Individual recognition in a jumping spider (*Phidippus regius*)

Christoph D. Dahl[1,2,*,†] and Yaling Cheng[2,*]

[1] Institute of Biology, University of Neuchâtel, Neuchâtel, Switzerland

[2] Graduate Institute of Mind, Brain and Consciousness, Taipei Medical University, Taipei, Taiwan

* joint senior authorship

† corresponding author: Christoph D. Dahl <christoph.d.dahl@gmail.com>

Summary

Individual recognition is conceptually complex and computationally intense, leading to the general assumption that this social knowledge is solely present in vertebrates with larger brains, while miniature-brained animals in differentiating societies eschew the evolutionary pressure for individual recognition by evolving computationally less demanding class-level recognition, such as kin, social rank, or mate recognition. Arguably, this social knowledge is restricted to species with a degree of sociality (sensu [1], for a review [2]). Here we show the exception to this rule in an asocial arthropod species, the jumping spider (*Phidippus regius*). Using a habituation - dishabituation paradigm, we visually confronted pairs of spatially separated spiders with each other and measured the 'interest' of one spider towards the other. The spiders exhibited high interest upon initial encounter of an individual, reflected in mutual approach behaviour, but adapted towards that individual when it reoccurred in the subsequent trial, indicated by their preference of staying farther apart. In contrast, spiders exhibited a rebound from habituation, reflected in mutual approach behaviour, when a different individual occurred in the subsequent trial, indicating the ability to tell apart spiders' identities. These results suggest that *P. regius* is capable of individual recognition based on long-term social memory.

Keywords

Recognition memory, long-term social memory, individual recognition, flexible learning, arthropod, invertebrate, salticid, jumping spider, *Phidippus regius*

Main text

Recognising individuals is a complex cognitive process requiring flexible learning and recognition memory. Arthropod species possessing the social ability of individual recognition would, thus, stand in stark contrast to the commonly accepted notion that animals with smaller brains are cognitively less advanced due to reduced computational power of nervous systems with smaller and fewer neurons [3]. And yet, there is evidence for an arthropod species displaying face learning [4] and long-term social memory [5]. That is, a social wasp species (*Polistes fuscatus*) showed mammal-like face learning [4, 6], arguably providing social benefits by reducing aggression and stabilizing social interactions. With this, being one of the few reported cases of individual recognition in arthropods (also see [7]), it is considered unlikely that asocial arthropod species would evolve such complex cognitive processes. The reasons being high energy consumption, long processing times and, thus, increased predation risk that would never be outweighed by the few social encounters between individuals and the additional survival benefit [2, 8]. The general consensus, thus, is that a certain degree of sociality sensu Wilson [1] is required for the emergence of individual recognition [8]. Here, we challenge this consensus: In a naturalistic experimental procedure, we put to the test the ability of individual recognition in a notoriously asocial and miniature-brained arthropod species, a member of the *Salticidae* family, the jumping spider (*Phidippus regius*).

In a first step, we assess the ability of *P. regius* to individually recognise other members of its species, commonly referred to as individual recognition [9] or individuation of conspecifics [10]. For this purpose, we used a habituation - dishabituation procedure, where, in general terms, one individual habituates to the presence of another individual in its close proximity and dishabituates when, after a short phase of visual separation, another individual is present in close proximity, assuming that the one individual is capable of discriminating the identities of the two individuals it was confronted with [11, 12]. In other terms, with this habituation - dishabituation paradigm we expect to see that the rebound in 'interest' following changes in a spider's identity is greater than the rebound in 'interest' following a repetition of identity. To experimentally control the animal pairs, we placed the individuals in separate containers with one side and the top panel being transparent. We then pairwise confronted the individuals by placing the containers such that the transparent sides faced each other in the following fashion:

Individual A and individual B were exposed to each other for 7 minutes, triggering an initial 'interest' in each other, and were then visually separated by means of an opaque slider for 3 minutes. Subsequently, they were either exposed to the same individual again (A vs B, *habituation* trial) for 7 minutes, or to a different individual (A vs C, or B vs D, *dishabituation* trial) for 7 minutes, followed by a 3-minute period of visual separation. The relative interest is quantified by approximating spatial distances between the spider pairs in the xy-plane, where high interest is reflected in smaller values (i.e. spiders go close) and low interest in larger values (spiders stay apart). Therefore, under the assumption that the spiders are capable of individuating each other, we predict that in the *habituation* condition, involving the same individuals, the relative interest in each other decreases and, hence, spiders' distances increase (Figure 1a-c; 'Habituation', dashed line: towards maximal distance; solid line: medium distance), while in the *dishabituation* condition, involving a different individual, the relative interest in each other increases and spiders approach each other, hence, distances decrease (Figure 1a-c; 'Dishabituation'). We divided a total of 20 individuals into five groups of four individuals each. Each individual of each group was exposed to the three group members in both habituation and dishabituation trials, resulting in six trials per session, equivalent to one hour of recording. We repeated this procedure twice, resulting in 18 trials across three sessions and an exact repetition of a given trial (and pairing of individuals) in 1-hour intervals (for a detailed description of the procedure see Materials and Methods and Tables 1-2). We found that *habituation* and *dishabituation* trials (i.e. predictor variable *condition*) were significantly dissociated as a function of inter-individual distances (i.e. predictor variable *distance*), leading to a significant improvement of model fitting the interaction of the predictors *distance* and *condition* (LRT: $\chi^2_{\Delta 3} = 63.66$, $p < 0.001$; Figure 2a, Supplementary Table 1): *dishabituation* trials (blue discs) showed a greater proportion of close-distance values than *habituation* trials (red discs), whereas *habituation* trials showed a greater proportion of far-distance values. The interaction between the predictors *distance* and *condition* further significantly interacted with the predictor *session*, modulating the level of the dissociative effect of *condition* over the progression of the testing period, showing the strongest modulation in session 1 and the weakest modulation in session 3 (LRT: $\chi^2_{\Delta 6} = 34.14$, $p < 0.001$; Figure 2a, Supplementary Table 1, exemplar trial: Figure 1 d-f). The systematic dissociation of distance values between *habituation* and *dishabituation* trials

suggests that *P. regius* possesses the ability to individuate conspecifics (see Video 1 and Supplementary videos 1, 2 in the OSF repository (https://osf.io/gpnct/)).

The question arises whether *P. regius*'s decreasing interest over session repetitions is caused by a general fatigue effect due the prolonged testing procedure or whether, in later testing sessions, *P. regius* actually recognises the current individual after having seen it before at least once (when encountering it again in session 2) or twice (when encountering it again in session 3) and, thus, would not dishabituate any longer. Such recognition capability would further emphasise the role of long-term memory representations in the individuation of conspecifics, due to the prolonged retention interval beyond the minute range into the hours. In a second step, we therefore assessed the extent to which a presentation of an individual novel and unseen across the three experimental sessions would trigger a rebound in interest at the end of session 3, henceforth referred to as *dishabituation [long-term]* trials, as opposed to the *dishabituation* trials of sessions 1-3, henceforth referred to as *dishabituation [short-term]* trials (see Table 3). If such rebound occurs, we conclude that the habituation across sessions is the result of recognition of repeatedly presented individuals and not the result of a fatigue effect due to prolonged testing procedures. In other words, such rebound would suggest a 'cognitive' fatigue towards seeing the same 'old' individuals, subserved by long-term memory formation, rather than a 'physical' fatigue effect. To this end, we re-ran the experiment in an additional 16 spiders, arranged to four groups and added a memory *dishabituation [long-term]* trial at the end of session 3. The memory *dishabituation [long-term]* trials were generated by cross-combining individuals from two groups (group 1: A, B, C, D; group 2: E, F, G, H; Table 3), which were run in parallel, at the end of session 3, resulting in novel pairings (A - E, B - G, C - F, D - H). We replicated our previous results and found a dissociation of the factors *distance* and *condition* (LRT: $\chi^2_{\Delta 3} = 29.52$, $p < 0.001$; Figure 2b, Video 2 and Supplementary videos 3, 4 in the OSF repository (https://osf.io/gpnct/), Supplementary Table 2), showing a greater proportion of close-distance values for dishabituation (blue discs) than for habituation trials (red discs) and a greater proportion of far-distance values for habituation than for dishabituation trials. Critically, we also found that the *dishabituation [long-term]* trials at the end of session 3 elicited a rebound in interest that exceeded the rebound in the *dishabituation [short-term]* trials of session 3 by far, reflected in the interaction of *condition* (i.e. *dishabituation [short-term]* vs *dishabituation*

[long-term]) and *distance* ($F(3,127) = 3.91$, sum sq. $= 0.92$, mean sq. $= 0.31$, $p < 0.01$, Figure 2b (right subfigure, white diamonds; exemplar trials: Figure 1g-i, j-l, Videos 3 - 5 and Supplementary videos 5, 6 in the OSF repository (https://osf.io/gpnct/)). Thus, the habituation across sessions reflects a decrease in interest for the same repeatedly presented individuals on the basis of long-term memory capabilities.

Our findings show, firstly, that *P. regius* recognised individuals to which it was exposed to for a short period of 7 minutes and that reoccurred after a visual separation period of 3 minutes. Secondly, *P. regius* habituated in the long-term, i.e. 1 hour and 2 hours after initial presentation of a given individual. Thirdly, despite long-term habituation, *P. regius* showed an unprecedented rebound in interest towards an entirely novel individual, ruling out a physical fatigue effect in favour of a cognitive fatigue on the basis of long-term social memory capabilities. For these reasons, our results are the first to suggest that *P. regius*, an asocial arthropod species, possesses long-term memory, which allows it to individuate conspecifics and recognise novel individuals.

Recognising members of one's own species is crucial for survival and a requirement for various social behaviours. Individual recognition allows the receiver animal to distinguish between friend and foe, to identify a mating partner, its offspring or a kin member. Individual recognition is achieved via the production of individually-distinct features (e.g. visual) or signals (e.g. acoustic) by the sender and extracting those features and signals by the receiver [13]. Individual recognition bears particular significance for *social* animal species mainly in three contexts: territoriality, aggressive competition and parental care [9]. However, jumping spiders, as many other spider species, are solitary and aggressive towards conspecifics, raising the question about the biological relevance of individual recognition in *P. regius*: One of the few social instances in the life of a jumping spider occurs during reproductive communication, encompassing a complex visual courtship display of coordinated movement patterns of the body and bodily features. It is believed that the typical colouration of the appendages (*Chelicerae*) and the colouration and facial hair characteristics serve as important features for species and sex classification in jumping spiders and as a general indicator about the quality of an individual as a mating partner [14, 15]. Hence, colouration (sender) and the ability to distinguish certain colours (receiver) seem to be sufficiently beneficial to sexual selection [16, 14].

Similarly, in aggressive interactions, often due to territorial disputes, fighting abilities are largely associated with the size and colour of the *Chelicerae* [16, 17], rendering territoriality and aggressive competition needless as an ultimate explanation [18] for individual recognition in *P. regius*. Some jumping spiders exhibited parental care [19], protecting the nest through the spiderlings' first molt. One particular jumping spider (*Toxeus magnus*) has been documented to provide a nutritious milk-like substance to the spiderlings, which compares functionally and behaviourally to lactation in mammals [20]. Whether individual recognition solves a survival problem in this context, is however questionable. The remaining solitary behaviours of *P. regius* give little additional reason to predict that individual recognition is a requirement for survival, setting the minimal recognition needs (*Minimum needs hypothesis* [21, 2]) at the basic-level of classification [22], e.g. colour-based distinction, size assessment of *Chelicerae*. Moreover, the neural implementation of a subordinate-level classification [22] system that operates at the level of abstraction required for a more detailed classification, such as individual recognition, involves specialised processing in dedicated neural correlates [23]. For all these reasons it is therefore more likely to assume that the ability of recognising conspecifics is related to *P. regius*'s general learning capabilities via pleiotropy, also referred to as the 'generalised learning hypothesis' [21]. For example, salticids' rather complex foraging and navigation strategies [24, 25, 26], requiring high degrees of learning and adaptability, may translate into the flexible learning ability required for recognising conspecifics, at a level of abstraction more fine-grained than their minimum recognition needs [13]. In other words, while for *social* animal species, including social arthropod species [6, 4, 7], there is an ultimate explanation [18] addressing the function (or adaptation) of individual recognition, we cannot conclusively infer the survival benefits gained by individual recognition in *P. regius*. Instead we put forward the idea that individual recognition in *P. regius* is a byproduct of fairly sophisticated cognitive processing capabilities. Critically, individual recognition relies on recognition memory, a form of long-term memory, where a previously encountered event or entity, here an individual, stored as memory representation is neuronally activated upon re-experiencing that event or entity [27]. Such memory representation might well serve as guidance to *Portia fimbriata*, allegedly the most intelligent jumping spider, when, after scanning the access route to a prey target, it follows the path to the prey under lack of visual control [28]. In our study, we demonstrated retrieval of

information from memory representations in various ways: First, *P. regius*'s dissocative behavioural responses upon perceiving an individual for a second time in succession as opposed to perceiving a different individual suggests recognition of individually distinct characteristics or cues, which manifest in solid memory representations. Moreover, *P. regius* systematically reduced the overall interest over a series of repeated exposure to the same individuals at a 1-hour presentation interval to the point where it became indifferent to the presented individual, suggesting that *P. regius* successfully retrieves memory-stored information at least one hour after memory consolidation. Thirdly, *P. regius*'s interest in novelty was restored at the end of session 3 upon perception of individuals that had not been encountered before, highlighting that the loss of interest in the long-term was not due to a general physical fatigue, but a 'cognitive' fatigue, i.e. to literally perceive the same individuals over and over again. A novel individual, consequently, did not activate memory representations of individuals, and led, as a response, to dishabituation, a fortiori amplifying the notion of memory representation in *P. regius*.

Together, our study challenges the notion of spiders being stimulus-response driven automata, by not only contributing to an increasing body of evidence that spiders and saliticids in particular produce a wide spectrum of intelligent behaviour [29], but by pinpointing the presence of two fundamentally important mechanisms for any higher cognitive processing: flexible learning and recognition memory. The key building blocks of these mechanisms are representations, mental images of external entities, that are not present to the sense organs, allowing more elaborate information processing, such as in complex decision making and goal-directed behaviour. The existence of which in arthropods in general and spiders in particular triggers rethinking of miniature brain cognition [29].

Materials and methods

Subjects

Our subjects were 36 jumping spiders (*Phidippus regius*), kept individually in enclosures (7 x 7 x 12 cm) at room temperature (21 - 25°C) and supplied with a moist water-pad, exchanged every other day, and two small-sized cockroaches (*Shelfordella lateralis*) per week. All spiders were adult laboratory-bred and had no direct encounters with conspecifics

during adulthood. Behavioural enrichment [30] was provided by means of climbing and nesting structures (i.e., natural wood branch) and by interaction with human caretakers and experimenters during handling and maintenance procedures. In Experiment 1, spiders were assigned to five experimental groups, three of which contained females, two of which males; in Experiment 2, spiders were assigned to four experimental groups, i.e. two groups per sex.

Apparatus

In the following we describe how pairs of spiders were brought into direct visual contact under controlled conditions and in a manner that allows to reassign individuals easily and without interruption to form novel pairings. To this end, we built a cubical experimental arena of 60 by 46 bx 65cm dimensions (L x W x H), consisting of white polypropylene plastic panels, mounted in a frame of T-slotted aluminium profiles (20 Series; Misumi Group Inc., Bunkyo City, Tokyo, Japan). Two LED light sources (Mettle® SL400, 45W, 2100lm, 350 x 250mm surface area, Mettle Photographic Equipment Corporation, Changzhou, China) were placed outside the cubicle at 25cm distance from the side panels of the cubicle, illuminating the inside of the cubicle uniformly. We also mounted two FLIR® 1.3MP, Mono Blackfly USB3 cameras with a 1/2" CMOS sensor (BFS-U3-13Y3M-C, FLIR® Integrated Imaging Solutions, Inc, 12051 Riverside Way, Richmond, BC, Canada) equipped with 8mm UC Series lenses from Edmund Optics® (Stock #33-307, Edmund Optics®, Barrington, New Jersey, USA) on T-slotted aluminium profiles, facing downwards onto the arena surface at a distance of 60cm. For each spider we 3D-printed a white container with outer dimensions (L x W x H) of 7 x 7 x 5cm and inner dimensions of 6.3 x 6.3 x 4.5cm. The upper side of the container and one of the four side walls were made of a transparent .5mm thick acrylic sheet. While the acrylic sheet on the upper side of the container was screwed onto the side walls of the container, the acrylic sheet on one of the sides of the container can be lifted up to open the container, allowing easier transfer of the spider from the home enclosure.

Procedure

In Experiment 1, each group involved four same-sex spiders, with each spider being placed inside a container prior to the experiment. During the experiment, the spiders remained

in their own container. We allowed the spiders sufficient time (10-15min) to get used to the new environment. We then placed the containers of the four spiders such that the transparent side walls of two containers were facing each other, resulting in two pairs of spiders with direct visual contact to each other. During the process of arranging the containers and prior to the initiation of every new trial, visual contact was prevented by an occluder slid between the transparent side walls of the containers. Each trial was initiated by removing this occluder, allowing visual contact. For simplicity, let the four individuals be symbolised by the letters 'A', 'B', 'C', and 'D': An arrangement of trials where each individual is opposed to each other individual is described in Table 1. To tease apart, whether or not *P. regius* was capable of visually discriminating other individuals two types of trials were required: (a) a *habituation* trial, where the same individual was presented in the trial preceding the current trial, and (b) a *dishabituation* trial, where a different individual was presented in the trial preceding the current trial. Therefore, every *dishabituation* trial followed a *habituation* trial, forming a *habituation* or *dishabituation* phase, respectively, as shown in Table 2. A trial, e.g. A - B (and in parallel C - D), lasted for 7 minutes allowing the spiders to visually inspect each other, before isolating the spiders visually for 3 minutes with a non-transparent white occluder, fully covering the transparent side wall. After the occluder phase, another exposure phase of 7 minutes was initiated, which consisted of either the same individual (*habituation* trial) or another individual (*dishabituation* trial) than the individual in the preceding trial. During each trial, the individuals distance to each other was quantified at 10Hz temporal resolution, and taken as a measure reflecting the 'interest' in each other: Short distances between individuals signal greater 'interest' in each other, while large distances signal reduced 'interest' in each other. We predict a dissociation of distances between *habituation* and *dishabituation* trials. With the outlined procedure (Table 2), we can form sequences of exposure phases, where each first of two exposure phases is a habituation phase, and every second of those exposure phases is a dishabituation phase and at the same time a habituation phase for the subsequent exposure phase. In this manner, we created a trial list, containing 12 trials in total, six of which result in *habituation* phases and six of which result in *dishabituation* phases (Table 2). This session of trials was repeated twice, resulting in a total of 36 trials per experiment. Each experiment lasted 180 min, where each trial contained 7 min exposure and 3 min visual separation. Each group of spiders

was subjected to this protocol. Two amendments were introduced in Experiment 2: (a) We ran two groups of four individuals in parallel, and (b) additional *cross-group* trials were introduced at the end of session 3. This resulted in a modified procedure described in Table 3.

Data logging and analysis

Camera control and image acquisition were done using Matlab (Mathworks®, Natick, Massachusetts, USA) and the image acquisition and processing toolboxes. The frame rate was set to 10Hz. Cameras were placed perpendicular to the xy-plane at a distance of about 60cm from the ground. The lens aperture was set to f/4, allowing a sufficient depth of field. Analysis was done with Matlab (Mathworks®, Natick, Massachusetts, USA). We pre-processed the video recordings by segmenting the spider body from the background in each frame using functions for image intensity adjustment, image enhancement, image binarization and image properties measurement to extract the largest available 'region', the spider body, and its centroid. For each trial we approximated the distance between the individuals in the xy-plane as a function of time, using the Euclidean distance weight function based on the centroid coordinates of the two individuals. We then pooled the distance values of each trial into 4 equally-sized and non-overlapping bins (bin centers [mm]: [20, 60, 100, 140]; bin size 40mm; maximal distance $\approx$ 160mm) and calculated the proportion of time spent at a given distance. Each bin was normalised by the total number of events. Differences between proportions were then calculated for every trial comparison according to Tables 2, 3: For instance, the proportions of time spent at a given distance for individual A in trial 1 was subtracted from the proportions of time spent at a given distance for individual A in trial 2, resulting in an assessment for the relative rebound of interest following a repetition of exposure to the same spider B (*habituation*). Subsequently, the proportions of time spent at a given distance for individual A in trial 2 was subtracted from the proportions of time spent at a given distance for individual A in trial 3, resulting in an assessment for the relative rebound of interest following changes in spider's identity (*dishabituation*). We used linear mixed-effects models, where the differences in proportions served as the dependent variable. We fitted two separate models for each experiment (*Full model 1* and *2*), and followed a commonly accepted model fitting procedure [31]: To fully account for the

dependent variable, we fitted three predictor variables: (1) The bin number ([1 to 4]), reflecting a discretised distance measure and henceforth referred to as factor *distance* ([1 to 4]), (2) the *session* of comparisons ([1, 2, 3]), as outlined in the Procedure above (Table 2, 3), and (3) the *condition*, referring to whether the given comparison was a *habituation* or *dishabituation* comparison. We also fitted all two-way interactions between the three main predictors: *distance*:*session*, *distance*:*condition*, and *session*:*condition*, as well as the three-way interaction *distance*:*session*:*condition*. Of particular interest are the two-way interaction between the factors *distance* and *condition*, since we predict a modulation of *distance* values by *condition* as a function of *distance*, and the three-way interaction between the factors *distance*, *condition* and *session*, since we predict a modulation of *condition* as a function of *distance* which becomes weaker over time and repetitions, i.e. *session*. We further defined *sex* of the subjects and *subject* as random factors in all models. We fitted a linear mixed-effects model (fitlme function in Matlab) with normal error structure and identity link function to our data set. We then created a null model for each corresponding full model, which consisted of the similar structure as the full model, however leaving only *distance* as fixed effect, while preserving all random effects. Using likelihood ratio test (LRT), we compared the null models with the corresponding full models. Assuming a significant improvement for the full model over the null model, the non-significant interaction terms were removed from the full model, reaching a model containing only significant interaction terms and both significant and non-significant main effects [32, 33], henceforth referred to as the final model. Evaluation of fixed effect were on the basis of the final models and are referred to as the *Final model 1* (Experiment 1), and *Final model 2* (Experiment 2). This procedure resulted in the following models (Wilkinson notation):

Final model 1 and *2*:

'Response ∼ 1 + Distance + Session + Condition + Distance:Condition + ...
Distance:Session:Condition + (1|Sex) + (1|Subject)'

An additional analysis of variance was performed comparing the *dishabituation [long-term]* trials at the end of session 3 with the *dishabituation [short-term]* trials from session 3 (Table 3) as a function of *distance*. No statistical methods were used to predetermine

sample size. The experiments were not randomized. The investigators were not blinded to allocation during experiments and outcome assessment.

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Author contributions

CDD: study design, data collection, analysis and interpretation, writing article, provision of necessary tools; YC: data collection, writing article, provision of resources.

Competing interest

The authors declare that they have no competing interest. The authors have no affiliations with or involvement in any organization or entity with any financial interest, or non-financial interest in the subject matter or materials discussed in this manuscript.

Additional information

All authors have seen and approved the manuscript. The manuscript has not been accepted or published elsewhere. Supplementary Information is available for this paper. Correspondence and requests for materials should be addressed to Christoph D. Dahl. Codes and materials are available (https://osf.io/gpnct/).

Ethical approval

According to Taiwan's Animal Protection Act, issued by the Council of Agriculture (Executive Yuan), experiments on invertebrates are allowed to be conducted without any special permission in Taiwan.

Tables

Table 1: Pairwise comparisons.

Trial	Pair 1	Pair 2
1	A - B	C - D
2	A - C	B - D
3	B - C	A - D

Table 2: Procedure of Experiment 1.

Trial	Pair 1	Pair 2		
1	A - B	C - D	Habituation	Dishabituation
2	A - B	C - D		
3	A - C	B - D	Habituation	
4	A - C	B - D		Dishabituation
5	B - C	A - D	Habituation	
6	B - C	A - D		Dishabituation
...				
3 sessions				

Table 3: Pairwise comparisons as habituation and dishabituation trials.

	Group 1		Group 2			
Trial	Pair 1	Pair 2	Pair 1	Pair 2		
1	A - B	C - D	E - F	G - H	Habituation	Dishabituation [short-term]
2	A - B	C - D	E - F	G - H		
3	A - C	B - D	E - G	F - H	Habituation	
4	A - C	B - D	E - G	F - H		Dishabituation [short-term]
5	B - C	A - D	F - G	E - H	Habituation	
6	B - C	A - D	F - G	E - H		
...						Dishabituation [long-term]
3 sessions						
7	A - E	B - G	C - F	D - H		

Figure

Figure 1

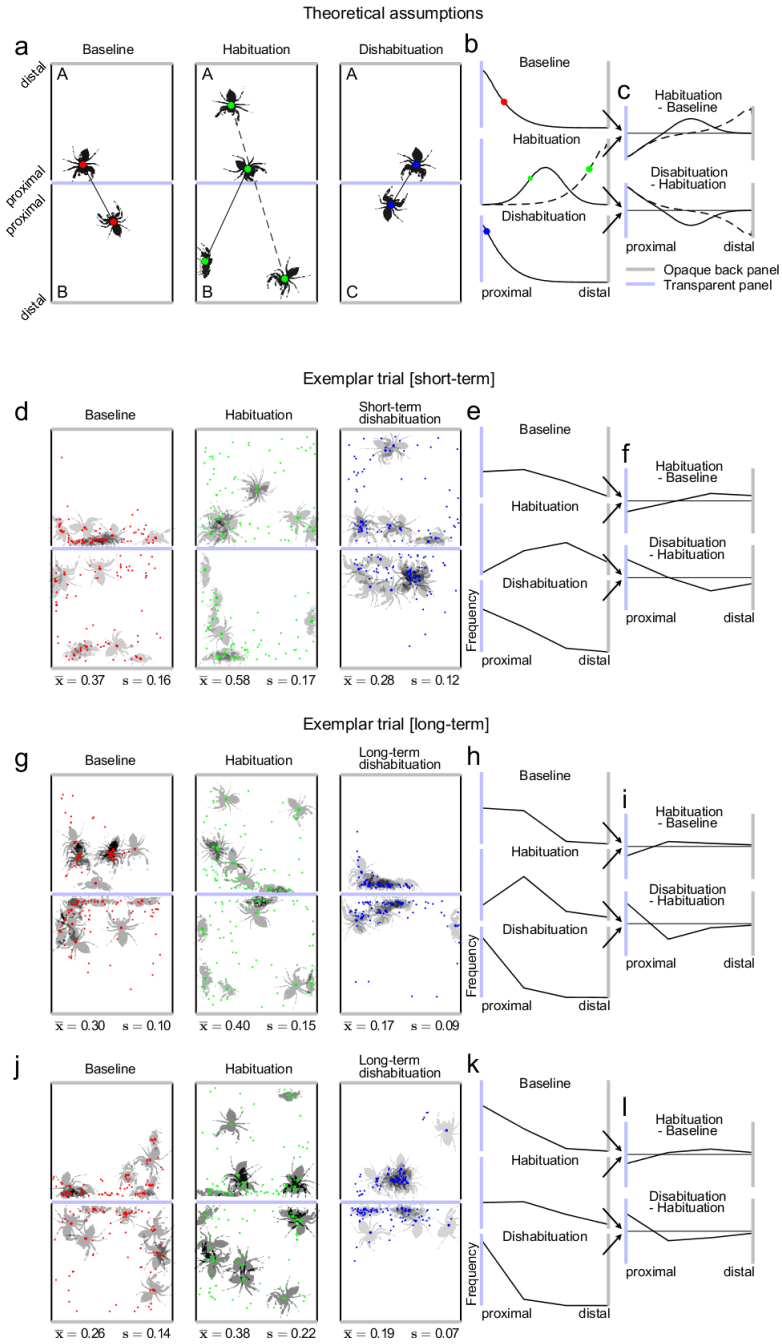

Figure caption 1: Theoretical assumptions and exemplar trials. a-c Predicted spider

distances for *baseline* (red dots), *habituation* (green dots) and *dishabituation* comparisons (blue dots). Habituation can manifest either in equal inter-spider distances (solid line) as in the *baseline* comparison or in an increase of distances (dashed line). What is referred to as *baseline* in this context is the *dishabituation* trial of the previous comparison (see Table 2). Distance samples are predicted to fall into distributions as shown in b. Contrasts between *baseline*, *habituation* and *dishabituation* comparisons would result in distributions as shown in c. d-f An exemplar trial consisting of *baseline*, *habituation* and *dishabituation* comparisons from the first session of trials is shown. The *short-term dishabituation* comparison shows a decrease of inter-spider distances, indicating increasing interest in a different individual than the previously perceived one (*habituation* comparison). g-i; j-l Two exemplar trials from the third session of Experiment 2 are shown, where a presentation of an individual novel and unseen across the three experimental sessions triggered a great rebound in interest (i,l, 'Dishabituation - habituation').

Figure 2

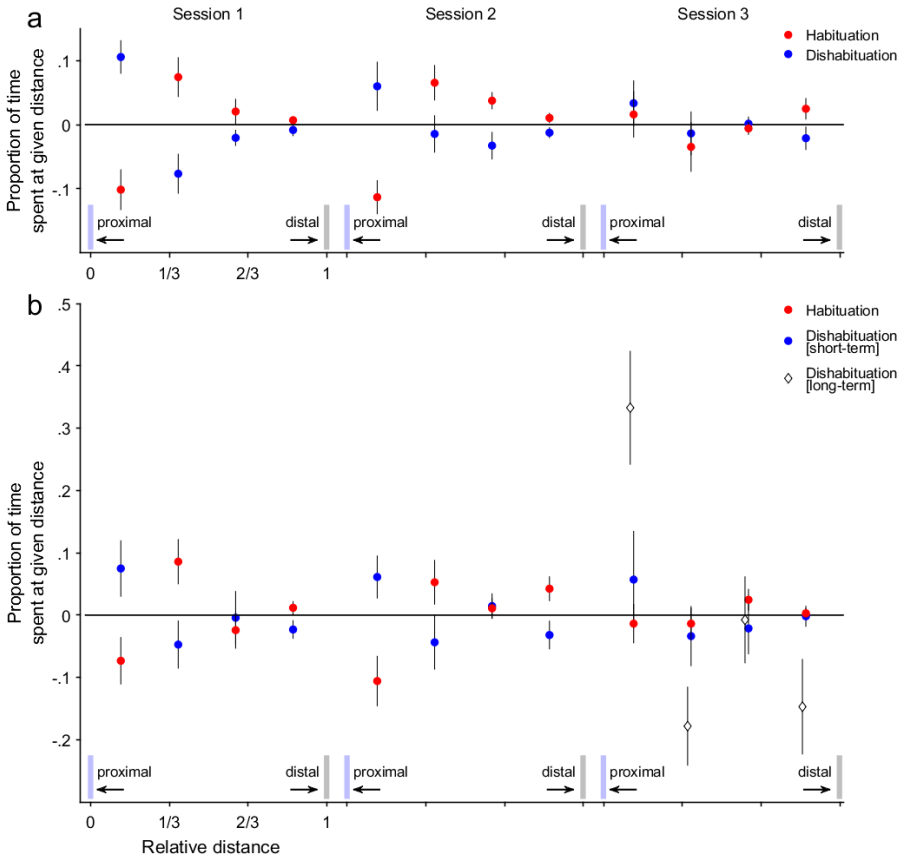

Figure caption 2: The relative change in distance between pairs of individuals, upon being confronted with the same individual as in the preceding trial (habituation trial; red discs) or a different individual from the individual in the preceding trial (dishabituation trial; blue discs). Each panel refers to an experiment (panel a. for Experiment 1; panel b. for Experiment 2), consisting of three sessions of trials. The dependent data is shown as the proportion of time spent at a given distance binned into 4 equally spaced bins. The x-axis labels refer to the proportional distances from the transparent acrylic sheet, ranging from 'proximal' to 'distal'; the y-axis refers to the proportion of time spent at a given distance, i.e. the relative number of samples that fall into a given bin. Discs show the mean proportion across all individuals (i.e. 20 for Experiment 1; 16 for Experiment 2). The whiskers indicate the standard errors of the mean. White diamonds in the lower right subfigure b show the long-term dishabituation trials. Light blue bars indicate the side of the transparent acrylic sheet (proximal); grey bars indicate the back wall of the

container (distal).