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A behavioral analysis of achromatic cue perception by the ant *Cataglyphis aenescens* (Hymenoptera; Formicidae)

Volkan AKSOY*, Yılmaz ÇAMLITEPE
Department of Biology, Faculty of Sciences, Trakya University, Edirne, Turkey

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Abstract: Behavioral responses of *Cataglyphis aenescens* foragers to various monochromatic light stimuli were tested. Foragers were trained to associate lights of 370 (UV), 440 (blue), 540 (green), and 640 nm (red) with a food reward on a circular orientation platform and were then tested to determine the threshold intensity values of these wavelengths they could perceive. Foragers significantly responded to all wavelengths at training intensities but their homeward orientation diminished with decreasing stimulus intensity. The results showed that UV and green lights could be perceived at lower intensities compared to blue and red lights. Foragers were further trained in a Y-maze apparatus to discriminate 2 monochromatic light stimuli of the same wavelength but different in their intensities. The results showed that they failed to make a significant discrimination except for the 440 and 640 nm pairs. Overall results revealed a broad spectral sensitivity for foragers ranging from at least 370 nm (UV) to 640 nm (red) mediated by both chromatic and achromatic cue perception.

Key words: *Cataglyphis aenescens*, achromatic vision, intensity threshold, intensity discrimination

1. Introduction

The visual world offers insects a wide variety of cues to orient, one of which is light. Light has hue, saturation, and intensity dimensions that constitute its chromatic (hue and saturation) and achromatic (intensity) components. The light guiding structures of insect compound eyes, the rhabdoms, bear the photosensitive visual pigments that make the eye itself a photon counting device. Color vision (chromatic vision) is based on differences in photon counts by these receptors differing in their spectral sensitivities (Land and Osorio, 2003). Unlike chromatic vision, achromatic vision is sensitive to intensity changes but not to changes in the spectral composition of light stimuli. Chromatic vision is achieved by color-opponent (subtractive) interactions between receptor signals, while achromatic vision is based either on the summation of receptor responses or on the signal of a single receptor type (de Ibarra et al., 2000).

Color vision is well documented in some insect groups [for a review, see Briscoe and Chittka (2001) and Kelber et al. (2003b)], but what we know today comes from the studies on the honeybee *Apis mellifera*. The trichromatic visual system of honeybees allows them to learn and discriminate colors of rewarded flowers in nature. Although bees are good at color learning and discrimination tasks, some attempts showed that it was hard to train bees to intensity differences (von Helversen, 1972; Backhaus and Menzel, 1987; Chittka, 1999). All models of bee color vision are 2-dimensional and they do not include a brightness dimension (Vorobyev and Brandt, 1997). However, when extensively trained, bees were shown to discriminate stimuli differing from each other only in intensity characteristics (Labhart, 1974; Menzel and Backhaus, 1991). For instance, Labhart (1974) tested honeybees in a Y-channel and found that bees could discriminate between white lights of different intensities. Moreover, the accuracies of intensity discrimination in the UV, green, and blue ranges were approximately identical. Similarly, Kelber (2005) showed that moths of the species *Macroglossum stellatorum* learned to discriminate between 2 light stimuli of the same wavelength with different intensities.

Some ant species have been investigated for their spectral sensitivities and mainly chromatic vision was questioned within these studies while achromatic cue perception was partially evaluated (Tsuneki, 1953; Marak and Wolken, 1965; Kiepenhauer, 1968; Roth and Menzel, 1972; Wehner and Toggweiler, 1972; Meznel, 1973; Menzel and Knaut, 1973; Kretz, 1979; Camlitepe and Aksoy, 2010; Aksoy and Camlitepe, 2012). As in many insects, ants

* Correspondence: volkanaksoy@trakya.edu.tr

tend to orient towards a light stimulus, and this tendency increases with increasing intensity of the stimulus (Kretz 1979). In an early study, Tsuneki (1953) showed that light intensity played a major role in orientations of *Camponotus obscuripes* and *Leptothorax spinosior*. Light intensity also influenced the responses of *Solenopsis saevissima* foragers when they were tested to obtain an action spectrum (Marak and Wolken, 1965). Desert ant *Cataglyphis bicolor* foragers were tested for their abilities in a discrimination task between 2 light stimuli of the same spectral compositions (340, 434, 493, and 574 nm) but with different intensities (Kretz, 1979). Foragers could discriminate the stimuli but the rate of the correct choices for the trained stimulus decreased with decreasing intensity difference between the 2 stimuli. More recently, Aksoy and Camlitepe (2012) showed with behavioral experiments that *Formica cunicularia* foragers have a UV-green dichromatic color vision system that also allows them a broad range of color sensitivity from 370 to 640 nm.

We have recently started to investigate the spectral sensitivity characteristics of *Cataglyphis aenescens* foragers with behavioral experiments. The results of color discrimination experiments showed that foragers had a dichromatic color vision system operating with UV and green sensitive photoreceptors and were capable of making fine color discrimination in these ranges (Çamlıtepe et al., 2008; Camlitepe and Aksoy, 2010). In the present study we trained *C. aenescens* foragers to associate a food reward with monochromatic light stimuli of 370, 440, 540, and 640 nm to evaluate their responses to achromatic cues to 1) determine the minimal intensity threshold values of these wavelengths that initiate a positive orientation response by foragers and 2) to determine if foragers can discriminate between 2 same wavelengths on the basis of intensity differences.

2. Materials and methods

2.1. The ants

Live specimens of *Cataglyphis aenescens* were obtained from a nest in the village of Sazlıdere (41°36′0″N, 26°40′59″E) of Edirne Province, Turkey. Several large colonies were transferred in an open-topped container to a laboratory. Collected colonies were divided into 4 portions and then transferred to arenas (600 × 600 mm) with Fluon-coated Perspex walls (200 mm high) in which the ants constructed their nests with their original nest material. Escape from the containers was prevented by Fluon-coating their walls. The laboratory was artificially illuminated by fluorescent lamps to provide a 12:12 light-dark regime and the indoor air temperature was kept at 28–30 °C. A humidifier (Vapac MV4) was used to provide a relative humidity of 50%.

2.2. Experimental apparatus

Experiments were performed in a Y-maze choice apparatus and on a circular orientation platform.

The Y-maze was made of glass (30 mm in diameter) with the 2 arms at 120° (Figure 1). The base of the Y (500 mm long) was connected horizontally to the nest via a

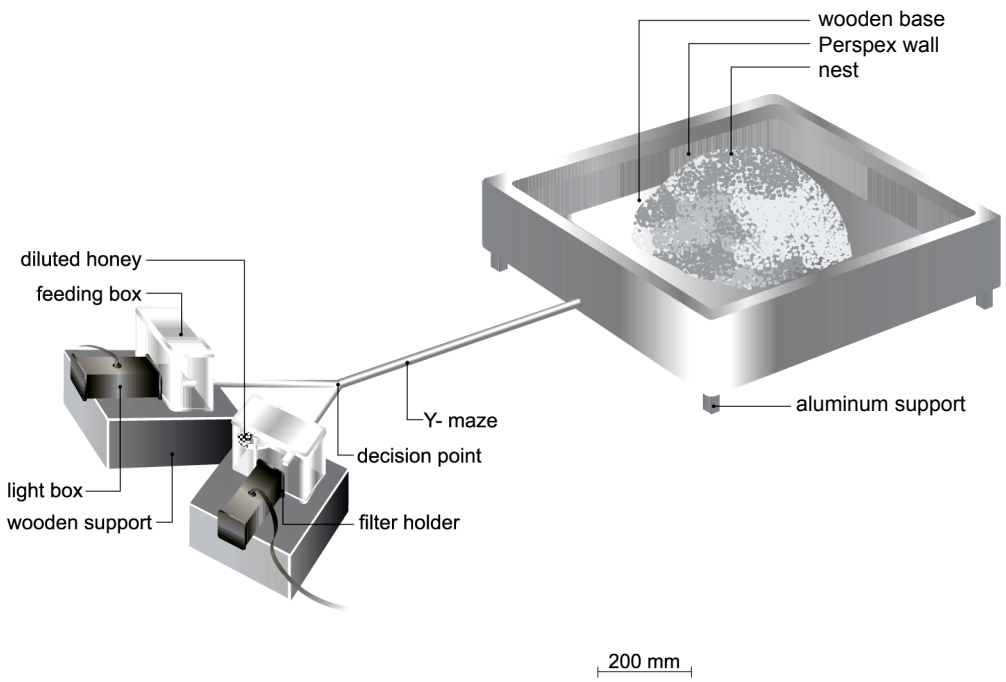

Figure 1. The spatial arrangement of the Y-maze binary choice apparatus.

hole in the wall of the arena at floor level. Each arm of the Y extended horizontally for 200 mm and terminated in clear Perspex feeding box (100 mm width × 150 mm high), from which escape was prevented with a Fluon barrier. This arrangement permitted foragers to explore boxes and return to the nest. The foragers had to walk along the floor of the Y-maze towards the decision point, which allowed them to see both spectral stimuli at the same time. The spectral stimuli delivered to the Y- maze were produced by light boxes attached to the backside of the feeding boxes. The light box contained a halogen lamp (Philips Focusline 24 V-250 W) and had a built-in ventilator to remove the heat produced by the lamps. Interference bandpass filters with 10 nm of bandwidth (Thorlabs Inc., CWL, 370, 440, 540, and 640) were attached to holders in front of the light boxes to obtain monochromatic test stimuli. An adjustable DC power supply (Maksimel, model #LPS–991) was used to energize the lamps. This power supply with the digital panel meters provided precise control of the output voltage and current with a high stability and very low ripple. Light intensity was measured with a calibrated spectroradiometer (International Light Inc., model #RPS 900). During training and tests, all stimuli were adjusted to have equal physical intensities ($I = 1.1 \times 10^{11}$ photons) at the decision point since absolute spectral sensitivities of the receptors of an experimental subject is not known (see Kelber and Henique, 1999; Kelber et al., 2003b). Absorptive neutral density filters (Thorlabs Inc.) were used to reduce the intensities of the stimuli by varying factors. Since all tests were performed in darkness, a digital video camera (Sony TRV520E) with NightShot vision was used to monitor the ants.

2.3. Orientation platform

The orientation platform consisted of a circular plastic vessel (17 cm in diameter) connected to the nest via a silicon pipe (Figure 2). The pipe was fixed into a hole at the center of the platform. A filter paper was used on the platform. Escape from the platform was prevented by Fluon-coating its walls. A hole was opened at one point of the wall of the platform, which led the ants to a feeding box through a short plastic pipe. Diluted honey and dead insects were provided in the feeding box as food. Foragers, after reaching the platform at the center, could freely forage for food. Light boxes were placed behind the feeding boxes. When a forager exited the silicon pipe and reached on the platform she could see the light beam passing through the filter.

2.4. Elimination of cues

It was necessary to prevent foragers from using any kind of possible orientational cues during training and tests, except the light stimuli. All training and tests were performed in darkness to eliminate use of possible visual cues. This also made the foragers positively phototactic. Since ants were shown to orient themselves using a magnetic field sense (Camlitepe and Stradling, 1995; Camlitepe et al., 2005) and kinesthetic cues (Aksoy and Camlitepe, 2005), test stimuli were interchanged between the arms of the Y-maze after every 15th forager. Light boxes and thus the stimuli on the orientation platform were also reversed by 90° during tests. Food was removed during tests and feeding boxes were changed with alcohol-wiped new ones. Y-mazes and filter papers on the orientation platform were replaced with new ones after every 5 foragers tested to eliminate any kind of possible chemical cues they could deposit. The orientation platform was also wiped with alcohol after every 5 workers

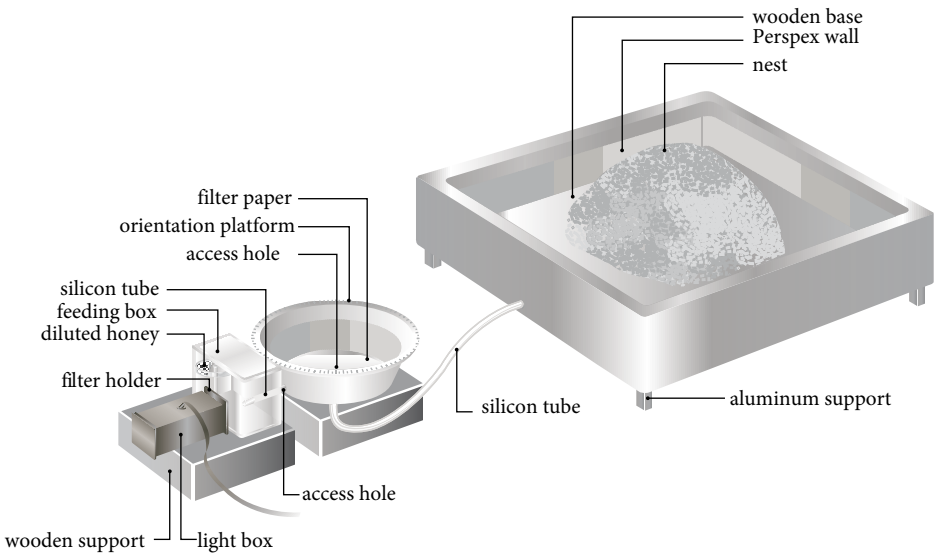

Figure 2. The spatial arrangement of the circular orientation platform assembly.

tested. All experimental set-ups were placed on wooden supports and leveled to preclude the use of gravitational cues. Therefore, on entering the maze and reaching the orientation platform, foragers were denied any point of reference with which to orient themselves.

2.5. Intensity threshold experiments

2.5.1. Training

Foragers were trained for a 2-week period to wavelengths of 370, 440, 540, and 640 nm on the orientation platform to test the threshold light intensities of these wavelengths that they could perceive and, in turn, show a significant orientation response to. The training intensity was 1.1×10^{11} photons for all wavelengths. For the first week of the training, workers were left free to use both chemical cues they deposited on the platform and the light stimulus to reach the food. By the second week, the orientation platform was wiped with alcohol and the filter paper on it was replaced with new ones regularly to remove the chemical cues and force the foragers to orient only using the light stimulus.

2.5.2. Tests

The first unrewarded test was performed with training intensity conditions (control test), followed by critical tests performed by decreasing the intensities gradually. Each test trial started when a forager exited onto the platform and lasted when she traversed the platform. Only one individual was allowed on the platform for each trial to prevent possible interpretation as social facilitation. Foragers were observed with the digital camera during tests and their compass angles and tracks were recorded. The angle at which each forager reached the edge of the orientation platform was recorded and the forager was gently removed with a paint brush. All tested foragers were kept in a moist box and put back into their nests when each experimental condition ended. The tracks of foragers during tests were transferred to computer media and combined with a program (Macromedia Freehand 10.0). Thirty individuals were used for each test and the distribution of compass angles of foragers on the platform was analyzed using a circular statistical method (Batschelet, 1981). The analysis derives the mean vector angle, a, and its length, r. The length indicates the amount of agreement among individual estimates such that if all estimates are in precisely the same direction, r = 1, and if they are uniformly spread over 360°, r = 0. The *V* test was used to determine whether or not the distribution of foragers tested was different from a uniform one.

2.6. Intensity discrimination experiments

2.6.1. Training

Foragers were trained in the Y-maze for a 2-week period to discriminate a food-rewarded monochromatic light stimulus from an alternative nonrewarded one of the same wavelength but different in intensity. The brightest of the stimuli were used as the food rewarded ones. Foragers were allowed to forage freely for food for the first week of the training period, during which they could use both the light stimuli and the chemical cues that they deposited inside the maze for their orientation to the food reward. By the second week of the training, mazes were replaced with new ones regularly to remove the chemical cues and the foragers were thus forced to pay attention only to the light stimuli to orient. The training intensity differences were not same for all stimuli. The positive training intensities were brighter by a factor of 40 for 370 nm and 540 nm and by a factor of 10 for 440 and 640 nm.

2.6.2. Tests

At the end of the training period, workers were tested with training conditions for their performances to discriminate between intensity differences. Each test trial started when a forager entered the maze and lasted when she entered one of the feeding boxes. Foragers spending more than 2 min inside the maze without any choice for either of the stimuli were not included in analysis. Each tested individual was gently removed with a paint brush and kept in a moist box until an experimental condition ended. Choice frequencies of at least 30 ants between the stimuli were recorded and a binomial test was used to evaluate whether the choice frequencies differed from chance or not.

3. Results

3.1. Intensity threshold experiments

The results of control tests of intensity threshold experiments showed foragers significantly oriented to all stimuli at training intensity (I) (1.1×10^{11} photons) (Figures 3 and 4). The mean vector angle for each trial was inside the 95% confidence interval. The results of the critical tests revealed different threshold values for each stimulus. Foragers significantly oriented to 370 and 540 nm when the intensity was decreased by 1.4 and 1.6 units, but when the decrease was 2 log units they dispersed randomly on the platform (Figures 3 and 4), showing that the minimal intensity threshold value for 370 and 540 nm was 2.75×10^{9} photons. On the other hand, when test wavelengths were 440 and 640 nm, foragers' significant orientation disappeared with an intensity decrease by 1 log unit (Figures 3 and 4).

3.2. Intensity discrimination experiments

Foragers were tested for their performances in a discrimination task between 2 lights of the same wavelength but differing in their intensities. When the test wavelength was 370 nm, the intensity of the rewarded stimulus was 1.1×10^{11} photons and that of the unrewarded stimulus was 2.75×10^{9} photons. The results of the control test performed with training conditions showed that foragers could not discriminate between 2 stimuli of 370 nm with different intensities (Figure 5a). Foragers also

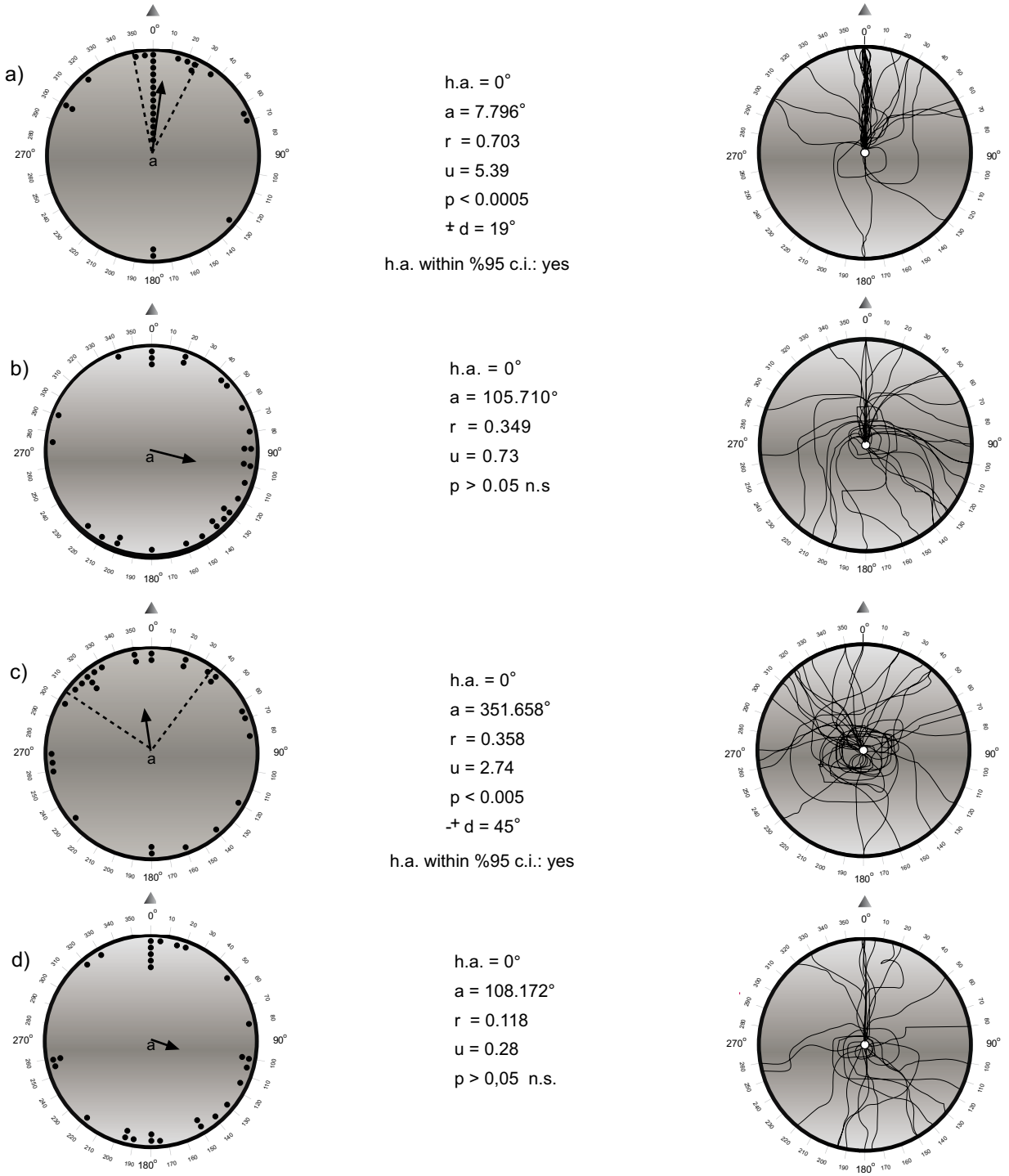

Figure 3. Angular distributions and tracks of foragers on the orientation platform during intensity threshold experiments with 370 nm (a, b) and 440 nm (c, d). Only the results of the control tests and the last critical tests with which the ants' homeward orientations were lost were given for each stimulus. **a)** 370 nm control test, I = 1.1×10^{11} photons, P < 0.0005; **b)** last critical test, I = 0.44×10^{10} photons, P > 0.05, not significant (n.s.); **c)** 440 nm control test, I = 1.1×10^{11} photons, P < 0.01; **d)** last critical test, I = 1.1×10^{10} photons, P > 0.05, n.s. The triangle above each circle indicates the home angle. The dots around the circumference show the actual distribution of angles of foragers. Sample size = 30; h.a. = home angle; a = mean vector angle; r = mean vector length; u = critical values of the V test; d = deviation values around the 95% confidence interval. The dashed lines denote the 95% confidence interval around each sample mean.

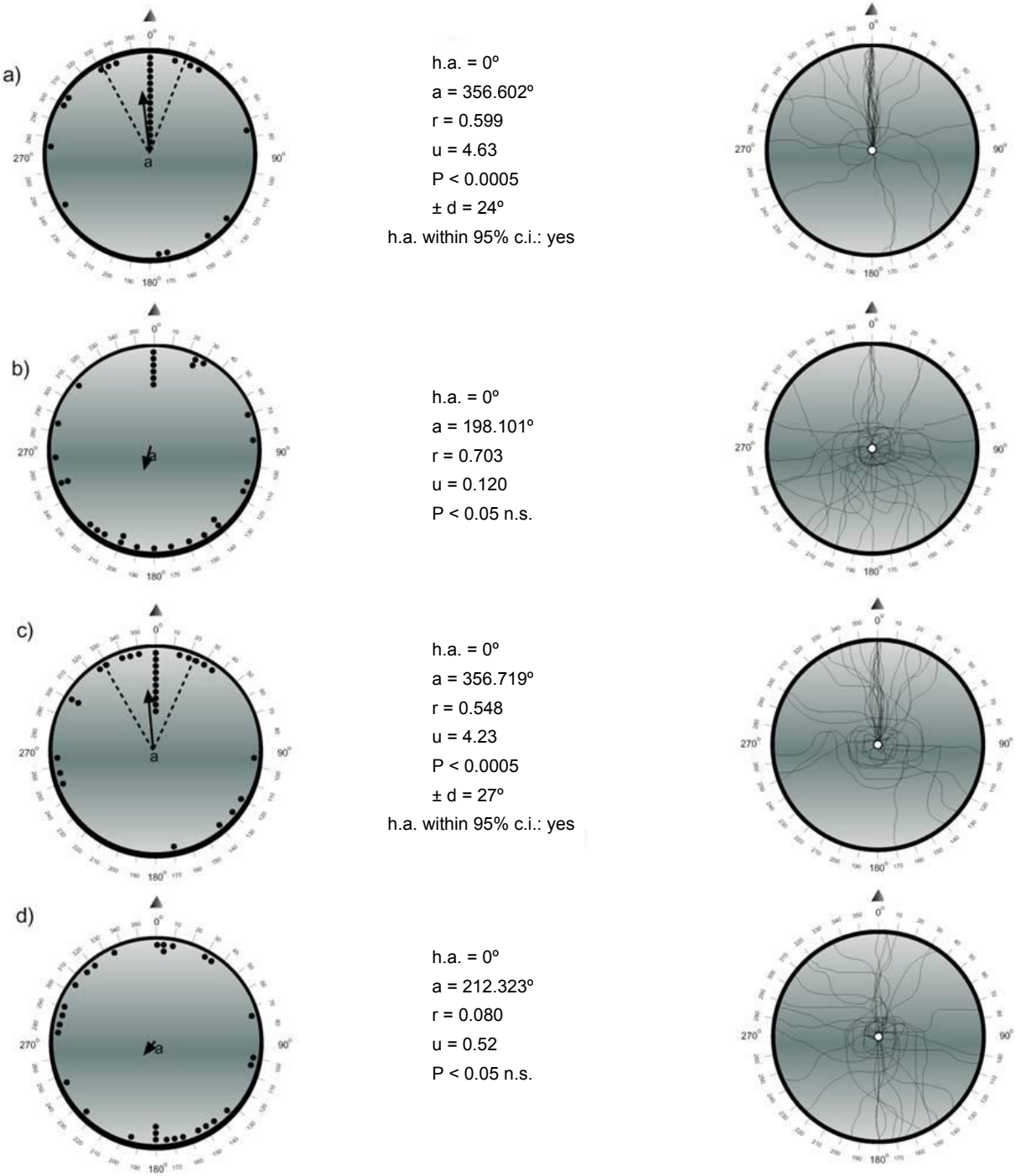

Figure 4. Angular distributions and tracks of foragers on the orientation platform during intensity threshold experiments. Only the results of the control tests and the last critical tests with which the ants' homeward orientations were lost were given for each stimulus. **a)** 540 nm control test, I = 1.1×10^{11} photons, P < 0.0005; **b)** last critical test, I = 2.75×10^{8} photons, P > 0.05, n.s.; **c)** 640 nm control test, I = 1.1×10^{11} photons, P < 0.0005; **d)** last critical test, I = 1.1×10^{11} photons, P > 0.05, n.s. The triangle above each circle indicates the home angle. The dots around the circumference show the actual distribution of angles of foragers. Sample size = 30; h.a. = home angle; a = mean vector angle; r = mean vector length; u = critical values of the V test; d = deviation values around the 95% confidence interval. The dashed lines denote the 95% confidence interval around each sample mean.

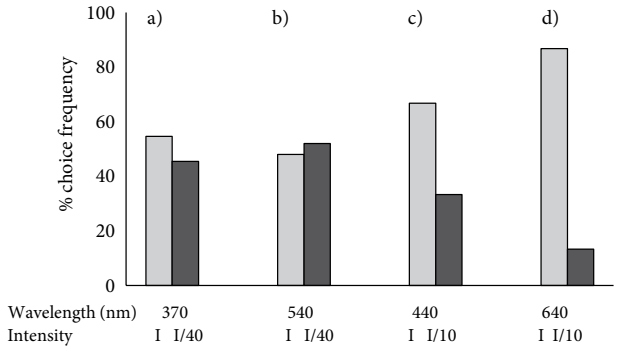

Figure 5. Choice frequencies of foragers in intensity discrimination experiments. Test wavelengths and intensities are given under the abscissa. The gray bars represent the choice frequencies for the rewarded intensities and the black bars represent the choice frequencies for the nonrewarded intensities. I = 1.1×10^{11} photons for 370 and 540 nm and I = 1.1×10^{12} photons for 440 and 640 nm. **a)** Test wavelength 370 nm, N = 44, the rewarded intensity was brighter by a factor of 40, binomial test, $P > 0.05$, n.s. **b)** Test wavelength 540 nm, N = 50, the rewarded intensity was brighter by a factor of 40, binomial test, $P > 0.05$, n.s. **c)** Test wavelength 440 nm; N = 30, the rewarded intensity was brighter by a factor of 10, binomial test, $P < 0.05$. **d)** Test wavelength 640 nm; N = 30, the rewarded intensity was brighter by a factor of 10, binomial test, $P < 0.0001$.

could not discriminate between 2 stimuli of the same wavelength when the test stimuli were 540 nm (1.1×10^{11} vs. 2.75×10^{9} photons, Figure 5b). On the other hand, they were successful when tested to discriminate between 2 wavelengths of 440 or 640 nm presented with an intensity difference of 1 log unit (1.1×10^{12} vs. 1.1×10^{11} photons) (Figures 5c and 5d).

4. Discussion

The present results showed that *Cataglyphis aenescens* foragers could learn to associate a food reward with monochromatic light stimuli over a wide range of spectrum, respond to these stimuli when presented above a certain threshold intensity value, and distinguish between 2 same wavelengths with differing intensities, but only in the long wavelength range. Previous results obtained in color discrimination tasks proved that *C. aenescens* foragers are capable of making color discrimination in UV and green ranges irrespective of changes in stimulus intensities (Çamlıtepe et al., 2008), and the present results revealed a broad spectral sensitivity for this dichromatic species ranging from at least 370 nm (UV) to 640 nm (red) mediated by achromatic cue perception.

Although foragers did not see 440 and 640 nm as colors, these 2 wavelengths still could be perceived via achromatic cues when presented with a threshold intensity value. How, then, could foragers lacking blue- and red-sensitive photoreceptors orient to these wavelengths? The sensitivity of a photoreceptor depends mainly on the absorption properties of its photopigment/photopigments and also to some extent upon other factors, i.e. screening pigments and positive electrical coupling between retinula cells (Menzel, 1975). Menzel and Blakers (1976) found that the majority of the UV cells of honeybees have some sensitivity at longer wavelengths (440 nm) where the UV pigment no longer absorbs, suggesting a linkage with long wave-absorbing pigment systems. It is also known that the high secondary sensitivity found in most UV and green cells originates from some kind of positive electrical interactions between retinula cells of different spectral types. Spectral sensitivity characteristics of photosensitive receptors of *C. aenescens* foragers are not known currently, but despite this, we propose that some type of electrical interaction between UV and green photoreceptors causing secondary peaks for these photoreceptors might account for blue sensitivity. Sensitivity of foragers to 640 nm is also interesting since such long wavelength sensitivity is not common among insects, except for some Lepidoptera species with tetra- and pentachromatic vision systems (see Briscoe and Chittka, 2001). We trained foragers in another experimental paradigm in dual choice conditions to discriminate between 2 long wavelengths (590 and 640 nm). Foragers' preferences between these 2 stimuli in control and critical tests appeared to be mediated by perception of achromatic cues, not by the wavelengths of the stimuli (Çamlıtepe et al., 2008). This result, as well as the significant response of foragers to 640 nm in present experimental conditions, led us to conclude that foragers most probably employed a photon catch mechanism by their green receptors to perceive long wavelengths by their sensitivity curves, possibly extending towards longer wavelengths. Foragers of *Formica cunicularia* were also shown to have similar long wavelength sensitivity (Aksoy and Camlitepe, 2012). As stated by Chiao et al. (2000), it is beneficial to shift the sensitivity of the L pigment as far as possible to the long wavelength part of the spectrum and a spectral tuning of L-receptors may be involved in tasks for achromatic vision.

The intensity discrimination performances of ants were poor in the present experimental conditions. Foragers failed to discriminate intensity differences in 370 and 540 nm pairs, but they were successful in 440 and 640 nm pairs. In an earlier study, Kretz (1979) tested *Cataglyphis bicolor* foragers to discriminate 2 same wavelengths (340, 434, 493, and 574 nm) with different intensities and found, in contrast to our results, that foragers could discriminate between intensities of 2 same wavelengths and that their responses to intensity differences were the same for all stimuli. Did *C. aenescens* foragers really fail to discriminate different intensities of UV (370 nm)

and green wavelengths (540 nm) or just disregarded the intensity-related cues, especially for these ranges of the spectrum that also provided chromatic information that might have been weighed more? The latter assumption seems reasonable considering the results that ants relied on intensity differences when no chromatic perception was possible, as in the case of 440 and 640 nm pairs. Therefore, foragers' failure in intensity discrimination in UV and green wavelengths was most possibly due to the presence of chromatic information that led foragers to disregard intensity differences. For instance, when *F. cunicularia* foragers were trained to discriminate 2 same wavelengths with differing intensities, their discrimination performance was better with the 440 nm pair, a wavelength not seen as color by foragers (Aksoy and Camlitepe, 2012). Animals can pay more attention to chromatic cues when they are presented simultaneously with achromatic ones and can also respond to achromatic cues when they are presented alone (Kelber, 2005). Thus, the intensity discrimination success of foragers with 440 and 640 nm could be explained by the possibility that foragers paid more attention to achromatic cues when they were required to discriminate these 2 wavelengths stimuli providing them with no chromatic perception.

In nature, visual tasks may depend either on achromatic contrast or chromatic contrast, or both. When the task is object recognition, achromatic contrast, caused by objects and shadows, is considered a less reliable cue than chromatic contrast, especially under changing light conditions (Kelber et al., 2003a). Therefore, diurnal species rely mainly on chromatic contrast and nocturnal species rely on achromatic contrast. Although we do not know whether *C. aenescens* ants use chromatic and/or achromatic vision for specialized visual tasks in nature, the UV-green dichromacy, which seems to be common at least for the ant species tested so far, may be related to separation between natural objects as foreground and the sky as background through a contrast mechanism involving UV and green receptors. In honeybees, for instance, achromatic visual pathways have been described, such as the e-vector analysis driven by the S-receptor (UV receptor) or motion perception performed by achromatic signals provided by the L-receptor (green receptor) (Vorobyev and Brandt, 1997; de Ibarra et al., 2001). The input by UV receptors also mediates polarization vision in *Cataglyphis* ants (Duelli and Wehner, 1973). The study of Petrov (1993) on foraging strategy of *C. aenescens* revealed evidence that foragers relied on dead reckoning, most probably involving a UV input to define a celestial compass, and landmark piloting to guide themselves in their orientations in open field.

Voss (1967) and Chameron et al. (1998) reported for the wood ant *Formica rufa* and the desert ant *Cataglyphis cursor*, respectively, that ants could respond to black patterns presented on a white background leading to an increased achromatic contrast. Recently, Yanoviak and Dudley (2006) concluded that the high contrast between tree trunks and the darker surrounding foliage provides the preferred visual target for falling *Cephalotes atratus* ants. Achromatic properties of objects in nature can be detected and used by ants as long as they enhance the objects' saliency. As long as the achromatic contrast between an object and its foreground is strong enough, then this object will be easily detected and discriminated from the background (de Ibarra et al. 2000). Achromatic contrast between objects as foreground and a background may be used to discriminate between them. Möller (2002) suggested that a UV-green contrast mechanism will allow landmark navigation for an insect under the open sky. However, insects have to depend on an intensity-based contrast mechanism for landmark navigation in artificial laboratory conditions where UV light is missing.

In conclusion, our results showed that *C. aenescens* foragers have a broad range of spectral sensitivity enabling them to respond to, in addition to chromatic, achromatic cues, as well. The results also showed that foragers could discriminate 2 long wavelength stimuli differing in their intensities. Therefore, we suggest that researchers reconsider the general assumption that hymenopteran insects are red-blind (see also Reisenman and Giurfa, 2008). Future behavioral and electrophysiological experiments on spectral sensitivities of ants will provide more data for clear conclusions and to define evolutionary and adaptive aspects of color sensation within this navigationally successful invertebrate group.

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