Living up to optimal expectations

C. M. P. Muller
Faculty of Human Movement Sciences, Vrije Universiteit, Amsterdam, The Netherlands

E. Brenner
Faculty of Human Movement Sciences, Vrije Universiteit, Amsterdam, The Netherlands

J. B. J. Smeets
Faculty of Human Movement Sciences, Vrije Universiteit, Amsterdam, The Netherlands

Natural visual scenes contain several independent sources of information (cues) about a single property such as slant. It is widely assumed that the visual system processes such cues separately and then combines them with an averaging operation that takes the reliabilities of the individual cues into account. Does that mean that people lose access to information about inconsistencies between the cues, or are all inconsistencies revealed in a distorted surface appearance? To find out, we let observers match the slant and appearance of a simulated test surface to those of an identical, simultaneously visible, simulated reference surface and analyzed the variability in the settings. We also let observers match surfaces under conditions that were manipulated in ways that were expected to favor certain cues (monocular or binocular) or to selectively disrupt certain comparisons between the surfaces (slant or structure). The patterns in the variability between the settings were consistent with predictions based on the use of all available information. We argue that information about discrepancies is only “lost” during cue combination if there is no benefit in retaining the information.

Keywords: cue combination, optimal, slant, binocular vision, texture


Introduction

We do not process everything that is within our field of view equally thoroughly. Part of the vast stream of incoming visual information is lost because of the limitations of the anatomy and physiology of the visual system. For instance, we will not see a stimulus if it is too small, too far from where we are looking, changing too fast, or only visible in UV light. Another part of the incoming information is ignored by the visual system as it extracts the properties of interest, thereby automatically “losing” any information that is deemed irrelevant. Examples of this are not noticing the color of the stairs as you climb them or not recognizing a friend as you swerve to avoid colliding with him or her when running to catch a train. We will hereafter refer to any kind of loss other than the two kinds mentioned above as “unnecessary loss.”

Having determined the property of interest, there may be several ways to extract this property from the vast stream of visual information. We refer to these different ways as using different cues for that property. Extracting properties of interest independently in different ways makes it possible to optimize the processing for each cue separately. It is known that the visual system processes unrelated cues separately (Livingstone & Hubel, 1988; Lueck et al., 1989). Processing related cues separately has the advantage of making it possible to accommodate different encodings for different cues (Landy & Kojima, 2001) and makes it possible for the visual system to independently estimate each cue’s reliability at each moment for each position in the scene so that the relevant reliability can be considered when the cues are later combined (Hillis, Watt, Landy, & Banks, 2004; Knill, 2003). However, combining the cues is, in itself, a process during which information may be lost.

Surface slant

Slant is a property for which there are many cues. Slant estimates can, for instance, be obtained from the distribution of points and orientations within the retinal image (assuming that the surface’s texture is isotropic), from binocular disparity, and from motion parallax (assuming that the surface is rigid and that you can judge its motion). Given independent processing of slant cues, with independent errors, the different cues are likely to indicate slightly different values. Such discrepancies must somehow be harmonized. Without feedback, the visual system cannot know which of the estimated values is correct, but it can judge the reliability of each estimate (Knill & Pouget, 2004). Weighted averaging could be used to combine the cues in a way that takes the individual cues’ reliabilities into account so that the variability of the combined estimate is minimized (Landy, Maloney, Johnston, & Young, 1995;
van Beers, Sittig, & Denier van der Gon (1996, 1999). Hillis, Ernst, Banks, and Landy (2002) suggest that different pairs of cue values that are combined to give the same weighted average give rise to indiscernible percepts.

The abovementioned weighted average is often referred to as optimal cue combination because in a statistical sense, no information about the property of interest is lost. However, a discrepancy between cues could, in itself, be considered to be additional information because certain causes for such inconsistencies are more likely than others; for instance, the texture could be anisotropic, which would selectively disrupt the foreshortening cue. Thus, in some cases, it may be more reasonable to assume that one of the estimates is completely inconsistent between cues could still influence the interpretation of the surface’s structure (shape and surface texture). Thus, even if the slant cues are combined in a statistically optimal manner (Hillis et al., 2004; Knill & Saunders, 2003), based on the assumption that discrepancies between the cues are all due to sensory error, information about the discrepancy need not be lost. Whether such information is lost can be revealed by asking observers to report about the surface’s appearance. If no information is lost, the conflict will influence the perceived surface structure, even when the discrepancy as such is not noticed. For instance, the texture on the surface can appear to be slightly anisotropic.

**Surface structure**

Even when the lack of consistency between the slant cues is small enough to be attributed to independent errors in judging the slant in different ways, the small differences between the cues could still influence the interpretation of the surface’s structure (shape and surface texture). Thus, even if the slant cues are combined in a statistically optimal manner (Hillis et al., 2004; Knill & Saunders, 2003), based on the assumption that discrepancies between the cues are all due to sensory error, information about the discrepancy need not be lost. Whether such information is lost can be revealed by asking observers to report about the surface’s appearance. If no information is lost, the conflict will influence the perceived surface structure, even when the discrepancy as such is not noticed. For instance, the texture on the surface can appear to be slightly anisotropic.

**The task**

In this study, we examine whether we can find any evidence for unnecessary loss of information when combining slant cues under conditions in which the conflicts are small enough to be considered to be caused by sensory errors. Determining whether potentially useful information is lost is not trivial. Cue combination can seem to be suboptimal if cues have correlated sources of errors (Oruc, Maloney, & Landy, 2003). Moreover, it is almost impossible to present a cue in the same manner both alone and together with one or more other cues. We have, therefore, chosen a rather unconventional methodology. Previous studies on slant perception have taken measures to ascertain that observers had no other way to perform the task than the one that the experimenters had in mind. For instance, surfaces have been rendered at random depths to make it impossible to rely directly on binocular disparity (Hogervorst & Brenner, 2004; Knill & Saunders, 2003), and the aspect ratios of surfaces have been randomized to make sure that observers did not use retinal size ratios to perform the task (Hillis et al., 2002). Such precautions have clear advantages, but they also introduce sources of errors that are not directly related to the resolution of the individual cues (this issue will become clearer when we interpret our results).

We asked observers to match the slant and structure of a simulated test surface to those of a simultaneously visible simulated reference surface. They could do so by independently manipulating the slant indicated by the monocular cues and that indicated by the binocular cue. In our main (baseline) condition, the pattern of dots that defined the surface was identical for the two surfaces and they were shown simultaneously, side by side, at the same distance. In this condition, it was extremely easy to match the surfaces in both slant and structure. Beside this condition, we also designed conditions with a lower reliability for either the monocular or the binocular cues, as well as conditions in which it was more difficult to match either the slant or the surface properties. We examined whether each of these conditions elicited the pattern of errors that is to be expected from an optimal combination of the cues—without any unaccountable loss of information or more complex interaction between the cues—by looking at the variability within observers’ settings (Hogervorst & Brenner, 2004). This is conceptually equivalent to measuring thresholds in many directions (as in Hillis et al., 2002), if one is willing to assume that the errors form a two-dimensional normal distribution. Although one may expect a more complicated distribution of errors on the basis of the relationships between slant and binocular disparity and between slant and monocular deformation (Hillis et al., 2002), for the modest errors in our simple matching task an ellipse is probably a good enough approximation of the distribution.

**Methods**

**Observers**

Five observers participated in this study. One was an author and the other four were experienced psychophysical observers who were naive with respect to the purpose of the experiment. All observers had normal or corrected-to-normal vision and a stereo acuity of better than 50 arcmin (Randot Stereo Acuity Test).

**Experimental setup**

Images were presented on a CRT screen by a Silicon Graphics Onyx Reality Engine (frame rate: 120 Hz;
Observers sat in a dark room, with their chin placed on a chin rest so that their eyes were 44 cm from the screen (Figure 1a). The images were viewed through liquid crystal shutter spectacles that were synchronized with the refresh rate of the monitor. Alternate images were presented to the left and right eyes so that each eye received a new image every 16.7 ms (60 Hz). These images were calculated on the basis of individual observers' interocular distances. Only the red gun of the monitor was used because the shutter spectacles work best for red images (transmitting more than 50 times as much light when open than when shut). The observers' heads were restrained by a chin rest, but they were free to move their eyes as they pleased.

Stimuli

Each stimulus consisted of two simultaneously visible simulated surfaces that were placed side by side (Figure 1b). The slant of each stimulus was indicated both by binocular disparity and by monocular cues (assuming an isotropic texture and a circular outline; except in one condition that will be discussed later). For the reference surface, the two kinds of cues always indicated the same slant. For the other surface, the observer manipulated the two slant cues independently so that they did not necessarily indicate the same value (observers could set any amount of conflict between the cues that they liked). The simulated surfaces were slanted around a horizontal axis at the screen center. The surface on the left was always the reference surface. It was slanted backward at the top relative to the CRT screen by 30°, 45°, or 60°. The slant and structure of the test surface on the right were set by the observer to match the reference (as explained further in the Task and instructions section).

The same condition was the main condition of the experiment. In this condition, both the test and the reference surfaces were 10-cm-diameter simulated discs consisting of identical patterns of 500 randomly distributed dots. A new distribution of dots was generated for each trial. If no information is lost when the cues are combined in the ways needed for matching slant and surface structure, then the values set for each cue will only be determined by the resolution of that cue (irrespective of how the cues are later combined). Four other conditions were designed to examine whether the patterns of errors in the cue settings change as expected (based on there being no loss of information) when the uncertainty about specific aspects of the stimulus is increased. These conditions (described below) were designed to make either the binocular or the monocular cue less reliable or to make the comparison of one of the properties (slant or surface structure) more difficult.

To make the monocular cues less reliable, we simply reduced the number of dots on the two surfaces from 500 to
50 (few points condition). Reducing the number of dots is hardly expected to compromise the reliability of the binocular cue, but it is expected to make the monocular cues less reliable (Hillis et al., 2004). We changed the texture on both surfaces in the same way so that the two surfaces were still identical. Thus, we only expect more variability in the settings for the monocular cues when compared with the same condition.

In the three other conditions, the reference was the same as in the same condition, but the test surface was different. To make the binocular cue less reliable, we moved the simulated test surface 2 cm further away from the observer (to a distance of 46 cm; other distance condition). We increased the size of the simulated surface and dots slightly so that the test surface gave rise to almost the same image in each eye as in the same condition. As a result, the monocular cues should not become less reliable. However, an estimate of the viewing distance is needed to interpret binocular disparities in terms of slant. When two surfaces are at the same distance, errors in judging the viewing distance are irrelevant for the accuracy of a comparison between the surfaces’ slants because disparities are misinterpreted in the same way for both surfaces so that the surfaces are matched correctly even if their slopes are not estimated correctly (Brenner & Landy, 1999). This is not so when the surfaces are at different distances. Additional errors as a result of misjudging the viewing distance are likely to make the binocular cue less reliable in this condition. Moreover, binocular disparity is less reliable at a larger distance, although moving the surface from 44 to 46 cm can only be expected to have a very small effect. Thus, in this condition, we only expect to find more variability in settings for the binocular cue than in the same condition.

To make it harder to compare the slants of the two stimuli, we tilted the rotation axis of the test surface by 30° (from the original horizontal orientation) in a counterclockwise direction within the plane of the screen (other direction condition) so that the surfaces were slanted in slightly different directions. Otherwise, both the test and reference surfaces were identical in all respects. We expect the difference in direction to make the slants more difficult to compare, but neither of the cues themselves should become less reliable by this manipulation. If observers make errors in matching the slants for different tilt angles, then we may expect to see additional errors in judging slant, but there is no reason to expect additional errors in judging the surface structure. Thus, we may expect some additional variability due to covariation of the two cues as observers match an incorrect slant, with no additional conflict between the cues. Note that this covariation will increase the variability for both cues.

Making surface properties difficult to match is complicated because we cannot directly control the assumptions that observers are willing to make. Thus, for instance, asking observers to match surfaces with different widths may lead to systematic errors in slant judgments rather than to more uncertainty about the structure of the surface. We chose the following solution: In the lines condition, observers had to match the reference surface with a square plane of which only two horizontal rectangles located at its top and bottom edges were visible. Each rectangle was 10 cm wide and 2 cm tall; hence, they were separated by 6 cm. This condition provided binocular disparity cues for slant both from within and between the rectangles, and monocular cues for slant from the shapes and relative sizes of the rectangles, as well as possibly from the assumption that together they form the edges of a square. Although observers could still notice cue conflicts, they no longer had the possibility to compare the two surfaces in terms of surface structure; hence, we expect them more reliably to match the slant than to avoid conflicts between the cues. Thus, in this condition, we expect to see the consequences of weighted averaging of the two kinds of slant cues because a too high setting for one cue will sometimes be compensated for by a too low setting for another cue. The precise relationship will depend on the relative weights given to the two cues. The accuracy of the monocular cue may also be slightly different because of the use of a different kind of test surface.

**Task and instructions**

The reference surface on the left and the adjustable test surface on the right were visible simultaneously. Observers were asked to set the slant and structure of the test surface to match the reference surface as closely as possible. In terms of matching the slants, we specified that the angle with respect to the frontal plane had to be matched. For the same, few points, and lines conditions, this meant that the two surfaces were to lie in the same plane. For the other distance condition, the two surfaces were to lie in parallel planes. For the other direction condition, the angles were to be matched, but they had no special relationship other than the fact that they had the same angle with respect to the frontal plane. In terms of surface structure, the task in the same, few points, other distance, and other direction conditions was self-evident: The two surfaces had to look alike (though viewed from different angles). In the lines condition, the task was (intentionally) ambiguous because the purpose of that condition was to make it difficult to match the surface structure. Subjects were instructed to match the surfaces as well as they could. In all cases, we made sure that the subjects understood the task before they started to match the surfaces.

**Procedure**

At the start of each trial, each cue indicated a random slant of the test surface. The observers could adjust the test
surface’s slant independently for each cue by moving the mouse. Moving the mouse left to right changed the slant as indicated by binocular disparity; moving the mouse forward and backward controlled the slant indicated by monocular cues. Both cues could be set to indicate a slant between 20° and 80°. The binocular cue’s range was assigned to a 20-cm stretch of table; thus, the stereo-indicated slant changed by 3°/cm. The monocular slant cue’s range was assigned to a 15-cm stretch of table, which resulted in a 4° slant change per centimeter of mouse movement. As soon as observers were content with the match, they clicked on the mouse button to start the next trial. Observers could not manipulate the surface structure directly, but, of course, a setting with a conflict between the slant cues is equivalent to a simulation of a surface with a different structure (shape and surface texture).

We did not provide the observers with feedback about their performance. Each of the five conditions was presented 40 times for each of the three different reference slants. The total of 600 trials was presented in several blocks containing all three slants of one or several conditions.

Data analysis

Data were initially collected as pairs of settings (in degrees of slant). Pairs of settings were excluded from further analysis if either of the two differed by more than 2 SD from the mean for the slant set for that cue in that condition. This resulted in exclusion of about 6% of the 3,000 pairs. For each condition and reference slant, we plotted the settings with the monocular and binocular cues on orthogonal axes and fit a confidence ellipse to the resulting distribution using a principal components analysis (Figure 2). The ellipse’s elongation (the ratio of the lengths of the major and minor axes) and its orientation were used to evaluate the relationship between the cues.

Predictions

Assuming that there is no unnecessary loss of information, we can make several qualitative predictions for comparisons between the variability of settings in the same (baseline) condition and in the other four conditions.

For the main same condition, an optimal use of the two kinds of cues for both tasks predicts that the resolution for setting each of the individual cues fully determines the variability because no information is left unused. Any discrepancy between the cues that is averaged away in an optimal judgment of slant is used to judge the surface structure (Hogervorst & Brenner, 2004). If performance only depends on the resolution of the individual cues, we expect the orientation of the ellipse to be either 0° or 90°, depending on which cue has the lowest resolution. The magnitude of the elongation indicates the extent to which one of the cues is more reliable than the other. If no information is lost, then there is no reason to expect any correlation between the cues (diagonally oriented ellipses), even if surface structure is processed completely independently of slant but from the same input (note that in terms of error propagation, completely independent processing of slant and surface structure from similar rather than from the same input is not completely equivalent to noticing the conflict between the slant cues; see Hogervorst & Brenner, 2004).

In the two conditions in which one of the cues was made less reliable (few points and other distance conditions), we expect the variance to increase in the direction of that cue, without a change in the variance of the other cue. The elongation of the confidence ellipses will change, but the orientations should still coincide with the axes of the separate cues (i.e., orientations of 0° and 90°).

In the two more interesting conditions, we make the following predictions. When the surfaces’ structures could not really be matched because the equivalent properties for the two surfaces are not well defined (lines condition), we expect observers to mainly match the slant. They may also
try to avoid cue conflicts, but because this was not explicitly part of the task, we expect more variability in matching the surface structure. We therefore expect to always see a negative correlation between the settings for the two cues and a higher variance for each of the cues than in the same condition because setting a slightly larger slant in one cue can be compensated for by setting a slightly smaller slant in the other cue. Because judgments of slant are based on a weighted average, the precise orientation of the ellipse will vary between observers and reference angles.

When the slants are more difficult to match, because the directions in which the surfaces are tilted differ (other direction condition), we expect observers to have more variability in setting the slant, without being more variable in matching the structure of the two surfaces. Consequently, the two cues should be set as consistently as in the same condition, but they will vary together as the estimated slant varies. This covariation will give rise to an elongation of the confidence ellipses with an orientation of about 45° (as shown in Figure 2).

Results

Figure 3 shows a summary of all the data for the same condition. The bar charts show average standard deviations of the settings for each cue and reference slant. In the polar plots, each line connecting two points describes the orientation and elongation of the confidence ellipse for one subject and reference slant.

For the 30° reference slant, observers were, on average, slightly less precise in their settings (larger standard deviations) for the monocular cue, leading to orientations of the corresponding ellipses near 90° (red bars and lines). For the larger reference slants, the precision was similar for both cues. The elongations of the ellipses were quite modest (note that the elongations are displayed on a logarithmic scale). There is no indication of a systematic correlation between the settings for the two cues (no systematic elongation in a direction other than along the axes in the polar plots; significant correlations are indicated by large discs at the ends of the lines).

In the few points condition, we simply expected less precise settings for the monocular cues than in the same condition. The bar charts in Figure 4 show that this is indeed the case. The standard deviations for the binocular cue were similar to those in the same condition. As a consequence, the orientations in the polar plots are more clearly grouped around 90°, and the elongations are considerably larger in this direction (up to almost 10 times larger variability).

In the other distance condition, we simply expected less precise settings for the binocular cue than in the same condition. The bar charts in Figure 5 show that the standard deviations of the settings for the binocular cue are larger (although not significantly so) in the other distance condition than in the same condition. There is no systematic difference for the monocular cues. In the polar

![Figure 3](http://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/932845/) Results for the same condition. Bar chart shows standard deviations of settings for each cue and reference slant, averaged across all observers (with standard deviations across observers). Each line in the polar plot shows the orientation and log(elongation) of the confidence ellipse for one subject and reference slant. An orientation of 0° (or 180°) means that the ellipse’s major axis is oriented along the axis of the binocular cue (see Figure 2). An orientation of 90° (or 270°) means that the elongation of the ellipse’s major axis is along the axis of the monocular cue. Large discs at the end of the lines indicate that the correlation is significant.
plots for the other distance condition, we see more lines oriented toward 0° than in the same condition, in accordance with observers having a larger variability in their binocular cue settings. This is especially evident for the largest reference slant, for which the monocular cue is the most precise (green lines).

In the lines condition, we predicted that the variability in the settings would be larger than in the same condition for both cues. We expected a negative correlation between the cues and, therefore, ellipse orientations between 90° and 180°. The standard deviations were larger than those in the same condition for both cues (Figure 6), although not always significantly so, and the orientations of the ellipses were almost all between 90° and 180°. The precise orientations differed considerably between the observers (and reference angles), probably at least partly because of variability in the weights assigned to the two cues.

In the other direction condition, we also expected more variability in setting both cues with a positive correlation between the settings for the two cues. Figure 7 shows that the variability was indeed larger for both cues and that at least part of the increased variability arises from correlated variability in both cues (orientations between 0° and 90°; also, see example in Figure 2). The ellipses’ major
axes were more closely clustered than in Figure 6, in accordance with the relationship between the cues not depending on any weights in this case.

**Discussion**

In the same condition, there was no consistent correlation between the settings for the two cues and, therefore, no evidence for an unnecessary loss of information. This was an easy task with standard deviations of only 2°. In this condition, we were confident that there was no added uncertainty through factors such as memory or differences in distance or dimensions between the surfaces. In the four other conditions, we examined whether the pattern that arises from adding uncertainty in various ways gives rise to the errors that one would expect under the assumption that no information is unnecessarily lost.

The few points and other distance conditions were designed to each make one slant cue less reliable. In these two conditions, the resolution of setting the more reliable cue was retained when the other cue was set less reliably. In the other two conditions, the stimuli were manipulated in such a way as to introduce uncertainty in the comparison of the slants (other direction) or of the surface.

Figure 6. Results for the lines condition. For details, see legends of Figures 3 and 4.

Figure 7. Results for the other direction condition. For details, see legends of Figures 3 and 4.
structure (lines). We argued that this would result in a correlation between the settings. The results show that this did indeed happen.

It is tempting to interpret the negative correlation in the lines condition (orientations between 90° and 180°; Figure 6) as a loss of information. An incorrect setting in one cue is compensated for by adjusting the setting of another cue, suggesting that information about the cue of origin is lost. However, we only found this negative correlation in the condition in which it was impossible to match the surface structure. In that case, our observers could set a combination of conflicting slants for the two cues that resulted in the perceived slant of the test surface matching the reference, while the structure of the test surface looked different than we had intended. Because the observers could not know that the surface looked different than we intended (because we provided no reference for the surface structure), they were unable to use the perceived structure that arises from the cue conflict to improve their settings for the individual cues. Thus, the lines condition demonstrates weighted averaging for slant judgments but not a concomitant loss of information. Although all information is used, observers do lose knowledge about the information provided by each cue for each attribute. This makes sense in terms of optimal cue combination, because if one has the best estimate for each attribute, why retain the (less reliable) elements?

The polar plot in Figure 6 shows quite a variable ellipse orientation. Such variability is to be expected because the slope associated with the negative correlation between the cues depends on the weights given to the two cues, which can differ between observers and should differ between reference slants. That the variability in the ellipse orientations between various observers and slants is due to variability in the weights is evident from a comparison with the settings for the other direction condition (Figure 7). In that case, we are not dealing with a weighted average (each cue provides essential rather than equivalent information); hence, we expect much more consistent ellipse orientations across observers and reference slants, and indeed, the orientations are much more consistent across observers and slants for the other direction condition than for the lines condition. The orientation of the ellipse is determined by the relative magnitudes of the standard deviations in the two cues and by the correlation between the cues. If the deviation from the mean had always been the same for both cues, then the ellipse orientations would have been centered on 45°. In fact, we find slightly lower angles, indicating that the variability in the binocular cue is larger than that in the monocular cues (in contrast to what we found for the same condition).

One might argue that observers in our experiment performed the task by matching other aspects of the scene than the slant. For example, they could match the relative depths (binocular cue) and heights in the visual field (monocular cue) of the lower edges of the circles. This seems unlikely because our manipulations had the effects that we would expect on the basis of judgments of slant and surface properties (which was also what observers were instructed to match). We intentionally did not take precautions to ensure that observers could not compare other aspects of the stimuli because of the risk that doing so would introduce new sources of errors (as explained earlier).

A large number of studies have found that the visual system weighs cues according to their reliabilities. Most studies found that the visual system does so in a statistically optimal fashion (Backus, Banks, van Ee, & Crowell, 1999; Hogervorst & Brenner, 2004; Knill, 2003; Knill & Saunders 2003; Landy & Kojima 2001; Landy et al., 1995; van Beers et al., 1999; Young, Landy, & Maloney, 1993). One study found weighting according to reliability but with weights that are not statistically optimal (Rosas, Wagemans, Ernst, & Wichmann, 2005). Other studies (Atkins, Fiser, & Jacobs, 2001; Atkins, Jacobs, & Knill, 2003; Ernst, Banks, & Bulthoff, 2000; Poom & Borjesson 1999) showed that the weights for slant perception can be subject to adaptation and can become context sensitive. In a number of studies, the statistically optimal combination seemed to entail a loss of information (Hillis et al., 2002, 2004). Our results could appear to imply that there is never an unnecessary loss of information after the first stages of visual processing, but remember that we carefully designed the experiment to minimize further loss. Thus, we intentionally chose a baseline task that does not involve memory or generalization across different kinds of simulated surfaces, distances, or orientations. We show that if no additional sources of noise are introduced, the loss of information can be fully explained by the single-cue resolutions. This may sound trivial, but it shows that cue combination itself does not automatically lead to a loss of information.

**Acknowledgments**

This research was supported by the Netherlands Organisation for Scientific Research (NWO; MaGW Grant 452-02-007).

Commercial relationships: none.
Corresponding author: Chris Muller.
Email: C.Muller@sbv.vu.nl.
Address: Van der Boechorststraat 9, 1081 BT Amsterdam, The Netherlands.

**References**


