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Some Experiments on Colour Vision in Ants¹⁾

By

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(With 1 Textfigure)

In comparison with the recent knowledge concerning the colour vision in the flying social Hymenoptera, it seems rather strange to say that little is known in this field in the walking relatives. This is probably due to difficulties of experiment, especially in method, compared with the case in the flying insects. Indeed, the classical works of Lubbock (1882), Turner (1907) and Forel (1910) undertaken in hope of analyzing this problem are all utterly valueless, since no proper attempt was made to control either the brightness or odour factor. Recently I have had an opportunity to make some experiments pertaining this problem. Though the experiments here attempted are rather preliminary in constitution, some results presented are, as it seems to me, worthy to publish.

I express here my deepest thanks to Professor Tohru Uchida, for his kind direction in the course of the present study. I am also indebted much to Professor Sajiro Makino, for the valuable advice in preparing the paper.

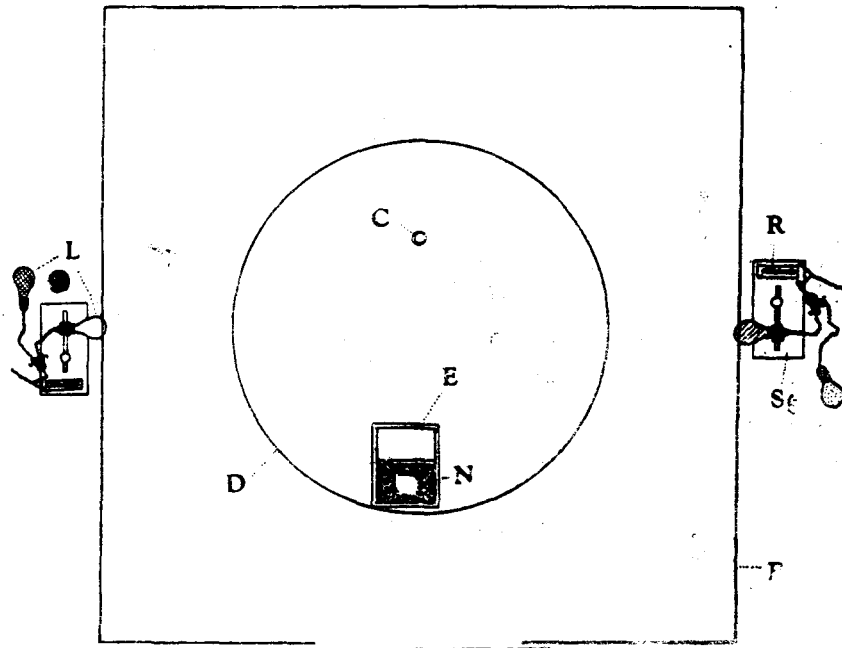
Material and Method

Leptothorax congruus spinosior Forel, reared in one of my Lubbock-Fielde nests (11 × 8 × 0.2 cm), was adopted as the material. An ant which was specially selected for the study was the largest worker marked with No. 3. The reasons for this are that, on the one hand, large workers have been commonly admitted among the myrmecologists to be more excellent in psychical ability than smaller ones, and on the other hand, they are

1) Contribution No. 234 from the Zoological Institute, Faculty of Science, Hokkaido University, Sapporo, Japan.

expected to transport burdens more easily; accordingly the experiments can be more smoothly carried out than in smaller ones. In the previous experiments it has been ascertained that the ants, in their homing behaviour, have a strong tendency to depend much more upon the light than upon the odour. Their orienting response to light in such a case was utilized by the writer for the colour vision experiments. Scores of larvae, taken out of the nest of No. 3, were put on a cardboard and placed some distance away from the nest. No. 3 was caught in the nest and was put to the cardboard. She examined the larvae, took one of them and went to the nest. Soon she came back, empty handed, to the cardboard and again carried a larva to her nest. Thus the transportation journey was repeated thereafter between the cardboard and the nest. While she was doing so, the cardboard was gradually shifted far and far until it attained to the necessary distance for the experiment. On the other hand, while she was at work, a coloured light was thrown upon her working ground from one side of her pathway, or two different coloured lights, one from each side. After several journeys were repeated and when she was in her nest or on the cardboard, the light (or lights) was changed either in colour or in intensity, or in both. Sometimes, furthermore, the light was shifted to the symmetrical position in the opposite side. The behaviour of the ant, caused by such changes of the condition of the light, especially the direction of her progress, was observed. The apparatus used in the experiments was arranged as shown in the annexed Figure. B is a cubic box, 70 cm in side, made of white poster paper, with the wooden outside frame and tightly fixed on to the table. The paper of the upper wall is removable in case of necessity. The northern wall consists of three sheets of hanging paper. The median sheet is laid slightly over the lateral sheets and not fixed below so as to permit the observer to treat, if necessary, the apparatus and the ant inside the box. In the middle of the eastern and western walls of the box, is opened a circular hole, which is 4 cm in diameter and situated at the height of 20 cm above the horizontal surface of the table. Through the holes coloured lights can be cast over the working ground of the ant. L shows the lamp (coloured bulb), S its stand and R its regulator. The colours of light used are five kinds, namely red, pink, yellow, green and blue. The intensity of illumination was measured in each experiment with the Matsuda Luxmeter. D is a rotating disc, the working ground of the ant, made of veneer, 40 cm in diameter and is covered with the paper of the same size. N is the nest, with the entrance (E) at its interior side. C denotes a small circular cardboard, 2 cm in diameter, on which are put a number of larvae to be transported. Just above the centre of the disc, at the height of 2 m 30 cm, is situated a ceiling lamp of 200 W. with a white cover. On account of its special

situation, this lamp is very convenient to control other light factor which may otherwise guide the ant in her journey. Furthermore, to the south of the apparatus is prepared a black screen which is specially made and is also useful to get an uniform luminosity over the sides of the box. The manoeuvre of the ant was observed through a small hole, with a diameter of 7 mm, opened in the centre of the median sheet of the northern wall.



Explanation of the Annexed Tables

1) No. of learning (L) or experiment (Exp. or E). Numbers within parentheses show one and the same experiment. 2) Direction and colour of light. The direction of illumination and the colour of light were shown by the combination of two initial letters, namely the first symbol representing the direction of illumination (U : upwards, E : eastwards, W : westwards) and the next symbol the colour of light (R : red. P : pink. Y : yellow. G : green. B : blue. W : white). The relative intensity of light is shown, for instance in yellow, as follows: $Y' > Y > Y' > Y > y > y$. Accordingly the combination of E.r,W.Y indicates that the red light from the east is weaker than the Yellow light from the west. If the light was

switched off, were put the symbols -- in that place. 3) Other conditions. dist. : distance between E and C (vide Figure). stop. e. c. : casual stoppage of the electric current. d.t. 180° : the disc was turned around 180°. pap. ch. : the paper covering the disc was changed. 4) Time. The numerals

Table I

No. of L. or Exp.	Direct. & colour of light	Outward journey			Return journey		
		time	behaviour	direct.	time	behaviour	direct.
		m s			m s		
L 1	U, W				8.38	Se	c(d)
L 2	" "	17.07	Se R(3)	α-D	13.46	Se, R(4)	D-c
L 3	E, R, W, b	11.57	Se(St)	D-c	4.44	Se	c(d)
L 4	" "	2.57	Se	c	1.35	Sm	C
L 5	" "	1.40	Sm	C	1.50	Sm	C
L 6	" "	1.28	Sm	C	1.13	Sm	C
L 7	" "	1.24	Sm	C	1.11	Sm	C
E 1	--W, b	(?)	H, R				
E 2	E, R --	2.29	Sm-Se	C-c	1.41	Sm-Se	C-c
L 8	E, R, W, b	1.29	Sm	C			
E 3	--W, b				(?)	H	
L 9	E, R, W, b				6.30	St-Se	D-c
E 4	E, R, W, Y'	(?)	Se-R(4)	O-D-O			
E 5	E, R, W, Y'	(?)	Sm(Se)-R	O-d-O			
E 6	E, R --	3.09	Se-St-Se	c			
E 7	E, R, W, Y'				(?)	Sm	O
E 8	E, R, --				(?)	R	C
" (2)	" "				2.30	Sm	C
E 9	E, R, W, Y'	(3.20)	Sm-R	O-d-O			
" (2)	" "	(1.10)	Se-R	c-O			
" (3)	" "	(1.10)	Sm-R	O			
" (4)	" "	5.30	Sm-Se(R)	O-d-O-c			
E 10	" "				10.37	Se(R)-St-Se	c-d-O-c
L 1'	" "	2.36	Se(R)	c	1.20	Sm	C
L 2'	" "	2.26	Se(R)	c	1.48	Sm(Se)	C
L 3'	" "	2.28	Sm-Se	c	.57	Sm	C
L 4'	" "	1.57	Se	c	1.00	Sm	C
L 5'	" "	1.42	Sm-Se	c	.59	Sm	C
L 6'	" "	2.24	Se-St-Se	c(d)	.58	Sm	C
L 7'	" "	2.06	Se(St)	c	1.24	Sm(d)	C
L 8'	" "	1.33	Se-Sm	c	1.15	Sm-d	C
E 11	E, R, W, Y'	2 17	Sm(St)-Se	c(d)	1.05	Sm	C
L 9'	" "	3.14	Sm-P-St-Se	c(d)	1.01	Sm	C
L 10'	" "	1.19	Sm(St)	C(d)	1.18	Sm-d	C
E 12	--W, Y'	1.41	Sm(St)	c(d)	1.14	Sm-d	C
L 11'	E, R, W, Y'	1.25	Sm-Se	C			
E 13	E, R, --				2.21	Sm-Se	O-c
L 12'	E, R, W, Y'	(1.50)	Se-R	D			
" (2)	" "	4.59	St-R-Se	d-c-c	1.52	Sm-P	C
L 13'	" "	(2.51)	St-Se-R	D			
" (2)	" "	5.45	Se-St-R-Se	c-d-c	1.02	Sm	C
L 14'	" "	1.41	Se	c			
E 14	--W, Y'				(?)	Sm	C
E 15	E, R --				(5.20)	St-Se	d-O
E 16	E, R, W, Y'				(?)	Se-Sm	C
E 17	--W, Y'				1.20	Sm	C
E 18	" "	1.25	Se-Sm	c-C			
E 19	U, W, W, Y'				(2.50)	R(4)	O
E 20	--W, Y'				(4.00)	St-R(2)	D-O-c

Table II

No. of L. or Exp.	Direct. & colour of light	Other conditions	Outward journey			Return journey		
			time	behaviour	direct.	time	behaviour	direct.
L 1	U.w, W.R	dist. 7cm				m s		
L 2	" "	" 13				1.30	H-Se(R)	c(d)
L 3	" "	" 19	5.14	Se-St	c(d)	1.04	H-Se(R2)-Sm	D-c
L 4	" "	" "	1.31	Se	c	2.20	Se	c
L 5	" "	" "	1.57	Sm (Se)	C-c	1.13	Sm(Se)	c
L 6	-- WR.					4.35	Se-R-St-Se	c-D-c
L 7	" "		1.25	Se-Sm	c	1.50	Se	c
L 8	" "		1.53	Se	c(d)	1.10	Sm	C
L 9	" "		1.18	Se-Sm	c-C	5.25	Sm-d-St	C-D
L 10	" "		1.30	Sm-Se	c			
E 1	-- W.g					1.30	Sm-d	C
E 2	" "		1.08	Sm	C	55	Sm	C
E 3	-- W.Y	(stop. e.c.)	1.10	Sm	C	(7.00)	Sm-St	C-D
E 4	E.P, --					(1.00)	Sm-St	O
E 5	-- W.Y					(?)	Se-R	c-d
E 6	" "					2.17	Se(St)	c(d)
E 7	E.P, W.Y		6.33	Se(R)(St)	c(D)	1.01	Sm	C
L 1'	" "	(stop. e. c.)	(4.12)	Se(St)	c-D			
L 2'	" "		1.28	Se	c	1.10	Sm	C
L 3'	" "		1.08	Sm	C	1.04	Sm	C
L 4'	" "		1.38	Sm-Se	C-c			
E 8	E.P, W.y					(7.00)	Sm-St-R	O-D
E 9	E.P, W.Y					(?)	Sm(St)-R	O-D
" (2)	" "		.57	Sm	C	1.40	Sm	C
L 5'	" "		.54	Sm	C	1.49	Sm	C
L 6'	" "							
E 10	-- W.Y					.59	Sm	C
L 7'	E.P, W.Y		3.01	Sm-P-Se	C-d	.53	Sm	C
L 8'	" "		1.42	Sm-P	C(d)	.58	Sm	C
L 9'	" "		.44	Sm	C			
E 11	E.P, --					(?)	Sm-St-R	O-c-O
" (2)	" "					.50	Sm	C
E 12	E.p, W. g		1.11	Sm-Se	C-c	(2.30)	Sm-R	O
" (2)	" "					(2.54)	Sm-R	O-d-O
" (3)	" "					.63	Sm	C
E 13	" "		9.05	Sm-St-R	O-d-O-d			
E 14	" "					(4.02)	Sm(St)-R	O-d-O
" (2)	" "					(1.45)	Se-Sm-St-R	c-d-O-d
" (3)	" "					1.42	Se	c

within parentheses represent the time consumed during the straying when the ant could not reach the destination. 5) Behaviour. Se : searching manner. R : returning to the starting point. R (2) : returning twice. St : straying. Sm : smooth. H : hesitation. P : passing over near-by. d : difficulty in finding the entrance to the nest, though smoothly arrived at. Sp : special manner, that is, the manner in which the ant faced very frequently against the light on the way of her excursion. Parenthesized symbol represents the behaviour shown in part. 6) Direction. C : correct, that is, in the outward journey, towards the larvae ; in the return journey,

Table III

No. of L. or Exp.	Direct. & colour of light	Other condition	Outward journey			Return journey		
			time	behaviour	direct.	time	behaviour	direct.
L 1	U.w, E.R, W.Y		m s			m s		
L 2	" " "		3.40	Se(St)	c((d)	2.40	Se	c
L 3	" " "		1.42	Se	c	2.00	Se	c
L 4	" " "		6.45	Se-R-St	C-D	1.14	Sm-d	c
L 5	" " "		6.35	Se-R(2)-P	c-c(d)	4.54	Se-F(3)-Se	d-O(d)-c
L 6	" " "		.58	Sm	C	2.06	H-Se-d	d-c
L 7	" " "		1.16	Se	C	1.40	Sm-d	C
L 8	" " "		1.25	Se	c	1.13	Sm-d	C
L 9	" " "		3.10	Se-P-St	c-d	1.08	Sm	C
L 10	" " "		1.17	Se	c	.58	Sm	C
L 11	" " "		1.50	Se(St)	c(d)	.45	Sm	C
L 12	" " "		3.33	Se	c	.43	Sm	C
E 1	" " "	d. t. 180°				(brought a friend)		
L 13	" " "	d. t. 180°				(?) Sm		O
L 14	" " "					.57 Sm		C
" (2)	" " "		3.00	Se(St)	c(d)	(imprisoned)		
L 15	" " "					1.39 Se		c
L 16	" " "		1.08	Sm-Se	C	.45 Sm		C
L 17	" " "		1.02	Sm	C	1.03 Sm-d		C
L 18	" " "		2.04	Sm-Se	C-c	.42 Sm		C
L 19	" " "		1.01	Sm	C	.45 Sm		C
L 20	" " "		1.03	Sm	C	.50 Sm		C
E 2	U.w, - - W.Y		.58	Sm	C	.43 Sm		C
E 3	U.w, E.R -		1.06	Sm(Se)	C	.50 Sm		C
L 21	U.w, E.R, W.Y		4.26	Se-R(2)-Se	O-d-Se	(2.30) Se-L-R		O-d
L 22	" " "		.53	Sm	C	.38 Sm		C
L 23	" " "		1.04	Sm	C	.44 Sm		C
E 4	U.w, - - - -		1.57	Se	c	.30 Sm		C
L 24	U.w, E.R, W.Y					(4.00) Se-St-R(2)		c-D
L 25	" " "		1.07	Sm-Se	C	.38 Sm		C
L 26	" " "		.58	Sm	C	.39 Sm		C
L 27	" " "		.45	Sm	C	(?) Sm		C
E 5	U.w, E.R - -		5.31	R(4)-Se(St)	O-c	1.44 Sm-Se		C-d
L 28	U.w, E.R, W.Y					(3 20) Se-R(2)		c-O-c
L 29	" " "		2.18	Se-P	c-d	.35 Sm		C
E 6	U.w, - - W.Y		.50	Sm	C	.55 Sm		C
E 7	U.W, E, b, W, r					.53 Sm		C
L 1'	" " "	pap. ch.	1.49	Sm-Se	C-c	2.01 Sm-Se		c
E 8	" " "					(?) Sm(St)		c
E 9	U.W, - - W, r					(?) Sm		O
L 2'	U.W, E, d, W, r					(?) St		D
L 3'	" " "		5.23	St-R(2)-Se	D-c	2.15 Se		c
L 4'	" " "		1.25	Se	c	1.35 Se(Sp)		c
E 10	U.W, - - W, R		1.30	Se	c	1.37 Se(Sp)		c
L 5'	U.W, E, b, W, r		4.01	Se-St	O(3)-d	1.48 Se(Sp)		c
L 6'	" " "		.54	Sm	C	1.30 Se		c
L 7'	" " "		1.11	Sm-Se	C-c	1.27 Se		c
L 8'	" " "		1.25	Sm-Se	C-c	1.04 Sm		C
L 9'	" " "		2.55	Se-St	c(d)	1.01 Sm		C
L 10'	" " "		1.06	Sm	C	2.20 H-Se		d-c
L 11'	" " "		1.05	Sm	C	.52 Sm		C
L 12'	" " "		2.00	Se	c	.47 Sm		C
L 13'	" " "		1.09	Sm	C	1.40 Se		c
L 14'	" " "		1.03	Sm	C	2.40 Se(Sp)		c
E 11	U.W, E, b - -					1.12 Se(Sp)		o-C
E 12	" " "		1.09	Sm	c			c
E 13	U.W, - - W, r					3.02 Se		c

L 15'	U.W, E.b, W,r		1.09	Sm	C	.43	Sm	C
L 16'	" " "		2.46	Se(St)	c(d)	1.14	Sm-d	C
L 17'	" " "		1.35	Sm-Se	c			
E 14	U.W, E.b - -					1.05	Sm (Sp)	C
L 18'	U.W, E.b, W,r		2.10	Sm(St)	c(d)	1.27	Sm-d	C
L 19'	" " "		1.03	Sm	C			
E 15	U.W, - - W,r					2.34	Sm-d	C
E 16	U.W, - - - -	d. t. 180°	4.13	St.	D-Se			
L 20'	U.W, E.b, W,r	d. t. 180°				1.02	Sm	C
L 21'	" " "		.58	Sm	C	.55	Sm	C
E 17	" " "	d. t. 180°	1.08	Sm	C			
E 18	U.W - - - -	d. t. 180°				2.20	Se	c
E 19	" " "		4.58	Se-st	c(d)	2.02	Se	c

towards the nest. c : approximately correct. D : remarkably disordered. d : more or less disordered. O : opposite, that is, opposite to the correct direction. Symbol within parentheses is the same as above.

When the records of the return journey are not put in the same line of the table as those of the outward journey, they would be in the next line. When the records of the return journey are put independently, not relating to the preceding outward journey, it means that the ant was transported by the observer to the cardboard. But even in such a case, if the preceding line bears R in the column of behaviour, the return journey is shown as the continuation of the preceding line.

Experiments

Experiment I. The experiment was made on Oct. 4. 1949, from 4 to 9.30 p. m. The upper wall of the box was removed. The distance between E and C was 27.5 cm. The nest was placed northwards. Intensity of illumination is as follows :—R' : 10, R : 4, b : less than 1, Y' : 100, Y : 40, Y' : 10, W : 60 (Lux). The detailed records are as shown in Table I.

Experiment II. The experiment was carried out on Oct. 5. 1949, from 2.50 to 9.30 p. m. The upper wall of the box was remained *in situ*. The nest was located northwards. The distance between E and C, below L 3 of the table II, was 19 cm. Intensity of illumination is as follows :—w : 4, R : 10, g : less than 1, Y : 100, Y : 40, y : 10, P : 40, p : 16 (Lux). The detailed records are as shown in Table II.

Experiment III. This experiment was made on Oct. 7. 1949, from 10.20 a.m. to 7.50 p.m. The upper paper wall of the box was *in situ*. The distance between E and C was 19 cm. The nest was located southwards. Intensity of lights is as follows :—Y : 10, R : 10, r : less than 1, but much brighter than b, b : less than 1 (Lux). The ceiling lamp (4 Lux on the table) was shining throughout the experiments. The records are as shown in Table III.

Results of Experiments

The results obtained from the experiments will be summarized as follows :

A. In the experiments in which the light was thrown from one side alone of the passage : (1) When the colour was altered from Red (10 Lux) to green (less than 1 Lux), and also from green to Yellow (100 Lux), the ant showed no reaction whatever to the change of colours (excepting for a slight hesitation which is probably due to the sudden change of intensity of illumination) (Table II, E 1, E 2, E 3, E 6). (2) When the ant was on the cardboard, yellow light was replaced by pink light of the same intensity (40 Lux) coming from the opposite side. Then the ant departed in the opposite direction and went far and far away from the nest (Table II, E 4).

B. In the experiments in which two different coloured lights were thrown, one from each side of the passage : (1) When the weaker light of the two was switched off, whatever colours may be chosen, no remarkable change occurred upon the behaviour of the ant [Table I, E 2, E 12, E 14, E 17; Table III, E 10, E 13. Exception: Table III, E 9, —vide (7)]. (2) When the stronger light of the two was stopped, irrespective of colours, (a) the ant took the opposite direction in her progress [Table I, E 13, E 15; Exception: Table III, E 11, E 14 — vide (7)]. or otherwise, (b) the ant fell into confusion (Table I, E 1, E 3, E 6, E 8). (3) When the stronger light of the two (Red, 4 Lux) was untouched and the weaker light (blue, less than 1 Lux) was changed by the strongest light of another colour (Yellow, 40 Lux), the ant went in the opposite direction (Table I, E 4, E 5; E 7, E 9). (4) When the weaker light of the two (Pink, 40 Lux) was untouched and the stronger light (Yellow, 100 Lux) was reduced to the weakest intensity (10 Lux), the ant started from the cardboard in the opposite direction (Table II, E 8). (5) When the combination of Red and Yellow or that of Pink and Yellow of the equal intensity was applied (R, 10; Y, 10; P, 40; Y, 40 Lux), Yellow affected upon the ant as if it were much stronger than the other, namely as follows : (a) The results corresponded to (1) of B (Table II, E 10; Table III, E 2, E 6). (b) The results corresponded to (2a) of B (Table II, E 11; Table III, E 3, E 5). In the above combinations, if Yellow is treated as a stronger source of light than Red or Pink, it might be needed to add the following facts to the above accounts. (6) When the weaker light of the two (pink, 40 Lux) was left shining and the stronger light (Yellow, 40 Lux,) was changed by the weakest light of another colour (green, less than 1 Lux), the ant proceeded in the opposite direction [Table II, E 12-

(2) and (3), E. 13, E 14 (1) and (2). Exceptions: Table II, E 12 (outward journey)]. (7) If the two lights were altered in position with each other and the weaker light (Red, 10 Lux) was left *in situ*, but much reduced in intensity, while the stronger light (Yellow, 10 Lux) was replaced by the weakest light of another colour (blue, less than 1 Lux, but much darker than the reduce red), the ant went in the correct direction (Table III E 7, L 1'). (8) In the preceding case, however, after several journeys were repeated, the behavior of the ant came to be somewhat disturbed. Sometimes she fell more remarkably into confusion when the weaker light (blue) was switched off than the stronger light (red) put out (Table III, E 8, E 9, E 11 — E 15).

Remarks The ant here considered, belongs to one of the species which do not establish the so-called "street" on their working ground. So that their trails are changed in each journey between the nest and the booty. Though the orientation in their homing behaviour is dependent in the main on the light factor, when very frequent changes of the direction of the light occurred, the effect of odour becomes the most important factor to lead them (Table III, E 16, E 17). In the course of the foregoing experiments, therefore, it was ascertained that the ant proceeded its way always depending upon the light, by means of either rotation of the disc (Table III. E 1) or the perfect control of the light factor.

Discussion

Judging from the evidences obtained in the foregoing experiments, it is presumable, under the proper consideration on the effect of scent of the path, that the ant, in its orienting behaviour to light, does not respond to the colour of lights, but merely to the direction of lights. It is also evident that, when the source of light is more than one, the light of the strongest intensity alone effects the behaviour of the ant. In case the light is only one and is held in a certain direction, the ant is indifferent, within a certain extent, to the change of the intensity of illumination. The facts obtained in (5) and (8) of B indicate that at least the lights, R or P give less effects on the ant than the lights, Y and B ¹⁾. From these facts it can be presumed that the ant is of colour blindness and receives the light like a photographic (orthochromatic) plate. If the ant has the capacity of colour vision, the colour of light especially when two different coloured

1) This fact, though is partly concerned with the colour range in this case, is in fair accordance with the evidence pointed out by Lubbock (1882).

lights came one from each side of her pathway, must exert an influence upon the orienting behaviour of the ant, quite independently from the intensity of illumination.

Conclusion

So far as the scope of the present investigation is concerned, it will be able to say that the ant, *Leptothorax congruus spinosior* Forel, has not the sense of colour vision, but is only sensitive to the intensity of light.

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