

Perspective vision in workers of *Myrmica sabuleti* MEINERT, 1861 (Hymenoptera: Formicidae)

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Abstract

My previous work demonstrated that *Myrmica sabuleti* MEINERT, 1861 workers see their environment with perspective. The stereovision of this species, which has rather small and laterally located eyes, cannot be explained by binocular vision. In the present study I show that – under UV light alone or yellow light alone – these ants do not perceive perspective, while under combined yellow and UV light as well as under natural light they perfectly perceive perspective. Motion parallax is probably not the mechanism giving *M. sabuleti* workers depth perception. Perspective detection in these ants is also not based on visible overall length, this has been experimentally checked. Therefore, I suggest that *M. sabuleti* workers see their environment with some perspective based on their sensitivity both to visible light (or perhaps long wavelengths) and to UV light (or perhaps short wavelengths). This interpretation requires experimental confirmation.

Key words: Depth perception, light, *Myrmica*, operant conditioning, vision, vision in 3D.

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Introduction

Even though many ant species primarily use chemical signals to communicate and inform congeners, many also use visual cues to accomplish a variety of tasks (e.g., foraging, collecting food, returning to the nest) (COLLETT & al. 1992, MCLEMAN & al. 2002). To date, the visual perception of ants is less well investigated than their chemical sensitivity. Moreover, the ant species studied for their visual perception generally have large eyes (for example: *Cataglyphis bicolor* (FABRICIUS, 1793), *Formica* spp., *Gigantiops destructor* (FABRICIUS, 1804); WEHNER 1981). Little work has been done on ants with small eyes such as the genus *Myrmica*. Since several years, my study therefore focuses on *M. sabuleti* MEINERT, 1861 workers' visual perception. I initially dealt with certain characteristics of this perception (CAMMAERTS 2004a), then studied other visual abilities of these ants (CAMMAERTS 2006a), examined their sensitivity to light intensity (CAMMAERTS 2005), and finally concentrated on *M. sabuleti* workers' visual perception of colours and sensitivity to UV light (CAMMAERTS 2006b). In the initial study (CAMMAERTS 2004a), I demonstrated that *M. sabuleti* workers are able to distinguish vertical segments that slope upwards and away from the viewer at different distances: these ants can see at least some part of their environment with perspective. However, they possess only rather small eyes located laterally on their head. Such eyes will have only a very small or nearly no common visual area. This excludes the existence of stereovision based on binocular vision, a mechanism commonly found in other organisms. Another possible mechanism allowing depth perception is motion parallax. CAMMAERTS (2006b) however, experimentally demonstrated that *M. sabuleti* workers distinguish colours from one another and from several greys and also perceive, under UV light, a black experimental apparatus (a specific shape drawn on

black paper, then cut and folded to yield a hollow cube; CAMMAERTS 2005: fig. 1). That approach showed that *M. sabuleti* workers are differently sensitive to several wavelengths and to UV light. A plausible hypothesis for these ants' depth perception is on one hand a sensitivity to visible (for humans) light and, on the other hand, to UV light. In other words, perspective perception by *M. sabuleti* workers might involve different photoreceptors with different spectral sensitivities and different locations. Here, I test ethologically this hypothesis, carrying out five experiments.

Material and methods

Collection and maintenance of ants

Four colonies of *M. sabuleti* were collected from Höhes Martelingen (Luxembourg; 49° 49' 30" N, 5° 45' 00" E) and from the Aise valley (Belgium; 49° 49' 39" N, 5° 15' 26" E). The determination of *M. sabuleti* was done by B. Seifert. The collected colonies were divided into a total of 30 experimental colonies (five series, labelled A to E, of six colonies numbered 1 to 6), demographically similar, containing each a queen, 250 workers and brood. These experimental colonies were maintained in a laboratory at a constant temperature (20 °C) and humidity. The ants nested into artificial nests made of one or two glass tubes half-filled with water, with a cotton-plug separating the ants from the water (Fig. 1A). The glass tubes were placed into a polyethylene tray (43 × 23 × 7 cm) serving as a foraging area (Fig. 1A), where food was provided ad libitum. Food consisted of pieces of dead cockroaches as well as of sugared water delivered into a small glass tube plugged with cotton. Four days before an experiment and during each experiment, no meat was provided because this food was used as a reward to condition the ants during the experiments.

Experimental apparatus and design

Each experiment was performed simultaneously on the six colonies of a series and, in order to perform an experiment, two different experimental apparatus were deposited on the foraging area of each colony (Fig. 1A). Three kinds of experimental apparatus were constructed in total, two kinds being used for performing one experiment. Each experimental apparatus was constructed of very strong white paper. The first kind of apparatus was a piece of paper ($4\text{ cm} \times (4 + 2 + 3.46)\text{ cm}$) with a black rectangle ($0.5\text{ cm} \times 3\text{ cm}$) drawn in the middle of the lower $4\text{ cm} \times 4\text{ cm}$ area. This was folded (and glued) to yield a polyhedron on which the black rectangle appeared sloping upwards and away from the viewer at an angle of 30° (Fig. 1B). The second kind of apparatus was a piece of paper ($4\text{ cm} \times (4 + 3.46 + 2)\text{ cm}$) with an identical black rectangle drawn at the same place, also folded (and glued) into a polyhedron: here, the black rectangle sloped upwards and away from the viewer at an angle of 60° (Fig. 1C). A third type was a piece of paper ($4\text{ cm} \times (6.2 + 5.4 + 3.1)\text{ cm}$) with a black rectangle ($0.5 \times 5.2\text{ cm}$) drawn at the same place, again folded and glued into a polyhedron where the black rectangle sloped upwards and away from the viewer at 60° (Fig. 1D), but where it reached the same height as the rectangle in type 1 (30°). The dimension (3 cm) of the first rectangle as well as the 30° and 60° slopes were deliberately chosen. All the other dimensions (of the last rectangle and of the three parts of the pieces of strong paper) were precisely calculated using trigonometry (Appendix as digital supplement to this article, at the journal's web pages). For each experiment, two series of six apparatus of one kind and six apparatus of another kind were built: one series was used to condition the ants, the other series to perform the control experiment and the two tests (see below: experimental protocol).

Experimental device

Each experiment (from the control to the two training phases and the two tests, see below: experimental protocol) was performed under a different lighting. One experiment was performed under UV light alone (a fluorescent tube emitting some violet light at low intensity and essentially A, B, and C UV light). Such lights are commonly used for anti-septic purposes, whereby eye and skin protection have to be used. Another experiment was performed under exclusively yellow light (OSRAM, 220 volts, 45 watt lamp commonly used in darkrooms). The spectrum of the broadband emission of the yellow lamp was measured using a 0.5 m triple grating monochromator / spectrograph, type 500i, Actor Research Corporation. Successive sections of 80 nm, with an overlap of 20 nm, were registered, then assembled to obtain the entire spectrum. The resulting broadband spectrum presented a maximum at 864 nm. It decreased rapidly towards the shorter wavelengths, being very low at 520 nm and finishing at 500 nm. It decreased slowly towards the longer wavelengths, finishing around 1,100 nm.

A third experiment was performed under combined UV and yellow light. Figure 2 shows the experimental device used to obtain each of the different lighting conditions described above. A fourth and a fifth experiment were conducted under natural light, in a different room from the three first experiments. This natural light was delivered by the sun through a polyacetate window located on the ceiling of the room. This natural light was therefore composed of both visible (for humans) and UV light.

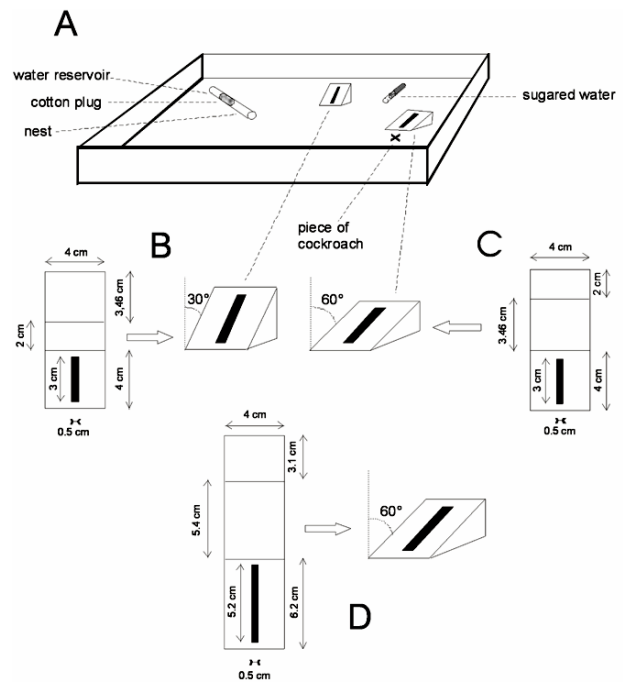


Fig. 1: Experimental design (A) and apparatus (B, C, D).



Fig. 2: Experimental device allowing the ants to be conditioned under either only UV light, or only yellow light, or combined UV and yellow light.

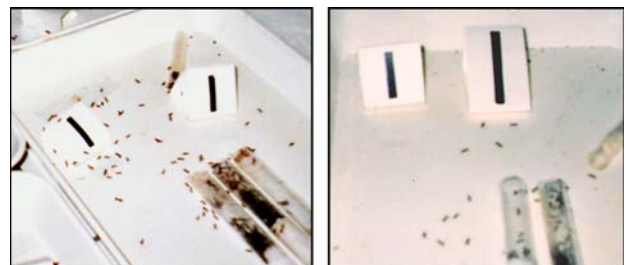


Fig. 3: Ants' response to two black rectangles, one ($0.5 \times 3\text{ cm}$) sloping at an angle of 30° , the other ($0.5 \times 5.2\text{ cm}$) at 60° , after conditioning under combined UV and yellow light (photo on left) or under natural light (photo on right) to find food in front of the 60° rectangle. More ants were recorded in front of the latter (= correct) rectangle.

Experimental protocol

For each of the five experiments, the ants of the six colonies of a series were conditioned (differential operant conditioning) to find their food in front of an experimental apparatus on which the black rectangle sloped upwards and away at an angle of 60° (in the presence of an experimental apparatus on which the rectangle sloped at an angle of 30°). This conditioning involved an initial four-day period of starvation followed by exposure to two kinds of experimental apparatus (those to be used for the control and the two tests) and a control experiment was performed (see below: quantification of the ants' responses). Next, the ants were confronted, during 6 days, with the apparatus to be used during the training phases. A piece of dead cockroach was deposited, on a small piece of glass, in front of the 60° rectangle. The two apparatus were relocated 6 to 10 times during the course of the six training days because the ants can acquire spatial learning (CAMMAERTS 2004b). Care was also taken to not reinforce the ants at 12- or 24-hour intervals because these insects can acquire temporal learning (CAMMAERTS 2004b). Meat was replaced as necessary during the training phase. Following this training, a first test was conducted using the apparatus built for the control and the tests (see below: quantification of the ants' responses). The ants were then conditioned again during three more days in the presence of the apparatus built to perform the training phases, these apparatus being randomly relocated 3 to 6 times during the three training days, intervals of 12 and 24 hours being once again avoided. After this period, a second test was conducted in the presence of the appropriate apparatus (those to be used for the control and the tests).

Quantification of ants' responses; statistical analysis

In the control and the two tests, the ants present in front of each experimental apparatus were counted during 15 minutes, at the end of each experimental minute (i.e., 15 times) for each colony. An ant was judged to be in front of an apparatus when it stayed or moved within a 4-cm long and 2-cm wide rectangular area directly in front of the apparatus. To help visualise this area, a small dot was drawn with a pencil, each time, on the ants' foraging area (i.e., on their tray, Fig. 1A), 2 cm away from the apparatus. No other mark or material was used in order to avoid any modification of the ants' movement. The mean value of the 15 counts was calculated for each experimental apparatus and for each colony. The statistical analyses used these mean values (see below). Then, the mean value together with the standard deviation of all the counts was calculated for each experimental apparatus and for all of the six colonies. These means allowed the mean proportion of ants present in front of each experimental apparatus to be calculated. The mean test values obtained for each colony and for each experimental apparatus were compared to the corresponding control mean values (those from the previous control experiment) using the non-parametric Wilcoxon test (SIEGEL & CASTELLAN 1988). Control values were not analysed statistically but are briefly commented upon in the discussion.

Results

Visual perception under UV light alone (Tab. 1, series A)

After having been conditioned (two rectangles types) under only UV light, *M. sabuleti* workers (series A) continued

responding to the two kinds of experimental apparatus as they did during the control experiment. They did not go preferentially in front of the rectangle that sloped upwards and away the most from the viewer (the one associated with the reward) as would have been expected had they been conditioned and seen the difference between the two apparatus. Thus, they could not distinguish the differently sloping objects and consequently did not see them with perspective. Towards the end of the experiment, they were even somewhat more numerous in front of the "wrong" segment: this behaviour is explained in the Discussion.

Visual perception under yellow light alone (Tab. 1, series B)

After having been conditioned under only yellow light, *M. sabuleti* workers (series B) were more numerous in front of the rectangle previously not associated with the reward. These ants could not differentiate between the two rectangles and simply went to the segment that appeared the longest to them (the "wrong" segment). Thus, under yellow light (with no UV light), *M. sabuleti* workers did not perceive the different slopes of the two rectangles and lacked visual perspective.

Visual perception under combined UV and yellow light (Tab. 1, series C)

After conditioning under the combined lights, *M. sabuleti* workers (series C) during the two tests were most numerous in front of the rectangle sloping upwards and away from the viewer at an angle of 60° (i.e., the one associated with the reward during the training phases) (Fig. 3, photo on left). They distinguished the two kinds of rectangles, perceiving very probably the different slopes, thus seeing with perspective. However, they might have perceived only the height difference between the two rectangles. So, a supplementary experiment was performed (see below).

Visual perception under natural light (Tab. 1, series D)

After training under natural light, *M. sabuleti* workers (series D) during the two tests significantly preferred the most strongly sloping rectangle (previously associated with the reward). They thus perceived the difference between the two rectangle slopes, correctly perceiving perspective. Again, to exclude the possibility that they only distinguished the different heights of the two targets, a supplementary experiment was conducted (see below). Nonetheless, the ants' possible perspective perception was slightly more efficient under natural light ($P < 0.016$) than under a combination of UV and yellow light ($P < 0.031$).

Visual perception under natural light, supplementary experiment (Tab. 1, series E)

Myrmica sabuleti workers (series E) were trained, under natural light, as above, but this time the more strongly sloping target was longer so that the two targets had exactly the same height. During the two tests, the ants were more numerous in front of the most strongly sloping rectangle (associated with the reward during the training) (Fig. 3, photo on the right). The ants had thus acquired operant conditioning and perceived the difference between the two rectangles. Here, only slope, not height was decisive. This capability requires visual perception of perspective.

Tab. 1: Responses of *M. sabuleti* workers to black rectangles sloping at an angle of 30° or 60° during a control experiment, then during two subsequent tests made after that the ants were conditioned, under four different lighting conditions, to find food in front of the rectangle sloping 60°. The difference between the fourth and the fifth experiment is detailed in the text. Each experiment was performed on a series of six colonies. Provided are (1) the mean number (and *standard deviation* σ) of ants present in front of each rectangle (2) the mean proportion of ants present in front of the "correct" rectangle (60° slope), (3) the results of non-parametric Wilcoxon tests between the test and the corresponding control values obtained for each of the six colonies (N, T, P are given according to the nomenclature of SIEGEL & CASTELLAN 1988). * illustrations of these results are given in Figure 3.

series	lighting conditions	steps	(1) mean number (<i>and</i> σ)		(2) mean proportion	(3) statistics		
			30°	60°		N	T	P
A	UV light	Control	2.95 (2.19)	2.72 (2.25)	48 %			
		Test 1	2.87 (2.39)	2.46 (2.12)	46 %	6	-14	NS
		Test 2	2.36 (1.20)	1.74 (0.72)	42 %	5	-11.5	NS
B	yellow light	Control	1.02 (0.89)	1.47 (1.57)	59 %			
		Test 1	1.31 (1.21)	0.72 (0.52)	35 %	5	-20	0.016
		Test 2	2.65 (1.96)	1.31 (0.81)	33 %	6	-21	0.016
C	UV + yellow light	Control	3.26 (2.64)	2.45 (1.66)	43 %			
		Test 1	0.72 (1.33)	2.92 (3.10)	80 % *	5	15	0.031
		Test 2	0.73 (1.04)	3.45 (4.67)	83 %	5	15	0.031
D	natural light	Control	1.00 (1.06)	0.56 (0.58)	36 %			
		Test 1	0.51 (0.77)	2.00 (1.29)	80 %	6	21	0.016
		Test 2	0.90 (1.05)	3.07 (2.85)	77 %	6	21	0.016
E	natural light	Control	0.86 (0.95)	0.54 (0.37)	39%			
		Test 1	0.45 (0.48)	2.38 (1.12)	84% *	6	21	0.016
		Test 2	0.28 (0.33)	2.17 (1.36)	89%	6	21	0.016

Discussion

Earlier experiments demonstrated that *M. sabuleti* workers perceive their environment with perspective (CAMMAERTS 2004a), which was originally explained based on the position of the eyes on the workers' head. My subsequent studies of these ants' visual perception and eye structure, however, cast doubt on this as the sole explanation. *Myrmica sabuleti* workers can see colours and are sensitive to UV light (CAMMAERTS 2006b). This turned the focus on the interplay between visible and UV light. The present study demonstrates that, under UV light alone or yellow light alone, *M. sabuleti* workers do not perceive perspective. Under combined UV and yellow light, however, they do see their surroundings with perspective. The same holds true under natural light (containing visible and UV light). Potentially, the ants might have perceived the two black rectangles (as well as the entire targets), which sloped differently upwards and away from the viewer, as merely having different heights (and thereby different apparent sizes). This was addressed with a supplementary test in which two differently sloping rectangles were given the same apparent size (reaching the same height). The ants successfully distinguished the two rectangles. They perceived the difference based on slope and therefore have 3D vision. This visual perception of perspective in *M. sabuleti* wor-

kers is apparently related to their sensitivity to different kinds of light (in this case UV and visible light). This interpretation will require further experimentation.

The strong, rough white paper used in the present experiments reflects light without changing its polarisation. Moreover, the experimental apparatus presented to the six colonies of ants were variously deposited among the colonies and were relocated several times during the training phases. The apparatus therefore received UV light, yellow light, a combination of both, or natural light under angles that differed between the colonies and varied over the course of the training phases. The ants' choice did not involve the quality (i.e., the polarisation) or the quantity of light reflected by these apparatus. Future experiments will incorporate the effect of light polarisation. In summary, the experimental apparatus, design and protocol minimised all those characteristics other than those requiring 3D vision to distinguish the two targets. The ants could acquire operant conditioning only by having some 3D vision, and they did so under natural light as well as under a combination of yellow and UV light.

During the controls and during the tests of the two experiments in which the ants did not demonstrate perspective, the ants were more numerous in front of the "wrong" rectangle (lesser slope). This "wrong" rectangle appeared somewhat longer to the ants. When an animal has the choice

between two elements – one larger, the other smaller – it instinctively chooses the larger one, a phenomenon known as instinctive response to supra-normal stimuli (GOULD 1982, MANNING & DAWKINS 1998). Prior to operant conditioning (= during the controls) and each time perspective perception was not possible, the ants generally preferred the rectangle that sloped less upwards and away from the viewer, this ("wrong") rectangle appearing longer and more visible to them.

The failure to perceive perspective under yellow light alone was not due to its low intensity (700 lux, lamp located about 50 cm away: Fig. 2). Earlier work (CAMMAERTS 2005) showed that, after having been kept for 9 days under 1,350 lux, *M. sabuleti* workers acquired a visual threshold of about 35 lux. After 9 days under 300 lux, the threshold value was 15 lux. Accordingly, the 700 lux conditions should yield a visual threshold of about 25 lux. Based on the relationship previously found between light intensity and *M. sabuleti* workers' visual thresholds (CAMMAERTS 2005), the value at 700 lux can be calculated as follows:

$$\text{thr}_{700} = 11.62 \text{ lux} \times e^{0.027 \times \sqrt{700}} = 11.62 \text{ lux} \times 2.71^{0.027 \times 26.46} \\ = 11.62 \text{ lux} \times 2.71^{0.714} = 11.62 \text{ lux} \times 2.038 = 23.68 \text{ lux}.$$

This threshold and the 700 lux conditions clearly enabled *M. sabuleti* workers to see their environment normally and to sufficiently perceive the two targets presented.

Under high light intensity, *M. sabuleti* workers are sensitive to yellow (and to blue) (CAMMAERTS 2006b). The yellow lamp effectively emitted yellow light. Its broadband spectrum emission had a maximum at 864 nm, extended until about 1,100 nm (thus containing red light, not well seen by the ants) as well as until 520 nm but finished at 500 nm, therefore containing no wavelengths corresponding to green light. For the ants, this light consisted of the longest wavelengths they can perceive, all other (shorter) wavelengths being absent.

It is not surprising that *M. sabuleti* workers have some degree of perspective perception, although it is unusual that this is based on different sensitivities to different wavelengths. Some information is available on perspective perception and its mechanism(s) in insects. In some species (for example in Odonata), the somewhat lateral position of the two eyes on the head yields 3D vision, i.e., true stereo-vision. WEHNER (1981) clearly explains this phenomenon. Based on morphology, I estimate that the eyes of *M. sabuleti* workers are located too laterally to provide efficient binocular (and 3D) vision. In mantids (ROSSEL 1996), whose eyes are positioned less laterally, the high spatial resolution and the small ommatidial angle are crucial for stereovision ability. This system differs in *M. sabuleti* workers which have lateral eyes and probably lack high spatial resolution because they are unable to discriminate between some lines or forms (CAMMAERTS 2006a). Moreover, based on own, unpublished morphological data, their ommatidial angle is not very small. I used corneal replicates of the eyes, which I photographed at 50 to 60 successive levels, and then analysed these photos using a new logiciel (similar to Image J). The ommatidial angle is rather large and differs according to the position of the ommatidia in the eye. This explains the experimentally assessed, rather large minimum visual angle of 5° 12' (CAMMAERTS

2004a). This rules out a system of perspective perception based on high resolution and small ommatidial angles for *M. sabuleti* workers. My supplementary experiment also rules out that they assess the relative size of elements. Another potential mechanism is motion parallax: some animals that lack binocular vision due to wide eye placement use the apparent relative motion of several stationary objects against a background while moving or moving their head to estimate relative distance. LEHRER & al. (1988) suggest this type of a motion cue to explain how bees see their world in 3D. Two facts argue against this mechanism in *M. sabuleti* workers. First, in my experiments, *M. sabuleti* workers acquired operant conditioning (association of the reward to the "correct" target) only while eating, i.e., remaining motionless in front of the target. Motion parallax would not (or only minimally) have come into play during such feeding. Second, a motion cue mechanism should have – but did not – functioned also under yellow light alone and UV light alone.

In *M. sabuleti*, the use of different sensitivities to different wavelengths requires the existence of different photoreceptors in each eye. It also requires the addition of a supplementary dimension to the animal's visual perception as a result of these different sensitivities. Regarding the first point, ommatidial heterogeneity in a compound eye has been revealed, among others, by BRUNNERT & WEHNER (1973), LABHART (1986) and MOTE & WEHNER (1980) in the ant *Cataglyphis bicolor* (FABRICIUS, 1793), by QIU & al. (2002) in a pierid, by RIBI (1978) in a wasp, by LIN & al. (2002) in moth larvae, as well as by YAMASHITA & TATEDA (1976) in a spider. No small-eyed ant has yet been studied. In *M. sabuleti*, this calls for searching for different kinds of ommatidia (differently sensitive to light) at specific places in each eye, and / or for different photoreceptors (having different spectral sensitivities) in each (or several) ommatidia. My morphological study of *M. sabuleti* workers' eyes (still on course) will probably bring information about this point. Regarding the second point, a third (or fourth) visual dimension as a result of different (and differently located) photoreceptors has not yet been demonstrated in insects. In birds, some photoreceptors are very sensitive to UV light, while others are not. This might give a supplementary dimension to the birds' visual perception (VLADYSLAV 2005).

If my hypothesis on perspective perception in *M. sabuleti* workers is correct, the ants might have depth perception in only one eye. Future work will involve observing the movement and behaviour of workers in which one eye is inactivated.

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Zusammenfassung

In einer früheren Arbeit konnte ich zeigen, dass Arbeiterinnen von *Myrmica sabuleti* MEINERT, 1861 perspektivisch sehen. Die Stereowahrnehmung dieser Art, deren vergleichsweise kleine Augen lateral positioniert sind, ist nicht durch binokulares Sehen erklärbar. In vorliegender Arbeit zeige ich, dass diese Ameisen bei UV Licht alleine und bei gelbem Licht alleine nicht perspektivisch sehen, sehr wohl aber, wenn UV Licht und gelbes Licht kombiniert werden, sowie bei natürlichem Licht. Bewegungsparallaxe ist wahrscheinlich nicht der Mechanismus, der *M. sabuleti* die Tiefenwahrnehmung erlaubt. Die sichtbare Gesamtlänge ist ebenfalls nicht die Ursache für das perspektivische Sehen, wie experimentell gezeigt. Ich bringe daher das perspektivische Sehen von *M. sabuleti*-Arbeiterinnen in kausalen Zusammenhang mit ihrer Empfindlichkeit für sowohl sichtbares Licht (oder eventuelle generell lange Wellenlängen) als auch UV Licht (oder eventuell generell kurze Wellenlängen). Diese Interpretation bedarf experimenteller Bestätigung.

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