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Individual recognition is associated with viewpoint-independent face recognition in a species-specific way

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Identifying three-dimensional signals (e.g. faces) can be challenging because the signals appear different when seen from different viewpoints. One simple solution is to always view signals from a particular viewpoint. A more flexible but also more cognitively challenging solution is viewpoint-independent recognition, where receivers can identify signals from multiple viewing angles. Here, we use same/different concept learning to test viewpoint-independent recognition for conspecific and heterospecific faces in two species of *Polistes* paper wasps that have three-dimensional visual signals. *P. fuscatus* use conspecific facial patterns for individual recognition, while *P. dominula* use conspecific facial patterns as a signal of fighting ability. Previous work has shown that *P. fuscatus* are able to identify novel viewpoints of conspecific faces through extrapolation. Here, we show that *P. fuscatus* and *P. dominula* differ in their capacity for viewpoint-independent recognition. *P. fuscatus* exhibit viewpoint-independent recognition for both *P. fuscatus* and *P. dominula* faces. In contrast, *P. dominula* do not have viewpoint-independent recognition for conspecific or heterospecific faces. These results suggest that viewpoint-independent recognition through extrapolation may be an adaptive strategy to facilitate individual face recognition across a wide range of taxa.

1. Introduction

Recognition is important in many contexts, including identifying conspecifics, kin, mates, individuals and nestmates [1]. During recognition, the receivers have a ‘template’ of what individuals in a category look, sound or smell like [2]. For example, many social insects have a ‘template’ of nestmate odour. If an approaching individual smells enough like a nestmate, the guard will accept them as a nestmate. If the individual smells too dissimilar, the guard will reject them and treat them as a non-nestmate [3,4]. Although the behavioural outcomes of recognition are typically clear, less is known about the mechanisms involved in perceiving, processing and matching a receiver phenotype to the recognition template. In some situations, the processes involved in matching a template to a signal may be quite complicated [5,6].

Visual recognition has the potential to be particularly challenging because visual signals appear different when seen from different viewpoints, distances or under different conditions [7–10]. A receiver’s viewpoint changes as they move, so the same signal may appear very different at different distances, positions or illuminations. Differences in viewing angle have a particularly strong impact on the appearance of three-dimensional signals [11,12]. For example, the front and profile views of a human face have very different characteristics. As a result, the front views of two different people are more similar than the front and side views of the same person [13]. Nevertheless, humans are adept at identifying individuals from different viewing angles

[14,15]. The way animals recognize three-dimensional objects from different viewing angles and in different conditions has been a focus of research in psychology, computer science and neuroscience [8,16]. Thus far, less is known about recognition of three-dimensional objects in wild animals and how recognition may vary across species and stimuli.

Three factors may influence the capacity for viewpoint-independent recognition: signal characteristics, receiver cognition and the context in which signals are used. Some signals have characteristics that make them easy to assess from different viewpoints. For example, non-structural colours appear the same regardless of viewing angle. In contrast, other signals, like three-dimensional shapes, will appear very different from different angles [11,12]. As a result, signal properties probably influence how easily signals can be assessed from different angles [7].

Receiver cognition could also influence the capacity to perceive and process signals from multiple angles. Some animals can identify novel viewpoints of a signal by extrapolating from previous knowledge [17–19]. Extrapolation is flexible, as it allows animals to identify objects with new viewpoints never seen before. However, extrapolation is thought to be relatively cognitively challenging [20]. As a result, the capacity for extrapolation may be more strongly developed in taxa where viewpoint-independent recognition is critical for success. In other taxa, individuals may always view signals from a particular perspective. Always viewing a signal from the same perspective is a less flexible type of recognition, though it is likely less cognitively challenging than viewpoint-independent recognition [9,13]. Therefore, some taxa may have perceptual adaptations that facilitate viewpoint-independent recognition, while other taxa may not.

The contexts in which signals are used may also influence the capacity for viewpoint-independent recognition. Recognition from a single viewpoint may be more common when signals are used in stereotyped contexts. For example, aggressive contests and mating displays often involve ritualized signalling behaviours, where signals can be viewed from a relatively consistent perspective [1]. As a result, signal phenotypes and receiver perception and processing may be adapted for viewing the signals from a consistent perspective. In contrast, viewpoint-independent recognition may be more common when signals are used in multiple contexts. For example, humans rely on individual face recognition throughout the day in many social contexts. As a result, it would be impractical if humans could only identify faces when viewed from a single perspective. Thus far, we lack data comparing the effect of viewpoint on visual recognition across taxa and signal types.

Polistes paper wasps provide a good model system to study how viewing angle influences visual recognition because they have three-dimensional visual signals of individual identity and fighting ability (figure 1) [21,22]. *Polistes fuscatus* have variable facial patterns that signal individual identity [21]. Wasps use individual recognition during interactions on and off nests to manage dominance interactions and division of work, reproduction and food [21,23,24]. Previous work has shown that *P. fuscatus* use viewpoint-independent recognition through extrapolation to identify novel views of conspecific faces [25]. *Polistes dominula* have facial patterns that are a signal of fighting ability. *P. dominula* wasps have variable black spots in the centre of their face that provide information about fighting ability [22,26]. Signals of fighting ability are used to mediate conflict between unfamiliar rivals but are not used during on-nest interactions between known individuals [26,27]. Previous work has not tested whether *P. dominula* can use viewpoint-independent recognition to identify conspecific faces or whether either species can use viewpoint-independent recognition to identify heterospecific faces.

Here, we test the viewpoint dependence of recognition by assessing how *P. fuscatus* and *P. dominula* apply the concept of sameness and difference to images of wasps taken from different viewpoints. Previous work has shown that *P. fuscatus* can learn the concept of sameness or difference and apply the concept to new samples and types of stimuli [28]. During training, wasps are exposed to two stimuli concurrently that are either the same (AA) or different (BC). Then, wasps must select a novel stimulus set representing the same relationship (same or different) between stimuli as the trained stimulus pair. For example, an animal trained to select a pair of different stimuli (BC) would be asked to choose between (DD) and (EF) with (EF) being the correct choice. We trained wasps using pairs of colours, then tested their capacity to apply the same/different concept to pairs of face pictures taken from different perspectives (0/0°, 0/30° or 0/60° rotation; figure 1). For example, wasps were asked to choose between two sets of pictures: (i) two pictures of the same wasp taken at different angles (wasp 1 at 0° and 30° rotation) or (ii) two pictures of two different wasps taken at different angles (wasp 2 at 0° rotation and wasp 3 at 30° rotation). If wasps are capable of viewpoint-independent recognition, we predict wasps will apply the concept of sameness and difference to different viewpoints of the same wasp. Therefore, the wasp will choose the pair of face pictures with the correct relationship. However, if recognition is viewpoint dependent, we predict wasps would not be able to apply the concept of sameness and difference to novel viewpoints and the wasp will choose randomly.

This study tests how viewpoint-independent recognition varies with species and stimuli in *Polistes* wasps. Our previous work has shown that *P. fuscatus* use extrapolation to identify novel views of conspecifics faces [25]. The current study addresses two questions. First, can *P. dominula* apply the concept of sameness and difference to novel views of conspecifics? We predict *P. dominula* will not identify conspecific faces from multiple viewpoints because *P. dominula* signals are primarily used during ritualized assessment of unfamiliar rivals rather than during interactions with familiar conspecifics [26,27]. As a result, there may be little benefit associated with viewpoint-independent recognition in *P. dominula*. Second, are differences in viewpoint dependence between *P. fuscatus* and *P. dominula* due to signal phenotype or receiver cognition? If differences between taxa are due to receiver cognition, we predict *P. fuscatus* will be more adept at viewpoint-independent recognition for all stimuli than *P. dominula*. If differences between taxa are due to signal phenotype, we predict both species will exhibit viewpoint-independent recognition for *P. fuscatus* faces but not *P. dominula* faces.

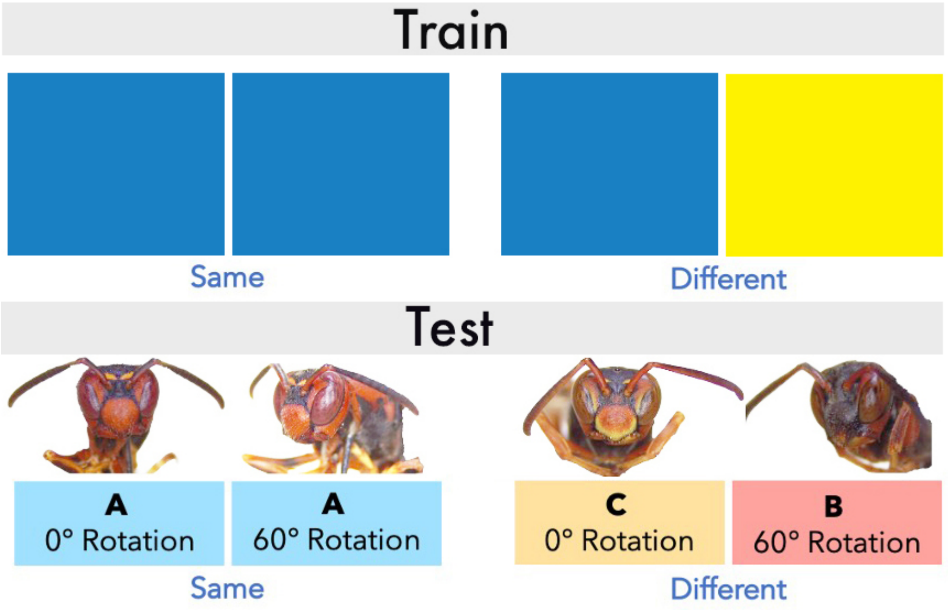

Figure 1. Examples of stimuli used during training and testing. Wasps were trained on the concept of sameness and difference using 10 unique pairs of colour stimuli (five pairs same, five pairs different). Either pairs of the same colour were associated with shock and pairs of different colours were associated with safety or vice versa. Then, wasps were tested on two pairs of face images that were either from the same wasp or from different wasps. In each pair of faces, one face image was unrotated and the other face image had one of three orientations (unrotated, rotated 30° and rotated 60°). Some wasps were tested on pairs of *P. fuscatus* images (brown and yellow), while others were tested on pairs of *P. dominula* face images (black and yellow).

2. Methods

Wasp nests used in this experiment were collected from sites around Ann Arbor, MI. Prior to the experiments, wasps were housed in the laboratory with *ad libitum* water, sugar and waxworm caterpillars. Wasps had no previous social experience with heterospecifics or with the wasps photographed for the trials. As a result, they were unable to learn different views through experience prior to the experiment.

Wasps were trained and tested using a simultaneous two-item same-different task. Simultaneous two-item tasks are commonly used to test abstract concept learning because they require subjects to learn the relationship between stimuli, rather than a representation of a perceived stimulus through simpler elemental cues [29,30]. In previous work, we showed that wasps can learn a general concept of sameness or difference and apply the concept to new samples and types of stimuli [28]. Wasps were trained using five different sets of stimuli of the same type (e.g. five pairs of the same colours and five pairs of different colours). After training, wasps were tested on novel stimuli (e.g. pairs of face pictures or pairs of odours). We found that wasps successfully transferred the concept learned on one type of stimuli (e.g. colours) to other types of stimuli (e.g. wasp faces or odours). The successful transfer tests across stimuli and sensory modalities show that wasps do not use stimulus generalization to solve the problem. Instead, they learn and apply the abstract concept of sameness and difference. In this study, we trained wasps using the same method and colour stimuli previously used for same/different concept learning [28]. However, instead of testing wasps with unrotated faces and/or odours, we tested how wasps apply the same/different concept to pairs of unrotated and rotated faces.

(a) Stimuli

All wasps were trained with pairs of the same or different colour stimuli using the following combinations: different—purple/grey, black/green, black/grey, purple/grey, blue/purple; same—black/black, purple/purple, grey/grey, green/green and blue/blue. The reflectance and the RGB values of the colours are shown in the electronic supplementary material, figure S1. The same stimuli were used to test same/different concept learning in previous experiments in *P. fuscatus* [28]. Stimuli were printed on photo paper on a Xerox AltaLink C8035 colour printer.

Like previous studies testing how viewpoint impacts recognition, we tested responses to two-dimensional printed stimuli. Perception of two-dimensional pictures is typically not completely equivalent to that of three-dimensional objects [31,32]. In *Polistes*, wasps that excel at social recognition of three-dimensional conspecifics also excel at learning and remembering two-dimensional conspecific face pictures (e.g. wasps with normal social experience from MI), while wasps that are not capable of conspecific recognition in social contexts are unable to learn to differentiate between two-dimensional pictures of conspecific faces during training (e.g. socially isolated wasps, wasps from some non-MI populations, *P. metricus*) [33–35]. Furthermore, *P. fuscatus* queens have better memories for individuals during social interactions and learn to discriminate face pictures better than workers [36]. Therefore, current data suggest that wasps can generalize between conspecific face pictures and real conspecifics based upon shared features.

Wasps were tested with pairs of *P. dominula* or *P. fuscatus* face images (figure 1; electronic supplementary material, figure S2). Face images were photographs of wasps from Michigan, USA. Pictures were taken head-on (0° rotation), rotated 30° and rotated

60°. Pairs of face images were either entirely unrotated (0/0°) or one face unrotated and one face rotated (0/30°, 0/60°). Face pictures were sized to ensure the head width was the same across all stimuli and the same as live wasps (3.5 mm wide). Wasps used in the experiment had no social experience with the wasps that were photographed to ensure they trained wasps had no experience with the different viewing angles. All tests involved pictures of three different wasps. The specific pair of stimuli varied across trials to ensure results were not influenced by the specific pictures. For example, in some trials where wasps chose between one unrotated face and one face rotated 30°, two pictures of wasp A would be used for the 'same stimuli', while one picture of wasp B and one picture of wasp C would be used for the 'different stimuli'. In other trials, two pictures of wasp B would be used for the 'same stimuli' and one picture of wasp A and one picture of wasp C would be used for the 'different stimuli'.

(b) Training

Wasps were initially trained to approach either 'same' or 'different' stimuli (figure 1) using methods similar to [25,28]. During training, wasps were placed in a 4 cm wide × 4 cm long × 0.7 cm height wood and plexiglass box with eight stimuli glued onto the inside walls. Wasps were alternately exposed to 'same' stimuli, where the box had the same colour squares on the walls and 'different' stimuli, where each side of the box had two different colour squares on the walls. For half of the wasps, the different stimuli was associated with a mild shock (CS−) and the same stimuli was associated with safety (CS+). In the other half of the wasps, the same stimuli was associated with a mild shock (CS−) and the different stimuli was associated with safety (CS+). Electric shock was provided by an electrified pad made of anti-static conductive foam electrified by two copper wires connected to a Variac transformer. The pad provided a continuous 0.4 V current. The boxes 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. In trials with no shock, the Variac transformer was turned off so the foam was not electrified. Between each 2 min bout, the wasp was given a 1 min break in a holding container. This sequence of one CS+ and one CS− bouts was repeated five times per wasp, so wasps experienced five CS+ and five CS− bouts in total. After training, the wasp was given a 45 min break in a holding container with access to sugar and water.

Each wasp was tested using pairs of faces from conspecifics or heterospecifics (figure 1; electronic supplementary material, figure S2). Performance was assessed by measuring whether the wasp approached the correct or incorrect image pair over 10 trials. Wasps were tested on the same stimuli for all 10 trials and there was no reinforcement during testing trials. Testing occurred in a 3 cm wide × 10 cm long × 0.7 cm high rectangular box. One end of the rectangle displayed the correct pair of stimuli while the other end of the rectangle displayed the incorrect pair of stimuli. Pairs of face images were either entirely unrotated (0/0°) or one face unrotated and one face rotated (0/30°, 0/60°). The centre of the rectangle had two removable, clear partitions that confined the wasp. At the beginning of each trial, the wasp was placed in the centre of the rectangle between the clear partitions; both partitions were removed simultaneously and the wasp was free to walk through the rectangle. A choice was scored when the wasp's head and thorax entered one of the 2.5 cm zones closest to each stimulus at each end of the rectangle. Wasps typically choose rapidly, within 2 s. After a wasp made a choice, it was removed from the testing arena and given a 1 min break in a holding container. The placement of the stimuli (right or left side) was determined randomly and changed between trials. This ensures that wasps did not associate a particular direction with correct choices.

Data on *P. dominula* and *P. fuscatus* response to conspecific and heterospecific faces were collected concurrently. *P. fuscatus* response to conspecific faces was published previously [25]. This study adds data on *P. dominula* response to *P. fuscatus* and *P. dominula* faces as well as *P. fuscatus* response to *P. dominula* faces.

(c) Statistical analysis

The data were analysed in SPSS v. 29. Learning was measured as the total number of correct choices (out of 10). General linear models (GLMs) were used to test how performance varied across independent variables like receiver species, stimuli or degree of rotation. For all GLMs, the dependent variable was the number of correct choices (out of 10). We describe the statistics used for each analysis.

Polistes dominula rotated conspecific faces*:* we used a GLM to compare choice accuracy in *P. dominula* for conspecific faces only. The independent variable was degree of rotation (categorical: 0/0°, 0/30° 0/60°). Least significant difference post hoc tests were used for post hoc pairwise comparisons between the three rotation categories. Year was originally included as an independent variable, but year had no effect and was removed from the final model.

Polistes dominula and *P. fuscatus* rotated conspecific and heterospecific faces: we used a GLM to compare choice accuracy of both *P. fuscatus* and *P. dominula* on both types of face stimuli at all three rotations. The independent variables were receiver species (categorical: *P. dominula* or *P. fuscatus*), stimuli species (categorical: *P. dominula* faces or *P. fuscatus* faces), degree of rotation (categorical: 0/0°, 0/30°, 0/60°) and all two and three way interactions. As there was a significant three way interaction between receiver species, stimuli species and degree of rotation, we split the data by the species of the wasp being trained. Within each species, we ran separate GLMs with the independent variables of stimuli species (categorical: *P. dominula* faces or *P. fuscatus* faces), degree of rotation (categorical: 0/0°, 0/30°, 0/60°) and their two way interaction. Year was originally included as an independent variable, but year had no effect and was removed from the final model.

We also compared the number of correct choices to the 50:50 random expectation using one-sample *t*-test with the test value set at 5. The one-sample *t*-test assesses whether the number of correct versus incorrect choices differs from the 50:50 random expectation of 5 out of 10 trials correct.

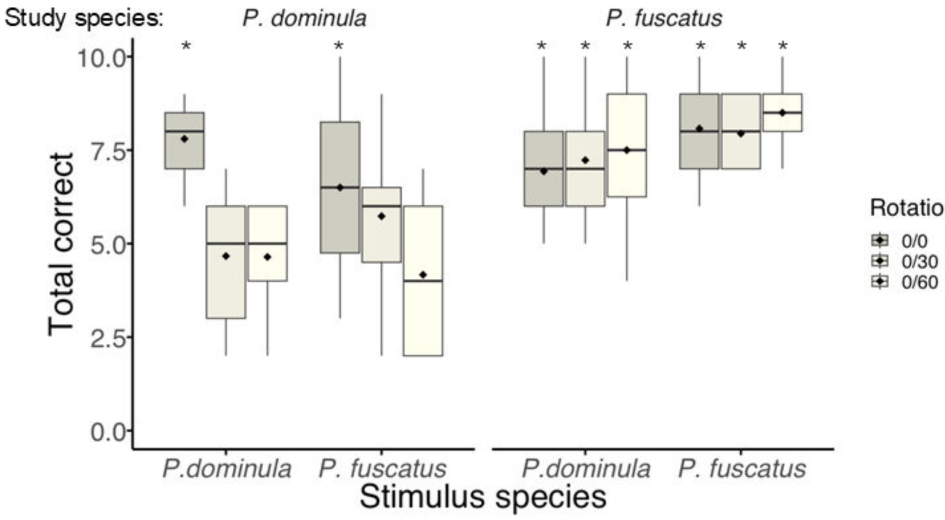

Figure 2. Performance of *P. dominula* and *P. fuscatus* wasps tested on pairs of conspecific and heterospecific face images. *P. dominula* were more adept at identifying whether face pictures reflect the same individual or two different individuals when the face pictures were unrotated than when one face image was rotated. *P. fuscatus* identified whether pairs of faces reflect the same individual or two or different individuals with similar accuracy when both pictures are unrotated and when one picture is unrotated and the other is rotated 30° or 60°. Boxes reflect first and third quartiles with median as the middle bar and triangles as the mean. Bars reflect 25th and 75th percentiles. *Performed better than chance ($p < 0.05$).

3. Results

(a) *Polistes dominula* rotated *conspecific faces*

In contrast to *P. fuscatus* [25], *P. dominula* were unable to identify novel views of the same conspecific face (figure 2). Accuracy was influenced by whether wasps compared a pair of unrotated faces or a pair of one unrotated face and one face rotated 30° or 60° ($F_{2,41}$=28.24, $p < 0.001$). Post hoc pairwise analysis shows that wasps chose more accurately when both face images were unrotated than when one face was unrotated and the other face was rotated (0° versus 30°, $p < 0.001$, 0° versus 60° $p < 0.001$ and 30 versus 60 $p = 0.96$). *P. dominula* were more likely to choose the correct pair of faces than expected based on chance when both faces were unrotated ($t_{14} = 10.7$, $p < 0.001$). However, wasps chose at chance level when one face image was unrotated and the other face image was rotated (0/30°, $t_{14} = 0.8$, $p = 0.42$; 0/60°, $t_{13} = 1.0$, $p = 0.34$).

(b) *Polistes dominula* and *Polistes fuscatus* rotated conspecific and heterospecific faces

We tested how the species being trained and the species of the stimuli pictures influence the viewpoint dependence of recognition by comparing *P. fuscatus* and *P. dominula* performance on conspecific and heterospecific faces. The ability to identify the relationship between faces was influenced by the three way interaction between the species trained, the species of the stimuli pictures and the degree of rotation ($F_{2,163} = 3.1$, $p = 0.048$). Performance was also influenced by the two way interaction of rotation species trained ($F_{2,163} = 1615.9$, $p < 0.001$) and the species being trained × the species of the stimuli pictures ($F_{1,163} = 6.3$, $p = 0.013$), but not rotation × the species of the stimuli pictures ($F_{2,163} = 1.5$, $p = 0.23$). In this model, performance was also influenced by rotation ($F_{2,163} = 8.7$, $p < 0.001$), the species being trained ($F_{1,163} = 780.0$, $p < 0.001$), but not the species of the stimuli pictures ($F_{1,163} = 2.3$, $p = 0.13$). To better understand the basis of the three way interaction, the data were split by the species being trained. Then, we compared relationships within each species.

Polistes fuscatus were able to identify novel views of both conspecific and heterospecific faces (figure 2). *P. fuscatus* performance accuracy was not influenced by the interaction between stimuli species and degree of rotation ($F_{2,82} = 0.20$, $p = 0.82$). The lack of interaction indicates that *P. fuscatus* responded similarly to the rotation of conspecific and heterospecific faces. Performance is also not influenced by rotation alone, as *P. fuscatus* are equally adept at comparing a pair of unrotated faces or a pair of one unrotated face and one face rotated 30 or 60° ($F_{2,82} = 1.1$, $p = 0.32$). Performance is influenced by stimuli species, as *P. fuscatus* performed better on *P. fuscatus* faces than on *P. dominula* faces ($F_{1,82} = 11.02$, $p = 0.001$).

One-sample *t*-tests show that *P. fuscatus* accurately applied the same/different concept to both *P. fuscatus* and *P. dominula* faces. Wasps chose the correct pair at higher than chance levels regardless of whether wasps compared two pairs of unrotated faces or a pair of one unrotated face and one face rotated 30° or 60° (all $p < 0.01$)

Polistes dominula were unable to identify novel views of conspecific and heterospecific faces. *P. dominula* performance accuracy was influenced by the interaction between stimuli species and degree of rotation ($F_{2,81} = 3.6$, $p = 0.032$). The two way interaction indicates that viewpoint dependence differs between conspecific and heterospecific faces. *P. dominula* are more adept at comparing pairs rotated/unrotated heterospecific faces than pairs of rotated/unrotated conspecific faces. Furthermore, rotation influences performance on both conspecific and heterospecific faces ($F_{2,81} = 18.9$, $p < 0.001$). Post hoc pairwise analysis shows that wasps chose more accurately when comparing pairs of unrotated faces than when comparing pairs of one rotated and one unrotated face (0/0° versus 0/30°, $p < 0.001$, 0/0° versus 0/60° $p < 0.001$, 0/30° versus 0/60° $p = 0.10$). Stimuli species did not influence performance ($F_{1,81} = 0.39$, $p = 0.53$).

One sample *t*-tests show that *P. dominula* accurately applied the same/different concept to unrotated *P. fuscatus* faces ($t_{15} = 2.6$, $p = 0.02$) and *P. dominula* faces ($t_{14} = 10.7$, $p < 0.001$). However, *P. dominula* were unable to apply the same/different concept to pairs of conspecific or heterospecific faces when one face was unrotated and one face was rotated (*P. dominula* 0/0° versus 0/30° $t_{14} = 0.8$, $p = 0.429$; *P. dominula* 0/0° versus 0/60° $t_{13} = 1.0$, $p = 0.34$); *P. fuscatus* 0/0° versus 0/30° $t_{14} = 1.5$, $p = 0.17$, *P. fuscatus* 0/0° versus 0/60° $t_{11} = 1.5$, $p = 0.17$).

4. Discussion

Both *P. fuscatus* and *P. dominula* learn the concept of sameness and difference and apply that concept to conspecific and heterospecific face images. However, *P. fuscatus* and *P. dominula* differ in their ability to apply this concept to different viewpoints of the same individuals. *P. fuscatus* exhibit viewpoint-independent recognition for both *P. fuscatus* [25] and *P. dominula* faces (figure 2). *P. fuscatus* identify a pair of pictures of the same wasp as the 'same', even if the pictures are taken from different viewpoints (e.g. one face picture at 0° rotation and one face picture at 60° rotation). However, *P. dominula* cannot identify pictures of conspecifics or heterospecifics taken from different viewpoints (figure 2). These results suggest that the capacity for viewpoint-independent recognition is influenced by receiver cognition.

Our results indicate that wasps can apply the concept of sameness and difference to novel views of faces rather than choosing between faces based on simple, elemental cues. Wasps were trained using a simultaneous two-item tasks, which requires subjects to learn the relationship between stimuli, rather than a representation of a perceived stimulus through simpler elemental cues [29,30]. In previous work, wasps were trained to the abstract concept of sameness and difference using the same methods and colour stimuli used in this study [28]. After training, wasps were able to apply the same/different concept to different stimuli (e.g. pairs of unrotated wasp face pictures) and sensory modalities (e.g. pairs of odours), showing that wasps do not use stimulus generalization or elemental cues to solve the problem. Instead, they learn the abstract concept of sameness and difference and applied the concept to diverse stimuli types. In this study, wasps applied the same/different concept to both rotated and unrotated face pictures. Furthermore, the face pictures associated with sameness and difference varied across trials to ensure that the specific stimuli characteristics did not influence performance.

A notable aspect of our results is that *P. fuscatus* can recognize novel viewpoints of both unfamiliar conspecific and heterospecific faces. In primates, experience viewing faces from multiple perspectives enhances face recognition [37]. Familiarity enables the formation of robust individual face representations that apply across different perspectives and viewing conditions [11]. As a result, humans and chimpanzees exhibit more accurate recognition of novel viewpoints for familiar faces than for unfamiliar faces [37]. In this study, the wasps had not previously encountered the individuals in the pictures and had no opportunity to view the faces from different viewpoints prior to testing. Nevertheless, *P. fuscatus* accurately identified whether pairs of unfamiliar face images were from the same or different wasp within seconds. *P. fuscatus* also accurately identified pairs of heterospecific, *P. dominula,* face images from different viewing angles, though they identified heterospecific faces with lower accuracy than conspecific faces. The ability to identify novel viewpoints of *P. dominula* faces is particularly interesting because *P. fuscatus* used in this experiment were raised in the lab and had never encountered a live *P. dominula*. Our results suggest that *P. fuscatus* wasps may readily generalize their capacity for viewpoint-independent recognition across different face stimuli. Future experiments will be important to test whether *P. fuscatus* primarily excel at viewpoint-independent recognition of face stimuli or whether they also excel at identifying non-social stimuli from multiple different perspectives.

In contrast to *P. fuscatus*, *P. dominula* are not capable of viewpoint-independent recognition. *P. dominula* were adept at forming and applying same/different concepts to pictures of conspecifics and heterospecific taken from the front. However, *P. dominula* were unable to identify pairs of wasp pictures taken from different viewpoints. These results indicate that *P. dominula* may need to view conspecifics from the front to effectively assess the black facial patterns that signal conspecific fighting ability [22,26]. Viewpoint-dependent recognition, like that found in *P. dominula* is less flexible, but it may also require less cognitive sophistication than image extrapolation used by *P. fuscatus*.

Mechanistically, the different capacity for viewpoint-independent recognition in *P. fuscatus* and *P. dominula* may be influenced by the processes these species use for face recognition. *P. fuscatus* wasps use a type of specialized, configural processing known as holistic processing to identify the faces of other wasps [38]. *P. fuscatus* identify faces using both facial features and the spatial relationships among features, which are bound together in a gestalt that is more than the sum of their parts. *P. fuscatus* also excel at viewpoint-independent recognition. In contrast, *P. dominula* are not capable of configural face processing or viewpoint-independent recognition [38]. Species differences in both configural processing and viewpoint-independent recognition suggest that configural processing could facilitate identification of faces from different observer viewpoints. However, *P. fuscatus* do not use configural processing to identify *P. dominula* faces and still have some capacity for viewpoint-independent recognition of *P. dominula* faces. As a result, configural processing may not be essential for some level of viewpoint-independent recognition.

Evolutionarily, the different capacity for viewpoint-independent recognition in *P. fuscatus* and *P. dominula* may be due to different selective pressures faced by each species. *P. fuscatus* depend on individual face recognition to mediate a wide range of social interactions both on and off nests [21,23,24]. The ability to identify conspecifics from novel viewing angles likely provides substantial fitness benefits because effective individual recognition minimizes aggression and stabilizes social interactions [39] (E. C. Laub, N. Pinter-Wollman & E. A. Tibbetts 2025, unpublished data). In contrast, *P. dominula* use facial patterns to assess the fighting ability of unfamiliar rivals [26,40]. *P. dominula* assess conspecific facial patterns using ritualized behaviour that involves standing face to face and rocking back and forth. *P. dominula* ignore conspecific facial patterns in other social contexts, including during on-nest interactions [27] or when competing over high value resources [41]. Given the limited contexts where *P. dominula* assess conspecific facial patterns, the ability to assess rivals from multiple viewing angles may provide little benefit. Using viewpoint-dependent recognition may simplify the sensory and cognitive processing required for signal assessment. In future work, it will be interesting to explore the selective pressures that shape variation in viewpoint-independent recognition across additional taxa.

The capacity for viewpoint-independent recognition was more strongly linked with receiver cognition than stimuli characteristics. *P. fuscatus* exhibited viewpoint-independent recognition for both conspecific and heterospecific faces. In contrast, *P. dominula* was unable to recognize either conspecific or heterospecific faces across viewpoints. Although this study did not find strong evidence that stimuli characteristics influence the accuracy of recognition from different angles, there is some evidence stimuli characteristics may influence recognition accuracy. *P. dominula* performance was influenced by the two way interaction between stimuli and rotation angle, suggesting that *P. dominula* may be better at viewpoint-independent recognition of *P. fuscatus* faces than of *P. dominula* faces. *P. fuscatus* facial patterns may be easier to assess from multiple perspectives because there is a high level of variation across the front and side of the face. In contrast, *P. dominula* facial patterns are much less variable and the variation is limited to size and shape of the black spot in the centre of the face. For this study, we chose *P. dominula* with distinct black spots, so recognition from different orientations was possible. However, most *P. dominula* appear similar enough that accurate discrimination from different viewpoints would be difficult [26,42]. Future work is needed to rigorously analyse the links between signal function, signal phenotype and the ease with which signals can be assessed from different viewpoints [7].

Previous work in other taxa indicates that most animals use either interpolation or extrapolation for viewpoint-independent recognition. Receivers use interpolation when they only identify novel views that fall within stored views [17]. For example, receivers learn 0° and 60° views, then interpolate to identify novel 30° views. Receivers use extrapolation to identify novel views that fall outside stored views. For example, receivers learn 0° views, then extrapolate to identify novel 30° views. Vertebrates use both interpolation and extrapolation to generalize over different viewpoints of the same individual [18,20,43]. Two previous studies tested how insects recognize rotated objects. Honeybees can learn to recognize novel viewpoints through image interpolation [44], while *P. fuscatus* probably identify novel viewpoints of unfamiliar faces by extrapolating from previous knowledge [25]. This study provides additional evidence that *P. fuscatus* are capable to extrapolation, as they identify novel views of heterospecifics that fall outside known views. The evidence of image extrapolation in *P. fuscatus* suggests that extrapolation may be a more taxonomically widespread mechanism for viewpoint-independent recognition than previously thought.

This study was designed to test how viewpoint-independent recognition varies across species and stimuli. It does not test exactly which cues wasps use to assess sameness versus difference of the conspecific and heterospecific pictures. We expect that wasps likely rely on facial patterns given the extensive evidence that wasps are highly attuned to conspecific facial patterns and ignore other cues like antennae or leg position [26,38,45]. However, future experiments where multiple cues are independently varied (e.g. brightness, leg position and antennae position) would be needed to test the specific cues that wasps use to identify sameness versus difference of the stimuli.

Overall, *P. fuscatus* can apply a concept of sameness and difference to both rotated and unrotated conspecific [25] and heterospecific faces. *P. fuscatus* are able to rapidly extrapolate to novel views of both conspecific and heterospecific faces. In contrast, *P. dominula* can only identify unrotated conspecific and heterospecific faces. *P. dominula* cannot apply the concept of sameness and difference to novel, rotated views of conspecifics or heterospecifics. These results suggest that the capacity for viewpoint-independent recognition is influenced by receiver cognition. Taxa with individual face recognition or other three-dimensional visual signals may commonly have the capacity for viewpoint-independent recognition.

Ethics. No permits or approvals are required for insect research.

Data accessibility. The datasets supporting this article have been uploaded as part of the supplementary material [46].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. E.A.T.: conceptualization, data curation, formal analysis, funding acquisition, methodology, project administration, writing—original draft; C.W.: conceptualization, data curation, investigation, writing—review and editing; J.P.-S.: investigation, visualization, writing—review and editing; A.N.V.: investigation, writing—review and editing.

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