Interference in early dual-task learning by predatory mites

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Animals are commonly exposed to multiple environmental stimuli, but whether, and under which circumstances, they can attend to multiple stimuli in multitask learning challenges is elusive. Here, we assessed whether simultaneously occurring chemosensory stimuli interfere with each other in a dual-task learning challenge. We exposed predatory mites *Neoseiulus californicus* early in life to either only conspecifics (kin) or simultaneously conspecifics (kin) and food (thrips or pollen), to determine whether presence of food interferes with social familiarization and, vice versa, whether presence of conspecifics interferes with learning the cues of thrips. We found that *N. californicus* can become familiar with kin early in life and use kin recognition later in life to avoid kin cannibalism. However, when the juvenile predators were challenged by multiple stimuli associated with two different learning tasks, that is, when they grew up with conspecifics in the presence of food, they were no longer capable of social familiarization. In contrast, the presence of conspecifics did not compromise the predators' ability to learn the cues of thrips. Memory of experience with thrips allowed shorter attack latencies on thrips and increased oviposition by adult *N. californicus*. Proximately, the stimuli for learning the features of thrips were apparently more salient than those for learning to recognize kin. We argue that, ultimately, learning the cues of thrips at the expense of impeded social familiarization pays off because of negligible cannibalism risk in the presence of abundant food. Our study suggests that stimulus-driven prioritization of learning tasks is in line with the predictions of selective and limited attention theories, and provides a key example of interference in dual-task learning by an arthropod.

Learning is defined as experience-based change in behaviour and memory retention over time (Alcock, 2005; Dukas, 2008; Lincoln, Boxshall, & Clark, 1998), and an omnipresent phenomenon in animals including arthropods (Alloway, 1972; Papaj & Lewis, 1993; Smid & Vet, 2006). The ability to learn allows animals to adjust to changing environments and is largely assumed to have positive effects on evolutionary fitness (Papaj & Lewis, 1993). However, learning is only beneficial to fitness as long as the benefits outweigh the costs (Dukas, 1999; Stephens, 1991). Neuronal activity during learning, that is, collecting, processing and storing information, as well as recalling and connecting different bits of information, requires energy, which is traded off against energy needed for other activities and cognitive tasks. These trade-offs represent the costs of learning (Bernays, 1998; Dukas, 1999; Jaumann, Scudelari, & Naug, 2013; Laughlin, 2001). For example, Mery and Kawecki (2003, 2004, 2005) showed for the fruit fly *Drosophila melanogaster* that an improved learning ability may come at the expense of poorer competitive ability, reduced oviposition rate and shortened longevity, and Snell-Rood, Davidowitz, and Papaj (2011) observed that adult cabbage white butterflies, *Pieris rapae*, had lower oviposition rates when they had to learn to search for a rare host plant type than when they fed exclusively on the common type. Along with physiological trade-offs, learning may incur cognitive trade-offs. Cognitive trade-offs may be, but are not necessarily, linked to energetic deficits caused by energy-demanding learning (Jaumann et al., 2013) and are commonly due to processing limitations of the cognitive system and associated resources. Cognitive trade-offs are especially likely to occur when animals are challenged to simultaneously process multiple unimodal stimuli within the same or across different learning tasks (Cohen, Konkle, Rhee, Nakayama, & Alvarez, 2014; Duncan, Martens, & Ward, 1997).

Animals are usually exposed to multiple, simultaneously occurring stimuli rather than to single stimuli occurring in isolation. Exposure to multiple stimuli does not imply that the animals

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divide their attention equally among those stimuli; they may rather selectively pay more attention to one stimulus or learning task and neglect the others (Dukas, 2002, 2004; Johnston & Dark, 1986; Lavie, 2005; Wiederman & O'Carroll 2013; Van Swinderen, 2007). Since the perceptual and neuronal systems are limited, it is simply not possible to process every piece of information that is available at a given time. Focusing on one stimulus or task may improve learning, whereas dividing attention to different stimuli may compromise it (Dukas, 1999, 2002). Owing to the interrelated physiological and cognitive benefit–cost trade-offs of learning, animals should be selected to flexibly attend to, focus on and learn those stimuli that promise the highest fitness gains, and filter out information of lower relevance. Which stimuli are ultimately more important than others depends on the contexts, tasks and circumstances. Which stimuli prevail over others depends, proximately, also on the predisposition of the sensory system and the salience of the stimuli. Multiple simultaneously occurring stimuli may be associated with different sensory modalities, such as vision, audition, touch or chemosensation, or the same sensory modality. While exposure to, and integration of, multiple multimodal stimuli may lead to cross-modal facilitation of learning and enhancement of memory formation (see, for example, synergistic interactions between olfactory and visual stimuli in learning by *Drosophila* (Guo & Guo, 2005), or Higham and Hebets (2013) for the advantage of multimodal signals in animal communication), exposure to multiple unimodal stimuli may result in interference (Duncan et al., 1997; Cohen et al., 2014; but see Rubi and Stephens (2016) for no difference in learning of multi- and unimodal signals by blue jays, *Cyanocitta cristata*, in the context of communication). Interference among multiple unimodal stimuli (Duncan et al., 1997) may be due to limitation at the perceptual and/or neuronal levels (e.g. Cohen et al., 2014; Pashler & Johnston, 1998).

Interaction between multiple stimuli within the same learning task, such as overshadowing and blocking, is well known from classical conditioning (Mackintosh, 1971). Typical examples of interaction between multiple, simultaneously occurring stimuli across learning tasks are the effects of the presence of conspecifics on learning performance in foraging tasks. The mere presence of conspecifics has frequently been shown to profoundly affect individual learning, in both a negative way, due to distraction, and a positive way, due to social facilitation (Chabaud, Isabel, Kaiser, & Preat, 2009; Zajonc, 1965). For example, the presence of conspecifics may compromise food-learning performance in birds (Klopfer, 1958) but enhance it in sea snails *Aplysia fasciata* (Schwarz & Susswein, 1992). While the effects of the mere presence of conspecifics on foraging learning tasks are widely documented, we are not aware of any study that assessed whether the presence and learning of food cues affects social familiarization, that is, learning the features of conspecifics.

We assessed interference in early dual-task (social and foraging) learning by the predatory mite *Neoseiulus californicus* (Acari: Phytoseiidae). Most animals, including predatory mites, in their early life phases are highly sensitive to environmental stimuli. Experiences made in this phase may have profound and persistent consequences for developmental and behavioural trajectories (e.g. Strodl & Schausberger, 2012, 2013). Phytoseiid mites develop through five life stages (egg, larva, protonymph, deutonymph, adult), are eyeless and primarily use chemo- and mechanosensory modalities (Sabelis & Dicke, 1985). Recent studies revealed that phytoseiid mites, such as *Phytoseiulus persimilis, Amblyseius swirskii* and *N. californicus*, are especially well able to learn chemosensory cues as larvae and early protonymphs, and able to retain memory through several moulting events into adulthood. Early learning of chemosensory cues occurs in social (*P. persimilis*: Schausberger & Croft, 2001; Schausberger, 2007; Rahmani, Hoffmann, Walzer, &

Schausberger, 2009; Strodl & Schausberger, 2012, 2013), foraging (*N. californicus*: Schausberger, Walzer, Hoffmann, & Rahmani, 2010; *A. swirskii*: Christiansen, Szin, & Schausberger, 2016) and intraguild predation (*P. persimilis, Amblyseius andersoni, N. californicus*: Walzer & Schausberger, 2011) contexts. Learning in social contexts is especially relevant for predatory mites living, at least temporarily, in groups, which are mostly species adapted to exploit patchily distributed spider mites as prey. The focal animal of our study, *N. californicus,* is a generalist predator with a ranked diet preference for spider mites (Castagnoli et al., 2003; Croft, Monetti, & Pratt, 1998; McMurtry & Croft, 1997). The patchy distribution of the spider mites may result in clumped distribution of the predators, allowing frequent mutual encounters among conspecifics but also entailing the risk of cannibalism (Schausberger, 2003). Such conditions promote the evolution of kin recognition abilities (e.g. Fellowes, 1998).

To enhance survival in times of food scarcity and/or to eliminate conspecific competitors, most predatory mites, including *N. californicus*, engage in cannibalism (Walzer & Schausberger, 1999; Schausberger & Croft, 2000; Farazmand, Fathipour, & Kamali, 2014; for review see Schausberger, 2003). Cannibalism is a widespread phenomenon in both vertebrates and invertebrates (Elgar & Crespi, 1992; Fox, 1975) and occurs primarily, or intensifies, when other food is unavailable or of low quality and/or rare (Schausberger, 2003). When both conspecific and heterospecific predatory mites are present, many generalist predatory mite species, including *N. californicus,* use species recognition abilities to preferentially feed on heterospecifics (Schausberger, 2003). Regarding conspecific prey, due to the risk of inclusive fitness loss (Hamilton, 1964), potential cannibals are expected to avoid kin cannibalism when they have other diet options. This has, for example, been shown for *P. persimilis*, which is more strongly adapted to spider mite prey, and which exhibits a stronger tendency to aggregate and live in groups than *N. californicus* (Schausberger, 2007; Strodl & Schausberger, 2012, 2013). In general, kin recognition can be based on contextual cues, recognition alleles and/or prior learning of the features of kin (Mateo, 2004). Among these principal perceptual mechanisms, recognition alleles are extremely rare, presumably because of green beard effects (Dawkins, 1976), whereas kin recognition based on prior learning of the features of kin is most widespread (Mateo, 2004). Accordingly, also in predatory mites such as *P. persimilis, Phytoseiulus macropilis* and *Iphiseius degenerans,* kin recognition, allowing avoidance of kin cannibalism, is learned and primarily based on prior association (Faraji, Janssen, van Rijn, & Sabelis, 2000; Schausberger & Croft, 2001; Schausberger, 2007). Commonly, juvenile predators become familiar with each other early in life, by direct contact, and later remember and recognize familiar individuals (Schausberger, 2007). *Neoseiulus californicus* has not yet been tested for kin recognition but, like other predatory mites, has a highly sensitive phase early in life, in the facultative-feeding larval stage (Schausberger & Croft, 1999), allowing imprinting on prey: exposure to thrips, which are difficult to grasp, early in life improves foraging on this prey later in life, by shortening attack latencies and increasing predation rates (Schausberger & Peneder, 2017; Schausberger et al., 2010). Depending on food availability, ovipositing *N. californicus* females aggregate or disperse their eggs, with the emerging juvenile mites growing up in the same or different sites (McMurtry & Croft, 1997; Schausberger, 2003; Walzer & Schausberger, 2011). It is not known whether young *N. californicus* are also able to learn in social contexts and, if so, whether the stimuli for learning to recognize particular conspecifics such as kin and those for learning the features of prey interfere with each other. Addressing these questions should at the proximate level provide information about the mites' ability to set