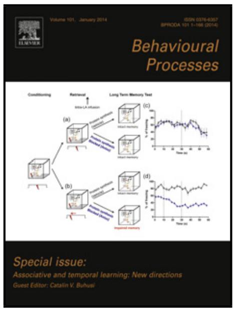

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Individual differences in exploratory activity relate to cognitive judgement bias in carpenter ants

Short title: exploration and cognitive bias in ants

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Highlights

- Individual ants show consistency in their exploratory behaviour
- Ants learn to associate a positive or negative stimulus with spatially distinct positions
- Cognitive judgment bias was tested with the stimulus in an intermediate position
- Fast explorers showed a pessimistic bias while slow explorers an optimistic bias
- Results suggest a link between personality and cognitive state in eusocial insects

ABSTRACT

Emotional state may influence cognitive processes such as attention and decision-making. A cognitive judgement bias is the propensity to anticipate either positive or negative consequences in response to ambiguous information. Recent work, mainly on vertebrates, showed that the response to ambiguous stimuli might change depending on an individual's affective state, which is influenced by e.g. the social and physical environment. However, the response to ambiguous stimuli could also be affected by the individual's behavioural type (personality), a question that has been under-investigated. We studied the link between individual differences in exploratory activity and the response to an ambiguous stimulus in the ant *Camponotus aethiops*. Exploratory behaviour, quantified with an open-field test, was variable among individuals but consistent over time within individuals. Individual ants learned to associate a spatial position to a reinforcement and another spatial position to a punishment. Once the ants had acquired this discrimination, cognitive judgement bias was tested with the stimulus in an intermediate position. Fast explorers in the open-field took significantly more time to approach the ambiguous stimulus compared to slow explorers, suggesting a negative judgement bias for fast explorers and a positive bias for slow explorers. This previously unknown link between individual difference in exploratory activity and cognitive bias in a social insect may help understanding the evolution and organization of social life.

Keywords: affective state, cognition; exploratory activity; learning; personality; social insects

1 INTRODUCTION

Animals show the ability to feel emotions that may induce long-lasting consequences (e.g., Désiré et al., 2002). For their assessment, indirect methods such as measuring stress hormones or quantifying abnormal behaviour are usually employed (Bateson and Matheson, 2007). It is increasingly acknowledged that affective state (driven by e.g., emotions) may influence cognitive processing in animals as in humans (e.g., Harding et al., 2004). In particular, the positive or negative valence of an affective state may bias cognitive processes such as attention, memory, and judgement (e.g., Novak et al., 2015). This phenomenon is generally referred to as ‘cognitive bias’. In the present study, we focus on ‘cognitive judgement bias’ following the definition by Mendl and co-workers (2009): “Judgement bias in this context refers to the propensity of a subject to show behaviour indicating anticipation of either relatively positive or relatively negative outcomes in response to affectively ambiguous stimuli” (Mendl et al., 2009, p.164).

Cognitive judgement bias can be studied using a simple go/no-go procedure, in which animals are first trained to discriminate between two distinct stimuli, then (after acquisition) their response to ambiguous stimuli is tested. Therefore, animals are requested to categorise an ambiguous stimulus as either positive or negative (see for a classical example in rats: Harding et al., 2004). For instance, European starlings (*Sturnus vulgaris*) were trained on a go/no-go task to discriminate between a white visual stimulus associated with palatable food and a dark grey stimulus associated with unpalatable food. Then, the birds were tested with unreinforced ambiguous stimuli (intermediate shades of grey) with the expectation that their response reflects their affective state (Bateson and Matheson, 2007). A positive cognitive judgement bias is therefore a high expectation of reward following an ambiguous stimulus. This "optimism" is usually observed when animals are in a positive affective state, following for instance the addition of an environmental enrichment. In this case, subjects would approach quickly the ambiguous stimulus. A negative cognitive judgement bias, instead, is a high expectation of punishment (or non-reward) in face of an ambiguous stimulus. This "pessimism" is usually observed when animals are in a negative affective state, triggered by e.g., stress or decrease in environmental quality. In this case, subjects would take long to approach (or not approach at all) the ambiguous stimulus. We adopt the pessimistic/optimistic terminology following operational definitions, such as in Douglas et al. (2012).

Studies of cognitive judgement bias have been carried out in several vertebrate taxa, such as birds (Bateson and Matheson, 2007), rats (Brydges et al., 2011; Harding et al., 2004), and pigs (Douglas et al., 2012). The subjects were tested with ambiguous stimuli after experiencing a change in environmental quality (removal or addition of enrichments). These studies have shown that environmental enrichment may induce a positive judgement bias, while a decrease in the quality of the environment may result in a negative bias. Similarly, stressful conditions induce a negative cognitive judgement bias (Burman et al., 2009; Mendl et al., 2009). In honeybees, to our knowledge the only invertebrate tested, individuals were trained to associate a given scent with a reward, and another scent with a punishment. The bees were then divided into two groups, one undergoing mechanical shaking for 30 seconds as a condition of stress, the other not undergoing any stressful procedure. The two groups were then exposed to an ambiguous stimulus, an intermediate odour (compared to the two learned odours). Stressed bees were more likely to interpret the ambiguous stimulus as predicting a punishment (Bateson et al., 2011).

Studying cognitive judgement biases may help developing new methodologies for evaluating emotions and therefore improving welfare in non-human animals (Mendl et al., 2009). One study, however, failed to clearly demonstrate a cognitive judgement bias: laying hens housed in an enriched environment did not respond positively to an ambiguous stimulus compared to hens in a standard environment. It was therefore suggested that if environmental differences are not large enough, inter-individual differences might exert a significant impact on the responses of animals (Wichman et al., 2012).

Animals show consistent inter-individual differences (personality) in e.g., boldness, aggressiveness, activity, sociability and/or exploratory tendency, and these personality traits are often correlated (behavioural syndrome). For instance, individuals that show high exploratory tendencies, are also highly aggressive towards conspecifics and bold when predators are present (Sih and Del Giudice, 2012). Cognitive processing should be influenced by individual differences in personality because these are predicted to affect fitness outcomes of individuals (Wolf and Weissing, 2012). Indeed, a link between cognition and personality has been postulated (Carere and Locurto, 2011; Sih and Del Giudice, 2012; Wolf et al., 2008), and empirical evidence in this direction is growing despite methodological challenges and limitations of experimental procedures (Griffin et al., 2015). Differences in personality traits could underpin affective states and this relationship could be bidirectional: for instance, individuals may be more prone to develop either positive or negative affective states depending on their personality, resulting in cognitive judgement bias. Such biases could then feedback on personality traits, as shown in humans (Mathews et al., 1997).

To our knowledge, only one study so far tested the link between personality and affective state in animals, suggesting that some personality traits modulate cognitive processing of environmental stimuli (attention bias) in psittacine birds, *Amazona amazonica* (Cussen and Mench, 2014). Once assumed a link between individual affective state and consistent inter-individual behavioural differences, a case for its directionality remains to be made. A key aspect of cognition that relates to consistent individual differences along the bold-aggressive-exploratory axis is the ecologically relevant speed-accuracy trade-off (Sih and Del Giudice, 2012): an individual may either use a fast/inaccurate strategy or a slow/accurate one, but cannot e.g., forage while being fast and accurate at the same time. Accordingly, we predicted that fast explorers (‘proactive style’, *sensu* Koolhaas et al. 1999), which are rather insensitive to environmental change and prone to set routines, should likely exhibit a negative cognitive judgement bias when facing uncertainty (ambiguous stimulus). These pessimistic individuals would not approach, or would take long time before approaching, an ambiguous stimulus. Conversely, slow explorers (‘reactive style’) should show a positive cognitive judgement bias, therefore being optimistic and approaching relatively quickly an ambiguous stimulus. We tested this hypothesis by: *i)* assessing the consistency of individual differences in exploratory activity in a large sample of individuals; *ii)* measuring exploratory activity in a separate set of individuals; *iii)* assessing the response of these same individuals to an ambiguous stimulus (cognitive judgement bias). Our study organism is a social insect, the carpenter ant *Camponotus aethiops,* which has been already tested for possible links between personality traits and learning ability (Udino et al., submitted).

2 MATERIAL AND METHODS

2.1 Animals and housing

Five queenright colonies of *Camponotus aethiops,* collected near Toulouse (Midi-Pyrénées, France, latitude 43.5°, longitude 1.516667°), were each housed in two Fluon®-coated plastic boxes connected by a hose. Colonies were kept under laboratory conditions (22±2°C, L12/D12, 40% humidity). One box, the nest (26x19x7cm), had a plaster floor and was darkened by cardboard; the other, the foraging area (29x26x8cm), was exposed to light. Colonies were fed twice a week with mealworms (*Tenebrio molitor*) and a mix of honey and apples, water was provided *ad libitum*.

Camponotus aethiops is a species that lives in hot, dry and open habitats and builds the nest in soil. Colonies are monogynous (only one queen) and medium size (500-3000 workers). They are omnivorous and eat preferentially dead insects, fruits and flower nectar, they also feed on extrafloral nectaries. Foraging workers usually avoid the warmest part of the day and are active early morning and late afternoon (Lenoir et al. 1990). Workers orient well using visual cues, especially when these are present in their horizontal field of view (Laffort et al. 1991) and are capable of visual discrimination learning (Yilmaz et al. 2014). It is not known whether this species uses chemical trails, like some other species of the same genus (Hölldobler and Wilson 1990), but there is evidence that *C. aethiops* workers perform group recruitment with leader, i.e., after having discovered a novel food source, a forager ant comes back to the nest and recruits several workers (1-20), which follow closely behind the leader to the food area (Suzzoni et al. 1991).

2.2 Exploratory activity test

One hundred and twenty five ants foragers were individually marked with dots of paint (uniPAINT©) on their thorax and gaster before the experiments started. Exploratory activity was evaluated in a circular open-field arena (Ø 6 cm), an adaptation of the classical open-field test (e.g. Prut and Belzung, 2003) with a floor of clean filter paper (replaced after each trial), in which an area of 4 cm diameter was considered as the central zone (Figure 1). An ant was taken from the foraging arena and introduced into an acclimatization tube placed in the peripheral zone for 120 seconds. Then, the tube was removed and the behaviour of the ant was observed for 300 seconds. We measured the time spent walking and resting in the central zone and in the peripheral by direct recording on a PC equipped with the software EthoLog (Ottoni, 2000). After the test, the ants were immediately returned to their respective colony. One week later, the open-field test was repeated with the same ants (n=125) to assess individual consistency over time.

A second batch of ants from the same colonies was used to study the relationship between exploratory activity and cognitive bias. These ants (n = 85) were tested in the open-field arena as described above and then returned to their colony. After about two hours they started the procedure described below (learning phase and ambiguous stimulus test), which was completed on the same day.

2.3 Cognitive judgement bias test

2.3.1 Learning phase

The apparatus consisted of a rectangular arena (18 x 12 x 5.5 cm) with a floor of filter paper (changed after each trial) and a visual pattern on the external part of one of the longest walls. Two microscope cover slips (20 x 20 mm, Menzel-Gläser, Germany) were placed one at each corner of this wall. Each slip had an identical little piece of plasticine as landmark (Figure 2A), but one slip was baited with an appetitive stimulus (a drop of sucrose solution, 30% w/w) and the other with an aversive stimulus (a drop of quinine solution, Sigma–Aldrich, 1% w/w, Guerrieri and d'Ettorre, 2010). The position of the two stimuli (left/right) was randomly chosen across individuals but remained the same for a given ant across the learning trials. For each trial, the ant was introduced into an acclimatization tube placed near the wall far from the stimuli at an equal distance from each stimulus for 120 seconds. The first phase of learning consisted of 6 trials in which both stimuli were present. After the removal of the acclimatization tube, the time the ant needed to discover the sugar solution was recorded (the trial was stopped after 10 min if the ant did not reach the sugar solution). Between each trial the ant was put back into its colony for about 5 min, and then it started the next trial. The ant should actively approach and taste both stimuli to ascertain their valence (positive or negative). When the ant reached the appetitive stimulus, it was left undisturbed until it finished drinking the sugar solution to avoid disturbance stress. If the ant did not get to the aversive stimulus at least once during the 6 trials (about 10% of the tested ants), the session was discarded and these ants did not continue to the second phase.

The second phase of learning consisted of 6 additional trials in which only one stimulus was present (3 trials with the aversive stimulus and 3 trials with the appetitive stimulus in a random order). The latency time to reach the stimulus was recorded during each trial, which lasted a maximum of 3 minutes. Between each trial the ant was put back into its colony, as in the first phase.

We considered that an individual learned the task if the sum of the latency time of the 3 trials with the appetitive stimulus was at least two times smaller than the sum of the latency time of the 3 trials with the aversive stimulus during the second phase of learning. The majority of the ants (90%) did not approach the aversive stimulus once during this phase, in which case they were assigned a latency of 180 seconds.

2.3.2 Ambiguous stimulus test

The ants that learned the task (74 of 85 individuals tested) were subjected to the test with the ambiguous stimulus. This test was carried out in the same rectangular apparatus used for the learning trials (with clean filter paper) but this time the cover slip was placed at the center of the wall (same distance from the right and the left corner, Figure 2B). A drop of water was placed on the slip instead of the appetitive or negative stimulus. The ant was placed in the acclimatization tube as usual and after the removal of the tube the latency time to reach the ambiguous stimulus was recorded. If the ant did not reach the stimulus the test was stopped after 10 min and a latency of 600 sec was assigned. This is an established paradigm called go/no-go procedure (Harding et al., 2004), in which the response is either approaching or not approaching (or approaching slowly) the ambiguous stimulus.

2.4 Data analysis

Intra-class correlation (Lessels and Boag 1987) was calculated to assess individual repeatability across the two sessions of the open-field test. We used LMM-based calculations by R package *rpt*R (Nagakawa and Schielzeth, 2010) and we assessed 95% confidence intervals (CI) by 1000 bootstrap steps. Individual was a random factor. P values were calculated by 1000 permutations (α level = 0.05).

For the ambiguous stimulus test, we calculated the median of the latency time to reach the ambiguous stimulus (97.01 sec) across all 74 subjects, and we then divided the 74 ants in two groups: fast optimistic (latency < median) and slow pessimistic individuals (latency > median). This was justified by the fact that the distribution of approach time was bimodal, with individual ants approaching the ambiguous stimulus very fast or not at all (Figure 3). Difference in exploratory activity (time spend moving the central area and total time spent in the central area of the open field) between optimistic and pessimistic ants was analysed with a t-test. We also looked at the correlations between individual latency time to approach the ambiguous stimulus and exploratory activity by Spearman correlation (data not normally distributed).

To investigate whether cognitive judgement bias might be related to learning ability, we calculated an index of learning performance by comparing the first 3 trials to the last 3 trials of the first phase of learning (these are the 6 trials in which the two stimuli, sucrose solution and quinine solution, were present). Given the sum of the time needed to reach the appetitive stimulus in the first 3 trials = A and the sum of the time needed to reach the appetitive stimulus in the last 3 trials = B, learning performance was calculated as (A-B)/A; the closer is this number to 1, the faster the animal approached the appetitive stimulus, i.e., the better the learning performance. We then looked at the possible correlation between learning performance and latency to reach the ambiguous stimulus.

3 RESULTS

3.1 Exploratory activity test

Ants showed significant consistency over time in their exploratory activity. The two variables reflecting the level of exploration during the open-field test were significantly repeatable across the two sessions (time spent moving in the central area: R = 0.384; CI = (0.222, 0.517); p = 0.001; total time spent in the central area: R = 0.289; CI = (0.121, 0.441), P = 0.003, Figure S1, supplementary material).

3.2 Cognitive bias

We observed substantial individual differences in the approach time to the ambiguous stimulus and the distribution of approach time was bimodal (Figure 3).

Ants that spent less time in exploratory activity (slow explorers) readily approached the ambiguous stimulus (optimists), while ants that spent more time in exploratory activity (fast explorers) were slow in approaching the ambiguous stimulus (pessimists). This difference between the optimist and pessimist group in relation to exploratory activities is statistically significant (time spent moving in the central area: t = 3.47, p < 0.001, Figure 4A; total time spent in the central area:

$t = 2.96$, $p < 0.01$, Figure 4B; these two variables are highly and positively correlated: $r = 0.78$, $p < 0.001$). This is confirmed by the positive correlations between latency to approach the ambiguous stimulus and both time spent moving in the central area ($r_s = 0.36$, $p < 0.01$) and total time in the central area of the open-field ($r_s = 0.38$, $p < 0.01$): ants that spent more time in exploring the open-field were slower in approaching the ambiguous stimulus during the cognitive bias test (Figure S2).

Cognitive bias was not related to learning ability, as shown by the lack of correlation between learning performance and latency to reach the ambiguous stimulus ($r_s = -0.122$, $P = 0.30$).

4 DISCUSSION

The aim of the present study was to test the relationship between cognitive judgement bias (measured as response to an ambiguous stimulus) and inter-individual differences in exploratory behaviour (a personality trait) in workers of the carpenter ant, *Camponotus aethiops*. We observed individual differences in the latency time to approach the ambiguous stimulus, with a clear bimodal distribution: ants were either very fast in approaching the ambiguous stimulus (optimistic) or they were very slow (or did not approach the stimulus at all within the cut-off time), i.e., pessimistic. In our go/no-go procedure, a non-approach is considered a response, as ants previously learned the discrimination between appetitive and aversive stimulus, and therefore not approaching is an appropriate response for the aversive stimulus. This bimodal pattern strikingly resembles the one observed in great tits, *Parus major*, for approach time towards a novel object and latency to return after a startle (indicating risk taking behaviour), which formed the basis to create genetic selection lines for avian personality (Verbeek et al., 1994; Drent et al., 2003; van Oers et al., 2004).

In general, proactive individuals are fast explorers but are relatively insensitive to new environmental information, whereas reactive individuals are slow explorers but adjust their behaviour to changes in the environment, or when signals have changed in meaning. Therefore, a trade-off between speed and accuracy occurs (see introduction, Sih and Del Giudice, 2012), which may result in a bimodal distribution. Both strategies (proactive/reactive) might entail their specific individual advantages when performing in stable (fast responders performing better) or unstable (slow responders performing better) environments, while individual with intermediate profiles would have certain disadvantages in both kinds of environment (Verbeek et al., 1994). Our results are consistent with studies in great tits, in which fast explorers appear to form more routines than slow explorers (Verbeek et al., 1994). Forming routines may explain why the behaviour of fast explorers is generally less flexible (Sih and Del Giudice, 2012). Indeed, in black-capped chickadees (*Poecile atricapillus*), fast explorers performed worse than slow explorers in a reversal learning task, which requires altering an acquired information (Guillette et al., 2010).

Our data suggest that the observed pattern of responses to the ambiguous stimulus could be explained by individual differences in the exploration test (open-field, which individuals performed before starting the learning phase and the cognitive judgement bias test). Individuals that spent significantly more time in the central area of the open-field were those showing a longer latency to approach the ambiguous stimulus. Thus, individuals who took the longest time to approach the ambiguous stimulus were those exploring most. Fast exploring individuals showed a negative cognitive judgement bias (pessimism), while slow explorers showed a positive cognitive judgement bias (optimism). In an ant colony, division of labour is based on age and/or morphology (Wilson, 1971). The foragers are older individuals but there is variability in foraging activity (see e.g. Beverly et al., 2009). We predict that fast explorer foragers may spend more energy than slow explorers as they cover a larger foraging area. Therefore, fast explorers are supposed to be less accurate in examining the environment and retain only information about high quality food. Conversely, slow explorer foragers may afford accurate evaluation of food sources (of varying quality) distributed in a relatively small foraging area. This is an example of speed/accuracy trade-off, also reported in bumblebees (Burns and Dyer, 2008).

We are not aware of any study relating affective states with personality traits in social insects. The results of the present study are among the first linking consistent individual differences (animal personality) to response to ambiguous stimuli (cognitive judgement bias). Most studies evaluating cognitive biases involved enrichment or impoverishment of the environmental quality, which induced a positive and negative cognitive bias respectively (Bateson and Matheson, 2007; Brydges et al., 2011; Douglas et al., 2012). Other studies have tested the effect of stress on the response to an ambiguous stimulus (Bateson et al., 2011; Burman et al., 2009; Salmeto et al., 2011). These studies aimed at finding a non-invasive and effective way to assess the affective states of animals in captivity. Since cognitive bias is considered an indicator of positive or negative affective states, it may also provide important information to assess and improve welfare in captive animals (Mendl et al., 2009). Our study suggests that personality should be taken into consideration when evaluating the welfare of animals since personality types are differently linked to affective states, for instance some personality types are likely to score more pessimistic than others in cognitive bias tests. Invertebrates are widely used in animal experimentation as well as in zoos and aquaria, and there is a growing interest and concern about their welfare upon realizing that many species possess advanced cognitive abilities, consciousness, individuality, pain suffering ability, etc. (Carere et al., 2011).

Finally, our data are in accordance with evolutionary explanations of strategies used by animals to cope with uncertainty (Mathot et al., 2012), which predict that if animals differ in their relative investment in sampling, individuals that sample more thoroughly would have lower exploration/activity scores, but exhibit greater plasticity than individuals that sample with less accuracy. In our study, readily approaching the novel ambiguous stimulus by slow explorers could be interpreted as sampling in an uncertain context, e.g. when in nature resources fluctuate in space and/or time.

5 CONCLUSIONS

The results support the postulated link between consistent individual profiles of exploratory activity (likely reflecting personality) and individual differences in affective states measured by cognitive judgement biases in response to ambiguous environmental stimuli. To our knowledge, this is the first experimental evidence of such a relationship in an invertebrate species. The next steps should focus on testing the possible consistency of affective states across subsequent trials and their potential impact on individual personality profiles, taking into account ontogenetic changes.

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FIGURE LEGENDS

Figure 1. Experimental set-up (open-field arena) used to study exploratory activity.

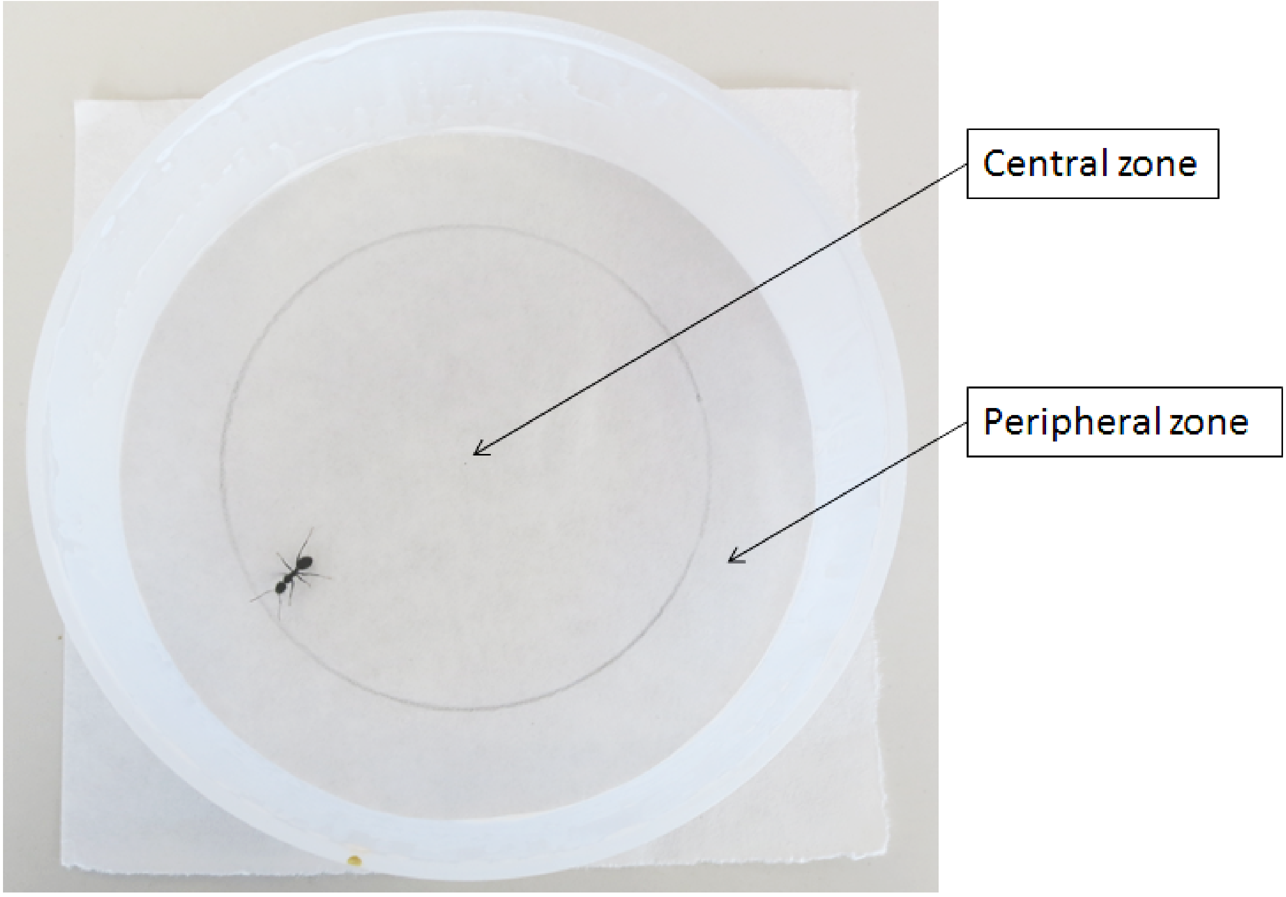

Figure 2. Experimental set-up used to study cognitive bias. A) First phase of learning, with the appetitive stimulus (sucrose solution) and one corner and the aversive stimulus (quinine solution) at the other corner (left/right balanced across individuals). B) Ambiguous stimulus test, with the neutral stimulus (water) placed at the center.

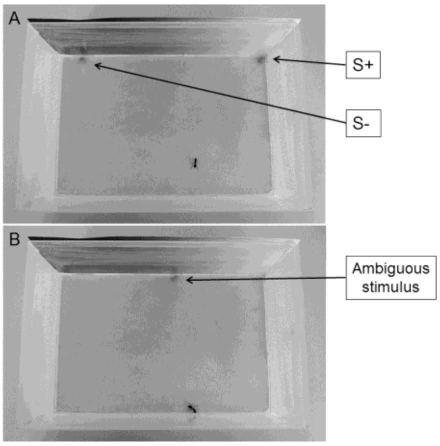

Figure 3. Frequency distribution of the latency time to approach the ambiguous stimulus during the cognitive bias test (n = 74).

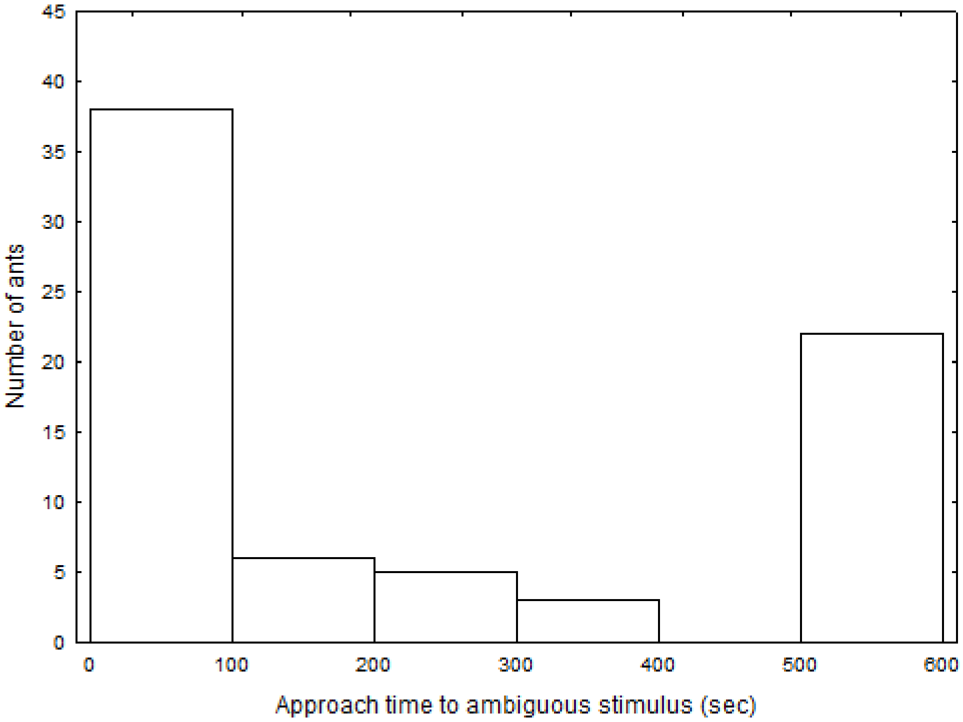

Figure 4. Approach time to the ambiguous stimulus during the cognitive bias test (ants are grouped in two categories: slow and fast) in relation to exploratory activity: A) time spent moving (mean and 95% CI) in the central part of the open-field; B) total time (mean and 95% CI) spent in the central part of the open-field (n = 74).