

equation [8] to facet number spatial resolution is reduced by 1.5%. Finally we note that *Drosophila* is one of the most important model organisms in biological science. Our observation that a complex trait, eye size, evolves appreciably over a relatively short time suggests that care should be taken when flies from long-term cultures are used as wild-type controls.

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Supplemental data

Supplemental data including experimental procedures are available at <http://www.current-biology.com/cgi/content/full/15/14/R542/DC1/>

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Moving observers, relative retinal motion and the detection of object movement

Simon K. Rushton and Paul A. Warren

Motion of the image of an object across the retina (or a camera sensor) may be due to movement of the object, movement of the observation point or a combination of the two. Humans are able to routinely distinguish between these causes and correctly perceive whether an object of interest is in motion or scene-stationary. The important question is how this ubiquitous and difficult problem is solved.

We have investigated whether the brain can resolve the ambiguity by comparing the retinal motion of the object of interest — the target — to that of scene objects. We find that relative retinal motion can indeed be used, and suggest that the processing may be done by cortical areas sensitive to optic flow [1,2].

Moving the scene relative to a stationary observer — rather than the observer within the scene — provides a way to focus on the role of relative retinal motion by excluding the contribution of other sources of movement information. Some particularly ingenious researchers have found ways to move physical rooms or their 'virtual' equivalents [3–5] around static observers. In this study, we employed an alternative, simpler solution and moved a virtual scene composed of an array of cubes (Figure 1, right panel), presented on a CRT to a stationary observer. The

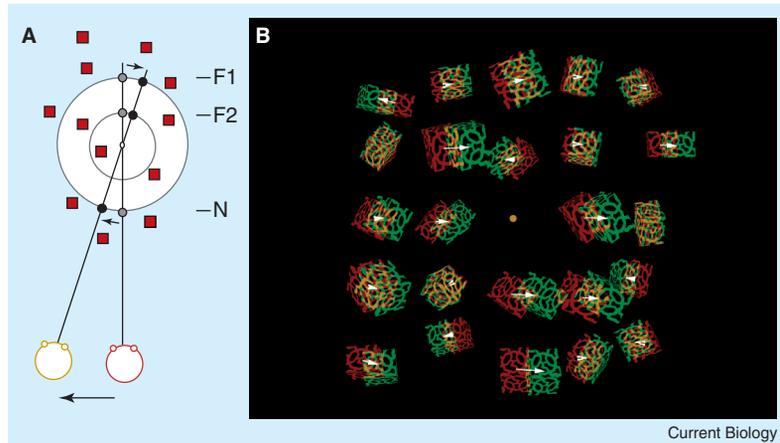


Figure 1. The experimental set up.

Left panel: plan view of the observer and simulated movement through the scene (two instances in time illustrated); a binocular viewpoint, indicated by schematic head, moves laterally while counter-rotating to keep pointing at the centre of the volume. Note that in the experiment, observer movement is simulated – the head remains physically stationary. The target sphere — indicated by filled circle and shown at distance F1, F2 and N — also remains directly ahead of the observer in the rendered scene and also on the CRT. The target sphere has movement relative to the scene only. Right panel: view of the scene from the left eye-point of the observer (two frames from movement illustrated in left panel). Arrows indicate the motion direction of scene objects (24 cubes randomly placed within a volume of 26 x 26 x 50 cm). Simulated speed of self-movement was 4.5 or 6.75 cm sec⁻¹ laterally with a counter-rotation to keep the centre (1.05 m from the observer) of the array of objects fixated. The stereo animation was presented on a CRT in a pitch-black room and viewed through shutter glasses. Each observer viewed 80 trials per distance (–0.2, –0.125 or 0.2 m relative to the centre of the array). In the natural environment there are multiple cues to depth order, in this experiment binocular disparity is the only reliable cue. Stereo deficits are common [7] so we would expect some observers to be unable to perform this particular task. Therefore, for inclusion we required that, in a parallel experiment with the probe at a fixed disparity-defined distance, an observer showed a strong ($r^2 > 0.6$) negative correlation between relative speed and response time.

scene was rendered in stereo and viewed through shutter glasses which produced a compelling percept of three-dimensional objects floating in space. In every presentation, a stationary target object was placed directly ahead of the stationary observer. Scene objects were moved over the screen to produce the pattern of retinal motion that would result if the observer undertook the natural action of maintaining fixation on the target object while moving sideways (Figure 1, left panel).

This is a particularly interesting action for two reasons: firstly, it produces a complex pattern of retinal motion (Figure 1, right panel); and secondly, because of the geometrical consequences of the relationship between target distance and scene-relative movement (Figure 1, left panel).

Examine the left panel illustrating the *simulated* observer movement and note that the target object is shown at three distances: F1, F2 and N (filled circles). Because the target remains directly ahead of the observer during the simulated movement, it must be moving within the scene. Geometry dictates that a target object at F1 is moving faster through the scene than a target object at F2. Further, a target object at N is moving in the opposite direction to target objects at F1 and F2. This is a very useful relationship because, if the brain does use relative motion to calculate scene-relative movement, then by simply changing the distance of the target object in our experiment, we should be able to produce predictable changes in perceived target velocity.

Rather than rely on a subjective report of perceived speed we attempted to tap the observer's immediate percept of movement. To do so, we made use of a measure employed in a similar situation by Smeets and Brenner [6]. It has previously been shown that the time it takes to detect movement is a function of speed; fast movements are detected more quickly [6]. Because of the

geometric considerations discussed above, if the brain uses relative motion and an observer is asked to press a button as soon as target movement is detected, then the button press should occur sooner when the target is at distance F1 than when it is at F2. Furthermore, we should be able to manipulate which of two buttons, indicating target direction, an observer will press by placing the target at either N or F1. Note that the motion on the retina is identical in all three cases; only the binocular disparity of the target differs.

The relative motion predictions were supported by the data. The average — mean median of five observers — response time at F1 (629 msec) was significantly ($t(4) = -2.77$; $p < 0.05$; one-tailed) shorter than at F2 (664 msec), consistent with the target being perceived as moving faster at F1. Furthermore, the reported direction of movement was consistent with the perception of the target moving in opposite directions at F1 and N: in the with-head direction 95% of the time at N compared to 6% of the time at F1 ($t(4) = -17.03$; $p < 0.001$; one-tailed).

These results are in line with the geometric predictions and indicate that observers can indeed use the relative retinal motion of scene objects to detect movement of an object of interest during self-movement. The results *do not* isolate an underlying mechanism or algorithm responsible for this ability but, as noted earlier, a candidate may have already been identified. Researchers interested in the visual guidance of locomotion have demonstrated the brain's sensitivity to optic flow — the patterns of relative motion that are characteristic of self-movement (see [2] for a recent review). If the retinal motion due to self-movement could be identified and isolated by such a mechanism, then only a simple calculation is required to separate it out. Any remaining motion can then be attributed to movement of an object within the scene.

Supplemental data

Supplemental data including a more detailed breakdown of the results and commentary on some of the response times are available at <http://www.current-biology.com/cgi/content/full/15/14/R540/DC1/>

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Supplemental Data: Moving observers, relative retinal motion and the detection of object movement

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Response times and perceived direction

The tables below report the reaction times for the various conditions. We present both raw and cleaned data (very high and very low RTs removed).

Percentage of targets perceived to be moving with the head

Target distance	Percentage with
F1	5.71
F2	6.39
N	94.39

Reaction times

Raw data, no cleaning. Times cited in paper.

Target distance	RT (sec)
F1	0.629
F2	0.664
N	0.684

Minimal clean: removal of RTs < 0.25 and > 1.5 sec (note 1.5 is considerably greater than the mean + 2SDs for all but one observer). All tables that follow are of minimally cleaned data.

It will be noted that N decreases somewhat after cleaning. This is due to the presence of a few very long response times when the target is at N — we are unsure

why there might be more of these trials at N than at F1 and F2.

Target distance	RT (sec)
F1	0.598
F2	0.643
N	0.623

Breakdown by speed

In each trial, the speed was selected randomly. Note that at all distances the RT decreases with speed.

Target distance	s1	s1.5
F1	0.612	0.584
F2	0.652	0.634
N	0.649	0.597

Mean RT by Observer

Only SKR (first author) is an experienced psychophysical observer.

Obs	Mean RT (sec)
SKR	0.398
ARB	0.544
CB	0.467
BM	0.800
JEM	0.896

A comparison of the response times to similar tasks

The response times reported in the paper may appear somewhat longer than expected. We make several comments on this:

From the Table S5 above it can be seen that the mean response time varies considerably between observers. Observer SKR (the first author) is the only experienced psychophysical observer and his response times are on the order of 400 msec. This observer's results are closest to those in the

Target distance	RT (sec)
F1	0.396
F2	0.407
N	0.391

literature where experienced observers are routinely used. Note SKR's pattern of responses (Table S6) is the same as the group's.

In this study we use a discrimination task (left vs right). In other studies — such as Smeets, J.B.J. and Brenner, E. (1994) The difference between the perception of absolute and relative motion: a reaction time study, *Vis. Res.* 34, 191-195 — a detection task is used. Discrimination tasks commonly take approximately 100 msec longer than detection tasks; see Figure 6 in Rushton, S.K. (2004). *Projectile interception, from where and when to where once. In Theories of Time-to Contact, Hecht, H. and Savelsbergh, G. J. P. eds. (Elsevier), pp. 327-354.*

Parallel experiment

In a parallel experiment we examined response times (for the same 5 observers) in 4 different conditions: absolute motion (motion of a target dot with no other visible objects; extra-retinal motion information), normal motion (motion of a target against a visible static background; retinal and extra-retinal motion information), relative motion (movement of a background against a static target producing relative motion; the same as normal motion but no extra-retinal motion signal), double absolute (the same as "normal" but with twice the extra-retinal signal, produced by independently moving the target and the background). The relative motion condition is the same as the relative motion manipulation used in the main experiment.

It will be noted that the response times in all the conditions decrease with speed as would be expected. Further, the response times for relative motion are approximately 15% slower than the normal motion conditions.

Therefore, we can be confident that the magnitude of the response times reported in the main experiment is appropriate, it reflects the expertise of the observers and their speed/accuracy trade-off; long response times do not reflect a

Table S7.

rel speed	abs	Nor	rel	rel+2*abs
0.5	1.1663	0.659	0.682	0.579
1	0.931	0.515	0.595	0.494
2	0.676	0.46	0.575	0.452
4	0.526	0.414	0.511	0.418

problem with the task or the
observers' understanding of task
requirements.