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The contribution of different parts of the visual field to the perception of upright

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ABSTRACT

We determined the relative effectiveness of different areas of the visual field in determining the perceptual upright. The perceptual upright was measured using the character 'p', the identity of which depended on its perceived orientation (the Oriented Character Recognition Test). The visual field was divided into left and right, upper and lower, and central and peripheral halves, with different backgrounds presented in each area. The left and right visual fields contributed equally to the perceptual upright while the lower visual field demonstrated a larger effect on the perceptual upright as compared to the upper visual field. The central and peripheral visual fields interacted with one another in a complex manner, although a separate experiment suggested that the peripheral visual field did not alter the perceived orientation of the central field.

1. Introduction

The perception of upright comes from a combination of cues including vestibular cues about the direction of gravity, an internal representation of the body, and the structure of the world as perceived visually (Mittelstaedt, 1983). Each of these cues is quite complex. Thus, the gravity cue is signalled not only by input originating from within the vestibular system (saccular and utricular macula) but also by the somatosensory system which relies on skin, neck and trunk receptors which are sensitive to points of pressure from the support surface (Angelaki, Gu, & DeAngelis, 2009). The internal representation of the body, indicating the direction of the head on the long axis of the body as a candidate for the "up" direction, must be learnt from interactions with the world and can be broken down into contributions from the trunk, torso, head and eyes (Mittelstaedt, 1991). In this paper, we consider the contributions to the perception of upright contained in visual input.

Different parts of the visual field have long been thought to be processed differently. The nature of the difference is dependent on how the visual areas are defined. Three particularly prevalent divisions of interest are left and right visual fields, upper and lower visual fields and central and peripheral visual fields.

The broad division into central and peripheral regions corresponds to a physiological difference. Central–peripheral asymmetries have been attributed to the biased distribution of retinal cones (Karim & Kojima, 2010). The density of the receptors in the visual system decreases as distance from the fovea increases (Curcio et al., 1987, 1990). One of the consequences of this is an increased sensitivity to foveal stimuli relative to peripheral stimuli (Duncan & Boynton, 2003; Hansen, Pracejus, & Gegenfurtner, 2009; Virsu & Rovamo, 1979). There are also differences between the cortical pathways to which each retinal area projects. Cells from the central retina project predominantly to the parvocellular pathway and ventral stream, whereas the peripheral region, with larger receptive fields and a particular sensitivity to movement, has cells that project into the dorsal stream (Danckert & Goodale, 2003). These two cortical streams have also been suggested to sub-serve perception and action functions respectively (Goodale & Milner, 1992).

It has correspondingly been suggested that these two streams may play a differential role in evoking vection, with stimuli in the periphery being more effective (Brandt, Dichgans, & Koenig, 1973). However, the idea that the periphery dominates in generating vection has been challenged (Howard & Heckmann, 1989; Paulus, Straube, & Brandt, 1984). There are also reasons we might expect the periphery to be important in determining perceptual orientation. In everyday life for example the periphery is less likely to be occluded by objects of interest. Also, features of more direct relevance to perceptual orientation, such as walls, floors, ceilings and the ground plane, are more likely to be visible in this region. The ground plane has been shown to greatly influence our ability to maintain balance and posture (Patla, 1998).

Similarly, there have been suggestions that the upper and lower parts of the visual field might be processed differently. Physiological differences include enhanced lower visual field representation in the posterior parietal cortex and enhanced upper visual field representation in the inferior temporal cortex (Previc, 1990). Also, the dorsal stream has been shown to contain a bias toward processing visual information that is derived from the lower visual field (Danckert & Goodale, 2003). There are also action differences

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between the fields. The optokinetic nystagmus reflex is not evoked so readily from the lower field (van den Berg & Collewijn, 1988), perhaps because the visual flow generated by forward locomotion would constantly be dragging the eyes downwards. However, more cues pertaining to orientation might be expected in the lower field, below the horizon. The lower visual field contains the ground plane, which is important for posture and balance (Patla, 1998), and it has also been shown that visual information from the lower visual field is important when walking on a complex terrain (Marigold & Patla, 2008).

Although there are differences in the nasal and temporal regions of each retina and their crossed and uncrossed cortical projections (Fahle & Schmid, 1988), there is no functional reason, when both eyes are open, to expect asymmetries between the left and right visual fields in the determination of the vertical.

Although the effectiveness of different parts of the visual field has been assessed as reviewed above, there has not been a study assessing their effectiveness in providing cues to orientation. We therefore compared the relative contributions of the left and right, upper and lower, and central and peripheral fields to the perception of up, using a conflict paradigm in which two areas of the visual field were made to signal different orientations at the same time. We also tested whether the effectiveness in providing orientation cues was greater if a larger part of the field is stimulated.

2. Experiment 1

2.1. Methods

2.1.1. Subjects

Eleven subjects aged 24–57 (six male) participated in Experiment 1. They either had no visual problems (by self report) or wore their normal optical correction. All subjects were recruited and gave their informed consent according to the ethical principles required by the Ethics Guidelines of York University which complies with the 1964 Declaration of Helsinki.

2.1.2. Apparatus

Visual stimuli were displayed on an Apple iBook laptop computer with a resolution of 48 pixels/cm (21 pixels/deg). Subjects viewed the screen at a distance of 25 cm through a black circular shroud that reduced the viewing area to a circle subtending 27° of visual arc and served to preclude the frame cues provided by the shape of the screen. Observers responded by pressing the left or right buttons on a game pad (Gravis Gamepad Pro).

2.1.3. OCHART

We used OCHART to assess the perceived direction of up. The Oriented CHAracter Recognition Test (OCHART) exploits the fact that the perceived identities of some objects depend on their orientation (Dyde, Jenkin, & Harris, 2006). Such an object is the ambiguous symbol 'p'. In its "upright" position this character is identified as a 'p'. If the symbol is rotated 180° it is recognized as a 'd'. By measuring the orientation of the transition points between the 'p' and 'd' percepts a direction of up, the perceptual upright, the orientation half way between these points, can be determined. We presented the character, which subtended approximately $3.1 \times 1.9°$ of visual arc, six times at 20 different orientations within the ranges of 45–135° and 225–315° at 10° increments, where 0° is an upright 'p'. Subjects were asked to report whether they perceived a 'p' or a 'd' using two buttons on the gamepad.

2.1.4. Calculating the perceptual upright (PU)

We calculated the percentage of the time subjects responded 'p' and plotted it as a function of the orientation of the character. Points of Subjective Equality (PSE) were determined by fitting two sigmoid functions to the data. The sigmoids were defined as

$$y = \frac{100}{1 + e^{-((x-x_0)/b)}}\% \tag{1}$$

where x_0 corresponds to the 50% point (PSE) and b is the standard deviation (so that b^2 is the variance). A smaller variance corresponds to a steeper slope of the sigmoid which indicates an easier, more reliable discrimination by the observer. The PSEs are the points where the character is maximally ambiguous, i.e. where the p-to-d and d-to-p transitions take place. The average of the two angles at which these transitions occur was taken as the perceptual upright (PU) (Fig. 1). The mean of the standard deviations of each of the sigmoid fits (the b value) was taken as the standard deviation of the subject's response.

One of our subjects failed to produce data that could be fit by sigmoid functions. We therefore could not determine the orientations of their perceived transition points and could not establish a measure of PU. This subject's data has been excluded from our results section.

2.1.5. Visual stimuli

The circular visual field visible through the shroud was divided into two equal areas of left/right, upper/lower, and centre/periphery (Fig. 2b). Three orientations of a highly polarized scene (0°, 112.5° and 247.5°), and a grey control background (of equal average luminance and spectral content) (Fig. 2a) were presented in each half region, for each of the three experimental sets. These values of background orientation were chosen because Dyde, Jenkin, and Harris (2006) had found them to produce the largest shifts of the perceptual upright. This combination of stimuli yielded three sets of 16 backgrounds. Four background combinations, where the two halves matched (Fig. 2a), were common to each set. Fig. 2b shows a few examples of combinations in each set. When combining half-field images, a distinct contour was evident where the images met (Fig. 2b). In the cases of the left/right and upper/lower sets, these contours provided distinct orienting cues that might have potentially biased subject responses. Therefore these contours were blurred (see Fig. 2b) using a Gaussian blur function in Adobe Photoshop CS3 Version 10.0. In the case of the centre/periphery set, the contour was circular and therefore did not provide any cues to up and was left unaltered. It should be noted however, that even after blurring, these contours could still have provided low-level orientation cues which may have interacted with the probe independently of high-level scene orientation. Similarly, the image itself contained many tall straight trees which

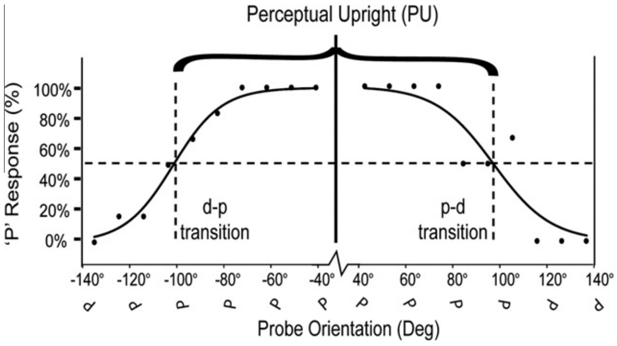

Fig. 1. Typical psychometric functions obtained from a single background orientation (in this case upright). The percentage of times the character was identified as a 'p' is plotted against its orientation. Sigmoids were plotted through the data from which the two points of maximum ambiguity (the 50% points) were found (indicated on the graph by vertical dashed lines). The perceptual upright is defined as being half way between these two orientations (illustrated by the solid line).

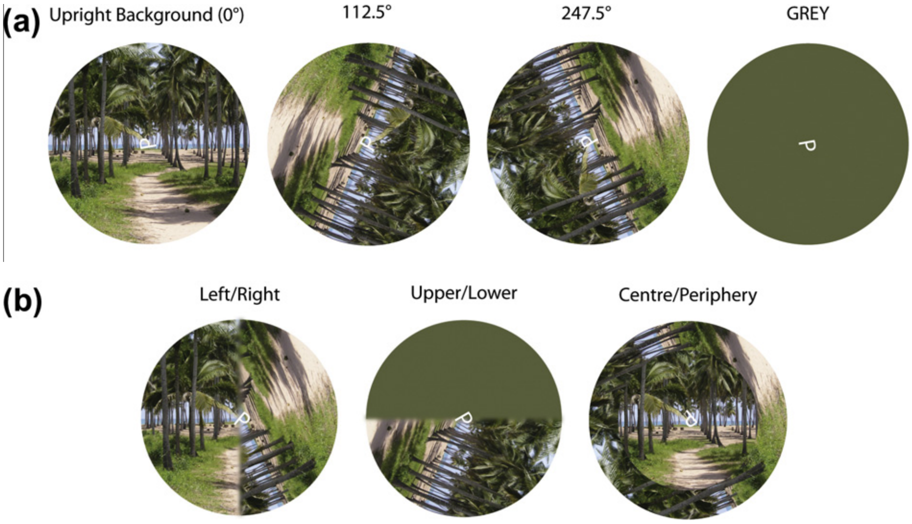

Fig. 2. This figure illustrates examples of the background stimuli used. (a) The four full-field backgrounds consisting of the Upright Background "0°", that background tilted CW "112.5°", tilted CCW "247.5°", and a control background of equal average luminance "grey". (b) Examples of each half-field division. Left 0°/right 247.5°, upper grey/lower 112.5° and centre 0°/periphery 247.5°. The contours where the conflicting left/right and upper/lower backgrounds met have been blurred to reduce the orientation cues they might provide. The 'p' character was presented in the centre of the display.

served to provide an abundance of vertical contours. These contours may have also interacted with the probe at low-levels independent of high-level scene orientation effects. Such low-level effects are unlikely to have confounded our results since they are expected to have been similar within each visual field. Nonetheless, it is important to consider the likelihood that such low-level effects may have been influencing the perception of the probe.

2.1.6. Calculating the visual effect (VE)

In 2006, Dyde et al. found that the orientations of a background which produced the greatest shifts in the PU were +112.5° and −112.5° (247.5°). They then defined the visual effect (VE) as the difference in the measured PUs found in the presence of these two background orientations. The VE assesses the total effectiveness of visual orientation cues on the perceptual upright. In this experiment, the VE for any given half field can be measured up to four times. The VE of each half-field is measured with the other half-field being held at a constant orientation (Fig. 3b). The constant orientation may be one of grey, 0°, 112.5° or 247.5°, and therefore results in four estimates of the VE for each half-field.

2.1.7. Procedure

Participants were seated at a desk with their heads positioned against the shroud approximately 25 cm from the computer screen. A button press on the game pad triggered a 500 ms visual stimulus which consisted of the 'p' character superimposed on one of the previously described backgrounds (see Section 2.1.5). Subjects were not able to respond during the 500 ms stimulus presentation time. After stimulus presentation, an inter-trial circular fixation point subtending approximately 0.45° of visual arc appeared and subjects were asked to respond whether they perceived a 'p' or a 'd'. Subjects indicated their response by button press on the game pad and were able to take as long as they wished to respond, but were encouraged to answer with their initial immediate percept. A new trial was initiated upon their response. Each unique background orientation and character orientation combination was presented six times. Stimuli were presented in a randomized order resulting in a total of 4800 trials. Participants were run in sessions of four equal blocks of 1200 trials each. Subjects took about 1 s/trial to respond, meaning that a typical session took about 20 min to run.

2.1.8. Convention

The orientations of all character and background stimuli were defined with respect to the body mid-line of the observer. Zero degrees refers to the orientation of the body axis. The character was an upright 'p' at 0° and an upright 'd' at 180°. Positive orientations are clockwise ('rightwards') while negative orientations are counter-clockwise ('leftwards') as seen by the observer.

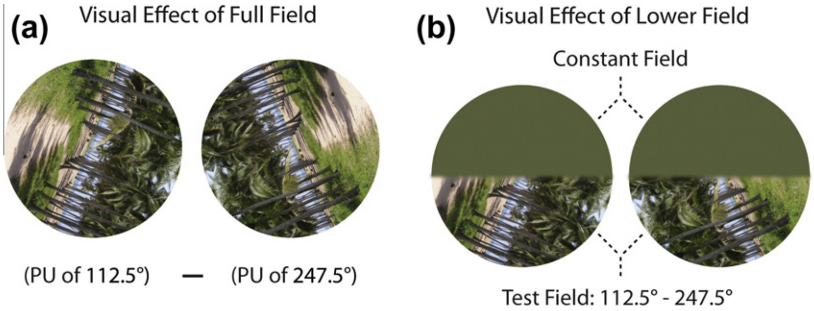

Fig. 3. (a) The difference between the PU measure in the presence of the full-field 112.5° and 247.5° backgrounds is the full-field VE. (b) To calculate a half-field VE, the same reasoning outlined in (a) is applied to one of the half-fields, in this example the lower field, while the remaining field is held constant. The orientation of the constant field can be any of the four background orientations: 0°, 112.5°, 247.5° or grey (shown here), resulting in four measures of VE for each half-field. The half-field VE measure illustrated here is "Lower VE (grey)".

3. Results

3.1. The effect of the visual background regions on the PU

Fig. 4 illustrates the relationship between the orientation of the visual background and the PU measured with different combinations of stimuli in the visual field divisions of left/right (a), upper/lower (b), and centre/periphery (c). In each case, the shift in the PU was related to the orientation of the background. The data were analyzed using three separate 3×3 ANOVAs, one for each of the left/right, upper/lower and centre/periphery conditions. The visual half-fields served as the independent variables and the visual background orientations served as the levels (Field A; 112.5°, 0°, 247.5° × Field B; 112.5°, 0°, 247.5°) for each of the left/right, upper/lower and centre/periphery experiments. There were main effects present for each region in each of the three experiments [left/right, $F(2,18) = 25.6$, $p = 0.001$/$F(2,18) = 8.4$, $p = 0.003$; upper/lower, $F(2,18) = 7.2$, $p = 0.005$/$F(2,18) = 14.0$, $p = 0.001$; centre/periphery, $F(2,18) = 9.6$, $p = 0.001$/$F(2,18) = 7.7$, $p = 0.004$, respectively]. There was also an interaction effect present in the centre/ periphery experiment [$F(4,36) = 3.8$, $p = 0.011$].

These results indicate that the background orientation of each of the half-fields had an effect on the perceived identity of the superimposed character. As the orientation of the background shifted in a particular direction, the perceptual upright generally shifted in the same direction. The absence of interaction effects for the left/right and upper/lower background conditions implies that the total effect of the stimuli on the probe can be approximated by simply adding the effects of each half-field stimulus. This is not the case, however, for the centre/periphery stimuli which shows a negative slope when the centre field was held constant at 0° (see Fig. 4c). The presence of an interaction in the centre/periphery condition means that the simultaneous influence of the centre and periphery backgrounds on the probe is not additive. That is to say, the relationship between each of the half field stimuli and the PU depends on the specific orientation of one half-field background with respect to the other.

3.2. Visual effect (VE)

The visual effect (VE) is defined as the difference between the PU measures with background orientations of 112.5° and 247.5°.

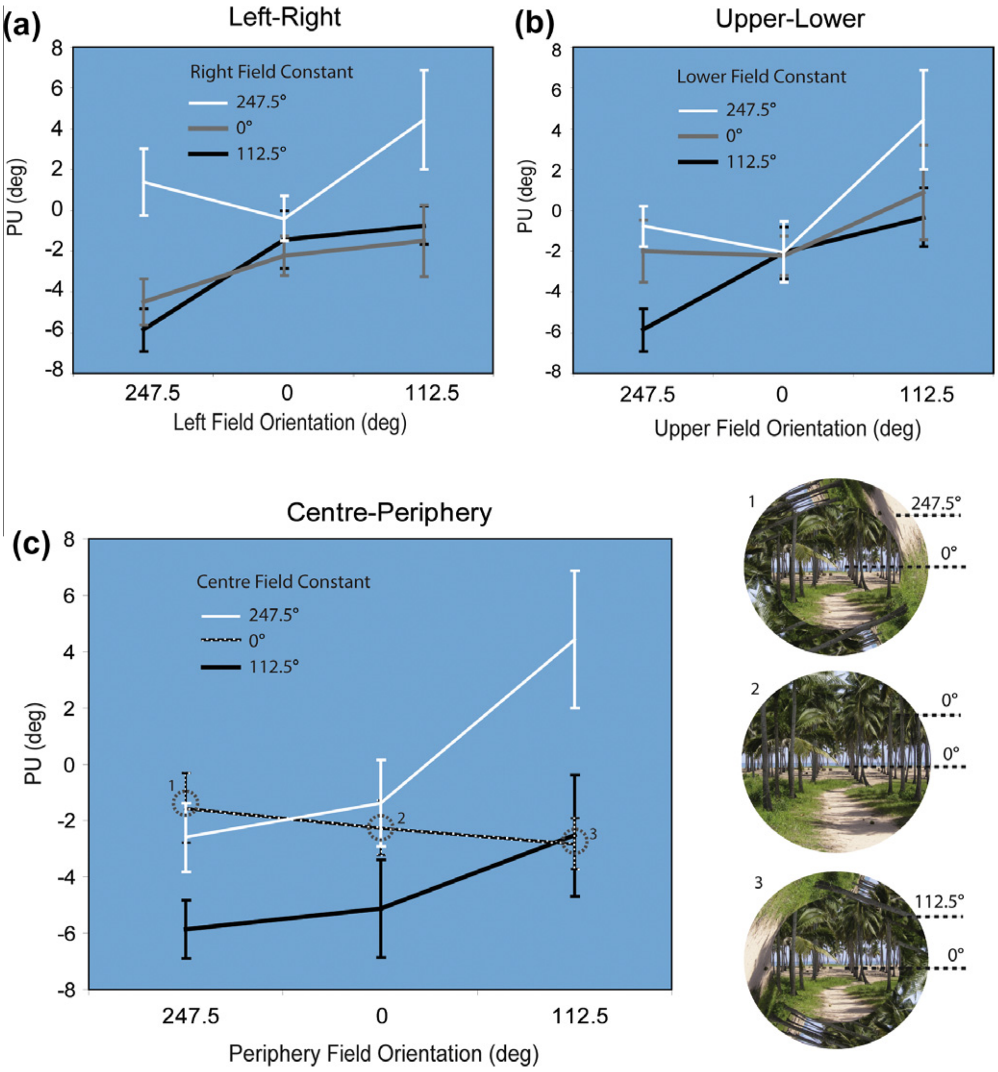

Fig. 4. This figure illustrates how the PU shifts with a change in orientation of the background scene with half-field divisions: (a) left/right, (b) upper/lower and (c) centre/periphery. For each graph one of the fields is held at a constant orientation (white-247.5°; grey/spotted-0°; black-112°) while the orientation of the other field varies along the *x*-axis. The PU is represented on the *y*-axis. Three sample backgrounds are illustrated as inserts to (c) numbered according to the data points to which they correspond. Error bars reflect standard errors of the means across subjects.

For each half field this was obtained four times as the constant field could be each of four background orientations (see Fig. 3b). To measure the relative effect of each half field, we ran a 4 × 2 ANOVA on the VE measure for each of the left/right, upper/lower and centre/periphery sets of backgrounds. The independent variables were: the orientation of the constant half field (with levels; 112.5°, 0°, 247.5° and grey) and test half field (with levels; Half Field A or Half Field B) (see Fig. 3b for clarification of "test half-field" and "constant half-field"). The left/right set of backgrounds showed no main effect of test half-field, $F(1,9) = 0.1$, $p = 0.739$, or constant half-field orientation, $F(3,27) = 1.6$, $p = 0.208$ (Fig. 5a). This result indicates that there is no difference in the measured VEs of the left and right visual fields.

There was, however, a main effect of test half-field for the upper/lower set of backgrounds, $F(1,9) = 9.5$, $p = 0.013$. Fig. 5b illustrates the greater influence of the lower field on the measure VE. The average VE of the lower field is 4.5°, which is significantly greater than the 2.8° VE of the upper field, $t(9) = 2.4$, $p = 0.031$. The visual effect size of the lower visual field was more than one-and-a-half times that of the upper visual field.

For the centre/periphery set of backgrounds, a main effect of test half field approached, but did not quite reach, significance ($p < 0.05$), $F(1,9) = 4.4$, $p = 0.064$. There was however, a main effect of the constant half-field stimulus on the VE, $F(3,27) = 7.1$, $p = 0.001$. This main effect of constant half-field orientation suggests that the constant background which appears in the opposing field is exerting an effect on the VE. Further complicating the interpretation of these results is the presence of an interaction effect, $F(3,27) = 3.5$, $p = 0.029$. This means that the influence of test half-field and constant half-field orientations on the VE may differ depending on specific combinations of the these two independent variables. One such interesting combination is the periphery VE with a constant half-field orientation of 0° (see Fig. 5c). The VE for this particular instance is negative. This result may provide a possible explanation for the main and interaction effects observed for the centre/periphery condition and is explored further in Section 4.

3.3. The effect of stimulus area on the perceived direction of up

The combinations of background stimuli which contain orientation cues in only half of the visual field (those where the constant half-field was grey) allowed us to assess the effect of stimulus area on the VE. We compared the VE of the full-field condition (Fig. 3a) to each of the six half-field (constant field grey) VE measures using a series of *t*-tests (Fig. 6). The full field had a significantly larger VE than each of the half-fields with the exception of the centre field at $p < 0.05$. These results suggest that an increase in stimulus area results in an increase in the size of the visual effect.

4. Experiment 2

Interaction effects present in the centre/periphery backgrounds for both PU and VE measures suggest that there is a complex

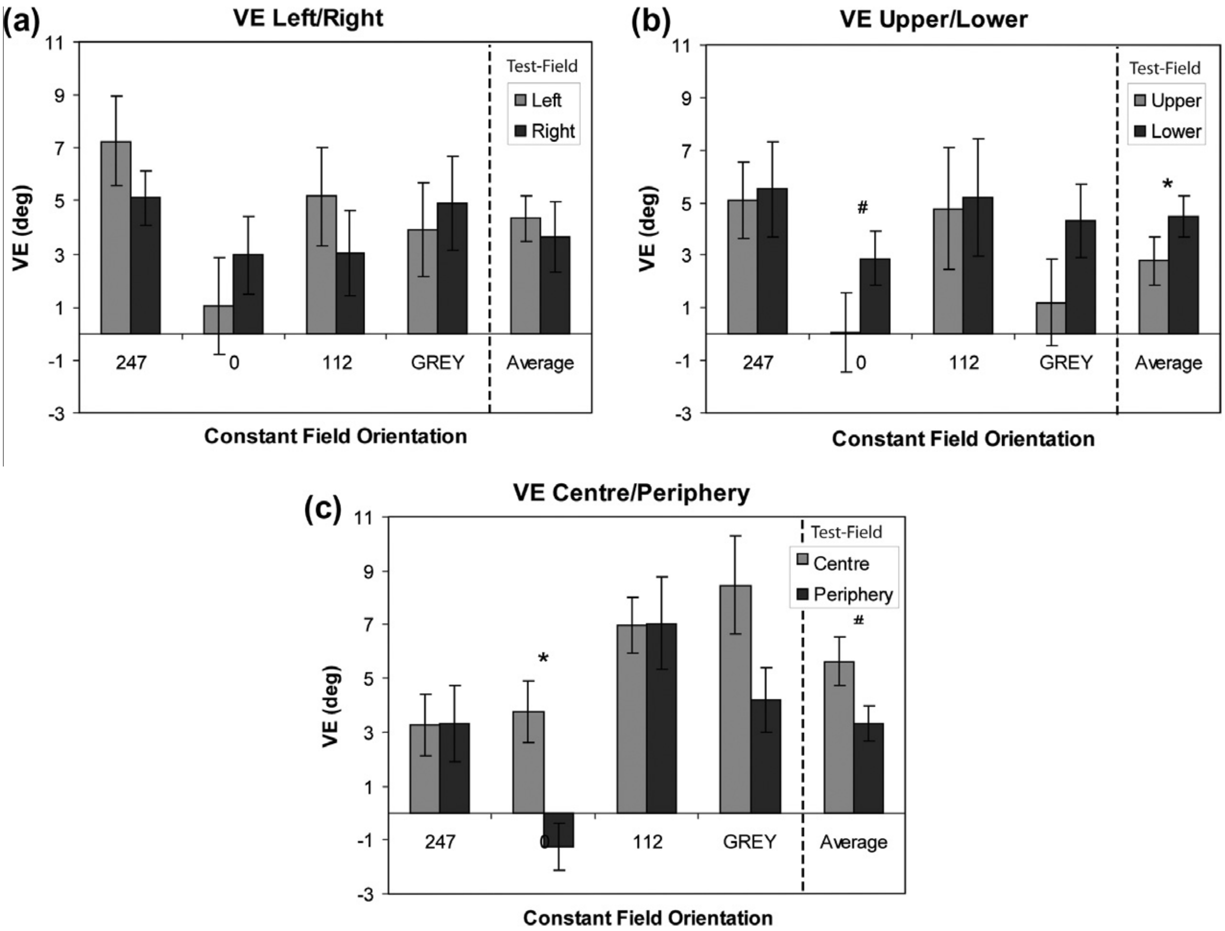

Fig. 5. The four half field VE measures of each half field for each field division (a) left/right (b) upper/lower and (c) centre/periphery. Each bar of the histogram represents the VE for one of the half fields while the other field is held at a constant orientation as indicated on the *x*-axis (see Fig. 3b for an example). The VE is represented on the *y*-axis. The final comparison on each graph is the mean of each of the four respective half-field VEs. Error bars reflect standard errors of the mean across subjects. * indicates statistically significant comparisons: upper/lower "VE Average" $t(9) = 2.4$, $p = 0.031$ and centre/periphery "VE (0°)" $t(9) = 3.6$, $p = 0.006$, # indicates comparisons which approach significance: upper/lower "VE (0°)" $t(9) = 2.2$, $p = 0.052$ and centre/periphery "VE Average" $t(9) = 2.1$, $p = 0.064$.

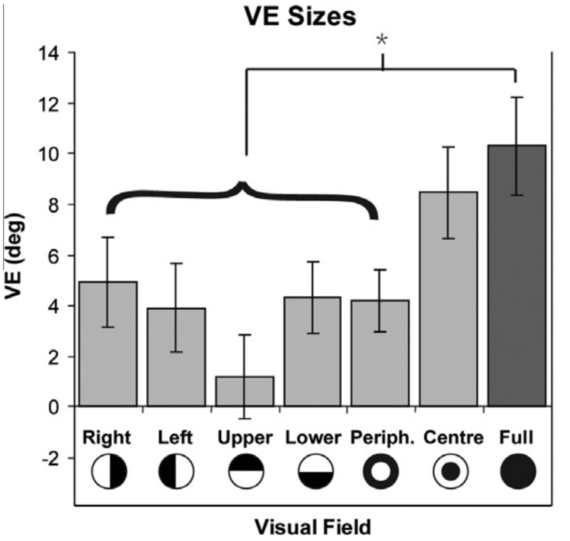

Fig. 6. This figure illustrates the difference between half-field and full-field VE sizes. VE is represented on the *y*-axis while the tested half field is represented on the *x*-axis. The final bar represents the full visual field. Right $t(9) = 3.4$, $p = 0.008$. Left $t(9) = 3.1$, $p = 0.012$. Upper $t(9) = 5.8$, $p = 0.001$. Lower $t(9) = 2.5$, $p = 0.034$. Periphery $t(9) = 2.4$, $p = 0.037$. Centre $t(9) = 0.8$, $p = 0.467$. All reported *t*-tests are compared against the full-field VE. Error bars reflect standard errors of the means across subjects.

relationship between the central and peripheral visual fields and their effect on the perceived orientation of the superimposed character. Unlike the effects of backgrounds in the left/right and upper/lower fields, the sum of the responses to each of the centre/periphery areas tested alone did not well predict the full-field response. Fig. 4c suggests that the PU interaction effect is being driven by the set of stimuli which contain upright backgrounds in the centre field (Fig. 4c, spotted line and illustrated backgrounds). The VE interaction may also be driven by the same stimulus set, as the VE in the periphery was negative (−1.3° ± 2.8°) when it was paired with an upright background in the centre field (Fig. 5c, constant field = 0). These observations suggest the presence of an additional effect in which the perceived orientation of the centre may be influenced by the orientation of the periphery stimulus surrounding it. If that were the case then the altered perception of the orientation of the centre stimulus may have in turn influenced the perception of the orientation of the probe character. Experiment 2 addresses this point directly.

It has been shown that a tilt of one part of a scene can influence the perceived tilt of another (Dyde & Milner, 2002). We therefore ran a control experiment for the centre/periphery division assessing the perceived orientation of the centre background itself in the presence of a tilted surround.

4.1. Method

Ten of the eleven subjects who ran in Experiment 1 also ran in Experiment 2. The same apparatus was used to run a modified version of OCHART. The procedure for Experiment 2 was the same as outlined in Section 2.1.7 except that the visual stimuli no longer included the ‘p’ character and subjects were asked to indicate if the centre field itself was tilted to the left or right of gravity-defined vertical. A set of backgrounds similar to those used in the centre/periphery condition in Experiment 1 were utilized in the centre/surround control experiment. The surrounding area consisted of three scenes, 112.5°, 247.5° and the grey control background (the same periphery stimuli utilized in Experiment 1) while the centre contained eleven tilted scenes from −5° to +5° in steps of 1°. All combinations of centre and surround scenes yielded 33 distinct combinations, each of which was presented nine times, resulting in 297 trials. Participants were run in a single session and took about 1 s/trial to respond, meaning that a typical session took about 5 min to run.

To obtain psychometric functions we plotted the number of times subjects reported the centre scene as tilted to the left of upright (as defined by gravity) as a function of the orientation of the centre scene. Using the sigmoid function described in Eq. (1), we determined the point of subjective equality and took it as the orientation at which the centre scene appeared most upright. We then compared the “perceived scene uprights” for the different orientations of the periphery (112.5°, 247.5° and a grey control). One of our subjects failed to reach points of subjective equality due to their inability to perform the task as their responses to each stimuli did not significantly differ from chance, $t(26) = 1.153$, $p = 0.260$. As a result their data could not be fit to a sigmoid function. We therefore could not determine the orientation at which they perceived the centre scene to be most upright. This subject’s data has been excluded from our results.

5. Results

In this experiment, subjects judged the orientation of the centre field itself in the presence of a surrounding stimulus at orientations of 112.5°, 247.5° and a grey control background. The perceived upright orientation of the centre stimulus in the presence of a leftward (247.5°) and rightward (112.5°) tilted peripheral background was +0.16° and +0.55°, respectively (Fig. 7). The difference between these two measures approached significance $t(8) = 2.092$, $p = 0.077$. However, the difference between the two percepts of the centre scene was less than half a degree. Although the direction of this difference was in line with the direction we would expect to cause a negative periphery VE, the size of the difference was much too small to explain the observed reversal in trend as seen in Fig. 4c. The VE of the centre alone (periphery stimulus grey) was 8.5° ± 5.8° (Fig. 5c). The difference between the centre scene orientations for these two backgrounds is 225° [112.5° − (−112.5°)]. By dividing the VE by this difference, we can determine the size of the

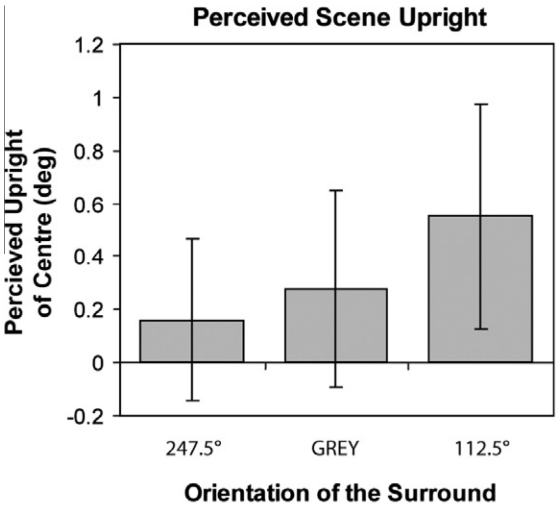

Fig. 7. This figure illustrates the lack of a significant perceptual difference between upright centre scene judgments when surrounded by a leftward tilted (247.5°) rightward tilted (112.5°) and grey control background. The perceived upright of the scene is represented on the *y*-axis and the orientation of the surrounding scene is represented on the *x*-axis. Error bars reflect standard errors of the means across subjects.

VE per degree of tilt of the background. This value is 0.038°/deg of background tilt. This means that in order for the peripheral VE to reach the observed −1.3°, the perceived difference in the centre background orientations would have to have been at least 34.2°.

6. Discussion

The tilted background images in Experiment 1 evoked shifts in the perceptual upright (PU) when presented in each of the left/right, upper/lower and centre/periphery sets of backgrounds. Visual effect (VE) measures indicated that the left and right visual fields were approximately equal in their ability to induce shifts in the perceptual upright, while stimuli in the lower visual field had a larger effect compared to these stimuli in the upper visual field. Both the PU and VE measures provided evidence for an interaction between centre field and peripheral field stimuli. Interaction effects between the stimuli in the centre and periphery suggested the possibility that the periphery stimulus may affect the perception of the orientation of the centre background. Quantification of the effect of a tilted periphery on the perception of the orientation of a centre background, however, indicated that any such effect was too small to explain our results.

6.1. Left/right symmetry

Our visual effect measure indicated no difference in effect size evoked by stimuli presented in the left field as compared to in the right field. The results of such a comparison suggest that the brain weighs visual information from the right and left fields equally in determining perceptual upright. While there are many cases where definite left/right asymmetries exist, it is not always the same field that is dominant across different types of tasks. For example, there is a right visual field advantage for verbal material (Beaumont, 1982) while there is a left visual field advantage for many types of non-verbal tasks (Bryden, 1982). In an informative review on visual field asymmetries, Bryden and Mondor (1991) drew the conclusion that no clear story emerges pertaining to left and right visual field dominancy. Instead, they proposed that asymmetries, or lack thereof, lie in the specificity of the task at hand and in the particular method in which tasks are carried out. Magnussen, Landro, and Johnsen (1985) specifically investigated line orientation discrimination in left and right fields and found no evidence for a right/left asymmetry. Our results provide supporting evidence for a lack of left/right visual field asymmetries in determining perceptual orientation. Although asymmetries do exist across right and left visual fields in clinical populations, for instance in unilateral spatial neglect cases, where patients with right brain damage do not process visual cues on the left side of space (Gainotti, Messerli, & Tissot, 1972), there appears to be no right/left visual field asymmetry in processing visual orientation cues in neurologically intact individuals.

6.2. Upper/lower asymmetry

The visual effect size of the lower visual field was significantly greater than that of the upper field (see Fig. 5b), indicating an upper/lower asymmetry in processing visual orientation cues. These results suggest that the brain favours visual orientation cues presented in the lower visual field over those same cues presented in the upper visual field. A possible explanation for this may be the significance of the ground plane in determining self-orientation. As mentioned in the introduction, the ground plane is critically important in determining upright posture and maintaining balance as it contains information which affects our gait pattern and our ability to navigate obstacles (Patla, 1998). It may be that the brain has evolved a preference for visual orientation cues in the lower field to extract the abundance of valuable postural and navigational information which is usually present there. The brain does demonstrate a preference, in general, for processing visual information in the lower visual field. For example, the discrimination of patterns, such as spatial frequency gratings, is superior in the lower visual field (Berardi & Fiorentini, 1991). Also, the segmentation of an image into figure and background is also performed better in the lower visual field (Rubin, Nakayama, & Shapley, 1996). Haji-Khamneh and Harris (2009) employed the OCHART technique to assess the importance of the brain's ability to extract intrinsic and extrinsic cues to orientation from a scene, thus outlining the importance of scene segmentation in determining the PU. It is appropriate that, if the lower visual field is superior in both scene segmentation and in the discrimination of orientation patterns, there would be a larger VE for the lower visual field. Our data confirm this is the case.

6.3. The centre/periphery relationship

Unlike our left/right and upper/lower field results, our centre/periphery field data do not provide a clear account of how the centre and peripheral fields may affect perceptual orientation. Results for the VE measure trend toward a difference between the effectiveness of central and peripheral stimuli, with a greater effect of the central stimulus. This goes against the early literature concerning the effectiveness of visual cues in central and peripheral areas. Visual cues in the periphery have been shown to be particularly effective in creating illusory self motion, a phenomenon known as vection (Brandt, Dichgans, & Koenig, 1973). Dichgans and Brandt (1978) concluded that the periphery dominates visually induced vection and spatial orientation. Also, research on postural adjustments induced by optical flow showed that spontaneous standing sway increased with the occlusion of peripheral vision but not with the occlusion of central vision, suggesting that the periphery played the dominant role in sway control (Amblard & Carblanc, 1980; Begbie, 1966; Dickinson, 1969; Dickinson & Leonard, 1967). Furthermore, peripheral vision plays a crucial role during our daily lives, apparently dominating our perception of self-motion and body orientation with respect to the environment (Bessou et al., 1999; Brandt, Dichgans, & Koenig, 1973; Johansson, 1977). The visual periphery is also more sensitive to stimuli in motion, and several investigations have cited the importance of the visual periphery in the control of posture, locomotion, reaching, and grasping (reviewed in Danckert and Goodale (2003)). It seems counter-intuitive then that compared to the effect of our central stimulus, the periphery seemed to exert a weaker effect on the perceptual upright. Overwhelming evidence suggests that the periphery would be expected to be play a *greater* role in determining the direction of up.

However, it may be the case that an interaction effect between the central and peripheral fields masked the total strength of the influence of the periphery in our experimental design. Our results showed that when a peripheral background was presented on its own (centre field grey) there was a VE comparable in magnitude to the VEs found in the left, right, upper, and lower fields (Fig. 6). It may be that when the periphery is combined with a centre stimulus the effect of the periphery is somehow masked or lost. To explore this hypothesis we took a closer look at the observed centre/periphery interaction effect. Fig. 4c suggests that the interaction may be attributed to those backgrounds which contain an upright central image surrounded by varying orientations of the peripheral scene. The direction in which the PU was shifted was opposite to the direction we would expect it to be shifted. It may be that the periphery still plays an important role in perceptual orientation but by exerting its effect on the perceived upright of the centre scene.

This hypothesis is in line with the "hierarchical organization principle" (Asch & Rock, 1990). Zoccolotti et al. (1997) studied the Double Rod and Frame Illusion (DRFI), a variation of the Rod and Frame Illusion (RFI) first studied by Witkin and Asch (1948) (see Fig. 8). They used the hierarchical organization principle to explain their findings. The principle proposes that the perceptual system organizes units of a field hierarchically, from the outer-most to the inner-most stimulus. Each stimulus in the field is perceived relative to its immediate outer frame of reference rather than to any other external frame (Asch & Rock, 1990). According to this principle, the outer frame in the DRFI causes a misperception of the inner frame which in turn affects the perceived orientation of the rod.

Experiment 2 sought to find evidence of such a hierarchically organized effect between our stimuli. However, our results indicated no such relationship, at least not of a significant size. The perceived difference in central stimuli for leftward and rightward tilted peripheral backgrounds was much too small (0.55°) to explain the reverse in trend present in our centre/periphery interaction. Further investigation into the DRFI and the hierarchical organization principle is required to uncover a possible explanation for our results.

A recent paper by Daini and Wenderoth (2008) challenges the simplicity of the hierarchical organization principle and provides a possible explanation for what might be occurring in our situation. They outline an effect to which our second experiment was insensitive. Daini and Wenderoth (2008) confirmed the observation of Zoccolotti et al. (1997) that when more than one frame is present there is an effect between the frames themselves. However, they performed multiple follow-up experiments to determine the exact nature of the inter-stimulus effect. What they found was that the effect of the tilted outer frame on the inner square frame is the same as that on the rod. Additionally they found that the outer frame acts differently on attended versus unattended stimuli. They proposed that there are different mechanisms which can arise from the same visual context whose influence depends on attention. As a consequence, they suggested that the effect of the outer frame on the inner frame was not relative to vertical when the inner frame itself was not the stimulus being judged. For our purposes, this means that the effect of the peripheral stimulus on the attended centre stimulus (Experiment 2) may be different from the effect of the peripheral stimulus on the unattended centre stimulus (Experiment 1). This position is supported by the findings of Jazayeri and Movshon (2007). They found evidence that the magnitude of illusions, and even whether they occur at all, depended on the observer's task, suggesting that some illusions can be a direct consequence of the particular decoding strategy used by the observer to make perceptual judgments. Therefore, we should not be hasty in drawing the conclusion that our second experiment confirms a lack of effect of the periphery on perceptual orientation judgments.

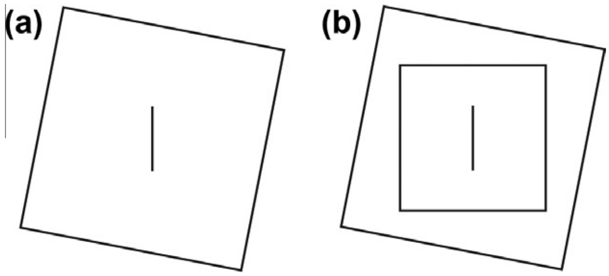

Fig. 8. (a) The rod-and-frame illusion (RFI). With the frame tilted 11° CW, the perceive orientation of the vertical rod is slightly CCW. (b) The double RFI (DRFI). With the outer frame tilted 11° CW and the inner frame vertical (0°), the perceived orientation of the inner frame is slightly CCW, and the perceived orientation of the vertical rod is CW (after Zoccolotti et al. (1997)).

Another possible explanation is that the effect of the periphery on the centre did not reverse the VE but simply neutralized it. Although the trend in VE in Fig. 4c is negative (centre field 0°, spotted line), it is not significantly different from zero, $t(9) = -1.45$, $p = 0.180$. It may be that when the peripheral stimulus exerts its effect on an unattended central background (Experiment 1) that the entire effect of the periphery is taken on by the centre stimulus, and in such a way that the centre's perceived orientation with respect to the vertical is unaltered. Such possibilities further complicate our efforts to draw conclusions about the centre and periphery half fields and their effects on perceptual orientation.

The means by which the centre and peripheral visual field were divided, into geometric halves by area, should also be taken into consideration in the interpretation of these results. Although the central and peripheral visual fields occupied equal retinal areas, the amount of cortical representation of each area was different. Due to M-scaling, the central field stimulated a much larger cortical area compared to the peripheral field. This may help to explain the unexpected trend towards dominance of the centre region.

Finally, it may also be that the periphery does not play as strong a relationship in determining the PU as measured specifically by the OCHART technique used in this study. The visual periphery is particularly sensitive to stimuli in motion (Danckert & Goodale, 2003) but OCHART employs a stationary background stimulus. There are also other limitations set by the study's design. The circular shroud eliminated a sizeable portion of peripheral vision, limiting vision to the central 27°. What we have chosen to call the periphery does not meet the classical definition of peripheral vision. It is peripheral only in relation to what we have labelled the centre region.

There has, however, been one clear result that has emerged from our exploration of the effects of the central and peripheral visual fields and that is that there is a complex interaction occurring between the two parts of the visual field which is both interesting and puzzling. Further research is necessary to explain this complex relationship between central and peripheral visual fields in determining the perceptual upright. We suggest a paradigm which stimulates the entirety of the visual field. Such a design could test central, peripheral and foveal vision without restraint.

6.4. The effect of stimulus area

Our left/right and upper/lower visual field experiments showed that the effect of visual cues on the PU increases with an increase in stimulus area (Fig. 6). This is in accordance with a study by Howard and Heckmann (1989) which concluded that stimulus area was a primary factor in achieving illusory self motion. Similarly, Nakamura and Shimojo (1998) found that the strength of vection increased linearly with the size of the visual area in which the moving pattern was presented. Could it be that there is linear summation of orientation cues across the retina in determining PU? Efforts to uncover recent studies involving retinal summation proved difficult. However, there was an older study regarding light detection which drew conclusion about retinal summation. Our ability to detect a faint light source increases with an increase in retinal stimulation (Hallett, Marriott, & Rodger, 1962). The authors suggested that there may be a spatial summation of signals across the retina. While our results do show that visual effect sizes grow with increased size of stimulus area, our study was not specifically designed to draw conclusions about retinal summation. It may be beneficial to further pursue the avenue of testing for spatial summation of visual cues to orientation across the retina.

7. Conclusions

From this study we conclude that an increase in stimulus area results in an increase in effectiveness in providing cues to the perceptual upright. The left and right visual fields are symmetric when assisting the brain in determining the direction of up, while the lower visual field is of greater importance as compared to the upper visual field. Finally, while both central and peripheral fields are important in determining the upright direction, there is a complex interaction taking place between these two fields which warrants further investigation.

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