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Individual recognition is associated with holistic face processing in *Polistes* paper wasps in a species-specific way

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Most recognition is based on identifying features, but specialization for face recognition in primates relies on a different mechanism, termed 'holistic processing' where facial features are bound together into a gestalt which is more than the sum of its parts. Here, we test whether individual face recognition in paper wasps also involved holistic processing using a modification of the classic part-whole test in two related paper wasp species: *Polistes fuscatus*, which use facial patterns to individually identify conspecifics, and *Polistes dominula*, which lacks individual recognition. We show that *P. fuscatus* use holistic processing to discriminate between *P. fuscatus* face images but not *P. dominula* face images. By contrast, *P. dominula* do not rely on holistic processing to discriminate between conspecific or heterospecific face images. Therefore, *P. fuscatus* wasps have evolved holistic face processing, but this ability is highly specific and shaped by species-specific and stimuli-specific selective pressures. Convergence toward holistic face processing in distant taxa (primates, wasps) as well as divergence among closely related taxa with different recognition behaviour (*P. dominula*, *P. fuscatus*) suggests that holistic processing may be a universal adaptive strategy to facilitate expertize in face recognition.

1. Introduction

Primates are particularly efficient at learning and remembering the unique faces of conspecifics [1,2]. For example, humans can learn an individual face in seconds, remember the face for years and recognize it again even if the face is shown from a new perspective. The remarkable capacity for face recognition has been attributed to configural processing of faces [1,3,4]. During configural processing, both the features and the spatial relationships among features influence recognition. For example, face recognition involves recognizing components of the face (e.g. big nose, brown eyes) and relationships among these components (e.g. wide-set eyes). There are three levels of configural face processing [1]. The first type is sensitivity to first-order relationships that define a face (i.e. two eyes above a nose and mouth). The second type is termed 'holistic processing' and implies that the features are bound together into a gestalt which is more than the sum of its parts. The third type is sensitivity to second-order relationships, which means that distances between facial features are perceived and used for discrimination.

Humans primarily rely on the first level of configural processing for categorizing visual objects, but use all three types of configural processing to identify human faces [1,3]. Incorporating the relationships among features into the visual representation of faces is thought to facilitate accurate face recognition [5]. Configural processing also allows humans to consistently identify individuals despite changes in viewpoint (e.g. front view versus rotated face) [6]. In particular, holistic processing increases sensitivity to subtle variations so

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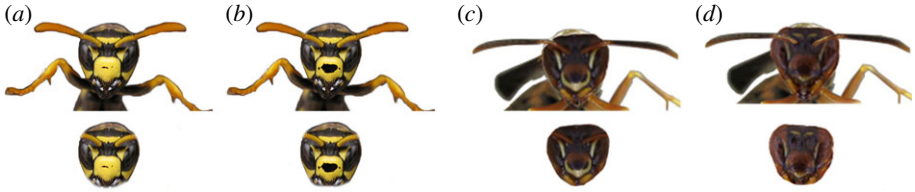

Figure 1. Images of *Polistes dominula* (*a*,*b*) and *Polistes fuscatus* (*c*,*d*) used for training and testing. All variation is in the inner part of the faces. The outer parts (legs, body position, antennae, background) are identical between the pair of faces from each species. (Online version in colour.)

humans can detect small differences in second-order relations between facial features (e.g. distance between eyes) [4]. There is much debate about how frequently holistic processing is used to recognize non-face objects [7–10]. While most non-face objects are not processed holistically, holistic processing may be used to help recognition of similar objects such as birds, dogs or cars [10]. Importantly, the viewer needs extensive experience identifying fine variation in the objects for holistic processing to occur [11]. Thus, the mechanisms originally evolved for face recognition may be mobilized to identify specific, non-face objects. Interestingly, neuronal networks thought to be specialized for face processing are also activated during recognition of non-face objects when the viewer has extensive experience with those objects [11].

Holistic processing is typically tested by assessing recognition of experimentally manipulated stimuli. For example, human face recognition is dramatically reduced when part of the face is presented in isolation rather than in the context of the whole face (part-whole effect). Humans easily discriminate between two noses when the noses are presented in a whole face, but have difficulty discriminating between the same noses when the noses are presented in isolation [3]. Similarly, holistic processing disrupts feature extraction, so it is more difficult to recognize that facial features are identical when the features are presented in a context of a different face (composite-face effect) [12]. Many primates were shown to rely on holistic processing to identify faces, as they are sensitive to both the composite and the part-whole effect specifically when discriminating faces [2,13,14].

Although diverse species recognize conspecifics using facial features, little previous work has tested whether non-primates use holistic processing during face recognition. Conspecific face recognition has been found in primates, sheep, dogs, fishes and paper wasps [2,15–18], but there is currently no evidence that holistic processing is used for conspecific face recognition in these taxa. Non-primates may use holistic processing to recognize heterospecific human faces with extensive experience. Dogs are sensitive to the part-whole effect with human faces [18] as are honeybees [19–21] and *Vespula vulgaris* wasps [20,22]. The research in honeybees and *Vespula* wasps is notable because it suggests that even small-brained insects can use sophisticated configural processing with sufficient experience. However, holistic processing in honeybees and wasps is not linked to individual recognition but rather to visual object expertize. Honeybees and *Vespula* wasps also do not naturally recognize human faces, so these species provide limited information about how face recognition strategies evolve.

Polistes paper wasps are ideal models for studying the evolution of configural face processing because some *Polistes* species use individual face recognition, while other species do not, despite similar visual abilities. *Polistes fuscatus* wasps recognize individual conspecifics based on facial pattern variation [16]. During individual recognition, *P. fuscatus* learn the unique facial features of conspecifics, associate the facial features with specific information about their rival, then recall both the face and the rival-related information during subsequent interactions. Previous work indicates that *P. fuscatus* may process conspecific faces differently than other visual stimuli, as *P. fuscatus* learn conspecific faces faster and more accurately than other images. Even minor alteration of face images (e.g. rearranging features or removing antennae) reduces face learning [23], which already suggested the involvement of configural processing. By contrast, other *Polistes* species, including *Polistes dominula*, do not learn and remember unique conspecific faces during social interactions [24]. Instead, *P. dominula* have facial patterns that signal fighting ability [25,26]. Strong wasps have different facial patterns than weak wasps. Although *P. dominula* are attuneded to conspecific faces, they assess rival fighting ability without learning and remembering specific conspecific facial patterns [26]. Previous work also suggests *P. dominula* do not use specialized mechanisms for learning conspecific faces [27], (but see [28]). The natural variation in face learning and face specialization makes paper wasps a perfect system to understand the evolution of configural face processing independently of the primate brain evolution.

Here, we test holistic face processing for conspecific and heterospecific face images in two *Polistes* species: *Polistes fuscatus*, which have individual face recognition, and *Polistes dominula*, which do not have individual face recognition. If holistic face processing is an adaptation to facilitate individual face recognition, we predict *P. fuscatus* will use holistic face processing for conspecific face images, while *P. dominula* will not. We also test the specificity of holistic face processing by assessing holistic processing for heterospecific face images. We predict that holistic face processing is highly specific, so neither species will use holistic processing for heterospecific face images.

We use an adaptation of the classical part-whole method that accounts for the wasp's visual acuity to test configural processing. The part-whole method provides evidence of holistic face processing when features (e.g. eyes, nose) are recognized more accurately in the context of a face than in isolation [1,12]. We trained wasps to discriminate between wasp face images that were experimentally altered so the outer part of the face (antennae, background, legs) were identical and the inner part of the face (clypeus, frons, inner eye) had natural levels of variation (figure 1). If wasps use featural mechanisms for face recognition, they will be equally adept at identifying the whole face and central face because all the featural differences between the two face images occur in the central part of the face. If wasps use holistic mechanisms for face recognition, they will identify the whole face more accurately than the central face.

2. Methods

(a) Species

P. fuscatus use visual face signals for individual recognition [16,29]. Wasps use individual recognition to minimize conflict in groups of cooperating foundresses [16,30] and to assess potential rivals via social eavesdropping [31]. *P. fuscatus* often nest in large cooperative groups where each foundress has a unique social role [32]. Individual recognition allows foundresses to keep track of individual social relationships, including division of aggression, food and work on nests [16]. Outside nests, individual recognition is used to assess rivals via social eavesdropping and memory of past interactions [31].

Polistes dominula also have visual signals, but these signals convey information about fighting ability rather than individual identity. Strong *P. dominula* have more broken black facial patterns than weaker *P. dominula* [25]. Signals of fighting ability are used to minimize the costs of conflict when animals interact with unfamiliar rivals [26]. Signals of fighting ability are quite different from signals of individual identity. First, the facial patterns that signal fighting ability have insufficient variation for individual recognition [24]. Second, signals of individual identity require wasps to learn and remember unique faces, while signals of fighting ability do not require learning and memory. For example, during individual recognition, wasps learn the unique facial features of conspecifics, associate the facial features with specific information about their rival, then recall both the face and the rival-related information during subsequent interactions. Effective signals of fighting ability only require wasps to assess whether the signal of an unknown rival indicates that the rival is strong or weak, not to learn or remember the faces of social partners [26]. As a result, having a signal of fighting ability is unlikely to influence their ability to learn and remember faces, as quality signalling does not involve face learning and previous experiments have shown that *P. dominula* are not capable of individual face recognition in any sensory modality [24].

(b) Collection

P. fuscatus and *P. dominula* wasps used in the experiment were collected from areas surrounding Ann Arbor, MI. After collection, wasps and their nests were housed in individual containers under a natural day/night cycle and fed *ad lib* with sugar and caterpillars. All experiments were performed with nest-founding queens prior to worker emergence.

(c) Stimuli

Wasps from both species were trained to discriminate between pairs of *P. fuscatus* or *P. dominula* face images species and then tested for their recognition abilities both with the whole faces or with the inner part only (figure 1). The particular face was chosen as the correct stimulus was swapped across wasps. Face images were photographs of wasps from Michigan, USA. Face images were altered in Adobe Photoshop so all the differences between the two face images occurred in the central inner part of the face. The outer part of the faces (antennae, background, legs) was identical between both faces, while the inner part of the face (colours on the clypeus, frons, inner eye) had natural levels of variation. All images were printed at life size (face approx. 3.5 mm wide) using a commercially available Sony Picture Station photo printer that uses ink cartridges.

(d) Training and testing procedure

Wasps were initially individually trained to discriminate a pair of whole face images (figure 1) using the same setup used in [27,33] (electronic supplementary material, figure S1). During training, wasps were placed in a 2.5 wide × 4 long × 0.7 height cm wood and plexiglass box with six identical stimuli glued onto the inside walls. Two longer sides had two face pictures each, while two shorter sides had one face picture each. In half of the bouts, the wasp was placed in the box with only incorrect face stimuli (CS+) and received a mild electric shock from an electrified pad for 2 min. The entire floor was electrified. The electrified pad was made of anti-static conductive foam electrified by two copper wires connected to a Variac transformer, which provided continuous 0.4 volt AC 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 the other half of the bouts, the wasp was placed in a box with only the correct face stimuli (CS−) for 2 min while the pad was not electrified. Between each bout, the wasp was given a 1 min break in a holding container. This sequence of one CS+ and one CS− bouts was repeated three times per wasp, so wasps experienced three CS+ and three 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 then tested twice: once using whole face stimuli and once using inner face stimuli. The testing order was randomized so that half the wasps were initially tested on whole faces and half were initially tested on inner faces. Whether a stimulus was tested first or second did not influence performance (see results). Learning performance was assessed by measuring whether the wasp approached the correct (CS−) or incorrect (CS+) image over 10 trials separated by 1 min breaks. After the first bout of 10 testing trials, each wasp was given a 45 min break, then tested for 10 trials on the second set of stimuli. Testing occurred in a 3 × 10 × 0.7 cm rectangular box. One end of the rectangle displayed the correct stimulus (CS−) while the other end of the rectangle displayed the incorrect stimulus (CS+). The entire floor of the rectangle was electrified except the 2.25 cm zone closest to the correct stimulus, the 'safety zone'. The correct choice was associated with safety to ensure learned preferences from the initial training were not extinguished during the 10 trials test. Receiving a shock while choosing a preferred stimulus can rapidly extinguish learned preferences.

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, the electric shock was turned on for five seconds, both partitions were removed simultaneously, and the wasp was free to walk through the rectangle. Providing an electric shock ensured wasps' motivation to look for the correct, 'safe', stimulus. Wasps who learned to discriminate the faces during the training phase typically turn toward the correct stimulus while confined in the centre and quickly walk toward it as soon as the partitions were removed. A choice was scored when the wasp's head entered one of the 2.5 cm zone closest to each stimulus, at each end of the rectangle. The stimuli subtended a visual angle of approximately 30° at the 2.5 cm distance. Wasps are scored as making a choice before they reach the non-shocking safety zone to ensure wasps made choices based on learned stimuli preferences rather than directly assessing the presence or absence of shock. Wasps made quick choices (typically less than 5 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 correct (CS−) and incorrect (CS+) 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.

(e) Statistical analysis

Twenty-three *P. dominula* were trained on *P. dominula* faces. Twenty-three *P. dominula* were trained on *P. fuscatus* faces.

Twenty-one *P. fuscatus* were trained on *P. dominula* faces. Fifteen *P. fuscatus* were trained on *P. fuscatus* faces. Each wasp was tested on both whole and inner face stimuli.

The data were analysed using generalized mixed linear models (GLMM) with a binomial error structure—logit-link function (*glmer* function of R package *lme4*) [34]. The dependent variable was the number of correct choices out of 10. The independent variables (fixed factors) were *Species* trained (categorical: *P. fuscatus* or *P. dominula*), *stimuli* species (categorical: *P. fuscatus* or *P. dominula*), whole versus inner face (called *test*, categorical: whole or inner) and *order* (continuous: first or second stimuli tested). *Wasp ID* was included as a random factor to account for the repeated-measure design as each wasp was tested on both whole and inner faces. Several models were run by testing interactions between factors and by dropping each factor subsequently to select the significant model with the highest explanatory power (i.e. the lowest AIC value) (See statistical tables in electronic supplementary material).

Tukey post hoc tests using the *ghlt* function (*multicomp* R package) [35] were run on the best models after splitting the data between species to compare tests performance between conditions. A Wilcoxon test was used to compare directly the performance of both species for the *P. fuscatus* faces.

We finally compared performance in each test to the 50 : 50 random expectation using a binomial test. The binomial test provides an exact test of whether the number of correct versus incorrect choices differs from the 50 : 50 random expectation.

All statistical analyses were performed with R 3.4.2 (R Development Core Team, 2016).

3. Results

There are significant differences in how *P. fuscatus* and *P. dominula* process faces (figures 2 and 3). Face recognition was influenced by the three-way interaction between species trained, stimulus species and whole versus inner face (χ^2 = 14.35, $p = 0.006$; electronic supplementary material, table S1). However, discrimination performance was not influenced by the order of the tests (χ^2 = 0.04, $p = 0.85$; electronic supplementary material, table S1). We further analysed the data by examining the performance of each species separately.

P. fuscatus process conspecific faces holistically but do not use holistic processing for heterospecific faces (figure 2). Indeed, there was a significant interaction between the stimuli species and the whole or inner face stimuli tests (χ^2 = 7.94, p = 0.005; electronic supplementary material, table S2). The significant interaction occurs because *P. fuscatus* recognize whole *P. fuscatus* faces more accurately than they recognize inner *P. fuscatus* faces (figure 2, $Z = 4.05$, $p < 0.001$). By contrast, *P. fuscatus* recognize whole and inner *P. dominula* faces with similar accuracy (figure 2, $Z = 0.50$, $p = 0.96$). Indeed, *P. fuscatus* succeeded in discriminating whole *P. fuscatus* faces (0.69 ± 0.03% of correct choices (mean ± s.e.m.); $p = 0.006$) but not partial *P. fuscatus* faces (0.46 ± 0.02%; $p = 0.36$). *P. fuscatus* also discriminated both whole and inner *P. dominula* faces better than expected by random chance (whole: 0.61 ± 0.03%, $p = 0.01$; inner: 0.59 ± 0.03%, $p = 0.01$).

P. dominula do not process either conspecific or heterospecific faces holistically and face processing consequently did not differ across stimuli. Performance was not influenced by the interaction between stimulus species and whole versus inner face (figure 3, χ^2 = 0.06, $p = 0.81$; electronic supplementary material, table S3), by the stimuli species (χ^2 = 0.005, p = 0.95), the type of test (whole versus inner face, χ^2 = 0.11, $p = 0.74$) or the order of the tests (χ^2 = 0.13, $p = 0.72$). The lack of significant interaction illustrates that *P. dominula* use the same processing mechanisms for learning conspecific and heterospecific faces. *P. dominula* discriminated all types of stimuli: *P. dominula* faces (whole: 0.59 ± 0.03%, $p = 0.01$, inner: 0.60 ± 0.03%, $p = 0.002$) and *P. fuscatus* faces (whole: 0.60 ± 0.02%, $p = 0.006$, inner: 0.60 ± 0.02%, $p = 0.004$).

Finally, *P. fuscatus* learned to discriminate whole conspecific faces more accurately than *P. dominula* discriminate the same stimuli ($W = 250$, $p = 0.02$), consistent with holistic face processing providing a learning advantage.

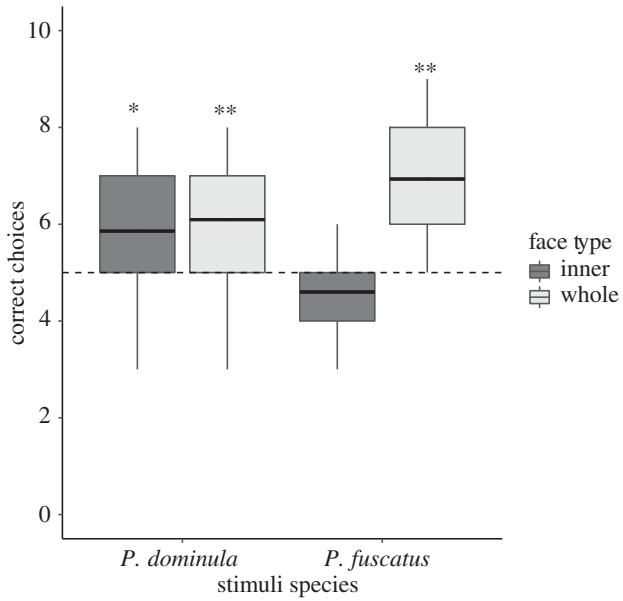

Figure 2. *P. fuscatus* face discrimination when wasps are tested on *P. dominula* and *P. fuscatus* whole and inner face stimuli after being trained with the whole faces. Box: 1Q, mean, 3Q. Whiskers: min/max. Dotted line represents the 50 : 50 random choice expectation. Stars reflect significant difference from random choice $*p < 0.05$, $**p < 0.01$.

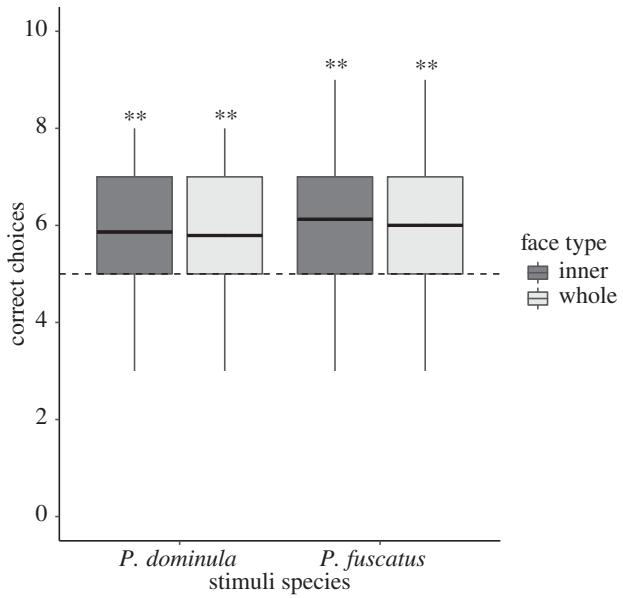

Figure 3. *P. dominula* face discrimination when wasps are tested on *P. dominula* and *P. fuscatus* whole and inner face stimuli after being trained with the whole faces. Box: 1Q, mean, 3Q. Whiskers: min/max. Dotted line represents the 50 : 50 random choice expectation. Stars reflect significant difference from random choice $**p < 0.01$.

4. Discussion

P. fuscatus wasps use holistic processing to identify conspecific, but not heterospecific faces. *P. fuscatus* easily differentiated whole conspecific face images. However, *P. fuscatus* were unable to differentiate faces when only the inner part of the face was available. The inability to discriminate inner face images was somewhat surprising because the images were experimentally manipulated to ensure the inner face images contained the same amount of information as whole face images because the outer part of the face was identical across stimuli. Further, there is nothing inherently difficult about recognizing inner face images, as *P. fuscatus* recognized whole and inner heterospecific faces with similar accuracy. Therefore, results of part-whole face discrimination tests suggest that *P. fuscatus* wasps use holistic processing to identify conspecific but not heterospecific faces. *P. fuscatus* encode conspecific facial features as integral parts of the face rather than as separate features. As a result, wasps do not identify conspecific facial features outside of the context of a face.

Although many taxa may use first-order configural information during object recognition [2,21,36], this study provides the first evidence to our knowledge of holistic processing of conspecific faces in a non-primate species. Holistic face processing is key to fast, accurate individual face recognition in humans [1,5] and likely serves a similar function in paper wasps. Individual face recognition is indeed an important aspect of the social life of *P. fuscatus*, as wasps learn and remember the unique facial patterns of many individuals on and off nests [16,31]. The species specificity of holistic face processing in *P. fuscatus* matches previous work in primates [2]. Like wasps, humans naturally use holistic face processing to identify conspecific faces, but do not naturally use holistic processing for heterospecific faces [37].

Our results also demonstrate that *P. dominula*, a related species of *P. fuscatus*, do not use holistic processing to identify conspecific or heterospecific faces (figure 3). Instead, *P. dominula* use featural processing to identify all face images. The lack of holistic processing in *P. dominula* is consistent with the hypothesis that holistic processing is an adaptation to facilitate individual face discrimination. *P. dominula* provide a particularly interesting comparison to *P. fuscatus* because they are closely related and both species use facial patterns for social interactions. Nevertheless, the species differ in holistic processing for conspecific faces, likely because *P. fuscatus* learn and remember the unique faces of many conspecifics, while *P. dominula* do not. Instead, facial patterns in *P. dominula* are status badges that signal fighting ability. Strong wasps have different facial patterns than weak wasps [25,26]. Wasps gain information about fighting ability without learning and remembering specific conspecific facial patterns. Consequently, holistic face processing likely provides no evolutionary benefit to *P. dominula* wasps, in contrast with *P. fuscatus*.

Importantly, the difference in performance between species and face stimuli probably do not arise from the characteristics of the face stimuli. Both *P. fuscatus* and *P. dominula* faces have general characteristics that are thought to facilitate configural processing. Previous work suggests that features are more likely to be processed using configural mechanisms when features are predictably arranged with variation in specific areas [21]. For example, human faces have a predictable arrangement (eyes above nose above mouth). Face variation occurs in the size and shape of features as well as their spacing. In *P. dominula*, wasps vary in the size and shape of black clypeus spots [25]. *In P. fuscatus*, faces vary in the brown, black, and yellow coloration in four facial areas (clypeus, frons, inner eye and outer eye) [16]. The predictable variation facilitates categorization and visual search because it is straightforward for receivers to focus on the most informative visual features. As a result, stimuli that have predictable configurations may favour the evolution of specialized mechanisms to extract relevant information [38].

This study thus adds to previous work in wasps suggesting that individual recognition is linked to specific face processing mechanisms. For example, *P. fuscatus* learn normal conspecific faces faster and more accurately than altered faces (jumbled facial features, antennae digitally removed), other biologically relevant visual objects such as prey items or simple geometrical forms [23]. Less work has examined face processing in *P. dominula*, though *P. dominula* seem also to have difficulty in learning face stimuli when the antennae are removed [28]. The current study used controlled stimuli with identical antennae and body position, finding no evidence of specialized face processing in *P. dominula*.

Paper wasps also allow us to study the role of experience in the development of specialized face processing. Testing the role of experience in face specialization is difficult in primates [7,39,40]. Previous studies have shown that *P. fuscatus* wasps raised in isolation without social contact lost their facility for individual face recognition [33]. Additionally, raising *P. fuscatus* wasps with *P. dominula* prevented the development of specialized conspecific face processing [27]. In parallel, *P. dominula* individuals raised with *P. fuscatus* did not show specialized processing for *P. fuscatus* faces but did improve *P. fuscatus* face learning performance [27]. Therefore, face specialization is influenced by both experience and innate, species-specific differences.

In conclusion, this study illustrates that species-specific evolutionary adaptation plays a key role in the development of holistic processing. Selection for efficient individual recognition has favoured the adaptive evolution of holistic face processing in *P. fuscatus*. Our results also confirm that holistic processing did not emerge with the development of large, sophisticated brain in primates. Instead, holistic face processing provides a remarkable example of convergent evolution between wasps and mammals. Although mammals and wasps have different sensory and neural structures, holistic processing has arisen independently in both groups suggesting the efficiency of such mechanism for accurately learning a large number of similar visual objects. Future work should explore whether face-processing specialization in wasps relies on the development of specific neuronal networks as found in primates.

Ethics. Our protocols comply with standard welfare practice in our field.

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

Authors' contributions. A.A.W. conceived the project. A.A.W. and E.A.T. designed the experiments. J.R.M. performed the experiments. E.A.T. and A.A.W. analysed the data. A.A.W., E.A.T. and J.P.S. wrote the manuscript.

Competing interests. We declare no competing interests.

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