Tilt aftereffect for texture edges is larger than in matched subjective edges, but both are strong adaptors of luminance edges

Sarah J. Hawley
School of Psychology, University of Wales, Bangor, United Kingdom

David R. Keeble
Department of Optometry, University of Bradford, Bradford, United Kingdom

The tilt aftereffect (TAE) has been used previously to probe whether contours defined by different attributes are subserved by the same or by different underlying mechanisms. Here, we compare two types of contours between texture surfaces, one with texture orientation contrast across the edge (orientation contrast contour; OC) and one without, commonly referred to as a subjective contour (SC). Both contour types produced curves of TAE versus adapting angle displaying typical positive and negative peaks at ~15 and 70 deg, respectively. The curves are well fit by difference of Gaussian (DoG) functions, with one Gaussian accounting for the contour adaptation effect and the other accounting for the texture orientation adaptation effect. Adaptation to OC elicited larger TAEs than did adaptation to SC, suggesting that they more effectively activate orientation-selective neurons in V1/V2 during prolonged viewing. Surprisingly, both contour types adapted a luminance contour (LC) as strongly as did an LC itself, suggesting that the second-order orientation cue contained in the texture edge activates the same set of orientation-selective neurons as does an LC. These findings have implications for the mechanisms by which the orientations of texture edges and SCs are encoded.

Keywords: tilt aftereffect, texture edges, subjective contours

Introduction

Texture surfaces in natural visual scenes are often bounded by contours composed of aligned line endings where surfaces abut or overlap. Textures separated by a boundary contour in this way may differ in properties such as their orientation or frequency spectra. Such boundaries are often referred to as “texture edges.” However, another type of texture edge occurs when the two abutting textures are identical. In this case, the boundary between them is revealed by aligned line endings only, as the surfaces on either side are identical. This type of contour is more usually described as a subjective contour (SC). The comparison of SCs of this type with the case where adjacent textures surfaces differ in orientation is rarely made as the two types of contour, “at first glance,” appear to be so different. The detection of orientation contrast, for example, across a border, is considered to be “preattentive,” that is, strongly perceived without conscious effort (cf. Treisman, 1985). In comparison, the appearance of SCs is usually considered to be more phenomenal, perhaps dependent on observer interpretation, and not unambiguously preattentive (for a review, see Pritchard & Warm, 1983). Hence, contours defined by texture orientation contrast would appear to be “stronger” visual stimuli in some way.

Nevertheless, despite differences in their perceptual qualities, the two types of contour have some important physical similarities. In both cases, there are no local first-order cues as to the orientation of the contour, such as a luminance or color discontinuity. Integration of local information is necessary for the orientation percept of even a luminance contour (LC), as the initial input of visual information is in the form of discrete localized points of information, which cannot unambiguously signal global properties (Nothdurft & Li, 1985). However, in the case of an LC, its orientation could be conceived to be the result of “linking” of first-order information already represented at a local level. For both of the texture surface boundaries described, the orientation attribute of the boundary is clearly a result of processing subsequent to the initial input. In many ways, both types of texture boundary, both with and without orientation contrast, could be described as “subjective” (cf. Bergen, 1991). However, for the remainder of this paper, texture edges with orientation contrast will be described as “orientation contrast contours” (OCs) and those without will be described as subjective contours (SCs).

Despite the well-documented phenomenon of effortless texture segmentation due to orientation contrast (Beck, 1966; Julesz, 1981; Julesz & Bergen, 1983; Landy & Bergen, 1991; Nothdurft, 1985), it is not clear that the strong visibility of a region of different orientation necessarily implies that orientation contrast across a texture edge elicits a stronger border percept than without, that is, where only an SC remains. SCs and texture orientation-defined
contours show similar orientation discrimination thresholds (Regan, 1995; Vogels & Orban, 1987; Westheimer & Li, 1996, 1997), and the orientation of both types of contour may first be encoded in the response of V2 neurons (Baumann, van der Zwan, & Peterhans, 1997; Leventhal, Wang, Schmolesky, & Zhou, 1998; von der Heydt & Peterhans, 1989; von der Heydt, Peterhans, & Baumgartner, 1984). While differences in perceptual qualities suggest that the two types of second-order contour described may differ in their processing, the end result of the processing in terms of the site of contour orientation encoding may not be different. Hence, we pose the question, does the addition of orientation contrast across the texture edge alter the encoding of contour orientation in the final percept?

We address this question using the tilt aftereffect (TAE), a misperception in orientation following prior viewing of an oriented stimulus. The TAE and related tilt illusion (TI) have both been used extensively to probe whether contours defined by different attributes are subserved by the same or by different underlying mechanisms (Berkley, Debruyne, & Orban, 1994; Bockisch, 1999; Clifford, Pearson, Forte, & Spehar, 2003; Georgeson & Schofield, 2002; Paradiso, Shimojo, & Nakayama, 1989; Poom, 2000; van der Zwan & Wenderoth, 1994). The basic premise of such experiments is that changes in perception of a test stimulus caused by a previously or simultaneously presented “adaptation” stimulus are attributable to a common stage of orientation representation of the two stimuli. In the case of the TAE, prolonged viewing of an “adaptation” line or grating causes a shift in the perceived orientation of a subsequently viewed “test” line/grating. A maximal repulsive effect is seen for adapt and test stimuli differing in orientation by 10–20 deg, using either gratings (Poom, 2000; van der Zwan & Wenderoth, 1995) or lines (Blakemore, Carpenter, & Georgeson, 1970; Carpenter & Blakemore, 1973; Paradiso et al., 1989; Skottun, Johnsen, & Magnussen, 1981). A less prolonged misperception of test angle can also be seen with very short “adaptation” presentations (e.g., Harris & Calvert, 1989). This repulsive misperception has been termed the “direct” effect and is generally accepted to be the result of altered patterns of activity in orientation-selective neurons in V1/V2, most likely due to inhibitory interactions (Blakemore et al., 1970; Carpenter & Blakemore, 1973; Magnussen & Kurtenbach, 1980a, 1980b; Morrone, Burr, & Maffei, 1982; Wenderoth & Johnstone, 1987). Hence, the existence and magnitude of the direct effect between contour types can be considered a measure of their shared sites of encoding in at this early level.

An attractive misperception, whereby the test orientation appears shifted towards the adapting orientation signal, is sometimes also seen. This effect peaks at an adapt-test orientation difference of approximately 70 deg. The mechanism of this “indirect” effect is more disputed. It may also be due to inhibitory interactions, but in this case between orientation-selective mechanisms in higher cortical areas involved in the processing of global stimulus properties (Poom, 2000; van der Zwan & Wenderoth, 1995; Wenderoth & Johnstone, 1988).

In this study, we measured TAEs for two types of contour between textured areas, both of which elicited the percept of abutting or overlapping surfaces. One type of contour demarcated two identical textures; hence, the edge was defined by aligned texture line endings only (SC; Figure 1). The other type of contour demarcated two texture surfaces of different orientations; hence, there was also an orientation contrast across the edge (OC; Figure 2). TAEs have previously been observed using both “single” SCs (Paradiso et al., 1989; van der Zwan & Wenderoth, 1994, 1995) and gratings defined by SCs (Berkley et al., 1994; Bockisch, 1999; Montaser-Kouhsari & Rajimehr, 2004). They have also been shown to interact with LCs (Berkley et al., 1994; Bockisch, 1999; Paradiso et al., 1989). Tilt aftereffects using texture edges defined by orientation contrast have not, to our knowledge, previously been investigated. However, the existence of filters tuned to the orientation of such texture edges is strongly suggested by the effect of adaptation to orientation-defined form on its perceived spatial location (Prins & Mussap, 2001) and on contrast thresholds for its detection (Kwan & Regan, 1998).

Stimulus presentation times in our study were sufficient for contour orientation resolution to reach a maximum, as measured in an initial orientation discrimination experiment (Experiment 1). We wanted to test the encoding of fully processed contours, and we took the time required for maximal orientation discrimination as an indicator of the time required for maximal orientation encoding of our

![Figure 1. An adapting stimulus for the SC condition. The contour presented here is at 15 deg anticlockwise and is within a texture that is at 90 deg to the contour. Test SC stimuli were very similar, differing only in that the texture was always horizontal, regardless of the angle of the SC contour.](Image)
contours. This time was then used when presenting the contours in the TAE parts of our study. In Experiment 2, we measured the intra-contour-type TAEs (adapt-test conditions OC–OC and SC–SC) over a range of adapting angles to verify that both contour types displayed misperceptions of contour angle following adaptation. This experiment allowed us to quantify the variation of TAE with adapting angle for comparison with previous studies and to locate the adapting angle for which maximum misperception of a test contour occurred. We also measured the adaptation effect of texture stimuli that did not contain an adapting central contour (Figure 3) on the same texture contour test stimuli. This control condition was conducted because the contour stimuli contained both a second-order orientation cue in the form of the contours themselves and also a first-order orientation cue in the form of the abutting textures that induced the SC and OC contours. While we wished to observe the effect of adapting to the SC and OC contours, it became apparent that adaptation to the textures themselves could also affect subsequent misperceptions of the test contour orientation. This effect was quantified, and it was shown that the direct TAE observed with the texture contours was not due to adaptation to the orientation of the composing textures.

In Experiment 3, we measured the TAE at the maximal adaptation angle found in Experiment 2 (15 deg) for cross-adaptation conditions between OC and SC. Total transfer of adaptation effects between our matched SC and OC contours would indicate that the presence of orientation contrast does not affect the final encoding of orientation of a texture surface edge, whereas nonexistent transfer would point to mutually exclusive mechanisms for the orientation encoding of the two texture contours. Although both types of contour contain aligned line endings, it could be that the presence of orientation contrast across the edge is a “strong” cue, which effectively “overrides” weaker mechanisms processing SCs. Incomplete transfer of adaptation between contour types would suggest limited shared sites of orientation encoding. We also measured the interaction of the texture contours with an LC. An LC can be expected to elicit response in cells tuned to the orientation of the contour in both V1 and V2, and so a comparison of the adaptation effect of LC compared to OC and SC will indicate the extent to which the texture contours activate this population of neurons.

**Methods and results**

### Observers

Four observers participated in these experiments. The authors, SH and DK, were experienced psychophysical observers. Observers JI and AB were inexperienced observers who were naive to the purpose of the experiment. All subjects had normal or corrected-to-normal vision.

### Stimuli and apparatus

Stimuli were produced using a G3 PowerMac computer and were displayed on a ProNitron monitor that had...
a pixel resolution of 30 pixels deg\(^{-1}\) at a viewing distance of 58 cm. All stimuli were presented within a circular aperture with a diameter of 20 deg, created by placing a dark card over the monitor. The display was viewed in a dark room, and the monitor edges and other cues to vertical and horizontal were not visible when attending the stimulus. Observers’ head position was stabilized by use of a head and chin rest.

Two types of texture contour stimuli were used as adapting and test stimuli. Textures were composed of randomly placed line elements, of lengths drawn from a square distribution ranging from 2 to 25 arcmin. Line widths were always 1 pixel, or 2 arcmin. Line elements were presented at a Weber contrast of 50% on a uniform grey background at 33 cd m\(^{-2}\). Contours passed through the central point of the display, which was marked by a maximum contrast fixation point during all phases of stimulus presentation. A central fixation point was used to maximize localization of the “adaptation” effect within retinotopically mapped V1 and V2. SCs demarcated two texture areas of identical orientation and were defined only by the alignment of line endings (Figure 1); if a randomly placed line element extended to the contour, it was terminated at that location. This was achieved by creating two full-screen textures and then splicing them together at the location of the contour, hence avoiding luminance artefacts that could result from anti-aliased line endings. For SC-adapting stimuli, texture was always oriented at 90 deg to the contour, but for SC test stimuli the texture had a fixed texture orientation of 90 deg regardless of the contour orientation so as to prevent texture orientation from cueing the test contour orientation. OCs were similarly defined by the alignment of line endings, and also by a change of texture orientation across the contour (Figure 2). The two areas of texture were oriented at ±75 deg relative to the OC for adapting stimuli, and at an absolute value of ±75 deg to vertical for OC test stimuli, with the order of the two texture orientations across the contour being randomized. (Again, the use of fixed texture angles for test stimuli meant that texture orientation could not cue contour orientation.) The total orientation contrast across the contour was therefore 30 deg, which elicits a maximum perception of two distinct regions (Motoyoshi & Nishida, 2001). The high density of line endings throughout both SC and OC stimuli meant that an isolated cluster of line endings was unlikely to signal the presence of the contour to observers. It was intended that integration of local components on a larger scale should be required to indicate the presence of an SC. An LC was also used in some conditions. This was a dark line of 2 arcmin (1 pixel) width presented at 50% Weber contrast on the same grey background. All contour types extended across the full diameter of the circular viewing aperture.

To ascertain whether adaptation effects after viewing OC and SC stimuli were due to adaptation to the contour orientation, or to adaptation to the first-order orientation cue of the texture lines, two control texture stimuli were created. The possibility that the lines inducing an SC, rather than the SC itself, may be contributing to the observed TAE has not, to our knowledge, been previously considered. The control texture stimuli were matched to the textures composing the SC and OC stimuli but did not contain a central contour; textures continued uninterrupted across the screen (Figure 3). The SC-matched control (SCC) consisted of unbroken texture at the same angle as would have been used to induce an SC in any given stimulus presentation. The OC-matched control (OCC) could have one of two texture orientations, as the OC contour stimulus contained two texture orientations. In this case, the texture orientation is any single 500ms presentation period was chosen randomly from the two available orientations. The SCC and OCC textures were used as adapting stimuli in trials with SC and OC test contours, respectively.

**Experiment 1: Time course of orientation discrimination for OCs and SCs**

Experiment 1 measured orientation discrimination thresholds for OCs and SCs as a function of stimulus presentation duration. This experiment was conducted to compare the orientation resolution of the two contours and to find the presentation duration required for maximal orientation resolution. A presentation duration that produces maximal orientation resolution, presumed to equate to maximal low-level orientation encoding, would be used for the later TAE experiments. Subjects SH and DK were used for this experiment.

The method of constant stimuli was used to present contours at a range of orientations close to vertical. Contours orientations ranged from −3 to 3 deg, at intervals of 0.75 deg. Observers indicated, by means of a key press, whether the presented contour was tilted clockwise or anticlockwise. Observers were free to respond in their own time, with response initiating the next stimulus presentation. Contours were presented for 50, 100, 200, 500, or 1000 ms. Trials were blocked for contour type and presentation duration, with a total of 360 observations completed for each combination of contour type and presentation time. Probit analysis (Finney, 1971) was used to fit psychometric functions to the data, giving the position of perceived vertical (PV) and the standard deviation of the PV, also called the orientation discrimination threshold (the orientation yielding a performance of 84% correct for a PV of 0).

**Results of Experiment 1**

Both subjects showed a bias in PV, with observer SH judging contours to be tilted clockwise and observer DK tilted anticlockwise. Biases for both observers were <1 deg and did not differ with contour type or presentation...
time. These biases can be a true misperception of PV or because clockwise and anticlockwise responses were always indicated by the same key presses, a bias in response. However, as the bias was constant for each observer, this does not affect our later comparisons of TAE.

The results for the orientation discrimination threshold are displayed in Figure 4. Both observers showed a decrease in threshold with time. Thresholds initially drop sharply but then plateau, showing little further decrease beyond presentation times of 300–400 ms. At presentation times beyond 100 ms, threshold values are not significantly different between the contours. As we wished to observe adaptation effects for borders that were maximally encoded, we subsequently used presentation times of 500 ms for both contour types when measuring PV before and after adaptation and a corresponding presentation frequency of 2 Hz when refreshing contour stimuli during adaptation. Shorter stimulus presentation times may give larger TAEs (Wolfe, 1984), but this would defeat the purpose of our experiment, to compare the orientation encoding of the two types of second-order contour at a point in time when they are maximally encoded. In addition, the misperception of orientation observed using short (<100 ms) stimulus presentations may in fact be subserved by different mechanisms to those underlying the misperception seen with the longer stimulus presentations (Wolfe, 1984) that are more usually used in TAE studies.

Figure 4. Orientation discrimination thresholds for the two texture contours used in the TAE experiments. The data sets are fit with a function of the form $y = c + x^m$ for illustrative purposes only, with data points weighted by their standard errors (error bars shown).

**Experiment 2: Tuning curves for the TAE using SCs and OCs**

In Experiment 2, we measured the TAE for OCs and SCs at adapting angles from 0 to 90 deg. The experiment was replicated using the texture control stimuli, OCC and SCC, as adapting stimuli while testing with the matched contour stimuli. Observers SH, DK, and AB participated in Experiment 2.

Each trial consisted of three phases: preadaptation measurement of PV, adaptation, and postadaptation measurement of PV. During the adaptation phase, the adapting stimulus was presented for 60 s, with the stimulus refreshed at a rate of 2 Hz. The refresh changed the individual lines composing the textures on either side of the adapting contour, without changing the contour orientation. Rather than the refresh occurring instantaneously, stimuli were presented for 400 ms and interleaved with a 100-ms blank screen. The blank screen itself was not perceived; the impression was of a stimulus onset at 500-ms intervals. Both the change of texture local composition and the nature of the stimulus onset served to increase the saliency of the adapting contour, as it was effectively “reformed” at rate of 2 Hz. Additionally, changing the local texture composition limited adaptation caused by local luminance differences while maintaining the adaptive influence of the contour under investigation. Subjects were instructed to direct their gaze at the central fixation spot at all times but to attend to the entire contour, that is, to maintain awareness of the contour presence during the prolonged initial adaptation. TAE was measured using adapting contours presented at 5–20 deg at intervals of 5 deg, and then to 90 deg at intervals of 10 deg. Three measurements were made for each adaptation angle presented in the clockwise direction, and three measurements were made in the anticlockwise direction, except for observer SH who made 5 TAE measurements in each direction for the SC–SC and OC–OC trials.

The pre- and postadaptation measurements of PV used a single staircase method. In an experimental session, both PV measurements started with a contour presented to the same side of vertical, which was nominally the direction of the adapting stimulus. On the first trial of each staircase, the orientation of the test contour was chosen randomly to be 4, 5, 6, or 7 deg from vertical. On subsequent trials, the contour was rotated in the direction opposite to that reported by the observer, such that presentations converged to PV. The contour was rotated by 2 deg until the first reversal in observer response, 1 deg until the second reversal, and 0.5 deg thereafter until 10 reversals had been made. Contour orientations at the last six reversals were averaged to find the subject’s PV. During the preadaptation measurement phase, observer response initiated the next presentation. In the postadaptation measurement phase, observer response initiated a 6 s period of “top-up” adaptation, which was of the same form as the initial adaptation. The next test presentation followed after a 500 ms blank screen. The preadaptation
PV was subtracted from the postadaptation PV to give the magnitude of the TAE, and the absolute value of the TAE was averaged over clockwise and anticlockwise trials at each adaptation angle. This removed any bias in observer judgement caused by the direction from which the contour approached PV, as the approach direction was the same for the pre- and postadaptation measurements.

The use of a single staircase and the length of initial and “top-up” adaptation periods were designed to limit the total adaptation time while maintaining adaptation effects. Prolonged periods of adaptation have long-term measurable aftereffects (Wolfe & O’Connell, 1986), a problem we wanted to be sure of avoiding so as not to require long breaks between experimental sessions. However, if adaptation is insufficient, TAEs are not seen. Our experimental design resulted in a ratio of top-up adaptation to non-adaptation time of approximately 75%, depending on the delay before observer response (as this determined the interval between test stimulus offset and the start of the next top-up period). This ratio was found by Wolfe and O’Connell (1986) to be sufficient to induce adaptation using luminance-defined contours, not just maintain it. Pilot work confirmed that this ratio was also sufficient to induce adaptation using SC and OC contours. Each trial required roughly 20 top-up adaptations, which, together with the initial 60 s of adaptation, made a total adaptation time of 3 min. The TAE on LCs after this duration of adaptation was found to drop off rapidly by Wolfe and O’Connell (1986), returning to less than a quarter of its maximum after 5 min, with minimal long-term adaptation. Accordingly, our observers were required to rest for 5 min between trials. As a further precaution against cumulative adaptation effects, clockwise and anticlockwise adaptation stimuli were interleaved.

Results of Experiment 2

Graphs of TAE versus adaptation angle are shown for SCs (adapt-test condition SC–SC; Figure 5) and OCs (adapt-test condition OC–OC; Figure 6). It can be seen that both contour types show TAE curves with a positive peak at approximately 15 deg and a negative peak close to 70 deg, typical of luminance contrast contours (e.g., Gibson & Radner, 1937) and also previously shown with SCs (van der Zwan & Wenderoth, 1995). Figures 5 and 6 also show the results of adaptation using matched texture control stimuli (for example stimulus, see Figure 3), which gave negligible TAEs for SC and OC test contours in the region of 0–30 deg. The results of curve fitting, as detailed in the following paragraphs, suggest that adaptation to the texture orientation, as composes the control-adapting stimuli, cannot account for the TAE seen in this region for the SC–SC and OC–OC conditions. However, the texture controls do elicit a significant negative TAE peaking at ~70 deg. This strongly suggests that the negative TAE seen for the SC and OC contours at approximately 70 deg can also be attributed to adaptation to the first-order orientation cue of the textures and is not a consequence of adaptation to the contours themselves.

The data sets for SCs and OCs were fit with a difference of Gaussian (DoG) function:

$$y = \frac{Ax e^{\frac{-x^2}{2B^2}} + C(x-90)e^{\frac{-(x-90)^2}{2D^2}}}{2},$$  

where $A$ and $C$ are the mean amplitudes of the two Gaussian contributions (which are of opposite polarities), and $B$ and $D$ are their respective standard deviations. Curve fitting was achieved using Kaleidagraph™ data.
analysis software, which uses the Levenberg–Marquadt algorithm (Press, 1992), and data points were weighted by $1/\text{SE}^2$. The DoG function gave a good fit to the data, with Pearson’s correlation coefficient (“$R$ values”) $>.95$ in all cases (Table 1; SC–SC and OC–OC). The first Gaussian represents the adapting effect of the contour, a second-order cue to orientation. The second Gaussian is taken to represent the first-order adapting effect of the texture lines, which are oriented at 90 deg to the contour (this value is exact for SC and an average for OC as texture orientation had two values). Linear summation of two populations of activity has been used previously to model cross-orientation interaction (Blakemore et al., 1970), and the linear summation of Gaussian functions in particular has been used to model the interaction between first- and second-order orientation processing (Skillen, Whitaker, Popple, & McGraw, 2002). While we do not assume validity of the Gaussian function in representing underlying adaptive processes, both the strength of the fit and the outcome of various manipulations of the function parameters described suggest that the summation of two functions representing the first- and second-order orientation adaptation cues present in our stimuli provides a robust description of our data.

In Equation 1, the second Gaussian is at a fixed offset of 90 deg from the first. When the “offset” of the second Gaussian was set as a free parameter, it converged to $90 \pm 5$ deg in all cases, and the fit of the function to the data (as shown by $R$ values) did not systematically improve, suggesting that the source of the attraction is indeed located at an angle of 90 deg to the source of the repulsion effect. Secondly, we explored holding the two Gaussian bandwidths equal, that is, $B = D$. While this modification of the function was not detrimental to the fit of SC data, it resulted in lower $R$ values for fits to orientation contrast data. When the two bandwidths were allowed to vary independently, the bandwidth allocated to the OC, texture (D, centered at $\sim 70$ deg), was considerably greater than that allocated to the OC contour itself (B, centered at $\sim 15$ deg).

The difference between the two bandwidths was much smaller for the SC condition, hence holding the contour and texture bandwidths equal made little difference to the strength of the fit. We would suggest that the larger bandwidth for adaptation attributed to the first-order cue of the texture in the OC stimulus was because the texture at any given spatial location was randomly presented at one of two different orientations that were 30 deg apart. This possibility is supported by the finding of smaller amplitudes for the first-order texture orientation Gaussian (parameter C) in the OC case compared to the SC case, that is, the adaptive effect of the OC texture was less strong but more “spread out”.

The second two row sections of Table 1 describe fits to the control conditions (SCC–SC and OCC–OC). As well as fitting the data with the DoG function, it seemed logical to fit the data with just the negative Gaussian portion of the DoG, as the source of the hypothesized positive portion (the SC or the OC contour) is not present in the control stimulus. For observer AB, the fit achieved with the single, negative Gaussian was nearly as good as the DoG fit. Note that fitting with a single Gaussian means that there are less free parameters and so the goodness of fit is likely to be decreased. However, for observer DK, the fit with the negative Gaussian was very poor and the reason for this is not known.

Finally, we looked at the effect on the curve fit of subtracting the control data (SCC–SC and OCC–OC) from the SC–SC and OC–OC data, which should this time...
leave just the positive portion of the curve (last two row sections of Table 1). The data were therefore fit with the single, positive Gaussian as contained in DoG, as well as with the DoG itself. The single Gaussian gave a good fit to the data in most cases.

In summary, and to return to the main finding of Experiment 2, while OC–OC and SC–SC gave a significant positive Gaussian (parameter A in Table 1), the control conditions OCC–OC and SCC–SC did not. This indicates that the direct TAE seen peaking at an adaptive angle of ~15 deg for SC and OC stimuli cannot be accounted for by adaptation to the texture orientation but is caused by the second-order contours themselves.

**Experiment 3: Cross-adaptation effects for SCs, OCs, and LCs**

In Experiment 3, we measured the TAE at an adaptation angle of 15 deg, the peak of the SC and OC adaptation effect found in Experiment 2, for cross-adaptation conditions between SC and OC. This investigated the extent to which the two types of second-order contour activate the same set of orientation-selective neurons. In addition, several adapt-test contour combinations among SC, OC, and a luminance-defined contour (LC) were tested, similarly, to investigate the overlap of orientation encoding between the two second-order contours and a first-order contour. Observers SH, DK, AB, and JI participated in this experiment.

The procedure was identical to that of Experiment 2. All subjects were tested with the adapt-test combinations of subjective–subjective (SC–SC), orientation contrast–orientation contrast (OC–OC), and matched texture controls (SCC–SC and OCC–OC) to ascertain that they perceived TAEs attributable to the texture contours. All possible adapt-test combinations of LC, SC, and OC contours were tested, allowing a comparison of (i) cross-adaptation between texture contours (OC–SC, SC–OC) compared with the within-contour conditions (OC–OC, SC–SC); (ii) adaptation to an LC compared to adaptation to texture contours, on texture test contours (LC–OC versus OC–OC and LC–SC versus SC–SC); and (iii) adaptation on a luminance test contour by all three adapting contours (LC–LC,

<table>
<thead>
<tr>
<th>Adapt-test condition</th>
<th>Observer</th>
<th>Data range (deg)</th>
<th>Type of fit</th>
<th>A (repulsive mean height)</th>
<th>B (repulsive SD)</th>
<th>C (attractive mean height)</th>
<th>D (attractive SD)</th>
<th>R (Pearson’s correlation coefficient)</th>
</tr>
</thead>
<tbody>
<tr>
<td>SC–SC</td>
<td>SH</td>
<td>0–90</td>
<td>DoG</td>
<td>0.235 ± 0.045</td>
<td>14.174 ± 1.672</td>
<td>0.313 ± 0.032</td>
<td>18.475 ± 1.1272</td>
<td>.991</td>
</tr>
<tr>
<td></td>
<td>AB</td>
<td>0–90</td>
<td>DoG</td>
<td>0.378 ± 0.093</td>
<td>14.137 ± 2.007</td>
<td>0.203 ± 0.076</td>
<td>16.140 ± 3.552</td>
<td>.971</td>
</tr>
<tr>
<td></td>
<td>DK</td>
<td>0–50</td>
<td>DoG</td>
<td>0.293 ± 0.088</td>
<td>14.456 ± 5.617</td>
<td>0.146 ± 0.430</td>
<td>25.363 ± 25.068</td>
<td>.959</td>
</tr>
<tr>
<td>OC–OC</td>
<td>SH</td>
<td>0–90</td>
<td>DoG</td>
<td>0.400 ± 0.067</td>
<td>19.876 ± 1.102</td>
<td>0.126 ± 0.014</td>
<td>36.921 ± 5.348</td>
<td>.981</td>
</tr>
<tr>
<td></td>
<td>AB</td>
<td>0–90</td>
<td>DoG</td>
<td>0.538 ± 0.045</td>
<td>16.258 ± 1.1658</td>
<td>0.153 ± 0.049</td>
<td>18.934 ± 3.409</td>
<td>.979</td>
</tr>
<tr>
<td></td>
<td>DK</td>
<td>0–50</td>
<td>DoG</td>
<td>0.530 ± 0.179</td>
<td>18.830 ± 3.847</td>
<td>0.111 ± 0.127</td>
<td>41.610 ± 20.620</td>
<td>.973</td>
</tr>
<tr>
<td>SCC–SC</td>
<td>AB</td>
<td>0–90</td>
<td>DoG</td>
<td>0.045 ± 0.024</td>
<td>-35.144 ± 8.075</td>
<td>0.252 ± 0.046</td>
<td>22.992 ± 2.496</td>
<td>.970</td>
</tr>
<tr>
<td></td>
<td>DK</td>
<td>0–50</td>
<td>DoG</td>
<td>0.153 ± 0.122</td>
<td>23.602 ± 15.461</td>
<td>0.097 ± 0.158</td>
<td>39.465 ± 21.498</td>
<td>.938</td>
</tr>
<tr>
<td>OCC–OC</td>
<td>AB</td>
<td>0–90</td>
<td>DoG</td>
<td>0.118 ± 0.079</td>
<td>25 ± 8.279</td>
<td>0.090 ± 0.044</td>
<td>43.460 ± 11.113</td>
<td>.800</td>
</tr>
<tr>
<td></td>
<td>DK</td>
<td>0–50</td>
<td>DoG</td>
<td>0.253 ± 0.081</td>
<td>28.316 ± 21.298</td>
<td>0.204 ± 0.341</td>
<td>41.805 ± 17.021</td>
<td>.913</td>
</tr>
<tr>
<td>SC–SC minus</td>
<td>AB</td>
<td>0–90</td>
<td>DoG</td>
<td>0.514 ± 0.214</td>
<td>9.406 ± 2.223</td>
<td>-0.052 ± 0.039</td>
<td>31.512 ± 13.656</td>
<td>.913</td>
</tr>
<tr>
<td>SCC–SC</td>
<td>DK</td>
<td>0–50</td>
<td>DoG</td>
<td>0.327 ± 0.195</td>
<td>9.998 ± 3.175</td>
<td>-830.220 ± 1.038 e + 07</td>
<td>-8.026 ± 40.169</td>
<td>.904</td>
</tr>
<tr>
<td>OC–OC minus</td>
<td>AB</td>
<td>0–90</td>
<td>DoG</td>
<td>0.548 ± 0.065</td>
<td>16.142 ± 1.544</td>
<td>0.148 ± 0.168</td>
<td>10.311 ± 6.179</td>
<td>.968</td>
</tr>
<tr>
<td>OCC–OC</td>
<td>DK</td>
<td>0–50</td>
<td>DoG</td>
<td>0.381 ± 0.293</td>
<td>14.496 ± 5.731</td>
<td>-0.018 ± 0.054</td>
<td>70.048 ± 244.11</td>
<td>.964</td>
</tr>
</tbody>
</table>

Table 1. Parameters from the DoG curve fit to the TAE data. Amplitude and standard deviation of the repulsive and attractive parts of the curve fit of Equation 1 (DoG), the first “positive” Gaussian only (positive) or the second “negative” Gaussian only (negative). “-” indicates parameters that are not applicable to the fit.
OC–LC, and SC–LC). Adapt-test conditions were interleaved, and clockwise and anticlockwise adaptations at each orientation were paired within conditions and were alternated as before. TAEs were explored using within-subjects (repeated-measures) analysis of variance (ANOVA) to test for the significance of adapting contour and test contour factors. Where this resulted in a multiple comparison of a single adapt-test condition being made, the appropriate Bonferroni correction was made when testing for significance at the 95% level; two comparisons, $p = .0250$; three comparisons, $p = .0167$; four comparisons, $p = .0125$.

**Results of Experiment 3**

All adapt-test combinations, with the exception of adaptation to the matched texture controls (OCC–OC and SCC–SC), were significantly greater than zero. Figure 7 shows the magnitude of the TAE for the original intra-contour-type conditions, OC–OC and SC–SC, and their respective texture controls. A paired $t$ test (i.e., one-way within-subjects ANOVA with two levels) of the OC–OC and SC–SC conditions showed them to be significantly different (1.85 versus 1.04; $p = .006$), with the OC–OC TAE on average 0.81 deg greater than that for SC–SC. OC contours must be stronger adaptors of orientation-selective neurons in V1/V2 than SC contours, or must be more susceptible to adaptation effects, or both. The contour TAEs were not explained by the adaptive effect of the textures, confirming that the subjects perceived and adapted to the contours themselves as previously shown in Experiment 2. Hence, it is demonstrated that the TAE is larger for OC contours, which contained an orientation contrast cue, than for SC contours.

Figure 8 shows the results of cross-adaptation between the two texture contour types, and also the initial intra-contour-type conditions for comparison. On first inspection, there is no apparent difference in TAE between the two cross-adaptation conditions (OC–SC versus SC–OC), but a two-way (adapting contour, test contour) within-subjects ANOVA reveals that there is a strong effect of adapting contour ($F = 60.59, p < .005$). Planned orthogonal pairwise comparisons showed that this was due to a strong increase for OC–SC compared to the SC–SC condition (1.49 versus 1.04; $p = .00$) and a nonsignificant decrease for SC–OC compared to the OC–OC condition (1.55 versus 1.85; $p = .052$). The effect of test contour was also significant ($F = 22.24, p < .05$), with OC test contours displaying larger TAEs. This was mainly due to the strong increase for SC–OC compared to SC–SC (1.55 versus 1.04, $p = .005$), as the increase for OC–OC compared to OC–SC was nonsignificant (1.49 versus 1.85, $p = .072$). Hence, comparison of the cross-adaptation conditions with the original conditions adds weight to the initial suggestion that OCs are stronger adaptors and are more susceptible to adaptation effects than SCs.

Next we compared the TAE induced on an OC after adapting to an LC and after adapting to an OC contour (i.e., the within-contour-type condition). The equivalent comparison was made for an SC (Figure 9). Two separate paired $t$ tests showed that there was a trend for adaptation by an LC to produce larger effects on the texture contours than adaptation by the same texture contour, but neither comparison reached significance (LC–OC versus OC–OC, 2.09 versus 1.85, $p = .22$; and LC–SC versus SC–SC, 1.92 versus 1.04, $p = .059$).

Figure 10 shows the TAEs induced on a luminance test contour (LC) after adapting to the three contours (LC, OC, and SC). A one-way within-subjects ANOVA showed no difference between the three conditions, suggesting that OC and SC were as effective at adapting the population of neurons encoding the LC orientation as the LC contour itself was. As OC and SC contours are
second-order orientation signals and LC is a first-order orientation signal, this result was slightly surprising. Hence, we also compared the conditions OC–OC versus OC–LC and SC–SC versus SC–LC in two separate paired \( t \) tests. This comparison checked if the texture contours were as effective at adapting neurons encoding a first-order luminance-defined orientation signal as they were at adapting neurons sensitive to the second-order texture contour orientation. We found that OC–OC gave a greater TAE than OC–LC, but that SC–SC gave a smaller TAE than SC–LC, and that neither comparison reached the required significance level (OC–OC versus OC–LC, mean difference = 0.875, \( p = 0.026 \); SC–SC versus SC–LC, mean difference = 0.298, \( p = 0.499 \)). Hence, in this comparison, there was no significant difference in the ability of the texture contours (OC and SC) to adapt neurons encoding second-order texture contour orientation and first-order LC orientation.

The results of the present study confirm previous observations of a TAE using SCs (Berkley et al., 1994; Bockisch, 1999; Paradiso et al., 1989; van der Zwan & Wenderoth, 1994, 1995) and of their interaction with LCs (Berkley et al., 1994; Bockisch, 1999; Paradiso et al., 1989). We also found strong TAEs for our OC, a type of contour that to our knowledge has not been investigated in this way before. This result is compatible with the previously demonstrated orientation-tuned detection threshold elevation after adaptation for orientation texture-defined gratings (Kwan & Regan, 1998). Another novel result of this study is the finding of a stronger adaptive effect of texture edge contours with OC than without (SC). This answers our original question, showing that the addition of an orientation contrast cue across a texture edge strengthens the encoding of orientation at the level of V1/V2. This finding is not entirely to be expected, as the two second-order contours had comparable orientation encoding in terms of orientation discrimination thresholds. We did not seek to use contour stimuli matched for salience, a factor that is known to influence the magnitude of the TAE (Berkley et al., 1994). Rather, we sought to differentiate the relative salience of two kinds of texture contours. The contours were identical apart from the attribute under investigation, orientation contrast. Hence, differences in the adaptive strength of our two texture contours are an effect of orientation contrast only.

In addition to the primary aim of the experiment, we also further investigated the encoding of second-order contour orientation by comparisons with a first-order luminance-defined contour. We found that adaptation by an LC produced a TAE with OC and SC test contours, evidence of shared sites of orientation encoding between first- and second-order orientation signals. Note that adaptation by an LC induced slightly larger TAEs in SC and OC test contours than SC and OC adaptors themselves (although the difference was not significant), showing that an orientation signal defined by luminance contrast is equally effective at adapting the population of neurons encoding the orientation of the texture contours. Both Berkley et al. (1994) and Paradiso et al. (1989) also found that adaptation by an LC could induce equal or larger TAEs in an SC than adaptation by the SC itself.

However, more importantly, this study found no difference in the effectiveness of the LC, OC, and SC adaptors on an LC test contour. Likewise, there was no difference between OC and SC adaptors on an LC test contour compared to the OC–OC and SC–SC conditions. This is a surprising result when it is considered that luminance-defined orientation signals are first detected in V1, and it is generally accepted that the TAE seen with luminance-defined contours results from altered orientation-selective response in V1 and V2. For example, Paradiso et al. (1989) found that their SCs induced much weaker TAEs.
in LCs than those induced by LCs themselves. They explained their results in terms of the relative populations of V1 and V2 that might encode the two contours; while the LC could activate all orientation-tuned cells, including those that signaled SC orientation, they hypothesized that the SC could only activate a subset of the cells that encoded the LC orientation. Hence, they reasoned that the effect of adaptation by an SC would therefore be less notable within the entire population of cells signaling the orientation of a luminance test contour.

Although a few studies have found a small V1 response to SCs (Lee & Nguyen, 2001; Ramsden, Hung, & Roe, 2001; Redies, Crook, & Creutzfeldt, 1986; Sheth, Sharma, Rao, & Sur, 1996), it is more usually found that a robust response to both subjective and texture orientation contrast contours is first seen in V2 (Baumann et al., 1997; Leventhal et al., 1998; Sheth et al., 1996; von der Heydt & Peterhans, 1989; von der Heydt et al., 1984). LCs should therefore have a greater adaptive effect than OC and SC on luminance test contours, according to the explanation put forward by Paradiso et al. (1989). However, our results suggest that all three contours are equally effective at activating V1/V2 during prolonged viewing. A plausible explanation for this is that OC and SC activate orientation-selective neurons in V1 by feedback from V2 or higher cortical areas and thereby indirectly produce adaptation in V1. This line of reasoning and a possible explanation for the difference between the results of this study and those of Paradiso et al. (1989) is discussed more fully later.

The TAE "tuning curve"

Both SC and OC texture contours displayed typical “S”-shaped tuning curves (cf. van der Zwan & Wenderoth, 1995), with a “repulsive” peak centered at ~15 deg and an “attractive” peak centered at ~70 deg. Investigation of TAEs and TIs caused by stimuli with multiple axes of symmetry has suggested that the attractive effect, often attributed to “global” properties of the stimulus rather than local orientation signals, may be due to adaptation to the orthogonal axis of symmetry in line or grating stimuli (Johnstone & Wenderoth, 1989; Smith, Wenderoth, & van der Zwan, 2001; Wenderoth & Johnstone, 1987; Wenderoth, Johnstone, & van der Zwan, 1989; Wenderoth, van der Zwan, & Johnstone, 1989).

We propose that the “attractive” effect for our stimuli can be explained by adaptation to the first-order cue of texture orientation, and that it is unnecessary to hypothesize adaptation to an axis of symmetry orthogonal to the second-order contours (OC and SC). Rather than the test contour being attracted in the direction of the adapting contour, at large adapting contour angles, it appears to have been repulsed by the texture orientation. Hence, both portions of the curves shown in Figures 5 and 6 can be attributed to repulsive effects. However, we cannot rule out the possibility that there was a small adaptive effect of the contour axis of symmetry that was not observed due to the strong adaptation effect of the texture. Indeed, van der Zwan and Wenderoth (1995) observed an attractive effect peaking at 75 deg for their SCs, which consisted of offset concentric circles, and hence contained no global first-order orientation signal at all.

The relative adaptive strengths of SC, OC, and LC contours

We found considerable variations in TAE across subjects, both in the absolute magnitude and in the relative effectiveness of the different contour types. Similar variations have been noted before (Berkley et al., 1994), and these may reflect individual differences in perception of the contours. It could also be of particular relevance that the salience of SCs is decreased by strong fixation (Bradley & Dumais, 1984; Frisby & Clatworthy, 1975; Kanizsa, 1976; Soriano, Spillmann, & Bach, 1996). Indeed, all our observers reported difficulty in “seeing” the SCs during both the initial, and the shorter “top-up,” adaptation phases. The detrimental effect of fixation on SC visibility could be because fixation is limiting awareness of the global context that induces the contour. Awareness of global stimulus properties is known to heighten the later parts of neural response in V1 and V2 (Ito & Gilbert, 1999; Lamme, Zipser, & Spekreijse, 1998; Lee & Nguyen, 2001; Lee, Yang, Romero, & Mumford, 2002; Super, Spekreijse, & Lamme, 2001; Tanaka, 2001).

If we accept that the direct TAE is an aftereffect of orientation-selective activation in V1 and V2 (Blakemore et al., 1970; Carpenter & Blakemore, 1973; Magnusson & Kurtenbach, 1980a, 1980b; Morrone et al., 1982; Wenderoth & Johnstone, 1987), then variability in observers’ awareness of contours and the subsequent strength of contour representation in these cortical areas could explain some of the variability in TAE magnitudes.
Both the frequent change of the local composition of our contour-inducing textures, and also explicit instructions to observers, were intended to heighten awareness of the contours despite fixation. However, our observers may have maintained awareness of the contours to greater or lesser extents. Our reasoning that stimulus awareness could affect the encoding of our texture contours finds support in the work done by Montaser-Kouhsari and Rajimehr (2004). They found that the strength of the TAE induced by an SC was inversely related to the attentional demands of an irrelevant task that was performed by observers during the adaptation period. It was concluded that the attentional resources available for processing the SC affected the strength of adaptation. Similarly in the present study, reduced awareness of the contour could limit its adaptive strength. OC contours might be hypothesized to be less affected by attentional resources, as the preattentive nature of local orientation contrasts would continuously signal the presence of this type of contour.

The decreased visibility with time of SCs during the initial and top-up adaptation phases may have also contributed to the finding of weaker adaptation by SC contours than by OC contours. Consider that the magnitude of the TAE is determined by the relative contrast of the adapting and test stimuli when they are defined by luminance contrast (Parker, 1972). This principle also holds for positional adaptation (Whitaker, McGraw, & Levi, 1997) and detection threshold elevation (Snowden, 1994), and it can presumably be accounted for in terms of the relative activities of the population of neurons activated by the adapting and test stimuli that are defined by the same attribute. An SC that has perceptually weakened during adaptation would be less effective than a briefly presented SC in eliciting a neural response; the contour effectively has lower contrast. Note that we are suggesting that the decreased visibility of the SC is caused by a decrease in the top-down influences on the contour visibility, not by adaptation to the orientation signal. Hence, even if brief presentations of OC and SC contours were equally effective in activating orientation-selective neurons in V1/V2 (as also suggested by our finding of equal orientation discrimination thresholds at short presentations), decreasing visibility of SC contours during the adaptation phase would result in lower TAEs for SC adaptor than for OC adaptor conditions. The difference between the two contours as test stimuli is harder to explain, as OC test stimuli displayed larger TAE than SC despite being the “stronger” contour. However, the difference was only significant when SC was the previously presented adaptor, that is, SC–OC versus SC–SC. It may be that interspersed presentations of OC increased or “rejuvenated” the effectiveness of the SC “top-up” adaptations.

Decreased visibility with increasing presentation time is certainly not the only possible explanation for the weaker adaptive effect of SCs when compared to OCs. SCs of the type used here are widely accepted to activate a feedforward process whereby line endings are detected in V1, and aligned responses input to orthogonal “integrating” cells in V2 (Peterhans & von der Heydt, 1989). OCs could activate an additional feedforward process mediated by a separate population of neurons integrating local orientation contrast. Possible mechanisms are the “linking” of local orientation singularities (Li, 2000), or a second stage of filtering by second-order filters that detect the region of orientation contrast (Bergen & Landy, 1991; Graham, 1994; Malik & Perona, 1990; Popple, 2003; Wolfson & Landy, 1999).

However, the equal adaptive strength of OC and SC contours in V1/V2 compared to a first-order LC signal would be difficult to explain by feedforward mechanisms only. Our texture contours only give a second-order cue to contour orientation, which is likely to be first detected in V2 (Baumann et al., 1997; Leventhal et al., 1998; Sheth et al., 1996; von der Heydt & Peterhans, 1989; von der Heydt et al., 1984). However, it appears that the representation of the texture contours and an LC is very similar in its locus and strength within V1/V2. To adapt the same orientation-tuned neurons as an LC contour, the representation of SC and OC contours may therefore rely on feedback to some extent, possibly from V2 to V1 and also from higher cortical areas to both V1 and V2. This feedback appears to be sufficient to equate the SC/OC orientation-encoding response in V1/V2 with that caused by feedforward mechanisms responding to luminance contrast. It is slightly surprising that the relative strengths of the LC, OC, and SC adaptors could not be differentiated in Experiment 3, given that there were significant differences between OC and SC adaptors in Experiment 2. An alternative explanation for LC, OC, and SC adaptation equivalence in terms of a common site of orientation encoding beyond V2 might be viable but would not be compatible with the long-standing evidence that the first-order, luminance-defined TAE is generated in V1/V2.

Orientation discrimination thresholds for our texture edge contours (OC and SC) decreased with increasing presentation time, reaching a plateau in the region of 400–1000 ms. Similar results have been reported before for SCs, whereas LCs or contours containing a luminance cue attain threshold plateaus for presentation times of under 100 ms (Westheimer & Li, 1996, 1997). Prolonged processing may point to an involvement of iterative feedforward and feedback interactions (e.g., Lamme & Roelfsema, 2000; Lamme, Super, & Spekreijse, 1998; Lee & Mumford, 2003) in generating the texture contour percept. The proposal has been made before that V1 and V2 responses to SCs (Lee & Nguyen, 2001) and texture orientation contrast contours (Lee, Mumford, Romero, & Lamme, 1998) have input from delayed modulation due to feedback from higher areas that encode scene contours in a cue-invariant fashion. Indeed, V1 and V2 recordings in macaque show late modulation both in response to
figures defined by orientation contrast (“orthogonal” disc) and to matched subjective figures (“parallel” disc) similar to our OC and SC stimuli (Marcus & Van Essen, 2002). These findings support a possible role for feedback in generating the final orientation encoding of our SC and possibly also OC contours.

Both the SCs and the OCs were constructed so as to resemble abutting or overlapping texture surfaces. Hence, we could expect the stimuli to be more salient than simple line grating stimuli (such as used by Paradiso et al., 1989) to higher cortical areas that are responsive to figural surfaces and occlusion percepts (Baylis & Driver, 2001; Grill-Specter, Kourtzi, & Kanwisher, 2001; Gulyas, Cowey, Heywood, Popplewell, & Roland, 1998; Kourtzi, Tolas, Altmann, Augath, & Logothetis, 2003) despite being isolated contours. Feedback from higher areas could therefore be more active in modulating low-level response to our texture contours than for some other versions of an SC.

As it was found that the orientation contours were stronger adaptors than SCs, in the within-texture contours comparison at least (Experiment 2), either the perception of OC contours is less reliant on feedback and hence less susceptible to fading than the perception of SC contours, or feedback is more robust when adapting to OC contours. Additional feedforward mechanisms for OC contours were discussed previously. The alternative that OC contours could elicit more robust feedback than SC could be the result of the attentional properties of orientation singularities (Joseph & Optican, 1996; Nothdurft, 2002) or because of the first-order difference between the textures either side of the OC contour. In the SC condition, the generation of a feedback input that could increase contour salience relies on the contour already being “known” by the visual system, as there is no difference in texture surfaces either side of the contour.

Conclusion

To conclude, adaptation to orientation contrast contours (OC) elicits larger TAEs than does adaptation to SCs, suggesting that they more effectively activate neurons in V1/V2 during prolonged viewing. This could be due to the integration of orientation contrast signals in a feed-forward process, which provides a more robust contour orientation signal than can be compensated for by feedback from higher cortical areas. However, the encoding of orientation for both contour types may rely on feedback to some extent, as they adapted an LC as strongly as did an LC itself. This demonstrates shared sites of orientation encoding in V1/V2 between first- and second-order orientation signals. Hence, while SCs do not appear to be as robust an orientation signal as texture contours containing an additional orientation contrast cue, their orientation is at least encoded by the same population of low-level orientation-tuned neurons.

Acknowledgment

This research was supported by an EPSRC studentship and EPSRC grand no. GR/N26296/01. The authors wish to thank M. Cox for comments on an earlier version of the manuscript.

Commercial relationships: none.
Corresponding author: Dr. Sarah J. Hawley.
Email: harrison.sarahj@gmail.com.
Address: School of Psychology, Adelard Brigantia, University of Wales Bangor, Gwynedd, LL57 2AS, UK.

References


