Journal of Biology and Life Science
ISSN 2157-6076
2020, Vol. 11, No. 2

Weber's Law Applies to the Ants' Visual Perception

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Received: Mar. 17, 2020 Accepted: Apr. 7, 2020

doi:10.5296/jbls.v11i2.16896 URL: https://doi.org/10.5296/jbls.v11i2.16896

Abstract

Non-numerical distance and size effects have been previously observed in the ant *Myrmica sabuleti*. As such effects can be theoretically in line with Weber's law, we presumed that this law, until now examined in vertebrates, could also apply to ants. Using operant conditioning we trained then tested *M. sabuleti* workers faced with black circles having fixed diameters of 2, 3 and 4 mm against circles with diameters increasing by 0.5 mm until the ants perceived a difference between the smaller and the larger circles. This just noticeable difference occurred when the larger diameter reached 3.5, 5.5 and 7 mm respectively, what corresponded to a ratio larger/smaller surface of 3.06, 3.36 and 3.06. Owing to the degree of accuracy of the experimental methodology, this ratio is sufficiently constant for being consistent with Weber's law.

Keywords: distance effect, *Myrmica sabuleti*, operant conditioning, size effect, visual perception

1. Introduction

Distance and size effects are physiological characteristics of the individuals' assessment of a difference between two intensities of a stimulus. The distance effect accounts for the fact that two intensities are better discriminated when their difference in magnitude is large. The size effect explains that two intensities are less and less well discriminated when their magnitude increases. This has been largely documented in vertebrates, but not in invertebrates. However, distance and size effect were recently shown to be present in the ant *Myrmica sabuleti* Meinert 1861 (M.-C. Cammaerts & R. Cammaerts, 2020).

Distance, and above all, size effects are in line with Weber's law which mathematically expresses that the smallest change that can be perceived in a stimulus magnitude, dI (the just noticeable difference) is proportional to this magnitude (I), so that the ratio dI/I (i.e. the Weber fraction) is a constant. This law has been demonstrated in vertebrates and concerns all sensory perceptions (vision, hearing, taste, touch and smell). For instance, it concerns the weight perception (e.g. Ross & Brodie, 1987) and the tactile perception (e.g. Francisco et al., 2008).

Deviations from Weber's law can however be observed. Concerning acoustic perception in humans, when applied to a pure tone, Weber's law does not hold in the strict sense since the Weber fraction somewhat varies according to the intensity of the sensation level (McGill & Goldberg, 1968). Although for a signal duration of half a second this near-miss to Weber's law holds across all wavelengths (Jesteadt et al., 1977), the departure from Weber's law is more intense for short signal durations in the range of 30 ms, the fraction dI/I being then highest for high (over 5000 Hz) and moderate (50-60 dB) sound intensity. This can be explained by a bimodal distribution of auditory-nerve thresholds (Carlyon & Moore, 1984). Presence or absence of noise and idiosyncrasy in the perception of the 'just noticeable' auditory intensity are also parameters generating a near-miss to Weber's law (Doble et al., 2006).

As for spatial vision in humans, Weber's law holds for bisection, vernier acuity, separation and alignment (references in Hess & Hayes, 1993) as well as for size judgments (Whitaker & Latham, 1997). This is known as Weber's law for position, the positional accuracy varying in proportion with the separation of the sighted objects (Whitaker et al., 2002). However, in these cases, the validity of Weber's law depends not only on the stimulus separation, but also on the visibility of the stimuli (Levi & Klein, 1992). Weber's law also applies to visual perception of second-order structures such as moiré patterns (Maloney et al., 1987) and mirror symmetries (Van der Helm, 2010), but only in the middle range of regularity-to-noise ratios.

Regarding the ability in discriminating numbers, the validity of Weber's law has been demonstrated at a behavioral and a neural level, in humans, monkeys and birds (Dehaene, 2003; Nieder & Miller, 2003; Jordan & Brannon, 2006; Cantlon & Brannon, 2006; Merten & Nieder, 2008; Ditz & Nieder, 2016).

To come back to the present work, and to its purpose, since it was shown that the workers of the ant *M. sabuleti* are subjected to visual distance and size effects when they are faced with non-numerical stimuli (i.e. dots of different sizes: M.-C. Cammaerts & R. Cammaerts, 2020), we might presume that Weber's law can also be applied to these insects, even if it has never been shown in an invertebrate. The aim of the present work is thus to examine the hypothesis of the applicability of Weber's law to the perception ability of an ant, by defining the *M. sabuleti* workers' just noticeable difference between two dots of different size.

2. Material and Methods

2.1 Collection and Maintenance of the Ants

The experiments were performed on three colonies collected in September 2019 in an abandoned quarry located in Olloy/Viroin (Ardenne, Belgium). These colonies contained about 500 workers, a queen and brood. They were maintained in the laboratory, each colony in one to two glass tubes half filled with water, a cotton plug separating the ants from the water. The nest tubes of each colony were set in a tray (34 cm x 23 cm x 4 cm or 30 cm x 15 cm x 5 cm) which served as foraging area. On this area, pieces of *Tenebrio molitor* larvae (Linnaeus, 1758) were deposited three times per week, and cotton plugged tubes filled with sugar water were permanently set. The ambient temperature was *ca* 20°C, the humidity 80%, the lighting 330 lux while working on ants, and the electromagnetism 2 µWm^2. These environmental conditions were optimal for the species used in the experiments (R. Cammaerts & M.-C. Cammaerts, 2020).

2.2 Experimental Protocol

Using operant conditioning, the ants of each colony were trained then tested faced with a black circle having a diameter of increasing size over successive experiments *versus* a black circle having a constant diameter. The diameter of the later equaled, for colonies A, B, and C, respectively 2 mm, 3 mm and 4 mm. A series of successive choice tests in front of the two kinds of circles ended when the ants significantly responded for the first time to the circle with an increasing diameter. The ants were then in presence of their smallest perceptible difference between the two circles. If Weber’s law is verified, this smallest perceptible difference assessed by the ratio between the areas of the two just discriminated circles should be a constant, i.e. in the present work, be identical for the three used colonies.

2.3 Training and Testing the Ants

This is schematized in Figure 1; photos are shown in Figures 3, 4, and 5.

The ants were trained on their foraging area, over successive experiments, to a black circle of increasing size set near the food and to a black circle of unchanged size set far from food, the two cues being distant of about 8 cm. Each experiment lasted 48 hours. During that time, the ants present all around the two presented circles were counted 16 times, and the mean of the counts was established (this mean is given in the Appendix only). This counting did not require statistical analysis.

The ants were tested, after 7, 24, 31 and 48 training hours, in a separate tray (21 cm x 15 cm x 7 cm), the borders of which having been slightly covered with talc, and in which the same kind of circles presented to ants during training were set at about 8 cm from one another. To make a test, 25 ants were transferred from their nest to the tray devoted to test, and those approaching each kind of circle were counted 20 times in the course of 10 experimental minutes. These counts allowed calculating the ants’ proportion of correct responses (i.e. of choosing the kind of circle set near the food during training). These ants’ conditioning scores are given in the text. The average conditioning score corresponding to the four training hours was calculated by using all the numbers of counted ants. Half of the tests were made with the ‘correct’ circle set on the left, and half of the tests were made with this ‘correct’ circle set on the right. After each test, the ants were transferred again into their nest, being deposited very near their nest entrance. After having made the four tests on a colony, the average of the ants’ conditioning scores (% of correct responses) was calculated (Table 1, 2, 3 last column). The

Journal of Biology and Life Science
ISSN 2157-6076
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twenty numbers chronologically obtained for each kind of stand were summed by four, and the five values were compared to one another using the non-parametric test of Wilcoxon (Siegel & Castellan, 1989). These values can be found in the tables of the Appendix; the statistical results are given in the text and in the Appendix.

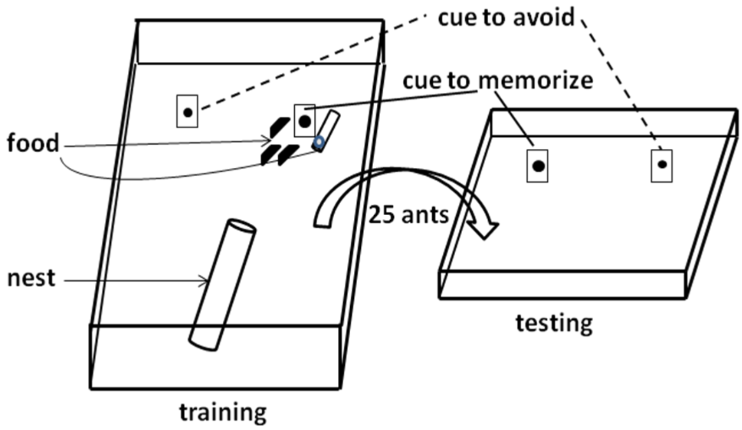

Figure 1. Experimental design used to train and to test the ants

The ants were trained in their foraging area with a cue near their food and another one far from food (left schema). They were tested in a separate tray containing two never used cues identical to those presented during training. The ants responding to each cue were counted twenty times over ten minutes, what allowed calculating the ants' conditioning score.

2.4 Cues Presented to the Ants

This is schematized in Figure 2; photos are shown in Figures 3, 4, and 5.

The circles presented to the ants were drawn each one into a 2.5 cm x 2.5 cm square using Word® software, which squares were then printed, cut and tied on the vertical front face of a stand (2.5 cm x 2.5 cm). Each stand was made of strong white paper (Steinbach®), and kept its verticality thanks to a duly folded horizontal part [2 x (1.25 cm x 0.5 cm)].

The cues presented to the three colonies were as follows. The ants of colony A were provided with, set far from food, a circle of 2 mm in diameter, and aside the food, with a circle the diameter of which equaled 2.5, 3, 3.5, and 4 mm in the course of four successive training and testing sessions. The ants of colony B were provided with, set far from food, a circle of 3 mm in diameter, and aside the food, with a circle the diameter of which equaled 3.5, 4, 4.5, 5, 5.5 and 6 mm in the course of six successive training and testing sessions. The ants of colony C were provided with, set far from food, a circle of 4 mm in diameter, and aside the food, with a circle of 4.5, 5, 5.5, 6, 6.5, 7 and 7.5 mm in diameter in the course of seven successive training and testing sessions. However, as explained in the section Results, the first planned experiment using a circle with a diameter of 4.5 was, after consideration, not performed.

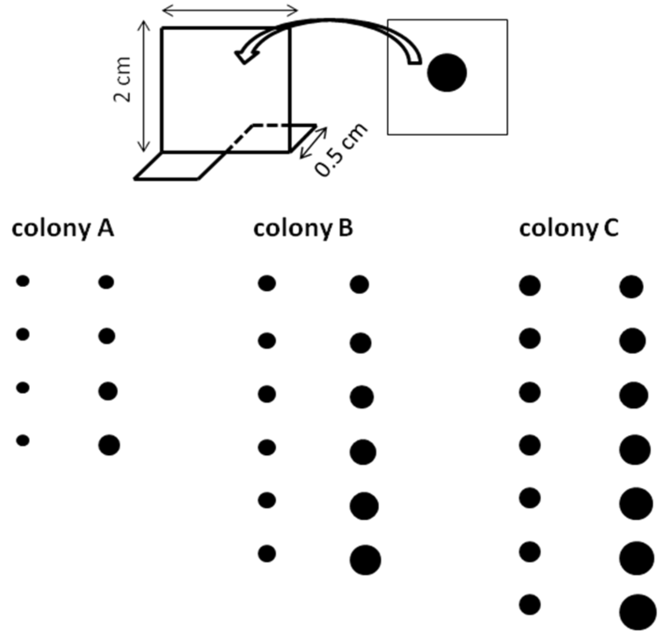

Figure 2. Cues presented to ants for tempting defining their just perceptible difference between two black circles of different dimension

The ants were trained and tested as schematized in Figure 1. The larger circle was set near the food during training and had a diameter of increasing dimension in the course of successive experiments (4 experiments for colony A, 6 for colony B, 7 for colony C). This allowed detecting for which dimension of the larger circle the ants perceived a difference between the two circles (i.e. correctly responded during testing). This information allowed checking if Weber's law can apply to ants.

3. Results

3.1 Colony A; Discrimination Between Circles Having a Diameter of 2.5, 3, 3.5, 4 mm and a Circle With a Diameter of 2 mm

Numerical results are summarized in Table 1; complementary information, among others the numbers of ants counted near each circle during the testing sessions, are detailed in the Appendix; photos are shown in Figure 3.

During their four training sessions, the ants of colony A were numerous enough all around the presented cues for seeing and memorizing them.

Trained to two circles the diameter of which equaled 2.5 and 2 mm, and tested after 7, 24, 31, and 48 hours, the ants presented a conditioning score of 47.7%, 49.1%, 54.7% and 45.0% respectively. For each training time, the numbers of ants sighted near the larger circle did not statistically differ from those sighted near the smaller circle (*cf* Appendix). The ants' average conditioning score equaled 50%. Thus, the ants did not perceive any difference between two circles the diameter of which were 2.5 and 2 mm.

Similarly experimented with two circles the diameter of which equaled 3 and 2 mm, the tested ants went nearly equally to the two circles, presenting a conditioning score of 48.2%, 45.9%, 47.6%, and 50.0% after 7, 24, 31 and 48 hours respectively. All these results were not significant (*cf* Appendix). The average conditioning score was 47.8%. Thus, the ants saw no difference between the two circles the diameter of which were of 3 and 2 mm.

Trained to a circle with a diameter of 3.5 mm *versus* a circle with a diameter of 2 mm, the ants went somewhat more to the former circle than to the latter. After 7, 24, 31 and 48 training hours, they reached a conditioning score of 66.1%, 59.7%, 65.2%, and 59.6% respectively. The result corresponding to 31 training hours was significant (P = 0.031); the three other ones were at the limit of significance (P = 0.063). The average conditioning assessed over their four testing sessions equaled 62.6%. Consequently, the ants saw some difference between the two presented circles, but this perception was weak, i.e. at its limit. The difference between circles with diameters of 3.5 and 2 mm could be, at least approximately, the 'just noticeable one' for these ants. For checking this estimation, the ants were experimented with circles the diameters of which were 4 and 2 mm.

Trained to such circles with diameters of 4 and 2 mm, the ants of colony A reacted essentially to the larger ('correct') circle, presenting a conditioning score of 67.1%, 72.5%, 70.9%, and 68.4% after 7, 24, 31 and 48 training hours respectively. All these results were statistically significant (N = 5, T = 15, P = 0.031), and the average conditioning score was 69.7%. Thus, the ants perfectly perceived the difference between the two presented circles, what confirmed that their just perceptible difference occurred between circles with a diameter of 2 and 3.5 mm.

Table 1. Ants discrimination between a circle with a diameter of 2 mm and a circle with a diameter increasing from 2.5 to 4 mm

Ø of the circle set near food ; far from it		Ants near the 'correct' *vs* the 'wrong' circle after… training hours				Ants' average conditioning score
		7	24	31	48	
2.5 mm	2 mm	21/23	28/29	41/34	18/22	50.0%
3.0 mm	2 mm	27/29	28/33	30/33	22/22	47.8%
3.5 mm	2 mm	39/20	46/31	45/24	34/23	62.6%
4.0 mm	2 mm	49/24	50/19	56/23	54/25	69.7%

The experiment was made on colony A. Photos are shown in Figure 3; results are given in the text, subsection 'Results' and are detailed in the Appendix. Briefly, the ants did not distinguish the two circles until the larger one reached a diameter of 3.5 mm. Then, the difference in magnitude between the two circles equaled the ants' 'just noticeable' one.

Table 2. Ants discrimination between a circle with a diameter of 3 mm and a circle with a diameter increasing from 3.5 to 6 mm

Ø of the circle set near food	; far from it	Ants near the 'correct' *vs* the 'wrong' circle after… training hours 7	24	31	48	Ants' average conditioning score
3.5 mm	3 mm	27/32	28/33	22/26	30/38	45.3%
4.0 mm	3 mm	23/28	24/29	19/24	27/34	44.7%
4.5 mm	3 mm	19/22	59/49	28/36	29/29	51.1%
5.0 mm	3 mm	43/53	30/30	43/53	47/48	47.0%
5.5 mm	3 mm	36/20	40/22	48/27	34/20	64.0%
6.0 mm	3 mm	68/42	43/15	49/22	49/18	68.3%

The experiment was made on colony B. Photos are shown in Figure 4; results are given in the text, subsection 'Results' and are detailed in the Appendix. Briefly, the ants did not distinguish the two circles until the larger one reached a diameter of 4.5 mm. The difference in magnitude between the two circles then equaled the ants' 'just noticeable' one.

Table 3. Ants discrimination between a circle with a diameter of 4 mm and a circle with a diameter increasing from 4.5 to 7.5 mm

Ø of the circle set near food	; far from it	Ants near the 'correct' *vs* the 'wrong' circle after… training hours 7	24	31	48	Ants' average conditioning score
5.0 mm	4 mm	18/24	23/32	24/31	20/24	43.4%
5.5 mm	4 mm	21/29	32/40	20/26	21/27	43.5%
6.0 mm	4 mm	23/29	21/29	20/27	32/34	44.7%
6.5 mm	4 mm	37/40	32/26	30/34	38/33	50.7%
7.0 mm	4 mm	38/18	24/15	30/20	33/20	63.1%
7.5 mm	4 mm	47/19	49/27	37/20	30/13	67.4%

The experiment was made on colony C. Photos are shown in Figure 5; results are given in the text, subsection 'Results' and are detailed in the Appendix. Briefly, the ants did not distinguish the two circles until the larger one reached a diameter of 7 mm. The difference in magnitude between the two circles then reached the ants' 'just noticeable' one.

3.2 Colony B; Discrimination Between Circles Having a Diameter of 3.5, 4, 4.5, 5, 5.5, 6 mm and a Circle With a Diameter of 3 mm

Numerical results are summarized in Table 2; complementary information, such as the numbers of ants counted in front of each circle during the testing sessions, are detailed in the Appendix; photos are shown in Figure 4.

We checked that the ants of colony B were numerous enough during their successive training sessions for being able to see and memorize the two presented cues.

Trained to circles with diameters of 3.5 and 3 mm, the ants never went statistically more to the 'correct' circle (the one with a diameter of 3.5 mm), on the contrary. They presented a conditioning score of 45.8%, 45.9%, 45.8, and 44.1% after 7, 24, 31, and 48 training hours respectively. The three first results were statistically not significant (NS (N = 2), P = 0.250, P = 0.188 respectively); the last one was at the limit of significance with more ants reacting to the 'wrong' circle (N = 4, T = -10, P = 0.063). On the basis of the numerical results obtained during the four testing sessions, the ants' average conditioning score equaled 45.3%. Consequently, the ants saw no difference between two circles with a diameter of 3.5 and 3 mm.

Experimented in the same way with a circle of 4 mm in diameter set near the food and a circle with a diameter of 3 mm set far from the food, the ants went slightly more to the later circle than to the former one, their conditioning score equaling 45.1%, 45.3%, 44.2%, and 44.3% after 7, 24, 31, and 48 training hours respectively. These four results were respectively not significant (N = 2), at the limit of significance with somewhat more ants reacting to the 'wrong' circle (P = 0.063), just under the limit of significance with somewhat more ants' reactions to the 'wrong' circle (P = 0.094), and not significant (P = 0.125). Calculated using the counts made during the four testing sessions, the ants' average conditioning score equaled 44.9 %. Thus, the ants did not distinguish the two presented circles which had a diameter of 4 and 3 mm.

Trained to a circle of 4.5 mm set near the food and a circle of 3mm set far from food, then tested in front of these two circles, the ants presented a conditioning score of 46.3%, 54.6%, 43.8%, and 50.0% after 7, 24, 31, and 48 training hours respectively. These results were respectively not significant (P = 0.219), significant with more ants reacting to the 'correct' circle (P = 0.031), significant with more ants reacting to the 'wrong' circle (P = 0.031), and not significant (P = 0.625). The ants' average conditioning score equaled 51.1%. Consequently, the ants did not unequivocally distinguish the two presented circles of 4.5 and 3 mm in diameter.

Trained in front of a circle with a diameter of 5 mm set near the food and a circle with a diameter of 3mm set far from the food, the tested ants went successively slightly more to the 'wrong' circle, equally to the two circles, again slightly more to the 'wrong' circle, and nearly equally to the two circles. They presented a conditioning score of 44.8%, 50%, 44.8% and 49.5% after 7, 24, 31, and 48 training hours respectively. These results were not significant with successively P = 0.094, P = 0.438, NS (N = 2), and P > 0.50. The ants' average conditioning score equaled 47.0%. In consequence, the ants did not yet significantly distinguish the two presented circles the diameters of which were 5.5 and 3 mm.

Trained to a circle with a diameter of 5.5 mm set near the food and a circle with a diameter of 3mm set far from food, the tested ants went mostly to the ‘correct’ larger circle. They presented a conditioning score of 64.3%, 64.5%, 64.0%, and 62.9% after 7, 24, 31 and 48 training hours respectively. These results were significant or at the limit of significance, with P = 0.031, P = 0.063, P = 0.031, and P = 0.031 respectively. The average conditioning score equaled 64.0%, the ants perceiving thus rather well the difference between the larger and the smaller circle, the diameters of which were 5.5 and 3 mm. They were probably at, or very slightly above, their just perceptible difference. To check this presumption, the ants were then experimented with a circle of 6mm in diameter and a circle with a diameter of 3mm.

Trained to a circle with a diameter of 6 mm set near the food and a circle with a diameter of 3mm set far from food, the tested ants of colony B went essentially to the ‘correct’ circle, presenting a conditioning score of 61.8%, 74.1%, 69.0%, 73.1% after 7, 24, 31, and 48 training hours respectively. All these results were significant (P = 0.031). The ants’ average conditioning score was 68.3%. Thus, the ants very well perceived the difference between circles of 6 and 3 mm in diameter. This difference was thus higher than the just noticeable one, which can be estimated as being situated between a circle with a diameter of 5.5 and a circle with a diameter of 3 mm.

3.3 Colony C; Discrimination Between Circles Having a Diameter of 4.5, 5, 5.5, 6, 6.5, 7, 7.5 mm and a Circle With a Diameter of 4 mm

We decided to not perform the initially planned training and testing sessions using a circle with a diameter of 4 mm and a circle with a diameter of 4.5 mm because at the end of the previous experiment with six successive training and testing sessions, we observed that colony B appeared somewhat affected by the duration of the experiment, no longer presenting its initial positioning of eggs, larvae and young workers inside the nest tube. A few dead old workers were also dispersed in the foraging area. We kept the six following planned training and testing sessions in order to be in accordance with the experiments on colonies A and B.

Numerical results are summarized in Table 3; complementary information can be found in the Appendix; photos are shown in Figure 5.

During each training session, the ants of colony C were numerous enough at any time in the vicinity of the two presented cues to see and memorize them.

Trained to a circle with a diameter of 5 mm set near the food and a circle of 4 mm set far from food, the tested ants went somewhat mostly to the ‘wrong’ smaller circle, presenting a conditioning score of 42.9%, 41.8%, 43.6%, and 45.5% after respectively 7, 24, 31, and 48 training hours. These results were respectively not significant (P = 0.156, P = 0.094), at the limit of significance with somewhat more ants reacting to the ‘wrong’ circle (P = 0.063), and again at the limit of significance (P = 0.063), but with slightly more ants reacting to the ‘wrong’ circle. The ants’ conditioning score was found to equal 43.4%. Consequently, the ants could not distinguish the two circles with a diameter of 5 and 4 mm.

Trained to a circle with a diameter of 5.5 mm set near the food and a circle with a diameter of 4mm set far from food, the tested ants reacted mostly to the 'wrong' smaller circle. They presented a conditioning score of 42.0%, 44.4%, 43.5%, and 43.8% after 7, 24, 31, and 48 training hours respectively. These results were respectively at the limit of significance (P = 0.063) with slightly more ants reacting to the 'wrong' circle, or not significant (P = 0.125, P = 0.250, P = 0.188). The ants' average conditioning score was found to equal 43.5%. We conclude that the ants did not acquire conditioning and consequently did not perceive a difference between the two circles of 5.5 and 4 mm in diameter.

Trained to a circle which had a diameter of 6 mm set near the food and a circle which had a diameter of 4mm set far from food, the tested ants reacted essentially to the 'wrong' smaller circle. Indeed, they presented a conditioning score of 44.2%, 42.0%, 42.6%, and 48.5% after 7, 24, 31, and 48 training hours respectively. None of the results was significant (P = 0.125, P = 0.125, P = 0.250 and P = 0.406 respectively). The ants' average conditioning was found to be of 44.7%. Consequently, the ants perceived no difference between the two circles of 6 mm and 4 mm in diameter.

Trained to a circle with a diameter of 6.5 mm set near the food and a circle with a diameter of 4mm set far from food, the tested ants responded nearly equally to the 'wrong' and the 'correct' circles. They presented a conditioning score of 48.1%, 55.2%, 46.9%, and 53.5% after respectively 7, 24, 31, and 48 training hours. These results were not statistically significant, with respectively N = 2 (NS), P = 0.125, N = 2 (NS), and P = 0.219. The ants' average conditioning score appeared to equal 50.7%. Consequently, although in the nick of acquiring conditioning, the ants not yet really saw a difference between the two presented circles which had a diameter of 6.5 and 4 mm.

Trained to a circle with a diameter of 7 mm set near the food and a circle with a diameter of 4 mm set far from food, the tested ants reacted somewhat more to the 'correct' circle than to the 'wrong' one. They presented a conditioning score of 67.9%, 61.5%, 60.0%, and 62.3% after respectively 7, 24, 31, and 48 training hours. These results were significant or at the limit of significance with respectively P = 0.031, P = 0.031, P = 0.063, and P = 0.031. The ants' average conditioning score appeared to equal 63.1%. Thus, the ants acquired some conditioning and detected for the first time a difference between the two presented circles which had a diameter of 7 and 4 mm. They were thus in presence of their just perceptible difference. For validating this conclusion, the ants were further experimented in front of a circle with a diameter of 7.5 mm and a circle with a diameter of 4 mm.

Trained to a circle with a diameter of 7.5 mm set near the food and a circle with a diameter of 4mm set far from food, the tested ants obviously responded essentially to the 'correct' circle. They reached a conditioning score of 71.2%, 64.5%, 64.9% and 69.8% after respectively 7, 24, 31, and 48 training hours. All these results were significant (P = 0.031). The ants' average conditioning was found to equal 67.4%. It could thus be concluded that the ants undoubtedly distinguished the two circles, perceiving a larger difference between them than a just noticeable one.

Journal of Biology and Life Science
ISSN 2157-6076
2020, Vol. 11, No. 2

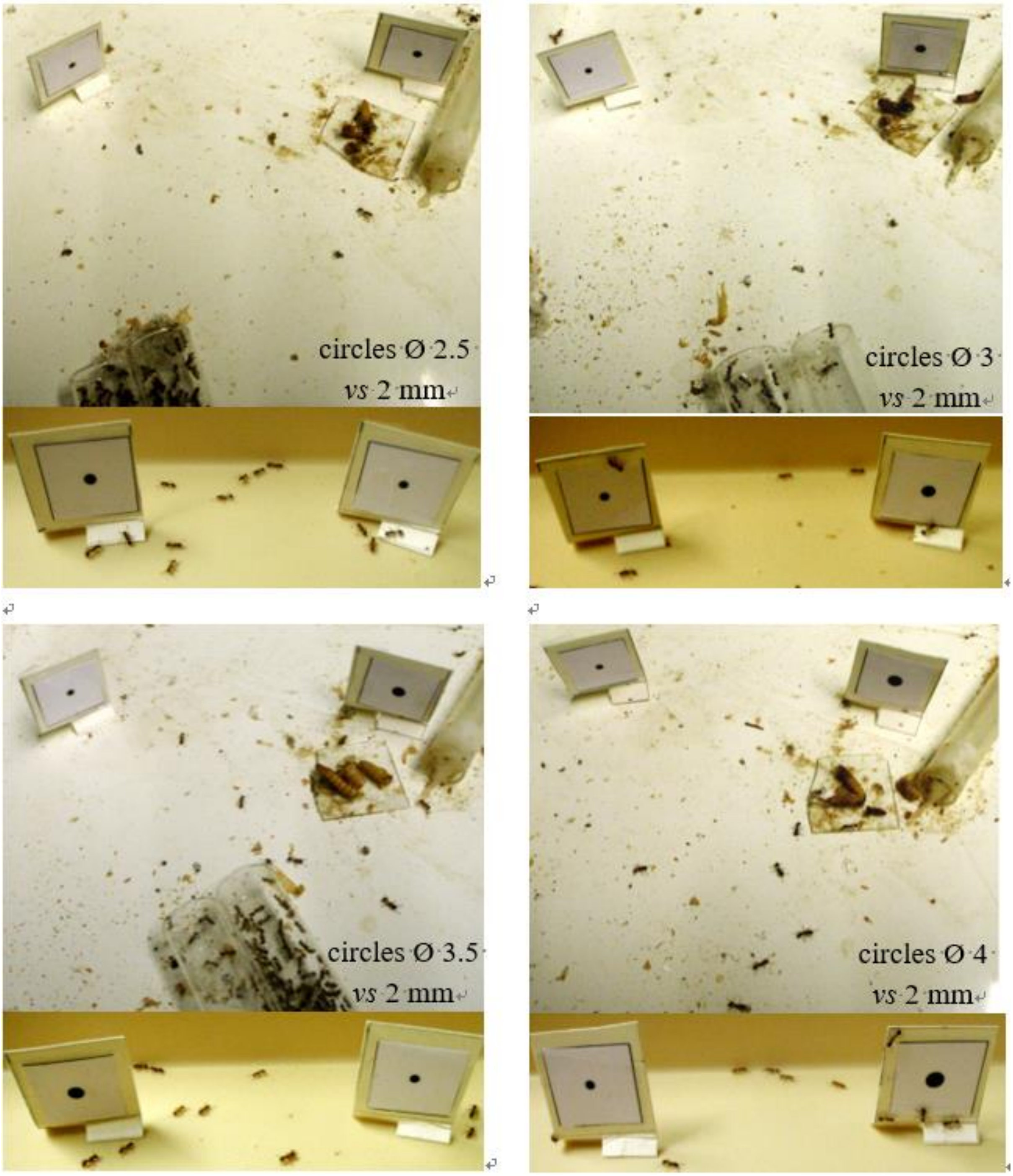

Figure 3. Some views of the experiments made using a circle with a diameter of 2 mm and a circle with a diameter increasing from 2.5 to 4 mm

Numerical results are given in Table 1; comments and details can be found in the text and in the Appendix. Briefly, the ants correctly responded for the first time to the larger circle when it had a diameter of 3.5 mm. The difference in magnitude between such a circle and a circle with a diameter of 2 mm was the difference the ants could just perceive.

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ISSN 2157-6076
2020, Vol. 11, No. 2

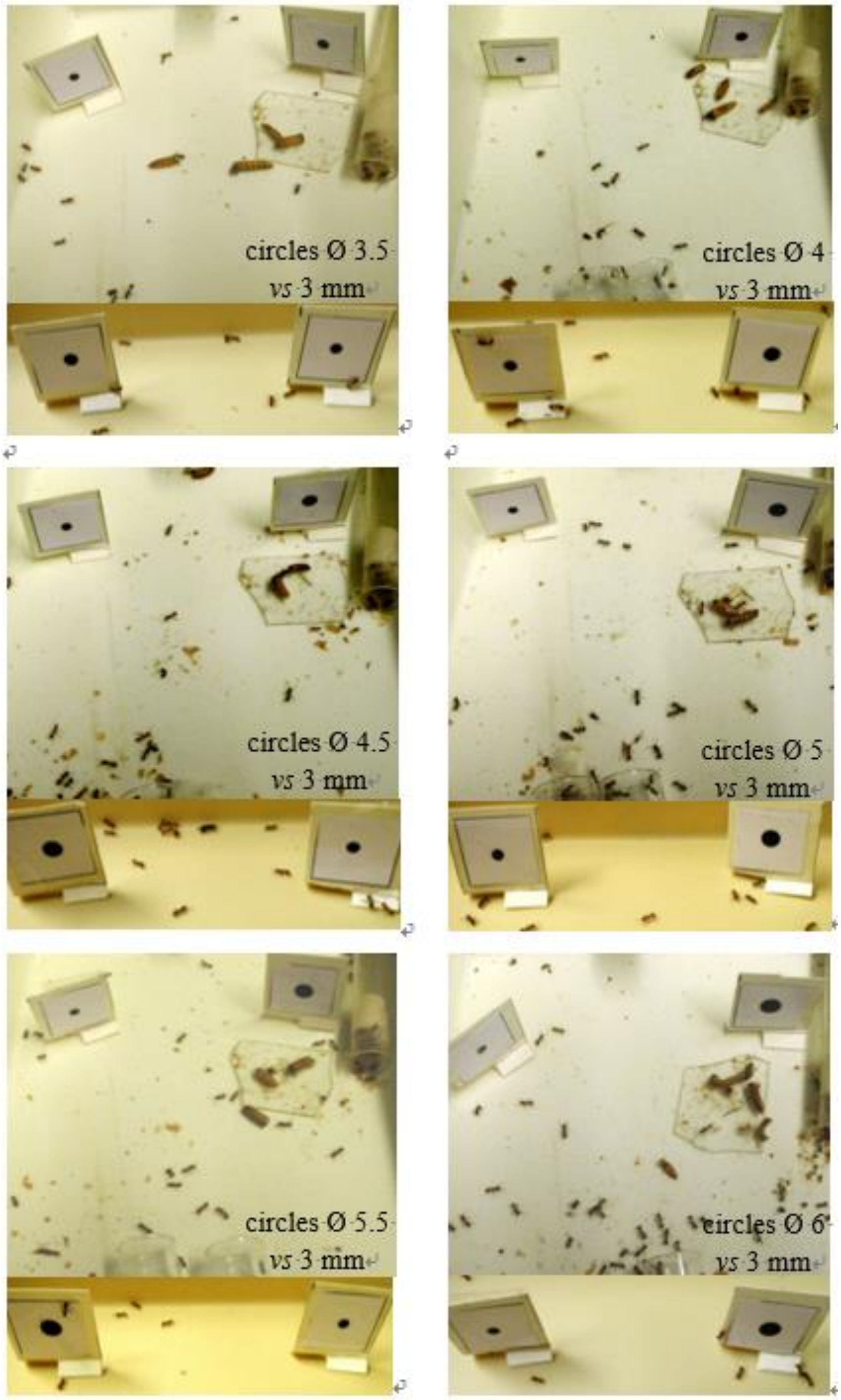

Figure 4. Some views of the experiments made using a circle with a diameter of 3 mm and a circle with a diameter increasing from 3.5 to 6 mm

Numerical results are given in Table 2, details in the text and Appendix. The ants correctly responded to the larger circle when the latter had a diameter of 5.5 mm. The difference in magnitude between this circle and that with a diameter of 3 mm was thus the difference they just perceived.

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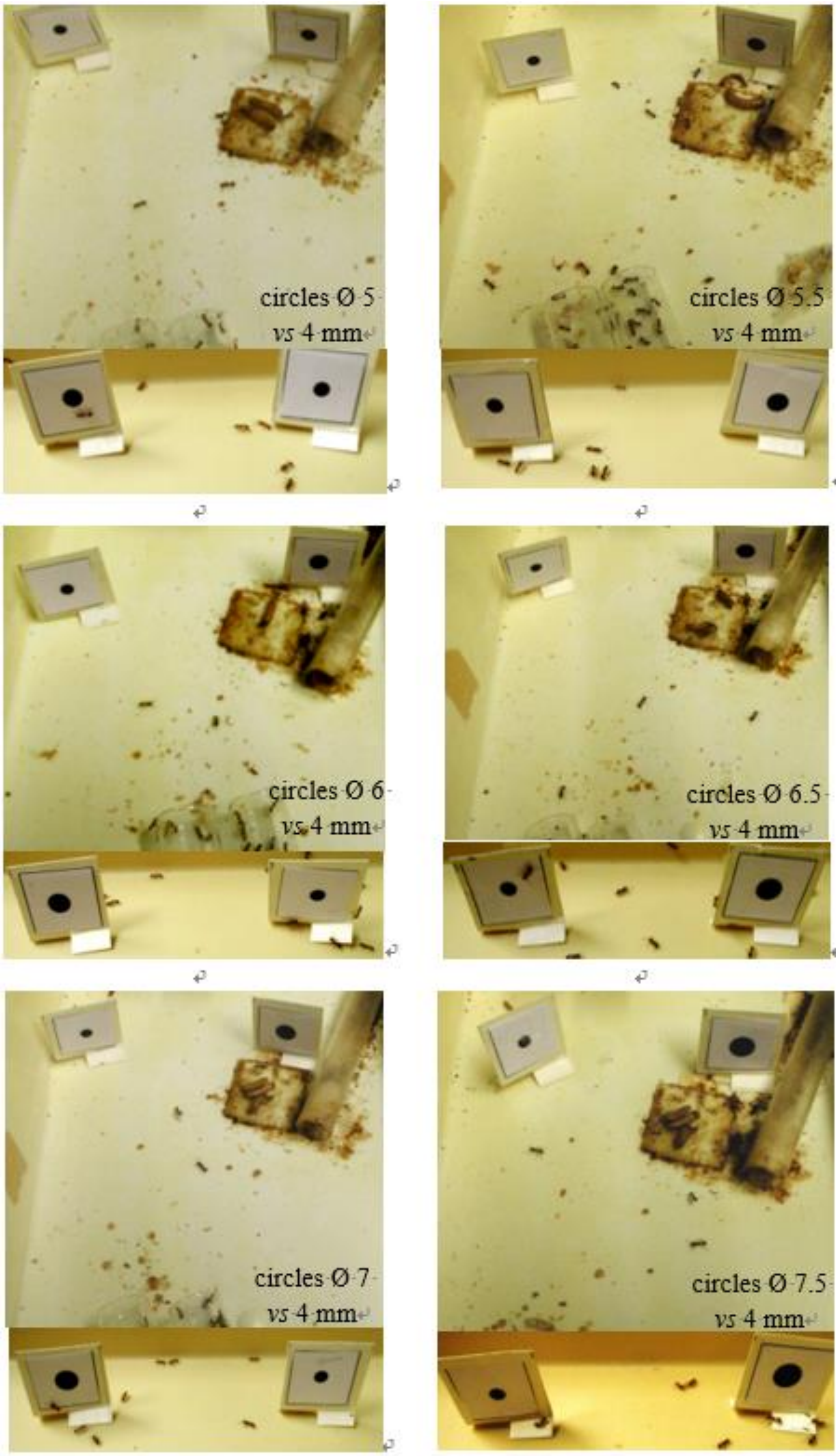

Figure 5. Some views of the experiments made using a circle with a diameter of 4 mm and a circle with a diameter increasing from 5 to 7.5 mm

Numerical results are given in Table 3; comments and details can be found in the text and in the Appendix. Briefly, the ants correctly responded for the first time to the larger circle when the latter had a diameter of 7 mm. The difference in magnitude between such a circle and a circle with a diameter of 4 mm was thus the difference the ants could just perceive.

3.4 Consistency of the Present Results With Weber's Law

Faced with a circle the diameter of which increased from 2.5 mm to 4 mm and a circle with a fixed diameter of 2 mm, the ants perceived a difference between the two circles when the larger diameter reached 3.5 mm. The ants' just noticeable difference was thus between two circles of 2 and 3.5 mm in diameter, thus between areas of 3.14 mm^2 and 9.616 mm^2, i.e. for a ratio of 3.06.

Faced with a circle the diameter of which increased from 3.5 mm to 6 mm and a circle with a fixed diameter of 3 mm, the ants perceived a difference between the two circles when the larger diameter was 5.5 mm. The ants' just noticeable difference was thus between two circles of 3 and 5.5 mm in diameter. The area of such circles equals 7.065 mm^2 and 23.746 mm^2, and their ratio 3.36.

Faced with a circle the diameter of which increased from 5 mm to 7.5 mm and a circle with a fixed diameter of 4 mm, the ants perceived a difference between the two circles when the diameter of the larger one reached 7 mm. The ants' just noticeable difference was thus between two circles of 4 and 7 mm in diameter. The area of these circles equals 12.56 mm^2 and 38.465 mm^2 respectively, and their ratio 3.06.

The ants' just noticeable difference between the areas of the presented circles was thus each time a similar proportion between the larger and the smaller sighted circles, i.e. in the range of 3.06 - 3.36, what, owing to the degree of accuracy of the experimental method, can be considered as consistent with Weber's law. The same result was obtained when taking into account the diameter of the circles instead of their area: the proportions between the diameters corresponding to the just noticeable difference were 1.75, 1.83 and 1.75 and, considering the degree of experimental accuracy, this also agreed with Weber's law.

4. Discussion & Conclusion

Weber's law states that a just perceptible change in the magnitude of a stimulus always corresponds to a constant ratio of the magnitude of the stimulus. We presumed that this law could apply to ants since we showed distance and size effects in these insects (M.-C. Cammaerts & R. Cammaerts, 2020). We thus faced *M. sabuleti* workers with black circles of increasing dimension. We found that they just perceived a difference between circles with a diameter of 2 mm and of 3.5 mm, as well as between circles with a diameter of 3 mm of 5.5 mm and between circles with a diameter of 4 mm and of 7 mm. The ratio between the magnitudes of these two just differently perceived circles was 3.06, 3.36 and 3.06, with corresponding average conditioning scores of 62.6, 64.5, and 63.3%. The average score of 64.5% corresponding to circles of 3 and 5.5 mm in diameter was slightly higher than the two other scores, what let us presuming that the ants' just noticeable difference for these circles was located between a circle of 3 mm in diameter and a circle with a diameter slightly smaller than 5.5 mm. Since we increased the magnitude of the larger circle by steps of 0.5 mm in diameter, it may well be that the just noticeable difference was situated between two of these steps, in this case it should have corresponded to a diameter of 5.25 mm. The observed 3.36 ratio could then have been somewhat lower and equaled to the two other obtained ratios, i.e. 3.06. With a constant ratio of 3.06, Weber's law would be perfectly verified. With the same adjustment when using the diameter instead of the area, a constant ratio of 1.75 would be found.

It can also be noted that before the ants began to distinguish the two presented circles (i.e. when the difference in magnitude between these circles was still too small), they somewhat, but not statistically, reacted more to the 'wrong' smaller circle than to the 'correct' larger one. We try here to explain this behavior. As long as the ants saw no difference between the two circles, the cue with the wrong (i.e. the smaller) circle presented during testing resembled the most to what the ants saw during training because the correct (i.e. the larger) circle was then, i.e. during testing, no longer associated to the view of the food items the ants saw during training (Figure 5). It may thus be that, before perceiving some difference between the two circles, the ants reacted somewhat mostly to the wrong, smaller circle because they simply reacted mostly to what resembled the most to what they saw during training. Such a reaction agrees with the fact that ants can rapidly acquire conditioning and retain it generally for a long time (e.g. Piqueret et al., 2019).

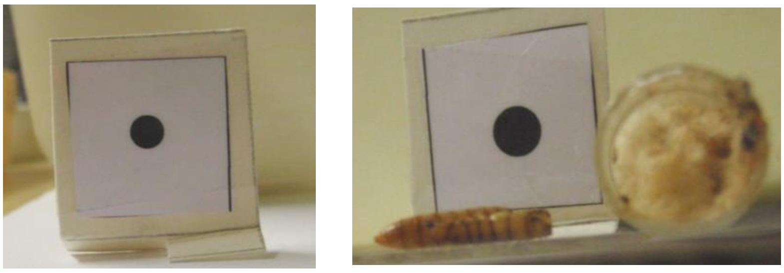

Figure 5. Cues as ants saw during training

As long as the two circles were considered as similar, among the smaller and the larger circles presented during testing, the smaller (left photo) corresponded the best to what the ants saw during training since then, the larger circle was surrounded by food items (right photo).

As habituation clearly occurred when day after day black circles were shown to the ants, the difference in magnitude between circles may have been less well perceived than if, without a previous presentation, two circles differing by their just noticeable magnitude difference would have been shown to the ants. However, since this occurred for each three pairs of used circles, the conclusion that Weber's law can apply to ants remains correct, although the three here observed just noticeable differences could be somewhat higher than the one obtained without habituation.

The fact that Weber's law is valid for ants, and maybe for other invertebrates, is not an exceptional finding, even if new. Indeed, Weber's law expresses a physiological trait common to all living organisms: the individuals' sensory reaction to a stimulus varies non-linearly with the intensity of this stimulus (Stevens, 1961; Wehner & Gehring, 1999, p 406).

As related in the Introduction section, cases of near-miss to Weber's law have been found in vertebrates. We presume that this may also occur in ants as for their perception of specific pheromones, such as those inducing trail-following and alarm reaction, since the individuals' sensitivity to such signals is particularly developed and their action on the ants is of the 'all or nothing' kind. Such a straightforward response to minute amounts of pheromone (e.g. minor workers of the ant *Atta texana* already detect their trail pheromone at a concentration of 0.08 picogram/cm: Tumlinson et al., 1972) may lead to the inapplicability of Weber's law. It has to be added that due to the non-linearity of the ants' quantitative response to their chemical trail, some slight increase of the latter signal can rapidly and considerably amplify the number of nestmates recruited on the trail to food (Detrain & Deneubourg, 2008).

Conclusively, Weber's law so far examined in vertebrates, for which it concerns sensory perceptions as well as numerosity ability, also applies to ants, at least as for their visual perception since their discrimination capability between cues of different sizes appeared to be constantly proportional to the size of these cues.

Conflict of interest

We declare having no conflict of interest.

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Appendix: details on results reported in the text and the tables 1, 2, 3.

Colony A; discrimination between circles with a diameter of 2.5, 3, 3.5 and 4 mm versus a circle with a diameter of 2 mm

Circle Ø of 2.5 mm vs circle Ø of 2 mm; data supplementing Table 1, line 1

Training: meanly 10.4 ants at any time around the two circles.

Testing:

Time	Ants' response	Summed by four, numbers of ants sighted near the larger circle	; near the smaller one	Wilcoxon test result N	T	P
7 h	21 *vs* 23 = 47.7%	3, 4, 1, 6, 7	4, 4, 4, 5, 6	4	-6	0.438
24 h	28 *vs* 29 = 49.1%	5, 8, 8, 4, 3	4, 7, 8, 5, 5	4	-6	0.438
31 h	41 *vs* 34 = 54.7%	9, 9, 8, 6, 9	8, 6, 8, 6, 6	3	-6	0.125
48 h	18 *vs* 22 = 45.0%	3, 4, 3, 5, 3	4, 5, 4, 4, 5	5	-11.5	0.188

Average score: 50.0% → no perception of a difference between the two circles

Circle Ø of 3 mm *vs* circle Ø of 2 mm; data supplementing Table 1, line 2

Training: meanly 10.2 ants at any time around the two circles.

Testing:

Time	Ants' response	Summed by four, numbers of ants sighted near the larger circle	; near the smaller one	Wilcoxon test result N	T	P
7 h	27 *vs* 29 = 48.2%	6, 5, 5, 5, 6	7, 4, 5, 6, 7	4	-7.5	0.251
24 h	28 *vs* 33 = 45.9%	5, 5, 4, 7, 7	7, 7, 7, 7, 5	4	-8	0.188
31 h	30 *vs* 33 = 47.6%	4, 6, 7, 6, 7	6, 7, 7, 6, 7	2	-	NS
48 h	22 *vs* 22 = 50.0%	4, 4, 4, 4, 6	6, 5, 2, 4, 5	4	-5	0.563

Average score: 47.8% → no perception of a difference between the two circles

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Circle Ø of 3.5 mm *vs* circle Ø of 2 mm; data supplementing Table 1, line 3

Training: meanly 10.2 ants at any time around the two circles.

Testing:

Time	Ants' response	Summed by four, numbers of ants sighted near the larger circle ;	near the smaller one	Wilcoxon test result N	T	P
7 h	39 *vs* 20 = 66.1%	8, 10, 9, 9, 3	3, 5, 3, 5, 4	5	14	0.063
24 h	46 *vs* 31 = 59.7%	9, 9, 19, 11, 7	6, 9, 5, 6, 5	4	10	0.063
31 h	45 *vs* 24 = 65.2%	8, 8, 10, 9, 10	3, 4, 6, 5, 6	5	15	0.031
48 h	34 *vs* 23 = 59.6%	9, 10, 5, 4, 6	5, 5, 4, 4, 5	4	10	0.063

Average score: 62.6% → just perception of a difference between the two circles

Circle Ø of 4 mm *vs* circle Ø of 2 mm; data supplementing Table 1, line 4

Training: meanly 10.2 ants at any time around the two circles.

Testing:

Time	Ants' response	Summed by four, numbers of ants sighted near the larger circle ;	near the smaller one	Wilcoxon test result N	T	P
7 h	49 *vs* 24 = 67.1%	8, 10, 11, 12, 8	3, 4, 5, 7, 5	5	15	0.031
24 h	50 *vs* 19 = 72.5%	9, 8, 9, 14, 10	3, 3, 3, 6, 4	5	15	0.031
31 h	56 *vs* 23 = 70.9%	7, 12, 12, 9, 16	1, 5, 4, 5, 8	5	15	0.031
48 h	54 *vs* 25 = 68.4%	10, 10, 9, 15, 10	4, 4, 5, 8, 4	5	15	0.031

Average score: 69.7% → obvious perception of a difference between the two circles

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Colony B; discrimination between circles with a diameter of 3.5, 4, 4.5, 5, 5.5 and 6 mm versus a circle with a diameter of 3 mm

Circle Ø of 3.5 mm *vs* circle Ø of 3 mm; data supplementing Table 2, line 1

Training: meanly 11.5 ants at any time around the two circles.

Testing:

Time	Ants' response	Summed by four, numbers of ants sighted near the larger circle	; near the smaller one	Wilcoxon test result N	T	P
7 h	27 *vs* 32 = 45.8%	6, 5, 6, 6, 4	6, 5, 8, 6, 7	2	-	NS
24 h	28 *vs* 33 = 45.9%	3, 9, 3, 7, 6	3, 7, 7, 10, 6	3	-5	0.250
31 h	22 *vs* 26 = 45.8%	3, 4, 4, 5, 6	4, 7, 3, 6, 6	4	-8	0.188
48 h	30 *vs* 38 = 44.1%	7, 5, 7, 7, 4	8, 7, 11, 8, 4	4	-10	0.063

Average score: 45.3% → no perception of a difference between the two circles

Circle Ø of 4 mm *vs* circle Ø of 3 mm; data supplementing Table 2, line 2

Training: meanly 11.0 ants at any time around the two circles.

Testing:

Time	Ants' response	Summed by four, numbers of ants sighted near the larger circle	; near the smaller one	Wilcoxon test result N	T	P
7 h	23 *vs* 28 = 45.1%	6, 3, 3, 5, 6	6, 3, 5, 5, 9	2	-	NS
24 h	24 *vs* 29 = 45.3%	5, 3, 4, 5, 7	6, 4, 5, 6, 8	4	-10	0.063
31 h	19 *vs* 24 = 44.2%	2, 3, 5, 5, 4	4, 5, 4, 6, 5	5	-13	0.094
48 h	27 *vs* 34 = 44.3%	4, 6, 5, 6, 6	6, 10, 5, 7, 6	3	-6	0.125

Average score: 44.9% → no perception of a difference between the two circles

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Circle Ø of 4.5 mm *vs* circle Ø of 3 mm; data supplementing Table 2, line 3

Training: meanly 12.0 ants at any time around the two circles.

Testing:

Time	Ants' response	Summed by four, numbers of ants sighted near the larger circle	; near the smaller one	Wilcoxon test result N	T	P
7 h	19 *vs* 22 = 46.3%	4, 3, 3, 3, 6	5, 4, 6, 4, 3	5	-11	0.219
24 h	59 *vs* 49 = 54.6%	10,13,11,12,13	9, 11, 9,10,10	5	15	0.031
31 h	28 *vs* 36 = 43.8%	3, 3, 7, 7, 8	8, 8, 8, 8, 4	5	-15	0.031
48 h	29 *vs* 29 = 50.0%	7, 5, 6, 5, 6	7, 8, 6, 3, 5	3	-3	0.625

Average score: 51.1% → no perception of a difference between the two circles

Circle Ø of 5 mm *vs* circle Ø of 3 mm; data supplementing Table 2, line 4

Training: meanly 12.0 ants at any time around the two circles.

Testing:

Time	Ants' response	Summed by four, numbers of ants sighted near the larger circle	; near the smaller one	Wilcoxon test result N	T	P
7 h	43 *vs* 53 = 44.8%	7, 9, 9, 11, 7	8,13,10,10,12	5	-13	0.094
24 h	30 *vs* 30 = 50.0%	6, 5, 8, 8, 4	4, 5, 6, 9, 6	4	6	0.438
31 h	43 *vs* 53 = 44.8%	9, 11, 9, 6, 8	9, 16, 9,11, 8	2	-	NS
48 h	47 *vs* 48 = 49.5%	11,12, 8, 8, 8	7, 7,11,10,13	5	7.5	>0.50

Average score: 47.0% → not obvious perception of a difference between the two circles

Circle Ø of 5.5 mm *vs* circle Ø of 3 mm; data supplementing Table 2, line 5

Training: meanly 10.6 ants at any time around the two circles.

Testing:

Time	Ants' response	Summed by four, numbers of ants sighted near the larger circle	; near the smaller one	Wilcoxon test result N	T	P
7 h	36 *vs* 20 = 64.3%	6, 11, 5, 7, 7	2, 6, 2, 5, 5	5	15	0.031
24 h	40 *vs* 22 = 64.5%	8, 9, 10, 8, 5	3, 4, 6, 4, 5	4	10	0.063
31 h	48 *vs* 27 = 64.0%	6, 11,10, 9,12	2, 7, 4, 5, 9	5	15	0.031
48 h	34 *vs* 20 = 62.9%	6, 7, 7, 9, 5	2, 6, 4, 5, 3	5	15	0.031

Average score: 64.0% → obvious perception of a difference between the two circles

Circle Ø of 6 mm *vs* circle Ø of 3 mm; data supplementing Table 2, line 6

Training: meanly 11.0 ants at any time around the two circles.

Testing:

Time	Ants' response	Summed by four, numbers of ants sighted near the larger circle	; near the smaller one	Wilcoxon test result N	T	P
7 h	68 *vs* 42 = 61.8%	9,15,16,17,11	5, 9,11,10, 7	5	15	0.031
24 h	43 *vs* 15 = 74.1%	7, 9, 7, 9, 11	1, 4, 2, 4, 4	5	15	0.031
31 h	49 *vs* 22 = 69.0%	11,11, 7,10,10	5, 4, 3, 3, 7	5	15	0.031
48 h	49 *vs* 18 = 73.1%	9,11,10,12, 7	2, 5, 5, 3, 3	5	15	0.031

Average score: 68.3% → perfect perception of a difference between the two circles

Colony C; discrimination between circles with a diameter of 5, 5.5, 6, 6.5, 7 and 7.5 mm and a circle with a diameter of 4 mm

Circle Ø of 5 mm *vs* circle Ø of 4 mm; data supplementing Table 3, line 1

Training: meanly 8.8 ants at any time around the two circles.

Testing:

Time	Ants' response	Summed by four, numbers of ants sighted near the larger circle	; near the smaller one	Wilcoxon test result N	T	P
7 h	18 *vs* 24 = 42.9%	5, 3, 4, 2, 4	6, 6, 2, 5, 5	5	-12	0.156
24 h	23 *vs* 32 = 41.8%	3, 5, 6, 3, 6	7, 11, 5, 4, 5	5	-13	0.094
31 h	24 *vs* 31 = 43.6%	5, 3, 4, 6, 6	8, 5, 5, 7, 6	4	-10	0.063
48 h	20 *vs* 24 = 45.5%	2, 4, 6, 4, 4	6, 5, 7, 2, 4	4	-10	0.063

Average score: 43.4% → no perception of a difference between the two circles

Circle Ø of 5.5 mm *vs* circle Ø of 4 mm; data supplementing Table 3, line 2

Training: meanly 11.0 ants at any time around the two circles.

Testing:

Time	Ants' response	Summed by four, numbers of ants sighted near the larger circle	; near the smaller one	Wilcoxon test result N	T	P
7 h	21 *vs* 29 = 42.0%	4, 4, 3, 5, 5	6, 6, 5, 7, 5	4	-10	0.063
24 h	32 *vs* 40 = 44.4%	7, 6, 6, 8, 5	12, 7, 8, 8, 5	3	-6	0.125
31 h	20 *vs* 26 = 43.5%	1, 3, 5, 4, 7	6, 6, 3, 4, 7	3	-5	0.250
48 h	21 *vs* 27 = 43.8%	2, 5, 4, 4, 6	6, 5, 6, 5, 5	3	-8	0.188

Average score: 43.5% → no perception of a difference between the two circles

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Circle Ø of 6 mm *vs* circle Ø of 4 mm; data supplementing Table 3, line 3

Training: meanly 11.3 ants at any time around the two circles.

Testing:

Time	Ants' response	Summed by four, numbers of ants sighted		Wilcoxon test result		
		near the larger circle ;	near the smaller one	N	T	P
7 h	23 *vs* 29 = 44.2%	3, 4, 5, 5, 6	7, 5, 6, 5, 6	3	-6	0.125
24 h	21 *vs* 29 = 42.0%	6, 4, 4, 2, 5	6, 5, 8, 5, 5	3	-6	0.125
31 h	20 *vs* 27 = 42.6%	3, 4, 5, 4, 4	8, 7, 5, 4, 4	3	-5	0.250
48 h	32 *vs* 34 = 48.5%	10, 7, 7, 5, 3	8, 6, 8, 6, 6	5	-9	0.406

Average score: 44.7% → no perception of a difference between the two circles

Circle Ø of 6.5 mm *vs* circle Ø of 4 mm; data supplementing Table 3, line 4

Training: meanly 10.9 ants at any time around the two circles.

Testing:

Time	Ants' response	Summed by four, numbers of ants sighted		Wilcoxon test result		
		near the larger circle ;	near the smaller one	N	T	P
7 h	37 *vs* 40 = 48.1%	7, 6, 9, 8, 6	9, 6, 9,10, 6	2	-	NS
24 h	32 *vs* 26 = 55.2%	5, 4, 6, 7,10	3, 5, 3, 5, 10	4	9	0.125
31 h	30 *vs* 34 = 46.9%	7, 5, 8, 4, 6	7, 10, 8, 4, 5	2	-	NS
48 h	38 *vs* 33 = 53.5%	10,10, 7, 5, 6	6, 8, 9, 6, 4	5	11	0.219

Average score: 50.7% → no or very slight perception of a difference between the two circles

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Circle Ø of 7 mm *vs* circle Ø of 4 mm; data supplementing Table 3, line 5

Training: meanly 11.7 ants at any time around the two circles.

Testing:

Time	Ants' response	Summed by four, numbers of ants sighted near the larger circle	near the smaller one	Wilcoxon test result N	T	P
7 h	38 *vs* 18 = 67.9%	12,10, 5, 5, 7	4, 4, 3, 3, 4	5	15	0.031
24 h	24 *vs* 15 = 61.5%	5, 4, 4, 7, 4	4, 3, 2, 4, 2	5	15	0.031
31 h	30 *vs* 20 = 60.0%	8, 5, 7, 5, 5	4, 4, 3, 5, 4	4	10	0.063
48 h	33 *vs* 20 = 62.3%	6, 7, 6, 7, 7	2, 5, 4, 5, 4	5	15	0.031

Average score: 63.1% → perception of a difference between the two circles

Circle Ø of 7.5 mm *vs* circle Ø of 4 mm; data supplementing Table 3, line 6

Training: meanly 10.8 ants at any time around the two circles.

Testing:

Time	Ants' response	Summed by four, numbers of ants sighted near the larger circle	near the smaller one	Wilcoxon test result N	T	P
7 h	47 *vs* 19 = 71.2%	8, 8, 9,13, 9	2, 4, 3, 6, 4	5	15	0.031
24 h	49 *vs* 27 = 64.5%	9, 14, 9, 8, 9	5, 6, 6, 5, 6	5	15	0.031
31 h	37 *vs* 20 = 64.9%	7, 6, 7, 8, 9	1, 4, 6, 5, 4	5	15	0.031
48 h	30 *vs* 13 = 69.8%	9, 6, 6, 5, 4	3, 2, 3, 3, 2	5	15	0.031

Average score: 67.4% → obvious perception of a difference between the two circles