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Sensitivity and adaptation of *Myrmica sabuleti* workers (Hymenoptera: Formicidae) to light

Marie-Claire CAMMAERTS

Abstract

Following up on previous studies on visual perception of *Myrmica sabuleti*, I intended to specify this ant species' sensitivity to light intensity. I therefore assessed the lowest light intensity necessary to induce a conditioned response to a visual cue in workers maintained during ten days under a given light intensity and then in the same workers maintained during one day under another light intensity. The visual threshold the ants acquired after a ten day-period under one light intensity appeared to be an exponential function of that light intensity's square root. After an additional one day-period under another light intensity, the ants acquired another visual threshold yet differing from the one presented after the ten day-period under that corresponding light intensity. Therefore, *M. sabuleti* workers adapt themselves to changes in light intensity initially rather rapidly, and then more slowly over the course of time.

Key words: *Myrmica sabuleti*, light and dark adaptation, vision, visual threshold

Dr. Marie-Claire Cammaerts, Faculté des Sciences, CP 160/11, Université Libre de Bruxelles, 50, Avenue F. Roosevelt, B-1050 Bruxelles, Belgique. E-mail: mtricot@ulb.ac.be

Introduction

Ants communicate primarily via chemical signals yet perform several tasks (foraging, returning from a new food source to the nest, etc.) using visual cues or landmarks (WEHNER & RÄBER 1979, MCLEMAN & PRATT 2002). For this reason I studied several characteristics of the visual perception of the ant *Myrmica sabuleti* MEINERT, 1861, such as the visual discrimination of different size cues, the maximum visual distance and therefore the subtend visual angle, as well as the visual discrimination of cues sloping down backwards at different extents (CAMMAERTS 2004d). I also analysed the visual discrimination by *M. sabuleti* workers between different numbers of an element, different shapes, different lines, and cues differently oriented (M.-C. Cammaerts, unpubl. data). All these observations were made in high light intensity. However, I sometimes had the opportunity to observe (without quantifying my observation) whether *M. sabuleti* workers could see cues when in low light intensity. It was obvious that they were indeed able to see these cues. Therefore, I intended to study these ants' sensitivity to light, and more precisely to detect the lowest light intensity under which *M. sabuleti* workers can see their environment after having been maintained during a given time period under a certain light intensity and to determine if these ants can adapt themselves to changes in light intensity.

The lowest light intensity allowing visual perception in an ant has not yet been specified. My work may thus bring new information to that subject. Systems allowing light and dark adaptation have already been largely studied in invertebrates, and especially in arthropods (see Discussion) (AUTRUM 1981, WARRANT & al. 1996). However, most Hymenoptera species studied for their visual perception have large eyes and good vision, contrary to *M. sabuleti* workers. My work might thus be of interest, to know to which extent a small-eyed ant species, living sometimes in darkness (inside of its nest) and sometimes in full light (while foraging in open areas) adapts itself to changes in light intensity.

Material and methods

Collection and maintenance of ants

Eight colonies of *M. sabuleti* were collected from Höhes Martelingen (Luxembourg; 49° 49' 30" N, 5° 45' 00" E) and in the Aise valley (Belgium; 49° 49' 39" N, 5° 15' 26" E). They were divided into 24 experimental colonies (four series labeled A, B, C, D of six colonies numbered 1 to 6) each containing 250 workers, a queen and brood. Each experimental colony was maintained in one or two glass tubes half-filled with water, with a cotton-plug separating the ants from the water. The glass tubes were deposited into a polyethylene tray (43 x 28 x 7 cm) serving as a foraging area (Fig. 1). The ants were fed with sugared water delivered into a small tube plugged with cotton. Meat (pieces of dead cockroaches) was delivered twice a week and only when no experiment was planned or performed.

Experimental design

A window-less room, located adjacent to another room without windows, was provided with a dimmer with which, using one to four lamps (Osram, concentra spot R63, 60 watts), any light intensity could be obtained. The light intensity was measured by assessing, with the help of a luxmeter (H&B), the brightness obtained on an experimental area. The photoelectric cell of that luxmeter could be placed far from the apparatus itself, and therefore on the experimental area, where six experimental colonies were successively placed in the course of our study of the ants' sensitivity to light.

Experimental protocol

Learning and conditioning are possible for ants (CHAMERON & al. 1998, HELMY & JANDER 2003). I have studied

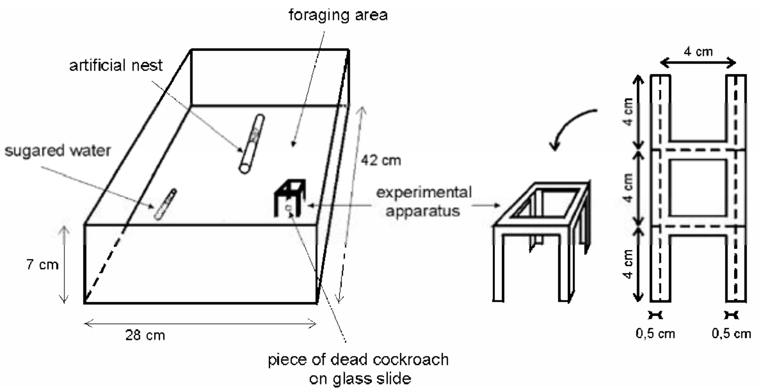

Fig. 1: Experimental nest in the course of a training phase and construction of an experimental apparatus used to condition the ants (this apparatus was in fact made of very strong black paper).

these abilities in *M. sabuleti* (CAMMAERTS 2004a, b, c) and I have also studied this ant species' vision using conditioning as a method (CAMMAERTS 2004d and unpubl. data). In the present study, I also used conditioning as a method for assessing *M. sabuleti* workers' sensitivity to light intensity.

Six experiments were performed, each one on six experimental colonies, as follows (Fig. 2). First, the six colonies were placed under a first light intensity (I 1) and a control experiment was performed (see below). The ants were then conditioned (operant conditioning; see below) during six days, after which a first test was performed. The ants' conditioning was then continued during three more days, and a second test was performed. Next, the ants were conditioned again during the course of one day, and their threshold was then assessed. This assessment consisted of trying to detect the lowest light intensity necessary to obtain the ants' conditioned response. In order to determine this light intensity, the ants' response was quantified several times under successively increasing light intensities. The six tested colonies were then placed under a second light intensity (I 2) and the ants were conditioned during the course of one day. Finally, the ants' threshold was assessed again.

Experimental apparatus – Conditioning of the ants

For each of the six colonies tested in the course of one experiment, a specific shape was drawn on very strong black paper, then cut and folded in order to obtain an kind of hollow cube (called the experimental apparatus) (Fig. 1). To condition the ants, one experimental apparatus was deposited into the tray of each of the six tested colonies and a small piece of dead cockroach was placed under each apparatus. The experimental apparatus were relocated several times in the course of the conditioning in order to avoid spatial learning as well as to avoid the establishment of a trail between the nest and the experimental apparatus. The relocations were performed about every 8 to 26 hours, and never twice in a row at the same daily time to avoid temporal learning. Spatial and temporal learning are in fact possible in *M. sabuleti* (CAMMAERTS 2004a). Meat (= the reward) was replaced whenever necessary. The ants' response consisted of coming onto the area located under the experimental apparatus (= the correct area).

Quantification and statistical analysis of the ants' response

To conduct the control, as well as all of the experimental tests (and this, several days after that sugared water had been offered to the ants), the experimental apparatus (without food) were placed elsewhere than during the training phases. The ants located at the correct area were then counted fifteen times in a row, and the mean value of the fifteen counts was determined, for each of the six tested colonies. The mean of the six mean values was then calculated. This procedure was chosen because the ants can come onto the correct area only if they see sufficiently the experimental apparatus (to which they are conditioned), so, only if the light intensity is higher than their visual threshold.

For each experimental tests, the six experimental mean values obtained were compared to the six control ones with the help of a Wilcoxon non-parametric test (SIEGEL & CASTELLAN 1988). The ants' response was considered to be significant when $P < 0.05$.

The mathematical relationship between the ants' threshold and the light intensity was analysed with the help of the software Statistica 99. Among the functions proposed, the one corresponding to the experimental data with the highest probability was chosen.

Study of the ants' locomotion

Six experimental colonies were conditioned as previously described during 10 days under 10,000 lux, and six other colonies were likewise conditioned under 300 lux. Afterwards, for each of the two series of experimental colonies, the ants' orientation towards the correct area and the ants' sinuosity of movement were quantified using a method described previously (CAMMAERTS-TRICOT 1973). The median, the mean and the standard deviation of the values obtained were then calculated each time using the program Excel 97 (Tab. 7). The orientation values as well as those for sinuosity obtained for the societies maintained under 10,000 lux were compared to those obtained for the societies maintained under 300 lux with the help of a non-parametric Chi-square test (SIEGEL & CASTELLAN 1988). The two distributions of values were considered to be statistically different when $P < 0.05$.

Under a first light intensity (I 1)

- a control (15 countings of the ants)
- a six day-period of conditioning
- a first test (15 countings of the ants)
- a three day-period of conditioning
- a second test (15 countings of the ants)
- a one day-period of conditioning
- the assessment of the ants' threshold →

Under another light intensity (I 2)

- a one-day period of conditioning
- the assessment of the ants' threshold →

detection of the lowest light intensity necessary to obtain the ants' conditioned response by making successive experiments with increasing light intensities

Fig. 2: Protocol of each experiment, performed simultaneously on six societies.

Results

10 days under 10,000 lux followed by one day under 1,350 lux (Tab. 1)

After six training days under 10,000 lux, the ants (series A) did not respond statistically but then did so after three additional training days. After a total of 10 training days, the lowest light intensity necessary for obtaining the ants' response was between 135 and 180 lux. On the basis of the results of the successive experiments made with increasing light intensity, the ants' threshold could be graphically specified as equalling 165 lux. After another training day under 1,350 lux, the ants' threshold was reduced to 90 lux, the ants having thus adapted themselves to a lower light intensity.

10 days under 1,350 lux followed by one day under 300 lux (Tab. 2)

After six training days under 1,350 lux, the ants (series B) were already conditioned, their response being even more pronounced three more training days later. After a total of 10 training days, the ants' threshold (that is the lowest light intensity necessary to induce the response) was equal to 35 lux. One should recall that, in the course of the previous experiment, the ants' threshold equalled 90 lux after a one day-period under 1,350 lux. As for the present experiment, after their 10 day-period under 1,350 lux and after having been trained during one day under 300 lux, the ants reacted statistically when the light intensity reached 22 lux, their visual threshold having thus decreased from 35 lux to 22 lux, when the light intensity changed from 1,350 lux to 300 lux.

10 days under 300 lux followed by one day under 1,350 lux (Tab. 3)

The ants (series C) were conditioned already after six training days, as well as after nine training days. After a total of 10 training days, their threshold equalled 15 lux, a lower value than that (22 lux) observed in the course of the previous experiment on ants maintained during one day under 300 lux. After an additional training day but this time under 1,350 lux, the series C ants gave their conditioned response when the light intensity equalled nearly 30 lux. They had thus adapted themselves to an increase in light intensity.

10 days under 1,350 lux followed by one day under 4,000 lux (Tab. 4)

The ants (series D) responded correctly statistically after six as well as after nine training days. After a total of 10 training days, they responded statistically when the light intensity equalled 35 lux. This value is the same as that previously obtained with series B ants maintained during 10 days under 1,350 lux, and it is somewhat higher than that observed for series C ants having lived during one day under that light intensity. In the present experiment, after having lived 10 days under 1,350 lux, followed by one day under 4,000 lux, the lowest light intensity necessary to induce the ants' conditioned response equalled 60 lux. Therefore, the ants' visual threshold increased from 35 lux to nearly 60 lux after a one day-period under 4,000 lux following a 10 day-period under 1,350 lux.

10 days under 4,000 lux followed by one day under 10,000 lux (Tab. 5)

After having been trained during six days the ants (series A) responded correctly statistically and did so even more obviously after three additional training days. After a total of 10 training days, the light intensity necessary for releasing their conditioned response was equal to 80 lux. One should recall that, in the course of the previous experiment, the ants maintained during one day under 4,000 lux had acquired a threshold of 60 lux. In the course of the present experiment, after having been trained during one more

Tab. 1: Sensitivity to light intensity of ants (series A) maintained under 10,000 lux during 10 days and then under 1,350 lux during one day. The ants were conditioned to come onto a given area when seeing a black apparatus. The table gives for each test (i.e., for each line): (1) for each experimental society the mean number of ants located on the correct area, (2) the mean value of these mean numbers and (3) the result of a Wilcoxon non-parametric test applied to the mean numbers (N, T, P according to SIEGEL & CASTELLAN 1988).

Series A		(1) experimental societies						(2) mean	(3) statistics		
		1	2	3	4	5	6		N	T	P
		10,000 lux									
Control		0.66	0.00	0.66	0.33	0.33	0.00	0.33			
Test 1		1.40	0.00	0.00	1.33	1.33	0.00	0.68	4	8.0	0.31
Test 2		1.60	0.66	0.80	0.53	0.46	0.13	0.70	6	21.0	0.02
		threshold assessment (after 10 days)									
lux:	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00			NS
	7	0.00	0.13	0.26	0.00	0.13	0.00	0.09	5	-14.0	0.06
	15	0.00	0.26	0.26	0.00	0.13	0.00	0.11	5	-13.0	0.09
	30	0.00	0.33	0.26	0.00	0.13	0.00	0.12	5	-12.5	< 0.16
	45	0.00	0.33	0.33	0.00	0.13	0.00	0.13	5	-12.0	0.16
	60	0.00	0.33	0.33	0.00	0.13	0.00	0.13	5	-12.0	0.16
	75	0.00	0.20	0.33	0.00	0.26	0.00	0.15	5	-13.0	0.09
	90	0.33	0.20	0.40	0.20	0.26	0.13	0.25	6	-13.5	< 0.09
	105	0.66	0.33	0.33	0.33	0.40	0.20	0.38	4	6.5	< 0.44
	120	0.33	0.46	0.46	0.40	0.40	0.20	0.32	6	12.5	< 0.42
	135	0.66	0.53	0.53	0.53	0.53	0.33	0.52	5	14.0	0.06
	180	0.93	0.66	0.53	0.53	0.53	0.40	0.60	6	20.0	0.03
	225	1.00	0.93	0.73	0.60	0.73	0.53	0.75	6	21.0	0.02
	345	1.33	1.07	1.00	1.00	1.20	0.80	1.03	6	21.0	0.02
	420	1.33	1.46	1.07	1.20	1.33	0.87	1.21	6	21.0	0.02
		1,350 lux									
		threshold assessment (after one day)									
lux:	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00			NS
	7	0.00	0.00	0.00	0.00	0.00	0.00	0.00			NS
	15	0.00	0.00	0.20	0.00	0.20	0.00	0.07	4	-10.0	0.06
	22	0.27	0.00	0.20	0.00	0.26	0.00	0.12	4	-10.0	0.06
	30	0.27	0.00	0.13	0.07	0.33	0.07	0.15	4	-9.0	0.13
	45	0.13	0.07	0.07	0.07	0.07	0.07	0.08	6	-18.0	0.08
	60	0.20	0.20	0.13	0.20	0.33	0.13	0.20	5	-10.5	< 0.31
	75	0.93	0.20	0.20	0.20	0.53	0.20	0.38	6	14.0	0.28
	90	1.13	0.40	0.53	0.60	0.60	0.40	0.61	6	20.0	0.03
	150	1.33	0.40	0.53	0.93	0.53	0.80	0.75	6	20.0	0.03

day under 10,000 lux, the series A ants presented their conditioned response when the light intensity was between 90 and 120 lux, or more precisely 115 lux. They had thus adapted themselves to an increase in light intensity.

10 days under 10,000 lux followed by one day under 4,000 lux (Tab. 6)

The series B ants trained during six as well as nine days under 10,000 lux gave statistically the correct response. After a total of 10 training days under 10,000 lux, they responded statistically when the light intensity was greater than 150 lux, or more precisely when equalling 165 lux. This value is the same as that obtained in the course of the first experiment with ants (series A) also maintained 10 days under 10,000 lux. This value (165 lux) is higher than the one (115 lux) presented by ants (series A) trained during one day under 10,000 lux in the course of the previous experiment. In the present experiment, after having been trained during an additional day under 4,000 lux, series B ants acquired a threshold equal to 110 lux (between 90 and 120 lux). They had thus adapted themselves to a decrease in light intensity. It should be noted that after a 10 day-period of training under 4,000 lux, the ants (series A, in the course of the previous experiment) presented a threshold of 80 lux.

Relationship between the ants' visual threshold and the light intensity (Fig. 3)

A curve was observed when plotting the six values of the ants' threshold obtained after a 10 day-period under a giv-

Tab. 2: Sensitivity to light intensity of ants (series B) maintained under 1,350 lux during 10 days and then under 300 lux during one day. Same legend as for Tab. 1.

Series B		(1) experimental societies						(2) mean	(3) statistics		
		1	2	3	4	5	6		N	T	P
		1.350 lux									
Control		0.20	0.07	0.13	0.00	0.00	0.20	0.13			
Test 1		0.20	0.66	1.60	0.40	0.20	0.30	0.56	5	15.0	0.03
Test 2		0.27	1.07	1.87	0.53	0.40	0.40	0.76	6	21.0	0.02
		threshold assessment (after 10 days)									
lux:	0	0.00	0.00	0.33	0.00	0.00	0.00	0.06	4	-6.0	0.44
	7	0.00	0.13	0.73	0.13	0.00	0.13	0.19	5	9.0	0.41
	15	0.27	0.13	0.87	0.20	0.00	0.13	0.27	5	12.5	< 0.16
	22	0.13	0.13	1.20	0.26	0.07	0.13	0.32	6	15.0	0.22
	30	0.20	0.26	1.20	0.26	0.13	0.20	0.38	4	10.0	0.06
	45	0.27	0.40	1.27	0.20	0.13	0.27	0.42	6	21.0	0.02
	60	0.33	0.33	1.53	0.26	0.20	0.27	0.49	6	21.0	0.02
	75	0.33	0.33	2.07	0.40	0.26	0.33	0.62	6	21.0	0.02
	90	0.33	0.40	2.73	0.67	0.47	0.80	0.90	6	21.0	0.02
	150	0.33	0.27	2.00	0.33	0.26	0.26	0.58	6	21.0	0.02
		300 lux									
		threshold assessment (after one day)									
lux:	0	0.00	0.00	0.40	0.00	0.00	0.00	0.07	4	-6.0	0.44
	7	0.00	0.00	0.67	0.00	0.00	0.00	0.11	4	-6.0	0.44
	15	0.07	0.13	0.87	0.07	0.13	0.27	0.26	6	14.0	0.28
	22	0.07	0.20	1.07	0.13	0.20	0.40	0.35	6	19.0	0.05
	30	0.20	0.27	1.53	0.20	0.27	0.67	0.52	5	15.0	0.03
	45	0.27	0.27	1.67	0.27	0.40	0.80	0.61	6	21.0	0.02
	60	0.27	0.27	1.80	0.27	0.40	0.93	0.66	6	21.0	0.02

en light intensity, in relation to the square root of that light intensity. The software Statistica 99 gives, with $P < 0.001$, an exponential function to describe that curve. According to this function, when the light intensity equals zero, the threshold equals 11.62 lux, which is the smallest threshold value the ants can acquire, and this is when living in darkness. The experimental data can also be fitted by a linear function with $P < 0.01$, the threshold value acquired in darkness then equalling 13.86 lux.

Ants' visual adaptation to changes in light intensity (Fig. 4)

Six adaptations to a change in light intensity could be graphically represented by using, as follows, the threshold values from the six experiments described above:

For t = 0 days, the threshold value obtained in the course of an experiment on ants of a given series maintained during 10 days under a given light intensity (I 1) was used.

For t = 1 day, the threshold value obtained in the course of the same experiment on ants of the same series maintained during one day under another light intensity (I 2) was used.

For t = 10 days, the threshold value obtained in the course of another experiment on ants of another series maintained during 10 days under that other light intensity (I 2) was used.

Each curve obtained represents the ants' adaptation, over the course of time, to a change in light intensity from I 1 to I 2. Whenever the light increased or decreased, the ants' adaptation always occurred rapidly at the beginning, then more slowly over the course of time. The kinetic of the ants' adaptation (and therefore the underlying physiological mechanisms) may differ according to the type of the light intensity variation (increase or decrease; large or small).

Ants' locomotion under 300 lux and 10,000 lux (Tab. 7)

The ants of the two series of experimental colonies tested oriented themselves towards the correct area. They thus saw the experimental apparatus under 10,000 lux as well as under 300 lux and moved in order to reach the area located under the apparatus (i.e., the correct area). To do this under 300 lux, the ants moved very sinuously; they often touched the edges of the apparatus before reaching the correct area. On the contrary, under 10,000 lux, the ants did not move sinuously, but reached the correct area rather directly. The ants might thus see differently under low and high light intensity.

Discussion

Thanks to operant conditioning as a method, I specified the visual threshold *M. sabuleti* workers acquired after a 10 day-period under 10,000 lux, 4,000 lux, 1,350 lux and 300 lux. These visual thresholds equalled 165 lux, 80 lux,

Tab. 3: Sensitivity to light intensity of ants (series C) maintained under 300 lux during 10 days and then under 1,350 lux during one day. Same legend as for Tab. 1.

Series C		(1) experimental societies						(2) mean	(3) statistics		
		1	2	3	4	5	6		N	T	P
		300 lux									
Control		0.00	0.07	0.07	0.00	0.00	0.00	0.02			
Test 1		0.27	0.33	0.53	0.07	0.13	0.07	0.23	6	21.0	0.02
Test 2		0.47	0.67	0.60	0.13	0.20	0.13	0.37	6	21.0	0.02
		threshold assessment (after 10 days)									
lux:	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2		NS
	7	0.00	0.13	0.13	0.00	0.00	0.00	0.04	2		NS
	15	0.20	0.20	0.33	0.13	0.07	0.00	0.16	5	15.0	0.03
	22	0.60	0.66	1.00	0.13	0.20	0.13	0.45	6	21.0	0.02
	30	0.73	0.73	0.86	0.20	0.20	0.20	0.49	6	21.0	0.02
	45	1.06	0.86	0.80	0.20	0.13	0.13	0.53	6	21.0	0.02
	60	0.93	0.80	0.67	0.07	0.07	0.00	0.42	5	15.0	0.03
		1.350 lux									
		threshold assessment (after one day)									
lux:	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2		NS
	7	0.00	0.13	0.00	0.00	0.00	0.00	0.02	2		NS
	15	0.13	0.20	0.13	0.00	0.00	0.00	0.08	3	6.0	0.13
	22	0.13	0.13	0.13	0.00	0.00	0.00	0.07	3	6.0	0.13
	30	0.80	0.40	0.26	0.13	0.13	0.00	0.29	5	15.0	0.03
	45	1.06	1.06	0.80	0.20	0.13	0.07	0.55	6	21.0	0.02
	60	1.00	0.67	0.53	0.12	0.07	0.13	0.42	6	21.0	0.02
	75	0.80	0.53	0.40	0.20	0.07	0.07	0.34	6	21.0	0.02
	90	0.86	0.53	0.33	0.07	0.07	0.07	0.32	6	21.0	0.02

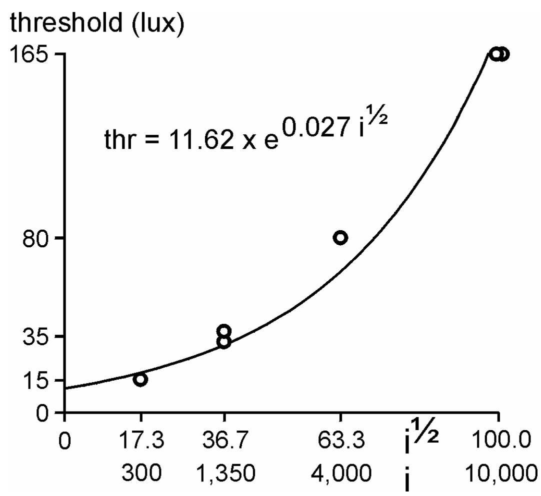

Fig. 3: Relationship between the light intensity and the visual threshold the ants then acquire.

35 lux, and 15 lux, respectively, being thus an exponential function ($P < 0.001$) (or a linear function with $P < 0.01$) of the square root of the light intensity. After a one day-period under a second light intensity, the ants acquired another visual threshold higher or lower than the previous one according to the change in light intensity, but this new threshold was not equal to the one demonstrated after a 10 day-period under the second light intensity. Therefore, the ants adapt themselves to any changes in light intensity initially rather quickly, then slowly and progressively in the course of time.

Many studies have been done on the vision of insects (WEHNER 1981) of which a few concern ants (e.g., VOSS 1967). However, assessments of any ant species' visual threshold and the relationship between such a threshold and the light intensity have not yet been reported. The present evaluation of an ant's threshold and its relationship to the light intensity may thus be of interest. On the basis of these results, the threshold the ants acquire in darkness was found to be equal to 11.62 lux. This value concords with the behaviour exhibited by ants maintained in darkness and then placed under either a low or a high light intensity. In low light intensity, the ants move slowly, come onto their food source, and return correctly to their nest, demonstrating that they see their environment sufficiently. In high light intensity, they move quickly and erratically, and young workers go out of their glass-nest, obviously being perturbed by light of too high an intensity. Consequently, finding a low visual threshold value for ants living in darkness is logical.

Concerning the ants' larger sinuousity of movement in low light intensity, it is interesting to note that, in domestic bees, the level of light has an impact on these insects' search times (CHITTKA & SPAETHE in press).

As for the ants' adaptation to light intensity, some very quick adaptations may occur. Indeed, ants came onto the

Tab. 4: Sensitivity to light intensity of ants (series D) maintained under 1,350 lux during 10 days and then under 4,000 lux during one day. Same legend as for Tab. 1.

Series D		(1) experimental societies						(2) mean	(3) statistics		
		1	2	3	4	5	6		N	T	P
		1.350 lux									
Control		0.20	0.13	0.13	0.07	0.00	0.00	0.09			
Test 1		0.60	1.06	0.53	0.13	0.07	0.20	0.40	6	21.0	0.02
Test 2		0.87	1.40	0.80	0.47	0.27	0.53	0.72	6	21.0	0.02
		threshold assessment (after 10 days)									
lux:	0	0.07	0.00	0.00	0.00	0.00	0.00	0.01	4	-10.0	0.06
	7	0.07	0.20	0.13	0.07	0.07	0.00	0.09	3	3.0	0.63
	15	0.07	0.20	0.13	0.07	0.07	0.00	0.09	3	3.0	0.63
	22	0.33	0.26	0.26	0.07	0.00	0.00	0.15	3	6.0	0.13
	30	0.47	0.53	0.47	0.20	0.00	0.00	0.28	4	10.0	0.06
	45	0.60	0.67	0.53	0.20	0.13	0.07	0.38	6	21.0	0.02
	60	0.40	0.40	0.33	0.27	0.13	0.07	0.27	6	21.0	0.02
	75	0.26	0.26	0.20	0.20	0.07	0.00	0.17	5	15.0	0.03
		4.000 lux									
		threshold assessment (after one day)									
lux:	0	0.07	0.20	0.07	0.00	0.00	0.00	0.06	4	-6.5	< 0.44
	7	0.00	0.20	0.07	0.00	0.00	0.00	0.05	4	-7.5	< 0.31
	15	0.07	0.27	0.13	0.00	0.00	0.00	0.08	3	3.0	0.63
	22	0.13	0.40	0.27	0.00	0.00	0.00	0.13	4	7.0	0.31
	30	0.20	0.33	0.27	0.00	0.00	0.00	0.13	3	5.0	0.25
	45	0.20	0.60	0.27	0.07	0.00	0.00	0.19	2	3.0	NS
	60	0.40	0.80	0.80	0.07	0.07	0.07	0.37	5	15.0	0.03
	75	0.60	1.20	0.47	0.13	0.07	0.07	0.62	6	21.0	0.02
	90	0.53	0.67	0.40	0.07	0.07	0.07	0.30	6	21.0	0.02
	120	0.20	0.67	0.27	0.07	0.07	0.07	0.23	4	10.0	0.06
	150	0.20	0.67	0.27	0.07	0.00	0.00	0.20	2	3.0	NS

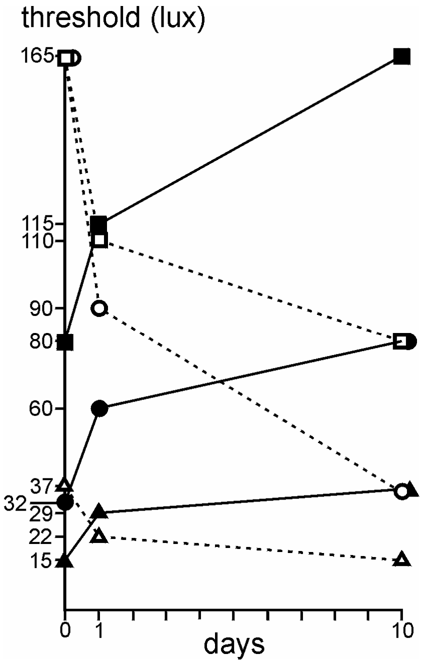

Fig. 4: Changes in the ants' visual threshold in the course of their adaptation to six changes in light intensity.

reward early, since they were conditioned again after a 24 hour-period, and therefore saw the apparatus well with nearly no delay.

Studies of cytological mechanisms allowing light and dark adaptations have been made by BRUNNERT & WEHNER (1973) on *Cataglyphis bicolor* and by MENZEL & LANGE (1971) on *Formica polyctena. Cataglyphis bicolor* foragers adapt themselves to light intensity with the help of radial (and probably also distal) movements of pigment granules within the retinula-cells as well as via changes of the cisternae volume along the rhabdomes. These mechanisms were revealed by comparing the fine structure of the eyes of foragers maintained during one day in darkness in one instance, and during 18 hours under high light intensity in another. Similar systems were shown to exist in *Formica polyctena*. In fact, many kinds of systems allowing light and dark adaptation have been described in many insects species (AUTRUM 1981). Some systems control the intensity of the light reaching the sensory cells, e.g., screening-pigments movements, intracellular cisternae, changes in the rhabdomes (BERNHARD & al. 1963, WHITE & LORD 1975). Other systems control the sensitivity of the sensory cells, e.g., changes affecting membranes, photo-pigments, ions (WALCOTT 1971, LAUGHLIN 1975). The numerous species studied have large eyes and the adaptation systems

Tab. 5: Sensitivity to light intensity of ants (series A) maintained under 4,000 lux during 10 days and then under 10,000 lux during one day. Same legend as for Tab. 1.

Series A		(1) experimental societies						(2) mean	(3) statistics		
		1	2	3	4	5	6		N	T	P
		4.000 lux									
Control		0.27	0.13	0.33	0.47	0.33	0.00	0.26			
Test 1		0.46	0.60	0.60	0.33	0.53	0.60	0.54	6	20.0	0.03
Test 2		1.40	0.60	0.60	0.73	0.80	0.60	0.79	6	21.0	0.02
		threshold assessment (after 10 days)									
lux:	0	0.00	0.07	0.00	0.00	0.07	0.00	0.02	5	-15.0	0.03
	7	0.00	0.27	0.00	0.00	0.13	0.00	0.07	5	-15.0	0.03
	15	0.07	0.27	0.00	0.00	0.27	0.13	0.12	6	-17.5	< 0.11
	22	0.00	0.40	0.00	0.07	0.27	0.27	0.17	6	-15.0	0.22
	30	0.07	0.27	0.13	0.20	0.13	0.13	0.16	6	-18.0	0.08
	45	0.20	0.33	0.13	0.33	0.13	0.13	0.21	6	-14.0	0.28
	60	0.13	0.40	0.27	0.20	0.27	0.13	0.23	6	-12.5	< 0.42
	75	0.13	0.33	0.40	0.47	0.60	0.27	0.37	5	13.0	0.09
	90	0.33	0.47	0.40	0.53	0.67	0.66	0.51	6	21.0	0.02
	120	0.33	0.67	0.40	0.53	0.67	0.66	0.54	6	21.0	0.02
	150	0.33	0.40	0.33	0.47	0.33	0.27	0.36	3	6.0	0.13
		10.000 lux									
		threshold assessment (after one day)									
lux:	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5	-15.0	0.03
	7	0.07	0.07	0.00	0.00	0.07	0.00	0.04	5	-15.0	0.03
	15	0.07	0.07	0.07	0.07	0.07	0.00	0.06	5	-15.0	0.03
	22	0.13	0.00	0.00	0.07	0.00	0.07	0.05	6	-20.0	0.03
	30	0.07	0.07	0.07	0.07	0.07	0.07	0.07	6	-20.0	0.03
	45	0.20	0.13	0.13	0.07	0.07	0.13	0.12	5	-13.0	0.09
	60	0.33	0.13	0.13	0.07	0.07	0.13	0.14	5	-12.0	0.16
	75	0.13	0.13	0.13	0.13	0.07	0.20	0.13	5	-12.5	< 0.16
	90	0.33	0.20	0.13	0.13	0.27	0.33	0.23	6	10.5	0.50
	120	0.60	0.40	0.40	0.53	0.40	0.27	0.43	6	21.0	0.02
	150	0.33	0.20	0.33	0.33	0.27	0.27	0.29	5	9.5	< 0.40
	180	0.20	0.20	0.13	0.27	0.27	0.27	0.22	6	-11.5	< 0.50

described generally function very rapidly. Compared to species generally studied for their vision, *M. sabuleti* workers have small eyes and present not only a quick but also a slow light and dark adaptation. It would be interesting to study cytologically the eyes of workers maintained during different time spans (one minute, one hour, one day, 10 days) under different light intensities (0 lux, 300 lux, 4,000 lux, 10,000 lux, for instance) in order to find the cytological mechanisms allowing these ants' adaptation to light intensity.

In the course of their adaptation to one light intensity, together with cytological mechanisms affecting their eyes, certain events might occur in *M. sabuleti* workers' brains. In other words, in addition to light receptor adaptation, simultaneously or after, some learning may occur as a response to a change in the light intensity. Concerning the latter hypothesis, it should be noted that behavioural changes due to light impact and resulting from learning have been shown to occur in bumblebees (LOTTO & CHITTKA 2005).

The light source used in the present paper does not include UV. Following this work, I studied *M. sabuleti* workers' colour vision and perception of UV (M.-C. Cammaerts, unpubl. data). On the basis of the latter data, I infer that experimenting with light including UV would lead to similar adaptation events though with somewhat different numerical results.

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Zusammenfassung

An bisherige Studien zur visuellen Wahrnehmung von *Myrmica sabuleti* anknüpfend habe ich hier die Empfindlichkeit der Art auf unterschiedliche Lichtintensitäten untersucht. Auf einen visuellen Reiz konditionierte Arbeiterinnen wurden 10 Tage lang unter einer bestimmten Lichtintensität gehalten. Danach wurde in einem Test die nied-

Tab. 6: Sensitivity to light intensity of ants (series B) maintained under 10,000 lux during 10 days and then under 4,400 lux during one day. Same legend as for Tab. 1.

Series B		(1) experimental societies						(2) mean	(3) statistics		
		1	2	3	4	5	6		N	T	P
		10.000 lux									
Control		0.13	0.13	0.13	0.07	0.00	0.00	0.08			
Test 1		0.26	0.53	0.67	0.60	0.07	0.13	0.38	6	21.0	0.02
Test 2		0.40	1.00	1.06	0.67	0.13	0.26	0.59	6	21.0	0.02
		threshold assessment (after 10 days)									
lux:	0	0.00	0.00	0.07	0.00	0.00	0.00	0.01	4	-10.0	0.06
	7	0.00	0.13	0.07	0.00	0.00	0.00	0.03	3	-6.0	0.13
	15	0.00	0.26	0.13	0.07	0.00	0.00	0.08	2		NS
	22	0.00	0.13	0.26	0.00	0.00	0.00	0.07	3	3.0	0.63
	30	0.07	0.20	0.20	0.07	0.00	0.00	0.09	3	5.0	0.15
	45	0.00	0.20	0.20	0.13	0.00	0.13	0.11	5	10.5	< 0.31
	60	0.07	0.26	0.26	0.13	0.00	0.07	0.13	5	13.5	< 0.09
	75	0.07	0.33	0.40	0.07	0.00	0.07	0.16	4	9.0	0.13
	90	0.13	0.40	0.40	0.07	0.00	0.00	0.17	2		NS
	120	0.07	0.40	0.53	0.07	0.00	0.00	0.18	3		NS
	150	0.13	0.53	0.60	0.53	0.00	0.13	0.32	4	10.0	0.06
	180	0.40	0.80	1.46	0.53	0.13	0.53	0.64	6	21.0	0.02
	210	0.60	1.00	1.53	1.06	0.20	0.53	0.82	6	21.0	0.02
		4.000 lux									
		threshold assessment (after one day)									
lux:	0	0.00	0.00	0.07	0.00	0.00	0.00	0.01	4	-10.0	0.06
	7	0.00	0.07	0.20	0.00	0.00	0.00	0.05	4	-7.5	< 0.31
	15	0.07	0.07	0.26	0.00	0.00	0.00	0.06	4	-6.0	0.44
	22	0.13	0.07	0.40	0.00	0.00	0.00	0.10	3	3.0	0.63
	30	0.26	0.26	0.40	0.07	0.00	0.00	0.17	3	6.0	0.13
	45	0.20	0.20	0.40	0.00	0.00	0.00	0.13	4	8.0	0.19
	60	0.20	0.20	0.46	0.00	0.00	0.00	0.14	4	8.0	0.19
	75	0.20	0.20	0.53	0.07	0.00	0.00	0.17	3	6.0	0.13
	90	0.20	0.26	0.53	0.07	0.00	0.00	0.18	3	6.0	0.13
	120	0.53	0.53	1.13	0.26	0.07	0.13	0.44	6	21.0	0.02
	150	0.60	0.66	1.46	0.40	0.13	0.26	0.59	6	21.0	0.02
	180	0.66	0.66	1.53	0.40	0.13	0.33	0.62	6	21.0	0.02

Tab. 7: Ants' locomotion under two different light intensities. The ants were conditioned under two different light intensities to go onto a given area. Then, their orientation (O) towards that area and their sinuousity of movement (S) were quantified. The table gives the numbers (n), the median, the mean and the standard deviation of the values obtained for each variable and each light intensity, as well as the results of non- parametric χ^2 tests applied to two distributions of values.

Societies series	Light intensity	n	O (angular degrees)			S (angular degrees / cm)		
			median	mean	σ	median	mean	σ
C	300 lux	24	46.8	49.8	14.2	155	157	34
			NS			P < 0.01		
D	10.000 lux	33	32.1	36.8	15.3	85	87	44

rigste Lichtintensität ermittelt, bei der sie noch die konditionierte Reaktion ausführten. Anschließend wurden die selben Tiere für einen Tag unter einer anderen Lichtintensität gehalten und der Test wiederholt. Der visuelle Schwellenwert der Ameisen nach der zehntägigen Periode war eine exponentielle Funktion der Quadratwurzel der Lichtintensität, unter der sie gehalten worden waren. Nach der anschließenden eintägigen Periode unter einer anderen Lichtintensität war der visuelle Schwellenwert der Ameisen nur geringfügig anders als jener nach der zehntägigen Periode bei der entsprechenden Lichtintensität. *Myrmica sabuleti*-Arbeiterinnen passen sich also an Änderungen der Lichtintensität anfangs recht rasch an, danach deutlich langsamer.

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