Virtual-Reality Techniques Resolve the Visual Cues Used by Fruit Flies to Evaluate Object Distances

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Summary

Insects can estimate distance or time-to-contact of surrounding objects from locomotion-induced changes in their retinal position and/or size [1–8]. Freely walking fruit flies (*Drosophila melanogaster*) use the received mixture of different distance cues to select the nearest objects for subsequent visits [9, 10]. Conventional methods of behavioral analysis fail to elucidate the underlying data extraction. Here we demonstrate first comprehensive solutions of this problem by substituting *virtual* for *real* objects; a tracker-controlled 360° panorama converts a fruit fly's changing coordinates into object illusions that require the perception of specific cues to appear at preselected distances up to infinity. An application reveals the following: (1) en-route sampling of retinal-image changes accounts for distance discrimination within a surprising range of at least 8–80 body lengths (20–200 mm). Stereopsis and peering are not involved. (2) Distance from image translation in the expected direction (motion parallax) outweighs distance from image expansion, which accounts for impact-avoiding flight reactions to looming objects. (3) The ability to discriminate distances is robust to artificially delayed updating of image translation. Fruit flies appear to interrelate self-motion and its visual feedback within a surprisingly long time window of about 2 s. The comparative distance inspection practiced in the small fruit fly deserves utilization in self-moving robots.

Results and Discussion

To investigate a fly's preference for near objects under virtual conditions, we allowed it to walk on a cross-shaped platform surrounded by light-emitting pixels on a cylindrical screen (Figure 1). Continuous tracking of its position marks the vertex of a solid angle, under which a given virtual object is made to appear when the currently subtending pixels are darkened. The actual

distance of the object's imaginary position before or behind the screen must be derived from locomotion-dependent "parallax" cues, i.e., image translation during motion at right angles to the object, or "looming" cues, i.e., image expansion/contraction during approach/retreat along this direction. Locomotion-independent "stereoscopic" or "peering" cues for the distance of a virtual object originate exclusively from the actual site of object generation on the screen. Such cues would fail to convey information about virtual distances, even if the screen were within the supposedly narrow range of locomotion-independent distance discrimination. Our experiments offered repeated choices between four bar-shaped objects in front of the four arms of the platform. Seen from the center, the objects were identical in their size and shape. A fly's preference for near objects can be expressed by the relative frequency of attempted visits. Expression of preference in the present experiments requires comparative distance valuation.

Equivalence of real and virtual distances was deduced from repeated choices between two real objects (black cardboard bars) displayed in opposite quadrants at a radial distance d_0 from the center and two virtual objects simulated to appear in the remaining quadrants at a selected distance d_-, d_0 or d_+ (Figure 2). The preference for virtual test objects P should approximate the maximum-rejection limit of its range from -1 to $+1$ if a walking fly locates these objects on the pattern-generating screen at about $4\times$ the distance d_0 of the real reference objects. However, *Drosophila* perceives simulated distances; the virtual test objects were preferred (P > 0) if they were nearer to the center than the reference objects ($d_- < d_0$) and were avoided (P < 0) if they were farther than the reference objects ($d_+ > d_0$). The preference for the test objects vanished completely (P ≈ 0) if they were simulated to appear at the distance d_0 of the reference objects. This exemplifies with surprising accuracy the identical valuation of real and virtual distances in the present experiments. The results confirm the conjecture that locomotion-dependent cues sampled en route are necessary and sufficient for far-field reconnaissance of distances in a stationary environment.

Allocation of distances under virtual conditions revealed a surprising phenomenon (Figure 3). En-route processing of distance cues suggests an ongoing comparison of self motion with the simultaneously evoked changes in the retinal image of the surrounding objects. The continuous updating of the strongly preferred nearest objects on the virtual screen trailed the fly's locomotion on the platform by only about 0.04 s (filled square). Yet an artificially increased delay up to about 2 s proved to be tolerable for distance reconnaissance (filled circles); the flies interrelate, in a still unknown manner, self motion and the resulting visual feedback within an unexpectedly generous time window. The ongoing search for a convincing interpretation of this result justifies an aside on the basic statistics of locomotion in freely walking fruit flies; the time course of delay tolerance resembles, presumably by chance, the time course

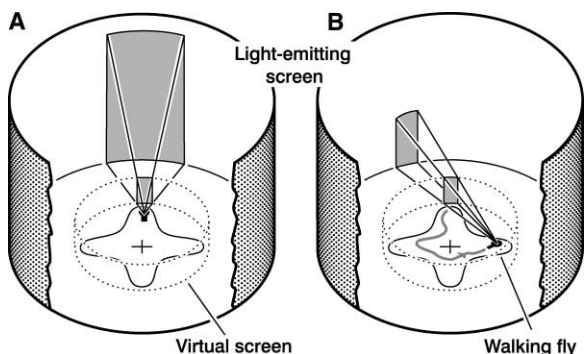[4]Correspondence: schustef@uni-freiburg.de

Figure 1. Visualization of a Virtual Object

Light-emitting pixels of a computer-controlled panorama screen convey the retinal image of an arbitrarily selected virtual object to the walking fly on a central platform. Shortened wings and a water-filled moat prevent its escape. (A and B) Visualization of a dark bar at an intended virtual distance from the center; a pixel is switched off whenever its connecting line to the walking fly intersects the object to be simulated. The height of the light-emitting screen determined the almost-constant vertical elevation ($48° \pm 4°$) of the bars shown to a fly in the present experiments. Simultaneous updating of the horizontal angular width (size) and position (azimuth) on a virtual screen with two identical bars took on average 0.04 s. For comparison, the fly's quickest steps last about 0.06 s. Virtual objects allow the dissection and manipulation of distance cues.

of the correlation function describing the most probable decrease in persistence, or predictability, of previously observed walking directions (Figure 3B, gray line; data from [11]; see Experimental Procedures). This function was derived from trajectories of random walking in an artificial environment without visual or tactile guidance. So far, a causal connection between the time window of delay tolerance and the average persistence time of a straight course cannot be entirely ruled out; mutual adaptation of the time constants would allow a walking
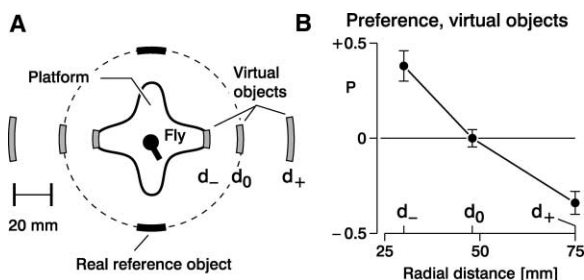

Figure 2. Preferences in a Choice between Real and Virtual Objects of Apparently Identical Size and Shape

(A) A top view of the platform and the surrounding objects indicates the actual position of two *real* bars (dark arcs) at a distance of 48 mm from the center and, simulated on the light-emitting screen at 200 mm distance (not shown), the position of two *virtual* bars (shaded arcs) at a selected distance of 30 mm (d_-), 48 mm (d_0), or 75 mm (d_+).
(B) The preferences P (mean $\pm$ standard errors) for the virtual test objects were obtained from N = 20 flies by evaluating n = 600 automatically recorded runs into one of the four arms of the platform. *Drosophila* preferred nearest objects without regard to their real or virtual nature. Equivalence of real and virtual distances was deduced from the lack of preference for the test objects programmed to simulate the distance d_0 of the reference objects.
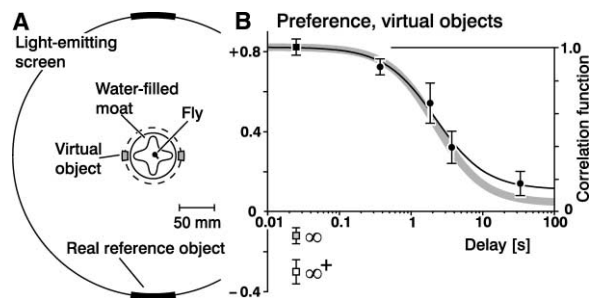

Figure 3. Tolerance of Artificial Delay in the Actualization of Virtual Objects

(A) Choice between apparently identical pairs of real bars (dark arcs) on the screen at 200 mm distance and virtual bars (shaded arcs) at 40 mm distance from the center. A 5:1 ratio of the distances was selected to intensify the preference for the near objects.
(B) Generation of the virtual test objects delayed their locomotion-induced visual feedback by about 0.04 s (filled and open squares; N = 22, n = 1194). This delay was artificially extended by the insertion of a programmable time shift into the feedback loop. The fly's strong preference P for nearest objects proved to be surprisingly delay resistant (filled circles; N = 34, n = 1316). The effect of increasing delay time on the preference P happens to resemble the effect of increasing interval time on the persistence of orientation. The latter was derived from random walks without guiding cues by correlation of walking directions at the beginning and the end of numerous intervals [11] (gray line and right ordinate). The hitherto stationary center of the virtual cylinder with its two simulated bars could be programmed either to follow the walking fly and thus to block self-induced image translation or to follow a 2-fold magnification of the fly's actual trace at twice its speed and thus to invert the self-induced image translation. Accordingly, the bars were expected to appear either at an infinite distance (∞) or at a "more-than-infinite" distance (∞^+). In both instances, the virtual bars were rated to be farther away than the real bars at a distance of 200 mm. Their rejection (preference P $<$ 0) suggests an amazing range of distance reconnaissance and, in contrast to results for peering locusts [5], a direction-sensitive evaluation of self-induced visual feedback.

fly to estimate distances of objects from translatory displacements of their retinal image that are not seriously contaminated by the rotatory components received during a deviation from a straight course [6, 7].

Neglect of looming cues in the present choice experiments was established by experimental dissection of the visual feedback into its looming-induced and parallax-induced components (Figure 4). Increasingly delayed updating of the angular width (size), the angular position (azimuth), or both simultaneously distinguished the virtual test objects from the otherwise indistinguishable virtual reference objects shown to a walking fly. The conspicuous delay-induced avoidance of the test objects identifies the azimuth, not the size, as the preference-determining feedback component; the flies ignore the looming cues received under these conditions. This is not necessarily the case if the upper limit of the cues' delay tolerance ranks in the range below the update time of a virtual screen (0–0.04 s) or above the highest delay tested in the experiment of Figure 4 (9 s to ∞). However, the first condition is incompatible with the well-established equivalence of real and virtual distances in Figure 2 and can be dismissed. The same holds for the second condition, which applies to an increasingly negligible remainder of the initial preference
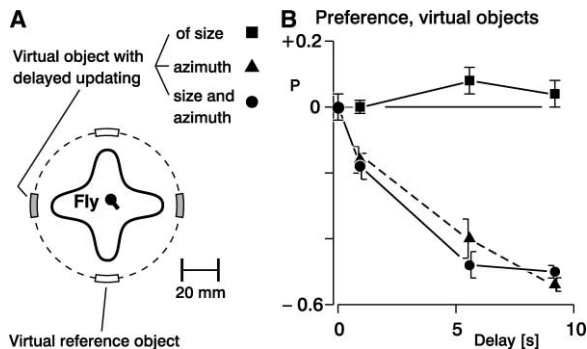
Figure 4. Separating the Contributions of Parallax and Looming Cues during Distance Reconnaissance

(A) Choice between two apparently identical pairs of virtual bars at 40 mm distance from the center. The delay of about 0.08 s in the updating of both the test objects (shaded arcs) and the reference objects (open arcs) was selectively extended for the test objects by a programmable time shift in the updating of angular width (size), angular position (azimuth), or both simultaneously.

(B) The preference P for the test objects decreases with increasing delay in the updating of their azimuth, not their size (N = 45, n = 4200). Intact parallax cues seem to be necessary and sufficient for the selection of nearest stationary objects; *Drosophila* could, but did not, utilize the otherwise indispensable looming cues received in the present experiments.

after its delay-induced decline, shown in Figure 3. This disqualifies looming as a relevant input for ambulatory distance reconnaissance, at least in experiments in which parallax cues are still available. Two facts suggest a context-specific neglect of "distance from looming". (i) The perceived width of the objects in Figure 4A varies between 10° at the most distal and 60° at the most proximal viewpoint on the platform. A fraction of this expansion already suffices to elicit landing responses during fixed flight [12] or orientation saccades during free flight [13]. Comparison of the average walking speed (22 mm/s; [14]) of fruit flies on the platform and the speed of expansion required to elicit these effects convinced us that the results in Figure 4B cannot be explained by a complete lack of appropriate looming cues. (ii) Deprived of feedback from motion parallax, the walking flies clearly preferred virtual objects expanding on approach over virtual objects expanding on retreat (P = 0.52 ± 0.06; N = 10, n = 200; $p < 0.001$; [15]). This requires the perception of looming cues and their utilization as a substitute for the missing parallax cues in walking fruit flies.

Distance reconnaissance beyond 200 mm was inferred from the avoidance of infinitely remote virtual test objects in favor of apparently identical reference objects at a 200 mm distance on the screen (∞ in Figure 3B; $p < 0.05$). The walking flies must have derived the distance of the reference objects en route from the backward-directed image translation (negative feedback), which decreases with increasing distance of the objects. Forward-directed image translation (positive feedback) is not encountered under natural conditions. Locusts, therefore, get all of the required information solely by estimating the distance of a target from the direction-independent magnitude of the feedback induced by their peering head movements [5]. This does not seem

to hold for fruit flies. Repeating the choice experiment in Figure 3A with artificially reversed feedback ought to have confirmed the strong preference for the nearest objects (filled square; P ≈ +0.8). The unforeseen rejection of these objects suggests an association of positive feedback with distances "beyond infinity" (∞⁺ in Figure 3B; $p < 0.001$). However, alternative explanations deserve to be discussed. Direction-dependent evaluation of image translation might be used to distinguish self-moving organisms from stationary objects, but it is still too early for a conclusive interpretation of these results. The time-tested principles of spatial guidance in *Drosophila* are not expected to be unique. Comparative distance inspection in walking ladybirds has been thoroughly investigated under both closed-loop and open-loop conditions in amazingly simple contrivances [3]. Their preference for near objects selected en route by backward-directed image motion within their visual field points to essential similarities of distance perception in remote insect orders.

The visual faculties of a fruit fly with only 0.001g body weight are restricted by the smallness of a visual system that simultaneously images 85% of the environment onto about 1400 retinal units: the presumed 200 mm range of distance reconnaissance on the ground (and its extrapolated increase by about one order of magnitude in the air) requires a sophisticated solution to get along with comparatively few retinal units. This solution has to support not only continuous surveillance of the surroundings but also selection, pursuit and inspection of nearest objects, avoidance of just-visited objects, and omission of objects beyond the range of distance perception [9]. The instrumentation of comparable solutions in automotive robots might benefit from the dissection of biological abilities with the new method described in the present account.

Experimental Procedures

Flight-disabled females of *Drosophila* wild-type "Berlin" were prepared at age 2–3 days by removal of 2/3 of the wings under cold anesthesia (4°C) and were tested 12 hr later after receiving water but no food. The position and orientation of a fly on a crossshaped platform (radial contour undulation 15–29 mm) were derived by a PC-based fly tracker from the signals of a red-sensitive CCD-camera above the platform (resolution 1/10 body length or 0.25 mm, refresh rate 20 Hz). A computer controlled the individual on/off state of the 5760 light-emitting diodes (LED's) of a surrounding panorama screen matched to the flies' resolving power [16]; the radius was 200 mm, the height was 224 mm, the contrast was 0.94, luminance was 60 cd/m², the spectral peak was at 565 nm, and frame rate > 1 kHz. The temporal limit for continuous updating of two virtual objects consists of a variable access time to the camera (on average 1/2 × 0.05 s) plus a fixed processing time (about 0.015 s). The crossshaped platform [9] supports forced choices between four dark bars on a yellow-green background. Seen from the center, the bars were identical in their subjective width (18°) and height (48°). The criterion for a valid choice was a departure of a test fly from a position 0–9 mm from the center toward the far end of the selected arm, and subsequent arrival within 120 s at its boundary at 22–29 mm distance. Automatic evaluation of a set of 20 valid choices between two test bars and two reference bars returned both the fly's choice frequency 0 ≤ r ≤ 1 and the corresponding preference P = 2r − 1 for the test bars. The graphs show preferences of N flies (mean ± standard error) on a scale between maximum rejection (P = −1) and selection (P = +1). The two pairs of bars were exchanged between successive sets to prevent hypothetical choice

reinforcement by olfactory traces. The correlation function in Figure 3B is based on time series of velocity vectors, each representing the actual orientation and speed of a walking fly. The comparatively low variability of walking speed in the present context justifies their interpretation as orientation vectors. The correlation of any two vectors is shown as a normalized function of their temporal separation [11]. The depicted function was derived from 23 series, sampled at a rate of 5 Hz during 40 s of unimpeded and uninterrupted random walking in a homogeneously illuminated featureless arena (diameter = 0.6 m).

Acknowledgments

References

1. Wallace, G.K. (1959). Visual scanning in the desert locust *Schistocerca gregaria* Forskål. J. Exp. Biol. *36*, 512–525.
2. Collett, T.S., and Harkness, L.I.K. (1982). Depth vision in animals. In Analysis of Visual Behavior, D.J. Ingle, M.A. Goodale, and R.J.W. Mansfield, eds. (Cambridge: MIT Press), pp. 111–176.
3. Collett, T.S. (1988). How ladybirds approach nearby stalks: a study of visual selectivity and attention. J. Comp. Physiol. [A] *163*, 355–363.
4. Lehrer, M., Srinivasan, M.V., Zhang, S.W., and Horridge, G.A. (1988). Motion cues provide the bee's visual world with a third dimension. Nature *332*, 356–357.
5. Sobel, E.C. (1990). The locust's use of motion parallax to measure distance. J. Comp. Physiol. [A] *167*, 579–588.
6. Srinivasan, M.V. (1993). How insects infer range from visual motion. In Visual Motion and Its Role in Stabilization of Gaze, F.A. Miles and J. Wallman, eds. (Amsterdam, The Netherlands: Elsevier), pp. 139–156.
7. Land, M.F. (1999). Motion and vision: why animals move their eyes. J. Comp. Physiol. [A] *185*, 341–352.
8. Esch, H.E., Zhang, S., Srinivasan, M.V., and Tautz, J. (2001). Honeybee dances communicate distances measured by optic flow. Nature *411*, 581–583.
9. Götz, K.G. (1994). Exploratory strategies in *Drosophila*. In Neural Basis in Behavioural Adaptations, K. Schildberger and N. Elsner, eds. (Stuttgart, Germany: G. Fischer), p. 47–59.
10. Götz, K.G. (1998). Processing of visual information in the fruitfly *Drosophila*. In From Structure to Information in Sensory Systems, C. Taddei-Ferretti and C. Musio, eds. (Singapore: World Scientific), pp. 431–456.
11. Schuster, S., and Götz, K.G. (1994). Adaptation of area covering random walk in *Drosophila*. In Sensory Transduction, N. Elsner and H. Breer, eds. (Stuttgart, Germany: Thieme), p. 304.
12. Waldvogel, F.-M., and Fischbach, K.-F. (1991). Plasticity of the landing response of *Drosophila melanogaster*. J. Comp. Physiol. [A] *169*, 323–330.
13. Tammero, L.F., and Dickinson, M.H. (2002). The influence of visual landscape on the free flight behavior of the fruit fly, *Drosophila melanogaster*. J. Exp. Biol. *205*, 327–343.
14. Strauss, R., and Heisenberg, M. (1993). A higher control center of locomotor behavior in the *Drosophila* brain. J. Neurosci. *13*, 1852–1861.
15. Schuster, S. (1996). Repräsentation visueller Objekte beim Suchlauf der Fliege *Drosophila*. PhD thesis. (Tübingen, Germany: Max-Planck-Institut für Biologische Kybernetik).
16. Strauss, R., Schuster, S., and Götz, K.G. (1997). Processing of artificial visual feedback in the walking fruit fly *Drosophila melanogaster*. J. Exp. Biol. *200*, 1281–1296.