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Social facilitation of insect reproduction with motor-driven tactile stimuli

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Tactile stimuli provide animals with important information about the environment, including physical features such as obstacles, and biologically relevant cues related to food, mates, hosts and predators. The antennae, the principal sensory organs of insects, house an array of sensory receptors for olfaction, gustation, audition, nociception, balance, stability, graviception, static electric fields, and thermo-, hygro- and mechanoreception. The antennae, being the anteriormost sensory appendages, play a prominent role in social interactions with conspecifics that involve primarily chemosensory and tactile stimuli. In the German cockroach (*Blattella germanica*) antennal contact during social interactions modulates brain-regulated juvenile hormone production, ultimately accelerating the reproductive rate in females. The primary sensory modality mediating this social facilitation of reproduction is antennal mechanoreception. We investigated the key elements, or stimulus features, of antennal contact that socially facilitate reproduction in *B. germanica* females. Using motor-driven antenna mimics, we assessed the physiological responses of females to artificial tactile stimulation. Our results indicate that tactile stimulation with artificial materials, some deviating significantly from the native antennal morphology, can facilitate female reproduction. However, none of the artificial stimuli matched the effects of social interactions with a conspecific female.

1. Introduction

Insects exploit multiple sensory modalities, including auditory, olfactory, gustatory and tactile sensing, in a wide range of behavioural contexts such as locating resources, avoiding predators, mate finding and mate choice [1,2]. Antennae are important multi-sensory organs in insects, largely because they are located at the anteriormost position of the insect, they often extend up to several body lengths and sweep and sample nearly 360° of space around the insect, and they can receive information about smell, taste, sound, humidity, temperature and various mechanosensory cues [3]. The antennae are also pivotal sensory organs in social interactions, especially in nocturnal insects.

Mechanoreceptive sensilla are broadly distributed throughout the body surface of insects, with particularly high density on sensory appendages, including the antennae [3,4]. Antennal mechanosensors have been studied most extensively in the contexts of obtaining position information and localization and feature discrimination of obstacles [5]. However, antennal mechanoreception is also important in courtship behaviour, where positional information is integrated with chemosensory signalling between the sexes, as shown for example in cockroaches, crickets and moths [6–10]. In the behavioural phase change of the Australian plague locust, *Chortoicetes terminifera*, tactile stimulation of the antennae appears to be the sole mechanism that evokes a shift from solitarious to the gregarious state and ultimately swarming [11]. The antennae also appear to be the main organ involved in adult phase change in the desert locust, *Schistocerca gregaria* [12]. In addition, maternal determination of progeny characteristics has been observed in *S. gregaria*, where tactile stimulation perceived by their antennae causes females to produce gregarious offspring [12].

In the German cockroach, *Blattella germanica* (L.; Dictyoptera, Blattellidae), the interchange of chemosensory and tactile signals during social interactions affects behavioural and physiological responses of nymphs and adults. Lihoreau & Rivault [13] showed that nymphs can discriminate siblings from non-sibs and that this kin recognition ability requires antennal contact between individuals. Social interactions also accelerate nymphal development in the German cockroach, and tactile stimulation of the antennae appears to be most important in eliciting this response [14–17]. Social facilitation of reproduction has been shown in both females and males of *B. germanica*. Females undergo an endocrine-regulated sexual maturation after adult emergence, and social interactions facilitate this process by lifting brain-imposed allatostatic inhibition of the corpora allata (CA), stimulating higher juvenile hormone (JH) production which, in turn, stimulates reproduction. Social interactions thus indirectly modulate all JH-related activities, including attainment of sexual receptivity, production of sexual signals, mating and the time course of oviposition [18–22]. Similarly, social interactions have a profound effect on certain aspects of male reproductive physiology and behaviour, such as JH biosynthesis, protein production in the accessory reproductive glands and sexual maturation [23].

Tactile cues are the primary sensory channel through which social conditions stimulate or accelerate reproduction in adult *B. germanica* females—with no evidence for involvement of the visual and olfactory systems—and the antennae play a prominent role in the reception of these tactile cues [24]. Moreover, tactile stimulation of the antennae with 'prosthetic' antenna-like artificial materials in place of the antennal flagellum can also accelerate oocyte growth [24], confirming that social interactions accelerate reproduction in *B. germanica* females via mechanosensory cues perceived mainly by the antennae. Although some features of antennal tactile communication involved in social facilitation have been described in phase-polyphenic locusts [11,12], to the best of our knowledge, the specific stimulus characters of tactile cues that facilitate reproduction in other arthropod species have not been investigated.

Our aim in this study was to identify the specific elements of a social tactile stimulus responsible for accelerating reproduction in *B. germanica* females. First, we evaluated the role of antennal contact in a social context. Then, we established a system for testing physiological responses of females to artificial, motor-driven tactile stimulation that mimicked the cockroach antenna. Finally, we dissected the tactile cues focusing on features such as speed of movement, duration of stimulation and morphology of the tactile stimulus.

2. Material and methods

(a) Insects and rearing conditions

Blattella germanica cockroaches, from a colony originally obtained from American Cyanamid in 1989 (also referred to as Orlando normal), were kept at $27 \pm 1°C$ and 40–70% ambient relative humidity, under a 12 L : 12 D photoperiod with continuous access to dry LabDiet rat chow (no. 5001; Rodent Diet, PMI Nutrition International, Brentwood, MO) and water. Newly eclosed females were selected from the colony on the day of adult emergence (day 0). Only females of similar size and degree of tanning and with intact wings were selected for each experiment and were maintained under the same conditions described above.

In all experiments, newly emerged females from the same cohort as the experimental females were either socially isolated (negative control) or paired for the entire experiment (positive control).

(b) Ovary dissection and oocyte measurements

Test females were ice-anaesthetized, and their ovaries were removed under cockroach saline [25]. In *B. germanica*, only a single basal (vitellogenic) oocyte matures in each ovariole and all basal oocytes mature synchronously in each of the approximately 40 ovarioles in the paired ovaries. A random sample of 10 basal oocytes of each female was selected, and oocyte lengths were averaged for each female. Measurements were done with an ocular micrometer in the eyepiece of a dissecting microscope.

(c) The effects of tactile cues on the reproductive response to social interactions

The antennae are essential in receiving sensory input, and the tactile stimuli that facilitate oocyte maturation in *B. germanica* are not species-specific [24]. A *Periplaneta americana* female was placed into a 15 ml plastic tube, with only the antennae protruding through a small hole in the tube. We covered the head of the cockroach with parafilm, so that only the antennae extended through the hole into a Petri dish (60 mm diameter, 15 mm high, Fisher Scientific, Pittsburgh, PA), where a newly emerged *B. germanica* female was placed with food and water ad libitum. In an additional treatment—using the same bioassay design—we bilaterally ablated the *P. americana* antennae to eliminate tactile stimuli by the antennae. *P. americana* females were briefly anaesthetized with CO_2, placed on ice and the flagellum of each antenna was cut with fine scissors just distal to the pedicel. Because *P. americana* females were necessarily starved and could not drink under these conditions, each female was used for only 2 days and replaced with a fresh female, so three females were used for each dish during the 6 day long experiment. On day 6, the oocyte lengths of 20−23 *B. germanica* females per treatment were measured.

(d) Motorized tactile stimulation system

To investigate features of tactile stimuli that ultimately accelerate oocyte maturation, we designed a motorized system that could stimulate isolated females with substrates that mimicked cockroach antennae. The system was comprised of a controller and 20 parallel stepper motors. The controller consisted of a microcontroller (PIC18F4520, Microchip Technology, Chandler, AZ), speed and direction controls, an LCD display showing the motor angular velocity and 10 microstepping bipolar stepper motor drivers (A4988, Pololu, Las Vegas, NV; figure 1). Each motor driver controls two stepper motors (ROB-09238, SparkFun Electronics, Boulder, CO). The output of the microcontroller could generate angular velocities of 0.1–30 revolutions per minute (r.p.m.), and each motor was set to rotate in a clockwise direction. Each motor was securely attached to the underside of a 6-mm thick acrylic sheet that held 10 motors. A Petri dish (90 mm diameter, 15 mm high) was placed on the acrylic sheet with a hole at its centre aligned with the hole in the acrylic sheet. The motor shaft thus penetrated into the Petri dish, and materials simulating insect antennae were attached onto the shaft. The acrylic sheet effectively thermally insulated the Petri dishes from the motors, and a room fan was used to ensure rapid dissipation of heat from the electronics.

(e) Validation and use of the motorized system

First, we determined whether the rotating motors influenced oocyte growth by producing heat, vibration or other confounding stimuli. Newly emerged females were either socially isolated or
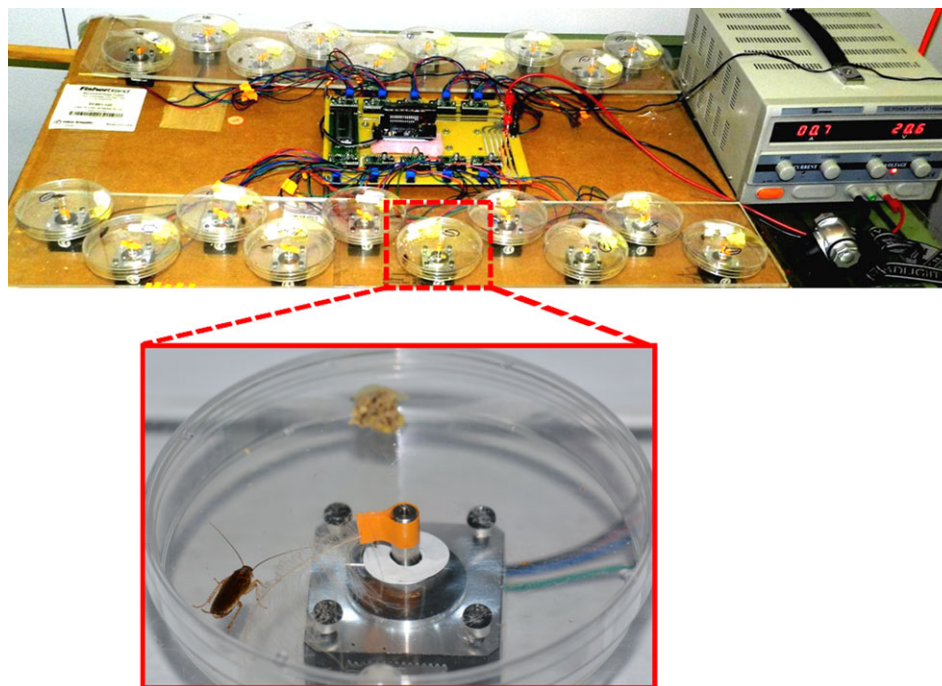
Figure 1. Motorized tactile stimulation system showing the power supply (right), controller (centre) and 20 Petri dishes each mounted on a stepper motor (top and bottom). The inset shows an isolated *B. germanica* female in a Petri dish with a duck feather mounted on the rotating motor shaft. (Online version in colour.)

paired in Petri dishes and placed either on the rotating motors or beside them with food and water ad libitum. Because social interactions stimulate oocyte growth only during the scotophase, when females are active, and not during the photophase when females aggregate in close contact with each other [24], the motors were turned on during the entire scotophase (12 h) at a maximum speed of 30 r.p.m. and with a bare motor shaft. The basal oocytes of 10 *B. germanica* females per treatment were measured on day 6. The temperature within similarly deployed Petri dishes was measured at 1 min intervals for 6 days with HOBO UX100-003 data loggers (Onset Computer Corp., Bourne, MA) positioned above motors running only during the 12 h scotophase at 0, 1 and 30 r.p.m. and in a Petri dish adjacent to the motors.

Movement of the antennae is necessary to glean tactile information from the surroundings [26]. The cockroach antennae are flexible and they regularly sweep through space, vibrate, palpate rhythmically and get deflected when the insect comes in contact with conspecifics, suggesting that movement is an important feature of the tactile cue. To determine the most effective motor speed and the optimal duration of stimulation, newly eclosed females were socially isolated in Petri dishes and placed on the motors with food and water ad libitum. Artificial tactile stimulation was provided by a commercially sanitized natural white Cul De Canard feather from the back of a duck (CDC201, Wapsi Fly Inc., Mountain Home, AR) attached to each motor shaft. Each set of females received stimulation for different durations (3, 4.5, 6, 7.5, 12 h (scotophase only) and 24 h) and at different motor speeds (0, 1, 5, 10 and 30 r.p.m.). Sample size was 16–20 females per treatment.

In addition to movement, some physical properties of the antenna such as the structural complexity may influence the reproductive rate of *B. germanica* females. Complexity of the antennal morphology was tested by manipulating duck feathers: either an intact duck feather, feather with its barbs cut to 1 mm, or bare feather with its barbs completely removed. Sample size was 10–18 females per treatment.

(f) Statistical analyses

Data were analysed with one-way ANOVA for multiple comparisons using SAS 9.1.3 software (SAS Institute Inc. 2002–2003,

Cary, NC). We used PROC GLM to test for the effects of social conditions on oocyte length as dependent variable. PROC GLM was also used to obtain the residuals from adjusted model and test whether residuals held the assumption of homogeneous variances within each treatment. Because data were unbalanced, LSMEANS and least significant difference test was used to compare means at 0.05 significance level. Variation around the mean is represented by the standard error of the mean (s.e.m.).

3. Results

(a) Antennal contact mediates the social facilitation of reproduction

To confirm the importance of antennal contact in social facilitation of female reproduction, each isolated *B. germanica* female was allowed to interact only with the antennae of a *P. americana* female whose body was bound in a tube outside the dish; these *B. germanica* females developed their oocytes significantly faster (1.29 ± 0.05 mm, $n = 23$) than females that were fully isolated (0.99 ± 0.07 mm, $n = 22$) or females that interacted with a *P. americana* female whose antennae were ablated (0.87 ± 0.06 mm, $n = 20$; ANOVA, $p < 0.0001$; figure 2). It is difficult to disentangle the relative significance of 'giving' social stimuli (touching) versus 'receiving' social stimuli (being touched). Nevertheless, it appears that active tactile sensing of social stimuli is crucial for accelerating oocyte maturation, because interaction with an immobile (freshly killed) female fails to stimulate oocyte growth, whereas tactile stimulation of the female with 'prosthetic' antenna-like artificial materials in place of the antennal flagellum induces faster oocyte growth [24].

(b) Validation of the motorized tactile stimulation system

We implemented artificial tactile stimulation with stepper motors, which have some intrinsic features that might confound
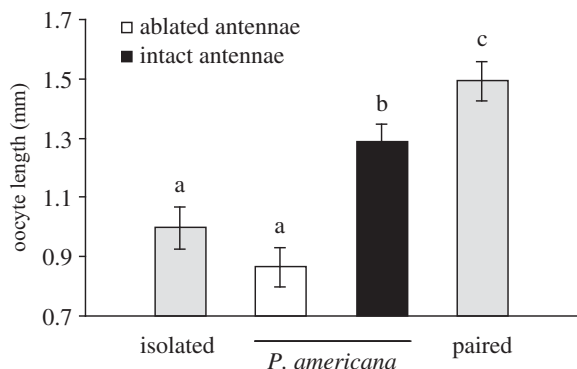
Figure 2. Effects of interaction with *P. americana* antennae only on oocyte maturation of *B. germanica* females. Newly emerged adult females were either socially isolated (negative control), or paired for the entire 6 day experiment (positive control; grey bars). An American cockroach female was bound in a plastic tube outside the dish with only its antennae protruding into the dish to interact with the otherwise isolated *B. germanica* female. In an additional treatment, the American cockroach female antennae were carefully ablated, eliminating antennal contact. Mean basal oocyte length $\pm$ s.e.m. Different letters above the bars indicate significant differences among treatments (ANOVA, $F_{3,83} = 21.78$, $p < 0.0001$; LSD, $p < 0.05$).

Figure 3. Validation of the motorized tactile stimulation system. Newly emerged adult females were either socially isolated or paired in Petri dishes and placed either on the rotating motors or beside them. The motors were powered during the entire 12 h scotophase at a speed of 30 r.p.m. and with no substrate attached to their shafts. The basal oocytes of *B. germanica* females were measured on day 6 and sample size was 10 females per treatment. Mean basal oocyte length $\pm$ s.e.m. Different letters above the bars indicate significant differences among treatments (ANOVA, $F_{3,36} = 4.99$, $p = 0.0054$; LSD, $p < 0.05$).

our results. For example, they might produce heat and vibration that might influence the female's reproductive rate. Social isolation significantly delayed oocyte maturation in both sets of solitary females, both on and off the motors, whereas both sets of paired females exhibited faster oocyte growth, regardless of whether they were on or beside the motors (ANOVA, $p < 0.05$; figure 3). There were no significant differences between isolated or paired females within each location, indicating that (i) the motors themselves did not affect the rate of oocyte growth, (ii) the rotating motor shaft was not an appropriate tactile facilitator of oocyte maturation in *B. germanica*, and (iii) our motorized system was thus suitable for testing physiological responses of females to artificial tactile stimulation. We confirmed that the mean 6 day temperatures were similar in Petri dishes positioned above non-rotating motors ($27.348 \pm 0.0640°$C, s.d., $n = 8640$ readings per dish), motors running during the 12 h scotophase at 1 r.p.m. (27.347 ± 0.0669) and 30 r.p.m. (27.357 ± 0.0612) and in a Petri dish positioned adjacent to the motors (27.357 ± 0.0683). These temperature differences were substantially smaller than the $\pm 0.21°$C technical accuracy of the data loggers.

(c) Stimulus features related to artificial 'antenna' movement

We recently found that 2 h of daily social interactions with another female in the middle of the scotophase were sufficient to induce faster oocyte maturation in *B. germanica* [24]. To determine the optimal conditions for artificial tactile stimulation, we fixed a duck feather to each motor and assessed the effects of various motor speeds and durations of daily stimulation on reproductive development in *B. germanica* females. The results again confirmed that movement is an important stimulus feature, because static feathers continuously present in the Petri dishes for 6 days failed to stimulate oocyte growth (figure 4, black bar). With dynamic tactile stimulation, oocyte maturation was inversely correlated with both motor speed and duration of stimulation (figure 4). Rapid tactile stimulation at 30 r.p.m. failed to accelerate oocyte maturation at all the stimulus
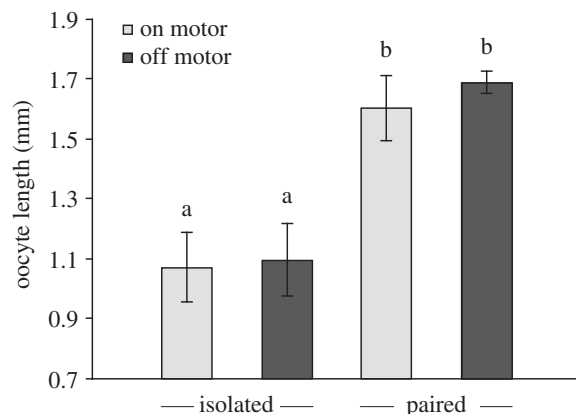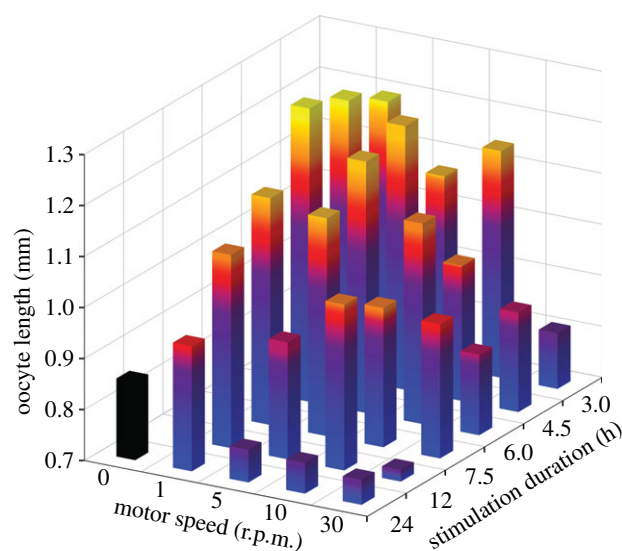

Figure 4. Dose–response histogram for the effects of motor speed and duration of stimulation on the rate of oocyte maturation in *B. germanica* females. Newly emerged adult females were socially isolated in Petri dishes and placed on the motors. Artificial tactile stimulation was provided by a duck feather attached to the shaft of each motor. Each set of females received stimulation for different durations in the scotophase (3, 4.5, 6, 7.5 or 12 h) or for the entire 24 h day and at different motor speeds (0, 1, 5, 10 and 30 r.p.m.). The black bar indicates a 'no movement' control treatment. Sample size was 16–20 females per treatment.

durations that we tested (average oocyte length across all stimulus durations: 0.80 ± 0.05 mm, $n = 59$, similar to 0.95 ± 0.05 mm, $n = 49$, in females that were isolated during the entire experiment). Decreasing motor speed to 1–5 r.p.m. or decreasing stimulation duration to 3–6 h resulted in maximal oocyte growth. In our 6 day assays, females responded with the fastest oocyte development (1.28 ± 0.09 mm, $n = 20$) to 6 h stimulation at 1 r.p.m. (figure 4). This combination was used in subsequent experiments.
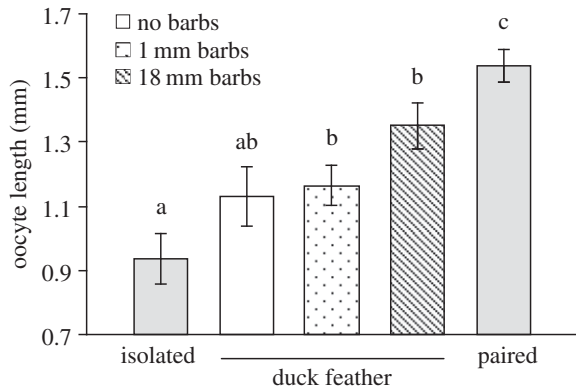
Figure 5. Evaluation of the significance of the structural complexity of an artificial tactile stimulus on the rate of oocyte *B. germanica* females. Newly emerged adult females were either socially isolated (negative control), or paired for the entire experiment (positive control; grey bars). Other newly emerged females from the same cohort were isolated in Petri dishes and placed on the motors. Each female received artificial tactile stimulation for 6 h at 1 r.p.m. by a duck feather attached to the shaft of the motor. Stimulus complexity was tested with either intact feathers with 18 mm barbs, feathers with short 1 mm barbs or feathers with the barbs completely removed leaving a bare feather rachis. Mean basal oocyte length $\pm$ s.e.m. Different letters above the bars indicate significant differences among treatments (ANOVA, $F_{4,85} = 12.21$, $p < 0.0001$; LSD, $p < 0.05$).

(d) Stimulus features related to artificial 'antenna' morphology

In previous research, we showed that slowly rolling glass beads failed to stimulate oocyte maturation in female *B. germanica* [24], suggesting that movement alone is not sufficient and that specific morphological features of the stimulus are responsible for socially facilitating oocyte growth in female cockroaches. To test for structural complexity, we used feathers with 18 mm barbs representing super-normal 'sensilla', short 1 mm barbs representing long 'sensilla' as well as a bare feather shaft (rachis) with no visible barbs. Stimulation with a bare rachis did not stimulate oocyte growth significantly more than in isolated females. However, 'sensilla'-bearing feathers elicited significantly faster oocyte development than in the isolated control females (ANOVA, $F_{4,85} = 12.21$, $p < 0.0001$; LSD, $p < 0.05$; figure 5).

4. Discussion

Numerous animal behaviour studies have used fabricated models to delineate key elements (stimulus characters) of relevant stimuli, dating back to Tinbergen's [27] elegant and rather uncomplicated studies, using cardboard models to define the relevant stimulus characters that comprise sign stimuli that guide bird and insect behaviours. However, such investigations have been heavily biased in the visual, auditory and chemosensory modalities. Examples of contemporary investigations using this approach include computer animations to explore the visual stimuli that guide mating behaviour of jumping spiders [28] and virtual computer-generated prey assemblages to explore the visual behaviour of predatory fish [29]. Robots have also been used to understand visually and chemically guided animal choices, including mate choice in grouse [30] and collective assembly in cockroaches [31]. Likewise, auditory biologists have

recorded and synthesized acoustic stimuli to understand key elements that convey specific information to the receiver, and chemosensory biologists have similarly conducted chemical structure–activity studies with synthetic analogues of odorants and tastants to understand the respective olfactory and gustatory receptors and the behaviours they drive. Near-range sounds and vibrational stimuli, which stimulate mechanoreceptors, have also been investigated, especially in arthropods [3]. Notably, however, it has been exceptionally challenging to fabricate synthetic tactile stimuli mainly, because the insect antenna is a compound sensory organ in which touch is but one component of a multi-sensory network, unlike the vertebrate whisker or vibrissa which is strictly tactile and inert with receptors located in the follicle at its base [32]. It has also been difficult to isolate and quantify the salient tactile features that elicit behaviour, including shape, fine structure, texture, friction, force and various spatiotemporal features of antennal contact. Moreover, tactile cues often involve complex and context-dependent active movements of both the signaller's and receiver's head and antennae, and unlike most communication messages that operate through a medium (air, water), the signaller in tactile communication can also be the receiver, as for example in reciprocal antennal fencing where the antenna both touches and is touched and processes both proprioreceptive and exteroreceptive information [3]. Finally, the insect antenna is endowed with multiple types of mechanosensory structures (e.g. hairs) that are differentially distributed across various antennal segments, and arranged as single sensilla or as specialized arrays of mechanosensory units (e.g. hair plates, chordotonal organs) [4], making it even more difficult to determine where and how socially relevant tactile stimuli are received.

Thus, it is not surprising that the relevance of most antennal mechanoreceptive sensilla in social interactions remains largely unexplored, as most investigations have focused on relatively instantaneous non-social behaviours such as steering and course control, obstacle navigation and escape responses [3]. These behaviours depend largely on object localization (i.e. where) and much less so on object discrimination and identification (i.e. what). The effectiveness of tactile stimuli in a social context is profoundly dependent on the receiver being able to identify the source of the stimulus (its shape, texture, biomechanics), and our endeavours to disentangle discrete social tactile stimulus characters are therefore considerably more challenging than in other sensory modalities. The challenge is substantially even more imposing in 'primer-type' responses that require multiple days of *in situ* tactile stimulation whose outcomes are physiological rather than behavioural, as in the slow contact-mediated social facilitation of reproduction in *B. germanica*. While the behavioural outputs of associative learning experiments can decode the tactile stimulus characters, more sophisticated paradigms are required to unravel the primer-type stimuli that drive slow physiological changes. This is apparent in *B. germanica*, where 24 h of social interactions on any day during the 6 day pre-oviposition period of otherwise isolated females is insufficient to elicit a 'grouping effect', and even 48 h of interactions on days 2–3 minimally facilitate reproduction in females [24].

We established and validated a motorized system that enabled us to investigate the effects of artificial tactile stimuli on reproduction of female cockroaches. *B. germanica* females

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respond to social interactions with conspecifics—and even with other insects—by elevating their rate of JH production and accelerating the rate of oocyte maturation, a form of phenotypic plasticity [18,19,21,22]. In a previous study, we established that visual and chemosensory cues play little, if any, role in this social facilitation of reproduction, whereas tactile stimuli alone can elicit faster reproduction [24]. In this work, we demonstrate that 'antenna'-like structures, driven by stepper motors, can also accelerate the rate of oocyte growth. Notably, however, all of our treatments were significantly inferior to normal social interactions with a conspecific female, indicating that other prominent features of this social facilitation system remain to be delineated. Because limited interaction only with the antennae of either *P. americana* or *B. germanica* was not as effective as interaction with a whole conspecific female [24], we infer that non-antennal tactile stimuli are also important facilitators of reproduction.

An emerging picture from our studies is that antennal movement and morphology are integral components of the tactile stimuli. In support of our *in situ* studies demonstrating that social facilitation of reproduction is gated with the photocycle and can be achieved with as little as 2 h of contact in the scotophase [24], we now demonstrate that the duration and magnitude of artificial tactile stimulation also impact oocyte growth. The effect of duration of artificial stimulation on oocyte maturation represents an upside-down (concave downward) parabola, with a peak at about 6 h of stimulation in the middle of the scotophase. We suspect that as the quality of the tactile stimulus increases, the minimal required duration of stimulation will diminish. We also demonstrated that the rate of oocyte maturation was inversely related to the frequency of stimulation, represented by motor speed. Thus, oocyte maturation was greatly suppressed by frequent tactile stimulation at 30 r.p.m. but considerably stimulated with slow intermittent contact with a duck feather. Coupled with the observations that reproduction in isolated females is not facilitated by an immobile feather or by the presence of freshly killed (i.e. immobile) females [24], these results indicate that stimuli related to kinematics of the insect antennal motor system and biomechanics and dynamic properties of the antennal flagellum play essential roles in facilitating reproduction.

The morphology of the artificial stimulus also had a bearing on oocyte maturation. Although the bare shaft (rachis) of a denuded feather stimulated oocyte development, greater structural complexity increased its effectiveness. Moreover, some exaggerated stimulus characters appeared to act as super-normal stimuli, as feathers with long barbs were slightly more effective than feathers with shorter barbs, and *P. americana* antennae were more effective than the native *B. germanica* antennae [24]. Antennal shape thus appears to be an important feature in tactile social stimulation, in support of our *in vivo* studies showing that certain insects with non-flagellar antennal morphology were less effective at

stimulating oocyte growth in *B. germanica* [24]. Further support for the importance of antennal morphology, flexibility and texture comes from male courtship behaviour in *B. germanica*. The female-produced contact sex pheromone readily elicits male courtship when placed on various flagellum-type antennae from a variety of insect species, but not on thick or club-shaped antennae or smooth surfaces such as a nylon line or a human hair [9], suggesting that an important feature of this sexual signal is the integration of chemical and tactile stimuli. The importance of textural cues in determining stimulus identity was also demonstrated in the cockroach *P. americana*, where cuticular surface properties of a wolf spider trigger escape, whereas touching a conspecific does not, even when both are solvent extracted to eliminate contact chemoreception [33]. The fine shape discrimination capabilities of the cockroach antennae remain to be determined, but it would not be surprising if the diversity and spatial organization of mechanosensory sensilla on the antenna enable feature discrimination comparable with that of rodent whiskers [32].

Our motorized tactile stimulation system represents an essential foundation for further studies of stimulus characters that socially facilitate reproduction in *B. germanica* and other species. Promising lines of investigation include mounting more realistic engineered jointed 'antennae' on robots programmed to execute species-specific and context-dependent behaviours in multiple axes. Decoding the tactile stimulus characters will further allow us to identify neuronal and endocrine circuit elements in the transduction pathway through which mechanoreceptors communicate relevant discrete tactile cues through the antennal nerve to sensory neurophils in the deutocerebrum and to higher brain centres, which ultimately accelerate female reproduction in *B. germanica* by disinhibiting the activity of the CA. This neuroendocrine pathway has been best described in phase transition in *S. gregaria*, where tactile stimulation of specific mechanoreceptive sensilla on the hind legs causes an increase in serotonin levels in the metathoracic ganglion which then leads to gregarization [34–36]. It will be fascinating to know whether biogenic amines also respond to social antennal contact resulting in the social facilitation of reproduction in *B. germanica* females.

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