

## ORIGINAL PAPER

T. Maddess · M. P. Davey · E. C. Yang

**Discrimination of complex textures by bees**

Accepted: 7 October 1998

**Abstract** A problem confronted by visual systems is that of discriminating textures. It appears that a recently described class of orientation-tuned neurones in the bee brain embody properties of mechanisms used by humans to discriminate complex textures. In particular these mechanisms would permit bees to discriminate a large range of textures by giving bees access to information related to higher-order correlations between texture elements. To determine if bees can exploit such textural information we have conducted behavioural experiments employing *iso-dipole* textures, that statistically speaking, differ from binary noise textures, and each other, only in their third-order correlation functions. While these textures are not themselves of any ethological significance their special properties permit us to show that bees can potentially use a very large palette of textures to classify textured objects. In electrophysiological experiments we demonstrate the requisite contrast sign invariance (rectification) of the orientation-selective neurones' responses and discuss other similarities of these neurones' responses to models accounting for human texture discrimination.

**Key words** Bees · Texture · Pattern · Orientation · Iso-dipole

T. Maddess (✉) · M.P. Davey  
Visual Sciences Group,  
Research School of Biological Sciences  
Australian National University  
Canberra ACT 0200, Australia  
e-mail: ted.maddess@anu.edu.au  
Tel.: +61-612-62494099; Fax: +61-612-62493808

E.C. Yang  
Institute of Zoology  
Academia Sinica  
Nankang  
Taipei 11529  
Taiwan, R.O.C.

**Introduction**

An important finding in our understanding of human texture segregation and discrimination was that of Beck et al. (1987) who showed that a previously reported trade-off between texture element size and contrast which affects texture segregation (Beck 1983) could be explained by spatial summation within oriented narrow-band spatial frequency channels whose output was later full-wave rectified (Sutter et al. 1989) (by full-wave rectification we mean that the units give similar responses to contrasts which are brighter or darker than average). These so-called "complex channels", are now well documented in the human (Graham and Sutter 1996; Graham et al. 1992; Landy and Bergen 1991). Experiments on texture-defined motion also indicate the presence of a "texture grabber" based on rectified, oriented spatial filters (Chubb and Sperling 1991), where the extracted textural information may form the input to the same motion-detecting mechanism as that for luminance-defined motion (Turano and Pantle 1989; Werkhoven et al. 1993, 1994).

Another approach to texture vision was initiated by Julesz et al. (1973) who hypothesised that humans could not discriminate briefly presented textures whose second-order correlation functions were the same, so called *iso-dipole* textures (note that although Julesz and colleagues use slightly different statistics to the standard autocorrelation function in fact the statistics are the same providing the textures compared have the same mean luminance as in the case of their binary patterns (Klein and Tyler 1986)). This lemma stood until a class of patterns was discovered, which can be highly discriminable, but which has identical third-order correlation functions (Julesz et al. 1978). Such *iso-trigon* textures by definition also have identical means and second-order correlations, i.e. they are also *iso-dipole* (Gilbert 1980). A variety of such textures have now been found (Gilbert 1980; Victor and Conte 1991). These textures' second-, (and frequently, third-order correlation functions are

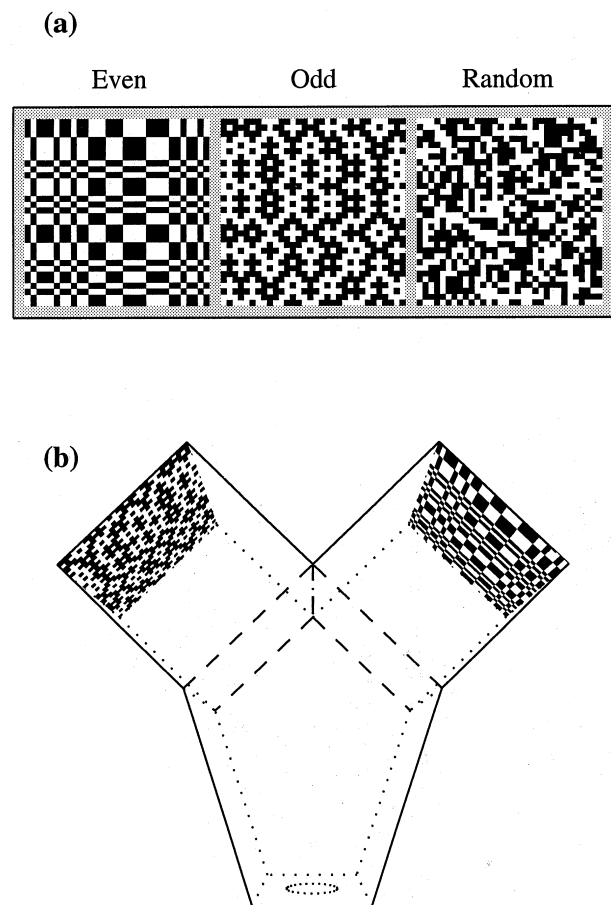
also indiscriminable from binary noise. Victor and Conte (1991) have constructed a parsimonious neural model whose performance matches human visual discrimination of these textures. The model accounts for human visual-evoked responses, those responses being dependent on the higher-order statistics of the textures. Victor and Conte's (1991) model contains model neurones similar to the complex channels described above, and involves a spatial sum of an array of oriented spatial filters which have their individual responses rectified, followed by a strong threshold non-linearity. It is interesting that such outwardly simple receptive field mechanisms are capable of making use of complex information in order to discriminate textures. If radically different animal species adopt similar texture processing methods this would provide evidence that the commonly selected mechanism was robust and efficient.

We recently reported neurones in the bee brain which appear to compute the spatial sum over many small oriented receptive fields (Yang and Maddess 1997). Orientation-sensitive neurones have also been reported in the dragonfly brain (O'Carroll 1993). Bees can discriminate the global orientation of textures (Giger and Srinivasan 1995, 1996; Srinivasan et al. 1993; van Hateren et al. 1990) and a system with at least three orientation channels separated by  $60^\circ$ , and with orientation bandwidths of about  $90^\circ$ , are required to explain the bee's orientation discrimination behaviour (Srinivasan et al. 1993, 1994). Bees discriminate pattern orientation even at presentation times as short as 20 ms, precluding the involvement of motion-sensitive channels (Giger 1997). The bee orientation neurones have the appropriate orientation-tuning properties (Yang and Maddess 1997) and they are appropriately fast, responding equally well (but not directionally) to bars moved at velocities over the range of  $100\text{--}2500^\circ\text{ s}^{-1}$  (Yang and Maddess 1997). The bee neurones (Yang and Maddess 1997) are thus similar to the required components of the texture-extraction mechanism proposed by Victor and Conte (1991). We have therefore investigated the rectifying nature of the neurones to confirm this final part of the story, and whether bees can discriminate the complex textures described by (Julesz et al. 1978) from each other and from random noise patterns. We also examine whether bees can transfer what they know about one class of textures to a new class. The relative merits of other potential mechanisms for discriminating these textures are also discussed.

## Materials and methods

### Behavioural stimuli

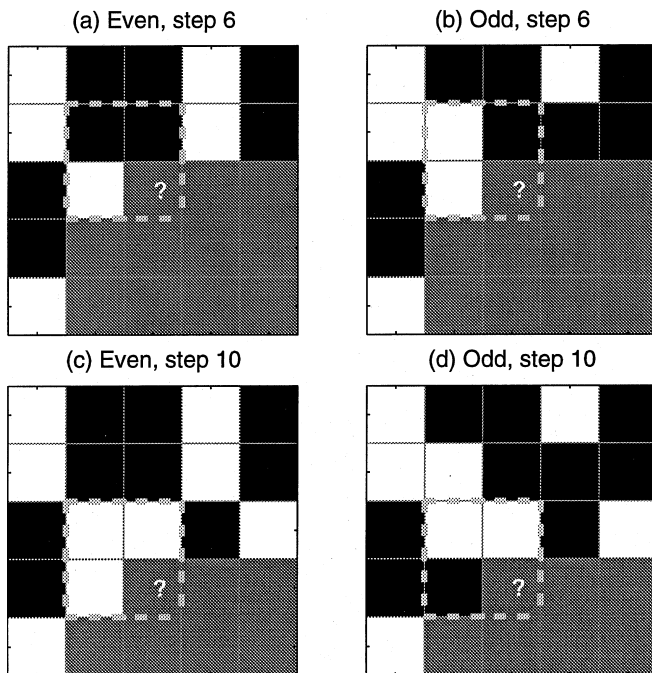
The patterns used here are of the type described by Julesz et al. (1978) as *even* and *odd* iso-trigon textures, and *random* noise textures (Fig. 1a). In the *random* patterns the probability of a given check being black or white is 0.5. Formally these patterns are best thought of as being created through a recursion process. To construct the *even* and *odd* patterns the checks in the first row and



**Fig. 1a, b** Stimulus presentation. **a** Examples of the *even*, *odd*, and *random*, visual stimuli used in the experiments. **b** Illustration of the bee maze viewed from above, the proportions of the top edge are correct. The *dashed lines* indicate the *decision plane* (at 26 cm from the target) beyond which a bee was deemed to have made a selection

column are first set randomly dark ( $-1$ ) or bright ( $1$ ). Then the other checks are coloured in by a recursion rule where the product of 2 by 2 blocks of checks must be either 1 for *even* textures or  $-1$  for *odd* (Julesz et al. 1978) as illustrated in Fig. 2. The statistics of the generated pattern does not depend on the initial set of checks or in which direction the recursion is operated (Gilbert 1980). The window over which the recursion rule operates can be altered to create a variety of iso-trigon textures [Victor and Conte 1991]. Rather than follow this general recursion rule a quick way to generate only *odd* and *even* textures is to create row and column vectors containing 1 or  $-1$  at random ( $P = 0.5$ ) and then take the outer-product of these vectors (also called the cross-product) to generate a matrix containing an *even* pattern. To create an *odd* texture multiply those pixels of the *even* pattern at the intersections of every other row and column by  $-1$ . Four different *odd* patterns can be created from each *even* by shifting the starting rows and columns each by one.

Although the *odd* and *even* textures are strikingly different in appearance, they differ only in their fourth- and higher-order correlation functions (Gilbert 1980; Julesz et al. 1978; Victor 1994). Optical blurring may affect the iso-trigon constraint but, since the patterns would thus have their power spectra multiplied by identical blurring functions, they will remain iso-dipole with themselves and with randomly coloured textures (Julesz et al. 1978; Klein and Tyler 1986; Victor 1994). Even though the effects of optical blurring were small (see below) this explains why we refer to the bees discriminating iso-dipole rather than iso-trigon statistics.



**Fig. 2a–d** Illustration of the recursion process to generate *odd* and *even* patterns. The first row and column of a matrix (5 by 5 in this case) are coloured black or white (i.e. assigned to be either  $-1$  or  $1$ ) with 50% probability. A window 2 by 2 pixels (*dashed box*) is then moved over the matrix in steps. At each step the value of the 4th pixel (white?) is determined by taking the product of the other three pixel values in the window,  $p$ , and then assigning the 4th pixel to be either:  $p$  for *even* textures (**a, c**), or  $-p$  for *odd* textures (**b, d**). **a–d** show the process at steps 6 and 10 of the recursion process

We emphasise that when we talk about a given *texture* we are referring in essence to the algorithm which generates that texture. For example, we can think of the *even* texture as a pattern of infinite extent where the particular images we have used here are selected *cut-outs* from the parent texture. Statements about the indiscriminability of these textures on the basis of higher order statistics hold for both the parent textures and also for spatial averages over ensembles of cut-outs from the parent image (Klein and Tyler 1986; Victor 1994), but do not hold for individual image pairs (Victor 1994; Yellott 1993). Therefore, we must take care that any discriminations attributed to higher order statistical properties, or equivalent measures, are based on averaged responses to ensembles of finite images selected from the parent textures. So, for example, in our first experiment we trained bees with a *set* of *even* patterns against a *set* of *odd* patterns and then assessed the ability of the bees to discriminate *odd* and *even* textures with new test sets that the bees had not seen before. Since the training sets were necessarily large this had the complication of making the training period long.

#### Behavioural experiments

Stimuli were presented to the bees (honey bees, *Apis mellifera*) at the ends of the two legs of a previously described (Srinivasan and Lehrer 1988; Srinivasan et al. 1993; van Hateren et al. 1990) Y-maze apparatus (Fig. 1b). Each stimulus pattern consisted of a square matrix of 32 by 32 square black or white elements. The viewing distance at the decision point for the bees was 26 cm. Each pattern thus subtended  $52^\circ$  horizontally and vertically at the bees' eyes making the characteristic spatial frequency  $0.31 \text{ cycles deg}^{-1}$ , which is within the range of bee visual acuity (Srinivasan and Lehrer 1988). Given the relative acuities of bees and humans the

blurring seen by the bees will be like that seen by humans viewing Fig. 1a at  $\approx 75 \text{ cm}$ .

Typically 15 bees were trained in each experiment. Bees were rewarded if they flew to the centre of the *positive* patterns from where a small tube lead to a reward chamber. The unrewarded (*negative*) patterns had an identical tube at their centre which was blocked at its far end. As in previous studies (Srinivasan and Lehrer 1988; Srinivasan et al. 1993; van Hateren et al. 1990) particular care was taken to eliminate olfactory and other possible cues. In most experiments the stimuli were the *odd* and *even* patterns described in the section above. Every 8 min the *odd* and *even* patterns were exchanged with a random selection from a set of six *odd* and six *even* training stimuli. Pattern orientation was also randomised to one of four states separated by  $90^\circ$  (texture element edges always being vertical or horizontal), thus providing 24 *odd* and 24 *even* stimuli. Individual bees frequented the maze about every 6 min, thus lengthy training periods of 7 or more hours were required to present a training set. A different set of six *odd* and six *even* patterns, also exchanged (and rotated) at random, was employed during the test period. Thus, the bees had to learn to discriminate the class of *odd* textures from the class of *even* textures. Only trials in which one bee was present in the apparatus were counted. Statistics presented are  $\chi^2$  statistics based on the raw decision counts. Two hundred discriminations were observed for each experiment. Note that if we had fit a more complex model with a subject-wise (bee) effect this would only have reduced the degrees of freedom by the number of bees while making the main effect more significant. By not accounting for possible subject-wise effects we are in fact presenting the most conservative estimate of the significance of our results.

#### Electrophysiology

In experiments designed to examine the rectification properties of bee orientation-selective cells to positive and negative brightness contrasts we measured separate orientation tuning curves obtained for thin dark bars and light bars moved through the visual field of bee orientation selective cells. Visual stimuli were produced on a Kikusui (P31 phosphor) driven by a Innisfree image generator under computer control. The background illumination was  $4.5 \text{ cd m}^{-2}$ . The bars were  $5^\circ$  wide and  $42^\circ$  high and moved at  $500^\circ \text{ s}^{-1}$  through  $42^\circ$  of the right eye's visual field. The mid-point of the traverse of the bars was centred on the equator of the eye at  $30^\circ$  horizontal retinal eccentricity. Previous experiments had shown that similar responses are obtained from these cells to moving lines presented at  $0^\circ$  (frontal),  $30^\circ$  and  $90^\circ$  (lateral) horizontal retinal eccentricity (Yang and Maddess 1997). The cells were recorded intracellularly with glass pipettes ( $180\text{--}200 \text{ M}\Omega$ , filled with  $2 \text{ mol} \cdot \text{l}^{-1}$  potassium acetate). The point of entry of the electrode was at the top of the head between the lateral ocellus and the right compound eye, the location being designed to access the anterior optic tract. Further details of the animal preparation and stimulus hardware are given elsewhere (Yang and Maddess 1997).

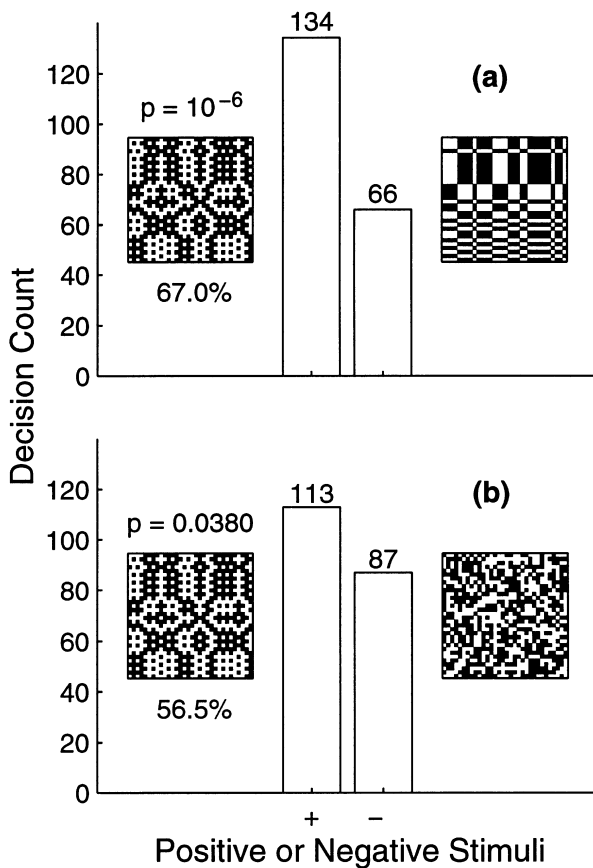
## Results

### Behavioural experiments

In the first of the behavioural experiments bees were rewarded if they flew to the centre of the *odd* patterns. After 9 h training (5 h on one day, 4 h the next), a previously unseen test set was substituted. We cannot stress strongly enough that the lengthy training periods did not reflect the bees learning performance but rather the requirement to train them on a large number of patterns presented in a random sequence, so that the bees learned to attend to what *on average* distinguished

the sets of patterns (see Materials and methods). In comparable experiments where bees had to learn to discriminate pattern orientation, their performance tends to saturate after 20 visits (about 2 h) (van Hateren et al. 1990). The bees' discrimination of the test set was 134 correct, 66 wrong (Fig. 3a), a success rate of 67.0% ( $P < 10^{-6}$ ), equal to human performance for some iso-dipole pairings (Victor and Conte 1991).

Having demonstrated that the bees could learn to discriminate iso-dipole patterns we next investigated whether they could learn to discriminate these patterns from *random* noise textures (e.g. Fig. 1a). We chose the *odd* patterns for this test because human subjects have more difficulty discriminating them from noise (Victor and Conte 1991). The *random* and *odd* textures also represent an iso-dipole stimulus pairing (Victor and Conte 1991). A new group of bees was trained and then tested with unseen sets of *odd* and *random* patterns;



**Fig. 3a, b** Results of the first two behavioural experiments examining iso-dipole texture sets. **a** The bees discriminate a previously unseen set of *odd* from *even* textures after being trained on a different set of *odd* and *even* patterns ( $P < 1e-6$ ). **b** Bees trained on *odd* and *random* patterns discriminate a new set of *odd* and *random* patterns ( $P = 0.038$ ). In each of **a** and **b** the *left* texture illustrates the positive, rewarded stimulus set, and the *right* texture the negative stimulus set (Materials and methods). The height of the two columns and the numerals atop each indicate the number of responses to the positive and negative stimulus set, respectively. Atop the positive stimulus example is the significance of the bees' performance (from chance), beneath is the percentage correct

performance was 113 correct, 87 wrong (Fig. 3b), a relatively poor success rate of 56.5% ( $P = 0.038$ ).

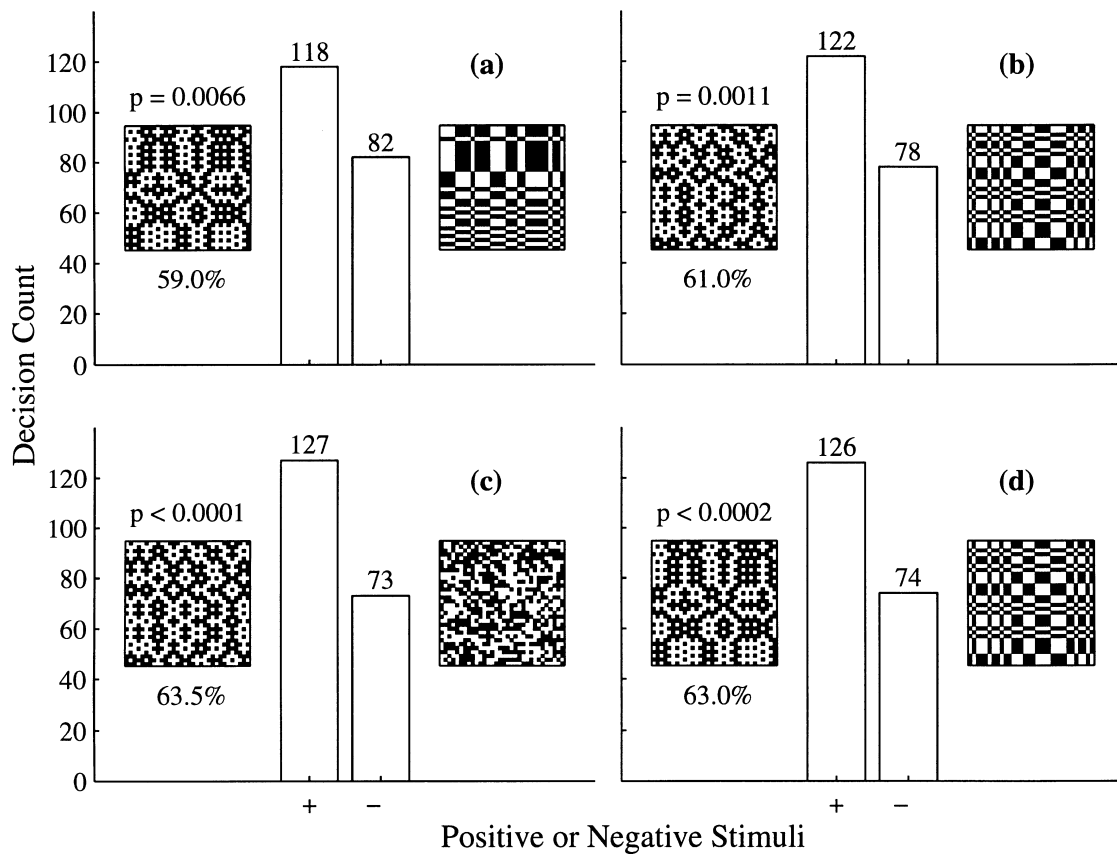
The question addressed in the third behavioural experiment was whether can the same bees spontaneously transfer what they have learned about discriminating *odd* from *even* patterns to immediately discriminate *odd* from *random* textures. This is a critical test of whether or not the bees are learning something related to the higher-order statistics of the patterns or not. To the human observer the *even* patterns have a distinctly more organised appearance than the *random* textures. Also, more *even* patterns need to be averaged to obtain an outcome which looks like random noise. By contrast individual *random* patterns are far more *ergodic*, that is individually having statistics close to the average for random noise (Gagalowicz 1981). The question is whether training with the quite different *even* and *odd* patterns can result in immediate discrimination of *odd* and *random* patterns, a task which was apparently a difficult one for bees to learn (Fig. 3b).

We also had not checked the performance on the training set before testing the bees and wished to assess whether performance changed on the switch to a related test stimulus set. Therefore, before conducting the actual experiment we assessed bee performance in the final 2 h of training with *odd* and *even* patterns. Performance was 118 correct, 82 wrong (59%,  $P = 0.0066$ , Fig. 4a).

The *odd* and *even* training sets were then swapped for a different *odd* and *even* set and (thus reproducing behavioural experiment 1) the bees' performance was 122 correct, 78 wrong (61%,  $P = 0.0011$ , Fig. 4b). On continuation of testing the following day, with the same bees, *odd/random* patterns were substituted producing 127 correct and 73 wrong responses (63.5%,  $P < 0.0001$ ). Finally, (different) *even* and *odd* patterns were reintroduced giving a performance of 126 correct, 74 wrong (63%,  $P < 0.0002$ ).

### Electrophysiology

Figure 5 shows a drawing of a lucifer yellow fill of an orientation-tuned cell from a whole mount. The cell has a presumptive dendritic field in the ipsilateral lobula and presumptive axonal fields in the contralateral mid-brain, possibly extending into the antennal lobe. We cannot rule out dye coupling to explain the smaller of the two contralateral fields as we could not see a connection between these fields. We had not previously reported (Yang and Maddess 1997) that the bee neurones we recorded from also have rectified responses to positive (bright) and negative (dark) image contrasts. The observation that the cells had rectified responses, that is ignoring the sign of the contrast, was first observed with hand-held and video stimuli employed in the course of finding our 14 previously reported orientation-tuned units (Yang and Maddess 1997). The present experiments were designed to extend this observation formally to demonstrate that orientation tuning, and temporal



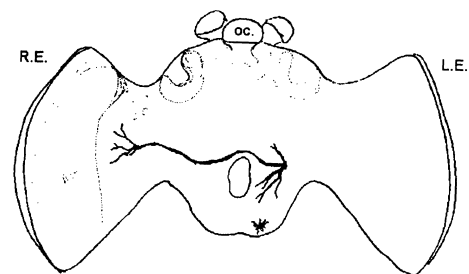
**Fig. 4a–d** Exchange of iso-dipole sets does not affect performance. **a** Bees discriminated their training set of *odd* and *even* patterns above chance performance ( $P = 0.0066$ ). **b** When a new set of *odd* and *even* patterns was introduced it was also discriminated ( $P = 0.0011$ ), as in the experiment illustrated in Fig. 3a. **c** Previously unseen *odd* and *random* patterns were introduced to the same bees the following day and these were immediately discriminated ( $P < 0.0001$ ). **d** Afterwards *odd* and *even* patterns are reintroduced and performance was unchanged ( $P < 0.0002$ ). Graphical conventions are as described for Fig. 3

response properties, are similar for stimuli which are either brighter or darker than the mean.

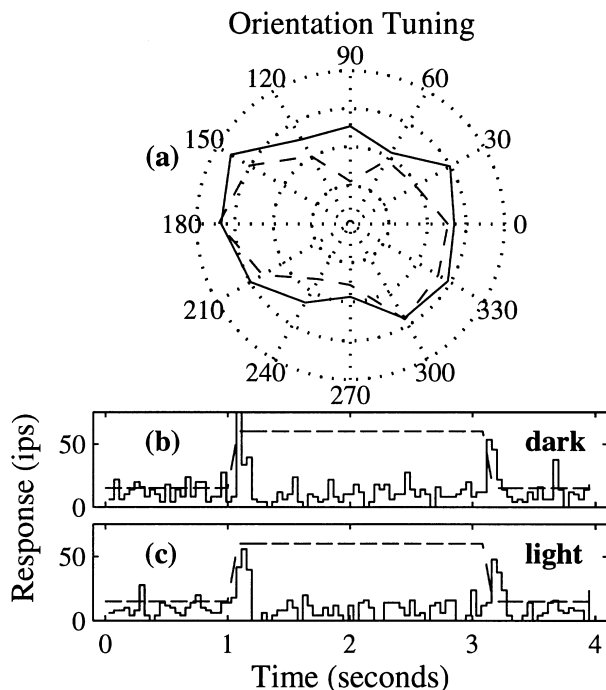
Recordings were analysed for ten experiments obtained from three cell penetrations in which one or more complete sets of orientation curves were obtained. We present data (Fig. 6) from our most stable recording in which seven complete orientation tuning data sets were obtained. In each data set seven orientations were each tested 12 times ( $0^\circ$  and  $180^\circ$  were tested as a control for recording stability internal to the data set). Since the trial time was 4 s this data set represents 1176 moving bar presentations over 39.2 min of intracellular recording time. For this cell stimuli were presented in three visual field locations along the equator ( $0^\circ$ , straight ahead;  $30^\circ$  and  $90^\circ$  lateral) and at bar contrasts of  $-50$ ,  $-20$ ,  $-10$ ,  $10$ ,  $15$ , or  $20\%$ . All responses in Fig. 6 are averages from 12 repetitions to contrast  $\pm 20\%$ , the standard errors in the responses were in the range 1–2 i.p.s. (not shown). Similar tuning curves were obtained

at  $\pm 10\%$  contrast. Low contrasts were used to prevent response saturation (Yang and Maddess 1997). For this cell the orientation tuning obtained for a bar contrast of  $-50\%$  was similar to those of Fig. 6a. The data of Fig. 6a have had their background responses removed, the background rate being computed for each stimulus presentation.

The first question is whether the responses to positive and negative contrasts both gave responses significantly different than the background rate. This was true: the mean difference from background, computed pair-wise



**Fig. 5** Drawing of an orientation-specific neuron filled with lucifer yellow. The drawing is of a whole mount as if looking at the face of the bee, hence the right eye (*R.E.*) is on the left side of the drawing and the ocelli (*oc.*) are in clear view. The neurone was recorded on right side and the axon appeared to run in the anterior optic tract. The presumptive dendritic field is in the lobula, while the presumptive axonal fields lie in or near the contralateral antennal lobe



**Fig. 6a–c** Illustration of the rectification properties of a bee orientation-selective cell to positive (bright) and negative (dark) contrast. **a** The orientation tuning curves obtained for thin, dark bars (*solid line*), and light bars (*dashed line*) moved through the visual field of a bee orientation selective cell (see Materials and methods). The *dotted circles* represent steps of 20 impulses  $s^{-1}$  (i.p.s.). **b, c** Peristimulus time histograms showing the response to movement of the bars along the 150° (*left response*) and 330° (*right response*) orientations for dark bars (**b**), and light bars (**c**). The *dashed line* gives the relative position of the line stimulus as it swept back and forth across 42° of the right eye's visual field. As is characteristic for these cells the results were similar at 0° and 90° eccentricity and the velocity tuning was also typical (not shown)

for each orientation, for light bars was  $22.9 \pm 1.72$  i.p.s. ( $P < 0.00005$ ; mean  $\pm$  SE); and for dark bars  $27.3 \pm 1.16$  i.p.s. ( $P < 0.00001$ ). The next issue is whether or not the responses to dark and light bars had exactly the same amplitude. This did not appear to be the case, the mean difference between light and dark bar responses being  $4.31 \pm 1.16$  i.p.s. ( $P = 0.005$ ), constituting a small but significant average difference of 17%. We also re-calculated the responses and statistics using two shorter temporal windows, and also using the maximum response, and the results were essentially unchanged. Based on the previously described principal component method (Yang and Maddess 1997) the preferred orientations for the light and dark bar cases were not significantly different at 169° and 171°, respectively. Despite the reversal of contrast sign response delay and temporal time-course are also similar in the 70 PSTHs obtained from our ten experiments (e.g. Fig. 4b, c). As with previously reported cells that were tested with dark bars only (Yang and Maddess 1997), position within the visual field also did not greatly alter the response character or orientation tuning.

## Discussion

Our previous electrophysiological study of bee neurones examined their orientation sensitivity and their temporal and spatial summation. The spatial summation of oriented subunits was studied by examining the summation properties of stimuli presented to divergent parts of the receptive field and also by examining the contrast response of small and wide field stimuli. In particular localised stimulation produced saturation of responses at contrasts of 30% and above but at spike rates well below the maximum for the summing cell, showing that individual subunits saturate. The present study indicates that not only are the cells computing a spatial sum over a set of many relatively small oriented spatial filters, but that those responses are also rectified. Stimulus contrast polarity has little effect on the time course or sign of the responses. This completes the main requirements for cells which could extract information equivalent to that found in the higher order correlation functions of iso-dipole and iso-trigon textures (Victor and Conte 1991).

The model of Victor and Conte (1991) has other similarities to our neurones which are worth discussing. Their model consists of a set of many small orientation-tuned subunits whose responses are averaged. The receptive fields of the orientation-tuned subunits were several times the size of the texture elements. A critical feature of their model is that there must also be *two* successive non-linearities. The first is the one we have discussed, the rectification of the oriented subunit responses. The second non-linearity is highly critical to the operation of the model, that is a strong threshold non-linearity operating on the summed subunit activity. Victor and Conte (1991) found that the threshold needed to be high to get good discrimination of random from other iso-trigon textures. This high threshold insured that the system tended to respond only when the subunits were behaving similarly, that is when the isotrigon textures were regular. Taken together these restrictions on the model mean that relatively linear summation of the subunit activity is required, followed by a high threshold. In fact the reader will appreciate from Fig. 6b that orientation cells, as we have reported before (Yang and Maddess 1997), all have a low spontaneous firing rates, and low response rates in general, indicative of a high threshold. Also, as mentioned above, subunit activity saturates well before the postsynaptic large field neurone (Yang and Maddess 1997), therefore the system is designed for fairly linear summation to occur before the high threshold. Victor and Conte (1991) found that their model matched human relative performance in discriminating the different iso-trigon texture types from noise. Electrophysiological measures from humans show that signals related to higher-order correlations are computed over the predicted spatial scales (Victor and Conte 1989).

The behavioural experiments show that bees can be trained to discriminate iso-dipole texture pairings such as *odd/even*, and *odd/random*. Furthermore, the control

at the outset of the last behavioural experiment showed that performance did not drop on going from the training to the test stimulus set. Therefore, having learned to discriminate one *odd/even* set the bees can immediately transfer their ability to a novel *odd/even* test set with no reduction in performance.

In the final behavioural experiments (Fig. 4) the bees transferred what they had learned about discriminating *odd* from *even* textures to the task of discriminating *odd* from *random* textures, again without a drop in performance, even out-performing a previous set of bees (Fig. 3b) which had first been trained on a large set of *odd/random* stimuli for 8 h before testing with *odd/random*. Finally, the 2-h period when *random* patterns were presented did not diminish the bees' ability to discriminate subsequently presented, different, *odd* and *even* patterns. Thus, it would appear that bees can discriminate iso-dipole textures from each other, and what they learn is transferable from one texture class to another rather than being dependent on the properties of a single textural class.

The question naturally arises whether these patterns be discriminated in some other way than measures related to their third-order correlation functions. Recall that whatever these other qualities might be they must allow a bee to classify a given pattern as belonging to a given set based on how the classes of patterns differ on average.

One mechanism will surely distinguish the patterns: a Singular Value Decomposition (SVD). A SVD of 2-D patterns consists of expressing the brightnesses of each pattern's checks as the sum of outer-products of pairs vectors each multiplied by a scalar (singular) value. That is the  $m$  by  $n$  pixel image  $I_{(x,y)}$  is expressed as:

$$I_{(x,y)} = \sum_1^n c_i r_i s_i, \quad (1)$$

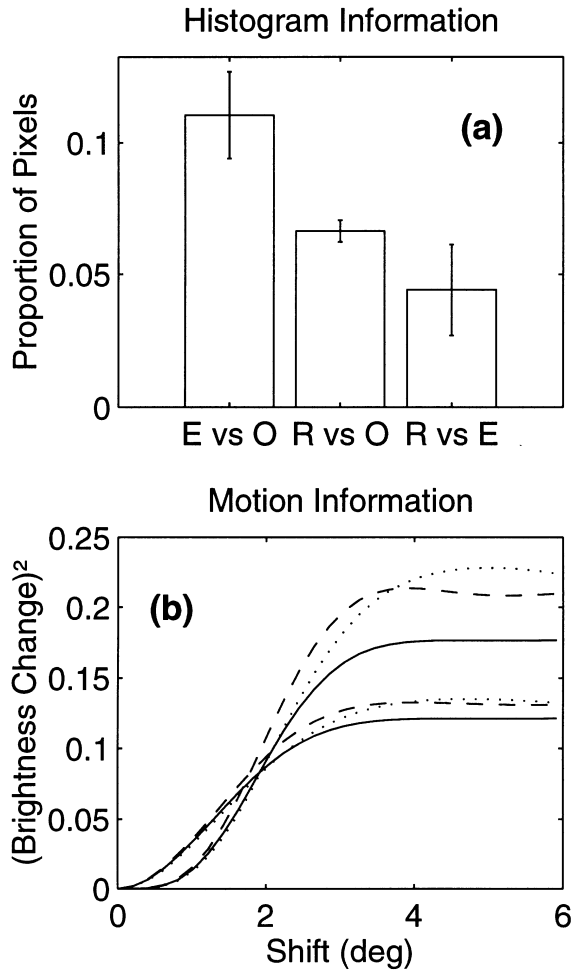
where  $c_i$ ,  $r_i$  are pairs of column and row vectors and  $s_i$  the singular values ( $n < m$ ). It can be seen by inspection that all *even* patterns, if expressed as having contrasts  $-1$  or  $1$ , are the outer product of a single pair of vectors, i.e. only one term of Eq. 1 is required. All the *odd* patterns we have examined require only two terms, while the *random* patterns have a full complement of terms with an exponentially decaying set of 32 singular values. While this would clearly distinguish the patterns it is unlikely that the bees can perform this calculation. Moreover SVD analysis says the *odd* and *even* patterns are more similar to each other (having only one or two singular values), the *random* patterns having many (32) singular values. The easiest discrimination based on SVD is thus opposite to the discrimination learned by the bees in the final behavioural experiment.

A more realistic quantity to compare might be the average intensity histograms of the collections of pattern types. Optical blurring by the bees' eyes means that more than two grey levels are present in the light received by the bees' retinas. We therefore mimicked blur by con-

volving all our patterns with a 2-degree, at half-height, circular Gaussian profile and computed the average histograms (not shown) for each of the *odd*, *even*, and *rand* pattern collections. The histograms had 20 bins between a brightness level of 0 (black) and 1 (white). It was the case that a few bins of the mean histograms systematically looked different for the three pattern collections. Figure 7a summarises the situation. We summed all the differences (always positive) of the putatively different histogram bins for different cases (*odd* versus *even*; *odd* versus *rand*, ...), computed the variances in the measures and then converted these numbers to the fraction of pixels showing the discriminating brightness. As shown in Fig. 7 the proportion of discriminating pixels was 10% or less. The calculation shows that this information could on average discriminate *even* from *odd* patterns but it would be difficult to use it to discriminate *rand* from *odd* or *even* given that the differences in these same grey levels are not significantly different in these patterns and they occur in similar proportions. One needs to bare in mind that the bees encounter each pattern individually and must categorise the presented pattern into a class; thus, the bee's task is in the realm of Discriminant Analysis where the determining factor as to whether or not a single sample can be categorised a given population group is the (co)variance of those populations and not the standard errors (Johnson and Wichern 1992).

It is also possible that information could be extracted from motion cues extracted from the patterns if the bees scanned across the target (Lehrer and Srinivasan 1994). This scanning behaviour is unlikely given our set-up, however, to examine this possibility we computed the sum of the squared differences of shifted versions of the blurred versions of the patterns. Thirty shifts were computed for each pattern and the mean and median squared brightness changes within each of the *rand*, *odd* and *even* classes were computed. Note that this process is equivalent to computing the output of an array of Reichardt half-cell motion detectors with either 30 different input separations or 30 different delays. Separate means for horizontal, vertical and diagonal shifts were obtained. The basic findings were that the means and medians (not shown) were very similar for all three texture types. Any small differences between the mean curves which could be used to classify a given pattern as being a member of any particular set were swamped by large standard deviations (Fig. 7b). The story was the same for vertical and diagonal translations.

It would appear that a number of simple cues which might be thought to be potentially useful in discriminating these textures in the way that the bees behaved cannot do the job. More sophisticated models might be able to achieve the desired outcome. It should be kept in mind, however, that the calculation which has been proposed to permit extraction of cues about higher order statistics (Victor and Conte 1991), is only slightly more complex than used for the calculation of the curves in Fig. 7b. The only additional feature being the calcula-



**Fig. 7a** Summary of investigation of the use of brightness histograms as a means of discriminating the textures. The mean histograms of the brightnesses found in blurred versions of the *random*, even and *odd* textures were computed with 20 bins over the range of the data. A small proportion of bins (grey levels) from the mean histograms for *random* and *even* patterns appeared to differ in the mean histograms. The bars represent the proportion of pixels within the images that differ in these particular grey levels. Comparisons at these particular grey levels are made for each pairing of textures. Thus, the large index for *even* and *odd* (*E vs O*) indicates that about 10% of pixels of a particular putatively characteristic brightness differed in abundance between the patterns. The same calculation for *random* and *even* patterns (*R vs E*), and *random* and *odd* (*R vs O*) reveals that a smaller proportion of these brightness differ in the same way between these patterns and so could not be used to distinguish *random* patterns from either of the other two textures. **b** Comparison of brightness changes for shifting blurred versions of the test patterns to mimic the effects of bee motion. The squared differences between the original position and various shifted position were computed and the means of the individual squared differences were stored. The *three lower curves* show how these means vary with shift distance for horizontal translation of the *even* (solid line), *odd* (dashed) and *random* (dotted) textures. The *upper three curves* represent the standard deviations in the means (same line conventions). Even when small differences between the means exist the variation across textures is too large for a given test pattern to be classified as being from any particular group

tion of *oriented* energy. An appeal cannot be made for the *local-statistics* to be different given that the correla-

tion functions are the same everywhere and therefore short-range correlations are identical as well.

Human visual performance in discriminating iso-dipole patterns from noise patterns has been assessed psychophysically (Victor and Conte 1991) and by visual-evoked potentials (Victor and Conte 1989, 1991; Victor and Zemon 1985). Evidence for orientation-tuned mechanisms was found to be necessary to explain the VEP response components related to higher order statistical properties of the textures (Victor and Conte 1989, 1991; Victor and Zemon 1985). Human performance in discriminating iso-dipole patterns (obscured by various forms and degrees of decorrelation (Victor and Conte 1989, 1991) from *random* patterns was found to be well described by a model corresponding to neurones spatially summing a large array of small detectors which individually show orientation tuning followed by rectification (Victor and Conte 1991). This is reminiscent of neurones in area 21a of the cat visual cortex (Dreher et al. 1993; Wimbome and Henry 1992).

The findings of Victor and co-workers were not too surprising given that human discrimination of other textures had been shown to be due to complex channels composed of rectified oriented receptive fields (Beck et al. 1987; Landy and Bergen 1991; Sutter et al. 1989). What was surprising is that these outwardly simple mechanisms are obviously very robust in that they can extract sufficient information even to discriminate textures which differ in mathematically very complex ways. It would be interesting if insects used a similarly robust strategy to discriminate textures. Such convergent evolution might suggest that the strategy is a computationally efficient one.

Taken together, our findings on the bee neurones and bee discrimination of iso-dipole stimuli, indicate that the class of neurones in insects displaying orientation tuning over wide portions of the visual field (Yang and Maddess 1997) may be part of a general texture discrimination mechanism. Bees have previously been shown to abstract the global orientation of textures (Srinivasan et al. 1993; van Hateren et al. 1990). Directionally selective neurones with small visual fields and orientation-selective neurones with very large visual fields have been described in dragonflies (O'Carroll 1993) and the inference has been drawn that these cells may form a basis for visual processing similar to that found in the vertebrate visual cortex (O'Carroll 1993; Srinivasan et al. 1993). By this it should not be construed that those authors meant that insects are attempting a wavelet-style transform of the image (Field 1994; Geisler and Hamilton 1986) where the goal is probably to encode the image with the fewest active neurones (Field 1994; Olshausen and Field 1996), but rather that insect *pattern vision* is accomplished by a mechanism which exploits orientation cues.

The ability of bees to use information equivalent to the higher-order correlation functions of images is a formal statement about the dimensionality of the total palette of textures (space) that can be discriminated by bees. Thus, our findings are not unlike discovering that

an animal previously thought to have two photoreceptor types actually has a third, and that it makes use of the potential extra chromatic information in its larger dimensional colour palette (space). The analogy extends to the stimuli used in both kinds of experiments. For colour vision work we commonly use quite unnatural stimuli to demonstrate functional trichromacy (Hemmi et al. 1998). We have similarly used quite unnatural textures, but with certain desirable quantitative features, to demonstrate the use of information contained in high-dimensional texture spaces by bees.

The advantages of using higher-dimensional spaces for image recognition are well understood (Schölkopf et al. 1998). For example, if we have an image of two pixels  $a$  and  $b$ , the second-order correlation contains information about  $\{a^2, ab, b^2\}$ , which can be thought of as casting the picture in terms of a three dimensional *feature* space. Third-order products yield a larger basis set  $\{a^3, ab^2, a^2b, b^3\}$ . In general if we consider products up to degree  $d$  for a picture of  $N$  pixels then the dimensionality of the feature space is  $(N + d - 1)! / d!(N - 1)!$  which grows as  $N^d$  (Schölkopf et al. 1998). We do not know yet over how many pixels the bee can compute this sort of information but if we take 16 for the moment then we find that as the order of products (correlations) is increased over the range  $\{1, 2, 3, 4\}$  the dimensionality of the corresponding feature spaces is  $\{16, 136, 816, 3876\}$ . Thus, our demonstration that bees can distinguish iso-dipole textures indicates that their feature space for texture discrimination is potentially  $N^3/N = N^2$  times bigger than if they use intensity information alone. If the slight optical blurring of our large textures leaves them as iso-trigon textures then the bee texture palette is  $N^3$  times bigger than if they use intensity alone. Further experiments are required to determine if they can use the whole of this space. Schölkopf et al. (1998) have shown that these higher-order correlations need not be calculated directly but can be obtained by short-cut computations resembling receptive field like operations upon images.

Our investigation was prompted by the demonstration that orientation-selective cells composed of the sum of many small oriented units occurred in bees (Yang and Maddess 1997). We have shown here that these neurones have the additional requisite qualities of rectifying the small field unit response, followed by spatial summation and a strong threshold. Spatial summation of small field units, each unit having independently regulated gain and dynamics, is characteristic of insect vision (Osorio 1991), such behaviour being well established in wide field motion sensitive neurones in vertebrates (Ibbotson et al. 1994) and invertebrates (de Ruyter van Steveninck et al. 1986; Ibbotson et al. 1991; Maddess 1986; Maddess et al. 1991; Maddess and Laughlin 1985). In humans the texture system appears to provide input to a motion detection system (Turano and Pantle 1989; Werkhoven et al. 1993, 1994) with slower dynamics than normal motion detection (Victor and Conte 1990) and may be the basis of slow higher-order motion detection for such

tasks as *feature tracking* (Lu and Sperling 1995). Neurones able to abstract figure from background motion occur in insects (Egelhaaf 1985). While it is not yet clear whether textural feature tracking systems also exist in insects, the present work demonstrates that the prerequisite ability for complex texture discrimination does exist in insects, suggesting that insect pattern vision may be more like our own than previously thought. Such computational parallels are perhaps not unexpected given that evolution would likely be driven to particular parsimonious solutions when they exist.

**Acknowledgements** We would like to thank J. D. Victor and B. Schölkopf for helpful discussions, and also our reviewers for providing insightful comments. This paper is dedicated to G. A. Horridge in his 70th year.

## Appendix

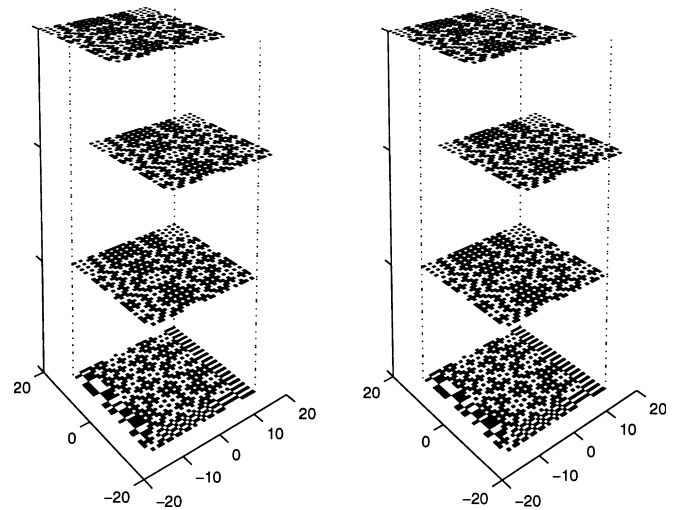
The first-order correlation function  $S_{1,f}$  of an image over  $x,y$  space is

$$S_{1,f} = \frac{1}{A} \iint f(x,y) dx dy. \quad (a1)$$

If the area of the checks is 1 then the total area  $A = N$

$$S_{1,f} = \frac{1}{N} \iint f(x,y) dx dy. \quad (a2)$$

So  $S_{1,f}$  is clearly the mean, i.e. the sum over all the checks ( $-1$  or  $1$ ) divided by  $N$ .



**Fig. 8** This stereo pair illustrates the central process in computing the third-order correlation function given by Eq. a4. The *upper figure* shows three copies of an *odd* texture in translated to three  $xy$  positions. The *figure at the bottom* is the pointwise products of the pixels of the three upper copies. That is:  $f(x, y) f(x + h_1, y + v_1) f(x + h_2, y + v_2)$  for a particular set of displacements  $h_1, v_1, h_2, v_2$ . According to Eq. a4 the whole of the bottom image is then summed and then divided by  $N$  to produce a point in the third-order correlation function  $S_{3,f}(h_1, v_1, h_2, v_2)$ . This process is repeated for every possible shift of three copies of the image where triple products exist. Note that this process is equivalent to calculating the average triple (trigon) product for every position in the original image. The units of the bottom axes are pixels, the labels having been left off to assist in achieving binocular fusion

The second-order correlation function or *autocorrelation function*  $S_{2,f}(h,v)$  is just

$$S_{2,f}(h,v) = \frac{1}{N} \iint f(x,y)f(x+h,y+v) dx dy, \quad (\text{a3})$$

the  $(x+h, y+v)$  term denoting that all possible horizontal and vertically shifted copies of the image,  $f(x+h, y+v)$  are multiplied, point-wise, with the image  $f(x, y)$ , and then the sum of all those products are placed at  $h_i, v_j$  in the output matrix. (Note: in our case there are fixed step sizes  $\Delta x$  and  $\Delta y$ , not infinitely small steps  $dx$  and  $dy$ ). The Fourier transform of  $S_{2,f}(h,v)$  is the power spectrum of  $f(x, y)$  (as opposed to the amplitude spectrum.)

The third-order correlation function  $S_{3,f}(h_1, v_1, h_2, v_2)$  is

$$S_{3,f}(h_1, v_1, h_2, v_2) = \frac{1}{N} \iiint f(x,y)f(x+h_1, y+v_1)f(x+h_2, y+v_2) dx dy. \quad (\text{a4})$$

Notice that  $S_{3,f}(h_1, v_1, h_2, v_2)$  is a two dimensional function also, where the sums of products of the image with every shifted version, and every shifted version (again), are computed. Notice that if  $f(x,y)$  can be negative  $S_{3,f}(h_1, v_1, h_2, v_2)$  can be also. When  $h_2$  and  $v_2$  are 0 the third-order correlation reduces to second order, so  $S_{3,f}(h_1, v_1, h_2, v_2)$  contains all the information of the lower-order correlations. Figure 8 illustrates one step in computing  $S_{3,f}(h_1, v_1, h_2, v_2)$ . The fourth-order correlation simply has another term in  $h_3, v_3$  vis.  $S_{4,f}(h_1, v_1, h_2, v_2, h_3, v_3)$ .

## References

- Beck J (1983) Textural segmentation, second-order statistics, and textural elements. *Biol Cybern* 48: 125–130
- Beck J, Sutter A, Ivry R (1987) Spatial frequency channels and perceptual grouping in texture segregation. *Comput Vision Graphics Image Process* 37: 299–325
- Chubb C, Sperling G (1991) Texture quilts: basic tools for studying motion-from-texture. *J Math Psychol* 35: 411–442
- Dreher B, Michalski A, Ho RHT, Lee CWF, Burke W (1993) Processing of form and motion in area 21a of cat visual cortex. *Vis Neurosci* 10: 93–115
- Egelhaaf M (1985) Figure-detection cells, a new class of visual interneurons. *Biol Cybern* 52: 195–209
- Field DJ (1994) What is the goal of sensory coding? *Neural Comput* 6: 559–601
- Gagalowicz A (1981) A new method for texture fields synthesis: some applications to the study of human vision. *IEEE Trans Pat Anal Mach Int* 3: 520–533
- Geisler WS, Hamilton DB (1986) Sampling-theory analysis of spatial vision. *J Opt Soc Am A* 3: 62–70
- Giger AD (1997) Analysis of pattern orientation in the honeybee: temporal constraints. *Naturwissenschaften* 84: 308–311
- Giger AD, Srinivasan MV (1995) Pattern recognition in honey bees: eidetic imagery and orientation discrimination. *J Comp Physiol A* 176: 791–795
- Giger AD, Srinivasan MV (1996) Pattern recognition in honey bees: chromatic properties of orientation analysis. *J Comp Physiol A* 178: 763–769
- Gilbert EN (1980) Random colorings of a lattice on squares in the plane. *SIAM J Algebra Dis Methods* 1: 152–159
- Graham N, Sutter A (1996) Effect of spatial scale and background luminance on the intensive and spatial non-linearities in texture segregation. *Vision Res* 36: 1371–1390
- Graham N, Sutter A, Venkatesan C, Humaran M (1992) Non-linear processes in perceived region segregation: orientation selectivity of complex channels. *Ophthal Physiol Opt* 12: 142–146
- Hateren JH van, Srinivasan MV, Wait PB (1990) Pattern discrimination in bees: orientation discrimination. *J Comp Physiol A* 167: 649–654
- Hemmi JM, Maddess T, Mark RF (1998) Spectral sensitivity of photoreceptors in an Australian marsupial, the tammar wallaby (*Macropus eugenii*). *J Comp Physiol A*
- Ibbotson MR, Maddess T, Dubois RA (1991) A system of insect neurons sensitive to horizontal and vertical image motion connects the medulla and midbrain. *J Comp Physiol* 169: 355–367
- Ibbotson MR, Mark RF, Maddess T (1994) Spatiotemporal response properties of direction selective neurons in the nucleus of the optic tract and dorsal terminal nucleus of the wallaby. *J Neurophysiol* 72: 2927–2943
- Johnson RA, Wichern DW (1992) Applied multivariate statistical analysis, 3rd edn. Prentice Hall, New Jersey
- Julesz B, Gilbert EN, Shep LA, Frisch HL (1973) Inability of humans to discriminate between visual textures that agree in second-order statistics – revisited. *Perception* 2: 391–405
- Julesz B, Gilbert EN, Victor JD (1978) Visual discrimination of textures with identical third-order statistics. *Biol Cybern* 31: 137–140
- Klein SA, Tyler CW (1986) Phase discrimination of compound gratings: generalized autocorrelation analysis. *J Opt Soc Am A* 3: 868–879
- Landy MS, Bergen JR (1991) Texture segregation and orientation gradient. *Vision Res* 31: 679–691
- Lehrer M, Srinivasan MV (1994) Active vision in honeybees: task-oriented suppression of an innate behaviour. *Vision Res* 34: 511–516
- Lu ZL, Sperling G (1995) The functional architecture of human visual motion perception. *Vision Res* 35: 2697–2722
- Maddess T (1986) Afterimage-like effects in the motion-sensitive neuron H1. *Proc R Soc Londser B* 228: 433–459
- Maddess T, Laughlin SB (1985) Adaptation of the motion-sensitive neuron H1 is generated locally and governed by contrast frequency. *Proc R Soc Londser B* 225: 251–275
- Maddess T, Dubois RA, Ibbotson M (1991) Response properties and adaptation of neurons sensitive to image motion in the butterfly *Papilio aegaeus*. *J Exp Biol* 161: 171–199
- O'Carroll D (1993) Feature-detecting neurons in dragonflies. *Nature (Lond)* 362: 541–543
- Olshausen BA, Field DJ (1996) Emergence of simple-cell receptive field properties by learning a sparse code for natural images. *Nature (Lond)* 381: 607–609
- Osorio D (1991) Mechanisms of early visual processing in the medulla of the locust optic lobe: how self-inhibition, spatial pooling, and signal rectification contribute to the properties of transient cells. *Vis Neurosci* 7: 345–355
- Ruyter van Steveninck RR de, Zaagman WH, Mastebroek HAK (1986) Adaptation of transient responses of a motion-sensitive neuron in the visual system of the blowfly *Callifora erythrocephala*. *Biol Cybern* 54: 223–236
- Schölkopf B, Smola A, Miller K-R (1998) Non-linear component analysis as a kernel eigenvalue problem. *Neural Comput* 10: 1299–1319
- Srinivasan MV, Lehrer M (1988) Spatial acuity of honeybee vision, and its spectral properties. *J Comp Physiol A* 162: 159–172
- Srinivasan MV, Zhang SW, Rolfe B (1993) Is pattern vision in bees mediated by 'cortical' processing? *Nature (Lond)* 362: 539–540
- Srinivasan MV, Zhang SW, Rolfe B (1994) Visual discrimination of pattern orientation by honey bees: performance and implications for 'cortical' processing. *Philos Trans R Soc Londser B* 343: 199–210
- Sutter A, Beck J, Graham N (1989) Contrast and spatial variables in texture segregation: testing a simple spatial-frequency channels model. *Percept Psychophys* 46: 312–332
- Turano K, Pantle A (1989) On the mechanism that encodes the movement of contrast variations: velocity discrimination. *Vision Res* 29: 207–221
- Victor JD (1994) Images, statistics and textures: implications of triple correlation uniqueness for texture statistics and the Julesz conjecture: comment. *J Opt Soc Am. A* 11: 1680–1684
- Victor JD, Conte MM (1989) Cortical interactions in texture processing: scale and dynamics. *Vis Neurosci* 2: 297–313

- Victor JD, Conte MM (1990) Motion mechanisms have only limited access to form information. *Vision Res* 30: 289–301
- Victor JD, Conte MM (1991) Spatial organization of nonlinear interactions in form perception. *Vision Res* 31: 1457–1488
- Victor JD, Zemon V (1985) The human visual evoked potential: analysis of components due to elementary and complex aspects of form. *Vision Res* 25: 1829–1842
- Werkhoven P, Sperling G, Chubb C (1993) The dimensionality of texture-defined motion: a single channel theory. *Vision Res* 33: 463–485
- Werkhoven P, Sperling G, Chubb C (1994) Perception of apparent motion between dissimilar gratings: spatiotemporal properties. *Vision Res* 34: 2741–2759
- Wimborne BM, Henry GH (1992) The visual response properties of cells in cortical area 21a of the cat. *J Physiol (Lond)* 449: 457–478
- Yang EC, Maddess T (1997) Orientation-sensitive neurons in the brain of the honeybee (*Apis mellifera*). *J Insect Physiol* 43: 329–336
- Yellott JI (1993) Implications of triple correlation uniqueness for texture statistics and the Julesz conjecture. *J Opt Soc Am A* 10: 777–793