



# Social experience drives the development of holistic face processing in paper wasps

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## Abstract

Most recognition is based on identifying features, but specialization for face recognition in some taxa 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. Although previous work suggests that extensive experience may be required for the development of holistic processing, we lack experiments that test how age and experience interact to influence holistic processing. Here, we test how age and experience influence the development of holistic face processing in *Polistes fuscatus* paper wasps. Previous work has shown that *P. fuscatus* use facial patterns to individually identify conspecifics and wasps use holistic processing to discriminate between conspecific faces. We tested face processing in three groups of *P. fuscatus*: young (1-week-old), older, experienced (2-weeks-old, normal experience), and older, inexperienced (2-weeks-old, 1 week normal social experience and 1 week social isolation). Older, experienced wasps used holistic processing to discriminate between conspecific faces. In contrast, older inexperienced wasps used featural rather than holistic mechanisms to discriminate between faces. Young wasps show some evidence of holistic face processing, but this ability was less refined than older, experienced wasps. Notably, wasps only required 2 weeks of normal experience to develop holistic processing, while previous work suggests that humans may require years of experience. Overall, *P. fuscatus* wasps rapidly develop holistic processing for conspecific faces. Experience rather than age facilitates the transition between featural and holistic face processing mechanisms.

**Keywords** Configural processing · Featural processing · Second-order relations · Visual cognition · Face recognition · Insect cognition

## Introduction

Rapid and accurate recognition of potential predators, prey, objects, and conspecifics plays an important role in an animal’s ability to successfully navigate their environment. Selection shapes responses to visual information such that animals are attuned to highly salient stimuli, like responding more strongly to stimuli that are animate rather than inanimate (Lorenzi and Vallortigara 2021). Recognition is often based on the specific features of an image, termed featural processing. During featural processing, animals use features such as color, contour, shape, and contrast to identify objects (Gothard and Brooks 2009). In contrast, conspecific face recognition in humans, some nonhuman primates,

and *Polistes* paper wasps is based on another mechanism, termed holistic processing (Tanaka and Farah 1993; Maurer et al. 2002; Tibbetts et al. 2021). During holistic processing, images are identified as a ‘gestalt’ or global representation where the whole is greater than the sum of its parts. Receivers simultaneously assess multiple facial features (e.g. eye color, mouth shape) and relationships among these features (e.g. large distance between eyes and mouth) (Tanaka and Farah 1993). Holistic processing is relatively rare, confined to a few taxa and stimulus types. As a result, there has been much interest in how and why holistic processing develops, particularly in the type and amount of experience required for the development of holistic face processing (Gauthier et al. 1998; Robbins and McKone 2007).

Much of the interest in the development of holistic face processing stems from long-standing debate over whether faces are processed differently than other stimuli because faces are inherently special or because individuals have an enormous amount of experience discriminating faces

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(Kanwisher 2000; McKone et al. 2007). Most current work suggests that both play a role: faces are inherently special, and experience facilitates holistic processing (Gauthier et al. 1998; Robbins and McKone 2007). Many taxa are inherently attuned to faces. For example, newly hatched chicks and newborn humans show spontaneous preference for face-like stimuli (Rosa-Salva et al. 2010; Rosa Salva et al. 2011). However, face recognition also changes with both age and social experience (Richler and Gauthier 2014). Thus far, it has been difficult to rigorously test the role of experience in the development of holistic face processing because it is difficult to experimentally manipulate face experience in humans and other primates. As a result, we lack the controlled experiments necessary to test how age and experience influence the development of holistic face processing.

Some research in humans suggests that experience influences holistic face processing (Richler and Gauthier 2014). First, holistic face processing continues to improve over childhood and into adolescence, suggesting that years of experience with faces may facilitate holistic processing (Mondloch et al. 1999). However, factors other than experience could account for how face processing changes as humans mature. A few creative experiments provide more clear-cut evidence that experience influences the capacity for holistic face processing. For example, humans with poor vision due to congenital cataracts have impaired holistic face processing (Robbins et al. 2010). Further, humans use more holistic processing to discriminate faces within their own race than faces of a different race, but this effect can be reversed through more experience with other race faces (Michel et al. 2006; Mondloch et al. 2010; Scott and Monesson 2010; Bukach et al. 2012). Finally, a few studies have altered human experience with monkey faces finding that infants given experience individually discriminating monkey faces exhibit more holistic processing for monkey faces than other infants (Pascalis et al. 2005). Therefore, there are multiple lines of evidence that suggest experience influences how humans process faces.

The second main type of evidence that experience plays a role in the development of holistic processing comes from studies that alter human exposure to non-face stimuli. Humans often use holistic processing for non-face objects after extensive experience with those objects. For example, adults trained to be experts in novel objects called “greebles” are more likely to use holistic processing to discriminate greebles than novices (Gauthier and Tarr 1997; Gauthier et al. 1998). Furthermore, expert chess players process chess boards more holistically than novice chess players (Boggan et al. 2012). However, other work has found no consistent relationship between experience and holistic processing. For example, Tso et al. (2014) report a U-shaped relationship between experience using Chinese characters and holistic processing. Bauser et al. (2011) found that humans do not

recognize bodies holistically despite encountering bodies as frequently as faces. Holistic processing may be more likely to develop when viewers have extensive experience assessing and discriminating objects using fine variation in the appearance of those objects. Therefore, expertise may facilitate holistic processing, but the relationship between experience and holistic processing is not straightforward (Bukach et al. 2006).

While many studies have explored the development of holistic processing, less is known about whether holistic processing is beneficial. Some argue that holistic processing leads to more robust face representations than featural recognition. As a result, holistic processing may allow faster recognition, better face memory, or more accurate recognition across different viewpoints or facial expressions (Calder et al. 2000; McKone 2008). Consistent with this hypothesis, humans have a better visual short-term memory for faces than other objects (Curby and Gauthier 2007). Some experimental work found a small but significant recognition benefit associated with holistic processing, as individuals with greater holistic processing ability had greater face recognition ability (Duchaine and Nakayama 2006; Richler et al. 2011). However more recent studies using a larger sample size and more sophisticated assessment of holistic processing found no recognition benefit linked with holistic processing (Konar et al., 2010; Richler et al., 2015). Therefore, while theory suggests holistic processing may improve recognition, we lack empirical tests of how holistic processing influences recognition accuracy or face memory.

Here, we use *Polistes fuscatus* paper wasps as a model to test both the role of experience in the development of holistic processing and whether holistic processing is linked with improved face memory. *Polistes fuscatus* are a good system to address these issues because they are the only non-primates known to use holistic processing to identify the individual faces of conspecifics (Tibbetts et al. 2021). Holistic processing was tested using an adaptation of the part-whole method that accounts for the wasp's visual acuity. 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 (Tanaka and Farah 1993). Consistent with holistic processing, *P. fuscatus* easily learn to differentiate between whole conspecific face images but are unable to differentiate faces when only the inner part of the face is available. Interestingly, *P. fuscatus* do not use holistic processing to discriminate between heterospecific face images, as wasps are equally adept at learning to discriminate between whole and inner images of *Polistes dominula* faces (Tibbetts et al. 2021). *P. fuscatus* wasps may have evolved holistic processing of conspecific faces to facilitate individual face recognition. Wasps individually recognize each other using variable facial patterns (Tibbetts 2002). Individual face recognition is an important

aspect of the social behavior of paper nest-founding queens and workers, as it is used to manage social relationships and minimize aggressive conflict on and off nests (Sheehan and Tibbetts 2009; Injaian and Tibbetts 2014; Tibbetts et al. 2020).

We tested the development of holistic face processing by independently controlling age and experience, then tested the wasp's capacity for holistic processing using the part/whole test. We trained wasps to discriminate between wasp face images that were experimentally altered so the outer part of the face (antennae, background, legs) was identical and the inner part of the face (clypeus, frons, inner eye) had natural levels of variation (Fig. 1). If wasps use featural mechanisms for face recognition, they will be equally adept at identifying the whole face and inner face because all the featural differences between the two face images occur in the inner part of the face. If wasps use holistic mechanisms for face recognition, they will identify the whole face more accurately than the inner face.

Wasps were reared in three treatment groups: (1) Young: wasps reared on their natal nest for 6–8 days, (2) Older, inexperienced: wasps reared on their nest for 6–8 days, then isolated until they were 15–18 days old, (3) Older, experienced: wasps reared on their natal nest for 15–18 days. Young and older, inexperienced wasps are different ages but have the same amount of social experience. Older, inexperienced and older, experienced wasps are the same age, but have different amounts of social experience. If experience with conspecific faces facilitates the development of holistic processing, we predict older, experienced wasps will use holistic face processing, while young and older, inexperienced wasps will not use holistic face processing.

We also tested whether holistic face processing is linked with improved face memory by assessing face memory eight days after initial training. If holistic processing is linked with improved face memory, we predict wasps that identify faces more holistically will have more accurate face memory than wasps that identify faces less holistically.



**Fig. 1** Example images of *Polistes fuscatus* used for training and testing. Legs, body, antennae, and background are identical in whole and inner faces. Both whole and inner faces have natural levels of facial color and pattern variation

## Methods

### Wasp rearing

Wasps and their nests were collected throughout south-east Michigan USA and were housed in the lab with ad lib water, sugar, and caterpillars. All wasps used in the experiment emerged from pupation in the lab from July 1, 2020 through August 9, 2020 and were workers. Nests were checked daily for newly emerged wasps. Wasps were assigned to treatment groups evenly to ensure that date of eclosion from pupation did not differ across the groups.

At emergence from pupation, wasps were uniquely marked using non-toxic modeling paint and placed in one of three treatment groups. Young wasps were raised on their natal nest until they were 6–8 days old. Older, experienced wasps were raised on their natal nest until they were 15–18 days old. Older, inexperienced wasps were raised on their natal nest until 6–8 days old and then isolated until 15–18 days old. Isolated wasps were housed in individual containers with ad lib water, sugar, and caterpillars. Wasps were trained and tested as described below when they reached the appropriate age for their treatment group. After training and testing, we returned wasps to their nests or isolation containers. We retested wasps eight days after the initial testing to assess memory.

*Polistes* are considered behaviorally mature when they are 5 days old because they engage in a range of adult *Polistes* behavior, including cooperative and competitive interactions with conspecifics, egg-laying, flying, hunting, and navigating (Reeve 1991; Giray et al. 2005; Shorter and Tibbetts 2009). Wasps usually enclose from pupation onto a nest full of other wasps and gain ample social experience as they mature. However, wasps occasionally experience social isolation when they emerge onto nests that were abandoned during their pupal period or leave their natal nest.

### Stimuli

We measured holistic processing by adapting the part/whole test for wasps (Tibbetts et al. 2021). The part/whole test has been used to assess holistic processing in primates, *Apis mellifera* honeybees, and *Polistes fuscatus* paper wasps (Tanaka and Farah 1993; Avargues-Weber et al. 2018; Tibbetts et al. 2021). 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. We adapted the part/whole test to account for a wasp's visual acuity by comparing a wasp's response to whole face vs inner faces.

Some research in humans compares responses to the whole face and to a single facial feature (e.g. nose), but single features may be difficult for wasps to discriminate from a distance. Wasps were trained 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 (Fig. 1). If wasps use featural mechanisms for face recognition, they will be equally adept at identifying the whole face and inner face because all the featural differences between the two face images occur in the inner part of the face. If wasps use holistic mechanisms for face recognition, they will identify the whole face more accurately than the central face. Four stimuli sets were used.

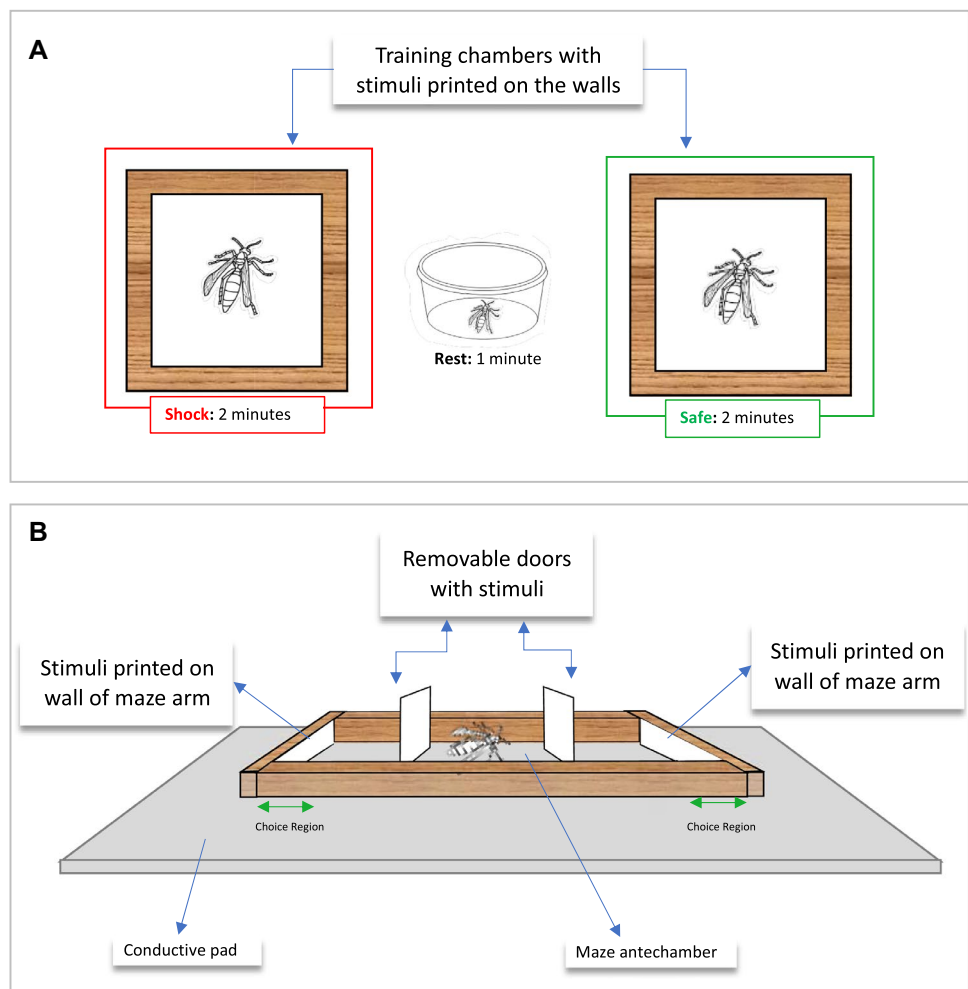
Wasps were trained to discriminate a pair of *P. fuscatus* whole face images. Then, we tested their ability to discriminate both whole face images and images with only the inner part of the same face (Fig. 1). To create the face images, photographs of wasps from Michigan, USA were taken and altered in Adobe Photoshop. Faces were altered so that

the antennae, legs, and background were identical across stimuli. The only variation between stimuli occurred in the inner part of the face (clypeus, frons, inner eye) (Fig. 1). All images were printed at life size (face approx. 3.5 mm wide) using a commercially available Xerox Altalink C8035 that uses ink cartridges.

## Training

We trained and tested wasps' ability to discriminate between a *neutral face* stimulus and a *shock associated face* stimulus using established methods (DesJardins and Tibbetts 2018; Tibbetts et al. 2019a, b, 2021). We trained wasps by placing them in  $2.5 \times 4 \times 0.7$  cm wood boxes with 6 identical face stimuli attached to the walls (Fig. 2). In half of the training trials, a wasp was placed in a box with only incorrect face stimuli (CS +) while receiving a mild electric shock for 2 min. An electrified pad made of anti-static conductive foam electrified by two copper wires connected to a Variac transformer conducted the shock. The Variac provided a continuous 0.4 V AC current which is not harmful to wasps.

**Fig. 2** Training and testing method. **a** Training occurs in smaller chambers with stimuli lining the walls. Wasps were placed in chambers with incorrect face images while receiving a mild electric shock. Then, wasps were placed in chambers with correct face images and did not receive an electric shock. **b** During testing, wasps were placed in a rectangle with the correct face image one end and the incorrect face image on the other end. Learning was tested by measuring whether the wasp approached the correct or incorrect stimulus pair over 10 trials. Stimuli location was swapped across trials to ensure wasps were responding to the stimuli rather than location. Figure modified from (Weise et al. 2022)



In the other half of the training trials, the wasp was placed in a box with only the correct face stimuli (CS–) for two minutes with no shock. The wasp received a one-minute break in a separate container between each trial. The sequence of one CS+ and one CS– trials was repeated five times per wasp, so wasps experienced five CS+ and five CS– trials in total. After training and prior to testing, the wasp was given a 45-min break in a separate container.

## Testing

After training, each wasp was tested once with whole face stimuli and once with inner face stimuli. Testing order was randomly assigned so half the wasps were initially tested with whole faces and half were initially tested with inner faces. Wasps performed better on the second test than on the first test ( $t = -2.14$ ,  $P = 0.018$ ,  $df = 52$ ). However, because testing order was randomized across treatments, the small order effect did not influence the overall results. Testing order was also included as a random effect in the statistical models.

Testing involved ten trials where the wasp was able to walk towards the correct (CS–) or incorrect (CS+) image. The same stimuli were used in all 10 trials. Between each trial, wasps rested for one minute in a separate container. Learning performance was measured as the number of correct choices over 10 trials. After being tested 10 times on one stimuli type (whole faces or inner faces), wasps were given a 30-min break in a separate container. Then, they were tested again to measure performance on the other type of stimuli (whole faces or inner faces).

Testing occurred in a  $3 \times 10 \times 0.7$  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+) (Fig. 2). The entire floor of the rectangle was electrified except the 2.25 cm closest to the correct stimulus to ensure that the learned associations from the training were not extinguished during testing. The rectangle was divided by two clear partitions. Wasps were placed in between the two partitions at the beginning of each testing trial. Then, the partitions were removed simultaneously to allow the wasp to walk to either side. A wasp was scored as making a decision when it entered a chamber in one arm of the maze. 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 do not change their choice behavior after approaching a “choice” zone, which suggests that they do not make choices based on minor differences in shock. Once a decision was made, wasps were removed and given a one-minute break in a separate container. We repeated this process ten times and randomly alternated the location of the stimuli to

ensure wasps made choices based on the stimuli rather than the location. There was no change in choice accuracy over the 10 trial test based on an analysis using generalized estimating equations with specific wasp ID as a subject variable ( $X^2 = 0.30$ ,  $p = 0.58$ ).

## Memory

We measured face memory by retesting wasps 8 days after initial testing. Wasps were housed in their regular treatment groups prior to the memory test. This means that *young* and *older, experienced* wasps were housed on their nest and *older, inexperienced* wasps were housed alone. Wasps were retested on the same whole face stimuli they were trained to discriminate during initial training and testing. Wasps were tested on whole face stimuli because whole face memory provides more information about natural recognition than inner face memory. The same methods were used for the memory tests as for the initial testing (see *Testing* section for additional information). The only methods difference is that no shock was used in the testing arena during the memory test. In the memory test, as in other tests, each wasp was tested 10 times. There was no change in choice accuracy over the 10 trials (generalized estimating equations with specific wasp ID as a subject variable,  $X^2 = 0.15$ ,  $p = 0.70$ ). Some wasps died between the initial test and the memory test, so they were not included in the memory analyses.

## Statistical analysis

There were 22 wasps in the young treatment group, 16 wasps in the old, experienced group, and 15 wasps in the old, inexperienced group. All analyses were performed using SPSS v. 24 and R v.4.1.2 (Team 2021). To compare holistic processing across groups, we used the formula  $([\text{whole face score} - \text{inner face score}] / [\text{whole face score} + \text{inner face score}])$  from Wang et al. (2012). A high score indicates whole faces are discriminated more accurately than inner faces, consistent with high levels of holistic face processing. A low score indicates whole and inner faces are discriminated similarly, consistent with featural rather than holistic face processing. Whole face score is the number of correct choices (out of 10) when wasps were tested on whole face stimuli. Inner face score is the number of correct choices (out of 10) when wasps were tested on inner face stimuli.

We compared holistic processing scores across wasps of different social experience using a mixed linear model. The dependent variable was holistic processing score. The independent variable was social treatment group (categorical: young, old and experienced, old and inexperienced). Random effects were the wasps' nest of origin, the specific face stimuli pictures used during training, and whether whole or inner face was tested first. The model gives a ‘singular fit’

warning because the random effects structure is complex. Removing whether whole or inner face was tested first as a random effect produces a model without a singular fit and with the same results. Pairwise posthoc analyses were performed with the Bonferroni correction. To facilitate visualization of the data, we plotted estimated holistic processing scores in Fig. 3. Estimates were calculated using the *effects* package in R, which absorbs the lower-order terms marginal to the term in question, and averages over other terms in the model (Fox and Weisberg 2019). Using estimated scores is valuable for visualizing the data when there are multiple independent variables and random effects. Estimates were not used for any statistical analyses. Instead, analyses were performed using raw holistic processing scores ([whole face score – inner face score]/[whole face score + inner face score]), see Wang et al. (2012).

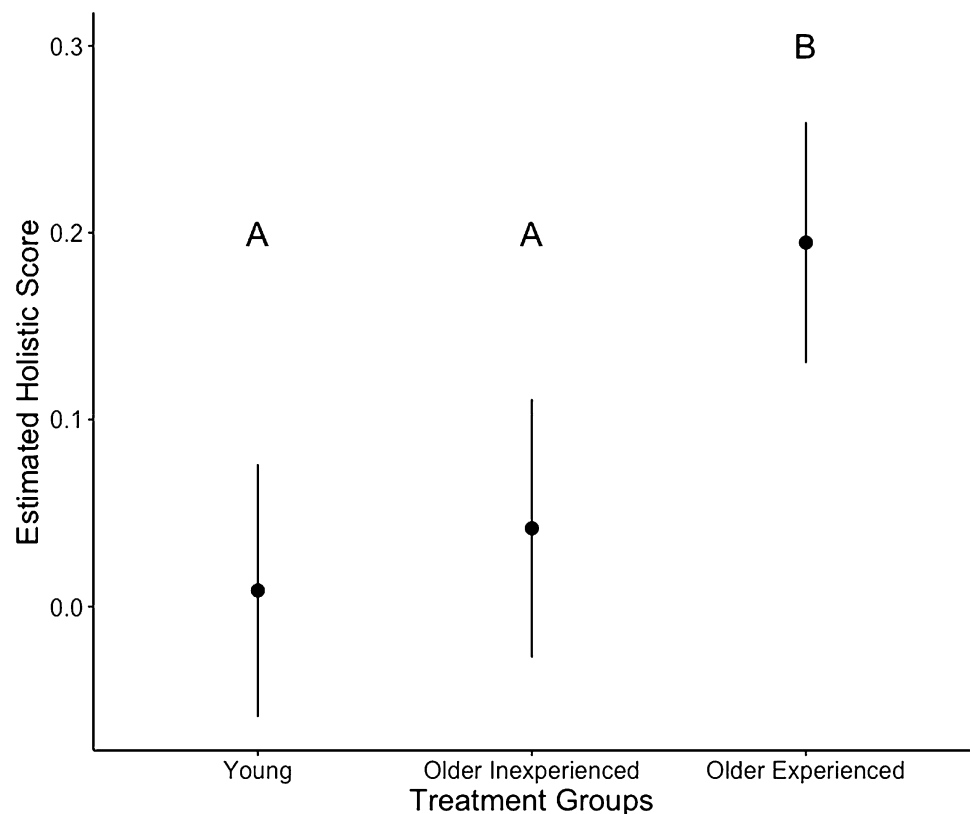
We tested whether differences in holistic processing score were caused by differences in whole face discrimination accuracy and/or inner face discrimination accuracy with mixed linear models where the data were split to separately analyze whole face and inner face learning. In both, the dependent variable was number correct (out of 10). The independent variable was social treatment group (categorical: young, old and experienced, old and inexperienced). Random effects were the wasps' nest of

origin, the specific face stimuli pictures used during training, and whether whole or inner face was tested first. Pairwise posthoc analyses were performed with the Bonferroni correction.

Within each social treatment group, we compared whole and inner face learning scores with a paired t-test. Finally, we used binomial tests to assess how performance in each treatment group and stimuli differed from the 50:50 random expectation. The binomial test provides an exact test of whether the number of correct vs incorrect choices differs from the 50:50 random expectation. Binomial tests provide p-values with no test statistics.

We analyzed the memory results using the same statistical tests. There were 15 wasps in the young treatment group, 13 in the old, experienced group, and 14 in the old, inexperienced group for memory testing. We tested whether wasps choose the correct choice more often than expected by chance using binomial tests. We also used a mixed linear model to test how performance in memory trials (out of 10) was linked with social experience (categorical: young, old and experienced, old and inexperienced) or holistic processing score during the initial training and testing (continuous). Random effects were the wasps' nest of origin and the specific face stimuli pictures used during training.

**Fig. 3** *Polistes fuscatus* holistic processing score (mean  $\pm$  SE). High holistic processing scores indicate wasps process faces more holistically, while lower scores indicate wasps process faces using featural mechanisms. Letters denote significant differences ( $p < 0.05$ ). Estimated holistic processing scores were estimated by including nest, stimuli set used for testing, and training order (whole or inner face first) as random factors in the *effects* R package



## Results

Experience influences holistic processing, as holistic process score differs across wasps with different social experience (Fig. 3,  $F_{2,40} = 5.8$ ,  $p = 0.006$ ; mean  $\pm$  st error young wasps =  $0.0712 \pm 0.03$ , old, inexperienced wasps =  $0.0516 \pm 0.04$ , old, experienced wasps =  $0.194 \pm 0.06$ ). Post-hoc pairwise analyses show that old, experienced wasps have higher holistic scores than young ( $p = 0.006$ ) and old, inexperienced wasps ( $p = 0.042$ ). Holistic scores of young and old, inexperienced wasps do not differ ( $p = 1.0$ ).

The high holistic processing score in old, experienced wasps is caused by experience decreasing inner face discrimination in old, experienced wasps rather than by a change in whole face discrimination. Whole face discrimination accuracy does not differ across treatment groups ( $F_{2,48} = 1.9$ ,  $p = 0.15$ ). In contrast, inner face discrimination accuracy differs across treatment groups ( $F_{2,42} = 9.9$ ,  $p < 0.001$ ), with old, experienced wasps having lower inner face discrimination than young ( $p < 0.001$ ) or old, inexperienced wasps ( $p = 0.01$ ). There is no difference in inner face discrimination between young and old, inexperienced wasps ( $p = 0.77$ ).

We also compared whole and inner face learning within each social experience group to test how age and experience influence whether wasps discriminate whole and inner faces with similar accuracy. Consistent with holistic processing, both old, experienced wasps and young wasps discriminate whole faces more accurately than inner faces (old, experienced  $t_{15} = 3.1$ ,  $p = 0.007$ , young  $t_{21} = 2.6$ ,  $p = 0.016$ ). However, there is no difference in whole and inner face discrimination in old, inexperienced wasps ( $t_{14} = 1.3$ ,  $p = 0.21$ ), consistent with featural processing.

Finally, we tested how social experience and stimuli type influenced whether or not wasps discriminated faces better than chance. Older, experienced wasps do not discriminate between inner face images, as they choose the correct inner face image at chance levels ( $p = 0.46$ ). However, wasps choose the correct face above chance level in other groups, including older, experienced wasps discriminating whole faces, young wasps discriminating whole and inner faces, older inexperienced wasps discriminating whole and inner faces (Table 1).

## Face memory

Wasps remembered the faces learned during initial training for at least eight days, as wasps performed better than chance when retested eight days after initial training (Fig. 5,  $p < 0.001$ , Table 1). Notably, when the data are

**Table 1** Results of binomial test analyses comparing how performance in each treatment group and stimuli differed from the 50:50 random expectation

| Treatment group     | Test type    | <i>p</i> -value   |
|---------------------|--------------|-------------------|
| Young               | Whole faces  | <b>&lt; 0.001</b> |
| Older experienced   | Whole faces  | <b>&lt; 0.001</b> |
| Older inexperienced | Whole faces  | <b>&lt; 0.001</b> |
| Young               | Center faces | <b>&lt; 0.001</b> |
| Older experienced   | Center faces | 0.69              |
| Older inexperienced | Center faces | <b>&lt; 0.001</b> |
| Young               | Memory       | <b>&lt; 0.001</b> |
| Older experienced   | Memory       | <b>0.03</b>       |
| Older inexperienced | Memory       | <b>0.002</b>      |

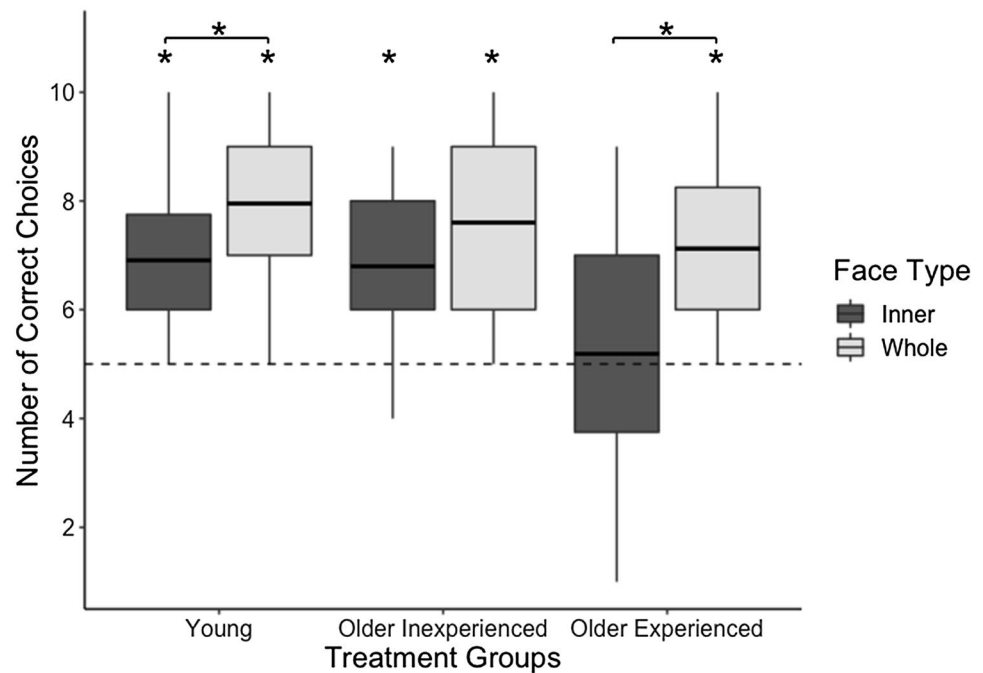
*p*-values bolded are significantly different than the 50:50 random expectation

split by treatment groups, wasps in all social treatment groups performed better than chance (Table 1). There is no evidence that holistic processing or social experience influences face memory. Whole face discrimination accuracy eight days after initial training was not associated with social experience ( $F_{2,38} = 1.0$ ,  $p = 0.37$ ) or holistic processing score ( $F_{1,38} = 0.004$ ,  $p = 0.95$ ).

## Discussion

Our results illustrate that experience with conspecifics plays an essential role in the development of holistic face processing. Notably, social experience, rather than age, is key to the development of holistic processing, as same age wasps with different amounts of social experience use different face processing mechanisms. Two-week-old wasps with normal social experience process faces holistically. These older, experienced wasps have the highest holistic processing score (Fig. 3). They also accurately differentiate whole wasp face images but are unable to differentiate inner wasp face images (Fig. 4). Two-week-old wasps with 1 week of normal social experience and 1 week of isolation (old, inexperienced wasps) use featural mechanisms to discriminate faces (Fig. 3). Old, inexperienced wasps have a low holistic processing score and discriminate whole and inner faces with similar accuracy (Fig. 4). Young wasps that are 1-week-old and have 1 week of normal social experience are just beginning to develop holistic face processing. These young wasps discriminate whole faces more accurately than inner faces, consistent with holistic face processing (Fig. 4). However, holistic face processing is less fully developed in young wasps than in older, experienced wasps. Young wasps

**Fig. 4** *Polistes fuscatus* whole and inner face test performance after wasps were trained to discriminate whole faces. Boxplots represents first quartile, mean, and third quartile. Old, experienced wasps and young wasps discriminated whole faces more accurately than inner faces ( $p < 0.05$ ). Old, inexperienced wasps discriminated whole faces and inner faces equally well ( $p = 0.21$ ). \* $p < 0.05$ . Dashed line shows the 50:50 random expectation



have lower holistic scores and discriminate inner faces more accurately than older, experienced wasps (Fig. 3).

A noteworthy aspect of our results is that increased social experience reduced inner face discrimination but had no effect on whole face discrimination. Experience typically improves performance, so we might naively predict that experienced wasps would be better at discriminating both whole and inner faces than less experienced wasps. However, a hallmark of holistic processing is that individuals encode conspecific facial features as integral parts of the face rather than as separate features. As a result, individuals that use holistic processing are unable to identify conspecific facial features outside of the context of a face (Tanaka and Farah 1993; Maurer et al. 2002). Therefore, experienced wasps' inability to discriminate isolated facial features is consistent with the development of holistic face processing. Importantly, the reduction in the inner face discrimination was not caused by differences in information available between whole and inner face stimuli. 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 (Fig. 1). In addition, recognizing inner face images was not inherently difficult, as 2-week-old workers with less social experience identified whole and inner heterospecific faces with similar accuracy (Fig. 4). Nevertheless, old, experienced wasps cannot discriminate inner faces, indicating that they encode conspecific facial features as integral parts of the face rather than as separate features.

Surprisingly little social experience is required for wasps to develop holistic face processing. After 1 week of

experience with conspecifics, young wasps were beginning to process faces holistically, as they identified whole faces more accurately than inner faces. After 2 weeks of experience with conspecifics, old, experienced wasps had more refined holistic processing. They were no longer able to discriminate facial features outside the context of a face. The 2 weeks of social experience required for wasp holistic processing is dramatically less than humans need to develop holistic face processing. Humans continue to refine holistic face processing through adolescence, after years of experience with hundreds of thousands of different faces (Mondloch et al. 2002). Perhaps the type and amount of experience needed for holistic processing varies across taxa that have different lifespans and social interactions. For example, the short timeline for developing holistic processing is consistent with wasps' relatively short lifespan. Wasp workers are considered behaviorally mature at 1 week and workers live for about 8 weeks (Reeve 1991; Giray et al. 2005; Shorter and Tibbetts 2009). Wasps also developed holistic processing despite only encountering a small number of unique individuals. Workers primarily interacted with nestmates, so they encountered approximately  $9 (\pm 6)$  other unique individuals based on censuses of the nests used in this experiment. Therefore, although experience may be required for the development of holistic processing in all taxa, the amount of experience likely differs based on the lifespan and social behavior of the specific taxa.

Older, inexperienced wasps are a crucial treatment group for understanding the role of age and experience in the development of holistic processing. Older inexperienced wasps had lower holistic processing scores than older, experienced

wasps (Fig. 3), providing strong evidence that experience rather than age plays a key role in the development of holistic processing. However, comparing older, inexperienced and young wasps is a bit more complex. Young and older, inexperienced wasps had similar holistic scores and similar amounts of social experience (Fig. 3), consistent with social experience influencing holistic processing. However, the two groups differ when whole and inner face learning is directly compared within each group using a paired *t*-test (Fig. 4). The paired *t*-test provides a more powerful test to identify any differences in whole and inner face learning than comparing the overall holistic scores across many wasps. The paired analysis shows that young wasps learn whole faces more accurately than inner faces, while older, inexperienced wasps learn whole and inner faces with similar accuracy. This result suggests that young wasps may begin to develop holistic processing after a week of social experience, but the initial low-level holistic processing may be lost after the week of social isolation experienced by the old, inexperienced wasps. Perhaps continued exposure to conspecifics is required for the maintenance of holistic processing.

Although much primate research has explored the role of experience in the development of holistic processing, this study is the first to test how experimentally altering social experience influences conspecific face processing. Altering conspecific face experience is not practical in primates. As a result, most work has tested how experience influences identification of other stimuli (e.g. non-face objects, faces of other primate species). This work has provided intriguing evidence that expertise can lead to holistic processing for stimuli including chess boards, greebles, and words (Gauthier and Tarr 1997; Wong et al. 2011; Boggan et al. 2012). However, experience does not always lead to holistic processing, as humans experienced with dogs do not use holistic processing to identify these stimuli (Gauthier et al. 1998; Robbins and McKone 2007). Similarly, *Polistes fuscatus* use holistic processing to identify conspecific faces but not heterospecific faces (Tibbetts et al. 2021). Therefore, both experience and stimuli type seem to influence the development of holistic processing. In future work, it will be interesting to test whether there are specific stimuli characteristics that are more likely to lead to holistic processing (Wong et al. 2009).

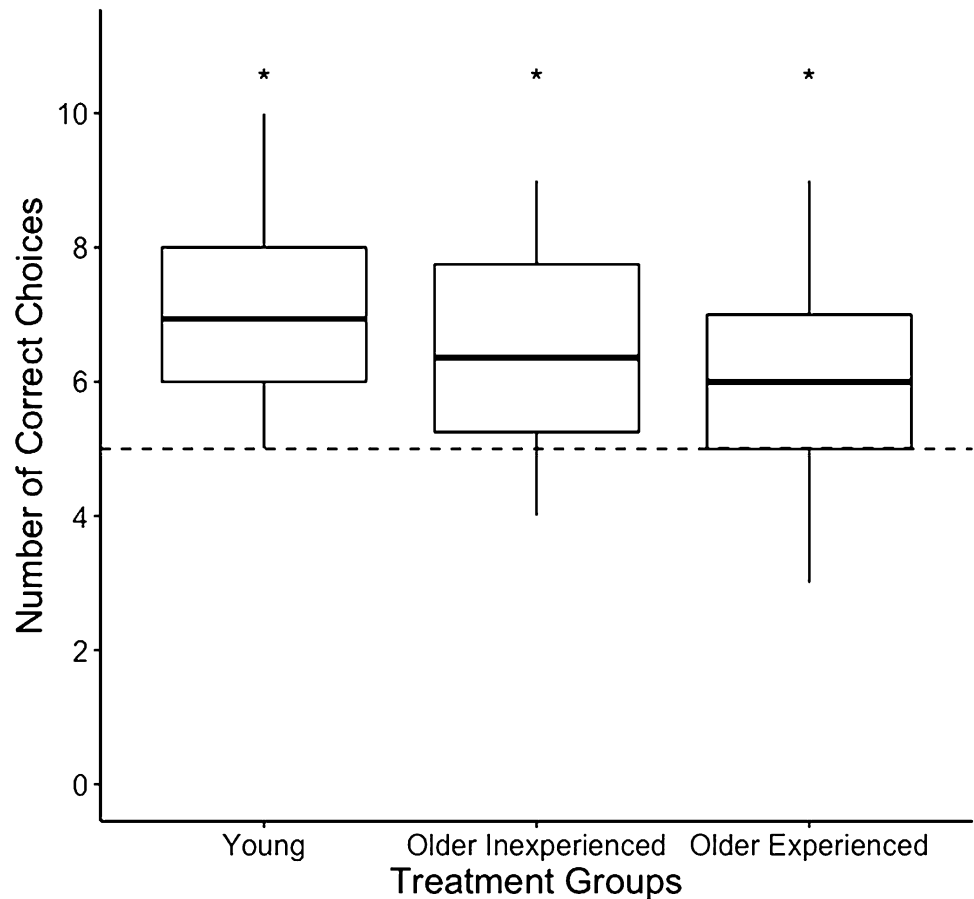
Previous research examining holistic processing in paper wasps focused on the nest founding queens (foundresses), while this study examined workers. Foundresses are more adept at face learning, as they require less initial training to learn conspecific faces than workers (Injaian and Tibbetts 2014; Tibbetts et al. 2018). Foundresses only require training with 3 sets of stimuli to discriminate faces with 70% accuracy, while workers require training with 5 sets of stimuli to perform similarly (Tibbetts et al. 2021; this study). The difference in face learning between queens and workers

may partially be due to experience differences between the castes. At the time of training, queens were approximately eight months old and we estimate that they had interacted with hundreds of wasps both on and off nests. Workers were only 1–2 weeks old and interacted with less than 30 individuals (maximum nest size = 20). Workers and queens are morphologically similar, and workers can become queens after overwintering, so there are unlikely to be fixed differences in the ability of workers and queens (O'Donnell 1998; Tibbetts 2007). In future work, it would be interesting to test whether workers can acquire queen-like recognition accuracy with sufficient experience.

We found no evidence that holistic processing is associated with a recognition benefit. Wasps that process faces more holistically were no better at remembering faces eight days after initial training than wasps that process faces less holistically. Although we did not identify a benefit associated with holistic processing, holistic processing could provide a recognition or memory benefit in other situations. For example, holistic processing could facilitate robust face recognition across different viewpoints or lighting (Calder et al. 2000; McKone 2008). Holistic processing could also improve memory over longer timescales or when a large number of individuals need to be remembered. This study assessed face memory at a single time point, eight days after training, using images taken from the same viewpoint with the same lighting. Therefore, additional research in different situations is needed to test whether holistic face processing provides benefits in terms of faster, more accurate, or longer lasting recognition. Finally, despite no relationship between holistic processing and face memory, it is notable that wasps were able to recall faces eight days after initial training (Fig. 5). Previous work has measured insect memory over shorter-times scales (Sheehan and Tibbetts 2008; Hourcade et al. 2009). Eight days is a relatively long time for a short-lived animal like a paper wasp especially because the initial training was relatively short (30 min). A memory for individuals that persists over multiple days of separation may not be beneficial for on-nest interactions among workers, but is likely to be valuable to wasps during off nest social interactions, including contests over dominance rank and social eavesdropping (Tibbetts et al. 2020) (see Fig. 5).

In conclusion, the development of holistic face processing is influenced by social experience rather than age. Two-week-old wasps with normal social experience use holistic processing to discriminate conspecific faces, while 2-week-old wasps with restricted social experience use featural mechanisms to discriminate conspecific faces. One-week-old wasps are beginning to develop holistic face processing, but this ability is less refined than more experienced wasps. While previous work in primates suggests that experience facilitates holistic face processing (Parr and Heintz 2006; Dahl et al. 2013), the challenge

**Fig. 5** *Polistes fuscatus* wasps memory for whole faces eight days after the initial training and testing. Boxplots represents first quartile, mean, and third quartile. All treatment groups remembered stimuli after 8 days ( $p < 0.05$ ). There was no difference in accuracy between the treatment groups. \*Indicates wasps discriminated stimuli significantly more accurate than expected by chance. Dashed line shows the 50:50 random expectation



of altering primate development has limited the types of experiments that are possible. Paper wasps are the only non-primate known to use holistic processing to identify conspecific faces, so they provide a valuable model for manipulative experiments that explore the mechanistic and evolutionary basis of holistic processing.

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## Declarations

**Conflict of interest** The authors have no competing or financial interests to disclose.

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