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1 **Olfactory and tactile cues can guide near-distance location of a refuge by whip spiders (Class**
2 **Arachnida, Order Amblypygi)**

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7 Whip spiders (Order Amblypygi) are arachnids with greatly elongated, antenniform first legs that serve
8 a sensory rather than locomotory function (Weygoldt, 2000). In their natural habitat, whip spiders
9 faithfully occupy home refuges, and if experimentally displaced from them, can navigate back (Beck &
10 Görke, 1974; Hebets, Gering, Bingman, & Wiegmann, 2014). If the tips of the antenniform legs (which
11 bear olfactory sensilla) are clipped off or coated in nail polish, experimentally displaced whip spiders
12 fail to return to their refuges (Beck & Görke, 1974; Bingman, Graving, Hebets, & Wiegmann, 2017;
13 Hebets, Aceves-Aparicio, et al., 2014). Thus, it has been proposed that olfactory cues guide the homing
14 behaviour of whip spiders (Beck & Görke, 1974; Bingman et al., 2017; Hebets, Aceves-Aparicio, et al.,
15 2014; Wiegmann et al., 2019). An element of this olfactory hypothesis has now been explicitly tested
16 by Wiegmann et al. (2019), which demonstrates the ability of whip spiders to learn and use olfactory
17 cues to locate a refuge in the laboratory, and that this ability is disrupted after the tips of the
18 antenniform legs are clipped.

19 In pursuit of this olfactory hypothesis the fact that whip spiders can also use tactile cues to
20 locate a home refuge in the laboratory (Santer & Hebets, 2009), and the possibility that these cues
21 might be important in the natural habitat, has been neglected. The tips of a whip spider's antenniform
22 legs are equipped with a range of sensillum types, including but not limited to, olfactory, contact
23 chemosensory, and mechanosensory hairs (Igelmund, 1987; Santer & Hebets, 2011). In field
24 experiments, clipping off the *ca.* 20 segments at the tips of the antenniform legs has been interpreted

25 as a primarily olfactory manipulation because it removes all olfactory sensilla whilst leaving some of
26 the other types present elsewhere (Bingman et al., 2017; Hebets, Aceves-Aparicio, et al., 2014).
27 Although the possibility of disruption to sensation in other modalities has been acknowledged
28 (Hebets, Aceves-Aparicio, et al., 2014), this interpretation overlooks the special importance of tactile
29 sensory structures at the antenniform leg tips. The antenniform legs of whip spiders are equipped
30 with an array of at least seven giant sensory afferents whose cell bodies are found within the distal
31 segments of the antenniform leg (Igelmund & Wendler, 1991a, 1991b; Santer & Hebets, 2011; Spence
32 & Hebets, 2006). Four of these giant neurons (GNs) have characterised mechanosensory functions and
33 receive inputs from known fields of mechanosensory sensilla at the antenniform leg tip. GN1 and GN2
34 each receive inputs from bristle sensilla in two overlapping fields that each includes some of the most
35 distal 20 segments of the antenniform leg (Igelmund & Wendler, 1991a, 1991b; Spence & Hebets,
36 2006). GN6 and GN7 are excited via a slit sensillum responding to movement at the articulation
37 between the 21st and 22nd segments of the antenniform leg tip (Igelmund & Wendler, 1991a; Spence
38 & Hebets, 2006). Furthermore, high-speed cinematography reveals that when examining surfaces,
39 whip spiders tap, press, and scrape the tips of their antenniform legs against the surface in a way that
40 might allow the spike trains of these four giant neurons to encode tactile information like shape and
41 texture (Santer & Hebets, 2009, 2011). There can be no doubt that clipping off or covering *ca.* 20
42 segments at the tips of the antenniform legs would disrupt tactile sensory input to these giant
43 neurons, and the former manipulation might damage or destroy the giant neurons themselves. Thus,
44 the disruption of tactile sensation might also contribute to the inability of whip spiders to locate their
45 home refuge after such an experimental manipulation. Most importantly, laboratory experiments
46 *have already shown* that whip spiders have the ability to learn texture cues and associate them with
47 a refuge (Santer & Hebets, 2009).

48 The motivation of this note is not to refute the findings of Wiegmann et al. (2019): that work
49 demonstrates that olfactory cues can be used by whip spiders to locate a refuge, and that clipping off
50 the tips of the antenniform legs disrupts that ability. However, this note does emphasise that there is

51 also physiological and behavioural evidence supporting the use of tactile cues in such near-distance
52 location of a refuge. In another extraordinary animal navigator, the desert ant *Cataglyphis*,
53 experiments show that visual (Collett, Dillmann, Giger, & Wehner, 1992), olfactory (Steck, Hansson, &
54 Knaden, 2009), and tactile cues (Seidl & Wehner, 2006), can all contribute to the accurate location of
55 the nest. Wiegmann and colleagues anticipate that whip spider navigation also relies on multimodal
56 sensory cues (Wiegmann, Hebets, Gronenberg, Graving, & Bingman, 2016), and in that multimodal
57 context the tactile sensing abilities of these fascinating animals should not be overlooked (c.f. Santer
58 & Hebets, 2009).

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