J Insect Behav (2019) 32:290–305
https://doi.org/10.1007/s10905-019-09735-8

Visually Guided Search Behavior during Walking in Insects with Different Habitat Utilization Strategies

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Received: 28 August 2019 / Revised: 1 November 2019 / Accepted: 13 November 2019 /

Abstract This review examines visually guided search behavior during walking in different species and developmental stages of insects having contrasting habitat utilization strategies. The discussion focuses on mantises, short-horned grasshoppers and crickets. Although generally short-horned grasshoppers are travelers, whereas mantises are ambush predators, all of these insects exhibit visually guided behavior during walking in the search for food sites and shelter. In crickets, which are central place foragers, visually guided behavior during walking is also important for nest site homing. Despite differences in habitat utilization, these three insect groups all use searches incorporating intermittent locomotion, where the distances traveled and duration of pauses have a distinct functional significance. However, there are also locomotion pattern variations, such as loops, zigzags, spiral patterns and straight lines. Search strategies during walking include searches with and without visual landmarks. The detection and recognition of stationary visual landmarks is based on self-induced retinal image displacement, with differing underlying neuronal mechanisms in the three insect groups. If a visual landmark is identified as a suitable target, a direct approach is elicited under either open- or closed-loop conditions, depending on the situation. In the presence of more than one suitable target object, the behavioral response can be temporarily restricted to stimuli associated with a particular area of the visual field, while information from other areas of the visual field is suppressed. The review concludes that there are gaps in knowledge concerning the various questions and thus further research is needed.

Keywords Insects · visual landmarks · intermittent walking · visual detection · visually guided approach · visual attention

Introduction

In insects, as in other animals, the underlying drivers of search behavior are hunger, the need for protection, and reproduction. Often searching must be conducted by walking. Observations of walking insects in the natural environment could lead to a superficial impression that their locomotion is random and aimless rather than directed and controlled. However, detailed consideration of the movement patterns in terms of space and time, and of the interaction between the insect and the environment, taking into account visual cues, can lead to valuable insights regarding visual search behavior algorithms. These could also be generally valid for animal orientation in the search for targets with the aid of visual cues. Variability in walking during visual searches in environments that are dynamic and fluctuating rather than constant can also provide valuable information in terms of behavioral ecology (Wehner 1981; Bell 1990; Hein et al. 2016; Knaden and Graham 2016).

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This review considers the search behavior during walking of various species of Mantodea and Orthoptera, also taking into account findings for species of other insect orders. As can be seen from the literature cited below, despite significant differences in the way of life of mantises, as sedentary ambush predators with powerful forelegs; short-horned grasshoppers, as herbivorous travelers with powerful hind legs; and crickets, as central place foragers that must find their way back to the nest; these insects all share the necessity of searching for resources during walking with the aid of visual cues. Likewise, all have compound eyes of the apposition type with an extensive field of view of almost up to 360° in the horizontal plane, but with differing adaptations in terms of spatial visual acuity, overlap of the visual fields, contrast sensitivity, and sensitivity to polarized light (Rossel 1979; Land 1997; Horridge 2005; Blum and Labhart 2000; Sakura et al. 2003). Search processes can therefore be expected to be governed by basic visual principles, but with details differing among the various species.

The following questions are examined in this review: 1) Special attention is paid to nest site homing and the search for targets that indicate shelter and food sources in an environment with or without landmarks as visual cues. 2) Emphasis is placed on locomotion patterns and their control, taking into account the special case of homing crickets, where visual experience and memory may also be an important element of visual searching. 3) The mechanisms responsible for the successful detection and localization of visual landmarks as targets are considered, together with the selective approach to visual targets. In this connection the critical role of visual attention processes is briefly discussed. 4) A separate section examines whether and how insects are affected by multiple target objects in the visual field, and how confusion is prevented to ensure efficient decision-making.

Search Behavior with and without Visual Landmarks

Mantises are primarily diurnal and have large forward-directed compound eyes with high acuity (Horridge and Duelli 1979; Rossel 1979). If mantises emerge from their oothecae at an exposed site, they must immediately search for dense vegetation such as grass or bushes as protection against potential predators. However, over the course of their lives it is also necessary for mantises, as sedentary ambush predators, to avoid any unnecessary movement so as not to attract the attention of predators or potential prey. Despite this necessity, mantises must often leave sheltered environments and travel to new areas to reduce the population density, find sufficient resources, and escape cannibalistic behavior which can arise in the absence of alternative food sources. In such situations, mantises must often traverse open terrain. In field studies, Battiston and Fontana (2010) found that in open natural habitats *Mantis religiosa* adult males can travel about 18 m/week and females about 8 m/week. Since no food is ingested during walking, the range of searching must be balanced with the energy reserves, and effective search strategies are required.

In *Mantis religiosa*, early nymphs behave very differently from adult males and females in searching for shelter. This has been observed (but without video recordings) in experimental studies in the laboratory (Kral 2014). When placed individually in the middle of a white homogeneous cylindrical arena (D: 100 cm), early nymphs spontaneously began walking in patterns of circles and loops of increasing size around the starting point, with integrated zigzag components. This behavior is innate, since it takes place immediately after emergence, and thus without previous experience and the opportunity of using learning or memory. Similar searching locomotion in spirals or loops when external stimulation is absent or not perceptible has also been observed in walking Colorado potato beetles searching for host plants (Visser 1988; see also Lönnendonker and Scharstein 1991). According to these authors, such idiothetic navigation may be due to proprioceptive and stored information being insufficient to permit a straight walking course. Searching via locomotion in spirals or loops has also been found in other walking insects engaged in homing. In an unfamiliar environment, leaf-cutting ants exhibit an innate preference for turning counter-clockwise when visual cues are absent (Endlein and Sitti 2018). When, despite path integration (see below), homing desert ants do not arrive exactly at the nest entrance, they perform a systematic search via locomotion in spiral loop patterns. In the process they can occasionally return to the starting point of the search to begin searching again with other loops (Wehner and Srinivasan 1981; Müller and Wehner 1994). Homing desert isopods (Crustacea) usually successfully find their sheltered burrows via visual landmarks, but in the absence of these can also use intrinsically controlled patterns of locomotion. When displaced from the burrow by an experimenter to a distance where the entrance is entirely undetectable, the isopod begins searching in spiral patterns and then in loops of increasing size with superimposed meanders, resulting in a successful return to the burrow (Hoffmann 1983, 1985). These examples show that the search behavior is not based simply on random Brownian-type locomotion with the risk of frequent passage across regions visited before. The zigzag components observed in the circular locomotion of early mantis nymphs during walking may reflect path control which is utilized due to the difficulty of navigating without landmarks. Desert ants have been described as turning with equal frequency to the right and to the left when returning directly to the nest, thus reducing the overall directional bias (Müller and Wehner 1988). However, it is not clear what internal factors trigger zigzag locomotion in the absence of outside influences. Finally, the above-mentioned examples in the literature suggest that in the case of early mantis nymphs, walking in circles of increasing diameter without external cues is based on an intrinsically structured search pattern. Apart from this mechanistic explanation, for early mantis nymphs walking in expanding circles can also be interpreted as reflecting an increase in search effort. Walking in circles or loops of increasing size enhances the probability of reaching surroundings with visual cues to indicate hiding places. It should be noted that a pattern of increasing circles or loops also prevents returning to already visited sites.

In contrast to early nymphs, after initial turning movements around a starting point, adult mantises travel more or less in a straight line (Kral 2014). This straightforward locomotion allows the large adult mantises to reduce the risk of predation by leaving exposed locations quickly. Experiments with a relatively small arena (D: 100 cm) did not permit investigation of how far adult mantises can or will walk in a straight line. It can be assumed that mantises, like other animals, cannot continue walking on a straight course over a long distance without the aid of external cues. In this regard, recent video recordings of spontaneously walking pre-adult mantis *Hierodula membranacea* females indicate that without any external cues, locomotion continues more or less on a straight course for approximately 90 cm, ending with a pause. However, in all cases, walking began to drift either to the left or to the right before the pause (see Fig. 1) (K. Kral, unpublished preliminary results). It is suggested that during idiothetic directed walking, variability in the descending neural drive results in deviations from straight line locomotion, followed by a drift toward random walking with seemingly indeterminable variability in turning maneuvers (see Cheung et al. 2007, 2008). On the other hand, deviations from straight line locomotion could hinder reaching suitable targets. However, as discussed below, walking is usually not continuous and constant over long distances, but rather is intermittent with stops and pauses ranging from milliseconds to minutes, which permit the resetting of straight line locomotion, or a change of direction for the next period of locomotion (Fig. 1). In addition, occasional periods of immobility during pauses can also reduce the likelihood of detection by predators.

Short-horned grasshoppers are terrestrial herbivores with well-developed compound eyes (Burtt and Catton 1969; Wilson et al. 1978). They usually jump or fly only if they are disturbed or are trying to escape exposed or dangerous situations. Grasshoppers normally use walking for locomotion, even if able to fly. An exception is migratory behavior in swarms over long distances, as in desert locusts in the gregarious phase. When fresh host plants are scarce or entirely lacking, grasshoppers must search for suitable new food sources, usually first in the immediate vicinity so as to save energy. Searching is also required in the case of negative changes in the habitat such as a loss of suitable oviposition sites. During searching, in fragmented habitats grasshoppers must often travel on the ground over relatively long distances. For example, flightless *Chorthippus pullus* grasshoppers can travel more than 40 m per day when living on sandbanks by mountain streams. Here there are areas covered with open vegetation as well as sand without any vegetation. Because this habitat can be associated with unstable living conditions, e.g. due to flooding (Schwarz-Waubke 1998), efficient search behavior is often necessary in order to locate suitable resources.

In open areas which lack suitable visual cues, grasshoppers can perform distinct intermittent search behavior. Bazazi et al. (2012) found that in a homogeneous experimental arena with minimal external cues, the individual search behavior of final stage nymphs of the desert locust *Schistocerca gregaria* is complex and adaptable. Between periods of locomotion are pauses which serve different functions depending upon their duration. For example, short periods of locomotion with long pauses were found to indicate local search

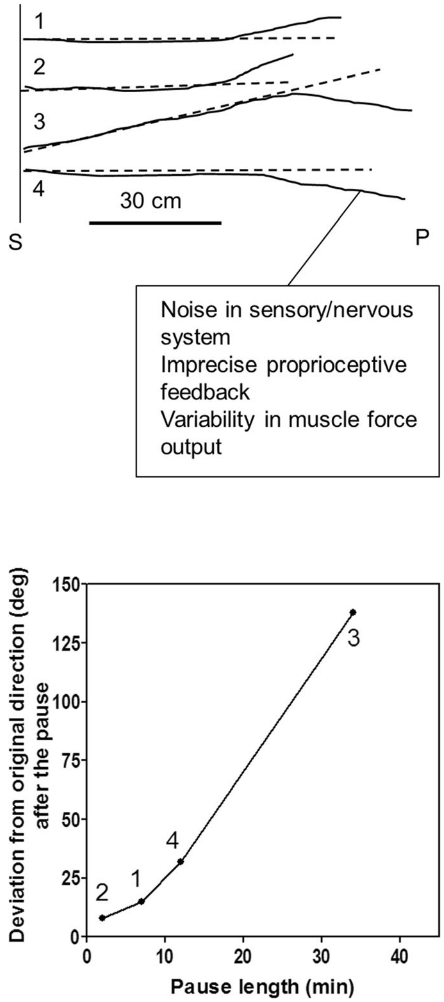


Fig. 1 Spontaneous walking on a straight course in the absence of external cues in praying mantis. In the top diagram, note the drift either to the left or to the right before the pause (P). Deviation from a straight course is caused by internal factors not yet fully understood; possible factors are suggested in the insert. Navigation via menotaxis can be excluded. For further details, see text. Four pre-adult females of the giant Asian mantis *Hierodula membranacea* (with body size between 78 and 80 mm) were released individually (without any external stimulus) in the middle of a circular arena (D: 300 cm) with a white homogeneous floor and wall. S indicates the starting point. The bottom diagram shows the relationship between the pause length and the degree of deviation from the original direction after the pause. Direction changes during pauses do not occur all at once, but in small steps

behavior, with visual scanning of the surroundings by means of head and body turns. Longer pauses are associated with a greater probability of turning movements during the pauses and changes of direction after the pauses (see Fig. 2). Relatively long pauses of up to an hour can be followed by a complete change in the direction of locomotion. In contrast, in extended locomotion with short pauses, the pauses can be used for visual relocation (without scanning). It is also postulated by Bazazi et al. (2012) that the shortest pauses (without turning movements) serve as resting periods for energy recovery. Since external cues were minimized in the experiments, it is suggested that the search behavior was governed mainly by internal factors, with the variable duration of pauses during intermittent locomotion being attributable to biochemical, physiological and neurobiological factors determined by the internal state of the insect. However, there is a lack of precise data with regard to the role of internal factors; more information could contribute to a better understanding of insect motor reactions to the environment. In this context, findings on nymphs of *Locusta migratoria migratorioides* may be mentioned which show that periods of light and darkness influence internal drivers for intermittent walking (Moorhouse et al. 1978).

Crickets have well-developed compound eyes (Sakura et al. 2003; see also below). They also exhibit distinct intermittent walking (e.g. Lambin 1984). However, visual search behavior occurs under different circumstances than is the case with mantises and short-horned grasshoppers. As central place foragers, crickets require the ability to return to the burrow after searching for resources such as food or mates, especially if the burrow is used permanently, or if there are no alternatives in the vicinity. In this situation, rapid direct homing can be critical for avoiding predators or bad weather. It is also necessary for the entrance of the burrow to be localized. Beugnon and Campan (1989) found that most of the *Gryllus campestris* field crickets observed were able to return directly to the burrow via self-generated navigation when the sky was blue. However, in most cases they were unable to do so under overcast skies. Nevertheless, even a small patch of blue sky visible among the clouds or through dense vegetation was found to be sufficient for navigation, in conditions with a low degree of polarization or low light intensity. Behavioral observations in the field, polarotactic responses under controlled experimental conditions, and the presence of a polarization-sensitive dorsal rim area (DRA) in the compound eyes and polarization-sensitive (POL) neurons in the optic lobe (Brunner and Labhart 1987; Herzmann and Labhart 1989; Henze and Labhart 2007) suggest that in crickets polarized light of the blue sky is used for path integration. This means that crickets may be able to navigate via the electric vector (e-vector)

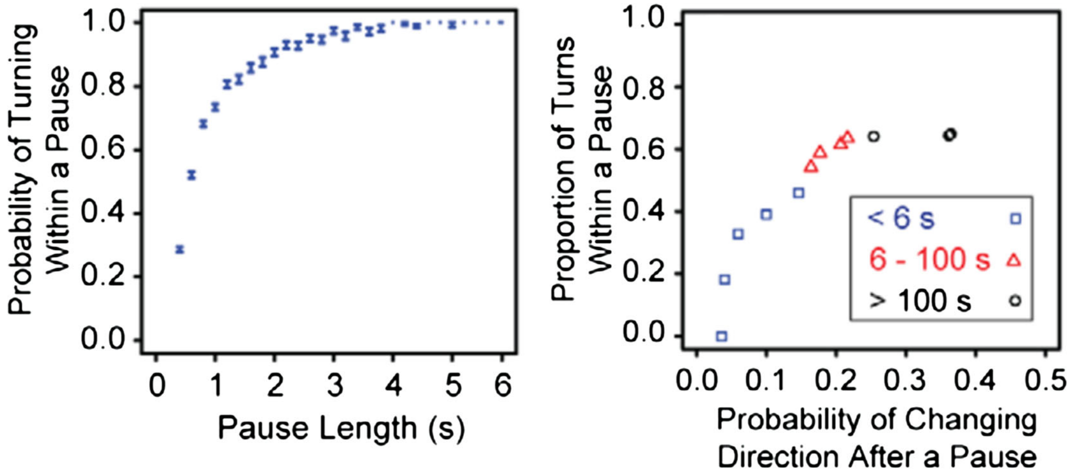


Fig. 2 **Intermittent walking in locusts.** Nymphs of *Schistocerca gregaria* were tested by Bazazi et al. (2012). Left: Mean probability of turning during a pause, for different pause lengths. Right: Relationship between the mean proportion of turns during a pause and the probability of changing direction after a pause, for pause lengths of <6 s (squares), between 6 s and 100 s (triangles) and > 100 s (circles). For more detail, see text. Diagrams reprinted from Bazazi et al. 2012, with kind permission

of linearly polarized light and to calculate distance by monitoring leg movements (e.g., the number of steps) or optical flow (i.e., the rate at which visual information moves across the retina). The neural basis for path integration may be associated with the central complex with four neuropils in the protocerebrum, which processes visual information from the dorsal rim area (DRA) (Wittlinger et al. 2006; Collett et al. 2013; Heinze 2014). It may be mentioned in this context that a similar DRA is also found in species of other orthopteran families, such as short-horned grasshoppers (Labhart and Meyer 1999). This also applies to POL neurons (Vitzthum et al. 2002). In the desert locust *Schistocerca gregaria* there is evidence that sun-derived celestial cues can be involved in maintaining the direction of walking (Homberg 2015); however, the purpose of this walking behavior remains unclear.

In addition to path integration, visual landmarks can also play an important role in the search strategy of homing crickets. This search strategy is evident in wingless Australian raspy crickets (which produce raspy sounds as a defense mechanism). The juveniles are associated with a particular burrow from an early age (Hale 2000) and thus have a well-defined home range with familiar landmarks. Although juveniles and adults typically forage at night and return to the burrow each morning, due to the high visual sensitivity of the compound eyes, visual landmarks may be used even under dim light conditions. This is also supported by the fact that landmarks can present a relatively high contrast against the brighter night sky (Warrant and Dacke 2016). However, Hale and Bailey (2004) found that in a simple two-choice maze, juvenile raspy crickets can use spatial cues as well as spatial landmarks to return to the burrow. Here it should also be noted that the use of sensorimotor routine memory independent of landmark identification was also found in tropical ants living in environments overloaded with landmarks (Macquart et al. 2008).

Visual landmarks also provide important cues for final localization of the burrow. This is shown by the fact that if there are several burrows in the immediate vicinity, homing raspy crickets are able to distinguish their own burrow from the burrows of conspecifics (Hale 2000). Particularly noteworthy in this regard are experimental studies of *G. bimaculatus* by Wessnitzer et al. (2008). In controlled laboratory experiments, these authors investigated the search behavior of adult females in a circular arena with a floor that was hot except for a cool spot on the floor which provided a target for escape from a hostile environment. [This is analogous to the Morris water maze, a paradigm for spatial memory testing in rodents (Morris 1984)]. In initial experiments, the target was either visible, invisible but marked by simple artificial visual cues (e.g., a black T shape, or horizontal and vertical stripes) on the wall, or invisible with no visual cues marked on the wall. In subsequent experiments with a larger arena (with a diameter of 40 cm rather than 30 cm), the cool spot was always invisible, with four visual cue conditions: simple black and white shapes on the arena wall; a detailed natural scene on the wall, as a complex visual cue; a wall with no visual cues, as a control; and a completely dark arena without visual cues. In the experiments with simple black and white shapes on the arena wall, it was observed that when the crickets stopped anywhere in the arena, they fixated on each of the distinct visual cues and then moved quite directly to the target. In the experiments with a natural scene on the wall, it was observed that this was the most helpful condition for finding the hidden target. Over the course of several trials, the crickets located the target approximately 60% to 70% more quickly. It was found that improvement in homing times was greater and learning was more consistent in the case of the natural scene. From the results of these experiments, Wessnitzer et al. (2008) suggest that adult females are capable of using surrounding visual landmarks to locate their nests, even if the nests themselves are hidden. Since the crickets were able to approach the hidden target location from various directions, the results suggest that memory of visual landmarks without internal spatial representation is sufficient. Thus, it seems that the crickets simply home in on a salient landmark near the hidden target, rather than learning the spatial layout of the various landmarks surrounding the target location. The crickets' knowledge of the target environment was found to improve with repeated searches (see also Doria et al. 2019). However, in similar arena experiments with cool spots and hot surroundings, recent studies of female Australian black crickets *Teleogryllus commodus* did not indicate spatial learning over successive trials (Anderson and Kasumovic 2017). These authors suggest that this discrepancy may be due to various rearing conditions, to the lack of ecological relevance of the experiment to female *T. commodus* fitness, or to other unknown factors. It should also be kept in mind that the two cricket species have different lifestyles, and that *T. commodus* has burrow and non-burrow strategies (Evans 2016).

On the other hand, as a result of homing from different directions, crickets may store multiple snapshots of burrow site landmarks from various geometric locations in their spatial memory. In the case of image matching, if a returning cricket noticed a deviation between the current view and the memorized retinotopic representation of the landmark constellation around the burrow, it could move to minimize the deviation in order to find the burrow. If the landmarks could barely be distinguished from the background, the cricket could use cues such as relative motion between the landmark and background, as has been suggested in the case of honey bees (Dittmar et al. 2010; see also Fauria and Campan 1998,"dynamic image matching"). It must be kept in mind, however, that in fast-flying bees and wasps, movement velocities and amplitudes are significantly greater than is the case for crickets walking or running on the ground. Therefore, image matching could be expected to be more accurate for bees and wasps, with a larger visual range (Goulet et al. 1981). It should be pointed out that image matching and the brain regions involved in visual memory have been studied much more extensively in the social Hymenoptera (Cartwright and Collett 1983; Collett et al. 2013) than in crickets. Thus, it is still unclear whether image matching is in fact used by crickets. For an overview of possible orientation aids for successful homing in crickets, see Table 1.

Estimation of the Position and Range of Visual Landmarks

As described above, the frequency of pauses increases when walking insects perform active searching. In addition, the duration and speed of locomotion decreases

Table 1 Overview of possible mechanisms for nest site homing and localization in crickets

Spatial orientation mechanisms	Prerequisites
Path integration[1]	Odometry for range estimation, for example using leg movements and optic flow, and use of the electric polarization vector (e-vector) of linearly polarized light of the blue sky as an external compass
Alignment retinal image matching	Memory of visual landmarks along the path, and internal spatial representation of the landmarks
Positional retinal image matching	Memory of visual landmarks at the nest site, and internal representation of the spatial constellation of landmarks
Use of landmarks simply as visual cues[2]	Repeated learning of visual landmarks at the nest site as seen from different directions; no internal representation of the spatial constellation of landmarks is necessary

[1] Henze and Labhart 2007

[2] Wessnitzer et al. 2008; for more details, see text

while the length of pauses increases. During pauses, insects keep their surroundings in a large area of the visual field (with a wide attention angle) to avoid overlooking important targets. If target objects are not easy to detect, for example, in a complex visual environment with target and non-target items of similar appearance, the duration of pauses increases because more time is required for target detection and recognition. The detection and recognition of an object as a behaviorally significant landmark necessitates an effective visual response, which means that the insect must then focus on a narrow visual attention angle (see Kramer and McLaughlin 2001; Dukas 2002).

In arena experiments it has been found that in mantises, short-horned grasshoppers and crickets, as soon as objects become visible as salient landmarks, turning toward these targets follows immediately. It is well known that luminance contrasts of vertically oriented structures, detected via vertical contrast detectors in the nervous system, serve as a strong stimulus for mantises and orthopterans (Wallace 1959; Rowell 1967; Goulet et al. 1981; Horridge 1986; Jeanrot et al. 1981; Bailey and Harris 1991; Kral and Poteser 1997; Hyden and Kral 2005). Vertical structures are frequently utilized as landmarks during orientation behavior. Although the information content of landmarks is simplified by the nervous system, they can indicate relevant resources such as hiding, resting, and feeding sites that occur, for instance, in dense high grass. In various *Melanoplus* species, Mulkern (1969) found that if a particular vertical structure is not well suited for one of these purposes, the grasshopper will leave it and orient itself toward another one. However, in a sparsely covered area where no other vertical target is available, the grasshopper will again begin to execute searching movements.

In mantises, it has been shown that when the head and prothorax are turned toward the target, the body is more upright, the prothorax is raised, and the abdomen is lifted off the ground. The forelegs are often raised and bent (Kral 2012, 2014). Such distinctive behavior appears to indicate increased visual attention directed toward the vertical structure (see below). This alert upright posture can also be observed in mantises in other situations associated with increased attention, such as prey detection, and deimatic display (Maldonado 1970; Cleal and Prete 1996). In this connection it should be noted that in mantises the reaction distance for vertically oriented black rods was found to be similar in early nymphs and adults, despite the much lower performance of the nymphs in terms of spatial vision. However, this is the case only if the contrast of the rods is not too low. According to Dukas (2002), this result can be explained by the phenomenon that objects with a more cryptic appearance give rise to increased attention, which leads to improved visual perception. This means that for these insects, visual attention is crucial for detection, recognition and focusing on target objects. In *Drosophila* fruit flies it has been found that an important internal factor associated with attention and decision making in active visual search behavior is the influence of the catecholamine transmitter dopamine (DA). Increased DA signaling results in enhanced reactions of visual neurons to stimuli, associated with increased coupling between optic lobes and the central brain, and increased motor activity resulting in hyperactivity (Hills 2006; Nityananda 2016; van Swinderen 2007; Yamamoto and Seto 2014; Koenig et al. 2016).

Target-related turning and fixation are often followed by side-to-side peering movements in the horizontal plane in both mantises and short-horned grasshoppers (Collett 1978; Sobel 1990; Kral and Poteser 1997; Kral 1999). First the walking legs on one side are extended while those on the other side are flexed and *vice versa*. In this way, the walking legs generally remain fixed in place during peering (Fig. 3). During the side-to-side peering movements, due to compensatory counter-rotation of the head about the yaw axis, the field of view remains directed straight forward and is thus oriented toward the contrast boundary of the target object. In this way, the peering movement consists of a translational motion component, which means that the horizontal displacement of the object image on the retina is inversely proportional to the distance of the object. The polyneuronal innervated musculature on each side of the neck is responsible for these versatile and accurately controlled head movements. Experiments of the author's research group have shown that mantises are able to judge the distance range of stationary objects by keeping the peering amplitude and peering velocity relatively constant (see e.g. Kral 1999). In the case of preparing for actions (such as jumping) relative to single objects in the visual field, the peering movement is adjusted by increasing the amplitude in relation to object distance to a saturation value. This permits accurate absolute distance estimation, if data from the visual system can be used in conjunction with past experience to achieve successful visually aided behavior, such as aimed jumps (Walcher and Kral 1994; Kral and Poteser

1997). The binocular ommatidia of both compound eyes take part in this evaluation process. Here the fronto-medial area (cf. fovea) of the compound eyes, which constitutes the region with the greatest acuity of vision, represents an important reference system (see also Rossel 1979, 1980). If the visually acute region is destroyed by photo-degeneration with sulfo-rhodamines, mantises lose the ability to estimate absolute distances (Walcher and Kral 1994). The neuronal control of image displacement on the retina is based on a motion-detecting mechanism which is sensitive to speed, rather than to the magnitude of image displacement in the frontal part of the visual field. Srinivasan et al. (1991) were able to show in tunnel experiments on a flying bee (the "centering response") that image speed is largely independent of image contrast and spatial frequency content. With reference to the autocorrelation model of Hassenstein and Reichardt (1956) and its later modifications, Higgins (2004) argues via a computational model that at an early stage of visual motion processing (in the lamina and medulla), non-directional rather than directional motion sensors may be the basis of speed sensitivity. Motion-sensitive neurons that respond independently to stimulus direction may in fact be present in the locust medulla (Osorio 1991). In higher visual pathways, distinct lobula giant movement detectors (LGMD) are found to be non-directional and motion-sensitive (Rind 1987; Bult and Mastebroek 1994; see also Berger 1985). Egelhaaf and Borst (1989) showed that the motion response of lobula plate tangential neurons can exhibit contrast saturation. Such contrast saturation would also have to be accommodated in the non-directional motion model by Higgins (2004) in order for responses to be speed dependent. In mantises, another important factor is that for the absolute estimation of object distance, the speed of retinal image displacement alone is not sufficient; proprioceptive feedback from the hair plate sensilla on both sides of the neck is also involved (Fig. 3). The speed of the head movement also appears to be related to the proprioceptive input. More detailed information about the peering behavior and underlying distance estimation mechanism in mantises is provided in Poteser and Kral (1995), Poteser et al. (1998), Kral and Poteser (2009), Kral (2012).

In 1959, Wallace found that in locusts, peering movements are used for visual range estimation. Later experimental studies with the aid of video recording techniques have confirmed these findings and provided more insight into the mechanisms involved (Collett 1978; Eriksson 1980; Horridge 1986; Sobel 1990; Collett and Paterson 1991). However, the peering mechanism of grasshoppers differs from that of mantises (Table 2). Because the eyes of grasshoppers are oriented more toward the side, the lateral visual field is involved to a greater extent in the control of lateral peering movements than is the case in mantises, where hair plate sensilla on each side of the neck serve as proprioceptors that measure dynamic and static head positions relative to the prothorax, in the horizontal plane (Collett 1978; Liske 1989; Poteser et al. 1998). In grasshoppers, retinal image displacement is kept as small as possible in the lateral visual field, to ensure linear head movements. It should also be mentioned that in grasshoppers often unilateral as well as bilateral peering movements can be observed (Kral 2008a). Here absolute range estimation via retinal image displacement is based on a monocular mechanism. This means that information obtained from a single eye is sufficient for a grasshopper to determine the direction and distance of a jump (Kral 2008b). This does not support the hypothesis that motion parallax signals from the left and right eye may be summed (see Sobel 1990).

In crickets, no distinct peering movements, as found in mantises and short-horned grasshoppers, are observable. Due to the difference in body structure, this behavior is not possible in crickets. However, Goulet et al. (1981) and Lambin (1984) suggest that in the wood cricket *Nemobius sylvestris*, the amplitude of translatory components of head or body oscillations is sufficient to elicit motion parallax cues suitable for obtaining spatial information about stationary objects. The speed or amplitude of target image displacement may be used for the estimation of relative distances, whereas a comparison of information obtained from both eyes is necessary for absolute distance determination.

Visually Guided Approach to Landmarks

If an object is identified as a suitable target, usually an approach is triggered. In mantises it has been shown that, with few exceptions, such an approach is not continuous (Kral 2014). As in the case of searching, during the approach locomotion is interrupted by pauses that are either motionless or are associated with target-related turning movements and saccades of the head in the horizontal plane, without turning of the entire body.

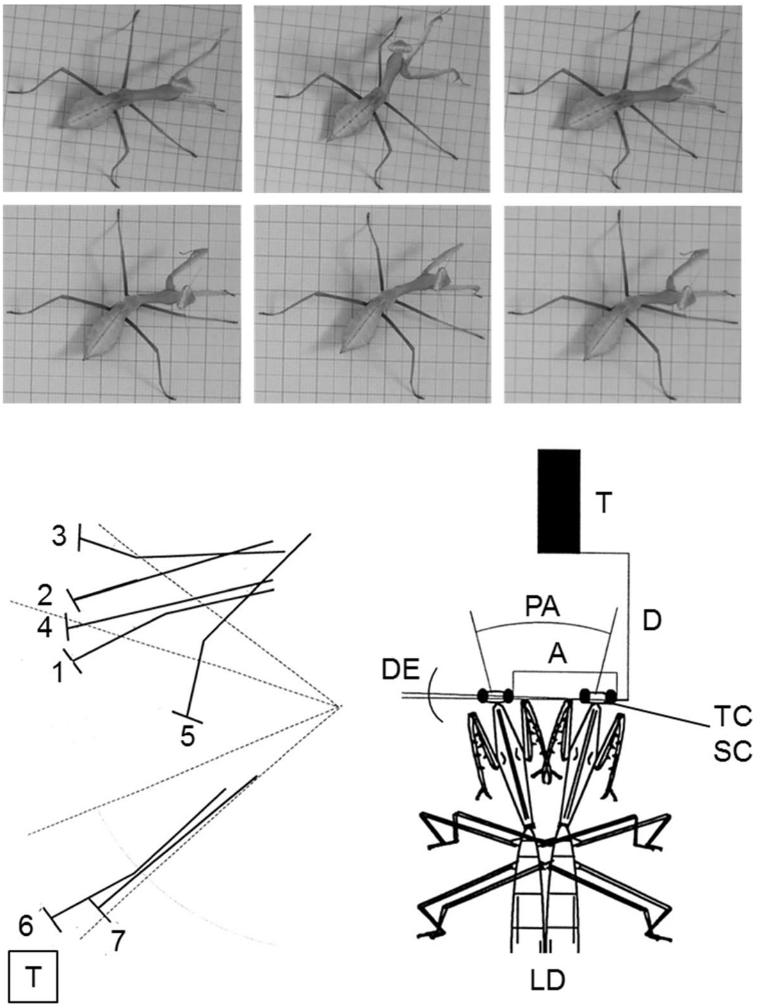


Fig. 3 Visual scanning in praying mantis. Top: Six images from a short video sequence of a *Hierodula membranacea* nymph. The scanning movements are initially directed toward unstructured space. Then, following a head turn to the right, peering movements are directed toward a vertical black object at a distance of approximately 15 cm. Bottom: Schematic drawings of peering movements of a *Polyspilota* sp. nymph. Bottom left: Peering movements are combined with locomotor movements. The lines indicate the angle of the medio-sagittal axis of the head and the longitudinal axes of the thorax and abdomen relative to one another, in seven steps during the search for target (T). Note that during scanning (1–5) the movement amplitude is larger than is the case when the insect is heading toward the target (6,7; see also above). This means that once a target object has been identified, scanning changes to object-related peering. Bottom right: T, target object; D, distance to the target object; PA, peering angle; A, amplitude of peering movement; DE, displacement error of compensatory turning of the head about the yaw axis; TC, tergo-cervical hair plate sensilla; SC, sterno-cervical hair plate sensilla; LD, lateral body displacement. (Drawings by M. Poteser). For further details, see text

Forward-and-backward rocking movements can also be involved. Whereas motionless pauses provide brief periods for stabilizing the visual field, turning and rocking movements permit fixation of the target object. The target is brought into the binocular visual field of both compound eyes, and peering can then be used to control positioning relative to the target. Pauses are also important for the reactivation of visual attention. The question arises as to what triggers the pauses between periods of locomotion. It appears that these pauses are controlled not only by the internal state of the insect but also by visual information. Particularly in early nymphs, there is often a positive correlation between the target contrast (stimulus strength) and the distance traveled between pauses. *Mantis religiosa* mantises travel more directly, with fewer pauses, the closer they get to the target

Table 2 Similarities and differences in mantis and short-horned grasshopper peering behavior for range estimation

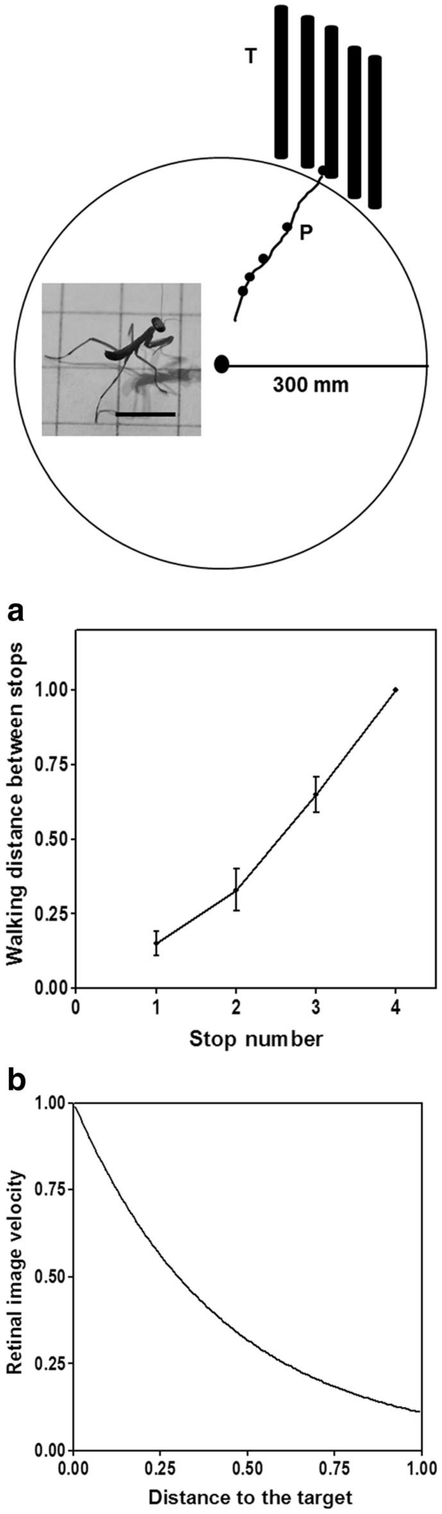
	Mantises[1]	Short-horned grasshoppers[2]
Peering movements	Bilateral	Unilateral/bilateral
Control of translatory horizontal component of peering movements	Feedback from frontal eye region (binocular ommatidia)	Feedback from lateral eye region
Control of amplitude of peering movements	Feedback from frontal eye region	Feedback from frontal eye region
Peering stimulus	Image speed	Image speed
Peering mechanism	Binocular	Monocular
Neuronal processing of image speed	Direction-independent speed-detecting mechanism	Direction-independent speed-detecting mechanism

[1] Walcher and Kral 1994; Poteser and Kral 1995; Poteser et al. 1998

[2] Collett 1978; Eriksson 1980; Kral 2008b; for more details, see text

(Fig. 4). This can be explained by the fact that with decreasing distance from the target, the available spatial information based on the velocity of retinal image motion becomes more accurate and reliable (Fig. 4b). This occurs sooner with adults than with juveniles, due to the better visual performance of the adults (Kral 2014; see also Köck et al. 1993; Figs. 2 and 3 in Kral and Poteser 2009). However, further experiments and analyses are required to gain more insight into this issue.

Target-oriented locomotion with intermittent pauses during walking has also been described for other insects, such as desert locusts, black bean aphids, and *Drosophila* larvae, where, in addition to stop-and-go movement patterns, alternating fast and slow movement phases can be observed (Mashanova et al. 2009; Bazazi et al. 2012; Gepner et al. 2015). The examples described indicate that the approach to targets is comprised of discrete behavioral steps: those which are undertaken "blindly", and those which involve high visual attention and decision-making. These steps occur consecutively, similarly to the way robots may be programmed. However, as mentioned above, in some cases mantises walk directly to the target object. Under high-contrast conditions, adult males have



◀ **Fig. 4 Approach to vertical black rods in early nymphs of *Mantis religiosa* under closed-loop control.** The number of pauses tends to decrease, the closer the nymphs get to the target. In the top diagram, dots represent pauses (stops), and P shows the location of a pause with target-related turning and peering movements for navigational control. Scale bar: 5 mm. The results are plotted in the middle diagram (**a**) (mean ± SD, $N = 5$). The bottom diagram (**b**) shows the relationship between the velocity of retinal image motion of the target object (due to translational peering movements of constant velocity within the distance range) and the target object distance, determined by the mean peering parameters (K. Kral, unpublished data). For further details, see text

even been observed jumping to the target object, with safe landing on a rod (Kral 2014). (Only adult males were tested in this regard, since adult females were too heavy to execute such a jump.) During jumping, mantises approach a target with an absence of sensory feedback for continuous updating of the direction of movement. Such an approach strategy is naturally much faster than an intermittent approach and could be beneficial for a quick escape. Continuous walking without pauses could be based on scototaxis (movement toward darkness), an innate behavioral response intermediate between negative phototaxis and the response to contrasting object edges (Bui Huy and Campan 1982). In an approach using scototaxis, a mantis would simply walk toward the darkest region within the visual field of its compound eyes. In doing so, straight forward movement would be mediated by stimulation of the lateral regions of the compound eyes. Similarly, Horn and Fischer (1979) have shown that when the fly *Calliphora erythrocephala* walks toward a target of black lines and stripes, a fixation-sensitive area of the compound eye located outside the binocular visual field plays an important role. Thus, a single eye can be sufficient in this case. When blinding of the lateral part of the compound eyes permitted only the frontal part of the eyes, associated with the binocular visual field, to be used, no preferred direction could be observed. Similar scototactic behavior has been described for walking crickets (Goulet et al. 1981; see also Atkins et al. 1987). When crickets focused on a black target, they fixated the image of one edge of the target in a region of the retina located at 10° to 25° laterally from the sagittal plane (Lambin 1984). In this context, it is of interest to mention that walking flies *Lucilia cuprina* fixate the edge (not the center) of a vertical bar as they approach it (Osorio et al. 1990). The fact that the edge of the target object is more attractive than the center can be explained by lateral inhibition. Under bright lighting conditions, lateral inhibition makes the edges appear darker than the center (i.e., via the Mach bands effect). Furthermore, the fixation is not frontal but slightly lateral, resulting in a spiral approach trajectory toward the edge of the target object. The results suggest that the approach of walking insects to stationary objects involves an interplay between edge fixation and scototaxis in early vision (Osorio et al. 1990). Finally, it should be mentioned that when grasshoppers are presented with a pattern of black stripes, scototactic behavior as well as phototactic behavior can be displayed. Edge fixation and edge-related peering are executed before landing at the center of a black stripe or at the center of a bright area between black stripes (Fig. 5) (Kral 2008a). It is possible that these alternative approach strategies represent a compromise between the need for shelter, and the need for a site that is open enough to permit freedom of movement.

In summary, in mantises the approach to a target object can be slow or fast. A slow strategy can be used for approaches where sensory information can help the insect to localize target objects exactly, even within an extended range. This permits distance-dependent changes of perception of the object (as perception improves with decreasing distance from the object) and the consideration of unforeseen obstacles on the path. It also aids in object detection and in the correction of false object identification at an early stage. Such an approach requires closed-loop coordination between the motor actions and sensory perception. In contrast, in the case of jumps or fast locomotion (e.g., running) toward a target object, open-loop conditions prevail. This means that following perception and decision-making regarding the direction of movement, the approach is “blind”. Such an approach is useful if rapid action is essential, as in urgent seeking of protection. This behavior is not based on detailed information concerning the features of the target object.

Is Switching between Targets Possible during a Visually Guided Approach?

What happens when during an approach to one target, other possible targets in the same or different categories appear in the visual field? Can the insect switch its attention between target objects? For example, can a new stimulus suppress the old one, directing the

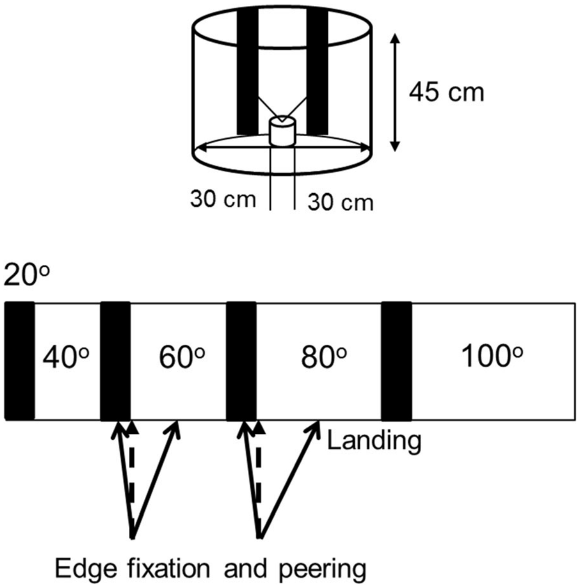


Fig. 5 Vertical stripe pattern used as jump target in short-horned grasshoppers (*Chorthippus brunneus, C. parallelus, Miramella alpina*). Top: Diagram of experimental arena, showing how the horizontal visual angles of the vertical stripes and spaces are measured in relation to the starting point at the center of the small circular platform. Bottom: Four vertical black stripes with different spacing between them. Broken arrows indicate the direction of fixation and peering toward the contrast boundary; solid arrows show the direction of jumping toward and landing at the center of black stripe or white space. A significant majority of landings occurred in the 60° and 80° white spaces. For these jumps the grasshoppers could view one black stripe frontally, with an additional black stripe to the left and right in the lateral visual field. However, this could mean that the distance between adjacent contrast boundaries is a critical factor in the selection of visual structures as jump targets. Redrawn according to Kral (2008a)

attention of the insect to a more up-to-date target? Is the visual system able to process data concerning multiple targets in the visual field at the same time? Or do limitations on visual processing in the brain make it impossible to recognize multiple targets? However, apart from a few initial approaches, these questions are largely unanswered in the case of mantises and orthopterans. Pinter (1979) studied the lateral inhibition of information from different parts of the visual field in desert locusts by investigating responses of the descending contralateral movement detector (DCMD) to small target movements. This mechanism may ensure that only signals from a distinct part of the visual field undergo neural processing, for motor control of the search behavior. Insight into attention switching between targets has been provided by various experiments on flies (Sareen et al. 2011; Koenig et al. 2016). A tethered *Drosophila* fruit fly was attached to a torque meter in the middle of a moveable circular arena that had dark vertical stripes on the wall. When two vertical stripes moving in opposite directions were presented to the fly at symmetrical positions to the left and right, the fly responded only to the stripe that was previously cued. The fly thus behaved as if only one of the two stripes was displaced. These authors hypothesize that this is due to inhibition of the central pattern generators (CPGs), neural networks for right and left turns. Thus, the CPG which is triggered first suppresses the other one. Insects are clearly able to restrict their behavioral responses temporarily to stimuli associated with a particular location in the visual field, while information from other locations is suppressed. During searches for particular targets by visual scanning of the surroundings via turning movements, this mechanism can prevent distractions by other stimuli. The paper by Wiederman and O'Carroll (2013) should also be mentioned in this context. It shows that a binocular neuron in the dragonfly visual pathway is associated with selective attention relative to two targets. Thus, as soon as the response has been locked onto one target, the other target has absolutely no influence on the response of the neuron. It is also apparent, however, that a response focused on a single target can be disrupted by the motion of an optically large structure, which can evoke optomotoric reactions (Liske and Mohren 1984; Kirszenblat et al. 2018). The reason for this could be that different kinds of stimuli (wide-field and small-field) are processed independently in different parts of the brain (Fenk et al. 2014).

Conclusions

A central question of the present review is whether, despite significantly different lifestyles (sedentary, traveling, and central place foraging), walking insects use similar strategies for visual searching, detection and recognition of landmarks, and approaching landmarks as targets. In general, this question can be answered in the affirmative, particularly with regard to intermittent locomotion, which seems to be a widespread strategy in insects as well as in other animals. However, there are also adaptive differences that depend upon the habitat utilization strategy, stage of development, and type of environment. In an environment where no visual cues are present, locomotion and pauses are triggered by internal factors. Differences between early nymphs and adult mantises in the use of spiral, zigzag and straight line walking locomotion patterns during searches in an environment without visual landmarks must be emphasized. Here the question arises as to whether these differences may be attributable to the post-embryonic development of proprioceptive and motor systems. In the case of crickets, behavioral observations and the ability of homing crickets to utilize polarized light vision suggest that they may perform path integration. However, it is not clear whether crickets can combine polarization cues and local landmark cues for navigation, or whether there could be potential conflicts between these information sources. Experimental studies seem to indicate that in homing crickets the memory of visual landmarks surrounding the burrow is sufficient, and that internal spatial representation of these landmarks is not necessary. Nevertheless, there are some contradictory findings. With regard to the spatial localization of visual landmarks, it should be noted that species of all three insect groups are attracted to vertically oriented contrast boundaries in their visual environment during walking. Here a form of visual attention plays an important role in guiding perception. Mantises and grasshoppers determine both relative and absolute distances based on the velocity of retinal image displacement arising from translational peering movements. The velocity of image displacement depends upon the distance of the object from the insect; however, different types of underlying neural processing are involved, which still require further clarification. The approach to a visual target that is the focus of attention can be associated with closed- or open-loop conditions, depending upon the situation. A key role is also played by the ability to focus on a single distinct target object, even if other similar objects are present in the current field of view.

Directions for Future Research

It is hoped that this review will stimulate further experimental studies of visually guided search behavior in other insect species with differing visual performance and different needs for visually guided behavior during walking under a variety of ecological conditions. For example, it could be investigated whether search behavior for a food, shelter or nest site displaced by the experimenter differs across various insect species and developmental stages. In this context, an important question would be to explore whether walking insects generally use leg movements for the purpose of odometry, or whether some may use other cues, such as energy consumption or optic flow. New insights in this regard could also provide an approach for investigating the little understood mechanisms of intermittent walking behavior in the search for visual targets.

Acknowledgments I would like to thank Mary Ansell for correction of the English and valuable comments. I also thank Drs. Sepideh Bazazi and Iain D. Couzin for kind permission to use Fig. 2d,e published in PLoS Comput Bio 8, e1002498 (2012).

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