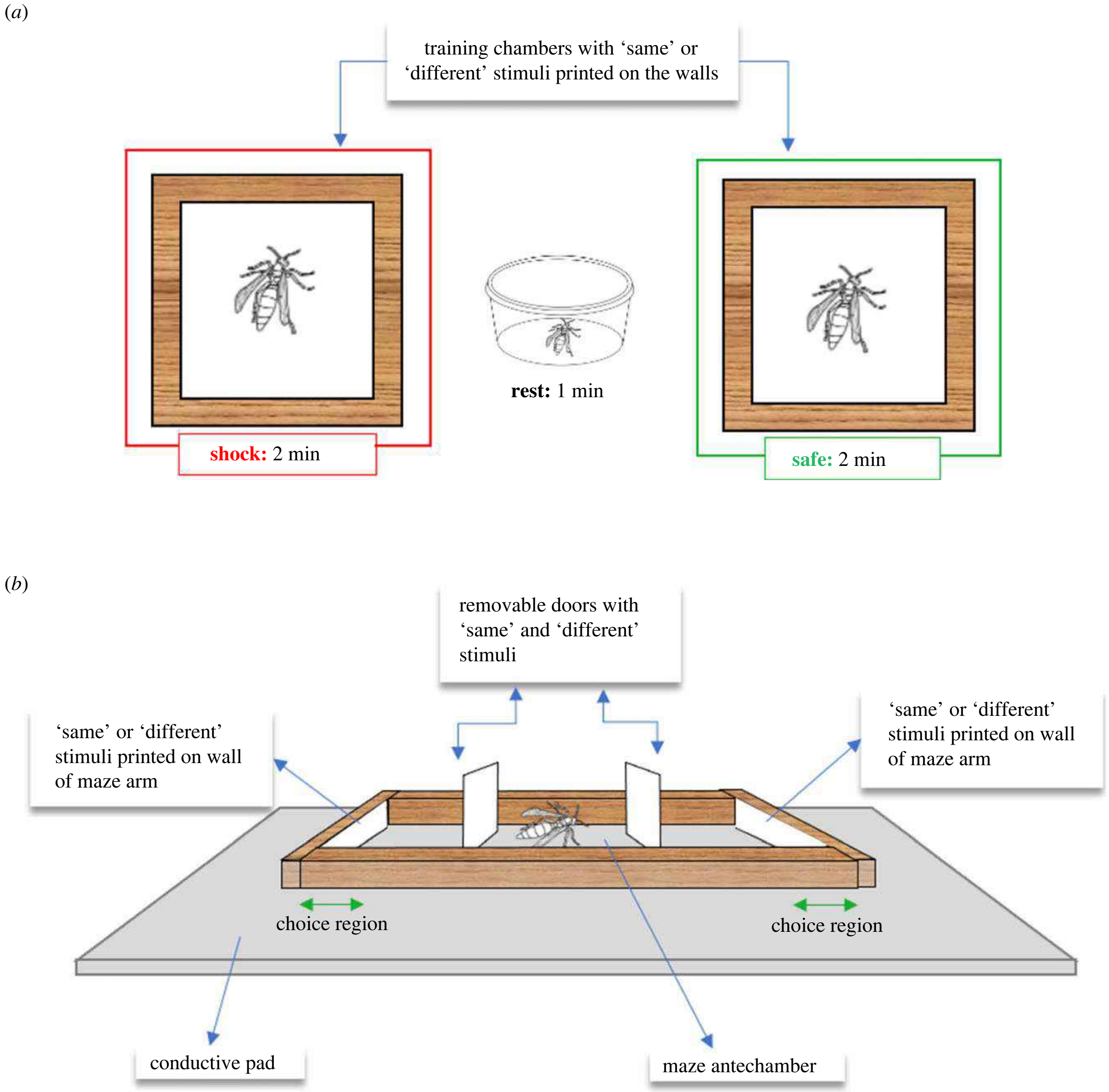

Figure 1. (*a*) Design of the training apparatus. During training, wasps were placed in 3.8 x 3.8 cm balsa wood 'chambers' with plexiglass ceilings and either electrified or neutral floors. Each wasp remained in the electrified chamber for 2 min, rested in a dark container for 1 min, and then was placed in the neutral chamber for 2 min. This cycle was repeated four times with different stimuli representing either the same or different relationships. (*b*) Design of the testing apparatus. During testing, wasps were placed in a balsa wood (for visual stimuli) or glass (for odour stimuli) rectangle with pairs of the same stimulus on one end and pairs of different stimuli on the other end. Learning was tested by measuring whether the wasp entered choice region with either the correct or incorrect stimulus pair over 10 trials. Location of the stimuli were swapped across trials to ensure wasps were responding to the stimuli rather than location. (Online version in colour.)

(CS0) and did not receive an electric shock. This sequence of one CS+ and one CS0 was repeated four times.

For example, a wasp trained to approach stimuli representing the 'same' relationship would be placed in shocking chamber with pairs of different stimuli (e.g. yellow and blue) for 2 min. Then, she would receive a 1 min break in her home container. Next, she would be placed in a non-shocking chamber with pairs of same stimuli (e.g. two green) for 2 min, followed by a 1 min break in her home container. This completes one training cycle. The subsequent cycles use different specific colour stimuli. Over four cycles of training, foundresses were exposed to a total of eight unique stimulus sets. Specific colours or face pictures were used more than once, but they were always used in equal frequency in both 'same' and 'different' sets to ensure that wasps learned the relationship between stimuli rather than associating certain stimulus with shock or safe outcomes. After training, wasps rested for 45 min before testing.

(ii) First transfer test

We tested whether wasps learned the concept of same-different by assessing performance in a 10-trial test using novel stimuli of the same type. For example, wasps trained with colours were tested on using novel colours never seen during the initial training. Wasps trained with faces were tested using novel face pictures never seen during initial training. We tested learning using a negatively reinforced rectangle, with an electrified floor (figure 1*b*; 3.8 cm width × 10.2 cm length × 0.48 cm height). The floor of the maze was electrified to maintain consistent conditions between the training procedure and the testing procedure. We ensured that choices were not influenced by shock avoidance by conducting control tests in which wasps were tested on an electrified pad without any prior training (electronic supplementary material, table S2). During testing, the only part of the floor that was not electrified was the 'safety zone' in one arm of the maze which was consistently associated with either two of the same stimuli (same), or two different stimuli (different). Stimuli location was swapped across trials in a predetermined, pseudo-random order to eliminate the possibility of a directional bias. In each trial of the 10-trial test, wasps were placed in the centre of the maze between two removable doors, with sets of 'same' stimuli on one door and sets of 'different' stimuli on the other door. The wasps were allowed to acclimate before the doors were removed and the wasp was released into the electrified maze (figure 1*b*). A wasp chose when it entered a chamber in one of the arms of the maze. After the wasp had made its choice, it was promptly removed from the maze and placed in a dark and neutral resting container for 1 min before the remaining trials.

The correct choice was associated with safety to ensure learned preferences from the initial training were not extinguished during the 10-trial test. Receiving a shock while choosing a preferred stimulus can rapidly extinguish learned preferences. Wasps were scored as making a choice before they reach the non-shocking safety zone to ensure wasps made choices based on learned stimulus preferences rather than directly assessing the presence or absence of shock. Wasps made quick choices (mean choice time = 3.15 s, s.e. = 0.37). Wasps did not change their minds after approaching a 'choice' zone, which suggests that they do not make choices based on minor differences in shock.

To confirm that wasps did not learn during the 10-trial test alone, we performed controls in which untrained wasps were tested on a shock pad without any initial training cycles. This is different from the regular training procedure because they were tested with no prior exposure to any stimulus. If the wasps learned during the 10-trial test or made choices based on the presence or absence of shock, they would perform better than chance during the 10-trial test. However, the untrained wasps did not perform better than chance during testing, confirming that wasps did not learn during the testing procedure alone, or choose based on shock avoidance (electronic supplementary material, table S2, all $p > 0.50$). It is likely that wasps do not learn during the 10-trial test alone because testing involves an extremely short period of reinforcement (3 s) compared to the 2 min of reinforcement wasps experience during training. We also performed a second control where 10 worker *Polistes* wasps were trained and tested on same-different colour concept formation, but there was no shock in any part of the testing arena. Wasps choose the correct stimuli more often than expected by chance when all 10 choices were included in the analysis ($p < 0.001$) and when only the first choice of each wasp was included ($p = 0.002$).

(iii) Second transfer test

We tested whether wasps were able to apply the same-different concept to a new type of stimuli with a transfer test. After the first transfer test, each wasp was allowed to rest for 45 min in a holding container with water and sugar before being tested on novel same-different stimuli. Wasps initially trained and tested using colour stimuli were tested with either face pictures ($n = 13$) or odours ($n = 20$) during the second transfer test. Similarly, wasps initially trained and tested with face stimuli were tested on colours during the transfer test ($n = 13$). The only methodological difference between first and second transfer tests were the stimuli used. All other methods were identical to ensure performance in the first and second transfer tests is directly comparable.

For both transfer tests, the wasps were tested by two researchers, one of whom was blind to the experimental treatment and predictions. There was no statistical difference in performance between the wasps trained by the two researchers ($p = 0.472$, s.e. = 0.460).

3. Materials

(a) Stimuli

Three types of stimuli were used in this study: (i) colours, (ii) wasp faces and (iii) odours (figure 2). The same stimuli were used in same and different trials across wasps to ensure that specific stimuli characteristics did not influence performance. The novel stimuli used during the transfer tests were a randomly selected subset of the stimuli shown in figure 2 and were not used during initial training:

(i) colours used during training included green, purple, light blue, dark blue, yellow, brown, black and grey (figure 2). Colour stimuli were printed on photo paper on a Xerox AltaLink C8035 colour printer, cut into rectangles (4.5 mm × 9 mm) to fit the height of the chamber and maze walls, and fastened to the interiors of mazes and chambers. Red, green and blue (RGB) values of the colours are provided in figure 2. Wavelength and per cent reflectance were assessed for each colour (electronic supplementary material, figure S1);

(ii) wasp faces used during training were pictures of *P. fuscatus* taken using a Leica Microscope. *Polistes fuscatus* use facial patterns for individual recognition [12]. Eight faces were selected with naturally occurring variation in facial patterns (figure 2). Backgrounds were removed from the face photos using Photoshop to ensure uniformity across all non-face aspects of the photos. Wasp faces were printed on photo paper on a Xerox AltaLink C8035 colour printer and fastened to the insides of training chambers and mazes. Face pictures were life sized (3.5 mm wide); and

(iii) odours used during training were alkanes: dotriacontane, octacosane and tetratriacontane (figure 2). The alkanes were non-volatile components of cuticular hydrocarbons that are readily discriminated by other social insects [22]. Concentration was based on proportional molarity. First, the molarity of 0.01 mg dotriacontane ml^{-1} pentanes was calculated, because dotriacontane has a molecular weight between the molecular weights of the other two hydrocarbons. The other mixtures were made to have the same molarity as the dotriacontane solution:

(a) to create 'same' odour stimuli (0.0088 mmol tetratriacontane, and 0.0088 mmol dotriacontane) 4.25 mg and 4.003 mg of each alkane, respectively, were serially diluted in pentanes to achieve equal molarities; and

(b) to create 'different' odour stimuli (one-half tetratriacontane, one-half octacosane; one-half dotriacontane, one-half octacosane) 0.0044 mmols of each were added to pentanes to create solutions with equal molarity (0.0088 mmol) to the 'same' stimuli.

Glass mazes were used for odour testing because the hydrocarbons used were dissolved in pentanes that would be absorbed and released by the balsa wood. Odours were added to glass mazes by saturating marking tape and

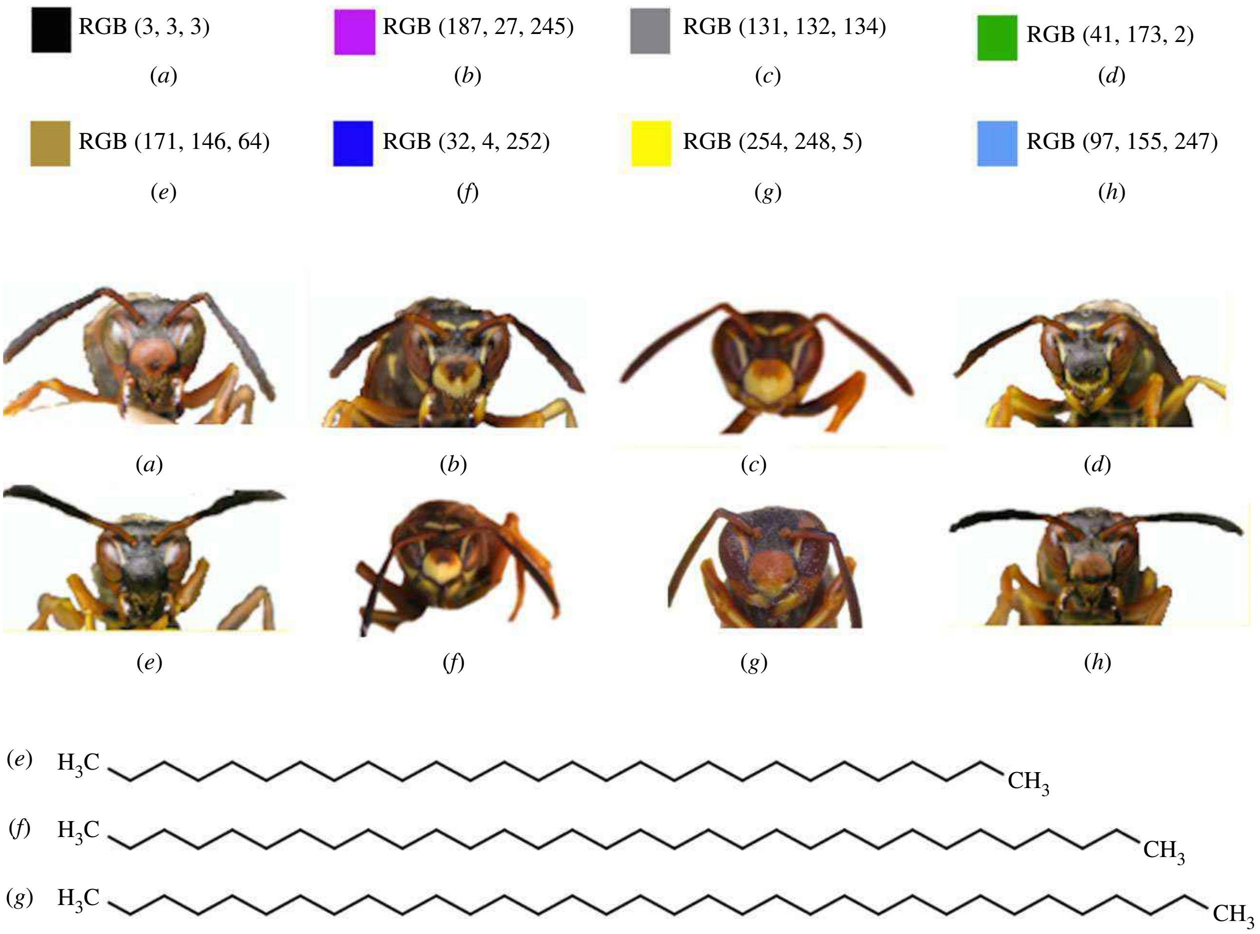

Figure 2. Colour, face and odour stimuli. Face stimuli were photographs of local *P. fuscatus*. Odours were non-volatile hydrocarbons. Stimuli were allocated uniformly across training and testing procedure. (Online version in colour.)

fastening the tape to the appropriate positions in the maze. Mazes were left for 24 hours before testing to ensure that the pentanes had fully evaporated, leaving only the prepared odours.

(b) Statistical analysis

The data were analysed in SPSS v. 26 and R statistical software (v. R 3.6 'Planting of a Tree'). Learning was measured as the total number of correct choices on each test. We compared performance to the 50 : 50 random expectation using binomial tests. The binomial test provides an exact test of whether the number of correct versus incorrect choices differs from the 50 : 50 random expectation. Binomial tests provide *p*-values with no test statistics. Two binomial test results are provided for each analysis, one where all 10 choices are included, and one where only the first choice of each wasp is analysed. General linear models (GLMs) were used to test whether the performance on first or second transfer tests were influenced by stimulus type and whether wasps were trained to approach 'same' stimuli or 'different' stimuli. For all GLMs, the dependent variable was number of correct choices (out of 10). For the first transfer test GLM, the independent variables were stimulus type during initial training (categorical: colours, faces), whether wasps were trained to approach 'same' stimuli or 'different' stimuli (categorical: same, different), and the two-way interaction. For the second transfer test GLM, the independent variables were stimulus type during transfer (categorical: colours, faces, odours), whether wasps were trained to approach 'same' stimuli or 'different' stimuli (categorical: same, different), and the two-way interaction. Finally, paired *t*-tests were used to compare performance on first to second transfer tests. 46 wasps were used in the experiment (13 colours transfer to faces, 13 faces transfer to colours, and 20 colours transfer to odours).

4. Results

Wasps learned the two-item same-different task. In the first transfer test on novel stimuli, wasps chose the correct stimulus pairs significantly more often than expected by chance (figure 3; faces mean = 8.15 ± 1.32 s.d., $p < 0.01$; colours mean = 7.9 ± 1.61 s.d., $p < 0.001$). In a second analysis, where only the first choice of each wasp was analysed, wasps also chose the correct stimulus pair significantly more often than expected by chance (faces mean = 0.92, $p < 0.01$; colours mean = 0.79, $p < 0.01$). Performance was not influenced by whether wasps were trained to approach pairs of the same stimulus or pairs of different stimuli ($F_{1,43} = 0.67$, $p = 0.42$) or whether the initial testing involved pairs of colours or pairs of faces ($F_{1,33} = 0.36$, $p = 0.55$). Wasps choose the correct stimulus set more often than expected by chance in all groups ('same' or 'different', colours or faces) (all $p < 0.001$).

We tested the wasps' capacity to abstract a general concept of sameness and difference with a second transfer test where wasps were tested on different types of stimuli without additional training. Over all trials, choice accuracy was similar in the first transfer test and the second transfer test

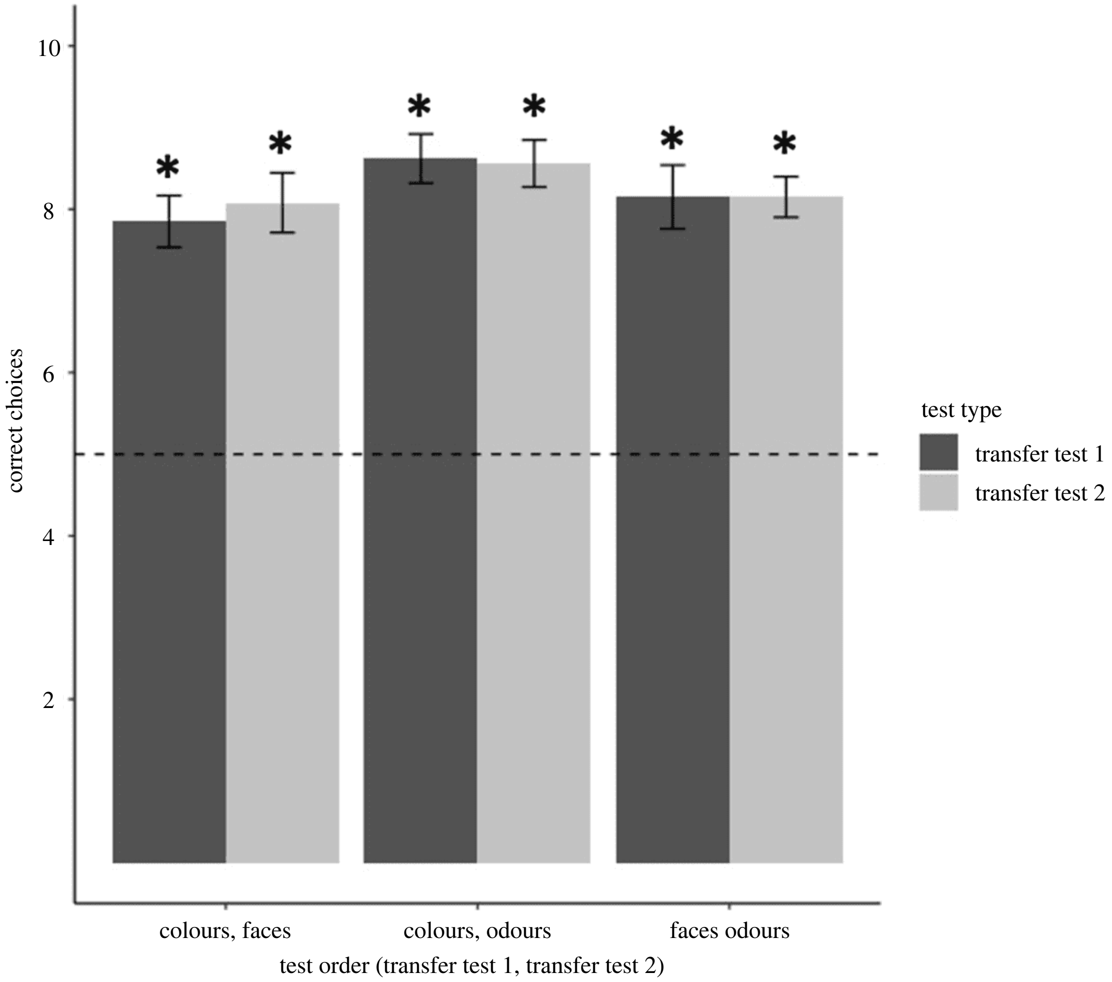

Figure 3. Mean ± s.e. correct choices made in first transfer tests (dark grey) and second transfer tests (light grey). 'Transfer test 1' refers to tests on novel stimuli of the same type as the training stimuli (e.g. novel colours for a wasp trained on colours). 'Transfer test 2' refers to tests on novel stimuli of different types (e.g, novel odours for a wasp trained on colours). The dashed line shows the 50 : 50 random expectation. Wasps performed better than chance on all tests, $*p < 0.01$. There was no difference in accuracy between first and second transfer tests ($p > 0.05$).

($t_{46} = 1.4$, $p = 0.15$, mean first transfer test = 8.0 ± 1.43 s.d., mean second transfer test = 8.30 ± 1.07 s.d.). There were also no differences between first and second transfer tests when the data were split by stimulus type. Wasps trained to discriminate pairs of same-different colours performed equally well on pairs of same-different faces ($t_{12} = 0.49$, $p = 0.63$, mean first transfer test = 8.07 ± 1.27 s.d.; mean second transfer test = 8.08 ± 1.21 s.d.). Wasps trained to discriminate pairs of same-different faces performed equally well on pairs of same-different colours ($t_{12} = 0.00$, $p = 1.0$, mean first transfer test = 8.15 ± 1.35 s.d.; mean second transfer test = 8.15 ± 0.86 s.d.). Wasps trained to discriminate pairs of same-different colours performed equally well on pairs of same-different odours ($t_{19} = 1.78$, $p = 0.09$, mean first transfer test = 7.9 ± 1.65 s.d.; mean second transfer test = 8.55 ± 1.0 sd). Wasps also performed better than chance on all transfer tests when all choices of each wasp were included in the analysis (faces mean = 8.07 ± 1.27 s.d., $p < 0.001$, colours mean = 8.15 ± 0.86 s.d., $p < 0.001$; odours mean = 8.56 ± 1.0 s.d., $p < 0.001$) and when only the first choice of each wasp was analysed (faces mean = 0.77, $p < 0.05$; colours mean = 0.85, $p < 0.05$; odours mean = 0.85, $p < 0.05$).

Performance on the second transfer tests was not influenced by whether wasps were trained to approach pairs of the same stimuli or pairs of different stimuli ($F_{1,42} = 0.26$, $p = 0.61$) or whether the second transfer test involved colours, odours or faces ($F_{2,42} = 0.95$, $p = 0.39$). In all cases, wasps choose the correct stimulus more often than expected by chance (electronic supplementary material, table S1).

5. Discussion

Polistes fuscatus learned the abstract concept of sameness and difference. Wasps were trained by simultaneously presenting pairs of *same* or *different* stimuli. Then, wasps were tested using two types of transfer stimuli: novel stimuli of the same type and novel stimulus types. Wasps performed better than chance (greater than 80% accuracy) on both types of transfer stimuli, showing that wasps learned a general concept of *sameness* or *difference* and applied the concept to new samples and new types of stimuli. Remarkably, wasps applied the concept of sameness and difference across sensory modalities, as they transferred concepts learned in the visual domain to the odour domain. Performance was not influenced by stimulus type (colours, wasp faces, odours) or whether wasps were trained to approach *same* or *different* stimuli. Therefore, our results illustrate that *Polistes* are able to master abstract interrelationships between stimuli.

Evidence of same-different concept learning in *P. fuscatus* is noteworthy because concept learning has traditionally been considered a cognitively sophisticated task. Concept learning requires the brain to independently encode the physical nature of objects as well as the relationships between objects. Concept learning is a cornerstone of challenging cognitive tasks like language, analogy and consciousness [1]. As a result, the ability to form abstract concepts is often thought to be restricted by taxonomic group and/or brain size. By taxonomic distribution, *P. fuscatus* are only the second invertebrate shown to form same-different concepts after honeybees. Paper wasps and honeybees have considerably smaller brains (less than 1 000 000 neurons) than vertebrates that form same-different concepts (pigeon 310 million neurons, macaque 6 billion neurons) [23–25].

Two aspects of this study stand out from previous work on same-different concept learning. First, our study is one of the few where subjects transferred a learned concept across both stimulus types and from the visual to olfactory modalities. Wasps trained using colours were able to transfer the same-different concept to odours without any decrease in performance. We have not yet tested whether wasps trained using odours are able to transfer the same-different concept to visual stimuli. The ability to apply a concept learned in one sensory domain to another domain provides strong evidence that wasps form concepts rather than using simpler mechanisms like choosing familiar stimuli, symmetrical stimuli or preferring variation and novelty [1,6]. The second notable aspect of this study is that we trained and tested paper wasps using a simultaneous same-different task. To our knowledge, this method has only been successfully used in a few taxa [1,4,9] and no other invertebrates. Species that form same-different concepts using the matching and oddity task do not always form same-different concepts using simultaneous stimuli presentation with relatively small stimuli sets [10,26,27]. Therefore, this study broadens our understanding of which taxa are capable of learning concepts with a simultaneous same-different task and applying those concepts across sensory modalities.

It is difficult to directly compare paper wasp performance during same-different concept learning with previous studies, as methods and type of reinforcement used for training and testing differ across studies. Nevertheless, wasp performance is consistent with work in other taxa. Wasps chose the correct stimulus pair with similar accuracy to pigeons, grey parrots, dolphins and chimps [1,6]. Interestingly, paper wasps reached greater than 80% correct choices after being trained using relatively few stimulus exposures. Paper wasps learned the same-different concept after training involving eight trials with eight stimulus pairs, while pigeons require 100 unique stimuli and thousands of trials to learn same-different concepts [1,5]. Wasps may learn with fewer trials because the reinforcement per trial (2 min of shock) is relatively intense compared with the positive reinforcement pigeons experience. Wasps could also learn relatively easily because they were trained using stimuli that are involved in same-different concept formation in the wild.

Animals may be more adept at rapidly forming concepts when trained using biologically relevant stimuli. We trained and tested wasps using wasp face images, colours and odours. All three types of stimuli are important in wild wasp behaviour. Wasps naturally excel at individual face recognition which probably involves forming same-different concepts of face images [28]. Wasps identify nestmate versus non-nestmate wasps using odours similar in their chemical structures to those used during training [29], and also learn flower colour during foraging [30,31]. By contrast, the pictures used for training other taxa may not be relevant to natural behaviour. For example, although pigeons are adept at visual discrimination, they may not be as attuned to human-centric stimuli like forks, whistles, rockets and Olympic flags [32]. Much previous work has shown that the ability to learn is shaped by selection, with animals learning salient stimuli more rapidly and accurately than less salient stimuli [33]. For example, individual face recognition is an important aspect of the social life of humans and wasps and both species are ‘specialized’ for learning conspecific faces. They learn faces more rapidly and accurately than non-face images [34,35]. In future work, it will be interesting to test whether an animal’s facility for concept learning is influenced by the specific stimuli used during training. Animals may be more adept at rapidly forming concepts when trained using stimuli similar to those used during concept formation in the wild.

Until now, the only evidence of an invertebrate species forming same-different concepts was in *A. mellifera* honeybees [6]. Like *P. fuscatus*, *A. mellifera* form concepts and transfer learned concept to novel stimulus types and sensory modalities [6]. However, Giurfa *et al*. [6] used delayed matching and oddity tasks to assess *A. mellifera* concept learning, while our study used a simultaneous same-different test. Because specific testing methods can influence a subject’s performance in unintended ways, evidence of same-different learning in another insect using different training methods strengthens the generality of the *A. mellifera* finding. Same-different concept learning may be more common in insects than previously anticipated [1,8].

The occurrence of same-different learning in both *P. fuscatus* and *A. mellifera* is interesting because the two species are distinct in many ways. First, the species last shared a common ancestor over 180 Ma [36], suggesting that the ability to form same-different concepts is either remarkably conserved or evolved independently in both lineages. *Polistes fuscatus* and *A. mellifera* also have different social behaviour. *Polistes fuscatus* live in relatively small colonies (less than 30 individuals), are behaviorally flexible, and lack strict morphological or behavioural distinctions between queens and workers. By contrast, *A. mellifera* live in large colonies (10 000 individuals) and have much stricter social organization, including pre-imaginal caste determination.

There are also behavioural and neural similarities between *P. fuscatus* and *A. mellifera* that could account for their shared ability to form same-different concepts. Both have impressive navigating abilities that allow them to travel long distances from their nest to forage. Navigation during these foraging flights involves flexible visual pattern recognition that allows them to navigate even when there are changes in the orientation or angle of viewing. Both taxa form configural representations of important stimuli like conspecific faces and flowers [20,37]. Bees and wasps also have similar general neuroanatomy, including mushroom bodies that integrate information from multiple sensory modalities [24,38]. Neural sensory integration may facilitate the development of conceptual rules valid across distinct sensory modalities and is found in both *P. fuscatus* wasps and *A. mellifera*.

Overall, *P. fuscatus* can form and use a concept of sameness and difference. Concept learning is a cornerstone of challenging tasks like language, analogy and consciousness [1]. As a result, the ability to form abstract concepts is sometimes thought to be restricted by taxonomic group and/or brain size [38]. However, our results add to a growing body of evidence that the miniature nervous systems of insects do not limit sophisticated behaviours. Future work in additional taxa will be useful to test the selective pressures that shape abstract concept learning as well as the cognitive mechanisms that underlie concept learning across taxa.

Data accessibility. Our data was submitted as supplementary material and can be accessed there [39].

Authors' contributions. C.W.: conceptualization, data curation, formal analysis, investigation, methodology, project administration, visualization, writing—original draft; C.C.O.: methodology, writing—review and editing; E.A.T.: conceptualization, formal analysis, methodology, supervision, validation, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interest.

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