POSSIBLE NEURAL SUBSTRATES FOR BINOCULAR RIVALRY

Rick van der Zwan
Department of Psychology

**A thesis submitted in fulfilment of
the requirements for the degree of
Doctor of Philosophy.**

February 1994
Faculty of Science
University of Sydney

ABSTRACT

Binocular rivalry is the perceptual consequence of dichoptic input which is not congruent between both visual inputs. There is some evidence, both theoretical and empirical, that the perception of binocular rivalry is mediated by interactions between binocular neurones, rather than by interactions between monocular neurones. This evidence suggests also a model of perception which predicts binocular rivalry as a consequence of normal interactions between binocular neurones in a retinotopic array. This model accounts for rivalry without postulating any additional interconnections beyond those already thought to exist between binocular neurones simply assumes an orderly mapping of tuning characteristics across groups of cells, as is typically observed in visual cortex. On the basis of this model, and findings already reported, it was hypothesised that binocular rivalry reflects extrastriate rather than area V1 processing (no process so far attributed to area V1 has yet been reported to be affected by binocular rivalry). It was hypothesised also that area V2 was the most likely area in which such processing first arises.

Area V2 has been associated with the perception of 'purely subjective contours'. It has been shown that some cells in area V2 are tuned for such contours, which are characterised by the absence of Fourier components at the orientation of the perceived contour, while no cells in area V1 have been found to be similarly sensitive (von der Heydt and Peterhans 1989). This characteristic of area V2 neurones enables purely subjective contours to be used to test the two hypotheses described above. Real contour tilt aftereffects, which are thought to arise in area V1, are not affected by rivalry during their induction. If purely subjective contour tilt aftereffects (Paradiso, Shimojo and Nakayama 1989) are subject to the same types of processing as their real contour counterparts, as suggested by the rationale and model of von der Heydt and Peterhans (1989), interactions between subjective contour tilt aftereffects and binocular rivalry should indicate the role, if any, of area V2 in rivalry.

It was found that purely subjective contour tilt aftereffects (Experiment One) and tilt illusions (Experiment Four) exhibit angular functions like those observed for real contour tilt aftereffects and illusions. Just as for real contour effects, these functions can be described in terms of direct effects (Experiment Two) and indirect effects (Experiment Three), suggesting purely subjective contours are processed as if they were real contours. Unlike real contour direct effects, purely subjective contour direct and indirect effects are reduced in magnitude by periods of rivalry during their induction (Experiment Five). In keeping with their suggested extrastriate locus (eg. Wenderoth, van der Zwan and Williams 1993), the magnitude of a real contour indirect effect is also reduced by periods of rivalry occurring during its induction (Experiment Six). These results suggest that rivalry does arise first in area V2. If this is true then complete interocular transfer of the purely subjective aftereffect, induced with or without rivalry, should occur because area V2 is almost exclusively binocular. This proved not to be the case, however, suggesting the ocular dominance observed in most binocular cells has to be taken into account in any explanation of rivalry (Experiment Seven). This was tested using real contours and found to be the case. These last results suggested also that rivalrous interactions occur between groups of binocular neurones only in extrastriate cortex (Experiment Eight). This hypothesis was tested by examining the effect of binocular rivalry on the duration of the plaid motion aftereffect, which is thought to arise no earlier than area MT, a visual cortical area which is also thought to be almost exclusively binocular. It was found that rivalry did reduce the duration of plaid motion aftereffects but not linear motion aftereffects, and that the impact of rivalry might be linked to plaid sensitive cells in area MT, although this last conclusion is tenuous (Experiments Nine and Ten). Finally, it was shown also that the magnitude of the reduction in duration of the aftereffect was proportional to the predominance of the plaid stimulus during rivalry, a finding which supports the mechanism of rivalry suggested by the binocular model.

The results together suggest that binocular rivalry does arise through binocular interactions, but that such interactions cannot be attributed to a single cortical area. All groups of binocular neurones may be subject to the processes that ultimately give rise to the perception of rivalry, a conclusion which does not invalidate the binocular model of rivalry. This has some consequences for binocular vision, particularly stereopsis, which might occur qualitatively during binocular rivalry.

Acknowledgments.

There are many, many people whom I'd like to thank for their help and support. A few are mentioned here.

First, in terms of intellectual contribution, is Dr. Peter Wenderoth. Peter has been an inspirational supervisor and colleague, providing sound advice and guidance when it was required. Despite what appears here, his ability and efforts should not be underrated. He is also a very good friend, and I thank him for his support and very good humour. I look forward to working with him again in the future.

Similar accolades are deserved by Benny Barnes, Thomas Haslwanter, Stuart Smith, Annie Swinbourne, and Annie Topple. Benny, with whom I've shared an office for three years, deserves a special mention. What a guy. He's more pleased I'm done than I am. He will, at last, have an office in which the bookshelf and both desks are tidy. It's not healthy, but it is what he wants.

A few other really good blokes are Darren Burke, Dave Alais and John Predebon. Consistently and persistently funny. I'm sure psychophysics will never seem quite the same again. Thanks guys. Others in the Department who should be mentioned are John Duckworth and Deb Buttenshaw. Thanks also to John Holden, who was an endless source of good advice and questionable jokes.

At home there is always Craig and Bev Sheffield, and Anthony and Hanan McLachlan. Better people don't exist. They are all wonderful and great friends. I must thank Anthony for always letting me look good at sport, and Craig for nearly always letting me. Thanks go to Craig also for not publishing any of this work before me. He's a man with all the answers. Girls, what can I say, marriage by choice.

I must thank also my family for their love and support. While I'm sure this stuff is a mystery to them most of the time, most of the time they've hidden it well.

Finally, I send my love to Jennifer Northam. I cannot imagine having been able to finish this without her support. She has been a constant source of love, comfort, encouragement, fun, and poverty for years. Thank you for every moment Gerty, of all my friends, you are the best.

vdZ.
1994

Papers and Proceedings Arising From This Investigation.

van der Zwan, R., Alais, D., Wenderoth, P. & Riddick, W. (1991) Are higher order motion aftereffects reduced by binocular rivalry? 18th Annual Experimental Psychology Conference, Flinders University of South Australia.

van der Zwan, R. & Wenderoth, P. (1992) Subjective contour/binocular rivalry interactions: Implications for the mechanism of rivalry. 19th Annual Experimental Psychology Conference, University of New South Wales.

van der Zwan, R. & Wenderoth, P. (1993) Mechanisms of purely subjective contour perception and the cortical location of the binocular rivalry mechanism. 20th Annual Experimental Psychology Conference, University of Melbourne.

van der Zwan, R. & Wenderoth, P. (1994) Does binocular rivalry arise via extrastriate mechanisms only? In preparation.

van der Zwan, R. & Wenderoth, P. (1994) Evidence that real and subjective contour tilt aftereffects are processed by the same neural mechanisms. Visual Neuroscience, submitted.

van der Zwan, R. & Wenderoth, P. (1994) Psychophysical evidence for area V2 involvement in the reduction of subjective contour tilt aftereffects by binocular rivalry. Visual Neuroscience, in press.

van der Zwan, R., Wenderoth, P. & Alais, D. (1993) Reduction of a pattern-induced motion aftereffect by binocular rivalry suggests the involvement of extrastriate mechanisms. Visual Neuroscience, 10, 703-709.

This research was supported by an Australian Postgraduate Research Award to Rick van der Zwan.

TABLE OF CONTENTS

GENERAL INTRODUCTION

The mechanisms used by the visual system to extract three dimensions from two are necessarily complex. Deciding where different objects begin and end, which objects obscure and which are (partially) obscured, which are moving and which are stationary are not trivial problems. The mammalian brain has achieved solutions through the development of mechanisms exploiting, for example, motion parallax, luminance and/or colour gradients, and binocular disparity. It should be remembered, however, that such terms represent a level of description separate from that which describes what is actually occurring neurophysiologically. These terms describe, but do not explain such mechanisms. It should be clear, therefore, that the response of the visual system to an effective input can be detailed either at a physiological level or at a psychophysical (that is perceptual) level, and a complete understanding of any visual process requires both (cf. Wenderoth and Latimer 1978). Thus it is significant that as understanding of the neural hardware in extrastriate regions of the cortex increases, so does the possibility of explaining psychophysical effects in terms of the operational properties of such hardware (Wenderoth 1992). For the psychophysicist this provides an advantage in that limitations which are imposed by increased physiological knowledge restrict the type and number of explanations that may be offered for a particular observation. This advantage presents several challenges. Interpretation of experimental results is inevitably guided by the assumptions underlying the research. In this way the implications of a set of findings are constrained by the working hypotheses of the research, and the more general theoretical environment in which the work has been conducted. These must be re-evaluated as understanding develops. Similarly, care must be taken not to over-interpret physiological findings in order to fit them to perceptions in the explanation of which they play an indeterminate role. Yet some attempt at linking neurophysiology and psychophysics and perception is necessary if visual perception is ever to be fully understood.

In a recent work Stoner and Albright (1993) questioned the efficacy of the conceptual modularisation of visual cortical functioning, particularly as it applies to motion perception, but more broadly as it applies to visual perception in general. They are not the first to express such concerns (DeYoe and van Essen 1988, van Essen, Andersen and Felleman 1992). Stoner and Albright (1993) noted that the facilitation of understanding provided by such an approach may be responsible, at least in part, for the development of this compartmentalisation of the visual system, and that it has been reinforced by distinctions in 'processing streams' described by the neurophysiologists (eg. Zeki and Shipp 1988). Describing the visual system as made up of motion channels, orientation channels, spatial frequency channels, etc, does make for ease of description, but does imply an isolation of function that does not really exist. Aside from their usually being studied in isolation, it is not the case that such processes work independently within the visual cortex, just as descriptions of the tuning characteristics of individual neurones as motion selective, or orientation selective, or contrast selective ignore a multiplicity of sensitivities that may be displayed by any one neurone. It is not surprising, therefore, that while this strategy may be generally successful, there are instances where it has failed to provide reasonable accounts of perceptual phenomena. Such failures may be temporary, awaiting only the arrival of more relevant data. Conversely, they may represent shortcomings inherent in an heuristically modular visual system. Which of these is true is an empirical question which will, no doubt, be solved on a case by case basis. It was one of the aims of the work reported here to provide an explanation for one such effect; the perceptual phenomenon described as binocular rivalry.

Binocular rivalry has long been the subject of psychophysical and, more recently, physiological investigation. There are plenty of data available, and the nature of explanations offered for the phenomenon have undergone several changes, roughly parallel with those described for illusions by Wenderoth (1992), as the amount and quality of such data has increased. Contemporary models of the processes giving rise to the perception of binocular rivalry have been developed within an information processing framework; a framework in which modularisation of function is an inherent characteristic. One consequence of this approach has been an ascription of function which may not be warranted. It is nearly always the case that when referring to the processes giving rise to rivalry workers refer to a "binocular rivalry mechanism". Intentional or not, this has accorded binocular rivalry the status of a process like those responsible for stereopsis, motion or colour perception. In other words, a special neural mechanism or process which acts on a certain type of visual information. As will be demonstrated, this can be shown to be wrong. It will be argued that binocular rivalry should be accorded the status of an illusion, or more correctly a misperception. That is, rather than a process which has developed specifically to deal with certain types of information, in order to increase the probability of survival of an organism, or make sense of the external world, or whatever, rivalry is more correctly thought of as the *perceptual consequence* of normal processing of 'abnormal' input. In some sense, rivalry is an emergent property (Oatley 1978) of normal cortical interactions, which is not to say that it arises via some 'cognitive' function, but rather that it arises as a by-product of the way the visual system is constructed.

Such a position implies that current models of rivalry mechanisms are limited in their explanatory value, and evidence for this is provided by the limited ability of any one model to account for the myriad of different findings in the area. The idea of distinct processing streams has allowed workers to investigate the effects on rivalry of individual parameters alone, or very occasionally interactions between two parameters. In turn, this has led to models capable of demonstrating rivalry for those parameters, but not others, and certainly not multiple parameters operating in concert. Claims by workers that other parameters "could be incorporated into an expanded model" (Mueller 1990, p. 63) may be valid, but could lead easily to an explosion of such mechanisms. Such a proliferation of 'rivalry mechanisms' is unnecessary. Careful examination of existing data reveals this to be true, and this is the task of the first part of the thesis. It is not sufficient, however, to adopt the obscurantist approach of highlighting shortcomings in existing work while offering no substitutes. Equally important is to provide a physiologically valid alternative. This can be done best when the neural substrates of the system being considered are well understood. Thus providing the general framework for such a model is only part of the task and defining the nature of the components is also required. This has been, in fact, a consistent problem for workers wishing to model rivalry. There have been few neurophysiological limitations placed on the components of the circuitry that might be involved. The experiments to be reported here were conducted with the general aim of understanding the nature of the neural correlates of binocular rivalry, and thus providing neurophysiological constraints for a model explaining rivalry. This has been achieved by examining interactions between extrastriate processes and the perceptual phenomenon of binocular rivalry with a view to linking binocular rivalry with a specific neural locus. This strategy has been employed several times previously, with limited success, but it has the advantage of potentially providing a coherent and restricted framework in which any model of rivalry may be developed. However, this can occur only when the components of the system are well understood.

[illegible]

mechanism or process which acts on a certain type of visual [illegible] demonstrated, this can be shown to be wrong. It will be argued that binocular rivalry should be accorded the status of an illusion, or more correctly a misperception. That is, rather than a process which has developed specifically to deal with certain types of information, in order to increase the probability of survival of an organism, or make sense of the external world, or whatever, rivalry is more correctly thought of as the perceptual consequence of normal processing of 'abnormal' input. In some sense, rivalry is an emergent property (Oatley, 1978) of normal cortical interactions, which is not to say that it arises via some 'cognitive' function, but rather that it arises as a by-product of the way the visual system is constructed.

PERSPECTIVES ON BINOCULAR RIVALRY

As stated, one of the principal contentions of this work is that binocular rivalry has generally been misinterpreted. In addition to the problems alluded to above, this can be attributed also to the compelling perceptions associated with rivalry. To clarify this; there is some evidence to suggest that researchers have confused descriptions of the percept with explanations of its mechanism. A brief consideration of the historical antecedents of current theories of binocular rivalry illustrates this while also providing perspective for contemporary research. It has not always been the case that rivalry has been attributed to interactions between parameter tuned units within the visual cortex, a development which occurred only after such distinctions were facilitated by early neurophysiological investigations (eg. Hubel and Wiesel 1959). Until then, a different level of description was applied to rivalry, and a failure to clearly distinguish between description and explanation may be the basis of some extant problems. The aim of the following review, therefore, is briefly to describe and evaluate the most noteworthy findings in the history of binocular rivalry research. It is not intended to be a comprehensive review or critique of early work in the area because such endeavours have already been completed by others (Levelt 1968, Lack 1978, Blake 1989). Instead it provides background, and highlights links between earlier findings and some of those of interest in contemporary research. It also describes a number of problems, and areas of controversy which will be addressed more fully when the results of the experiments in this investigation have been evaluated.

History and Background.

Research into binocular rivalry, while voluminous, can be divided arbitrarily into three periods. The first includes several works around the turn of the century, and lasts to the 1920's. During this period basic observations were made, and ideas that became popular later were first muted in simple forms, usually with 'mental' rather than neurophysiological explanations. Both Levelt (1968) and Blake (1989) recognise the first description of rivalry as being that provided by DuTour, in 1760, in which he noted that two colours presented separately to either eye resulted in an alternation of the perceived colour. A similar observation was reported much later by Sterling (1901). Stirling observed something much more complex than DuTour, however. He presented dichoptically two similar, but slightly different postage stamps, each of a different colour. Rivalry under these conditions was such that Stirling's subjects sometimes reported one stamp, or the other, and sometimes the picture of one stamp but the colour of the other. That is, subjects reported dissociations between form and colour. Creed (1935) and Hastof and Myro (1959) later verified 'Stirling's effect', while others have failed to find it (Ramachandran, Rao, Sriram and Vidyasagar 1973, Wolfe 1986). The experiments to be described provide a means of evaluating these two differing results, and the debate will be addressed more fully in the General Discussion. The first systematic inquiry into binocular rivalry was that conducted by Wheatstone (1838) during his investigation of stereopsis. Wheatstone also published what may be the first stereogram demonstrating rivalry. Breese (1899, 1909) published the most significant works of that time, however. In those he described and detailed many of the conditions necessary for the instigation of rivalry. Breese was the first to apply the terms 'predominance' and 'suppression' to describe the perceptual state of the available stimuli. Interestingly, a number of the techniques developed by Breese for measuring rivalry, but now thought to be flawed (cf. Wade 1975), were until recently still commonly employed.

Perhaps the most important thing to note from this early work is that at this stage descriptions of rivalry were being used in place of explanations. DuTour noted that perception during rivalry occurred *through one eye alone*. A similar description was provided by Wheatstone (1838). Breese (1899) similarly attributed rivalrous alternation to the predominance of *one eye or another*. Common to all these workers is the notion, either explicit or implicit, that rivalry arises through interactions between eyes, a theme echoed in contemporary research and models by the assertion that binocular rivalry is mediated by monocular neurones. There is no *a priori* reason why this is necessarily the case. It does appear during rivalry that the two eye views are in competition, that each monocular input is actively and often vigorously trying to suppress the other monocular input from conscious perception. Where it is successful, the image from one eye appears to reflect the monocular input to that eye, while the monocular input from the other eye is not visible. To the viewer, the one experiencing the rivalry, the visual field is filled with zones of apparently monocular perceptions which are temporally dynamic. As Levine and Scheffner (1991) describe it:

> "..*you see each region monocularly* with the one eye and then with the other, but the information from the two eyes does not fuse to form a single binocular percept. When the subject reports seeing the stimulus presented to the right eye, we say that eye is dominant, while the left eye is being suppressed." (italics mine)
>
> (p. 319.)

There is clearly some confusion between perception with process. It probably results from a simplistic association for which there is only a little evidence. Such descriptions are only (and can only be) of what is perceived, and what is perceived *appears* to be one or the other monocular input. For this reason, and others, almost every model of rivalry incorporates monocular units which ultimately are responsible for what is perceived when binocular fusion is not possible. However, while predominant stimuli do indeed appear to reflect monocular input, it is not clear that monocular neurones are responsible for such perceptions. Few would argue that conscious perception arises in visual area V1 (although equally few would argue that V1 is not involved in perception), and there is considerable evidence suggesting that processing in area V1 is not directly involved in the process of rivalry. Beyond V1 monocular neurones are scarce, in turn suggesting a significant role for binocular neurones in binocular rivalry, yet there are instances still where workers find it difficult to conceive of anything other than an area V1 locus for rivalry (eg. Blake 1989). As the following discussion will make evident, it is possible to describe a binocular array capable of behaving so as to give rise to the perception of rivalry. There is a substantial amount of empirical evidence to support such a model. In defence of early researchers, however, the complexities of the visual cortex were yet to be investigated.

The second period of rivalry research covers the middle part of this century and finishes in the late 1950's or early 1960's. It is characterised by a transition to more neurophysiological explanations of rivalry, but this became evident only later in this period. Earlier, in the 1800's, von Helmholtz (1924/1962), like Wheatstone, examined the relationship between stereopsis and binocular rivalry, concluding the two could co-exist. This conclusion was based, at least partially, on the observation that a simple object (eg. a cube), presented as a contrast reversed stereogram with disparity (Fig. 1.), is perceived in depth, but with 'lustre'. Levy and Lawson[A4] later redescribed this perception such that "non-fused contours appear in front of a metallic like [sic] background" (1978, pp. 239). Unfortunately, von Helmholtz (1924/1962) attributed binocular rivalry to 'mental' processes, particularly attentional ones. Hering (1920/1964) too ascribed his finding to cognitive processes. Again such accounts represent one level of explanation, but amount to little more than redescriptions of the perception of rivalry, and they have been criticised already (Levelt 1968). Perhaps the most significant finding reported by Hering was that if presented for a sufficiently brief period of time, stimuli that would normally rival vigorously would appear fused. He was. of course, unaware of distinctions between sustained and transient pathways, and more recently Wolfe (1983) has readdressed this effect.

Following those workers, Meenes (1930) was the first to report explicitly that complete predominance or suppression usually occurs only for small stimuli and he cited the now generally accepted observation that for stimuli larger than approximately 1° at the fovea piecemeal rivalry is generally the rule. Johannsen (1930) and Pickford (1947) systematically investigated the limits of colour fusion, continuing the work started

---

[A4] See Appendix Four.

initially by Breese. More recently it has been demonstrated that these simple investigations, in which stimuli were defined mainly by differences in perceived colour, are of limited explanatory use (eg. Crovitz 1964, Barrell and Parks 1969, Ramachandran and Sriram 1972), while others have demonstrated that in addition to wavelength, light intensity (Sagawa 1981) and stimulus structure (de Weert and Wade 1988) also affect colour rivalry.

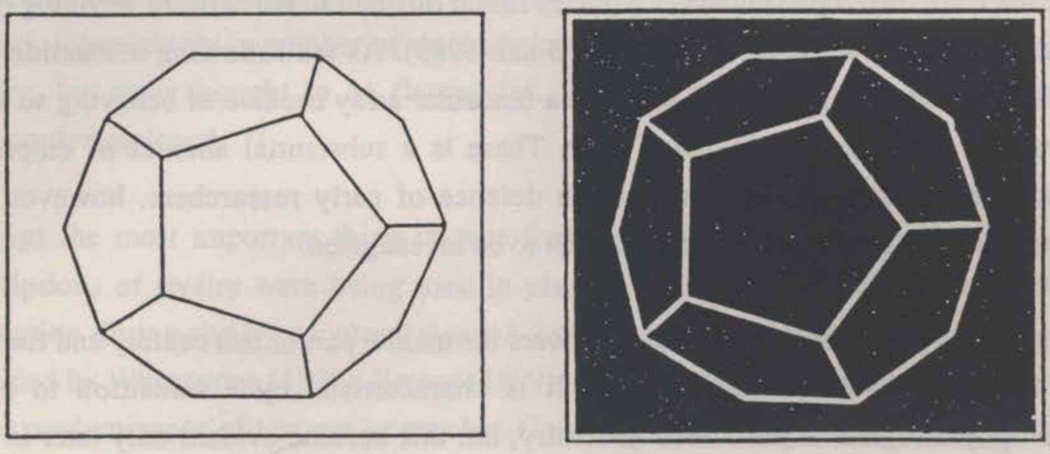


Fig. 1. A contrast reversed stereogram used by von Helmholtz (1924/1962). Viewed through a stereoscope the polyhedron appears in depth, but looks as if it has a metallic lustre (from von Helmholtz 1924/1962, pp. 512).

The complexity of explanation often required for perceptual phenomena that was becoming apparent around the beginning of the 1960's marked the beginning of the third period of binocular rivalry research. This period, which includes ongoing research, is characterised by neurophysiological accounts being offered for reported observations. The first major contribution of this period was that made by Levelt (1968). Levelt was concerned with brightness and contour relations, and his hypothesis was such that he argued that interactions between and within these two parameters were fundamental to the occurrence of rivalry. Drawing heavily on the available findings of Hubel and Wiesel (eg. 1962), Levelt considered no other parameters of a visual stimulus were necessary or sufficient to elicit rivalry, and he argued that this was true even for instances of colour rivalry. It remains one of the unanswered questions of rivalry as to whether completely isoluminant colours differing only in wavelength can generate rivalry like that observed between, for example, two fields of contours differing only in orientation.

There are findings which reinforce the suggestions of Levelt (1968): Short wavelength cones apparently do not contribute to the perception of borders (Ward and Boynton 1974, Tansley and Boynton 1976, Boynton 1978), and it has been reported that the rivalry mechanism is tritanopic (Hollins and Leung 1978, Rogers and Hollins 1982). Stalmeier and de Weert (1988) demonstrated contour information is unavailable for tritanopic pairs, and that rivalry may not occur for such pairs. Logothetis, Schiller, Charles and Hubert (1990) reported that at isoluminance colour sensitive parvocellular neurones show little sensitivity to wavelength differences, findings which Stuart, Edwards and Cook (1991) interpret in terms of the implications for stereopsis, arguing the necessity for contour information. It is not difficult to generalise their rationale further and suggest that colour edges are important for initiating rivalry, even at isoluminance. Yet there is other information (reviewed below) which suggests colour can act independently from any contour information it contains.

As the idea of processing channels became more accepted, particularly since neurophysiological evidence was accumulating in its favour, workers began to examine the relationships between some of the parameters for which such channels apparently existed and binocular rivalry in an attempt to link the neuophysiologically defined tuning characteristics of cortical cells to psychophysically defined performance. However, while visual cortical neurones, particularly those in area V1, were fairly specifically tuned, large differences between dichoptically presented stimuli could apparently be tolerated without eliciting binocular rivalry. For example, Blakemore (1970) found that spatial frequency differences of up to 20% could be tolerated by the visual system before rivalry would begin, although this depends on the spatial frequencies used. Kertesz and Jones (1970) and later Braddick (1979) found orientation differences of up to 15° visual angle could be tolerated. For moving stimuli, Wade, de Weert and Swanston (1984) reported direction of motion differences of up to 30° would not cause rivalry, while velocity differences, in degrees per second, could be up to 50% before rivalry was observed (Blake, Zimba and Williams 1985). Clearly rivalry was not linked to tuning in any simple way, and if it is argued that rivalry does arise via some type of comparator, these differences may be taken as evidence of an extrastriate origin for the interactions generating rivalry for only in extrastriate cortex are such broad tuning characteristics common. Nonetheless, some workers argue that differences between monocular neurones, which are common only in area V1, are some-how compared, and when these exceed certain tolerances rivalry is the result. The result has been a variety of different modelsof the visual system generally, or of a 'binocular rivalry mechanism' specifically.

Models of Binocular Rivalry

Any review of theories of binocular rivalry suggests that were the name not already used to describe a completely separate phenomenon, theorists would argue binocular rivalry might be more appropriately referred to as monocular rivalry. With only one exception (Cogan 1987), models of binocular rivalry (eg. Kaufman 1964, Sperling 1970, Abadi 1976, Wade 1978, Sugie 1982, Matsuoka 1984, Sloane 1985, Wolfe 1986, Lehky 1988, Blake 1989, Mueller 1990), or of binocular vision that purportedly accounts for rivalry (eg. Grossberg 1987) have been developed in which monocular neurones play a significant role in mediating rivalry. That is, activity in monocular neurones, and competition between them, is central to perception during periods of rivalry. The problem with this notion is that there exists a great deal of evidence that rivalry is an extrastriate rather than striate phenomenon, and monocularity is a characteristic mainly of visual area V1. Evidence in addition to that mentioned just above will be detailed in a moment, but it suggests the efficacy of attributing rivalry to monocular interactions is questionable. Less disputable is the notion that some form of inhibition plays a role in rivalry, and all models include various forms of inter-neurone inhibition. The nature of such inhibition, however, is equivocal. Several more recent models illustrate these points, but highlight also those factors which must be included in any thorough explanation of binocular rivalry[1].

Monocular or Binocular Interactions?

Blake (1989) argued that binocular neurones cannot distinguish the stimulus conditions that produce rivalry from those that do not, while monocular neurones are capable of this. He reasoned that during rivalry neural activity is inhibited in all monocular neurones receiving information from the region of the visual field which is at that moment suppressed and that "it is a region of an eye that is suppressed during rivalry, not information about a particular set of stimulus features" (p. 146). The model described by Mueller (1990) similarly describes spatial or zone suppression rather than feature suppression, and predicts rivalry on the basis of the level of excitation of monocular neurones. Grossberg's (1987) theory implies that what is suppressed during rivalry is a given stimulus feature, but suppression is still mediated in part by monocular cells. All these models seem to assume that binocular cells require binocular input in order to function (ie. change state), and this is not necessarily true. Neither is it

---

[1] The proposition of Kaufman (1964) and Wolfe (1986) that stereopsis and rivalry occur along parallel pathways, that the visual system is perpetually in a state of rivalry, will not be addressed here. This issue has already been the subject of debate (cf. Blake and O'Shea 1988, Wolfe 1988) and has been reviewed elsewhere (eg. Grossberg 1987, Blake 1989). The considerable differences that exist between models will similarly receive no direct consideration. As required, different aspects of different models will be elucidated and important aspects highlighted where they pertain to the current discussion.

necessarily true that monocular neurones are not necessary for perception once binocular fusion cannot be achieved. The view that binocular neurones are incapable of being sensitive to the conditions that generate rivalry (Blake 1989) would be true only if binocular cells had the characteristics of the 'purely binocular neurones' described by Wolfe and Held (1983), and there is evidence that such cells do not exist (eg. Burke and Wenderoth 1989). It has long been recognised that generally binocular neurones vary in their ocular dominance (eg. Hubel and Wiesel 1962, Hubel and Livingstone 1987, Tootell and Hamilton 1989), and such cells can be driven by a sufficiently strong stimulus in either or both eyes (depending on the relative weighting for each eye and the cells' firing thresholds). In addition to these 'classical' binocular cells, a second class of binocular cell is now also acknowledged. These cells are excited by input to one eye, and inhibited by input to the other (eg. Ferster 1986). For the sake of discussion, leave aside for a moment purely binocular cells, for even if they do exist they could, by definition, take no part in rivalry. Ignore also Ferster's binocularly inhibited cells and consider the behaviour of simple binocular neurones. Under normal circumstances, when input to two eyes is (effectively) equivalent, if a given neurones preferred stimulus (or stimuli) is present it will be excited and its firing rate will be proportional to the strength of the input it receives. If the two eyes receive different input, but the input to one of the eyes still contains parameters for which the neurone is tuned, the neurone's firing rate will still be proportional to the strength of that stimulus and the strength of the connection, the ocular dominance, of that eye. It will not be completely unaffected by a monocular stimulus. Such neurones form the basis of most binocular visual areas, and are all that is required to develop a model capable of explaining binocular rivalry.

An Hypothetical Binocular Array

In order to show monocular neurones are not required for rivalry it is necessary to describe an array of binocular neurones which is neurophysiologically realistic, and which can give rise to perceptions like those experienced during binocular rivalry. The array to be described should be considered to be one example of such a system. The exercise here is to demonstrate that it is possible *in principle*, and hence some variations to this model are likely. It should be borne in mind that this model is only a basic description of a group of binocular neurones tuned for various visual stimulus parameters, and which are the types of neurones that probably contribute to normal perception. This model is not, nor should it be considered to be a binocular rivalry mechanism, that is, a network in addition to those already in place in the cortex.

If a group of neurones were set up in an array, they would all be binocular if each received some input from each of two eyes. Assume that this is so. Assume also that for any neurone in the array the input from each eye[2] is not necessarily the same, some receive stronger input from the left eye, some from the right, and some equal input from both. The notion of ocular dominance as described by Blake (1989) in the third proposition of his model has the same spirit as that intended here, and this mirrors what is observed neurophysiologically (eg. Hubel and Wiesel 1962). Let each neurone have distinct tuning characteristics, such that some neurones may be tuned similarly to others, others differently, and many neurones will exhibit a multiplicity of tuning such that for some spatial frequency, say, a neurone will have a preferred orientation. The activity of any neurone will depend, at least, on the salience or the amount of energy in the stimulus deriving from the parameter(s) for which they are tuned. Other factors governing activity will be detailed later but include inhibition and fatigue. Finally, let the organisation of the array mirror that typically observed in visual cortical regions: neurones with similar tuning characteristics located together in a roughly retinotopic map of the visual field. This is the fundamental array and its performance can, in general terms, be described.

If the array receives similar dichoptic input, all cells with tuning characteristics sensitive to that input have the potential to respond proportionally to the strength of the stimulus. Those responding will be those receiving suprathreshold input. It is reasonable to assume that the cells linked with perception are those responding the most (eg. Carpenter and Blakemore 1973). What if the input is not the same, what if the input to one eye differs from that to the other? In this case, the tuning characteristics and ocular dominance of the cells becomes more important. Individual cells will respond proportionally to the strength of the stimulus for which they are tuned, but also proportionately to the strength of the input from the eye in which the stimulus is present. So, it would be possible to have some neurones responding only weakly to a very salient features of a stimulus in one eye because the strength of their connection to that eye is weak. At the same time, other neurones with strong connections to an eye might be responding vigorously to a less salient feature in the stimulus. Again, the cells responding most vigorously are those underlying perception. While no temporal variation can be expected in this array as it stands, clearly binocular neurones are able to distinguish (react differently to differences) between conditions normally giving rise to fusion and normally giving rise to rivalry without monocular mediation. This can, however, be only part of the story.

---

[2] The statement 'input to an eye' refers to the stimulus within the visual field of one eye. In terms of the input to a binocular neurone, this can be thought of heuristically as coming directly from an eye, or perhaps more realistically as coming from the monocular neurones servicing that eye.

The state of a neurone, its propensity to fire at any given moment, is affected not just by excitatory input but also by any inhibition to which it is subject. Most theorists have realised this and, as mentioned, included some form of inhibition in their designs. The role of inhibition in their models is usually to suppress one set of monocular neurones, allowing the contralateral non-inhibited neurones to give rise to the perception which predominates. The most common form is reciprocal inhibition, again usually between monocular neurones (Lehky 1988, Blake 1989, Mueller 1990), although such inhibition between binocular neurones has also been postulated (Cogan 1987), and also between both (Grossberg 1987). Assuming that they are not necessary for rivalry, inhibition between monocular neurones will not be considered further. This leaves just inhibition between binocular neurones, and Cogan's model, shown if Fig. 2, is of some interest for it describes a system by which binocular inhibition occurs in response to the type of input that normally elicits rivalry. While not equivalent to the array described here, it is similar in intent; activity in one set of binocular neurones inhibits activity in other binocular neurones. The are several types of inhibition to which binocular neurones can be subject; inhibition which occurs via co-lateral connections (eg. of the type described by Carpenter and Blakemore 1973) and may be considered to be inter-channel or intracortical (Braddick, Campbell and Atkinson 1978, Sekuler, Pantle and Levinson 1978), and inter-ocular inhibition of they type described by Ferster (1986, 1988). Lateral inhibition results from the activity of surrounding neurones and has received considerable treatment in the literature (eg. Blakemore, Carpenter and Georgeson 1970, Carpenter and Blakemore 1973, O'Toole and Wenderoth 1977, Nelson 1985), principally in relation to orientation selective channels. Without redescribing it, there is no reason to believe that lateral inhibitory interactions are confined to orientation channels, particularly as many orientation selective neurones are tuned also for other parameters (eg. motion). It is reasonable, therefore, to suppose that in an array of binocular neurones, all of which were tuned for certain parameters but for different values of those parameters (eg. different orientations, different contrasts, different directions of motion), while some neurones were maximally excited by the current stimulus, some others less so, and some neurones, at some location (both in terms of tuning characteristics and spatial location), would be inhibited. The amount of excitation, and hence inhibition, would be proportional to the strength of the stimulation. Ferster (1988) argues that spatial arrangement is critical in understanding inhibition, and has pointed out that there is some evidence to suggest that inhibition elicited by the activation of a certain population of neurones is far more broadly tuned than the corresponding activation from which it arises (Ferster 1988), and that this inhibition will decrease between neurones tuned as similarity in their tuning decreases (Ferster 1986). That is, for a certain stimulus, activation will be confined to a set of finely tuned neurones, but the concurrent inhibition arising from their activation will be much less specific. This implies that the inhibitory interconnections associated with a given neurone are not specific within a channel or to a small cortical region, but can be much more general; activity in a single binocular neurone may cause inhibition in many others, and conversely will be affected by activity in many others. Across the array, there may also be some neurones which are unaffected by the current stimulus, and these would be those cells tuned for values of the current parameters too different to be excited or inhibited, or those physically too far away from the excited neurones.

If different stimuli were simultaneously but dichoptically input, as is required for rivalry, different groups of neurones would be maximally excited. The pattern of excitation would not reflect just the tuning characteristics of the neurones responding to

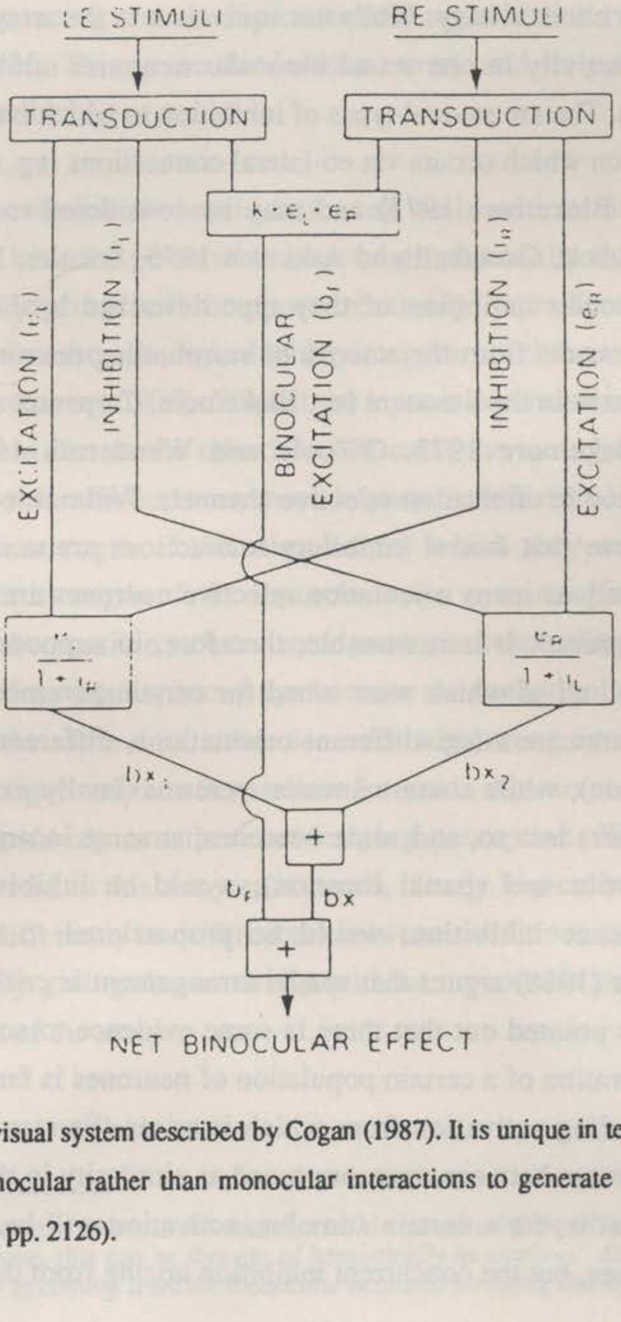


Fig. 2. The model of the visual system described by Cogan (1987). It is unique in terms of its explanation of rivalry, relying on binocular rather than monocular interactions to generate rivalrous perceptions (Taken from Cogan 1987, pp. 2126).

the two different inputs, but also their ocular dominance and the inhibition to which they are subject. If excitation and inhibition add up in some (not necessarily linear) way (eg. Carpenter and Blakemore 1973, O'Toole and Wenderoth 1977), then across the array the overall pattern of activity would reflect the sum of excitation and inhibition resulting from those characteristics. Remember, this is just the effect of inhibition, so if all neurones were initially in the same state and no other factors were operating, no temporal variation in that pattern would be observed. On the subject of lateral inhibitory interactions, it is important to realise that the architecture and multiplicative tuning of visual cortical neurones makes inhibition across parameters almost inevitable. Active neurones can inhibit spatially local neurones through inhibitory interneurones, and activity in response to some stimulus parameters will be impinged upon by activity in response to other parameters. Thus, across-channel excitation and inhibition will occur. In terms of neural architecture, certain areas will show excitation or inhibition just because of proximity to activated cells. This suggests that if one were to map excitation and inhibition, it could be done in terms of tuning characteristics, spatial location, or both. Perceptually, the result of this architecture would be a composite of both visual fields, with the features represented by the tuning characteristics of the most active neurones those which are perceived. These could correspond to components of either or both the input fields, but at any one point in the retinotopic array only one feature will predominate at any time.

As it stands, the states of the binocular neurones in the array are determined by input and inter-neurone interactions. While this arrangement is sufficient to generate 'piecemeal' perceptions, it does not account for the spatio-temporal variation characteristic of rivalry. Only changes in the input will cause temporal variation to the activity within the array at any moment, and while this must necessarily be true, another form of variation must be included. This variation is, of course, neural fatigue. For a given input (excitation and inhibition) the response of any neurone to that input at any time will be determined by its state of fatigue. This in turn will be determined by the neurone's recent history of activity and its response characteristics (sustained or transient responses). The effect of fatigue is such that a neurone's behaviour will not, over time, be constant, even for a static stimulus or stimuli. This variation will affect not only any excitation generated by a neurone, but also by inhibition resulting from its activity. The significance of neural fatigue is that it allows for changes, over time, in the pattern of activity within a group of neurones. This, in turn, leads to changes in the perceptions it has a part in generating, changes which could appear to be interocular competition when two dissimilar inputs are involved.

In summary, a group of binocular neurones with non-equal ocular dominances can predict both normal perceptions and binocular rivalry if excitation, inhibition and fatigue are all factored in. The most active neurones, which are determined by the stimulus and these three components of neural behaviour, underlie perception. Changes to patterns of activation are caused by stimulus changes and by neural fatigue, both of which usually operate in concert (particularly if normal eye movements are taken into account). A number of predictions arise from this model, and these will be examined. Before that, relations between the components outlined here can be semi-formalised[3].

Semi-formalising Relations Between Excitation, Inhibition, and Fatigue.

Consider the model developed by Mueller (1990), a generalised version of which is illustrated in Fig. 3., and to which the following discussion refers. In Mueller's (1990) original model, stimulus strength (S) and inhibition (a function of the function ag(X)) govern the state (X) of a neurone (equation (1)), and there is a propensity for all neurones to fatigue or habituate in response to prolonged stimulation (equation (2)). The elegance of Mueller's model lies in the predicted variation of firing rates of individual cells over time simply in response to the level of fatigue those cells are experiencing, even in response to static input. Its usefulness comes from the inclusion of all parameters likely to cause changes to the activity of a cell, and hence of an array of cells. In his model, however, the neurones represented by X1 and X2 are monocular in the sense that excitatory input is received only from one eye or the other, and for this reason Mueller refers to his neural array as a reciprocal inhibitory oscillator. Contralateral monocular neurones mutually inhibit activity in each other, and the strength of this inhibition is dependent upon ipsilateral activity. It is clearly the case, for the architecture depicted, that such neurones could in fact be the type of binocular cells referred to by Ferster (1988), as each receives pre- and post-synaptic inhibition, the latter of which is determined by the state of the contralateral monocular neurone. This aspect of Muller's formulation is rejected, and in the generalised version of the model presented here monocular cells are replaced by binocular cells. Thus X1 and X2 receive excitatory input from both eyes[4].

---

[3] The term 'semi-formalised' is used here because the model described is insufficiently detailed to provide any type of formal mathematical description. The relationships about to be described are, therefore, more or less proportional with some modifications for known neural interactions. Readers are referred to recent works by Koch and Segev (1989), McKenna, Davis and Zornetzer (1992), Reeke and Sporns (1993) and Selverston (1993) if they wish to gain some ideas of the complexities of attempting to model individual neural interactions.

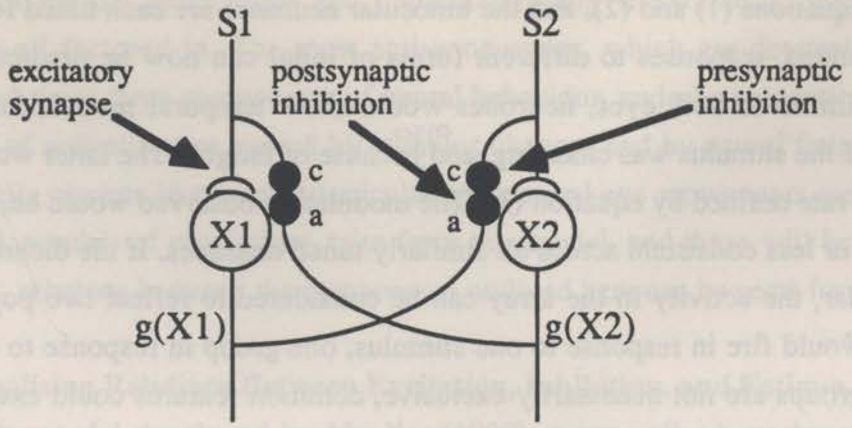
[4] The inhibitory interconnections depicted by solid black circles are not neurophysiologically realistic, extra synapses are required with inhibitory interneurones, and should be taken only to represent different types of inhibitory interconnection, rather than the exact connections themselves.

If the activity of individual neurones in the binocular model described above are defined by equations (1) and (2), and the binocular neurones are each tuned for various stimulus features, responses to different forms of input can now be predicted. If the input was similar to both eyes, neurones would show temporal modulation in their firing rates if the stimulus was changing, and also because of fatigue. The latter would cause changes at a rate defined by equation (2). The modulation observed would be, all things equal, more or less consistent across all similarly tuned neurones. If the dichoptic input was dissimilar, the activity in the array can be considered to reflect two populations. One group would fire in response to one stimulus, one group in response to the other. These two groups are not necessarily exclusive, common features could excite single neurones, and would show temporal modulation. Variation in the responses of individual neurones would depend on several factors, including stimulus strength and ocular dominance, which both affect 'S'. The pattern of modulation would depend also on the initial state of each neurone. If any were already in a state of fatigue, their response to the stimulus would have different temporal characteristics than initially unfatigued neurones.

Before proceeding, further consideration of input, 'S', is required. Mueller (1990) defined 'S' as the strength of input from a stimulus. For any cell, either monocular or binocular, this can be thought of as the sum of excitatory inputs to the cell. Cells can receive many excitatory inputs, many synapses are possible. With this in mind, 'S' can be defined more exactly as:

$$S = q\sum_{i=1}^{n} k(s_i) \qquad (3)$$

where: n = the number of excitatory inputs.
s_i = excitatory input.
q = a state variable, which is really a scaling factor allowing that the sum might not be linear.
k = a scaling factor weighting for ocular dominance.



$$\tau\frac{\partial X}{\partial t} = -h(X,f) + \ln(S) - a\left[1 - c\,\frac{\ln(S)}{\ln(100)}\right] g(X'') - X' \tag{1}$$

$$T\frac{\partial X'}{\partial t} = -X' + bg(X) \tag{2}$$

Fig. 3. A reciprocal inhibition oscillator of the type described by Mueller (1990). Mueller argues the fundamental neural units responsible for rivalry are mutually inhibitory contralateral monocular cells. These are depicted here as X1 and X2. The state of any such neurone over time is determined by its input, the inhibition to which it is subject, and neural fatigue. The way in which these are related are described by equations (1) and (2). Equation (1) describes the spike rate of a cell as a function of the time constant τ, the excitatory input to the cell S, the fatigue state of the cell X', and the inhibitory input ag(X") (which is shown here in a form accounting for both pre-synaptic and contralateral inhibition). Note g(X) is a threshold function which determines the cells minimum firing rate (cf. Mueller 1990, pp. 65). Equation (2) describes the rate of fatigue of cell X as a function of its spike rate. 'a' and 'c' are state variables which represent contralateral and presynaptic inhibition strength respectively. 'b' is a rate constant for that particular cell. 'h' and 'f' define the initial state of the cell at time t = 0. While these relations were developed for monocular neurones, they have been adapted here to describe the behaviour of binocular neurones. This requires the elaboration of certain terms. Without defining or specifying values of the state variable, these equations represent proportional relationships. In adapting the model for binocular interactions, the architecture described by Mueller, and depicted here, must be considered only a schematic representation of the possible interactions between neurones.

The 'q' term in this relation is important. It is an acknowledgment that the summation represented in equation (3) might not be linear. 'q' could be, in fact, a complex term and remains undefined. As stated, 'k' represents ocular dominance and so the term $k(s_i)$

represents the weighted input to a neurone from an excitatory source: As ocular dominance increases, 'k' increases. Having thus described excitatory input, it is possible also to redefine inhibitory input to a cell. Mueller defined 'g(X)' as a threshold function ensuring a minimum firing rate for a cell, and 'ag(X)' as the inhibitory effects experienced by the cell. Holding the threshold function constant, 'a' represents the inhibitory input to the cell. If this is then applied to the binocular model, 'a' represents all types of inhibition experienced by the cell. It is possible, therefore, to define 'a' similarly to 'S' in equation (3), however, the single summation could be split up into terms for pre- and post-synaptic effects separately depending on the nature of the inhibition being supposed (McKenna, et al. 1992).

After consideration of the relations described by the above equations the significance of neural fatigue should be apparent; it is one means by which the activity of neurones in the array, and hence the overall activity throughout the array, will vary over time even when input to the system is constant. The perceptual consequence of such changes will be alterations in the perceived visual field. Other factors will affect activity also. The most important of these, of course, is stimulus strength. If the parameters of a stimulus or stimuli change over time, then input into the binocular array will change causing a change in the activity of the neurones in the array. The actual neurones affected will depend on whether the change is a spatial one (ie. the elements of the input move with respect to each other) or a relational one (the elements of the input change with respect to one and other). Clearly, the more vigorously a stimulus changes (in terms of the speed of the change and/or the magnitude), the more vigorous will be the change in activity in the array in response. In terms of the perceptions which might arise from the system, such changes could be reflected as changes in the regions of the visual field which are becoming predominant, or changes in the features of the visual field which are becoming predominant.

It should be evident from this general description of binocular visual cortex that binocular interactions are sufficient to predict the perception of binocular rivalry under appropriate circumstances: differing input to each of two eyes still causes activity in binocular neurones. If the activity in such neurones is correlated with perception, then as activity levels change, so will perception. The elegance of this conceptualisation of rivalry is that it is neurophysiologically realistic and does not require the postulation of additional hardware within the cortex to account for the perceptions associated with rivalry. Binocular rivalry is just a perception like normal stereoscopic vision. It suggests also that perceptions associated with binocular regions of the visual cortex might be those most likely to reveal details of the processes of rivalry. The model, as it stands, may have some limitations: It may not, for example, be able to explain the perception of the sliding motion of plaid components instead of rivalry under appropriate circumstances (Alais, Wenderoth and Burke 1994). Such examples need to be considered on a case by case basis. The efficacy of this model is demonstrated by its ability to account for a range of findings already documented.

Evidence For 'Binocular' Rivalry.

While an explanation of binocular rivalry in terms of binocular interactions is theoretically possible the following discussion aims to provide further evidence in support of this notion by examining existing data on rivalry. A number of previously reported findings are reviewed and re-analysed in terms of the current model.

Tuning Characteristics and Inhibition.

Binocular organisms must always be able to tolerate small differences between their two eye views of the world. Indeed, these differences are thought to be the key to stereoscopic vision. The trick is matching slightly different views so to form a coherent unitary perception. A number of workers have investigated the ability of the human visual system to account for or tolerate differences in input and still achieve stereopsis. Some of these have been described already (eg. Blakemore 1970, Braddick 1979, Wade, de Weert and Swanson 1984, Blake, Zimba and Williams 1985), but there are others (eg. Blake and Lehmkuhle 1976, Hollins and Leung 1978). The point is that only when significant differences in the two eye views of these or any other parameters, or combination of parameters, occur, does binocular rivalry result and, as mentioned, the size of these differences does not fit easily with the fineness of tuning observed in many cortical neurones. This in itself suggests that the processing associated with rivalry might not involve point to point comparisons between monocular neurones receiving input from either eye, as suggested by various workers (eg. Blake 1989, Mueller 1990), and neither does it suggest specific comparisons are made between tightly tuned processing channels (eg. Grossberg 1987). Such assertions must be tempered by the knowledge that modifications to tuning characteristics can be achieved by inhibitory interconnections of various types (eg. Orban 1984, Ferster 1986). For example, it is possible that inhibition between cells during conditions which generate rivalry is such that the most inhibited cells in opposite eyes are those with the most similar tuning. On the other hand, Orban (1984) has argued that tuning characteristics of neurones may be sharpened by inhibitory interconnections, and it has already been mentioned that inhibition is far more broadly tuned than the excitation from which it arises (Ferster 1988). If this is the case, then it is not easy to see how neurones might exhibit more broad tuning during rivalry than they do otherwise. If inter-ocular inhibition is to be argued for, theoreticians must explain how these findings and the specific inhibitory interconnections they propose can be reconciled.

If the observation that rivalry results only in the presence of relatively large differences between the two eyes input is interpreted as evidence that the cells mediating rivalry lie in extrastriate cortex where more broadly tuned cells are more frequently found, the issue of comparisons still needs to be addressed unless a set of interactions like those proposed by the model described above are accepted. The interocular differences tolerable before rivalry arises can then be explained by combining the broader tuning characteristics of extrastriate cortical regions with the activity in the array. In the model, activity across the array results from some form of summation between excitatory and inhibitory inputs. It is accepted that a given stimulus will excite neurones with the most appropriate tuning the most, but neurones with similar tuning will also be excited, and this excitation will diminish as tuning becomes less appropriate (eg. Braddick 1979). Under conditions where the input to two eyes is dissimilar, this pattern of activation will still be true, but for all appropriate features in both eyes, and affecting all this will be inhibition which will modify the amount of activity in (probably all) the binocular cells. If input to each eye is similar, but not the same, then binocular cells reasonably close together will be stimulated. For example, let the right eye receive a grating stimulus of some fixed spatial frequency, luminance, contrast, and oriented at 20°. Let the left eye similarly view a grating with the same spatial frequency, etc., but oriented at 30°. If the bandwidth for these cells is, say, 5°, cells responding to the two inputs, because they are binocular, will be receiving excitatory input from both fields and a unitary percept may result. If the orientations were not 20° and 30° but 10° and 40°, while the cells are still binocular the strength of the excitatory input is likely to be much less and unitary perception can break down[5]. Under these conditions, perception will correspond with whichever cells are most active at any moment. In this way no comparisons are necessary, and no extra hardware required to account for different perceptions under different conditions.

Finally, and further complicating arguments for comparisons between similarly tuned neurones being the mechanisms of rivalry are observations suggesting that receptive field properties can change in response to stimuli beyond their 'classical' receptive field. Allman, Miezin, and McGuiness (1985a, 1985b) have described what they call 'total' receptive fields for some cortical neurones. A second stimulus within the total receptive field of a cell can affect the response of that cell to a stimulus within its classical receptive field, effectively altering the cells tuning characteristics. The impact of the

---

[5] This argument can be generalised to any domain.

second stimulus is observed only when a stimulus is in the classical receptive field, the stimulus beyond the classical receptive field has no effect when the classical receptive field is empty (Allman, et al. 1985a, 1985b). Under normal viewing conditions, when equivalent stimuli are in both eyes, the possible impact of the total receptive field presents no problems. However, under rivalrous conditions, where similar inputs are not necessarily available, the tuning characteristics of cells wired to one eye could be altered, while the characteristics of cells wired for the other eye are not. Under these circumstances it is difficult to see how point to point comparisons of individual stimulus characteristics could successfully be made. Nonetheless, in models of rivalry favouring some type of comparison mechanism these are interactions which may need to be taken into account. However, if rivalry arises from interactions between groups of binocular neurones, then even if the tuning characteristics of individual cells are altered, it should not cause a problem for the mechanisms of perception.

Temporal Characteristics of Binocular Rivalry

In addition to studies which have examined stimulus parameters and their relationship to rivalry, a number of intricate experiments have been conducted looking at changes in the pattern of rivalry in response to different stimuli. Blake (1977) demonstrated that if the contrast of one of a rivalrous pair of stimuli was reduced, the percentage of time for which that stimulus was predominant is also reduced. Blake and Overton (1979) showed prior monocular adaptation to a grating, which has the effect of weakening the apparent contrast of the grating, similarly decreases the time for which that grating will be predominant when subsequently presented in rivalry. Others too have noted congruent findings (Levelt 1965, Fox and Rasche 1969). Conversely, if contrast is increased, predominance is increased. A number of different explanations have been offered for these observations (eg. Blake 1989, Mueller and Blake 1989, Mueller 1990), yet all can be accounted for simply by the model offered here. Activity within the array depends on the strength of the stimuli currently presented and the fatigue state of the neurones. If a stimulus is weak (low contrast for example) the activation within the array corresponding to that stimulus will be reduced in comparison to a similarly constructed stimulus with higher contrast. As contrast increases more and more cells tuned for the features of that stimulus are recruited. Cells tuned for lower contrasts will be above their firing threshold more often, and as contrast increases the number of cells constantly above threshold will increase. If a high contrast stimulus is presented to one eye and a low contrast stimulus to the other, the signal from (ie. activity generated by) the former will more often be stronger than that from the latter. Sometimes fatigue combined with the inhibition generated by the lower contrast stimulus will cause the activity generated by the stronger stimulus to be diminished. In terms of perception, the stronger stimulus should be perceived (predominate) most of the time, while occasionally it will not (suppression). Braddick, et al. (1978) made a similar case when they suggested that neurones behave stochastically, at any moment there is a certain probability they will fire. This means that as input increases the probability of a neurone firing increases. Thus for a weak input there is less probability that the stimulus will generate a response, but this is not zero. As the strength of the stimulus increases, which is effectively what increasing contrast does, more cells are capable of firing, and the probability that they will do so increases. Prior adaptation to a stimulus will cause fatigue in neurones tuned for that stimulus. This will lead to an increase in their firing threshold, decreasing the probability of their responding to a stimulus. It seems unsurprising that changes in contrast are mirrored by changes in the duration of predominance and suppression.

The binocular model predicts that as fatigue decreases the probability that a neurone will respond above threshold to a stimulus increases: integrate equation (1) with respect to 'X'. This means that as time after adaptation progresses, fatigue (X') will decrease and the spike rate will increase. In perceptual terms, the stimulus should come to predominate for longer and more often until it reaches preadaptation levels. The rate of this 'recovery' is linked to the fatigue state and should parallel the reduction in amount of adaptation, which is indeed what happens (Blake and Overton 1979). The model also generates a second, more subtle prediction. Inhibition and fatigue are proportional to activity. If stimulus strength is increased, activity in the population of neurones tuned for that stimulus will increase, but at the same time so will the rate of fatigue[6]. Recall that the rate of fatigue will be less than the rate of increase in activity, but it will increase (equations (2) and (3)). It follows then, that under conditions of increased stimulus strength neurones should cycle through a pattern of high activity and fatigue more quickly than for a weaker stimulus. If luminance, or brightness, of a pair of rivalrous stimuli were increased they should appear to compete, to rival each other, much more vigorously. Levelt reported this to be the case (1965), as has Blake (1977) and Mueller and Blake (1989).

Colour and Binocular Rivalry

Breese (1899) first observed that the pattern of rivalry between differently oriented fields remained constant whether fields were achromatic, monochromatic, or of different colours. Wade (1975), using more subtle methodology, found that colour does affect the pattern of rivalry observed between two contoured fields. He reported that

---

[6] It should be evident from equations (1) and (2), Fig. 3., that excitation, inhibition and fatigue will be proportional to one and other, but that the time constants for each are different, and that none of the ratios for these are 1:1. If, for example, rate of fatigue was exactly equal to rate of excitation, no change in firing rate would be observed for a change in input.

periods of exclusive visibility of one field or the other increased when fields were complementary colours, compared to fields of the same colours. Hollins and Leung (1978) extended these data when they reported that differences between the wavelengths of two dichoptically viewed fields were directly correlated with the duration of exclusive predominance. While the interpretation of such findings is made difficult by the complications of colour vision (changes in isoluminance criteria across the visual field), these findings suggest that interactions between colour and other channels do exist, and that the more different the information being input to the system, the more energetic the interactions of rivalry become (cf. Sagawa 1981). In order to understand how the binocular model can account for such findings it is necessary to remember that cells are arranged in a retinotopic map, but that there is the additional orderly organisation of tuning characteristics. The neurones signalling each of two very different inputs will be further apart in the array than will the neurones signalling more similar inputs, so that in response to very dissimilar stimuli there will be fewer individual neurones responding strongly to both inputs. One consequence of this is that changes in the activity of neurones responding to one stimulus are less likely to interact with changes in activity in the neurones responding to the other stimulus, and at any one retinal location changes in activity are also more likely to result in a change in what is perceived at that location. If, on the other hand, there are similarities between stimuli, then at one location while the input for orientation tuned neurones, for example, may be sufficient to generate rivalrous interactions, if at that location spatial frequency and luminance information is consistent, the likelihood of rivalry is reduced. Similarly, different colour information increases differences between the two inputs.

In considering the work on colour/rivalry interactions it is interesting to note that while it is sometimes mentioned (eg. Blake 1989) workers rarely give extensive consideration to the observation that while 'processing channels' apparently exist, they are not observed to be independent during rivalry. The one exception is colour (eg. Stirling's effect). For some reason, colour is apparently less strongly tied to other stimulus features than are properties such as spatial frequency, orientation, and direction of motion. A neurophysiological explanation for this is possible; individual cells can show sensitivity to several parameters, and it is not really to be expected that orientation and spatial frequency, for example, should be perceptually independent. For now this observation should be considered to be evidence that at the site of rivalry the only distinctions between stimulus channels that exist are those between colour and the others. Whether this distinction is equivalent to parvocellular/magnocellular distinctions remains to be seen. As Livingstone and Hubel (1984) pointed out, colour is not determined purely by, nor can it be predicted purely by, the wavelength composition of light at any particular place in the visual field. Of area V1 they note:

> "blob cells....probably represent too early a stage and are probably too short range in their spatial coverage to generate the long range interactions that occur in colour perception."
>
> (1984, pp. 353)

Evidence For The Site of The Rivalry Mechanism.

Having determined that the binocular model can account for much of the existing binocular rivalry data, the most likely location within the visual cortex for these interactions to take place remains to be determined. Some evidence that it is extrastriate has already been reviewed and much of what follows reinforces that conclusion. It should be remembered, however, that while many cells in visual area V1 are monocular, a substantial number of binocular cells can be found there also. The contribution of this latter group to rivalry has not previously been examined in any specific way. It might be the case that the neural interactions generating the perception of binocular rivalry are common to all groups of binocular neurones. This is addressed more fully in Experiments Seven and Eight.

Psychophysical Evidence for the Site of Binocular Rivalry

The difficulty with interpreting psychophysical data in terms of its implications for neural processing is that assumptions have to be made about the nature of that processing. In particular, if sequences of events are to be inferred, the assumption must be made that serial and not parallel processing occurs. There is much evidence available that processing in the visual system is massively parallel (eg. Van Essen, Anderson and Felleman 1992), and yet there is a real sense in which it is serial also. Many of the more complex tuning characteristics observed in extrastriate regions are apparently built up from processes occurring in 'lower' cortical areas; cells tuned for subjective contours can be found in area V2 but not area V1 (von der Heydt and Peterhans 1989), cells signalling the direction of 'plaid' motion are unique to area MT (Allman, et al. 1985b, Maunsell and Newsome 1987), and neurones tuned for spiral motion are not found prior to visual areas in parietal cortex (Sakata, Shibutani, Ito and Tsurugai 1986, Tanaka and Saito 1989). For this reason, studies applying the rationale that processing which is sequential can be revealed by studying the presence or absence of effects retains validity.

Several studies have examined the impact of binocular rivalry on visual aftereffects in the belief that if rivalry does involve some form of suppression (ie. inhibition), and also precedes the aftereffect in terms of processing sequences, this will be reflected in the magnitude of the aftereffect. Wade and Wenderoth (1978) examined the effect of binocular rivalry on the tilt aftereffect. They found that rivalry during adaptation to a grating tilted 10° from vertical caused no change in the magnitude of the subsequent orientation aftereffect. They concluded the processes giving rise to the aftereffect occurred prior to those giving rise to binocular rivalry (Wade and Wenderoth 1978). The tilt aftereffect has been ascribed to lateral inhibitory interactions between orientation selective neurones in visual area V1 (Blakemore, Carpenter and Georgeson 1970, Carpenter and Blakemore 1973), suggesting that rivalry arises beyond V1, or at least does not involve those neurones sustaining the aftereffect. The work of others reinforces this. Blake and Overton (1979) found the threshold-elevation aftereffect, also ascribed to processing in V1, was similarly undiminished by periods of binocular rivalry during induction. Blake and Overton went on to argue that suppression during rivalry occurs at a site beyond the striate cortex, with the characteristics of rivalry not reflecting the nature of processing occurring in V1. Additionally, the linear motion aftereffect (Lehmkuhle and Fox 1975, O'Shea and Crassini 1981) and the spatial frequency shift aftereffect (Blake and Fox 1974), both believed to be V1 effects, are also undiminished by the periodic suppression, characteristic of rivalry, during their induction. Together these results point strongly towards binocular rivalry arising after the interactions sustaining these effects have occurred, that is, in extrastriate cortex.

Aside from the indirect evidence that rivalry and aftereffects can interact (Blake and Overton 1979), it was only recently demonstrated that there are aftereffects which do show the impact of rivalry. Interestingly these spiral motion aftereffects (Wiesenfelder and Blake 1990), are 'higher-order' effects and were found to be reduced by periods of rivalry during their induction. Wiesenfelder and Blake (1990) argue that the complex motion aftereffects they examined arise no earlier along the visual pathway than visual area MT in the superior central sulcus, and they point out that rivalry must arise prior to this neural locus. In combination with the previous results this places the processes of rivalry beyond V1, but not later than MT. Further discussion of these data follows in the experiments reported below, as does a detailed account of how the binocular model can account for such findings. At this point it is important to notice that binocular rivalry diminished the magnitudes of the aftereffects observed by Wiesenfelder and Blake, suggesting that activity during rivalry is reduced in comparison to activity without rivalry, and that such reductions are to be expected if the general level of inhibition within a group of binocular neurones is increased while the level of excitation is decreased.

Neurophysiological Evidence for the Site of Binocular Rivalry

There has been little direct physiological examination of cortical behaviour during rivalry. A notable exception is the work of Logothetis and Schall (1989) who reported that many neurones which are found in the superior temporal sulci of rhesus monkeys and which are tuned for motion, behave differently during binocular rivalry induced by oppositely moving gratings presented to the two eyes, compared with responses to gratings which moved in the same direction in both eyes. All cells they examined were binocular and driven almost equally by either eye and five cell types were reported. Class [1] cells showed no directional selectivity whether the same direction of motion was present in both eyes or whether opposite directions were presented to the two eyes. These cells constituted 25% of the sample. Class [2] cells (21%) were non-directional in the non-rivalrous trials but direction selective when rivalrous stimuli were presented. Selectivity in this case would require that the cell fire more when the monkey indicates that perceived motion is in one direction rather than the other (ie.. when the monkey's response indicates that rivalry is currently dominated by upward or downward motion). Class [4] cells (32%) were directional under non-rivalrous conditions but non-directional during rivalrous trials. This leaves the remaining 22% of cells, all of which showed direction selectivity in non-rivalrous trials but in the rivalrous conditions, half these cells showed the same direction selectivity as under non-rivalrous conditions (Class[3]) and half showed the reverse preference (Class [5]). Thus, Logothetis and Schall found most of all possible varieties of direction tuning with and without rivalrous stimuli. What could be concluded? Careful analysis showed that the neural responses were not due to eye movements but apart from that the conclusions drawn, as the authors admitted, were pure speculation. They suggested that the class [4] cells might be first order neurones that are not involved in rivalry. The class [2] cells might be "dynamic and adaptable to the perceptual requirements" (p.763) because though they were non-directional to non-rivalrous gratings moving up or down, they had horizontal or oblique preferred directions. This conclusion thus merely restates the observation. Class [3] cells "could mediate the perception of motion that was expressed in the behavioural response of the monkeys" (p.763), another restatement of the data. Finally, the cells which fired when the non-preferred direction was seen in rivalrous conditions ([5]) "might provide the inhibition to lower or higher visual centres to suppress the view of one eye during rivalry"(p.763). So might class [3], of course: while it is true that "the results of this study suggest the possibility of experimentally relating the activity of single neurones... to the internal perceptual state of the subjects" (p.763), this particular experiment allows only the conclusion that cells in the superior temporal sulcus behave differently during rivalry than they do otherwise. Variation in tuning characteristics under different viewing conditions is, however, becoming more widely recognised as a problem that researchers must address (Allman, et al. 1985a, 1985b, Peterhans and von der Heydt 1993).

Logothetis and Schall (1989) interpret their findings as indicating that the superior temporal sulcus contains the neural machinery mediating binocular rivalry induced with motion, describing a general model by which this may be achieved. While such conclusions do concur with the psychophysical findings of Wiesenfelder and Blake (1990) and van der Zwan, Wenderoth and Alais (1993), Logothetis and Schall may have overstated the case. Although the activity of the neurones examined by Logothetis and Schall seem to be correlated with perception, nonetheless mere correlation does not indicate whether the cells are involved in perceptual decisions (ie.. output) or input, if either (see Morgan, 1989; Wenderoth, 1994).

Logothetis and Schall acknowledged the activity they observed may have resulted from feedback from higher areas. They did not, however, consider feedforward explanations. Input to the superior temporal sulcus, particularly visual area MT, has been shown to come, directly and indirectly, from several areas hierarchically earlier in the visual pathway (eg. Van Essen et al., 1992). These areas include the motion segments of V1, V2 and V3. It is possible that rivalry arises in any of these areas although, as discussed, it seems unlikely that the requisite processes are located in V1. Given that binocular rivalry is now known to disrupt acquisition of some aftereffects but not others, and that these aftereffects may be tentatively categorised on the basis of their neural loci, examination of the effect of rivalry on processes arising in areas which feed into the superior central sulcus provides one strategy for testing the hypothesis put forward by Logothetis and Schall (1989), that binocular rivalry may, at least in part, arise via interactions between extrastriate neurones, particularly those in or feeding into area MT. Experiments Five and Six were designed for this purpose.

Neuroanatomy and Neurophysiology.

Much of the preceding discussion points to binocular rivalry being a perception arising from extrastriate processing. The only possible constraints so far available suggest that the binocular interactions of interest lie somewhere between visual area V1 and visual area MT or possibly even area MST. As recent reviews of visual neurophysiology and neuroanatomy reveal, this does not really narrow down the search area to only a few possibilities, particularly when the number of interconnections, both feed-forward and feed-back, between areas are considered (DeYoe and Van Essen 1988, Stoner and Albright 1992, Van Essen, et al. 1992). There are some clues which might be considered. Since binocular rivalry has been shown to be sensitive to various stimulus parameters, and these parameters have characteristics associated with either or both parvocellular and magnocellular pathways, the logical conclusion is that rivalry arises either in a number of cortical areas across these pathways, or in a region which receives input from both pathways. Area V2, as an anatomically and physiologically distinct region along the visual pathway receiving both motion and form and colour information from area V1 (Tootell, Silverman, De Valois and Jacobs 1983), seems a reasonable possibility. The case for area V2 is strengthened by the observation that, area V1 aside, no other area receives such substantial input from both the major processing streams. While the separation is not complete nor exclusive (Krubitzer and Kaas 1990, Zeki 1990), colour information separates from motion information after area V2, with the former travelling to infero-temporal cortex while the latter goes to parietal regions (eg. Livingstone and Hubel 1988). As Zeki (1990) also points out, while 'new constructs', or emergent properties (Oatley 1978) have been associated with area V2, information is still in a relatively simple form and one of the functions of area V2 seems to be to act as a "segregator, parceling out different signals to different prestriate visual areas" (pp. 99). Differences in stimuli sufficient to elicit rivalry are simple; all other parameters being equal rivalry will occur if two stimuli differ in spatial frequency, orientation, direction of motion, etc. This suggests that the stage at which differences between stimuli cause rivalry is one where these fundamental stimulus characteristics have yet to be incorporated into anything more complex. The binocular model reinforces this point. It predicts rivalry on the basis of different levels of activity in cells tuned for simple stimulus characteristics.

There is another feature of the model which suggests that area V2 might be a good place to look for the processes generating rivalry. The model predicts rivalry on the basis of binocular interactions, and it would not make sense for several levels of binocular processing to occur before the types of interactions described occur. In fact for rivalry to occur in the way predicted by the model it is almost necessary that the earliest binocular processing be involved in rivalry. On one hand this implicates binocular cells in area V1 in the mechanism of rivalry, but this has yet to be demonstrated. On the other, area V2 is the first cortical level in which there is massive convergence of monocular into binocular information (Tootell and Hamilton 1989). That is, there are two maps of the visual field mapped into area V1 and these separate maps can be traced through area V1 to the layers that project to area V2 (Tootell, Hamilton, Silverman and Switkes 1988b). This duality is maintained to the input layer of area V2, but after that it is lost, and extremes of ocular dominance all but disappear. Tootell and Hamilton described this change as a "discrete, step-wise transition between a monocular organisation and a binocular one....the transition....appears to be in the connection between striate layers 2 + 3 and layers 3B/4 of V2" (1989, pp. 2641), which is exactly the type of connection the binocular model would require. From that point, monocularity is rare both in area V2, where some cells have ocular biases (Burkhalter and Van Essen 1986) but monocular cells are generally not found (Hubel and

Livingstone 1987) and this remains the case throughout the rest of the extrastriate visual cortex.

Further to these arguments for area V2 as the site of the rivalry process, several workers have suggested that only small, circular concentric receptive fields display the characteristics necessary for piecemeal rivalry (Blake, O'Shea and Mueller 1992). In a series of experiments those workers presented dichoptically rivalrous pairs of circular stimuli, randomised for size and retinal position, and examined the patterns of complete predominance that resulted. When a stimulus is small and confined to the fovea, complete predominance can be observed. As stimuli are moved peripherally, the size of the stimulus that can be completely suppressed increases. Blake, et al. (1992) argue the units of area observed to alternate between complete predominance and complete suppression, which are described as 'zones of suppression', reflect something of the characteristics of the cortical units involved in generating such perceptions. In the past, the nature of piecemeal rivalry has tended to lead workers (eg. Levelt 1968, Blake 1989) again to ascribe rivalry to area V1, where receptive fields typically are smallest. Blake, et al. (1992) present data which they argue shows these zones of suppression correlate, in terms of area of the visual field covered, with foveal hypercolumns and peripheral hypercolumns in area V1. Cortical magnification, defined as the distance (in mm) between two recording sites divided by the distance (in degrees visual angle) between the centres of receptive fields recorded at those sites, is such that in a number of extrastriate areas, including area V2, approximately equal numbers of modules (columns and hypercolumns) will be stimulated by any stimulus at a given eccentricity (Gattass, Gross and Sandell 1981). Blake, et al. (1992) acknowledge the constancy of cortical magnification and state their zones of suppression correspond with it as fields are mapped from fovea to periphery. While correlation is not, of course, a demonstration of cause, the relationship implied is tempered by the finding that area V2 exhibits receptive fields not much larger than those observed in area V1, and with similar characteristics (Burkhalter and Van Essen 1986, Bauer, Hoffmann, Huber and Mayr 1989, Zeki and Shipp 1989), so they could easily fulfil the receptive field requirements described by Blake and his colleagues. Gattass, et al. (1981) showed that while the receptive fields of area V2 are slightly larger than area V1 and the cortical magnification slightly smaller, these differences are not significant. The situation is similar for area MT, in which even larger receptive field sizes are compensated for by a smaller magnification factor (Albright and Desimone 1987). These findings do not so much prove that area V2 is the site of rivalry, but rather show that there is no reason to believe that it or indeed any other extrastriate cortical area is not.

Despite the arguments of Blake, et al. (1992), there is no clear evidence which suggests an 'area' of the visual field suppressed at one moment and predominant the next will continue to be perceived as a single coherently alternating patch, nor that such areas correspond directly to the receptive fields generating the rivalry. Very careful measurements would need to be carried out to establish these claims, and the use of small fixed size rivalrous fields is not sufficient to do this. Blake, O'Shea and Mueller used only circular fields in their examination, and while they changed the size of these fields, using sufficiently small single fields at corresponding positions in each eye will inevitably lead to the conclusion that zones of suppression are constant. A link between the physiologically determined characteristics of cortical neurones and perception like that suggested by Blake, et al. (1992) may exist, but a definitive experiment has yet to be conducted. Given the constancies described above, it seems unlikely that such an experiment could distinguish between cortical regions if only simple stimulus fields are used.

Visual Area V2

Assuming area V2 is the site at which rivalrous interactions first arise, the question which must be considered is whether there are any psychophysically examinable characteristics of area V2 which are unique to that area (ie. cannot be attributed to area V1) and which can be applied to the task of revealing the effect of rivalry on processing in area V2? Area V2 is anatomically and physiologically distinct from its surrounding visual areas. It is large, almost the same size as area V1 (Van Essen, et al. 1992) and contains an orderly retinotopic representation of the visual field, just as does area V1 (Tootell, et al. 1983). A number of characteristics identify area V2. Lying antero-laterally to area V1, area V2 receives a complex set of projections from, and sends a number of projections to area V1 (Stoner and Albright 1992, Van Essen, et al. 1992). Just as cytochrome-oxidase staining reveals neurophysiologically distinct regions in area V1, area V2 so stained reveals a pattern of thick and thin stripes and pale 'interstripes' (Livingstone and Hubel 1982, Tootell, et al. 1983). In general terms, blobs of area V1 project to 'thin' stripes in area V2, interblobs to interstripes, and layer 4B to thick stripes in area V2 and also directly to area MT (DeYoe and Van Essen 1988). In turn, the thin and interstripe regions of V2 project to V4 (Shipp and Zeki 1985), with the former also projecting to V3 (Felleman and Van Essen 1987). Both MT and V3 receive projections from the thick stripe region of V2 (Burkhalter, Felleman, Newsome and Van Essen 1986, Felleman and Van Essen 1987, DeYoe and Van Essen 1988). It has also been suggested that interconnections link thin and thick stripes (Livingstone and Hubel 1984). These cytoarchitectonic distinctions are matched by distinctions in processing streams (Hubel and Livingstone 1987, Livingstone and Hubel 1988) and neurophysiology (eg. Tootell, et al. 1983). Most cells in thin stripes are wavelength selective (Hubel and Livingstone 1987), and have recently been reported to show some orientation selectivity for contrast borders (Peterhans and von der Heydt 1993). Thick stripes and interstripes exhibit large populations of cells sensitive for the orientation of contrast borders (De Yoe and Van Essen 1985). These differences mirror closely differences observed in area V1. Peterhans and von der Heydt (1993) reported more interesting observations, however. They found that many neurones in inter- and thick stripes were sensitive to borders defined by 'subjective' contours or to lines defined by coherent motion. No such cells were observed in thin stripes. Also exclusive to thick stripes were cells tuned for disparity and purely exclusively binocular neurones. Conversely cells that were direction selective or end-stopped were evenly distributed throughout the different segments of area V2.

The distribution of cells is interesting in light of observations made earlier about dissociations which are sometimes observed during rivalry[7]. Recall that the most frequently observed dissociation is that between form and colour: Colour can be perceived to rival while form remains constant, or colour and form can rival but independently of each other. These dissociations are not observed for other stimulus parameters, which can be taken as evidence that orientation and spatial frequency, for example, were more closely related than colour. In neurophysiological terms, cells tuned for orientation are likely to be spatial frequency selective, for example, and so activity caused by one recruits the other, while relations between colour and other parameters is not so tight. Activity in wavelength selective cells does not necessarily recruit spatial frequency, for example. These apparent distinctions are similar to those reported by Peterhans and von der Heydt (1993), although the relationships being suggested need to be more carefully examined as the situation is complicated. Not all parvocellular cells display just wavelength sensitivity (above), and magnocellular cells have been shown to signal changes in colour (Lee, Martin and Valberg 1989), although not the nature of those changes (Stuart, et al. 1991).

The other point of interest to be taken from this description of the properties of area V2 neurones is that they exhibit tuning characteristics not observed in area V1 neurones.

Subjective Contour Perception.

In two comprehensive papers von der Heydt and Peterhans (1989) and Peterhans and von der Heydt (1989) described the physiological concomitants of subjective contour

---

[7] The distribution of cells reported by Peterhans and von der Heydt (1993) may also help to explain the results of Ramachandran, et al. (1973) in which they claim to demonstrate the existence of stereopsis during colour rivalry. The issue of stereopsis during binocular rivalry is addressed in the general discussion.

perception. They demonstrated that distinctions between subjective contours that can be made in terms of their physical structure are mirrored in the processing to which they are subject within the visual cortex (see Fig. 4.). To briefly reiterate their results, they found that 'contours bridging gaps' (Fig. 4A.), which are characterised by having Fourier components at the orientation of the perceived edge, cause excitation of orientation selective neurones in both visual areas V1 and V2 (Peterhans and von der Heydt 1989). The nature of these responses was different, however. In area V1, neurones generally responded only when the inducing elements of the stimulus were in their receptive fields. If intersecting lines were added to the stimuli, so as to close the gap (Peterhans and von der Heydt 1989, Figure 10, p. 1757), most area V1 neurones continued to respond much as before. In area V2 32% of orientation selective neurones signalled the gap bridging contour even though the inducing elements were outside their receptive fields. Closing the contour caused activity in these neurones to be reduced or abolished. The point is that processing of such gap bridging occurs at the earliest stage of cortical processing. Their encoding is not unique to any extrastriate region. Compare that with the processing of 'purely subjective contours' (Fig. 4B.). In terms of their physical characteristics, such contours have no Fourier components at the same orientation as the perceived edge. von der Heydt and Peterhans (1989) reported no orientation sensitive neurones in area V1 responded to such contours. 44% of orientation sensitive neurones in area V2 did signal the purely subjective contour. Nearly 16% of such neurones did so without also signalling the orientation of the inducing elements. In evaluating their findings, von der Heydt and Peterhans highlight the uniqueness of stimuli which have no 'power' in the Fourier domain along the orientation of the subjective contour, and the distinctions that can be made between area V1 and area V2 neurones in response to such stimuli:

> "Many cells in V2 responded maximally to an anomalous-contour stimulus when the contour had the same orientation as the optimum bar stimulus; however, in the Fourier plane, the bar has all its energy concentrated near the axis perpendicular to its orientation, while the anomalous-contour stimulus has zero energy on this axis.....The cells thus signalled an orientation that is not represented at all in the Fourier spectrum. Conversely, often, they did not signal the orientation of the [inducing] gratings which is heavily represented [in the Fourier plane]."
>
> (von der Heydt and Peterhans 1989 pp. 1744)

It seems reasonable to conclude that purely subjective contours are not encoded in the visual system earlier than area V2, and while it must have a role in their processing, area V1 provides no unambiguous information about such contours[8]. Interestingly,

---

[8] Recently, Grosof, Shapley and Hawken (1993) reported that V1 cells *did* respond vigorously to purely subjective contours. However, their vigorous responses were obtained with interdigitated sine wave

Jefferys (1977) had suggested a similar pattern of results. In that study Jefferys examined the evoked potentials associated with subjective contour perception and found them around a prestriate area exhibiting retinotopic organisation. Jefferys suggested area V2 and/or area V3.

In attempting to explain their results, von der Heydt and Peterhans developed a model of contour perception such that real, purely subjective, and gap bridging contours all arise via similar processes. In essence, they assert the perception of edges, lines, or contours involves a two stage process, and the perception of contours or edges where they do not exist represents what is effectively an error or ambiguity in that process. Such errors arise, because the system has developed strategies for interpolating edges when they are sometimes occluded (von der Heydt and Peterhans 1989, Peterhans and von der Heydt 1989). The different stages of the process are thought to give rise to different types of error, and these are mirrored in the different types of anomalous edges; that is gap bridging contours represent an earlier stage in the process than do purely subjective contours, but both arise from the one process. If this is true, it follows that purely subjective contours, and gap bridging contours, are subject to ongoing processing like that experienced for real contours, a suggestion made elsewhere (Berkley, Debruyn and Orban 1994).

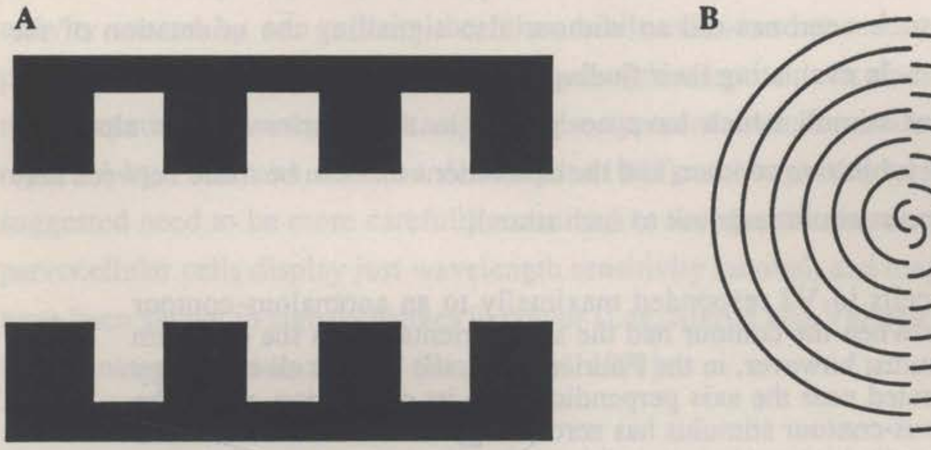


Fig. 4. Two different types of subjective contour. A: 'Contours bridging gaps', including those observed in Kanizsa figures (1955) and other similar stimuli (Weisstein, Maguire and Berbaum 1977, Smith and Over 1979) are sufficient stimuli for some area V1 neurones. B: 'Purely subjective contours' stimulate no area V1 neurones, but are sufficient for some area V2 cells.

---

gratings so that the line endpoints were rather elongated and could easily be imagined to be an adequate *real* contour stimulus - a dashed line. When they used stimuli composed of sparse and thin line endpoints, such as ours and those used by von der Heydt and Peterhans (1989), their V1 responses fell to about 20% of those obtained with their original patterns. It thus remains to be demonstrated in any convincing fashion that V1 cells respond strongly to purely subjective contours.

Leaving aside 'contours bridging gaps', while it remains to be demonstrated that processes associated with real contour perception are the same as those operating on subjective contours, there is available neurophysiological and psychophysical data linking the purely subjective contour tuned cells reported by von der Heydt and Peterhans with perceptual effects. von der Heydt and Peterhans (1989) found that neurones signalling the subjective contour showed response patterns which appeared to mirror perception. For example, subjective edges appear less compelling when fewer inducing elements are present (Lesher & Mingolla, 1993). The activity of purely subjective contour sensitive neurones could similarly be modulated. Fewer inducing elements led to decreased responses. Vogels and Orban (1987) showed that orientation discrimination for purely subjective contours and real lines is similar, a finding reflected in neurophysiological data (von der Heydt and Peterhans 1989, Peterhans and von der Heydt 1993), and Paradiso, Shimojo and Nakayama (1989) found they were subject to orientation aftereffects apparently similar to those observed in real contours.

Binocular Rivalry and Subjective Contours.

The importance of distinctions between types of subjective contours becomes evident when considering research already carried out on interactions between the perceptions of binocular rivalry and subjective contours.

Bradley (1982) reports that real triangles, shown in Fig. 5., when viewed dichoptically through a stereoscope, exhibit alternating contralateral suppression. This is especially prevalent at the six points of intersection of the two triangles. Predominance at any moment involves suppression of the non-dominant contours in the immediate vicinity of the predominant contours. This masking may occur at all six intersections such that one triangle can be said to dominate, or at only some intersections, with the other intersections dominated by the second triangle. Where one triangle dominates all intersections, the rivalry may be complete and none of the field containing the second triangle may be perceived. Alternatively, it may be that a single triangle is dominant at the intersections, but parts of the non-dominant field, away from the intersections, are also visible. All these effects are easily observed if Fig. 5. is reproduced and viewed through a stereoscope.

What of the subjective triangles in Fig. 5.? Bradley reports that when these are viewed through a stereoscope the effects are somewhat different. Under these conditions:

> "instead of showing rivalry, the monocular subjective contours merge to form the interior corners of a six-pointed star. The star represents a new subjective contour object generated by the binocular integration of the individual subjective triangles. This integration is not simple

> summation....selective portions of the monocular subjective contours are blended together to produce a new [binocular] subjective contour object. This....is not observed in [the real contour triangles]. In those instances....the centre portions of the sides of the triangles form a hexagonal shape in the centre of the combined view."
>
> (Bradley 1982 pp. 85-86.)

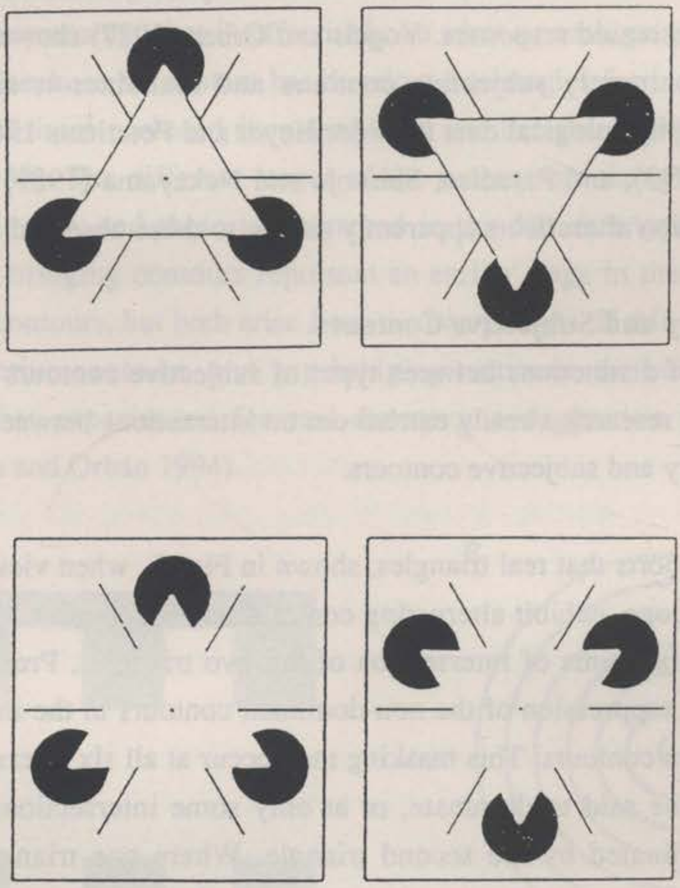


Fig. 5. Figures used by Bradley (1982 pp. 85) in his study of rivalry induced by subjective contours. While perceptually these figures are distinct from each other, in neurophysiological terms they represent processing from similar cortical locations. Peterhans and von der Heydt (1989) have argued that perception of gap bridging contours like those depicted above actually involves the same processes as give rise to the perception of real contours.

Bradley goes on to point out that in contrast to viewing the real contour triangles, for which perception of the rivalrous fields is inherently unstable, the subjective six pointed star is quite stable. Thus, rivalry would seem not to occur when the dichoptic objects are subjective, and it would be reasonable, therefore, to conclude that a number of significant differences exist between the pattern of rivalry that occurs in response to real contours and that which apparently does not occur between subjective contours.

Such a conclusion may be wrong. In what appears to be a contradiction to his earlier statements, Bradley also notes also that in place of the subjective six pointed star two subjective triangles, one superimposed on the other, with the subjective edges of the bottom triangle running up to the subjective edges of the top triangle, is sometimes observed. Actual differences between this last situation and that described as sometimes occurring for the real contour triangles are questionable, and the issue is clouded by Bradley's failure to provide any data to support his claims. He does assert that the situation described for the subjective fields cannot be attributed to rivalry as the same effects are observed when viewing an objective six pointed star nondichoptically. Bradley and Dumais (1975) attribute this result to the 'perceptual ambiguity' of the figure, which has a number of equally valid solutions; changes in the perceived field may be due 'simply' to the visual system providing an alternative solution for the veridical field. It is not made clear nor is it obvious how these two effects are related. If the model developed by von der Heydt and Peterhans (1989) applies, these results are not wholly unexpected. Among the suggested functions of such processes is the extraction of contiguity and discontinuity of three dimensional objects from a two dimensional 'view' of the world. If perception of occluded contours is achieved by a process with characteristics like those applied to real contours, interactions between sets of subjective contours should be similar to interactions observed between real contours. This is best explained by examining some more recent findings.

If one does as Bradley suggests, and views the subjective triangles through a stereoscope, the subjective six pointed star is readily apparent but so are the overlaid subjective triangles. Interestingly, and in conflict with Bradley's assertions, it is sometimes the case that rivalry, or what appears to be rivalry is observed. While this is a casual observation, a similar report has been made formally by Fahle and Palm (1991).

Fahle and Palm (1991) replicated the efforts of Bradley and Dumais (1975) and Bradley (1982). Fahle and Palm defined their illusory contours as "shapes which are not - or at least not along their extent - defined by transitions in luminance, wavelength, or any other physical parameter" (1990, pp. 1), and use to illustrate their definition variations of the Kanizsa triangle (their Fig. 1., pp. 2). Unlike those earlier workers they found that subjective figures; triangles, stars, squares, and other more complex multi-sided figures, do undergo binocular rivalry if presented dichoptically. They go further, however, and note that while all their subjects experienced rivalry, they did so "both under dichoptic conditions and, more surprisingly, during monocular and binocular viewing" (1990, pp. 2). Fahle and Palm are obviously vulnerable to the same criticisms as their earlier counterparts, and given the model developed by von der Heydt and Peterhans (1989) it is not surprising that they were able to observe rivalry with their stimuli when it was viewed dichoptically. Their statement above, however, suggests that the observations they reported may not have been rivalry at all.

Under monocular and binocular viewing conditions, the perceptions they describe as binocular rivalry could not have been, by definition. As to what they were, recall that Bradley (1982) attributed his findings to the 'perceptual ambiguity' of the subjective contour figures. It may be that all the observations made by both Bradley (1982) and Fahle and Palm (1991) are gap bridging contour equivalents of the Necker cube ambiguity. As Bradley suggested, 'more than one solution is possible' and so the alternations reported by him and Fahle and Palm as rivalry may really be alternations in perception, similar to the flipping of aspect observed when viewing a Necker cube. It is interesting to note that Fahle and Palm conceive of rivalry as an "unwanted side-effect in the perceptual system" (1991 p. 4), which is congruent with the conceptualisation of rivalry developed here. In the same sense, the conflicting solutions to the Necker cube reflect the existence of several valid alternatives.

The main points to be taken from this discussion is that there are virtually no useful data describing interactions between rivalry and subjective contour perception, and that unless careful definitions are observed, ambiguities and even erroneous interpretations can result. von der Heydt and Peterhans (1989) made clear the need for carefully designed stimuli in any attempt to localise effects being considered. They revealed also the likelihood that purely subjective contours and real contours arise via similar mechanisms, with the former resulting from ambiguities in the information usually used to process the latter. The degree of the similarity in processing is yet to be fully established. Nonetheless, using stimuli like that utilised by Paradiso, et al. (1989), for example, it is possible to generate effects which can confidently be described as arising after V1, but no later than V2. Examining interactions between effects elicited by these stimuli and effects caused by binocular rivalry may reveal whether binocular rivalry interferes with processing in area V2. If such effects are unmodulated by the occurrence of rivalry, as effects attributed to area V1 apparently are, the locus of the rivalry mechanism will be pushed more centrally than V2, a conclusion already suggested by others (Logothetis and Schall 1989). It is now possible to examine these issues empirically.

INTRODUCTION TO THE EXPERIMENTS

The discussion so far has demonstrated that there is no 'in principle' reason why rivalry does not arise as a product of the normal functioning of binocular neurones. It has reviewed evidence suggesting that monocularly mediated rivalry is an idea which is difficult to sustain. Finally, it has shown that there is some reason to believe that rivalry arises through extrastriate rather than striate processing and described a general model of binocular cortex capable of giving rise to perceptions like those experienced during rivalry. With this in mind, it has been suggested that area V2 may be a likely candidate for the site of the interactions giving rise to rivalry: It is predominantly binocular, and is the area where large scale integration of monocular information into a common binocular array is achieved. The exact nature of area V2 involvement has not been specified, but the binocular model described provides some hints to this. It must be remembered, however, that to formally describe any model of rivalry, general descriptions of binocular arrays such as the one provided, and the types of interactions occurring within them are not sufficient. That is, it is not enough to speculate on the types of mechanisms that could sustain sufficient algorithms because any number of such structures may be possible. As modellers of neural function are coming to realise, complexity increases almost exponentially with every additional cell included in an array (eg. Selverston 1993). To be able to provide a sufficiently constrained, physiologically realistic model, the neural locale of the interactions by which rivalry arises must be defined accurately. Demonstrating that area V2 is the site at which rivalry generating interactions occur would go some way towards this. That was the general aim of this series of experiments. It should be remembered that the work reported here was not designed specifically to validate all aspects of the model for rivalry so described. This can be done only by continually examining its ability to explain new data, and by examining predictions that arise from it. Instead, these experiments were intended to test the hypotheses that rivalry arises through binocular interactions and that the types of interactions eventually giving rise to rivalry are first observed in area V2.

The experiments reported here together form what Julesz (1971) would have described as a "psycho-anatomical" investigation of binocular rivalry. To provide the limitations described above, the strategy adopted here was to isolate the level of cortical processing with which rivalry may first correlated. This can be achieved psychophysically only when the neurophysiology underlying perception is well understood. This is the major limitation of this approach, and perhaps explains why other similar studies (eg. Blake and Overton 1979) have had limited success. Thus it was that misperceptions of orientation form the focus of the first part of this project. The nature of the interactions giving rise to both tilt illusions and tilt aftereffects are now reasonably well understood, and provide a starting point for this investigation. They were pressed into service here with another visual phenomenon, purely subjective contour perception, which has been linked with a sub-population of area V2 neurones.

So, the experiments which are shortly to be described can be divided into three groups. Those in the first group examine orientation misperceptions associated with subjective contours (eg. Paradiso et al. 1989). Purely subjective contours have been described as being encoded first in visual area V2 and are thought to arise via mechanisms designed for real contour perception (von der Heydt and Peterhans 1989). These experiments were conducted to provide fundamental information about the types of processing to which such contours are subject and the nature of the neural interactions in which they are involved. To pre-empt the results, it is clear that once encoded, purely subjective contours are subject to the same types of interactions as are real contours. It is as if the visual system regards such contours as edges. The experiments in the second group contain the critical experiments in terms of understanding the involvement of area V2 in binocular rivalry. These four experiments utilise earlier findings to examine the impact of rivalry on orientation misperceptions elicited with subjective contours. If periods of rivalry during the induction of such effects has an impact on the magnitude of the effects it seems reasonable to explain the result in terms of interactions between the components of visual area V2. As will become apparent, inhibitory interactions seem likely candidates for subserving the effects described here. The final three experiments briefly examine the effect of rivalry on other aftereffects, the neural determinants of which are similar to those of subjective contours in that they are reasonably well established and have been attributed to extrastriate processes. These last experiments were conducted first to verify some of the results of earlier work, and also as a means of confirming some of the predictions arising from earlier results.

GENERAL METHODS

Subjects

Unless otherwise noted (cf. Experiment Nine) all subjects used in these experiments were undergraduate psychology students at the University of Sydney. They took part either to obtain nominal course credit (these were first year students), or as the tutorial requirement of an advanced Perceptual Systems course (third year students). All had normal, or corrected to normal, acuity, and none of the subjects was stereoblind. Ocular dominance was also tested. Colour-blindness was not examined, nor were other aspects of visual performance.

All subjects were naive to the aims of the experiments in which they participated.

Apparatus

All stimuli were presented via a modified Gerbrands 4A four channel tachistoscope (Arlington, Massachusetts). Individual channels were used alone or in combination to present stimuli monocularly, binocularly or in rivalry. Each channel was aligned to ensure the centres of all displays coincided, and each had been modified in several ways. A circular black mask was inserted into each channel such that each field, as viewed by a subject, would lie within a circular boundary. This eliminated all cues to vertical and horizontal. Unless otherwise stated, to the end of each channel, behind each circular mask, was attached a metal plate. This plate, in turn, was attached to an externally mounted protractor. Each protractor had a fixed external reference, providing a limit of reading of 0.25°, and was manually controlled. This configuration allowed the experimenter, but not the subject, to monitor the orientation of the stimulus.

Within each channel was inserted a polaroid filter. A second set of polaroids was placed in the subject's viewing aperture, and together all filters could be adjusted to allow a stimulus in any channel to be viewed by a subject in either or both eyes. Surrounding the viewing aperture was a rubber mask which served to hold a subject's head steady throughout the experiment. Co-ordination of stimulus presentation was controlled by an external timer (Gerbrands 300 series millisecond timer) to which the tachistoscope was attached. The timer had a manual trigger controlled by the experimenter.

Both static and moving stimuli were employed in these experiments. Static stimuli were designed using Pagestream 2.0 (Soft-Logik Publishing Corporation) on an Amiga 2000 personal computer, and were output on an Apple Lazerwriter II. Once output, stimuli were glued to magnetised rubber discs, which were in turn affixed to the metal plate at the end of the required channel. Stimuli were aligned with gravitational vertical and offset appropriately with reference to the adjoining protractor. Subjective contours were constructed by generating a series of concentric circles, the luminance profile of which was a square wave and which subtended 3 arc minutes. The concentric circles were then bisected and the two resultant halves offset with respect to one and other such that each semicircular element terminated at a point midway between two contours in the opposite hemifield. The line of discontinuity defined by the terminators of the semicircles clearly defined a purely subjective contour of the type used by von der Heydt and Peterhans (1989). Around the outer edge of the stimulus was placed a black ring, defining the outer extent of the stimulus. This ring had an outer diameter of 8.5° and an inner diameter of 7.6°. Subjective contour test stimuli were defined by inducing contours such that the test subjective contour had an extent of 2°. The rest of the field, within the ring, was blank. Subjective contour adapting stimuli (aftereffects) and inducing stimuli (illusions, Experiment Four) had the subjective contour defined from one edge of the black ring across the entire field to the other edge of the black ring. A4 Examples of these stimuli are shown in Fig. 7. Real contour stimuli were similarly constructed, with the addition of an extra line along the terminations of the semicircular elements. Thus a real contour replaced a subjective contour in such displays.

The dark circular contours used to elicit the purely subjective contours and the surrounding black ring had an average luminance (L_{min}) of 0.2 cd/m^2. The white background against which they were observed had an average luminance (L_{max}) of 3.8 cd/m^2. Thus the Michelson contrast ($[L_{max} - L_{min}]/[L_{max} + L_{min}]$)for stationary stimuli used was 0.9. Blank fields etc. had the same space averaged luminance as the experimental fields, 3.0 cd/m^2.

Procedure

Before testing began, each subject was required to identify three objects - a disc, a horizontal rectangle, and a vertical rectangle in three random dot stereograms taken from Julesz (1971; figs. 8.1-1(D), 8.3.2 and 8.3.3 respectively). All three had to be correctly identified before the subject could take part in the experiment, and only one subject was rejected by this criterion (Experiment Seven). All subsequent testing took place in a darkened lab.

In all but the last experiments (Nine, Ten, and Eleven) subjects were required to judge the orientation of a contour, either real or subjective, as being tilted left or right of vertical. A staircase technique was used to establish each subject's point of subjective vertical (PSV), a pair of staircases being applied to each condition. Each treatment was preceded by a pretest staircase from which the subjects initial PSV for that treatment was established. It was followed immediately by the treatment staircase. Pretest/test pairs were pseudo-randomly ordered in each experiment. Each staircase commenced with the test contour oriented randomly within 10° of vertical. Step size was 3.0° initially, but reduced to 1.0° after 4 reversals. In all 10 reversals were run per staircase, with PSV calculated as the mean of the last 6. Pretest trials consisted of just the test contour, real or subjective. Following each stimulus presentation subjects viewed a blank field until their decision as to the orientation of the contour just presented was made. Such decisions were signalled verbally, and the orientation recorded manually by the experimenter, who also triggered the next presentation. The magnitude of the effect for any subject in a condition was calculated as the difference between their test and pretest means.

All subjects were tested individually. Unless otherwise specified, all subjects were tested monocularly, the test field being presented to their right eye. Adaptation and inter-ocular transfer was manipulated with respect to this.

Models and Statistical Analyses.

All the experiments reported here employed repeated measures designs in either simple or factorial designs. Data were therefore analysed using either a factorial or one-way analysis of variance (ANOVA). In all experiments planned comparisons (contrasts) were used to more fully partition the variance so as to completely examine independent variable effects. Unless stated, such comparisons were orthogonal, and employed the Bonferroni technique to restrict the type 1 error rate. Experiments One and Four utilised trend analyses in which the trend coefficients formed the contrasts. In addition to the analyses of variance, simple t-tests were often employed to examine differences between individual means, and between mean effects and zero. In such cases the nature of the tests make them independent of whatever contrasts were examined, and the repeated measures design allowed for the standard error to be calculated simply on the basis of the scores contributing to that mean. That is, all the variation within an effect can be attributed to that effect in a repeated measures design, unlike non-repeated measures designs where variance can be attributed to between subject differences (Kepple 1973).

In Experiment Five a rating scale was used in addition to other measures taken. Since the scale was continuous between zero and ten, and again employed a repeated measures design these data were analysed using a t-test for related samples.

[A4] See Appendix Four

Experiment Eleven employed, in addition to the above analyses, correlation analysis utilising Pearson's product-moment procedure. These correlations were done for individual subjects, rather than across subjects, to establish the constancy of the effects.

EXPERIMENT ONE

Before it can be established that rivalry has an affect on processes arising earlier in the visual hierarchy than those areas suggested by Logothetis and Schall (1989) it is necessary to understand the nature of those processes, that is, the mechanisms and interactions which give rise to them. The perception of purely subjective contours has been linked with neural processes in area V2, and von der Heydt and Peterhans (1989). among others, have argued that those processes are the same as those involved in real contour perception. Among the evidence which suggests this might be true is the observation that purely subjective contours, like real contours, undergo orientation misperceptions (Paradiso, et al. 1989). While much is known for real contour induced misperceptions of this type, little is known of purely subjective contour induced tilt aftereffects, and whether they are members of a single class of misperceptions, or whether their mechanisms differ. The aim of Experiment One was to measure the magnitude of a tilt aftereffect induced with purely subjective contours.

Psychophysical data reported by Paradiso et al. (1989) seems to support the physiological analysis of subjective contour processing described by von der Heydt and Peterhans (1989). Paradiso, et al. (1989) reported that adaptation to a purely subjective contour tilted away from vertical would induce a tilt aftereffect in a subsequently viewed subjective contour truly oriented vertically, and the magnitude of the aftereffect was proportional to the difference in orientation between the two contours. This suggests that the orientation tuned area V2 neurones sensitive to purely subjective contours may be subject to processes like cells encoding real contours, for which such effects are well documented (cf. Wenderoth and Johnstone 1987). Significantly, Paradiso and his colleagues reported that adaptation to a purely subjective contour would not induce a tilt aftereffect in a subsequently presented real contour, while adaptation to a real contour would produce a tilt aftereffect in a purely subjective contour. This pattern of results appears consistent with the hierarchically structured system described by von der Heydt and Peterhans (1989) and Peterhans and von der Heydt (1987). Real contours are encoded first in area V1, while purely subjective contours arise first in area V2. If adaptation at the point of encoding is required for the aftereffect to manifest, then adaptation further along the pathway might not corrupt an already encoded signal (Paradiso, et al. 1989). That is, if the two types of contour share some common processes, then adaptation of processing in the earlier area might be expected to impact on processing in the latter. Unless feedback from the later area to the earlier is in place, adaptation of the latter can have no effect on preceding processes. If such feedback is in place, it is not *necessary* that it affects the processing in the area receiving the feedback. Either of these alternatives is consistent with these results.

Indeed, the pattern of results reported by Paradiso et al. indicate that it is unlikely that orientation tuned area V2 neurones feedback to area V1 orientation selective cells in a way which affects their processing, and that describing purely subjective contours as an area V2 phenomenon has some validity.

This will become important later. The present experiment concerns the tilt aftereffects which can be induced with purely subjective contours. In their work, Paradiso et al. (1989) induced aftereffects using a range of orientations between vertical (0°) and 50°. Testing with a vertical subjective contour, they found a maximum aftereffect for orientation differences of approximately 15°, reducing to zero for differences between 45°-50°. This pattern of results appears very similar to those typically reported for real contour tilt aftereffects (see reviews by Howard 1982, Wenderoth and Johnstone 1987).

Thought to arise via common processes, real contour tilt aftereffects and tilt illusions reflect the operation of two distinct mechanisms (Wenderoth, van der Zwan and Williams 1993). Together these mechanisms combine to produce a distinctive asymmetrically 'S' shaped angular function (Fig. 6.) which can be explained heuristically as follows: all interactions between near contours are repulsion effects and all depend upon the contour's axes of symmetry. A single contour, or grating, has two axes of symmetry, one corresponding to its orientation, the other orthogonal to that axis. This is the virtual axis. Any angle formed by two real contours can be defined by the real contours or by one real contour and a virtual axis, or by two virtual axes. Repulsion effects make these angles look bigger than they really are. The magnitude of this effect is proportional to the actual angle between the components and the type of components involved (real or virtual). In this scheme, direct effects are defined as repulsion effects caused by real contours, indirect effects are repulsion effects caused by virtual axes. So, for example, a truly vertical test contour or grating (referred to as the test field) can be made to appear tilted away from vertical if it has around it a single non-vertical grating (the inducing field)[9]. The test field will appear tilted away from whichever axis of symmetry, real or virtual, of the inducing field is nearest vertical. The angular distance will be proportional to the proximity of the axis and its type (Wenderoth and Johnstone 1987). Real contours produce larger effects than virtual axes, which act like weak real lines. This is the one-dimensional (1-D) tilt illusion.

Because the vertical stimulus appears tilted away from whichever axis of symmetry of the inducing field is closest to it, as the inducing field orientation is rotated from

---

[9] Both the inducing and test fields are considered 1-D stimuli in that they have extent in the orientation domain in only one direction. That they have other qualities, like spatial frequency, luminance, etc, is not in question.

vertical to horizontal, the angular function of the apparent displacement of the test field is 'S' shaped, as first a real axes pushes it one way and then a virtual axis the other. This function is asymmetrical because real axis effects are stronger than virtual axis effects; the former correspond to real lines, the latter act as real, but weak lines. More recently, Wenderoth, van der Zwan and Williams (1993) have shown that this 'nearest-axis' hypothesis has predictive efficacy if the displacement of the test field is held to be the sum of both real and virtual axis effects.

This descriptive account is matched by neurophysiological evidence. Real and virtual axes have been equated with local and global mechanisms. The local process, lateral inhibition (Blakemore, Carpenter and Georgeson 1970, Carpenter and Blakemore 1973), generates apparent angle expansion or 'direct' effects (Gibson and Radner 1937, Howard 1982) for angular differences between 0° and approximately 55°, with a peak effect at about 15°. Wenderoth and colleagues noted that in addition to lateral inhibition a second, and probably extrastriate, process contributes a small component to the misperception experienced for these orientation differences. This second process may be involved in orientation constancy, and in the impoverished visual conditions encountered in the laboratory fails to function normally, thus compromising orientation constancy (Wenderoth and Johnstone 1988a, Wenderoth et al. 1993). 'Indirect' effects (Gibson and Radner 1937, Howard 1982) are apparent angle contraction effects observed for orientation differences between about 55° and 90°. The indirect effect is largest for differences of about 75°. Wenderoth and Johnstone (1988a) provided evidence that suggests indirect effects are the result of just extrastriate operations. Such processing is again thought to underlie orientation constancy. Wenderoth and Johnstone refer to the work of Allman, Miezin and McGuiness (1985) and Maunsell and Newsome (1987), in which are described striate and extrastriate mechanisms which modulate the tuning characteristics of classical receptive fields from well beyond them, and which may be involved in processing perceptual constancies. Significantly, there is no *a priori* reason to suppose so called 'total-receptive-fields' are confined just to the orientation domain. As should be evident from the General Introduction, they provide an example of precisely the type of mechanism that might be involved in binocular rivalry, thus providing a means of modifying neural responses from areas of the visual field thought classically to have no effect on the responses of individual neurones. In terms of orientation perception, however such processes, Wenderoth reasons, are of the type required to give rise to the indirect effect, and the extrastriate component of the direct effect. The differences between tilt illusions and tilt aftereffects is the temporal relationship between the test and inducing field. Tilt aftereffects are explained by assuming the effects of the inducing field are, for a short time, tonic (Magnussen and Johnsen 1986).

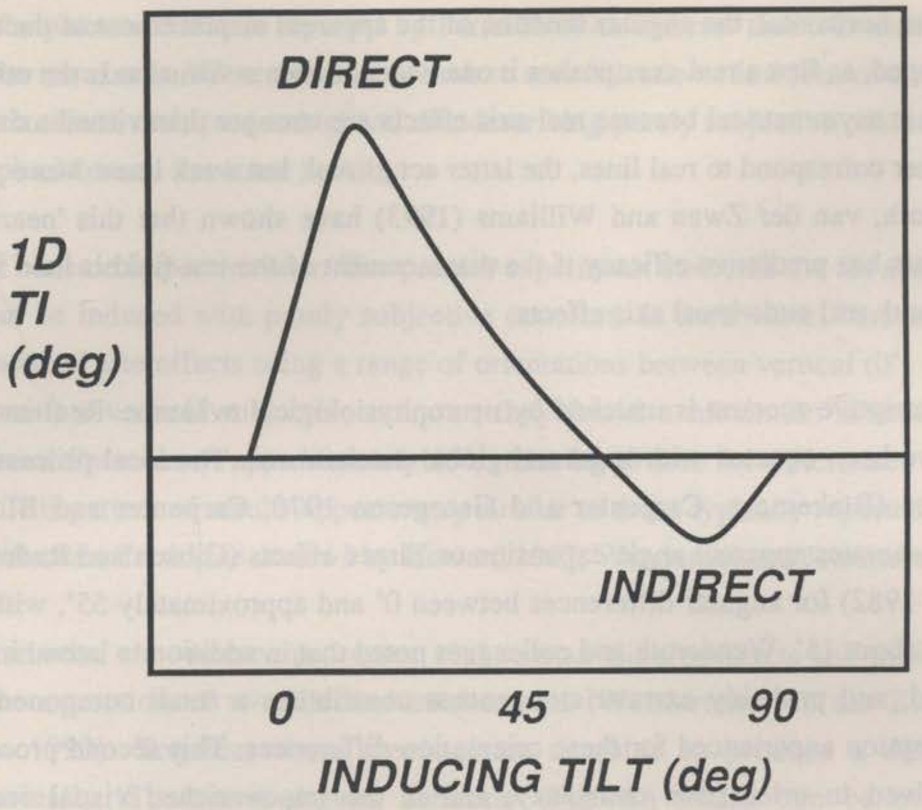


Fig. 6. The type of angular function typically observed for real contour tilt aftereffects and tilt illusions.

What of the purely subjective contour tilt aftereffects described by Paradiso et al. (1989)? Are the same mechanisms involved in producing those effects as are involved in the real contour aftereffects? There is some reason to expect that orientation tuned neurones in area V2 are subject to the same types of local processing as orientation sensitive neurones in area V1. Neurones in area V2 are grouped together in orientation columns (Livingstone and Hubel 1982, Hubel and Livingstone 1987) apparently analogous to orientation columns in area V1 (Tootell and Hamilton 1989). Further, there is no reason to expect that lateral inhibition is confined to orientation channels in area V1 (Braddick, et al. 1978). It is a real possibility, therefore, that lateral inhibitory processes contribute to the purely subjective contour tilt aftereffect. The function observed by Paradiso et al. (1989)beares a strong resemblance to the direct part of the real contour tilt aftereffect and illusion. Unfortunately, those workers did not examine a sufficiently large range of orientations to observe an indirect effect.

If purely subjective contour tilt aftereffects do arise via a mechanism like those giving rise to the real contour effects, then over a 90° range of inducing orientations it too should exhibit the asymmetrically 'S' shaped function predicted by the nearest-axis hypothesis. This would imply that subjective contours, once encoded, are subject to the same processes as real contours. That is, they are not qualitatively different in terms of some of the neural operations to which lines and edges are subject. More strong predictions are possible, however. It has been shown the angular function elicited by real contours exhibits significant linear, quadratic and cubic components (Wenderoth and Beh 1977). If similar mechanisms are operating, it is to be expected that they will produce similar perceptual effects, so the same trends should be evident in a subjective contour function. Further, if the mechanisms are indeed the same, then for orientations up to 50° (eg. 15°, 30°, 45°) significant direct effects should be evident, while for larger orientations (60°, 75°) significant indirect effects should be observed (O'Toole and Wenderoth 1977).

Method

Subjects: 16 third year undergraduates took part in this experiment.

Apparatus and Stimuli: The apparatus used in this experiment was as described above. The stimuli were constructed as described, the adapting purely subjective contour subtending 7.6° visual angle and the test subjective contour 2.0°. These stimuli are shown in Fig. 7.

Procedure: Using the staircase technique, each subject was tested under 7 experimental conditions, once at each inducing angle: 0°, 15°, 30°, 45°, 60°, 75°, 90°. These orientations are measured from vertical (0°), and were counterbalanced as clockwise (CW) and counter clockwise (CCW) rotations. The experiment utilised repeated measures in a simple one-way design, see Table 1. 1.

Table 1. 1. Adapting Orientations

Adapting Field Orientation	0°	15°	30°	45°	60°	75°	90°

As described above, each treatment staircase was preceded by a pretest staircase, thus each subject completed 14 staircases, with pretest/test pairs randomly ordered. Having completed the pretest staircase, subjects viewed the appropriate adapting field for 60 seconds. After 50 seconds the adapting field flashed off for 100 mseconds and then back on. This served as a cue to subjects that the test contour would soon be presented. After 60 seconds the adapting field disappeared, was replaced by a blank field for 500 mseconds, and then the test contour for 1.6 seconds. Subjects were then required, as quickly as possible, to decide whether the test contour was tilted left or right of vertical, and signal this to the experimenter. Immediately following their decision subjects were again presented with the adapting stimulus for a 10 second "top-up", before again being presented with the test stimulus. After each pair of staircases subjects were given a three minute break, during which they were encouraged to look around the darkened lab. Instructions to subjects consisted simply of a description of their task - to discriminate the test contour as tilted left or right of vertical, a description of the adaptation-test presentation procedure - including the requirement that they don't fixate during this period. Each subject was then given 5 practice trials, with the test contour being presented at random orientations within 10° of vertical. No feedback was given as to the success or otherwise of these judgements. Prior to commencement of the experiment the instructions were briefly reiterated, with clarification made as required.

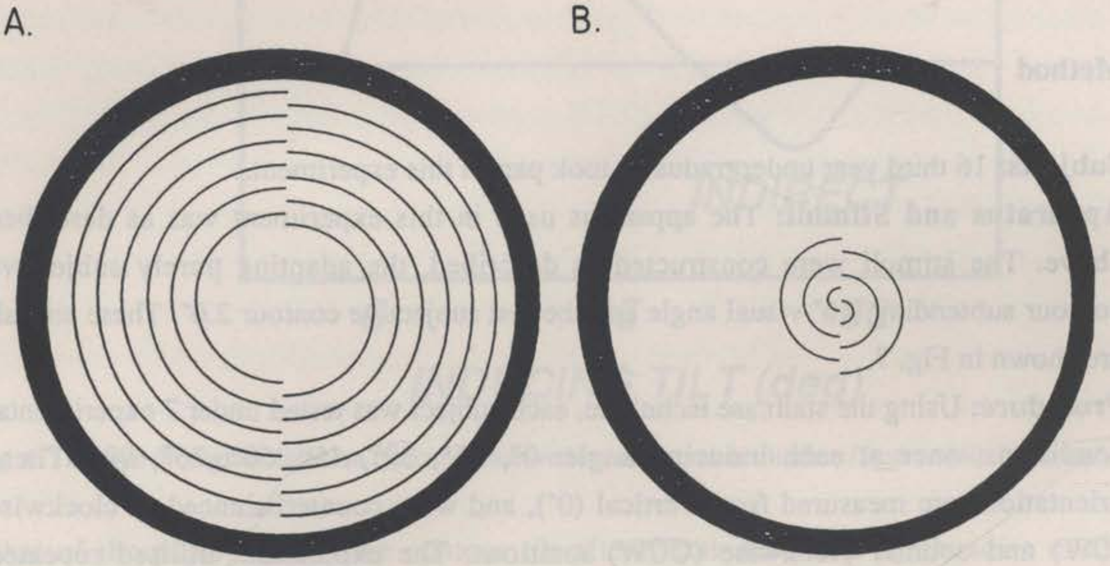


Fig. 7. The adapting and test stimuli used in this experiment. The adapting stimulus, A., was adjusted to the appropriate orientation for each condition. Subjects were instructed to "look to the centre" of this figure during adaptation. B., the test figure, had to be judged as tilted CW or CCW of vertical. The black ring was included as later experiments would require it for dichoptic fusion. Presented simultaneously, these stimuli were used also to measure the purely subjective contour tilt illusion in Experiment Four.

Results

For each orientation, a set of t-tests was used to compare the CW and CCW groups. None of these comparisons was significantly different, so scores were collapsed across direction of induction[10]. All measures have been normalised such that angle expansion effects are scored as positive values, while angle contraction effects are negative.

---

[10] All analyses are described in Appendix Two. There will be some instances where analyses are referred to, but not reported as results. These analyses too can be found in Appendix Two, but they deal only with questions with no bearing on the aims of the experiments

Means and standard errors at each of the orientations examined are illustrated in Fig. 8., and are summarised in Table 1. 2.

Table 1. 2. Mean Aftereffects and Standard Errors

Adapting Field Orientation	0°	15°	30°	45°	60°	75°	90°
Mean	0.011°	3.219°	1.917°	0.730°	-0.656°	-1.062°	-0.083°
Std. error	0.158	0.414	0.402	0.204	0.288	0.244	0.121

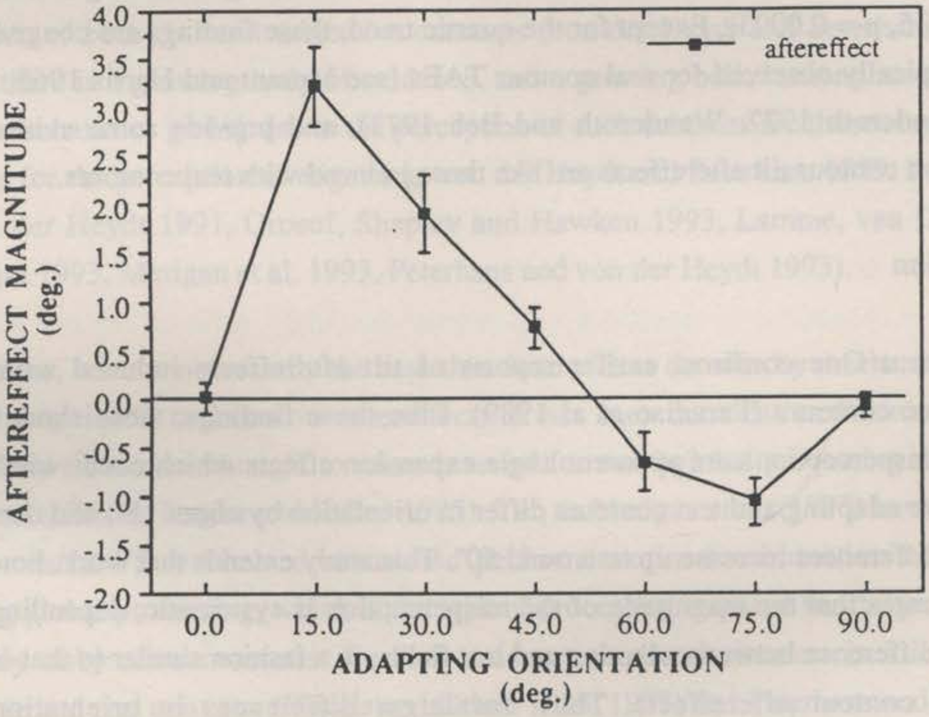


Fig. 8. The angular function of the purely subjective contour tilt aftereffect. Positive values are angle expansion (direct) effects, negative are angle contraction (indirect) effects. Bars represent ±1 standard error. Note the asymmetrical 'S' shaped function typical of that observed for real contours.

The function depicted is clearly asymmetrical and 'S' shaped, with the sign of the function (ie. nature of the effect) changing between 50°-55°. Up to approximately 50° the difference between the inducing and test contours looked bigger than it actually was; angle expansion. Beyond that point, and up to 90°, the angle looked smaller than it was; angle contraction. It is interesting to note that these expansion and contraction effects have similar sizes, proportionally, to real contour effects. That is, contraction effects are approximately half the size of expansion effects. An analysis of variance for repeated measures with trend analysis (trend co-efficients forming planned orthogonal contrasts, see Appendix Two) revealed significant linear ($F_{1,60} = 63.02$, $p \leq 0.0001$), quadratic ($F_{1,60} = 8.04$, $p = 0.0056$) and cubic ($F_{1,60} = 103.12$, $p \leq 0.0001$) trends. A quartic trend was also significant ($F_{1,60} = 8.22$, $p = 0.0052$), which was unexpected. The quartic trend accounts for less than 4% of the variance, however, and may simply be fortuitous in that the steps between treatments were of sufficient size to create this effect artificially. No higher trends were significant (quintic; $F_{1,60} = 2.796$, $p = 0.0979$, sextic; $F_{1,60} = 1.109$, $p = 0.2951$). A set of directional t-tests, which examined each mean separately, revealed that at all inducing orientations other than vertical (ie. 0°: $t_{15} = 0.067$, $p = 0.47$) and horizontal (ie. 90°: $t_{15} = -0.69$, $p = 0.25$), significant aftereffects were obtained and that these were in the predicted direction (15°: $t_{15} = 7.78$, $p \leq 0.0001$, 30°: $t_{15} = 4.77$, $p \leq 0.0001$, 45°: $t_{15} = 3.58$, $p = 0.0014$, 60°: $t_{15} = -2.88$, $p = 0.0057$, 75°: $t_{15} = -4.35$, $p = 0.0003$). Except for the quartic trend, these findings are congruent with those typically observed for real contour TAEs (see Morant and Harris 1965, O'Toole and Wenderoth 1977, Wenderoth and Beh 1977), and provide some evidence that subjective contour tilt aftereffects are like those induced with real contours.

Discussion

Experiment One confirms earlier reports of tilt aftereffects induced with purely subjective contours (Paradiso et al 1989). Like those findings, these show that the largest misperceptions are apparent angle expansion effects which occur when purely subjective adapting and test contours differ in orientation by about 15°, and decrease to zero as differences increase up to around 50°. This study extends that work, however. It demonstrates that the magnitude of the misperception is systematic, depending on the angular difference between adapting and test fields, in a fashion similar to that observed for real contour aftereffects. Thus, for larger differences in orientation, from approximately 55° and up to 90°, the angle between the adapting and test contours appeared smaller than it actually was. This angle contraction effect was largest at about 75°. So like the real contour tilt aftereffect, the purely subjective contour tilt aftereffect exhibits both angle expansion and angle contraction effects, and as the analysis revealed, both these expansion and contraction effects are significant across a range of inducing angles. The combination of the different trends revealed in the data has produced a function that is both asymmetrical and 'S' shaped, again mirroring real contour tilt aftereffects. On the basis of these results and in keeping with established nomenclature, purely subjective angle expansion effects will be referred to as direct effects. For larger orientation differences, up to 90°, angle contraction occurred; a purely subjective contour indirect effect. Such labelling is arbitrary, but the strong similarity between this function and that typically observed for real contour aftereffects (Wenderoth and Johnstone 1987) suggests it as appropriate.

It must be remembered that this experiment does not address the question of mechanisms directly. Understanding of the effects reported here is only in terms of the heuristic model provided by the nearest axis hypothesis. In terms of that model, the subjective contour direct effects can be attributed to interactions between the axes of the stimuli corresponding to the perceived contours. Indirect effects can be attributed to interactions between the real axis of the test field and the virtual axis of the adapting field, about which the subjective contour is also symmetrical. This analysis assumes subjective axes have the same effects as real axes. Neurophysiological support for this assumption is provided by the observation that there are area V2 cells that signal the orientation of both real and subjective contours (von der Heydt and Peterhans 1989). Indeed, there is a growing body of evidence, and a growing belief among researchers, that the mechanisms giving rise to the perception of such contours are those responsible normally for the perception of edges (eg. von der Heydt and Peterhans 1989, Peterhans and von der Heydt 1991, Grosof, Shapley and Hawken 1993, Lamme, van Dijk and Spekreijse 1993, Merigan et al. 1993, Peterhans and von der Heydt 1993).

Nonetheless, it is not necessarily the case that these effects do arise by mechanisms like those giving rise to real contour aftereffects. It has been demonstrated that area V2, where these effects are thought to arise, is tuned for more global processing than area V1 (Forster, Gaska, Nagler and Pollen 1985). Yet, as Merigan et al. (1993) have shown, lesions to area V2 result in decremented performance in discrimination of stimuli requiring global processing, which is the type of processing required for the perception of purely subjective contours. Further, orientation discrimination is similar for subjective and real contours (Vogels and Orban 1985, 1987) and Peterhans and von der Heydt (1993) found area V2 neurones do exhibit a high selectivity for orientation, particularly among those cells in which sensitivity for purely subjective contours has been demonstrated. Add to this the similarities which exist in cortical architecture between areas V1 and V2 and there seems little reason to suspect that similar local interactions would not occur in the two areas. That processing in area V2 has global characteristics could point to a role for it in orientation constancy, but such is speculation.

One interesting observation that does arise from these data is that apparently robust indirect effects have been observed. Using real contours a number of workers have found it difficult to elicit such effects when tilt illusions are generated by small acute angles (Carpenter and Blakemore 1973, Virsu and Taskinen 1975, Wenderoth and

Johnson 1985, Wenderoth, O'Connor and Johnson 1986). On the other hand, they do occur when the inducing stimulus is a large grating, or when there are relatively long, bisecting inducing and test contours (Gibson and Radner 1937, Morant and Harris 1965, O'Toole and Wenderoth 1977). This can be interpreted as reflecting the operation of global rather than local mechanisms (Wenderoth and Johnstone 1987), and that is the position accepted here. The stimulus configuration used in this experiment is more complex than a simple acute angle. The purely subjective contours, if considered in isolation, are not much more extensive; perhaps two acute angles. However, as a stimulus, the subjective contours alone most closely resemble two intersecting lines like those used by Morant and Harris (1965). While it is not conclusive, this suggests one alternative explanation of these results to be fallacious.

The model of purely subjective contour perception being applied here describes a two stage process in which oriented end-stopped cells, either in areas V1 or V2, encode the termination of the real contour inducing elements (von der Heydt and Peterhans 1989, Peterhans and von der Heydt 1989). In that model the relationship between the orientation of the end-stopped cell and the subjective contour they eventually signal is such that if the inducing subjective contour is tilted, say 15° CW of vertical, and the test contour is oriented truly vertically, the angular difference between the two subjective contours is the same as the angular difference between the oriented end-stopped cells signalling each of them (see von der Heydt and Peterhans, their Fig. 22, pp. 1746). One consequence of this might be that interactions between the end-stopped cells are responsible for the at least the direct aftereffects reported here, or some component of them. That is, the function depicted in Fig. 8. is not a subjective contour effect at all, but a real contour effect mediated by the oriented end-stopped cells. Two factors now suggest this not to be the case. First, end-stopped cells, like other orientation selective cells are set up in a structured retinotopic array. Most of the cells signalling the terminations of the inducing elements are separated by some distance, particularly those signalling the test contour and those signalling the inducing contour. Inhibitory interactions would be reduced, therefore, and direct effects arising from such interactions attenuated (Wenderoth and Johnstone 1988a). Secondly, real contour interactions do not generate indirect effects when induced with acute angles. At some inducing orientations, the terminations of the inner inducing elements are close to the terminations of the outer test elements. For the end-stopped cells signalling those terminations, the stimulus most closely resembles only an acute angle. It seems unlikely, therefore, that interactions between oriented end-stopped cells can account for the angular function described here, more likely it reflects interactions between neurones tuned for orientation and selective for subjective contours. This, of course, does not rule out completely interactions between end-stopped cells, just their ability to account for these effects.

It would be possible to further examine the usefulness of the nearest-axis hypothesis in predicting subjective contour aftereffects by increasing the number of subjective contours perceived in the inducing stimulus so two orthogonal contours were visible. If the hypothesis is indeed an appropriate way of thinking of these effects, then a quintic function typical of that observed for 2-D stimuli (Wenderoth and van der Zwan 1991) might reasonably be predicted. Such an investigation is incidental to the aims of this work, however, for it does not directly address the neural mechanisms underlying the observed effects. More appropriate experiments are possible. Before considering those experiments, and in summary, it is tentatively proposed that purely subjective contour direct effects arise from a combination of local and global processes, as do real contour direct effects. Similarly, global processes alone do not discriminate the purely subjective contour as different from a real contour or edge, and hence give rise to indirect effects. The next experiments were designed to establish the tenability of these assertions.

[illegible] occur when the inducing stimulus is a large grating, or when [illegible] exceeding inducing and test contours (Gibson and Radner 1937, Mitchell and Harris [illegible]

[illegible] orientation of the end-stopped cell and the subjective contour they [illegible] such that if the inducing subjective contour is tilted, say 15° CW of vertical, and the test contour is oriented truly vertically, the angular difference between the two subjective contours is the same as the angular difference between the oriented end-stopped cells signalling each of them (see von der Heydt and Peterhans, their Fig. 23, p. 1740). One consequence of this might be that interactions between the end-stopped cells are responsible for the at least the direct interactions reported here, or some component of them. That is, the function depicted in Fig. 8, is not a subjective contour effect at all, but a real contour effect mediated by the oriented end-stopped cells. Two factors now suggest this not to be the case. First, end-stopped cells, like other orientation selective cells are set up in a structured retinotopic array. Most of the cells signalling the terminations of the inducing elements are separated by some distance, particularly those signalling the test contour and those signalling the inducing contour. Inhibitory interactions would be reduced, therefore, and direct effects arising from such interactions attenuated (Wenderoth and Johnstone 1988a). Secondly, real contour interactions do not generate indirect effects when induced with acute angles. At some inducing orientations, the terminations of the inner inducing elements are close to the terminations of the outer test elements. For the end-stopped cells signalling those terminations, the stimulus most closely resembles only an acute angle. It seems unlikely, therefore, that interactions between oriented end-stopped cells can account for the angular function described here; more likely it reflects interactions between neurones tuned for orientation and selective for subjective contours. This, of course,

EXPERIMENT TWO

Experiment One demonstrated that the purely subjective contour tilt aftereffect can be described as having direct and indirect components, apparently similar to those observed for real contour tilt aftereffects, and the nature of which can be predicted in terms of an hypothesis developed to account for real contour aftereffects. The general aim of this and the following experiment was to determine whether purely subjective contour direct and indirect effects can be attributed to the same neural mechanisms as their real contour induced counterparts. A number of theories have been put forward to explain real contour effects (Gibson and Radner 1937, Kohler and Wallach 1944, O'Toole and Wenderoth 1977), but Wenderoth and Johnstone (1988a) demonstrated, in a series of experiments, that the neural mechanisms giving rise to apparent angle expansion effects are fundamentally different from those giving rise to apparent angle contraction effects. A brief description of the neural processes thought to be involved has already been given. A more detailed account will now be provided.

Gibson and Radner (1937) theorised the tilt aftereffect occurs because prolonged inspection of a tilted inducing stimulus results in its 'normalising' to the nearest primary meridian, horizontal or vertical. Normalisation caused a subsequently presented stimulus to be shifted in the same direction in which the normalisation had taken place, as if the entire orientation frame of reference was rotated. This theory has been criticised often (eg. Morant and Harris 1965, Wenderoth and Johnstone 1987), with its major shortcoming being its prediction of a symmetrical angular function. As already discussed, such a function is not observed, and Gibson and Radner's *ad hoc* account of the asymmetry has been dismissed. In place of normalisation, Kohler and Wallach (1944) developed their 'cortical satiation' theory to account for a number of effects, including the tilt aftereffect. While it would now be considered unrealistic in a physiological sense, 'satiation' can be seen as the forerunner to Carpenter and Blakemore's (1973) lateral inhibition theory. Lateral dis-inhibition was at one time suggested as the mechanism of the indirect effect (O'Toole and Wenderoth 1977), but like normalisation and satiation has since been discarded.

That different mechanisms might give rise to direct and indirect effects respectively has been noted for some time (Kohler and Wallach 1944), and is suggested by several observations. First, indirect effects are difficult to observe, depending critically on the particular stimulus configuration being used. Direct effects are robust, and can be measured in a large range of different inducing stimuli. Second, the presence or absence of vertical or horizontal edges can determine whether indirect effects occur; no cues to these meridia must be visible if the indirect effect is to be observed (Kohler and

Wallach 1944). The direct effect will manifest under almost any viewing condition. In contrast to these observations on the sensitivity of the indirect effect, the magnitudes of the tilt illusion, and the Zollner illusion, are reduced when the components of the inducing display are separated spatially. A separation of 1° completely eliminates the Zollner illusion (Wallace 1969), while others have shown that similar gaps in the display can reduce or eliminate the tilt illusion (Tolhurst and Thompson 1975, Virsu and Taskinen 1975).

Wenderoth and Johnstone (1988a) considered these observations and reasoned that if lateral inhibition gives rise to direct effects, while indirect effects arise from some other process, manipulations of stimulus parameters which are thought to reduce lateral inhibition should reduce the direct effect but not the indirect effect. Conversely, they argued, if a manipulation of the stimulus reduces the indirect effect, and the neural interactions to which it can be attributed do not include lateral inhibition, then the direct effect should remain unaffected. Manipulating differences in spatial frequency, spatial location and spatial extent did reduce direct effects (Wenderoth and Johnstone 1988a). As they predicted, indirect effects were not diminished by such changes. A luminance square frame around the stimuli reduced indirect effects but not direct effects, again as they predicted. Wenderoth and Johnstone explain this pattern of results by arguing that neurones in area V1 are systematically and tightly tuned for orientation, but also for spatial frequency, spatial location, etc. Introducing differences in spatial frequency, spatial location, etc serves to separate the groups of neurones signalling the orientations of the components within the stimuli. This, in turn, reduces lateral inhibitory interactions between these populations and thus the direct effect is reduced. That the indirect effect is not points explicitly to the operation of a second mechanism. Wenderoth and Johnstone assert the luminance frame acts like a "frame of reference", anchoring orientations. Both striate and extrastriate regions have been shown to contain neurones whose tuning characteristics are modulated by stimulus features outside the classical receptive field. It may be by the operation of such mechanisms that indirect effects arise (Wenderoth and Johnstone 1988a, Wenderoth et al. 1993). While these explanations were developed for operations arising in area V1, they are easily generalised for area V2.

A review of area V2 neurophysiology has already been provided, but some important features support the arguments developed here. First, orientation processing in area V2 closely resembles that occurring in area V1 (Burkhalter and Van Essen 1986, T'so, et al. 1990, Peterhans and von der Heydt 1993). Evidence for orientation columns and hypercolumns has been reported (Shipp and Zeki 1985, Tootell, et al. 1988), and while receptive fields may be larger for a given eccentricity, cortical magnification was statistically equivalent (Gattas, et al. 1981). Secondly, and importantly, area V2 shows more homogeneity of function across its three areas (thick, thin and pale stripes) than was originally suggested (Peterhans and von der Heydt 1993), an observation arising from behaving rather than anaesthetised and often paralysed animals. Thirdly, coarseness of tuning in the input to area V2 is similar to that at the output of area V1, so that there is little change in the amount of information. (Tootell and Hamilton 1989). Together, this suggests that area V2 does function similarly to area V1, at least in the orientation domain, and that interactions in the orientation domain are not exclusive to one area or another. On the other hand, it does ignore some substantial differences in the type of information processed in area V2, in particular, the tendency towards more global processing already discussed. The nature of such complexities indicates that in addition to 'low-level' information, area V2 may be a region where 'higher-order' processing arises for the first time. It is possible, therefore, that both the so-called local and global processes discussed co-exist within area V2. That is, in terms of the tilt aftereffect, both local (lateral inhibition) and global (mechanism of the indirect effect) effects occur together.

Now to demonstrate that the results of Experiment One reflect both local and global interactions, it is necessary to demonstrate the purely subjective contour direct effect is sensitive to stimulus parameters which are thought to modulate lateral inhibitory interactions between orientation sensitive neurones in area V2, in particular, interactions between orientation sensitive neurones tuned also for purley subjective contours. Similarly, manipulation of the stimulus such that global but not local processes are affected should reduce only purely subjective contour indirect effects while having no impact on purely subjective contour direct effects. To this end, it was decided the manipulations used by Wenderoth and Johnstone (1988a) could be applied to the mechanisms causing the purely subjective TAE. Of the four manipulations used by those workers, namely introduction of gaps between inducing and test fields, introduction of spatial frequency differences, changing inducing annulus thickness and introduction of a luminance frame oriented at or near the primary meridia, only the first and last were thought applicable to this study. It is not clear what the purely subjective contour equivalent to spatial frequency is. As for annulus thickness, it has been demonstrated, both psychophysically and neurophysiologically, that decreasing the number of inducing contours decreases the effective salience of a purely subjective contour (Lesher and Mingolla 1993, von der Heydt and Peterhans 1989). Thus a manipulation of this nature would confound subjective contour salience and inducing annulus thickness.

The aim of Experiment Two was to examine the effect of a gap between the inducing and test fields on the purely subjective TAE. Two alternative sets of predictions can be made. If lateral inhibition does produce purely subjective contour direct effects, then a gap between inducing and test fields should reduce the magnitude of such effects, just as for real contour direct effects. Introducing a gap between the fields will separate the retinotopically ordered neurones encoding the different components of the stimuli presented, in turn reducing inhibitory interactions which are thought to be giving rise to the effect. Similarly, if the purely subjective contour indirect effect arises via some other 'higher order' mechanism, one concerned with more global parameters of the stimulus, such effects should remain unaffected by the introduction of a gap between inducing and test fields; This just as for real contour indirect effects. Alternatively, if both direct and indirect subjective contour effects arise in area V2, they may share a common mechanism. Purely subjective contours are, after all, an 'emergent' property of the stimulus, and require global processing which real contours perhaps do not. If this is so, then induced changes in one effect may be matched by similar changes in the other. So, for example, decreasing lateral inhibitory interactions between purely subjective contour tuned neurones may reduce the subjective contour direct effect, but because indirect effects possibly arise via processesinvolving these same neurones, they too may be reduced. Such changes would be difficult to reconcile with the known orientation tuning characteristics of area V2, but would certainly highlight differences between the real contour effects and those observed in Experiment One.

Method

Subjects: 15 undergraduate psychology students, all from the volunteer population.

Apparatus and Stimuli: These were as for Experiment One, except that the adapting field was restricted in extent, and in its spatial relation to the test field. These differences are described in the procedure.

Procedure: Four conditions were tested: two gap sizes (0°, 1.4°) at two angles of inducing tilt (15°, 75°) in a simple one-way, repeated measures design. This is depicted in Table 2. 1.

Table 2. 1. Experimental Conditions

Adapting Field: Orientation/ Position	15° No Gap	15° Gap	75° No Gap	75° Gap

It was decided that just two orientations would be examined, one each representing direct and indirect subjective contour tilt aftereffects. 15° and 75° were selected for consistency with previous work on real contour effects, but also because at these orientations the largest effects were observed in Experiment One. The inducing stimulus differed from that used in the earlier experiments only in the introduction of the gap, all other stimulus parameters were as for the earlier experiments, see Fig. 9. There was some concern that introducing a 1.4° gap would reduce the salience of the purely subjective contour, just as decreasing the number of inducing contours does. In order to overcome this the same number of inducing contours (6) were used in the abutting annulus as were used in the annulus around the gap (the inducing stimulus described in the earlier experiments was modified in the abutting condition by removing the outer half of its diameter, the gap annulus by removing the inner half). In this way the number of inducing components were held constant. During the experiment subjects were given a five minute break between the second and third conditions, the condition order having been randomised for each subject. All other procedures were as described for Experiment One.

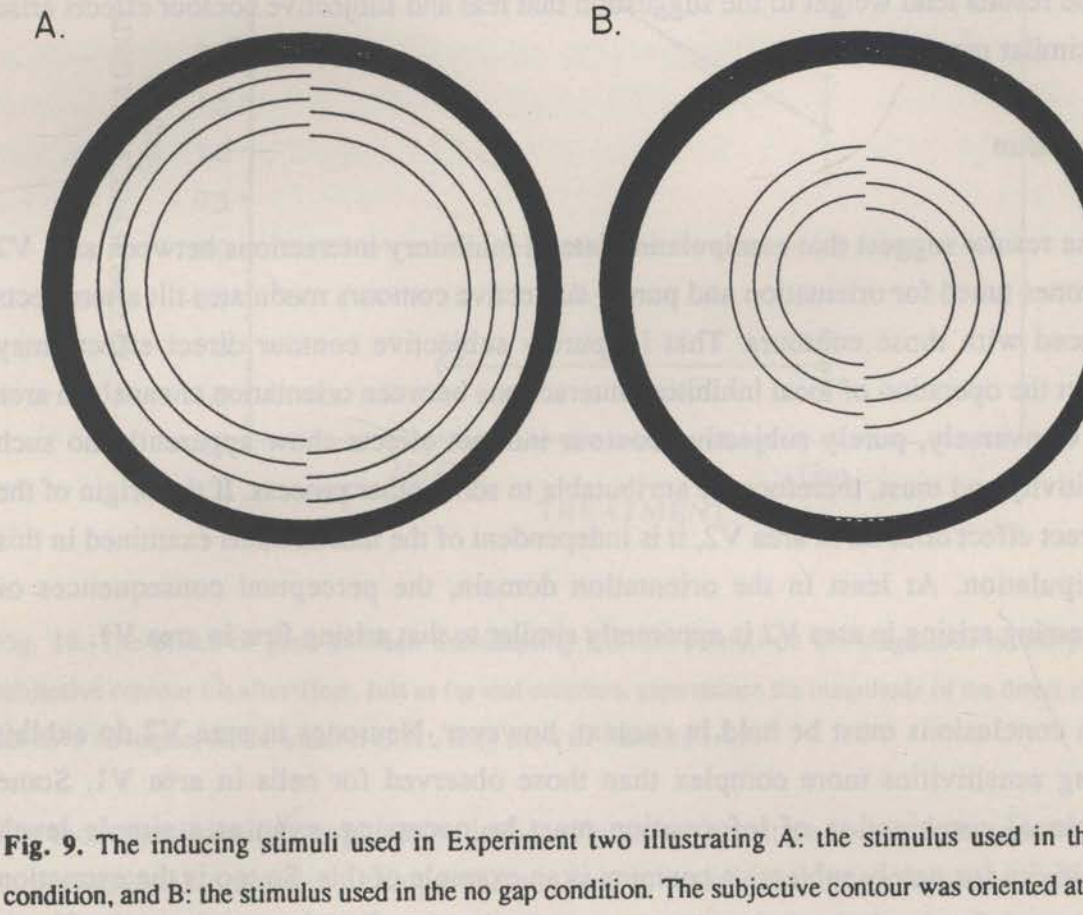


Fig. 9. The inducing stimuli used in Experiment two illustrating A: the stimulus used in the gap condition, and B: the stimulus used in the no gap condition. The subjective contour was oriented at either 15° or 75° CW of vertical.

Results

The mean illusions obtained under the four conditions are shown in Fig. 10. The data were analysed using a one-way repeated measures design with three planned orthogonal contrasts. The direct condition with no gap produced an aftereffect of 3.51° (s.e. = 0.389), similar to that obtained for the equivalent condition in Experiment One (3.22°). When the gap was introduced, this aftereffect was reduced to 1.21° (s.e. = 0.538). This reduction was significant ($F_{1,14} = 17.067$, $p = 0.0002$). Individual examination of the means revealed that although the direct effect was reduced by the introduction of the gap, it was still significantly different from zero (no gap: $t_{14} = 9.022$, $p \leq 0.0001$, gap: $t_{14} = 2.252$, $p = 0.0205$). That is, the gap reduced but did not eliminate the 15° induced aftereffect. Conversely, the corresponding indirect effect showed no modulation in response to the introduction of the gap. At 75° with no gap the aftereffect was -1.24° (s.e. = 0.335), again congruent with the similar condition in Experiment One (-1.06°). Even after introducing the gap, the indirect aftereffect was -1.222° (s.e. = 0.361). The difference between these was not significant ($F_{1,14} = 0.01$, $p = 0.9696$), and both means were significantly different from zero (no gap: $t_{14} = -3.708$, $p = 0.0012$, gap: $t_{14} = -3.381$, $p = 0.0023$). A final contrast showed the direct (15°) conditions were significantly different from the indirect (75°) conditions ($F_{1,14} = 193.747$, $p \leq 0.0001$). These results lend weight to the suggestion that real and subjective contour effects arise via similar mechanisms.

Discussion

These results suggest that manipulating lateral inhibitory interactions between area V2 neurones tuned for orientation and purely subjective contours modulates tilt aftereffects induced with those contours. That is, purely subjective contour direct effects may reflect the operation of local inhibitory interactions between orientation channels in area V2. Conversely, purely subjective contour indirect effects show apparently no such sensitivity and must, therefore, be attributable to some other process. If the origin of the indirect effect does lie in area V2, it is independent of the mechanisms examined in this manipulation. At least in the orientation domain, the perceptual consequences of processing arising in area V2 is apparently similar to that arising first in area V1.

Such conclusions must be held in context, however. Neurones in area V2 do exhibit tuning sensitivities more complex than those observed for cells in area V1. Some additional combination of information must be occurring, even at a simple level. Sensitivity for purely subjective contours is an example of this. So too is the extraction of edges defined only by texture or apparent motion (eg. Peterhans and von der Heydt

1993), and so is the combination of two monocular maps into a binocular map, thus allowing perception of binocular disparity (Burkhalter and Van Essen 1986, Tootell, et al. 1988, Tootell and Hamilton 1989). However, given that such information seems to be available for the first time at area V2, and that perception of the orientation of edges so defined is almost as accurate as for real contours (Vogels and Orban 1987), and that orientation aftereffects similar to real contour aftereffects can be elicited using such edges (Cavanagh 1989), it seems reasonable that orientation tuning does occur in area V2. Further, it is plausible that the processes by which it occurs are similar to those occurring in area V1. There is no reason to expect that such tuning would be achieved via different processes. Why would two separate mechanisms develop? It is certainly possible, but is perhaps unlikely. Orientation tuning could be achieved via feedback to area V1, but it is difficult to see how sensitivity for these 'higher order' edges would not then be observed in area V1. Certainly, psychophysical data suggest such feedback is not in place (Paradiso, et al. 1989).

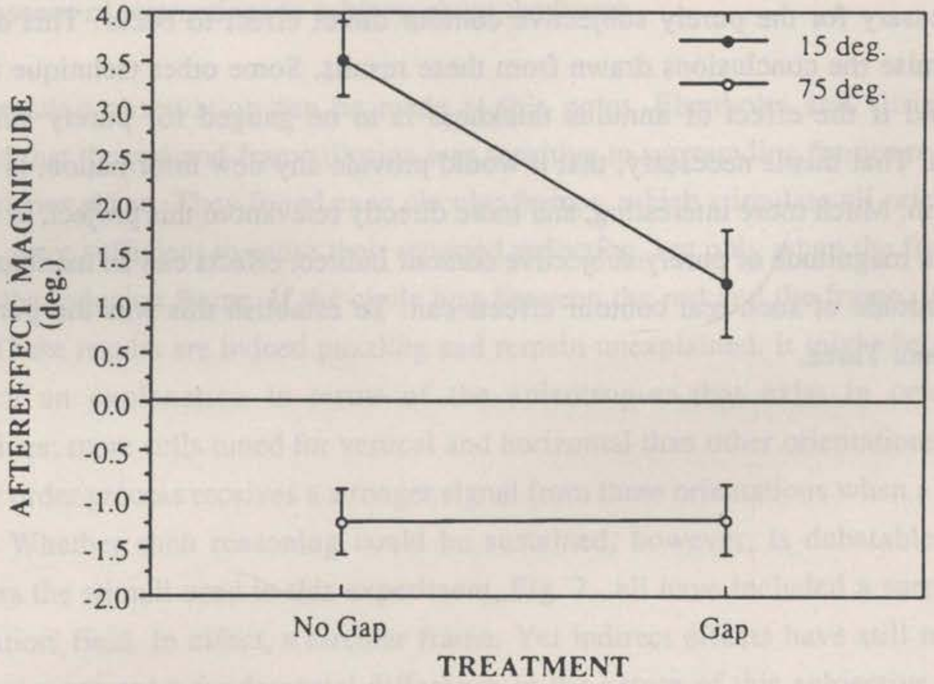


Fig. 10. The effect of gaps between the adapting and test stimuli on the magnitude of the purely subjective contour tilt aftereffect. Just as for real contours, gaps reduce the magnitude of the direct effect, but have no impact on the indirect effect. Bars show ±1 standard error.

The most parsimonious explanation is that orientation sensitive neurones in area V2 are subject to local interactions comparable to those to which orientation sensitive neurones in area V1 are subject. Whether such interactions, and the effects observed here, can be attributed to end-stopped cells or to subjective contour tuned cells has already been discussed (Experiment One). The arguments developed here need not be confined to one type of orientation sensitive cell or another, so while these effects are attributed to subjective contour tuned neurones, the conclusions are drawn more generally. That is, proximal neurones are mutually inhibitory, and such interactions are responsible for the direct effects described here and for real contours (Carpenter and Blakemore 1973). This tells us nothing about the origin of the indirect effect, other than to suggest it arises similarly for both real and subjective contours. This needs to be examined, however.

Prior to that, some mention of annulus thickness must be made. Wenderoth and Johnstone (1988a) demonstrated that for real contours, abutting inducing and test fields were *necessary* for direct effects to manifest, but that annulus thickness determined whether the stimulus was *sufficient* to elicit the full effect. For reasons mentioned in this experiment's introduction, annulus thickness cannot be varied with the type of adapting stimuli used here, as it confounds thickness and inducing element number. This experiment should, therefore, be taken only as a demonstration of what conditions are necessary for the purely subjective contour direct effect to occur. This does not compromise the conclusions drawn from these results. Some other technique must be developed if the effect of annulus thickness is to be gauged for purely subjective contours. That this is necessary, that it would provide any new information, is open to discussion. Much more interesting, and more directly relevant to this project, is whether or not the magnitude of purely subjective contour indirect effects can be manipulated as the magnitude of such real contour effects can. To establish this was the purpose of Experiment Three.

EXPERIMENT THREE

Kohler and Wallach (1944) observed they could only generate indirect effects while no rectilinear edges were visible in their stimulus. As soon as such contours were visible, indirect effects disappeared. Earlier Gibson and Radner (1937) mentioned, informally, that direct effects occurred even when the edges of the screen they used in their work was visible. They made no similar mention of indirect effects. More recently, the rod-and-frame illusion has been shown to be sensitive to surrounding fields also (Ebenholtz and Utrie 1983), while Wenderoth and Johnstone (1988a) in two experiments, demonstrated indirect tilt illusions can be eradicated if a 'frame-of-reference' is included in the stimulus field. They argued that if the direct tilt illusion was not affected by rectilinear frames, as suggested by Gibson and Radner (1937), but that indirects were (Kohler and Wallach 1944), that would be evidence against a common mechanism underlying both. They demonstrated that a frame-of-reference oriented along the primary meridian, or tilted up to 5° from that position, was sufficient to eradicate indirect tilt illusions while leaving direct tilt illusions unperturbed. This was true even in the absence of instructions to subjects about the frame.

An interesting observation can be made at this point. Ebenholtz and Utrie (1983) observed that the rod-and-frame illusion was sensitive to surrounding frames regardless of the frames shape. They found even circular frames, which stimulate all orientations equally, were sufficient to cause their reported reduction, but only when the frame was outside the inducing frame. If the circle was between the rod and the frame, it had no effect. These results are indeed puzzling and remain unexplained. It might be possible to couch an explanation in terms of the anisotropies that exist in orientation sensitivities; more cells tuned for vertical and horizontal than other orientations, and so a higher order process receives a stronger signal from these orientations when a circle is visible. Whether such reasoning could be sustained, however, is debatable. If one considers the stimuli used in this experiment, Fig. 7., all have included a surrounding 'registration' field. In effect, a circular frame. Yet indirect effects have still manifest. This may represent a fundamental difference in the nature of this subjective contour aftereffect and the rod-and frame illusion. The two different inducing stimuli are indeed very different, and presumably require some different processing.

Wenderoth and Johnstone (1987) examined direct and indirect tilt illusions induced with and without a surrounding circular frame. Direct effects were not at all affected. Indirect effects were reduced by approximately 45%, although they do not say whether this difference was significant. These reports suggest that while circular frames reduce the magnitude of indirect tilt illusions, unlike square frames, they are not sufficient to eliminate them. Perhaps because of lesser information about the primary meridia when compared to all other orientations. While comparable studies have not been conducted on tilt aftereffects, it follows that the magnitude of the purely subjective contour indirect effects reported here might be attenuated by the surrounding circle. The need for a registration stimulus in the following experiments precludes the need to examine if this is the case. It does raise the question, however, of just how effective a luminance frame might be in modulating the effects observed here.

The aim of this experiment was to measure the impact of a luminous square frame, oriented along the primary meridia, on purely subjective contour direct and indirect tilt aftereffects. If purely subjective contour tilt aftereffects are the perceptual consequence of processes similar to those giving rise to real contour aftereffects, inclusion of a frame around the stimulus should result in an attenuation of the subjective contour indirect effect, but no modulation at all of the direct effect. Alternatively, while the effect of a gap has apparently similar effects on real and subjective contour effects, two other predictions are possible. The luminance frame might have no affect on subjective contour indirect effects, which would suggest subjective contours are treated differently by, or subject to different higher order processes than their real contour counterparts. The exact nature of such a difference is an empirical question, but might be interpreted as showing subjective contours play no role in orientation constancy, or other global attributes of perception. The other alternative prediction is that both direct and indirect subjective contour effects will be modulated by the inclusion of the square frame. Both necessarily arise from higher order processing, and so the component of the direct effect attributable to such processes may be larger than is the case for real contour effects (Wenderoth, et al. 1993). Local and global mechanisms might contribute equally to subjective contour direct effects. This experiment examines these alternative predictions.

Methods

Subjects: 15 undergraduates were used, all volunteers from the first year population. As stated, all were naive, and all had normal or corrected to normal vision.

Apparatus and Stimuli: The apparatus was as for the previous experiments. The stimuli were those used in Experiment One, except that surrounding the adapting and test displays, in two of the four conditions, was a luminance square frame. This frame had sides that subtended 10° v.a., and presented a dark border around the stimulus. Like the inducing contours, the frame had a luminance of 0.2 cd/m^2.

Procedure: As for the previous experiment, four conditions were tested in a simple one-way, repeated measures design; Two adapting angles (15° or direct, 75° or indirect) each with and without a frame. These are shown in Table 3. 1. The frames were placed into the tachistoscope between trials when they were required. Identical frames were used in both the channel containing the adapting field and the channel containing the test field, and were placed in the same plane as the adapting and test stimuli. Insertion of the frames was achieved without the subjects being aware that anything was inserted into or removed from the tachistoscope by getting the subjects to turn their backs to the tachistoscope between conditions. As all were naive and inexperienced observers, this was for them not a departure from normal routine. At no stage was any reference to the frames made to the subjects. Condition order was randomised for each subject, and a five minute break given between the second and third conditions. All other procedures were as for Experiment Two.

Table 3. 1. Experimental Conditions

Adapting Field: Orientation/ Surround	15° No Frame	15° Frame	75° No Frame	75° Frame

Results

The mean aftereffects are shown in Fig. 11., and, as can be seen, the results were as predicted on the basis of subjective contour effects arising from cortical mechanisms like those generating real contour direct and indirect effects. A one-way repeated measures analysis of variance with three planned orthogonal contrasts was used to examine the data. Both the 15° and 75° inducing angles, without frames, produced misperceptions comparable to those observed in the previous experiments; 3.29° (s.e. = 0.36) and -1.37° (s.e. = 0.31) respectively. Introducing a square luminance frame had no significant effect on the direct effect, which under the 15°/frame condition produced a misperception of 3.44° (s.e. = 0.60) ($F_{1,14} = 0.100$, $p = 0.7533$). The introduction of a square frame did significantly reduce the indirect effect, which under the 75°/frame condition produced an effect of 0.17° (s.e. = 0.20) ($F_{1,14} = 10.118$, $p = 0.0028$). Clearly there is a difference in the impact of a luminous square frame on purely subjective contour direct and indirect tilt aftereffects. Finally, the average difference between direct and indirect effects again was significant ($F_{1,14} = 131.601$, $p \leq 0.0001$).

An examination of the individual means revealed all the aftereffects observed in this experiment were significant, except for the 75°/frame condition ($t_{14} = 0.88$, $p = 0.1974$) (see Appendix Two). The implies that the indirect effect was not simply reduced, but eradicated by the inclusion of the frame. That there was no suggestion that subjects had used the frame as a reference for making their judgements in the direct condition (15°/frame) suggests that this is a real effect, and not an artefact of a change in strategy.

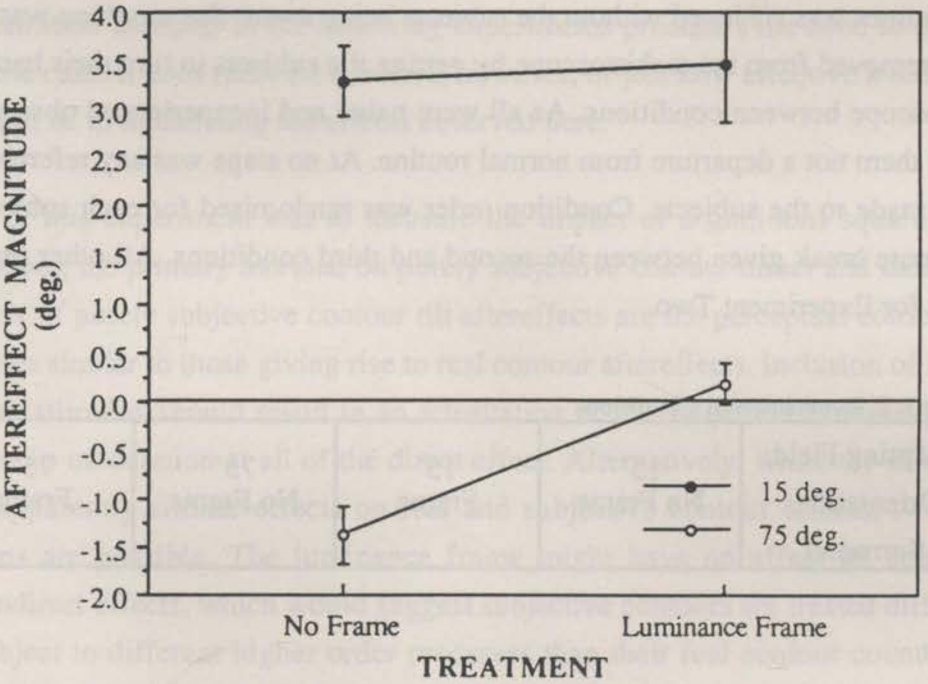


Fig. 11. The effect of a surrounding square luminance frame on the magnitudes of direct and indirect subjective contour tilt aftereffects. The subjective contour direct effect showed no variation in the presence of the frame. The corresponding indirect effect appeared to be eradicated. These results mirror those obtained under the same conditions using real contours. Bars are ±1 standard error.

Discussion

The results of this experiment indicate that a square luminance frame surrounding the inducing and test fields used to elicit purely subjective contour tilt aftereffects eliminate indirect effects, but do not cause any perturbation to direct effects. That is, purely subjective contour indirect effects occur only when markers of the principal axes are not visible. This supports the view that indirect effects arise via global mechanisms, possibly involving orientation constancy (Wenderoth and Johnstone 1987), and that the same mechanism operates whether the edge is real or higher order. There is no suggestion that subjective edges are ignored, that they are treated differently from real contours. Similarly, there is no suggestion that subjective contour direct effects contain a significant contribution from such higher order mechanisms. There was no attenuation of the subjective contour direct effect when a frame was included. Finally, if the registration field around the stimuli is causing any attenuation of these effects, it is sufficiently moderate to still allow the effects to manifest and be manipulated.

The previous experiment showed gaps reduced direct but not indirect subjective contour effects, giving a pattern of results that together resemble those for real contours (Kohler and Wallach 1944, Tolhurst and Thompson 1975, Virsu and Taskinen 1975, Wenderoth and Johnstone 1988). So, in addition to asserting that real and subjective contour effects arise via similar mechanisms, it is possible also to argue that direct and indirect subjective contour effects are, like their real contour counterparts, the product of different processes. It is the contention here that lateral inhibitory interactions between orientation selective, subjective contour tuned neurones, occurs in area V2, and these give rise to subjective contour direct effects. Like those in area V1, orientation selective neurones in area V2 are highly ordered, both in terms of retinotopic mapping, and in orientation preference (Gattas, et al. 1981, Shipp and Zeki 1985, Burkhalter and Van Essen 1986, Tootell, Born and Hamilton 1988, Tootell, et al. 1988, Tootell and Hamilton 1989, T'so, et al. 1990). Thus, changing differences in orientation changes inhibitory interactions between neurones (Experiment One), and increasing the difference in spatial location decreases these interactions (Experiment Two). Manipulating spatial relationships generally had no influence on the magnitude of the subjective contour indirect effect, however. As is the case for real contours, this suggests the basis of the indirect effect is different. It seems clear that indirect effects are not subject to local mechanisms, either for real or subjective contours. Therefore, just as global mechanisms have been offered in explanation for real contour indirects (Wenderoth and Johnstone 1988a, Wenderoth, et al. 1993), it is the assertion here that they can account also for subjective contour effects. The luminance frame which has been used here, is sufficient to eliminate errors in orientation constancy. Not only do similar interactions apparently occur in area V2 as in area V1, but once edges, real or subjective, are encoded, they are subject to more global operations. Models of purely subjective contour perception (von der Heydt and Peterhans 1989, Peterhans and von der Heydt 1989, Takahashi, et al. 1992) all frame their explanations in terms of processes able to distinguish objects from each other and from the background. There is no reason to expect, therefore, that once they are encoded, subjective contours are processed differently from real contours. Thus the explanation of Allman, et al. (1985), suggesting that facilitation and inhibition occurring in response to the total receptive field properties of some neurones (see also Maunsell and Newsome 1987), which might be the basis for figure-ground discrimination, perception of constancy's, etc, can not only be applied to subjective contour mechanisms, but must be equally as appropriate.

As discussed, area V2 has been implicated by considerable evidence in more global type processing than is observed in area V1. Generalisation of borders begins in area V2. These processes require the (not necessarily linear) summation of information across cortical space. The question arises as to whether any of those mechanisms might account for the types of interactions being considered? It is possible that cross orientation inhibition between area V2 neurones underlies the indirect effect. Morrone, et al. (1982) described how orthogonal contours presented simultaneously and detected by neurones in the striate cortex caused a decrease in excitation compared to levels observed in neurones when either contour was presented alone. If similar responses occur in area V2, local/global comparisons may be responsible for these effects. Similarly, it has previously been suggested that area MT exhibits properties that might be appropriate (Wenderoth and Johnstone 1987). That is, the pattern selective tuning of area MT neurones is consistent with the encoding of two dimensional stimuli (Movshon, Adelson, Gizzi and Newsome 1985, Stoner and Albright 1992), and so may mediate the real and virtual axes of symmetry interactions hypothesised by Wenderoth and Johnstone. If purely subjective contours are treated like real edges once they are encoded, it follows that their axes of symmetry too are encoded subsequently. Whether this occurs in area V2 or area MT, which receives considerable input from the thick stripes, and lesser input from the pale stripes of area V2 (Van Essen, et al. 1992) is open to debate. It should be remembered also that while there is evidence that the effects reported in these three experiments almost certainly do represent interactions between subjective contour encoding neurones, the inducing elements will also have axes of symmetry, and these will correspond in orientation with those of the subjective contours.

These results generate a number of questions, for example, could a frame defined only by anomalous edges, or purely subjective contours also provide enough information to eliminate such errors? The answers to these and similar questions might expose not only something of the nature of contour processing in the visual cortex, but also something of the nature of orientation perception. It seemed important, at this point, to conduct a simple test of the proceeding arguments. As already mentioned, the angular function of 2-D effects could be examined, but that could introduce new neural mechanisms which have yet to be considered. A more simple and direct test, which would include the neural mechanisms already explored, was to examine the angular function of the purely subjective contour tilt illusion.

EXPERIMENT FOUR

This is the final experiment designed to establish the similarities between the mechanisms of the real contour tilt aftereffect and the purely subjective contour tilt aftereffect. If the conclusions drawn from the foregoing experiments are sound, a simple prediction provides a means for testing them. Wenderoth, and others (see Wenderoth and Johnstone 1987 for a review), have argued that tilt aftereffects and tilt illusions arise via similar processes, and are part of a family of orientation misperceptions that include the rod-and-frame illusion, and the two-dimensional tilt illusion and two-dimensional tilt aftereffect. The mechanisms implicated have already been described. If this is so, then in addition to tilt aftereffects elicited with subjective contours, it should be possible to observe also a purely subjective contour tilt illusion. The aim of Experiment Four was to test the hypotheses that purely subjective contour tilt illusions similar to purely subjective contour tilt aftereffects can be elicited by the same stimuli presented appropriately, and that such illusions will be characterised by an angular function similar to that observed for tilt aftereffects. This will serve to verify the commonality of the mechanisms giving rise to real and subjective contour orientation misperceptions.

The same conditions were examined in this experiment as were in Experiment One. Based on those results it was predicted that the angular function thus described would exhibit significant linear, quadratic and cubic trends. Similarly, of the seven conditions examined (Table 4. 1.) all but horizontal (90°) and vertical (0°) were predicted to elicit significant illusions. These would be apparent angle expansions (direct effects) for the 15°, 30° and 45° conditions, and apparent angle contractions (indirect effects) for 60° and 75°.

The purely subjective contour tilt illusion examined in this experiment was set up using a configuration like that used to induce the aftereffect in Experiment One. That is, it was constructed as a test contour surrounded by an abutting annulus, in which was contained the inducing contour. Unlike the tilt aftereffect stimuli, which were viewed successively and in which the two subjective contours appeared quite salient, this was a more complex display. The stimuli were presented simultaneously, and the subjective contours were still easily perceived, but casual observation revealed that on first viewing it was a little difficult to separate centre and surround. Given that continuous viewing was not going to be used, some modifications to the design of the experiment were included. These are described below.

Experiment Four.

Methods

Subjects: 10 undergraduates from the volunteer population acted as subjects. For the reasons described above it was decided to use experienced, but naive observers. All subjects had taken part in previous experiments. None had been previously debriefed. The number of available subjects was thus constrained.

Apparatus and Stimuli: The apparatus remained unchanged from the previous experiments. Stimuli were also similar, depicted in Fig. 7.

Procedure: The important difference between this experiment and those carried out so far was that rather than successive presentation of stimuli, the test and inducing fields were presented simultaneously. A staircase presentation was used, with each trial consisting of a two second presentation of the inducing field surrounding the test field (Wenderoth and Johnstone 1988b have shown that for real contours the magnitude of the direct and possibly indirect effect can be modulated by stimulus-on duration, the magnitude varying for 'flash' durations up to 1600 ms. While it was not tested formally, a duration of 2s was used here as it seemed sufficiently long to approximate continuous viewing). As for the previous experiments, subjects were required to make a two alternative, forced choice decision; the test field appeared tilted left of right of vertical. The staircases again ran for ten reversals, with pretest and test staircases following each other at each of the seven inducing conditions, which were randomised. The conditions tested were as for Experiment One, with the inducing contour oriented at 0° (vertical), 15°, 30°, 45°, 60°, 75°, and 90° (horizontal), Table 4. 1. Again, the design used was a repeated measures, one-way design. Only CW rotations were examined in this experiment, given that no differences between CW and CCW had been found in Experiment One. Effects were calculated as for Experiment One. Intercondition intervals were three minutes, with consecutive trials commencing five seconds after subjects had made a decision for the previous trial. Test staircases followed pretest stairs' by five seconds also. Prior to commencing the experiment, subjects completed 10 practice trials; five with the test alone and five with the inducing field in place. The orientation of the inducing contour on these trials was randomised between 90° CW and 90° CCW of vertical. Test field alone, or both fields was also randomised for each subject, and no feedback as to accuracy was provided. All other procedures were as for Experiment One.

Table 4. 1. Inducing Orientations

Inducing Field Orientation	0°	15°	30°	45°	60°	75°	90°

Results

The angular function described by the mean tilt illusions obtained at each inducing orientation are illustrated in Fig. 12. The means and their standard errors are summarised also in Table 4. 2. Similar analyses were carried out on these data as those used in Experiment One.

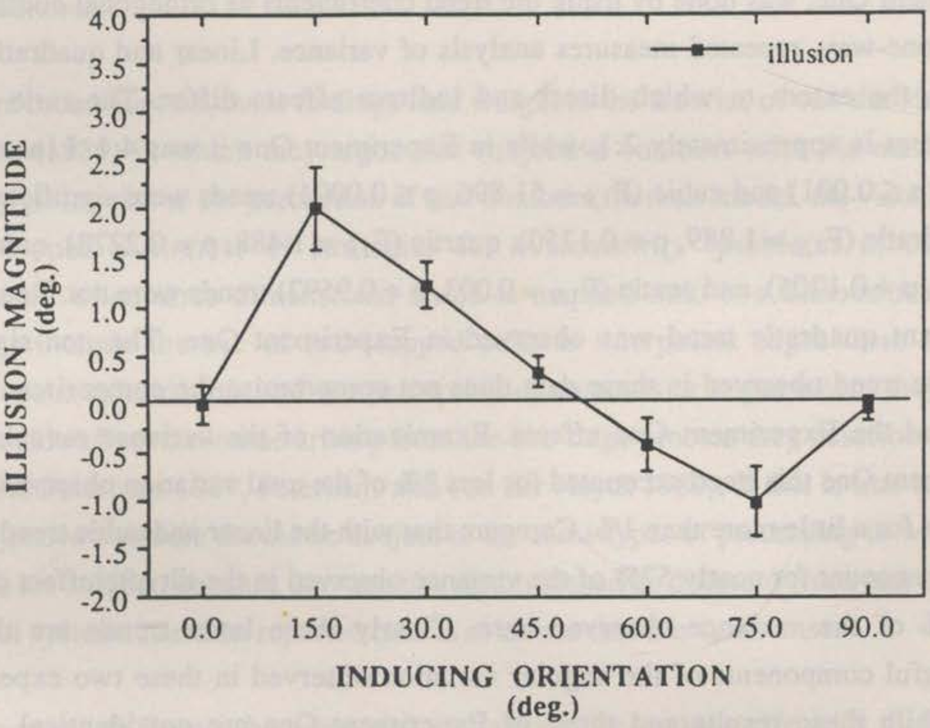


Fig. 12. The angular function of the purely subjective contour tilt illusion. Like its aftereffect counterpart this function is asymmetrical and 'S' shaped. It has significant linear and cubic trends, and all conditions except 0°, 90° and 60° produced significant illusions. The 60° condition produced an apparent indirect effect, albeit a small one, and may reflect a problem with the power of the experiment.

Table 4. 2. Mean Illusions and Standard Errors

Inducing Field Orientation	0°	15°	30°	45°	60°	75°	90°
Mean	0.001°	2.001°	1.218°	0.317°	-0.433°	-1.017°	0.050°
Std. error	0.199	0.427	0.239	0.162	0.277	0.350	0.124

Except for the 0°, 60°, and 90° conditions, all illusions were individually significant (0°: $t_9 = 0.005$, $p = 0.9961$, 15°: $t_9 = 4.684$, $p = 0.0005$, 30°: $t_9 = 5.089$, $p = 0.0003$, 45°: $t_9 = 1.955$, $p = 0.0412$, 60°: $t_9 = -1.563$, $p = 0.0763$, 75°: $t_9 = -2.903$, $p = 0.0088$, 90°: $t_9 =$

0.403, $p = 0.6967$). This result was as for Experiment One, except for the 60° inducing condition. Given that an apparent angle contraction, that is indirect effect, was observed, and that the magnitude of this effect was similar to that observed for the comparable tilt aftereffect, concluding that no effect was elicited at that orientation may be a type II error. This might be attributed to the power of this experiment to detect small differences, which is constrained by the number of subjects. A more extensive experiment could verify this conclusion, but does not seem critical.

More importantly, a series of trend analyses were carried out on the data. This, as in Experiment One, was done by using the trend coefficients as orthogonal contrasts in a simple one-way, repeated measures analysis of variance. Linear and quadratic trends indicate the extent to which direct and indirect effects differ. The ratio for this experiment is approximately 2:1, while in Experiment One it was 4:1. Linear ($F_{1,9} = 28.402$, $p \leq 0.001$) and cubic ($F_{1,9} = 51.896$, $p \leq 0.0001$) trends were significant, while the quadratic ($F_{1,9} = 1.889$, $p = 0.1750$), quartic ($F_{1,9} = 1.488$, $p = 0.2278$), quintic ($F_{1,9} = 2.489$, $p = 0.1205$), and sextic ($F_{1,9} = 0.003$, $p = 0.9592$) trends were not. Recall that a significant quadratic trend was observed in Experiment One. The non-significant quadratic trend observed in these data does not compromise the comparison between these and the Experiment One effects. Examination of the variance reveals that in Experiment One this trend accounted for less 3% of the total variation observed. Here it accounts for a little more than 1%. Compare that with the linear and cubic trends, which together account for nearly 57% of the variance observed in the tilt aftereffect data, and for 53% of the variance observed here. Clearly these latter trends are the most meaningful components of the angular variation observed in these two experiments. Thus while these results and those of Experiment One are not identical, there is sufficient similarity to assert they represent an interaction common to both the aftereffect and illusion. More generally, they support the thesis that real and subjective contour orientation misperceptions arise via similar processes.

Discussion

Certainly these first four experiments lend strength to the argument, made by Wenderoth and Johnstone (1988a), that theories of orientation misperceptions formulated in terms of striate cortex mechanisms (eg. Over 1971, O'Toole and Wenderoth 1977) are incomplete, and are unable to explain the full range of such effects. The results described here implicate area V2 mechanisms in such processes also. This experiment tested the hypothesis that subjective contour aftereffects arise via similar processes to their real contour counterparts by examining the similarity between subjective contour tilt illusions and tilt aftereffects, and together with the preceding experiments provided strong evidence that real and subjective contour aftereffects could be so equated. The similarity between the illusion function described here, and the function described in Experiment One is sufficiently strong to conclude that subjective contour illusions and aftereffects share a common origin. A range of other experiments could be carried out on subjective contour orientation misperceptions to further elucidate their mechansims, but on the basis of these four experiments there is sufficient evidence to conclude subjective contour tilt aftereffects can be regarded as equivalent to real contour aftereffects in more than just the similarity of their perceptual manifestation; the processes giving rise to these effects apparently are similar to those for real contours.

In a more broad context, these findings lend weight to the theories of von der Heydt and Peterhans (1989) in which they argue that subjective contours arise via mechanisms normally giving rise to the perception of real contours. In their model, the visual system has developed a number of strategies for overcoming problems of occlusion encountered when three dimensional space is mapped onto two dimensions. These strategies include the use of end-stopped cells to interpolate edges from spatially discontinuous information, and the perception of contours or edges where they do not exist is a side effect sometime arising from the two stage process they describe (von der Heydt and Peterhans 1989, Peterhans and von der Heydt 1989). If this is true it follows that subjective contours should be subject to the same types of processing to which real contours are subject, because they are not distinguished as different from real edges by the visual system. The data reported here is evidence that this is the case.

The important difference between real and subjective contour effects is their site of origin in the cortex, which was the point of examining their similarities. Subjective contours are encoded first in area V2, and thus provide information about the cortical interactions occurring in that area. Any differences that might be found between subjective contour effects and real contour effects can be attributed to differences in processing occurring in the two areas, which was the original purpose of these experiments. It is now possible to address directly any role area V2 might have in binocular rivalry. While real contour tilt aftereffects are not affected by periods of rivalry during their induction (Wade and Wenderoth 1978), subjective contour aftereffects have not been similarly examined. The usefulness in doing so is provided by the different sites of origin of these effects. These first experiments have demonstrated that any differences which might be observed cannot be attributed directly to differences between the mechanisms giving rise to real and subjective contour aftereffects.

EXPERIMENT FIVE

The previous experiments have provided the necessary information to allow the unambiguous interpretation of the results of this experiment. As already described, several studies have examined the impact of binocular rivalry on visual effects for which the underlying neural correlates are thought to be known. The fundamental assumption of all those studies, and of this experiment, is that effects which are reduced by rivalry during adaptation probably arise subsequently to rivalry along the visual pathway whereas effects not so reduced arise prior to the site of rivalry. For example, recall Wade and Wenderoth (1978) examined the effect of binocular rivalry on the tilt aftereffect and found binocular rivalry caused no change in magnitude. They concluded that the processes giving rise to the aftereffect occurred prior to those giving rise to binocular rivalry. Because the tilt aftereffect had, at that time, been ascribed only to lateral inhibition in area V1 (Carpenter & Blakemore, 1973), Wade and Wenderoth suggested that rivalry arises beyond area V1. The conclusions of other workers followed similar logic (eg. Blake and Overton 1979, Lehmkuhle & Fox, 1975; O'Shea & Crassini, 1981, Blake & Fox, 1974). The more recent report that spiral motion aftereffects (Wiesenfelder & Blake, 1990) are considerably reduced by periods of rivalry during their induction has effectively eliminated the possibility that the processes of rivalry, and those of aftereffects are independent of each other. The results of Blake and Fox (1974a) and Blake and Overton (1979) had already suggested, indirectly, that this was the case. Wiesenfelder and Blake (1990) argue that the complex motion aftereffects they examined arise no earlier along the visual pathway than visual area MT. In asserting that rivalry must arise prior to the neural loci responsible for the perception of spiral motion, which places the processes of rivalry beyond area V1, but not later than MT, Wiesenfelder and Blake again use reasoning based on the assumption that some form of serial processing can be assumed to occur in the visual cortex. The difference between the later application of this strategy, and the earlier ones is the increase in understanding of the complexity of the visual system that has occurred in recent years. Wiesenfelder and Blake (1990), among others (eg. Paradiso, et al. 1989, Berkley, et al. 1994) acknowledge that in some sense serial processing can be assumed. There is, therefore, some precedent for the rationale being applied in this experiment.

It has been argued here that rivalry is the perceptual consequence of normal neural operations which include excitation, fatigue and inhibition, and as the findings of Logothetis and Schall (1989) indicate, the way in which these factors combine is extremely complex. They suggest tuning characteristics are not fixed, and can depend upon the presentation of the stimulus, as do others (Hubel and Livingstone 1987, Rose, Blake and Halpern 1989, Peterhans and von der Heydt 1993). The difference between 'normal' perception and binocular rivalry is that a group of binocular cells receives two sets of almost congruent information under normal circumstances, but two different sets in conditions that elicit rivalry, and for some cells this is apparently sufficient to change their observed tuning characteristics (Logothetis and Schall 1989). Even without this complication if the perception of rivalry arises because of temporal variation in the amount of excitation, inhibition, and fatigue across the array, it follows that the difference between normal and rivalrous activity within the cortex is that binocular neurones tuned for one stimulus or the other during rivalry will be subject to different patterns of activity than would be the case if input to them from monocular sources was equivalent. Recall the description of activity in the model. One of the prime determinants of the state of any neurone will be the inhibition to which that neurone will be subject. Inhibitory interactions too may determine the nature of the tuning exhibited by neurones at any time (eg. Bauman and Bonds 1989). Further, under rivalrous conditions, the average amount of inhibition experienced by any neurone may be greater than under normal viewing conditions (Burr and Morrone 1987, Ferster 1988). This suggested increase in general inhibition is supported by various psychophysical findings. For example, the data of Wiesenfelder and Blake (1989) describes a reduction in aftereffect magnitude. Blake and Fox (1974b), Blake, et al. (1980), and Westendorf (1989) have all reported findings which show stimuli are more difficult to detect during rivalry. The consequence of an increase in inhibition is that, in general, cells will be less excited during rivalry than during normal perception. That is, they will fire less often and perhaps for shorter periods. In turn, this leads to a general decrease in the fatigue state of a cell so affected by rivalrous input[11]. On this basis, it must be predicted that if the site of adaptation resulting in an aftereffect lies prior to the site at which the rivalrous perceptions are first generated[12], no change in the magnitudes of those aftereffects should be observed. If the site of adaptation coincides or is subsequent to the site at which the rivalrous interactions first manifest, then less adaptation should be observed because of the decreased fatigue associated with reduced levels of activity (see Experiments Nine, Ten and Eleven for an explanation in terms of the binocular model).

---

[11] This type of reasoning is simply an extension of the findings and arguments developed by other workers (eg. Rose 1980, Blake, Sloane and Fox 1981) to account for apparently synergistic increases in sensitivity observed with congruent binocular inputs.

[12] This should not be taken to imply that the cortical locations nominated here are the sites directly responsible for perception. The intention is that at points along the visual pathway interactions occur which have perceptual consequences. These interactions may occur at any level, and the result of their occurrence is carried on through the visual system. Even if it were possible to nominate a particular cortical location before which perception does not occur (cf. Wenderoth 1992), processing in preceeding areas would still have perceptual consequences.

The aim of Experiment 5 was to examine the impact of binocular rivalry during the induction of purely subjective contour orientation aftereffects on the subsequent magnitude of those effects. It has been argued that the purely subjective contour direct tilt aftereffect arises through lateral inhibitory processes between subjective contour tuned neurones in area V2, and that the equivalent indirect tilt aftereffect arises either in area V2, or perhaps more centrally, but certainly not in area V1. The question as to the impact of binocular rivalry during induction on the magnitude of the subsequent subjective contour tilt aftereffect can now be considered, as it provides a way of investigating any contribution to rivalry made by the neural machinery in area V2. If the results of Logothetis and Schall (1989) can be generalised from motion and rivalry arises in superior temporal sulcus, purely subjective contour direct tilt aftereffects, like real contour direct tilt aftereffects and other aftereffects attributed to area V1 should show no modulation in response to periods of suppression during their induction, although purely subjective contour indirect effects, described only arising beyond area V1, may be reduced. If rivalry arises prior to MT, specifically in area V2 then, like the spiral and plaid motion aftereffects, both purely subjective contour direct *and* indirect tilt aftereffects should be diminished by rivalry during their induction. Experiment 5 tested these predictions.

Methods

Subjects: 15 subjects completed the experiment as part of a requirement for a 3rd year psychology course in which they were enrolled. All were naive as to the aims of the experiments, and all had normal or corrected to normal vision.

Apparatus and Stimuli: In general, the stimuli and apparatus of this experiment were as described for the previous experiments. However, there were several important additions.

This was the first experiment in which a rivalrous stimulus was presented concurrently with the adapting stimulus. The rivalrous stimulus was constructed similarly to the adapting and test stimuli, and presented via the third channel of the tachistoscope. In this channel the polaroid filters were oriented orthogonally to those in the other fields and hence the stimuli in this field could be perceived only by the eye not adapting to the subjective contour. The black rings surrounding all fields were sufficient to achieve registration of the stimuli during testing. Within the ring of the rivalrous stimulus were a number of randomly placed blobs. These blobs differed in size (between ~0.25° and ~2.0° diameter), but were all circular (Fig. 13B.) and thus stimulated all orientations equally. Luminance and contrasts were as for the adapting and test stimuli.

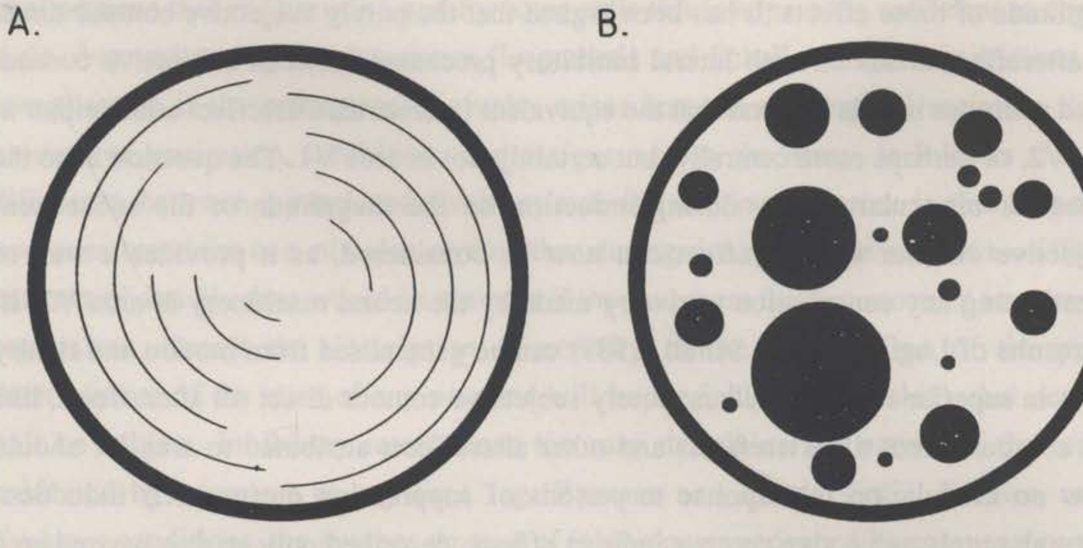


Fig. 13 The extra stimuli used in this experiment. The adapting and test fields used for this study were equivalent to those used in the previous experiments. A: The salience of the subjective contour during rivalry was measured by comparing it to the salience of any contour perceived in a stimulus which had the inducing elements modified so as to appear similar to the way the adapting stimulus sometimes appeared during rivalry. It is not suggested that this stimulus is a rivalry mimic. B: Binocular rivalry was achieved by presenting with the adapting field, but to the other eye, a field of random blobs of various sizes. This field was matched to the adapting field in terms of luminance, etc, and the use of blobs ensured there was no specific orientation cues.

Procedure: Just as for the apparatus, procedures for this experiment were kept as similar as possible to those of the previous experiments. The pretest/test staircase technique described was again utilised, each subject being tested on each of 4 experimental conditions. Thus each subject completed 8 staircases, with pretest/test pairs randomly ordered. The conditions tested were inducing orientation (15°, 75°) by rivalry (no-rivalry, rivalry). This is represented in Table 5. 1.

Table 5. 1. Experimental Conditions for subjective contour tilt aftereffect.

Adapting Orientation	15°	15°	75°	75°
Adapting Condition	No Rivalry	Binocular Rivalry	No Rivalry	Binocular Rivalry

As for Experiments Two and Three it was decided to use just two orientations, one each for direct and indirect tilt aftereffects.

Just as in the previous experiments 60s adaptation was used, but this period included rivalry as appropriate. Similarly, after 60 seconds the adapting field(s) disappeared and were replaced by a blank field for 500 msec, and then the test contour was presented for 1.6 seconds. In the rivalry condition, the rivalrous stimulus was presented only when the adapting subjective contour was present. Instructions to subjects were as for the previous experiments, except that they were told that on each of the rivalry trials they were required to monitor the amount of rivalry they experienced during the initial adaptation period. Subjects signalled those periods during adaptation in which the adapting stimulus predominated. They were instructed that complete predominance was not required, but that they should signal with a continuous button press those periods for which 50% or more of the adapting field could be perceived. The button was connected to a simple lab-timer which measured the cumulative time for which the button was pressed. Prior to the commencement of the first experimental condition, a measure of predominance was taken using a vertical adapting stimulus. Subjects monitored a vertically oriented adapting field for 60 seconds, indicating the time for which it was predominant. This trial was followed by a 3 minute rest period. A similar trial was conducted three minutes after the final experimental condition. This step was taken to monitor the amount of rivalry experienced by subjects throughout the experiment so as to ensure that it was constant. Were it not it would indicate that complete dissipation of adaptation Blake and Overton 1979) had not occurred during the rest period.

Finally, an additional set of measures were taken from ten of the subjects (selected at random) after they had completed all other measures. These measures required the subject to rate the strength of the subjective contour during rivalry, and were made to ensure that any decrement in the magnitude of the aftereffects could not be attributed to a reduction in the salience of the subjective edge during rivalry. Subjects viewed an inducing stimulus in rivalry for five 10 second intervals (intertrial interval 60 seconds), making a rating on each occasion. They were instructed to make a rating between 0 and 10, with the former being no perceived contour at all, and the latter a perceived contour of the same strength as a subjective contour seen without rivalry. Randomly interspersed between these trials were trials in which subjects rated the subjective contour without rivalry, and trials in which subjects were presented an inducing stimulus with the line of discontinuity removed. This was achieved by shortening each inducing element so that each terminated at a random position (Fig. 13A). These control stimuli were also presented with and without rivalry. Each subject thus produced four ratings of the perceived subjective contour salience, each of which was the mean of five measures.

Results

The means of the four measures of predominance taken for each subject are shown in Fig. 14. A one-way analysis of variance for repeated measures and with planned orthogonal contrasts revealed that the predominance of the subjective contour stimuli was not significantly different for the 15° (26.77s, s.e. = 1.17) and 75° (26.16s, s.e. = 1.19) inducing orientations ($F_{1,42} = 0.613$, $p = 0.4380$). At both orientations the inducing stimuli were predominant for approximately 44% of the adaptation period, indicating that any differences in the effect of rivalry at these orientations is attributable to neural mechanisms rather than to differences in the amount of rivalry for each condition. Similarly, there was no difference between the predominance of a vertically oriented subjective contour before (26.96s, s.e. = 1.25) and after (26.66s, s.e. = 3.57) the experimental conditions ($F_{1,42} = 0.148$, $p = 0.7024$). Pre- and post-adaptation predominances were not different from those obtained during the adaptation trials ($F_{1,42} = 0.393$, $p = 0.5342$). Together these data indicate no overall change in predominance throughout the experiment, suggesting that as the experiment progressed, no build up of aftereffects occurred (Blake and Fox 1974).

Means and standard errors of the purely subjective contour tilt aftereffect magnitudes are shown in Fig. 15. An analysis of variance for a factorial design with repeated measures was used to examine the data. Inspection of Fig. 15. reveals that subjective contour direct effects were again significantly different from subjective contour indirect effects ($F_{1,14} = 30.667$, $p < 0.0001$). The subjective contour direct tilt aftereffect, which without rivalry was 2.97° (s.e. = 0.35), showed a reduction in magnitude, down to 0.95° (s.e. = 0.48), in response to rivalrous suppression during the adaptation period. Similarly, the subjective contour indirect effect, -1.19° (s.e. = 0.45) without rivalry, also showed diminished magnitude, down to 0.31° (s.e. = 0.47), in response to periodic suppression of the inducing stimulus during adaptation. A set of t-tests examined each of these means, and revealed that all but the last were significantly different from zero (15°, no riv.: $t_{14} = 8.42$, $p \leq 0.0001$, 15°, riv.: $t_{14} = 1.984$, $p = 0.0336$, 75°, no riv.: $t_{14} = -2.635$, $p = 0.0098$, 75°, riv.: $t_{14} = 0.0668$, $p = 0.2574$). Thus while rivalry apparently reduced but did not eliminate purely subjective contour direct tilt aftereffects, it eradicated the comparable indirect effect completely. This conclusion must be tempered by consideration of the power of this experiment (Appendix Three). The interaction between viewing condition and orientation was significant ($F_{1,14} = 14.664$, $p = 0.0018$), indicating that while there was no main effect of rivalry condition ($F_{1,14} = 0.454$, $p =$

0.5112), when considered in conjunction with orientation the effect of rivalry was to significantly reduce the magnitudes of both direct and indirect effects.

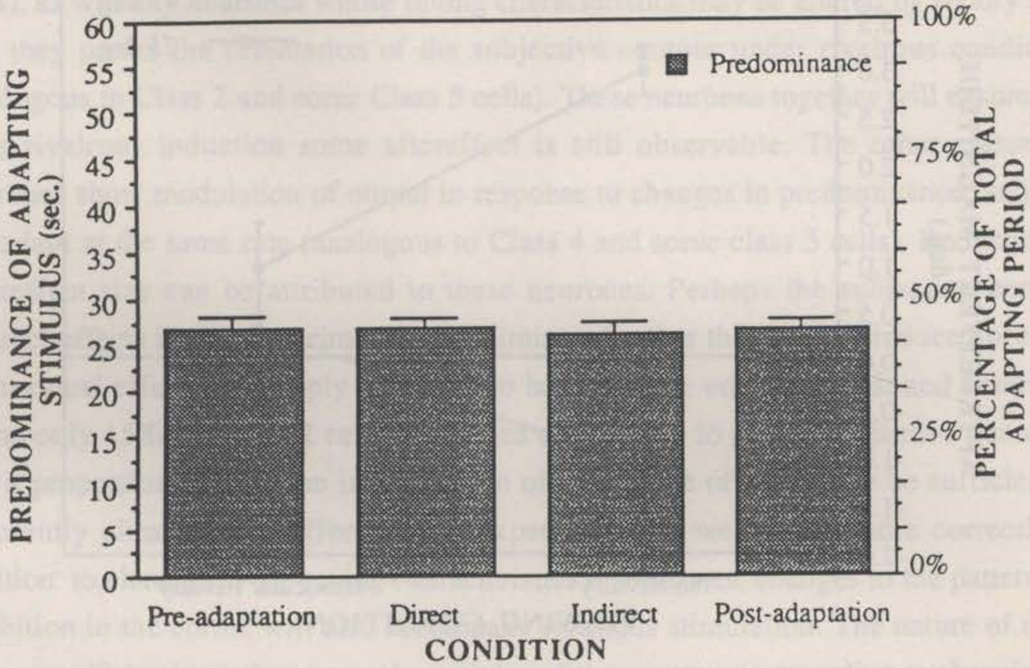


Fig. 14. Mean predominance of the adapting stimulus during induction of subjective contour direct and indirect effects, prior to the commencement of the experiment, and after the completion of the experimental conditions. Subjects were required to signal periods when the adapting stimulus was the most predominant stimulus, periods of exclusive predominance being extremely infrequent. The left-hand axis indicates predominance in seconds, the right-hand axis describes predominance as a percentage of the adapting period. No differences between any of the periods were observed. This indicates relatively constant rates of rivalry throughout the experiment, and suggests sufficient time was allowed for the dissipation of the aftereffects induced from the previous condition. Bars are 1 standard error.

This difference cannot be attributed to a change in the salience of the subjective contour during rivalry because planned contrasts revealed there was no difference between the salience of purely subjective contour in rivalry (mean rating = 9.33, s.e. = 0.29) and not in rivalry (mean rating = 9.5, s.e. = 0.38) respectively ($F_{1,27} = 0.107$, $p = 0.7465$). Similarly, there were no differences ($F_{1,27} = 0.130$, $p = 0.7217$) in the ratings given to the non-subjective contour stimuli with rivalry (mean rating = 1.38, s.e. = 0.48) and without rivalry (mean rating = 1.57, s.e. = 0.43). The mean salience of subjective contours under both conditions was greater than for the non-inducing stimuli under both conditions ($F_{1,27} = 482.65$, $p < 0.0001$). That is, rivalry during adaptation disrupts the acquisition of purely subjective contour induced direct and indirect tilt aftereffects, but does not decrease the salience of the contour when the adapting stimulus is visible. So, together these findings indicate that the occurrence of binocular rivalry during their induction reduced the magnitude of subjective contour tilt aftereffects.

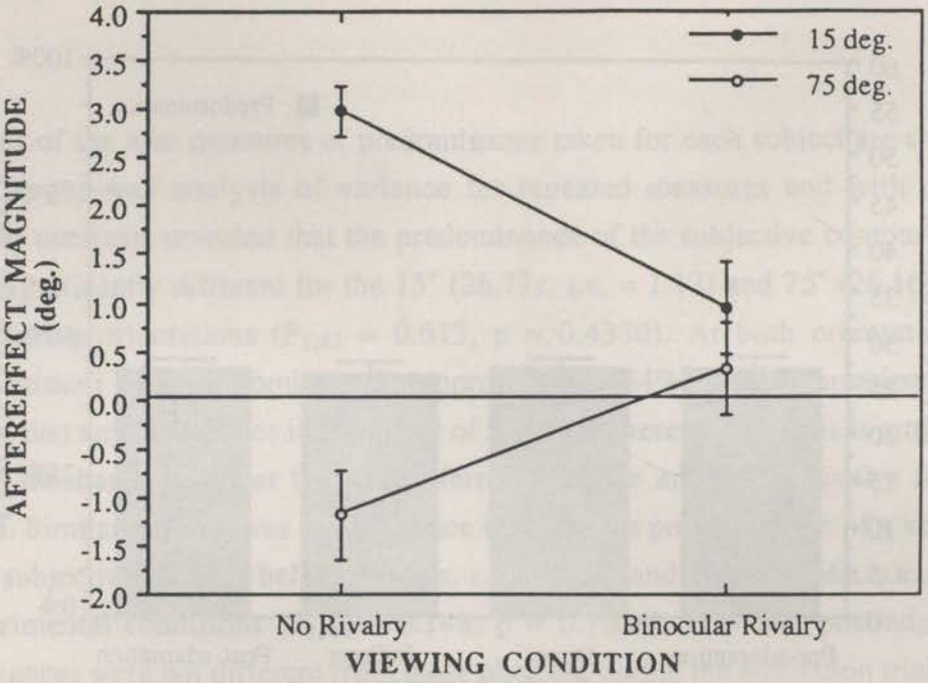


Fig. 15. The effect of binocular rivalry on purely subjective contour direct and indirect tilt aftereffects. It is clear that binocular rivalry disrupts both direct and indirect effects. These results are congruent with the explanation of rivalry offered here, and they indicate that while striate processing may not be disrupted by rivalry, extrastriate processing, even that occurring in the visual area immediately adjacent to area V1, apparently is. Bars are ± 1 standard error.

Discussion

These results indicate that orientation misperceptions induced with purely subjective contours are diminished in magnitude if periods of suppression occur during their induction. There is no suggestion this reduction is linked to a decrease in perceived salience of the inducing contour during rivalry. The data thus strongly support the suggestion that rivalry first manifests in the visual system in area V2, earlier than suggested by Logothetis and Schall (1989). At the same time, the results described are congruent with the types of neural responses to rivalry reported by those workers. There is some evidence suggesting area V2 neurones, like those in superior temporal sulcus, have little ocular dominance (eg. DeYoe and Van Essen 1985, Hubel and Livingstone 1987). If binocular neurones in area V2 behave similarly to those described by Logothetis and Schall (1989), then one possible account of these results can be developed as follows: Under normal (non-rivalrous) conditions, the subjective contour tilt aftereffects are mediated by all neurones tuned for the orientation of the subjective contour, with sensitivity dependent upon whether the stimulus is presented monocularly or binocularly. During rivalry, however, the populations adapting to the subjective contour stimulus change. Neurones that show no change in their tuning characteristics will adapt throughout the induction period (analogous to Logothetis and Schall's Class 3 cells), as will any neurones whose tuning characteristics may be altered by rivalry such that they prefer the orientation of the subjective contour under rivalrous conditions (analogous to Class 2 and some Class 5 cells). These neurones together will ensure that after rivalrous induction some aftereffect is still observable. The other classes of neurones show modulation of output in response to changes in predominance, and will not adapt at the same rate (analogous to Class 4 and some class 5 cells). Reduction in aftereffect size can be attributed to these neurones. Perhaps the subjective contour indirect effects in this experiment were eliminated rather than merely reduced because the residual effect was simply too small to be observed: von der Heydt and Peterhans found only 15% of area V2 cells responded exclusively to purely subjective contours, and a proportional reduction in adaptation of only some of these may be sufficient to apparently eliminate the effect in this experiment. As well as, or more correctly in addition to, changes to the tuning characteristics of neurones, changes to the patterns of inhibition in the cortex will also accompany rivalrous stimulation. The nature of these changes will be dependent upon the activity of the neurones responding to the stimuli, and as just outlined, this can be considered complex. In general it is probable that rivalrous stimuli will elicit more inhibition, in absolute terms, across the visual cortex, simply because there is more information, or proportionally more because facilitation accompanying binocular viewing is not occurring. It must be noted, however, that there is no strong and direct evidence provided by this experiment for the role of inhibition in rivalry. The actual reduction of the aftereffect magnitude points to some role for inhibition, but these data provide no means to evaluate it. Clearly such an analysis is speculative and only one of several that might be developed, but it does agree with known neural characteristics and suggests that, like direction of motion selective cells in superior temporal sulcus, orientation tuned subjective contour cells in area V2 may show differential characteristics during binocular rivalry. Validation of these hypotheses requires empirical, and probably neurophysiological investigation. Some preliminary investigations of interactions involving inhibition will described shortly. Before that, the findings of the present experiment need to be clarified.

The results indicate that any aftereffects attributable almost exclusively to extrastriate processes may be affected by rivalry occurring during their induction. Given that real contour indirect effects may arise via extrastriate processing (Wenderoth & Johnstone, 1987, 1988, Wenderoth et al., 1993), they too can be expected to be smaller in magnitude if rivalry occurs during their induction. The question is whether they will be eliminated like their subjective contour counterparts, or merely reduced. If the latter is the case, that the previous experiment had insufficient power to detect a small purely subjective contour indirect effect, increasing the population of cells contributing to the indirect effect by using real contours provides a first test of the explanation developed above. That is, real contour indirect effects should be reduced but not eliminated by periods of rivalry during their induction. With this in mind Experiment Six was designed to re-evaluate the work of Wade and Wenderoth (1978) who reported no effect of rivalry on the magnitude of the tilt aftereffect but who used orientation differences of only 10°, limiting their conclusions to direct effects only.

EXPERIMENT SIX

The stimuli and methods used in these experiments are quite different form those used previously (eg. Wade and Wenderoth 1978), and it is not clear whether the results of the last experiment can be attributed only to the rivalry mechanism. There is a possibility that some methodological factor may account for the impact of rivalry on the subjective contour aftereffects. This is one reason for requiring a control for the previous experiment. A second is the differences in the mechanisms of the direct and indirect effects already highlighted, and the predicted impact of rivalry on real contour indirect effects noted above. The aim of Experiment 6 was to re-examine the effect of binocular rivalry on real contour tilt aftereffects, taking into account differences in the proposed mechanisms for direct and indirect effects. In this way, this experiment acts as a control for the previous experiment, and also examines the hypothesis that indirect tilt aftereffects, whether induced using real or subjective contours, will exhibit sensitivity to periods of rivalry during their induction. It is predicted that direct effects, which have previously been examined (Wade & Wenderoth 1978), will be unaffected by rivalry during induction of the aftereffect. The magnitude of real contour indirect effects should be reduced, however, because their hypothesised extrastriate locus makes them susceptible to binocular rivalry.

There is one complication that must be noted. Recall that real contour direct effects, and probably subjective contour direct effects, mayalso have an extrastriate component. It follows from the predictions just made that some reduction in this component of the direct effect should be expected also, and thus some reduction in the direct effect observed. However, the predicted outcome of this experiment is merely a proportional reduction, not an elimination of effects arising from extrastriate processes. A proportionate reduction in an already proportionally small effect will in the first instance be hard to observe. Wenderoth and Johnstone (1988) allude to the effect being up to perhaps 0.5° of the total direct effect. As the power calculations in Appendix Three highlight, it is doubtful whether a 50% reduction in such a small effect would be observable using this protocol. Further, Berkley, et al. (1994) reported that interactions between real contours and those defined solely by 'higher-order' processes depend upon the perceptual salience of the contours being used. One of their findings was that such interactions are psychophysically strongest when the test contour is reduced in perceptual salience with respect to the inducing contour. While it is not clear what exactly those workers mean by 'perceptual salience', it appears to be something like subjective contrast. That is, higher order interactions can be observed most readily when differences are introduced between the channels processing the adapting stimulus and the channels processing the test stimulus. This explanation agrees with the results of both Wenderoth and Johnstone (1988) and Paradiso, et al. (1989). It might be argued that rivalry is in some way equivalent to adding noise to the adapting stimulus, noise which is not present during the test. That is, rivalry might be similar to reducing the subjective contrast of the adapting stimulus with respect to the test stimulus (which is never presented under rivalrous conditions). Under such conditions, Berkley, et al. (1994) had difficulty in detecting any higher order effects. So while there may indeed be an extrastriate or higher-order component to the direct tilt aftereffect generated in this experiment, it is unlikely any reduction it suffers because of rivalry will be observed.

Methods

Subjects: All subjects (n = 15) were naive, and taken from the same population as those in Experiment Five. All had normal or corrected vision.

Apparatus: This was as described for the previous experiment, except for a change to the inducing and test stimuli. These differed only in that the line of discontinuity of the inducing elements, which previously defined the subjective contour, was joined by a real contour over the same extent. The test stimulus is illustrated in Fig. 16.

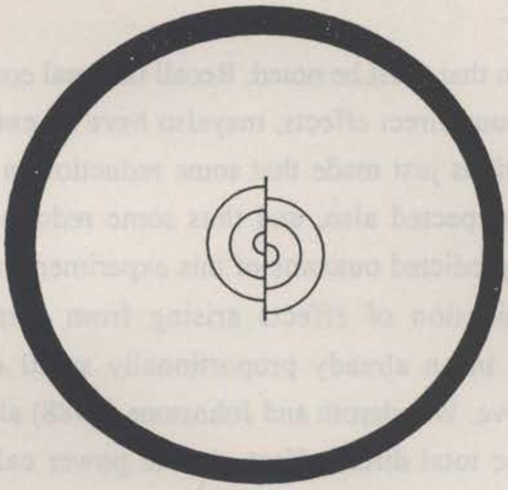


Fig. 16 The test stimulus (illustrated here), and the inducing stimulus used in this experiment were constructed exactly as the previous stimuli had been, except that the subjective contour was replaced by a real contour. That is, one defined by luminance edges.

Procedure: All procedures and conditions (Table 6. 1.) were as for Experiment Five. The same conditions were tested, with the real contour replacing the subjective contour used in the previous experiment. Subjects were instructed that they were required to judge the orientation of the real contour presented in the test as being tilted either left or right of vertical. No subjects had difficulty with this task. No measure of the salience of the real contour was made during the experiment.

Table 6. 1. Conditions examining real contour tilt aftereffects and rivalry.

Adapting Orientation	15°	15°	75°	75°
Adapting Condition	No Rivalry	Binocular Rivalry	No Rivalry	Binocular Rivalry

Results:

Just as for Experiment One, there was no difference between the predominance of the inducing stimuli before (31.78s, s.e. = 0.94) and after (31.53s, s.e. = 1.01) the experiment ($F_{1,42} = 0.56$, $p = 0.8139$). Similarly, there was no difference in predominance between the direct (30.52s, s.e. = 1.05) and indirect (30.10s, s.e. = 0.34) adapting conditions ($F_{1,42} = 0.15$, $p = 0.6980$). Finally, there was no difference between the predominance of the inducing stimuli during the adaptation trials and the inducing stimuli pre- and post-adaptation trials ($F_{1,42} = 3.04$, $p = 0.0888$). These results are illustrated in Fig. 17.

The real contour inducing stimuli were, on average, predominant for approximately 51% of the adaptation period compared with 44% in the last experiment. It has been argued previously that predominance during rivalry depends upon the 'energy' of each field (Levelt 1968, Sagawa 1981), contrast and luminance for example. The rivalrous stimulus was equivalent in both this experiment and in Experiment Five but the real contour adapting stimulus, with the extra real contour, can be thought of as actually containing more information (particularly at the orientation of the real contour), or more 'energy' (Levelt 1968), than the subjective contour stimulus, even if marginally so because there was only a single extra contour. Nevertheless, it should be expected that the time for which the adapting stimulus was predominant would be greater for this experiment than for Experiment Five. By treating the predominances of the two experiments as if they were from a single study, a t-test for independent groups revealed that this was in fact the case ($t_6 = -9.90$, $p \leq 0.0001$).

Means and standard errors of the real contour aftereffects are shown in Fig. 18. The magnitudes of the direct effects (no rivalry: 2.011°, s.e. = 0.229, rivalry: 1.911°, s.e. = 0.182) and indirect effects (no rivalry: -1.022°, s.e. = 0.176, rivalry: -0.455°, s.e. = 0.166) were significantly different from each other ($F_{1,14} = 142.082$, $p \leq 0.0001$). Just as for the subjective contour effects, the main effect of viewing condition (no rivalry vs. rivalry) was not significant ($F_{1,14} = 2.228$, $p = 0.1577$). Inspection of Fig. 18. shows that the real contour direct effects were not diminished in magnitude by rivalry, as reported by Wade and Wenderoth (1978). In contrast, real contour indirect effects, unlike their direct equivalents, were diminished by rivalry, and this is highlighted by the significant interaction between orientation and viewing condition ($F_{1,14} = 7.352$, $p = 0.0169$). Importantly, the indirect effect reduced by binocular rivalry was different from zero ($t_{14} = -2.74$, $p = 0.008$), which suggests that unlike the data for subjective contour indirect effects, binocular rivalry merely reduces, rather than eliminates, real contour indirect effects. All other real contour aftereffects were significantly different from zero (15°, no riv.: $t_{14} = 8.774$, $p \leq 0.0001$, 15°, riv.: $t_{14} = 10.501$, $p \leq 0.0001$, 75°, no riv.: $t_{14} = -5.812$, $p \leq 0.0098$). These data support the hypothesis that real contour direct aftereffects show no reduction in magnitude in response to binocular rivalry during their induction, while real contour indirect aftereffects, congruent with their supposed extrastriate locus, are disrupted.

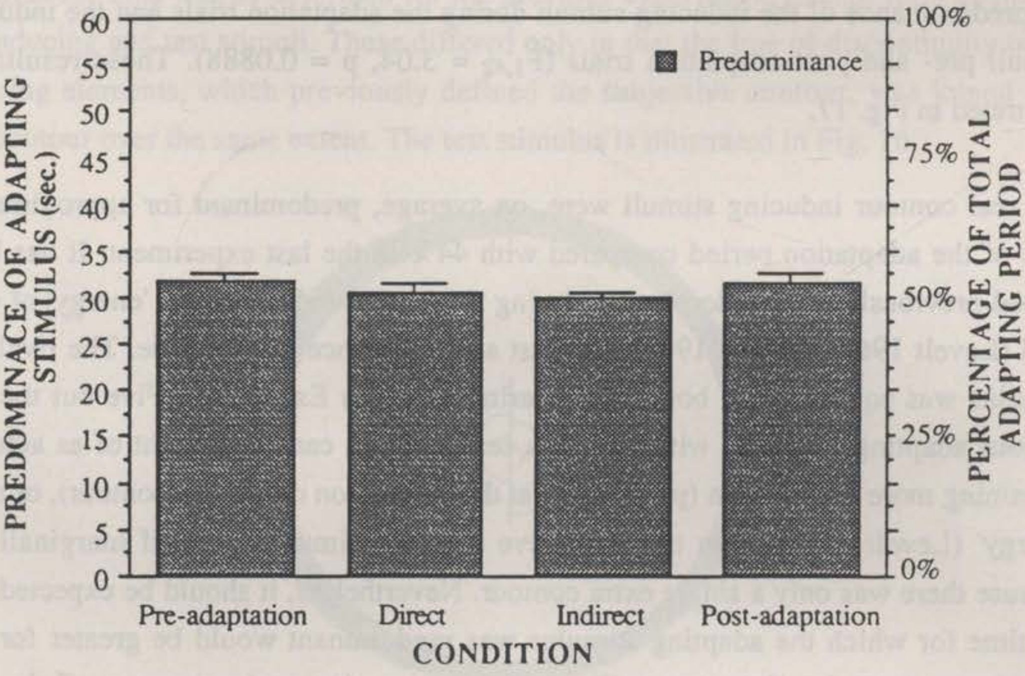


Fig. 17. The mean predominances of the adapting stimulus (in seconds and as a percentage of adaptation period) during induction of the aftereffects, and also prior to the commencement of and after the completion of the experimental conditions examined here. As for the previous experiment, no differences between these were observed, indicating relatively constant rates of rivalry throughout the experiment. Bars are 1 standard error.

Discussion

The results from Experiment Six demonstrate that previous reports suggesting real contour tilt aftereffects are unaffected by rivalry apply only to direct effects. Indirect effects, like other aftereffects believed to be attributable to extrastriate processes, do show a reduction in magnitude in response to periodic suppression during their induction. The data indicate also that the apparent elimination of the purely subjective contour indirect effect in Experiment Five might reflect a failure to discriminate a reduction rather than an eradication (Appendix Three). Generally, however, the indirect tilt aftereffect may now be included with purely subjective contour orientation aftereffects and spiral motion aftereffects as those which show modulation in response to periods of rivalrous suppression during their induction. Of the aftereffects known to be disrupted by rivalry, all are believed to arise in extrastriate cortex and in regions of strong binocularity. The spiral motion aftereffect has been ascribed to mechanisms in area MT and beyond, subjective contour effects have been ascribed to area V2, while the cortical locale of the indirect tilt aftereffect is undetermined but probably extrastriate (Wenderoth and Johnstone 1988, Wenderoth, et al. 1993). Clearly the impact of rivalry is not limited to motion processes (as may have been suggested by its effect on spiral aftereffects), although whether binocular rivalry is a product of just the magnocellular pathway, or both magno- and parvo-cellular pathways is yet to be conclusively determined.

Given these conditions, it is proposed that rivalry in response to dissimilar dichoptic inputs is the perceptual consequence of processing which arises through interactions between binocular neurones rather than involving interactions between monocular neurones (eg. Blake 1989, Mueller and Blake 1989). In normal circumstances binocular cells in extrastriate cortex, area V2 for example, receive similar inputs from both eyes, so all the cells tuned for the characteristics of the presented stimulus will respond and are also those which underlie perception. When the input from the two eyes is dissimilar, binocular neurones are still activated, by definition. However, as different stimulus characteristics are present in each visual field, binocular neurones will have dissimilar input to their receptive fields. This may cause no change in their activity, they may be less strongly and/or less frequently activated, or as suggested by the results of Logothetis and Schall (1989), may change their tuning characteristics altogether.

The outcome of this will be that under rivalrous conditions populations of neurones responding to the input will be different from the populations responding otherwise, and will be responding differently. More importantly, both the population of most active neurones and their responses will change over time. For any given pair of corresponding retinal locations, different neurones with different tuning characteristics

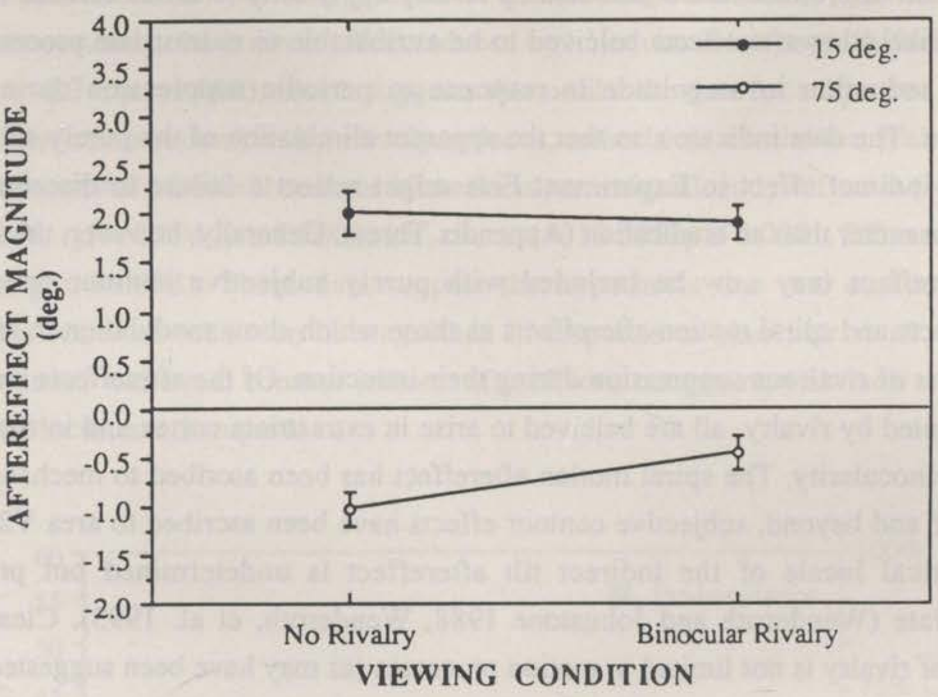


Fig. 18 The effect of binocular rivalry on real contour direct and indirect effects. As reported by Wade and Wenderoth (1978), rivalry has no impact on tilt aftereffects induced by luminance contours at smaller orientations. That is, direct effects are not affected by rivalry during their adaptation. The conclusion can be no more general than that however, as the equivalent indirect effect is disrupted by rivalry. This pattern is consistent with extrastriate processes, but not striate processes, being affected by the interactions giving rise to the perception of rivalry. Bars are ± 1 standard error.

will be stimulated. The strength of this response will be proportional to the strength of the input, the strength of the connection to that eye, the activity of other neurones and perhaps any inhibitory signals from other (differently tuned) neurones (Reinis et al., 1988). In this way each stimulus will excite a population of binocular neurones with specific (although not necessarily fixed) tuning characteristics and this 'double' population will be different from the population stimulated during normal non-rivalrous viewing because for many retinal locations, two different sets of features will coincide. If perception is correlated with the most active neurones it is not difficult to understand how the perceptual experience of rivalry arises. At each specific location a number of different neurones with overlapping receptive fields will respond uniquely. The pattern of rivalry, the alternating periods of suppression and predominance, reflects the changing response characteristics of the different groups of neurones responding to the two inputs. The pattern of predominance, or suppression, will change with time, just as the firing rate of individual neurones changes through excitation, fatigue, or inhibition . As the response (ie. firing rate) of one population of neurones, at one location and tuned for the characteristics of one stimulus, decreases relative to the response of the population of neurones with similarly located receptive fields but tuned for the characteristics of the other stimulus, so the likelihood of that group of neurones being 'suppressed' increases. The general trend of the observed rivalry will be constant for a given pair of rivalrous stimuli. However, since this is determined by the effect of the stimuli on the visual cortical neurones, the precise pattern of rivalry will depend also on the initial state of the neurones, and any scanning of the stimuli that occurs (because this will change the receptive fields responding at each location).

Viewed in this way rivalry arises through the normal operation of binocular neurones in response to abnormal input: no special apparatus is required, nor is it necessary to predict feedforward or feedback connections. It suggests that any model of the visual system that might be used to explain rivalry will require, at the very least, different sets of binocular units, each set with different tuning characteristics but with similarly located receptive fields. Conversely, rivalry might be used as a test of any system purporting to model the visual cortex.

As to the location of the interactions giving rise to rivalry, while the data described thus far suggest area V2 as the first location for rivalry generating processes, such processing may occur wherever populations of binocular neurones are located in the visual cortex. That is, there may be no specific, single site of rivalry. It may be, as the model suggests, a binocular phenomenon. If so, the suggestion by Logothetis and Schall (1989), that rivalry arises in superior temporal sulcus, may be in a certain sense true, at least for moving stimuli. Clearly, as area MT is predominantly binocular, neurones in that area may be subject to the interactions described here. This will be examined later. There is one constraint which must be applied to this conclusion however, and it depends upon the nature of interconnections between different cortical areas. Area V2 has reciprocal projections to area MT (van Essen et al., 1992) and if the stimulus features destined for perception are determined by responses in area V2, then behaviours of binocular area MT neurones might reflect changes in the processes operating in area V2. If this is the case, then rather than mediating rivalry *per se*, the activity of neurones in the superior temporal sulcus might reflect earlier strategies which are primarily responsible for the perceptual consequence of dissimilar dichoptic input. The reciprocity of the connections between these areas provides for the converse argument to be similarly valid, although it is difficult to speculate until the behaviour of area V2 neurones during rivalry has been definitively studied. That changes in response characteristics during rivalry should be expected in area V2 neurones is indicated by the reduction of the subjective contour aftereffects reported here.

EXPERIMENT SEVEN

The results of the foregoing experiments indicate that orientation aftereffects hypothetically attributable to area V2 mechanisms are disrupted by periods of binocular rivalry during their induction, and they suggest that the perception of rivalry arises via interactions and processes occurring first in area V2. These conclusions are based on the assumption that purely subjective contours of the type applied in these studies are first encoded in area V2. This does not imply that the stimuli used excite no area V1 neurones: the inducing elements are, after all, real lines. Instead it should be interpreted as meaning that, on the evidence currently available, it is probable that the subjective contour effects described cannot be attributed to processes in area V1. If tuning for subjective contours is one characteristic of area V2 neurones, a second is that almost all cells in area V2 are binocular, and what little ocular dominance has been observed is limited (DeYoe and Van Essen 1985, Burkhalter and Van Essen 1986, Hubel and Livingstone 1987). No anatomical ocular dominance architecture has been found (Tootell and Hamilton 1989). In line with the proposed model, it is therefore possible that the effects reported so far illustrate not an exclusively extrastriate effect, but a binocular effect. A more definitive psychophysical test of this hypothesis can be made by manipulations which isolate binocular cells. The general aim of this experiment was to test the notion that only binocular interactions in area V2 are needed to account for the interaction between rivalry and subjective contour tilt aftereffects, and thus to prove that such interactions implicate the substrate of rivalry to be interactions between binocular rather than monocular neurones.

The following discussion can be simplified by making a number of points before beginning. The first of these is that unless otherwise stated, the arguments made here assume that binocular rivalry does arise via the types of interactions described by the binocular model. Some of the following discussion considers the possibility of monocularly mediated rivalry, and where this is necessary the types of processes described by the model remain valid while the hardware would need to be re-thought. Secondly, the analysis assumes that perceived aftereffects are related to activity in populations of cells, and that aftereffect magnitudes are proportional to the ratio calculated by dividing the activity of all adapted cells tested psychophysically by the activity of all the cells tested. Of course the absolute magnitude of any aftereffect will depend also on the amount of adaptation exhibited by the cells involved. Finally, the methodology to be used in this experiment involves measuring aftereffects in adapted and unadapted eyes. While this does not bear directly on the underlying theories, predictions arising from these manipulations do. In the following analysis it is assumed that all adaptation occurs monocularly, and if the aftereffect is measured in the adapted eye this is 'monocular' testing. If the aftereffect is measured in the unadapted eye, it is measured 'interocularly'.

The decrement in aftereffect magnitude observed after adaptation with rivalry has been explained by the increased levels of inhibition within a binocular array in response to non-congruent dichoptic input, and by the concomitant decrement in excitation experienced by individual cells during rivalry relative to the levels of excitation experienced during periods in which congruent (ie. binocular) stimuli are input. Further, changes to tuning characteristics may be linked also to the processes of binocular rivalry. Basically the assertion is that after adaptation, cells tuned for the adapting stimulus are adapted less after rivalry than if rivalry does not occur. By considering the neurophysiological characteristics of area V2 cells some predictions are possible concerning the relative magnitudes of various aftereffects induced with and without rivalry. Assume that area V2 cells do exhibit some variation in their ocular dominance (Hubel and Livingstone 1987), but that most fall into categories 3, 4, and 5 of the Hubel and Wiesel system (Burkhalter and Van Essen 1986). Assume also that after one minute of monocular adaptation without rivalry these binocular cells are all more or less equally adapted. Any differential in the rate of adaptation caused by differences in ocular dominance has effectively been eliminated because cells are maximally adapted. The most simple prediction that can be made under these circumstances is that subjective contour tilt aftereffects induced without rivalry would transfer almost completely interocularly because they are mediated solely by binocular neurones. For example, if the left eye adapted to the tilted subjective contour, the magnitudes of the subsequent aftereffects would be observed to be equal whether measured monocularly (in the adapted eye) or via interocular transfer (in the contra-lateral eye). This was as observed by Paradiso, et al. (1989). Contrast this subjective contour prediction to that arising for real contour tilt aftereffects, or more correctly, real contour *direct* aftereffects. These have been shown to be reduced in magnitude by interocular transfer, and this reduction has been attributed to the significant monocular cell populations (categories 1 and 7) in area V1 (eg. Ware and Mitchell 1974). Similar results may be observed using subjective contours, but only if cells in one category, for example category 5, are adapted less than those in another, say 3, and these differences are demonstrated by monocular and interocular testing.

If subjective contour tilt aftereffects are just binocular (ie. have no monocular component) binocular cells are implicated in the process of rivalry, as the binocular model predicts. Predictions are now possible about aftereffects induced during rivalry. Monocular testing following rivalry has already been shown to reduce the magnitude of the subjective contour tilt aftereffect, and as just mentioned, this has been attributed to less adaptation of cells tuned for the adapting stimulus. Binocular cells are known to exhibit different ocular dominances, so consider more fully how rivalry affects these cells. One minute of adaptation without rivalry may induce more or less equal amounts of adaptation in all binocular cells in categories 3, 4, and 5. If this is not so, if one category is adapted less than the others, aftereffects measured interocularly will be smaller than those measured monocularly, and the assumption here is that this will not be the case. Because rivalry reduces the amount of adaptation in cells, after rivalry equal adaptation in cells with different ocular dominances is unlikely. Cells are no longer maximally adapted, or even nearly so. If the impact of rivalry is more or less even across all binocular cells, then after rivalry the cells that are most adapted should be those most strongly driven by the eye receiving the adapting stimulus and cells more strongly driven by the unadapted eye should now be less adapted. For example, if cells driven more strongly by the left eye are category 3 cells, and cells driven by the right eye are category 5, then after left eye adaptation with rivalry the most adapted cells would be those in category 3 and the least adapted would be those in category 5. The interesting question is what happens to the magnitude of the aftereffect in this situation if it is measured interocularly? In this situation, while the cells most strongly adapted are those in category 3, those contributing most strongly to perception during interocular testing are those in category 5. Since category 5 cells are now less adapted than category 3 cells because of rivalry, in addition to the monocularly measured decrement in aftereffect magnitude caused by rivalry an additional decrement must be predicted. Because differences between cells in ocular dominance categories 5, 4, and 3 are small, differences in the rates of adaptation will probably be small and the additional decrement should be expected to be small. Nonetheless it should be present. If no additional decrement in the interocularly transferred aftereffect measured after rivalry is observed, it indicates either that differences in ocular dominances between area V2 neurones are trivial in terms of their perceptual and psychophysical consequences, or that the methodology used here has been unable to detect such differences. Distinguishing between these alternatives would be an empirical task.

These behaviours are based, of course, on the hypothesis that complete interocular transfer of the subjective contour tilt aftereffect will be observed in the first place. While it may be unlikely (Paradiso, et al. 1989), it is possible that complete interocular transfer of the subjective contour tilt aftereffect will not be observed, and this could occur for several reasons. As noted, differences in the ocular dominances of area V2 neurones may be large enough to be measured psychophysically as reductions in the magnitude of interocularly measured aftereffects, because these differences will lead to different rates of adaptation. If a difference is observed between monocularly and interocularly measured aftereffects this possibility must be considered. The other is that there is a monocular contribution to the aftereffect. If this is the case, interpretation becomes more complicated.

If there is a monocular contribution to the subjective contour tilt aftereffect, it will be evident only when the aftereffect is measured in the adapted eye. The magnitude of the aftereffect measured interocularly will be reduced (cells adapted and tested / cells tested). Because rivalry reduces the aftereffect measured monocularly, the mechanisms of rivalry could in this case be attributed to either monocular or binocular interactions, or both. If rivalry involves interactions between monocular neurones alone, then the reduction in aftereffect magnitude caused by rivalry can be attributed to changes in the monocular contribution only. In this situation, interocularly measured aftereffects should remain constant, whether they are induced with or without rivalry, because the cells contributing to the interocular aftereffect are not adapted monocular cells. A small reduction might be observed if adaptation was not equal across all binocular cells (because of differences in ocular dominance), and additional investigations would be required to establish that this was the case. Importantly, if this is the case, the amount by which the monocularly measured aftereffect is reduced by rivalry cannot exceed the amount by which the aftereffect induced without rivalry is reduced by interocular transfer. It is not possible for rivalry to reduce the contribution of monocular neurones more than interocular transfer.

If rivalry is a binocular process and subjective contour effects have a monocular component, then in addition to a reduction in magnitude caused by interocular transfer, rivalry plus interocular testing should further reduce the observed aftereffect magnitude for the reasons described above. That is, the subjective contour tilt aftereffect induced without rivalry will be reduced by interocular transfer because the contribution of adapted monocular cells is eliminated. If aftereffects are induced with rivalry, then on top of the reduction caused by interocular transfer, decreased adaptation of binocular cells will contribute a further reduction. In monocular testing conditions, the aftereffect induced without rivalry will be larger than that induced with rivalry, because the latter will include a decreased binocular contribution. Finally, if rivalry involves both monocular and binocular cells and subjective contour aftereffects have both binocular and monocular components, largest effects should be observed with monocular testing of aftereffects induced without rivalry. Interocular transfer will reduce the aftereffect, and rivalry will reduce it even further. Monocular testing of an aftereffect induced with rivalry will also produce a reduced effect, but this aftereffect can be smaller than an interocularly measured aftereffect induced without rivalry. It cannot be smaller than an interocularly measured aftereffect induced with rivalry.

While these predictions may be complicated, each possible combination of effects yields a specific pattern of effects, and they are simply tested. The design of this experiment combined both monocular and interocular testing of subjective contour tilt aftereffects following adaptation periods without and with rivalry, as described below (Table 7. 1). In summary, the predictions for this experiment can be described thus: If the subjective contour tilt aftereffect is a binocularly mediated effect, monocular adaptation without rivalry will produce the same sized aftereffect whether it is measured 'monocularly' (in the adapted eye) or 'interocularly' (in the unadapted eye). If it is a binocular effect and if binocular rivalry is also a binocular process, a reduction in the aftereffect measured monocularly will be observed. An additional reduction will be observed if the aftereffect is measured interocularly because rivalry reduces the amount of adaptation in binocular cells, and differential rates of adaptation attributable to differences in ocular dominances will be revealed. If there is a monocular component to the subjective contour tilt aftereffect and rivalry is also mediated by monocular neurones then no additional decrement in the magnitude of the interocularly measured effect should be observed beyond that attributable to removal of the adapted monocular cells from contributing to the aftereffect. However, monocular testing should reveal a decrement, because the monocular cells involved in rivalry will be less adapted. This decrement cannot be larger than that generated just by interocular transfer. If the subjective contour tilt aftereffect has a monocular component, but rivalry is a binocular process, then interocular testing following adaptation without rivalry will cause a decrement in aftereffect magnitude, and a further reduction will be observed following adaptation with rivalry. In this situation, monocular testing following rivalry will reveal a significantly smaller aftereffect than monocular testing following no rivalry. Finally, if rivalry involves both monocular and binocular interactions, then all aftereffects measured after rivalry will be smaller than their counterparts induced without rivalry, and the largest reduction will be that measured monocularly.

Methods

Subjects: 15 naive volunteers from the first year population were used for this experiment. None had been tested in any of the previous experiments, although several had been subjects in psychophysical experiments in other laboratories. All had normal or corrected vision.

Apparatus and Stimuli: The apparatus and stimuli used in this experiment were the same as those used for Experiment Five. The same rivalrous stimulus was used as in that experiment. Several different polaroid filters were used (see Procedure), but these were of identical construction and specifications.

Procedure: The protocol for this experiment was similar to that used in all the foregoing studies, with only a manipulation of the polaroid filters to achieve interocular transfer being a significant deviation. As with all previous experiments, the test stimulus was presented to the subject's right eye. Under conditions of interocular transfer, therefore, subjects viewed the adapting stimulus with their left eye. Subjects were also tested under monocular conditions, which means simply that adapting and test stimuli were presented to the same (right) eye. The order of the conditions was randomised for each subject, and prior to the commencement of each condition the tachistoscope was opened and the polaroid filter currently in place in front of the adapting stimulus was removed. A second polaroid, apparently identical to the first was inserted in its place. The only difference between the polaroid filters was their orientation once inserted, with the filters used for interocular transfer being orthogonal to those used for monocular adapting and testing. The two alternative orientations matched either the orientation of the filter in front of the right eye in the viewing aperture for monocular conditions, or the orientation in front of the left eye in the viewing aperture for transfer conditions. The removal and replacement procedure was carried out prior to each condition whether or not the subsequent condition required a change in orientation of the filter. As all subjects were naive observers and received no information as to the nature or the purpose of the filters and changing the filters provided no clue as to the significance of the manipulation. Only one subject noted the stimulus 'looked different' during one of the interocular transfer conditions under which she was examined. She made no similar observations during the rest of the experiment, and her data are included in the study. The filters in all other channels remained untouched throughout the experiment.

Four conditions were examined in this study using a factorial design: Two monocular conditions, one with and one without rivalry, and two interocular transfer conditions similarly with and without rivalry. This design is illustrated in Table 7. 1.

Table 7. 1. Design for interocular transfer of subjective contour tilt aftereffects.

Adapting Stimuli	Purely Subjective Contours			
Adapting Orientation	15°	15°	15°	15°
Adapting Condition	Without Rivalry	Binocular Rivalry	Without Rivalry	Binocular Rivalry
Viewing Condition	Monocular Inducing/Test	Monocular Inducing/Test	Interocular Transfer	Interocular Transfer

Only a single orientation was examined, for both methodological and theoretical reasons. As an aftereffect experiment, completion of the eight staircases, with the accompanying breaks, required subjects to spend, on average, between 50 and 55 minutes at the task. Since these were naive observers with little or no experience this was considered long enough. Casual observation in the laboratory had revealed previously that naive observers experienced increasing difficulty completing their judgements as the experimental duration extended beyond the hour. This time restriction was not seen as an important limitation to the experiment however. Little additional information to that revealed by subjective contour direct effects seemed likely from an examination of subjective contour indirect effects. As previously discussed, small changes in the magnitude of subjective contour indirect effects can be difficult to observe using the protocol described here. More importantly, as the actual neural mechanism and the cortical locus of the indirect effect is more speculative than for the direct effect, inference from the results of the manipulations described here seemed unlikely to provide significantly more information. For these reasons, only subjective contour direct effects were examined.

All other procedures were as described for Experiment Five.

Results

A one way analysis of variance for repeated measures, and with planned orthogonal contrasts, revealed that as with all previous experiments, there were no differences in the reported predominance of the adapting stimulus for any of the rivalry conditions reported here. Thus, as illustrated in Fig. 19., there was no difference between the predominance of the adapting stimulus before the experiment (28.89s, s.e. = 1.020) and after (28.37s, s.e. = 0.811) ($F_{1,42} = 0.591$, $p = 0.4464$), indicating no build-up of fatigue over the course of the experiment. Similarly, there was no difference in the predominances measured prior to monocular (28.33s, s.e. = 1.011) and interocular (29.01s, s.e. = 0.758) testing ($F_{1,42} = 1.002$, s.e. = 0.3225), suggesting that there was no difference in perceived predominance of the adapting stimulus regardless of to which eye it was presented. The final comparison, comparing test and non-test predominances, also revealed no differences ($F_{1,42} = 0.007$, $p = 0.9322$).

The aftereffect data gathered for each subject were collapsed into condition means, and a two-by-two factorial design with repeated measures was used to analyse the variance. The means and standard errors are illustrated in Fig. 20., and are summarised in Table 7. 2.

The main effect of viewing condition (no-rivalry vs. rivalry) was found to be significant ($F_{1,14} = 26.461$, $p \leq 0.0001$), indicating that rivalry reduced the aftereffect magnitude whether testing was done in the same eye as that which was adapted or in the other eye. This was as predicted. Also confirming predictions, the main effect of interocular transfer was not significant ($F_{1,14} = 1.469$, $p = 0.2455$), which suggests that there was no difference in the average aftereffect whether it was tested in the adapted eye or in the other eye. This supports the assertion that just binocular neurones are mediating the aftereffects being examined here, and is further supported by the non-significant interaction between viewing condition and eye of testing ($F_{1,14} = 1.162$, $p = 0.2992$).

Table 7. 2. Means with rivalry and interocular transfer of subjective contour direct effects.

Inducing Condition	15° Monocular No Rivalry	15° IOT. No Rivalry	15° Monocular Rivalry	15° IOT. Rivalry
Mean	2.067°	2.156°	0.644°	0.178°
Standard Error	0.388	0.568	0.312	0.247

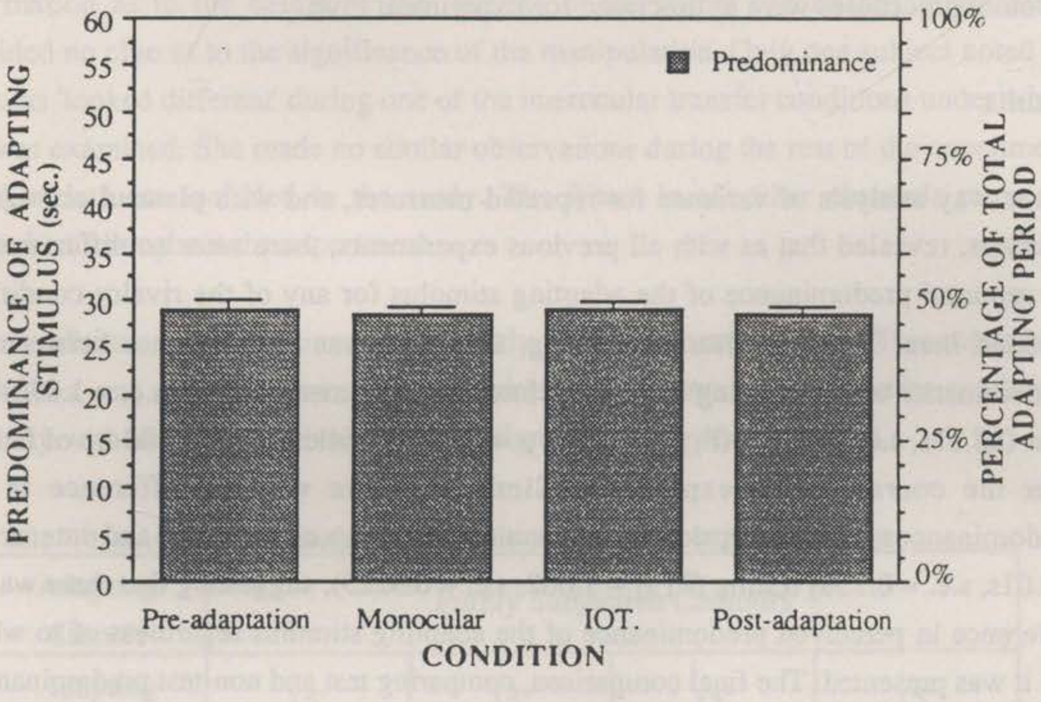


Fig. 19. Mean predominances (across subjects) for the four measures taken during this experiment. Just as for the two previous experiments, no differences were observed. Bars indicate 1 standard error.

Inspection of Fig. 20. indicates an apparent reduction in the magnitude of the aftereffect under conditions of interocular transfer and binocular rivalry, when compared to monocular testing with rivalry. While the analysis of variance has indicated this reduction is not significant, examination of the means reveals what appears to be a contradiction. All means were found individually to be significantly different from zero, when examined by one-sample t-tests, except for the rivalry and interocular transfer condition (Mon./no-riv.: $t_{14} = 5.333$, $p \leq 0.0001$, IOT./no-riv.: $t_{14} = 3.793$, $p = 0.001$, Mon./riv.: $t_{14} = 2.065$, $p = 0.0289$, IOT./riv.: $t_{14} = 0.720$, 0.2416). Thus while the analysis of variance does not indicate a significant reduction of the aftereffect magnitude for this condition, there is some reason to believe that this conclusion could in fact be a type II error. This aside, these findings generally concur with the predictions made on the basis of binocularly mediated rivalry.

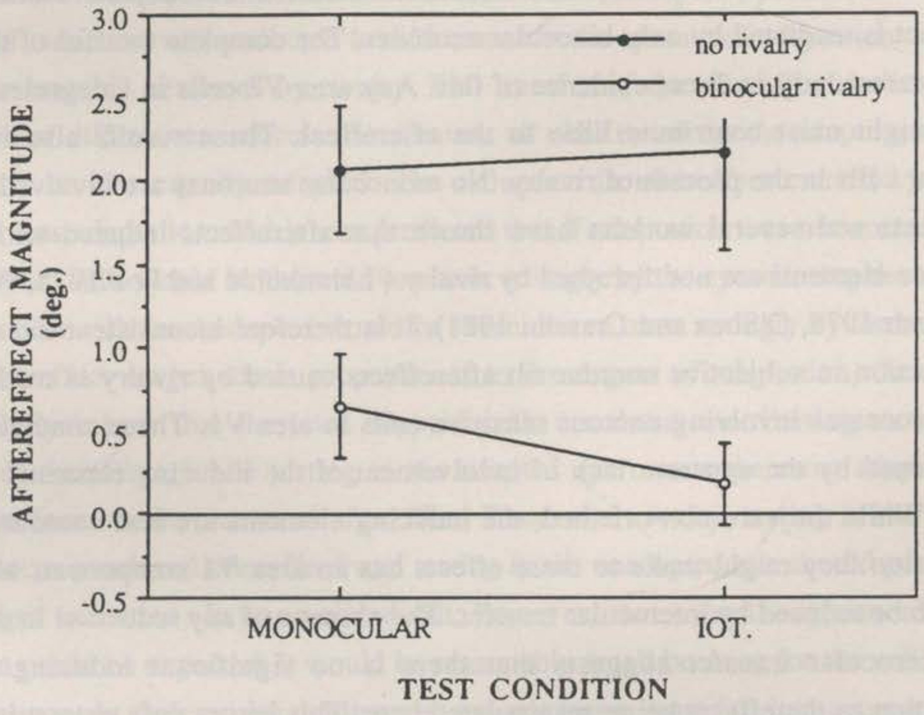


Fig. 20. Mean tilt aftereffects for the conditions examined in this experiment. Only direct effects were measured, and without rivalry or interocular transfer the subjective contour direct effect is about the same magnitude as in previous studies. Interocular transfer of the subjective contour direct effect is complete, suggesting it is binocularly mediated. The important feature to note is that while the Anova suggests no differences between the interocular transfer conditions, without rivalry the aftereffect is significantly different from zero, but with rivalry this difference disappears. Bars are ±1 standard error.

Discussion

Clearly the most intriguing aspect of these data is the ambiguity of the size of the reduction of the aftereffect magnitude that is associated with the combination of interocular transfer and binocular rivalry, compared to rivalry alone. This will be considered in a moment. First, it is useful to consider the results more generally. The rivalrous reduction of the subjective contour aftereffect observed in Experiment Five was again observed here. In that experiment, rivalry during adaptation reduced the aftereffect by approximately 68%, while here the reduction was 69%, comparable and consistent effects. In both cases, this reduction in aftereffect magnitude was achieved by a reduction in predominance of about 55%. That is, the adapting field was reported to be predominant during adaptation approximately 45% of the time in both this experiment and Experiment Five. To say more than this about the relationship between predominance and aftereffect magnitude is difficult on the basis of these data, particularly as the measures discussed are not measures of complete predominance[13].

There is little doubt, however, that these data indicate the subjective contour tilt aftereffect is mediated by only binocular neurones. The complete transfer of the direct effect interocularly is direct evidence of this. Any area V2 cells in categories 1 and 7 which might exist contribute little to the aftereffect. These results also implicate binocular cells in the process of rivalry. No monocular neurones are involved in these aftereffects and several workers have shown that aftereffects induced with simple luminance elements are not disrupted by rivalry (Lehmkuhle and Fox 1975, Wade and Wenderoth 1978, O'Shea and Crassini 1981). It is therefore inconsistent to argue that the reduction in subjective contour tilt aftereffects caused by rivalry is mediated by neural processes involving contour sensitive cells in area V1. These conclusions are strengthened by the apparent lack of involvement of the inducing elements in these effects. While they are non-oriented, the inducing elements are real contours so any contribution they might make to these effects has an area V1 component, which are known to be reduced by interocular transfer. The absence of any reduction in the effect with interocular transfer suggests that there is no significant inducing element contribution to the effects being manipulated here. This leaves only extrastriate cells, and as discussed, these are generally binocular. Interactions between subjective contour tuned cells in area V2 seem to provide the most likely and most parsimonious account for the effects reported here. So in addition to suggesting binocularly mediated rivalry, these data suggest, indirectly, that rivalry is an extrastriate process. These claims are examined more fully in Experiment Eight, and Experiments Nine and Ten provide

---

[13] All subjects were asked, informally, to describe their experience of rivalry after completing their testing. Very few reported <u>any</u> occasions where complete predominance occurred, all basing their decisions on changes in the patterns of piecemeal rivalry they were observing. This is congruent with findings previously reported (eg. Levelt 1968, Mueller and Blake 1990). Some attempt was made during these experiments to examine the correlation between predominance and aftereffect magnitude using variations of the rivalrous stimuli used in these experiments. It was originally thought that manipulating the number and/or size of the blobs of the rivalrous stimulus would be sufficient to vary predominance, which it was. However, this variation was only small and insufficient for a good estimation of correlation over a sufficiently broad range. Larger ranges could be achieved using variations in contrast but this confounds the experiment and was deemed inappropriate. This issue is addressed more thoroughly by Experiment Eleven.

additional evidence for this rationale. Digressing for a moment, it is reasonable to infer from this that the subjective contour indirect effect, more global in nature still, is also the product of binocular processes. To suggest the same for real contour indirect effects seems logically coherent, particularly in light of the results of the previous experiment, but would require empirical verification were it to be argued for more strongly.

Consider now the remaining, inconclusive, finding. Accounts involving monocular interactions can be rejected. None explain this pattern of results. In the situation where complete interocular transfer of the subjective contour aftereffect was observed, it was predicted that the effect of rivalry on the interocularly measured effect would be to further reduce it compared to the effect measured in the adapted eye after rivalry. This additional reduction was attributed to differences in the amount of adaptation caused in binocular area V2 neurones by rivalry. Full transfer of the aftereffect indicates that regardless of differences in ocular dominance, all cells tuned for the adapting stimulus were more or less equally adapted. The reduction in aftereffect caused by rivalry indicates less adaptation, and it was predicted that if adaptation was not complete, the most adapted cells would be those driven most strongly by the eye viewing the adapting stimulus. The cells least adapted would be those driven most strongly by the other eye. If the aftereffect magnitude is proportional to the degree of adaptation, then testing interocularly means that the least adapted cells are those contributing most to the measured aftereffect, while testing in the adapted eye means the most adapted cells contribute most to the measured aftereffect. Thus, after rivalry, testing in the adapted eye produces a reduced aftereffect, and testing in the unadapted eye should produce an even larger reduction. It was pointed out, however, that even though an additional reduction could be expected, it would be reasonably small because for the cells in area V2 differences in their ocular dominances are not large, most fall into categories 3, 4, and 5 (Burkhalter and Van Essen 1986). So while these results did not produce a statistically significant reduction, that reduction which was observed, and is suggested by the relative values of the means, may reflect the small differences described.

Until a more definitive demonstration is provided, however, this explanation is speculative. It remains to be seen whether the changes described can be measured using the current paradigm. One possible manipulation which could demonstrate these relations would be to use a shorter adaptation period. Under these circumstances, cells would be less adapted, just as is the case after rivalry. If the subjective contour aftereffect was measured in the adapted and unadapted eye following long and short adaptations, with no rivalry, then the pattern of results predicted would be the same as that observed here. As noted, however, there is not very much difference between the ocular dominances of cells in categories 3 - 5, so while expectation of some differences in the amount of adaptation is reasonable, it will not be large and might again yield an ambiguous result. Recall von der Heydt and Peterhans (1989) reported only 44% of cells they tested in area V2 signalled subjective contours, and while any link between these cells and the perceptions being examined here is speculative, there is no reason to expect a large effect from this small population. The other consideration to be taken into account in terms of such an experiment is that while it would provide a replication of these results, it would show conclusively only that binocular cells are mediating the subjective contour tilt aftereffect, and this experiment has already shown this to be the case. A more interesting experiment is possible; one which examines whether or not there is any monocular contribution to rivalry, and also whether or not striate cortex is involved in rivalry. Experiment Eight was designed with this in mind.

EXPERIMENT EIGHT

The previous experiment demonstrated that purely subjective contour tilt aftereffects arise in binocular neurones and have no apparent monocular component, and it suggested that rivalry is not only a binocular process, but one confined to extrastriate cortex. It is possible to examine these last claims more thoroughly. To do this it is necessary not only to include extrastriate neurones in the population being examined, but also area V1 cells, and Experiment Eight was designed to do this. The predictions of the last experiment described possible interactions between groups of neurones based on their behaviour under different testing conditions. While the interactions were complex, each possible combination of neurones and interactions between them produced a unique set of predictions. By examining the same manipulations used in the last experiment, but this time using real instead of subjective contours, a second set of predictions can be generated. Just as for the last experiment, each possible combination produces a set of unique predictions which examine the role of striate and extrastriate cortex in binocular rivalry as well as the possible contributions made to rivalry by both monocular and binocular neurones. Thus the aim of Experiment Eight was to measure the magnitude of the real contour tilt aftereffect measured in the adapted eye and interocularly following adaptation without and with rivalry. While this experiment was expected to demonstrate that rivalry is an extrastriate, binocular process, possible alternatives are discussed below.

Clearly the use of real contours recruits a population of neurones not previously included in these investigations directly. In particular, real contours are sufficient stimuli for both binocular and monocular cells in area V1, as well as for many binocular cells in area V2. In terms of the ocular dominances of real contour sensitive cells, those in area V2 can be described as falling mainly into categories 3, 4, and 5, (Burkhalter and Van Essen 1986). The situation in area V1 is somewhat different. In area V1 cells fall into all categories, with large numbers of cells in categories 1 and 7 (eg. Tootell, et al. 1988a). These cells are monocular. The results of this experiment will be determined, in part, by the role of these cells in binocular rivalry. As for the previous experiment, understanding the following discussion is simplified by a number of assumptions. First, all adaptation will again be monocular and testing aftereffects in the adapted eye will again be referred to as the monocular condition, testing in the unadapted eye will be referred to as the interocular condition. Again the analysis is based on the assumption that processing like that described by the binocular model underlies the perception of rivalry, and that the magnitude of the tilt aftereffect is proportional to the ratio of all cells both adapted and tested divided by all cells tested. On the basis of the results of Experiment Seven it is assumed that differences in ocular dominances are reflected as differences in rates of adaptation, even if these are small. Recall there is substantial evidence that processes in area V1 are not affected by rivalry. No aftereffects attributed to area V1 have been found to be reduced by rivalry during their induction (eg. Blake and Fox 1974a, Wade and Wenderoth 1978, O'Shea and Crassini 1981), and this suggests that rivalry does not occur in area V1. In particular, if rivalry arises via a process like that described by the binocular model, it suggests that the binocular cells in V1 do not contribute to rivalry. This has not been examined directly, at least in terms of orientation aftereffects, and that forms part of the aim of this experiment. Finally, the analysis will be couched in terms of cells and processes only in area V1 and area V2 simply to facilitate the discussion.

So what predictions can be made? Monocular testing following adaptation without rivalry will produce an aftereffect of some magnitude, and previous studies suggest this magnitude will be reduced if it is measured interocularly (Ware and Mitchell 1974). In terms of cells contributing to these effects, this pattern of results is explained such that when testing monocularly, all cells adapted are those that are tested. Interocular testing means that the cells both adapted and tested are just binocular cells, while all cells tested are all binocular cells, and contra-lateral (unadapted) monocular cells. This second ratio is some fraction of the first, and is observed psychophysically as a smaller aftereffect. More interesting, and more complex, are the predictions arising from monocular adaptation accompanied by binocular rivalry. If testing is done monocularly and interocularly then the possible outcomes are that rivalry will reduce the monocularly measured aftereffect but not the interocularly measured aftereffect, or it will reduce the interocularly measured aftereffect but not the monocularly measured effect, or it will reduce both, and which of these is actually observed depends on the mechanisms giving rise to rivalry. If no reductions are observed, either the methodology, or the theory, or both, will need to be carefully re-examined.

It is possible that all cells in areas V1 and V2 are involved in rivalry, and were this so the binocular model would need to be rethought. This seems unlikely, however, since it must be predicted that in this situation any aftereffect induced with binocular rivalry would be reduced in magnitude when compared to aftereffects induced when there was no rivalrous stimulus present. It is difficult to reconcile the observations that subjective contour tilt aftereffects and spiral motion aftereffects (Wiesenfelder and Blake 1990) are reduced in magnitude by rivalry during their induction, while tilt aftereffects, linear motion aftereffects and spatial frequency shift aftereffects, for example, are not, if all area V1 and area V2 cells are engaged in rivalry. Nonetheless, this is one possibility, and so it must be predicted that if this is the case there will be significant reductions in the magnitudes of aftereffects measured monocularly and interocularly if the aftereffect is induced while the adapting stimulus is in rivalry with some other stimulus.

Similarly, it seems unlikely that just monocular cells are giving rise to the perception of rivalry, even though this, in various forms, has been the previously favoured model (cf. Blake 1989). As has already been pointed out, if rivalry reduces the magnitudes of subjective contour and spiral motion aftereffects, one needs to explain how monocular cells mediate these effects. While it might be argued that subjective contour effects occur in area V2, and while this area has few monocular neurones it receives monocular input, this does not explain the impact on spiral motion aftereffects which are thought to arise in cortical regions beyond area MT (eg. Tanaka and Saito 1989). However, some complex mechanism may be in operation and so this possibility too must be considered. If rivalry involves some form of competition between monocular neurones, then adaptation with rivalry will cause monocular neurones to be less adapted than if adaptation occurs without rivalry. Now if testing is done monocularly, the less adapted monocular neurones will mean a smaller aftereffect. The magnitude of the reduction depends on what proportion of all cells contributing to the aftereffect are monocular, but since there are large numbers of monocular contour sensitive neurones in area V1, a significant reduction should be observed. The maximum possible size of this reduction equals that caused by testing interocularly. Interocular testing is equivalent to testing without any adaptation in the monocular cells. Because interocular transfer prevents adapted monocular cells from contributing to the aftereffect, if rivalry does affect monocular cells this affect will be removed by interocular transfer. Thus in this situation, rivalry combined with interocular transfer will produce the same magnitude aftereffect as interocular transfer without rivalrous adaptation.

A possibility more likely than either of the two just outlined is that binocular rivalry is a binocular process, and that it occurs between all binocular neurones. The binocular model can easily accommodate this alternative, and in fact provides no *a priori* argument against it. If this is the case, then following adaptation during rivalry all binocular cells will be less adapted than they would be following adaptation without rivalry. As described for the previous experiment, binocular cells with different ocular dominances will adapt at different rates, and if rivalry reduces the amount of adaptation in all binocular cells more or less equally, cells driven more strongly by the adapted eye will be more adapted than cells driven more strongly by the unadapted eye, and no cells will be adapted as much as they would be had rivalry not occurred. If the aftereffect is measured now in the adapted eye, that is monocularly, then all cells adapted and tested will be area V1 monocular cells for the adapted eye, area V1 binocular cells, and area V2 binocular cells. The cells tested will be the same, but if the level of adaptation in the binocular cells is reduced by rivalry, so too will the aftereffect be reduced when compared to the aftereffect measured monocularly after adaptation without rivalry. As before, the magnitude of this reduction will be proportional to the fraction of the total number of cells made up by binocular cells. A reduction beyond that normally associated with interocular transfer should also be expected. If interocular testing follows adaptation with rivalry cells adapted and tested are just area V1 binocular cells and area V2 binocular cells, while cells tested are both groups of binocular cells and monocular cells for the eye contra-lateral to the adapted eye. The normal decrement through interocular transfer occurs through the removal of the adapted monocular cells from the numerator and the addition of unadapted cells in the denominator. Added to this, however, is the reduction in the levels of adaptation exhibited by the binocular neurones. If rivalry reduces the levels of adaptation in all binocular cells, this reduction should be evident whether the aftereffect is measured monocularly or interocularly.

Finally, there is the possibility that rivalry is a binocular process, as described by the model, but that it is a process characteristic of only extrastriate neurones. That is, no area V1 neurones, monocular or binocular, contribute to rivalry. This is as suggested by the experiments reported here. The magnitudes of subjective contour tilt aftereffects are reduced by rivalry, while aftereffects attributed to area V1 are not. However, this can be tested more directly by the manipulations suggested here. If rivalry affects only extrastriate binocular cells, then adapting to a real contour during rivalry should reduce the levels of adaptation only in contour sensitive binocular cells in area V2. Remember, rivalry reduces adaptation, it does not eliminate it. No area V1 neurones will be affected by rivalry, all will be as adapted as they are after rivalry free adaptation. If testing of the aftereffect, following rivalry, is done in the adapted eye, the cells adapted and tested will be adapted monocular cells in area V1, adapted binocular cells in area V1, and the less than usually adapted binocular cells in area V2. The last group will contribute less to the effect than they would do without rivalry. The cells tested are the same. The impact on the magnitude of the aftereffect by the reduced adaptation of the area V2 binocular cells will be proportional to the size of the reduction in adaptation and to their contribution to the overall effect. Because most cells contributing to the aftereffect have not been affected by rivalry, and because the impact of rivalry on those cells it is affecting is limited, it seems reasonable to suggest that the effect of rivalry in this instance will be small. In terms of levels of adaptation, the area V2 binocular cells most adapted will be those driven most strongly by the adapted eye, while those affected least will be those contributing least to the measured aftereffect. Thus if rivalry is just an extrastriate process, a small, even negligible, reduction in the monocularly measured aftereffect can be predicted, but the size of this reduction will be limited. If the aftereffect is measured interocularly, then cells adapted and tested include only area V1 binocular cells, which will not be affected by rivalry, and area V2 binocular cells which will be affected. Cells tested include both these groups and unadapted contra-lateral area V1 monocular cells. Differences between ipsi- and contra-lateral monocular cells can account for some interocular transfer effect, but now the proportion of area V2 cells contributing to the measured aftereffect is larger than with monocular testing. In terms of the total number of adapted cells contributing to the aftereffect, fewer cells are unaffected by rivalry, and so the reduced adaptation in those cells which are affected is now proportionally more important in terms of their contribution to the aftereffect. This suggests that while the normal reduction in aftereffect magnitude associated with interocular transfer should be observed, an additional reduction caused by the reduced adaptation of the binocular area V2 cells should also be evident. This reduction, however, can be expected to be larger than for the monocular case.

In summary, these predictions indicate that if any area V1 cells are involved in rivalry this should be reflected in a reduction in the magnitude of aftereffects measured in the adapted eye. If rivalry is a monocular process, the rivalry induced reduction will not be carried over into interocularly measured effects. If rivalry is just a binocular process, significant reductions should be observed in aftereffects measured both monocularly and binocularly, and if rivalry is just an extrastriate process a larger rivalry induced reduction should be evident in effects measured interocularly than in effects measured monocularly.

Methods

Subjects: 15 students from the same population as the previous experiment were used in this study. None had taken part in any of the previous experiments and all were naive.

Table 8. 1. Design for interocular transfer of real contour direct tilt aftereffects.

Adapting Stimuli	Real Contours			
Adapting Orientation	15°	15°	15°	15°
Adapting Condition	Without Rivalry	Binocular Rivalry	Without Rivalry	Binocular Rivalry
Viewing Condition	Monocular Inducing/Test	Monocular Inducing/Test	Interocular Transfer	Interocular Transfer

Apparatus and Stimuli: The apparatus used in this investigation was as described for the previous study. The stimuli differed only in that the subjective contour was replaced in the adapting and test fields by a real contour in exactly the same position. Thus, the stimuli used here were equivalent to those applied in Experiment Six.

Procedure: The procedures for this experiment were identical to those used for Experiment Seven.

The conditions examined were similar also, and these are described in Table 8. 1. Again a two-by-two factorial design was applied, and as for the subjective contours in the previous experiment, only direct tilt aftereffects were examined, but using real contours here.

Results

As with all previous experiments involving rivalry, four measures of adapting stimulus predominance were made, under the same conditions outlined for Experiment Five. Just as for all previous experiments there were no differences between the measures made on any of the four conditions, as can be seen in Fig. 21. A one-way analysis of variance for repeated measures and with planned orthogonal contrasts proved this to be the case, and is summarised in Table 8. 1.

Table 8. 1. One-way Anova, with planned contrasts, examining predominance.

Source	SS	df	MS	F	probability
Subject	447.650	14	31.975		
Pre. vs. Post Non-adapt.	2.546	1	2.546	0.980	0.3279
Monocular vs. IOT	1.374	1	1.374	0.529	0.4712
Adapting vs. Non-adapt.	2.513	1	2.513	0.967	0.3311
Error	109.158	42	2.599		

As was the case in Experiment Six, the real contours used here were predominant for approximately 50% of the adapting period (means and standard errors are summarised in Appendix Two; Experiment Eight). Interestingly, the predominances of the subjective contours, which were around 45% under equivalent conditions in Experiment Five increased to approximately 48% here.

The mean aftereffects for the four conditions examined are depicted in Fig. 22. The real contour direct effect induced and tested monocularly without rivalry was 2.300° (s.e. = 0.284), comparable with the similar condition in Experiment Six (2.011°). This was reduced to 1.535° (s.e. = 0.162) by interocular transfer, a reduction of approximately 43%. This is consistent with previous studies. In contrast, rivalry during adaptation caused only a small, non-significant reduction in the magnitude of the real contour aftereffect, which was 2.144° (s.e. = 0.264). While not much can be made of this, it is not inconsistent with the hypothesis that rivalry affects only extrastriate binocular neurones. Interocular testing following rivalrous adaptation reduced the aftereffect to just 0.823° (s.e. = 0.215). This reduction represents a 65% reduction from the magnitude of the aftereffect observed with monocular testing and no rivalry, a 62% reduction from monocular testing with rivalry, and a 47% reduction from the magnitude observed using interocular testing following a non-rivalrous induction.

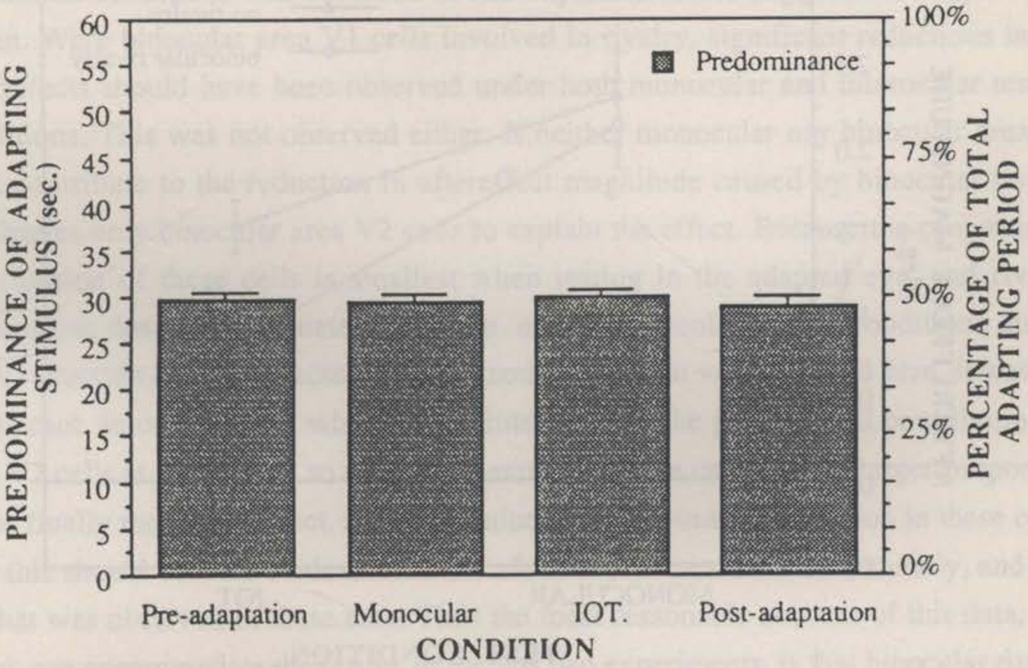


Fig. 21. Mean predominances, and their standard errors, for the real contours used in this experiment.

A two-way, factorial analysis of variance for repeated measures was used to examine these data and this revealed that the main effect of adapting condition (no-rivalry vs. rivalry) was significant ($F_{1,14} = 15.029$, $p = 0.0017$), indicating rivalry, on average, reduced the magnitude of the aftereffects. Similarly, testing condition (monocular vs. IOT) was significant ($F_{1,14} = 19.529$, $p = 0.0006$), which means interocular transfer reduced the average effect when compared to monocular adapting and testing. Finally, the interaction between these was significant also ($F_{1,14} = 5.113$, $p = 0.0402$). This suggests that interocular transfer after rivalrous induction significantly reduced the magnitude of the real contour direct effect when compared to the effect measured interocularly following non-rivalrous adaptation. This suggests that rivalry is mediated by binocular, but not monocular neurones. That no significant reduction in magnitude was observed under monocular testing conditions is evidence against the involvement of area V1 neurones in rivalry while conversely, it supports the argument for extrastriate binocular neurones mediating binocular rivalry. Importantly, in the context of the rationale for conducting this experiment, independent t-tests revealed that all effects were significantly different from zero (Mon/no-riv.: $t_{14} = 8.091$, $p \leq 0.0001$, IOT/no-riv.: $t_{14} = 9.473$, $p \leq 0.0001$, Mon/riv.: $t_{14} = 8.128$, $p \leq 0.0001$, IOT/riv.: $t_{14} = 3.82$, $p = 0.0009$). That is, none of the manipulations conducted here was sufficient to eliminate any of these effects completely.

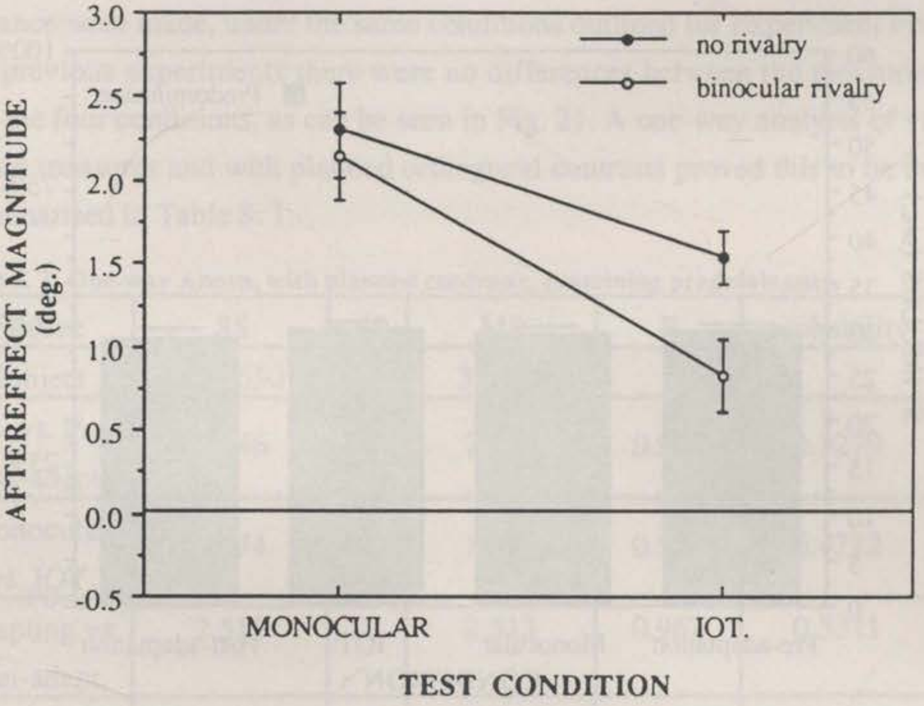


Fig. 22. Means and standard errors for the real contour aftereffects under conditions of binocular rivalry and interocular transfer. While rivalry does not reduce monocularly tested aftereffects it does reduce interocularly tested effects. This is evidence for binocularly mediated binocular rivalry, and may suggest that rivalry does manifest in area V1, but that it is difficult to observe because of the strong monocular component of any area V1 effect.

In summary, these results together provide evidence that binocular rivalry is mediated by binocular neurones in extrastriate cortex.

Discussion

These data confirm the prediction that rivalry is mediated by binocular neurones, a prediction made on the basis of the effect rivalry has on extrastriate processing. They suggest also that rivalry can be thought of as an exclusively extrastriate phenomenon, the incorporation of interactions between binocular cells in area V1 into the model being not supported. If rivalry arises from the types of interactions predicted by the binocular model, and were any area V1 neurones (monocular or binocular) involved in rivalry, smaller aftereffects should have been measured in the monocular test condition following adaptation with rivalry than were measured in the adapted eye following adaptation without rivalry. This was not the case. Other findings support this conclusion. Monocular cells are a characteristic of area V1. If monocular cells were those involved in rivalry, not only should a reduction be seen when comparing monocular test conditions but no reduction should be observed when comparing interocular transfer testing conditions. However, a significant difference in the interocular conditions was observed in this experiment, and suggested in Experiment Seven. Were binocular area V1 cells involved in rivalry, significant reductions in the aftereffects should have been observed under both monocular and interocular testing conditions. This was not observed either. If neither monocular nor binocular area V1 cells contribute to the reduction in aftereffect magnitude caused by binocular rivalry this leaves only binocular area V2 cells to explain the effect. Because the proportional contribution of these cells is smallest when testing in the adapted eye, and rivalry reduces but does not eliminate adaptation, under monocular testing conditions only a small reduction can be expected. While a small reduction was observed here, it was not significant. In comparison, when testing interocularly the proportional contribution of area V2 cells is larger, and so effects generated by these cells form a larger proportion of the finally measured effect. If rivalry reduces the amount of adaptation in these cells, then this should become evident when the aftereffect is measured interocularly, and that is what was observed in these data. Thus the most reasonable account of this data, one which can accommodate the results of the last two experiments, is that binocular rivalry is an extrastriate process occurring between binocular neurones, and its effect is more or less equal across all binocular cells regardless of their ocular dominance.

There are several additional implications of these findings. While it has not been discussed previously in such terms, principally because of disagreements in the literature as to the appropriate means for measuring binocularity and its association with disparity tuning (cf. Baizer, Robinson and Dow 1977, DeYoe and Van Essen 1985, Hubel and Livingstone 1987), these results can be interpreted in terms of disparity tuning. Perhaps cells most sensitive to small disparities are those most affected by, or involved in, rivalry, while cells tuned for larger disparities are involved less. This leads directly to predictions about stereopsis, and is elucidated in the General Discussion and Conclusions.

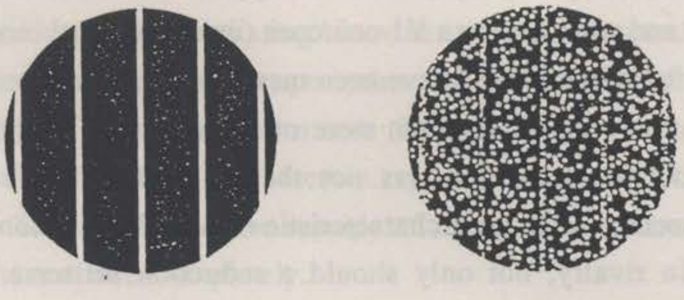


Fig. 23. Representations of the stimuli used by Berkley, et al. 1994 (taken from their Figure 1, pp. 210). The left hand stimulus depicts luminance defined contours, the right hand, the same contours with 25% noise. Note that with the addition of noise the subjective contrast of real contours changes, as does their luminance profile.

An interesting comparison which can be made here is that between these results and those described by Berkley, et al. (1994). Those workers reported that the failure to measure aftereffects induced using 'higher order' stimuli (ie. those induced using purely subjective contours for example) with lower-order (ie. area V1), luminance defined stimuli, as reported by Paradiso, et al. (1989), was dependent on the salience of the lower-order test stimulus. As the 'salience' of the luminance defined stimulus decreased, or as noise increased, so the ability to measure, using a lower-order stimulus, an aftereffect from a higher order adapting stimulus increased. If these findings are interpreted in terms of types of cells involved in the processing, then some similarities between those results and these emerge. Addition of random static noise of the type used by Berkley and colleagues may have the effect of reducing the specificity of tuning exhibited by area V1 cells to the real contour stimulus. Real lines and edges begin to look less like real lines and edges, their luminance profile changes (Fig. 23), and so fewer orientation selective cells in area V1 should be responding as they would to a noise free stimulus. Neurones in extrastriate regions might be less affected by the addition of noise because their wiring is such that they are able to extract a contour from a noisy background (eg. von der Heydt and Peterhans 1989, Stoner and Albright 1993). This results in a proportional increase in the contribution of such neurones to the aftereffect, and this is accompanied by a proportional decrease in the contribution of many area V1 cells. This change allows, in some way, the more higher-order component of the aftereffect to become manifest. The similarity to the work reported here is that by examining the real contour direct effect interocularly, the contribution of much of the area V1 population to the effect has been reduced, and this allows more subtle effects to be observed. It would be interesting to examine the effect of binocular rivalry on real contour tilt aftereffects using adapting and test stimuli accompanied by noise such as that used by Berkley. It is tempting to predict that the magnitude of tilt aftereffects induced during rivalry would be reduced when compared to aftereffects similarly tested but induced without rivalry.

Among the issues raised by these experiments is the nature of the relationship between what is perceived during rivalry and the processes associated with these perceptions. The evidence so far suggests that rivalry is binocularly mediated and involves some form of inhibitory interactions, or at least some decrease in the levels of activity experienced by such neurones, during rivalry. Similarly, the binocular model suggests predominance is linked with activity, the more active a group of neurones are, the more predominant the perception they underlie. One of the purposes of the remaining experiments was to examine more closely the nature of this hypothesised decrement in activity and its affect on perception. Prior to that, if rivalry is binocular, then visual phenomena (other than purely subjective contours) associated with binocular areas of the cortex should show effects similar to those described above. Experiment Nine was designed to investigate this hypothesis.

[illegible] cells. This strategy is used in some [illegible] higher-order [illegible] component of the aftereffect to be [illegible]. The similarity to the [illegible] here is that by examining the real contour direct effect interocularly, the contribution of much of the area V1 population to the effect has been reduced, and this allows more subtle effects to be observed. It would be interesting to examine the effect of binocular rivalry on real contour tilt aftereffects using adapting and test stimuli accompanied by noise such as that used by Berkley. It is tempting to predict that the magnitude of tilt aftereffects induced during rivalry would be reduced [illegible] compared to aftereffects similarly induced but without [illegible] rivalry.

Among the issues raised by [illegible] experiments is [illegible] relationship between what is perceived during rivalry and the processes [illegible] these perceptions. The evidence so far suggests that rivalry is binocularly mediated and involves some form of inhibitory interactions, or at least some decrease in the levels of activity experienced by each neurone, during rivalry. Similarly, the binocular model suggests predominance is linked with activity, the [illegible] group of neurones [illegible] the percept predominates the perception [illegible]. One of the purposes of the rivalry experiments was to examine more closely the nature of this hypothesised decrement in activity and its effect on perception. Prior to that, if rivalry is binocular, then visual phenomena (rather than purely subjective contours) associated with binocular areas of the cortex should show effects similar to those described above. Experiment Nine was designed to investigate this hypothesis.

EXPERIMENT NINE

The experiments so far described have considered the effect of binocular rivalry on processes ascribed to area V2, but also on binocular processes in area V1, and these experiments have provided evidence suggesting that rivalry is mediated not by cells in area V1 but by interactions between binocular neurones beyond the striate cortex. This raises several interesting, and related questions: Can the assertion that rivalry involves binocular interactions be generalised beyond area V2? Since area V2 exhibits a high degree of binocularity, do other areas with similar or greater binocularity exhibit rivalrous processing also? If that is the case, and if rivalrous processing causes psychophysically observable changes in perceptions associated with area V2, do perceptions associated with areas in the visual system heirarchically later similarly reflect rivalry? Finally, can perceptual predominance be correlated with the magnitude of the subsequent aftereffect, as suggested by the data described above and by Wiesenfelder and Blake (1990)? To answer these questions the general aim of these last three experiments was to test the hypotheses that (i) binocular rivalry is mediated by interactions between bincoular neurones at many levels in extrastriate visual cortex, and (ii) that activity within binocular neurones during rivalry is correlated with predominance.

The rationale for the first of these hypotheses arises from the previous experiment. The rationale for the second comes, as stated, from these and other experiments, but is also as a prediction from the binocular model. In the model, activity of a group of neurones depends upon input, inhibition and fatigue (equations (1), (2), and (3)). Inhibition depends upon the activity of other neurones, in a reciprocal relationship. Recall also that the most active neurones are those giving rise to perception. This means that during rivalry, the cells tuned for a predominant stimulus are those which at that moment are most active. Activity can be decreased by inhibition, and this can be achieved by increasing the input to other neurones, which in turn is increased by increasing the 'energy', or salience, of the rivalrous stimulus (Levelt 1968, Sagawa 1981). A consequence of decreasing activity is that the rate and amount of fatigue will be decreased. It follows, therefore, that if two stimuli are in rivalry and one is altered so as to predominate more, the inhibition generated by the cells tuned for that stimulus will increase and therefore decrease the activity in cells tuned for the other stimulus. This will decrease the time for which the second stimulus is predominant, at the same time decreasing the fatigue state of those cells. If aftereffect magnitude, or duration, is proportional to activity, then logically, a stimulus which predominates less frequently should subsequently generate a smaller or shorter aftereffect.

Considerable neurophysiological and psychophysical efforts have been expended on visual area MT and processing arising in association with it. Perhaps the most important finding associated with area MT, in terms of understanding visual neurophysiological functioning, is that neurones in area MT exhibit behaviour which suggests a solution to the *aperture problem* (Ullman 1986). Neurones earlier in the visual pathway have not been found to exhibit this property, and so in this sense the relation between drifing plaids and area MT is similar to that between purely subjective contours and area V2. Further, area MT was closely associated with the findings reported by Logothetis and Schall (1989). There is some reason to expect, therefore, that rivalry will have an impact on effects associated with area MT.

Plaid motion is more complex than it may at first seem. For any one-dimensional stimulus (a single contour or a grating) if the ends of the stimulus are not visible, only motion orthogonal to the orientation of the stimulus can be perceived. So in Fig. 24A., the vertical contour can be moving along any one of a family of motion vectors (represented by the fine arrows), but through a circular aperture will always appear to be moving along a single orthogonal vector (OR). It was this ambiguity of motion to which Ullman (1986) referred. Importantly, the family of vectors, of which OR could be a component of any, all terminate along a line (AB) parallel with the orientation of the original contour, but some distance from it. Adelson and Movshon (1982) describe this as *the line of constraint*. However, such ambiguities occur only for one-dimensional stimuli. Two-dimensional motion, created, for example, when two moving one-dimensional gratings with different orientations are superimposed, has a unique solution provided by the intersection of the contraint lines for each of the one dimensional stimuli. Such a stimulus is now commonly referred to as a plaid. Since the two component stimuli have different orientations, the lines of constraint also have different orientations, and where those two lines intersect determines the sole possible motion vector of the plaid. This is represented in Fig. 24B.

Plaids exhibit several characteristics which allow them to be studied either in terms of coherent wholes, or in terms of their components. While the components are similar in perceived contrast, the motion of the individual components will not be perceived, just the plaid as a whole. Under these circumstances plaid speed can be increased by increasing the speed of either or both the components; thus in Fig. 23B., OR can be increased to OR_1 by increasing OC_1 to OC_{11}, and OC_2 to OC_{22}. Alternatively, plaid speed can be increased by increasing the angle between the components; that is from a to b. The relationship between perceived coherence and contrast varies with velocity and spatial frequency, (Movshon, et al. 1985, Smith 1992). When coherence breaks down into *transparent motion*, observers will perceive the two independent one-dimensional gratings sliding over each other.

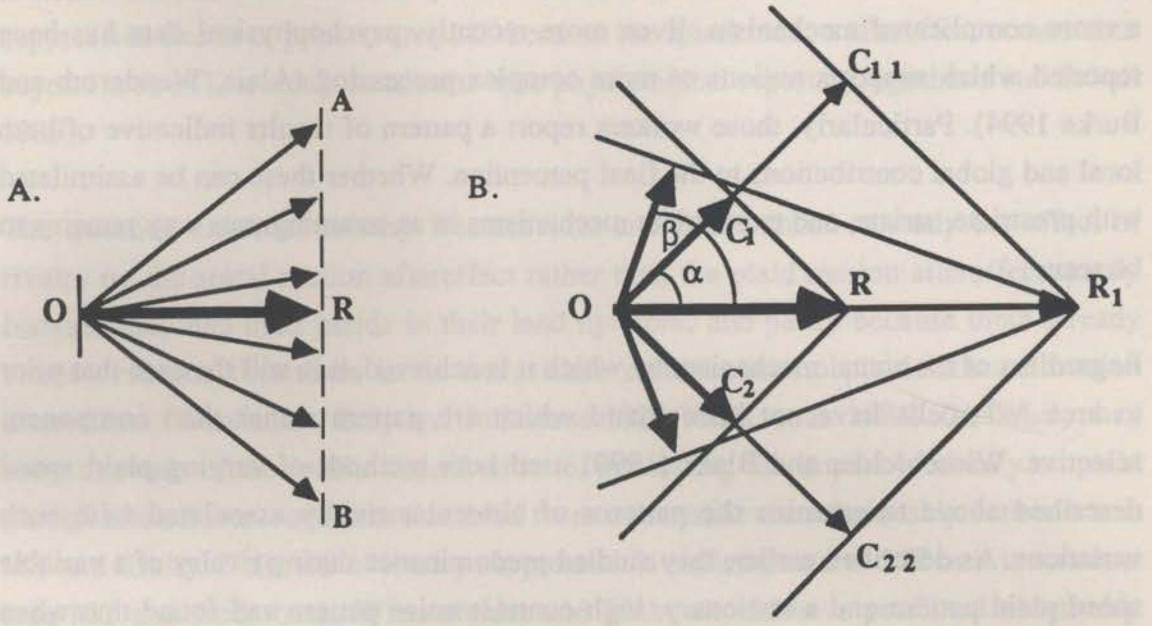


Fig. 24. A: A vertical grating moving in any of the directions represented by the fine vectors, and with a velocity equal to the length of the vector would appear, through a circular aperture obscuring the ends of the contour, to have direction and speed represented by vector OR. This is the aperture problem. B: A plaid, a 2-dimensional stimulus composed of two 1-dimensional stimuli like that depicted in A., will be perceived to have direction and speed OR. This perception is thought to arise from the solution of the intersection of the constraints of components C_1 and C_2. Plaid speed con be increased to OR_1 either by increasing component speed to C_{11} and C_{22} or by increasing the angle between the components from 2a to 2b.

In terms of the current study, understanding plaid perception is important because single neurones at different levels of the cortex have different response properties when stimulated with plaids. Area V1 cells signal only to the individual component gratings of which the plaid is comprised, responding only when either of the components is at the cell's preferred orientation and direction of motion. In area MT similar responses are observed, but approximately 25% of area MT cells are pattern selective, responding when either a single grating or a plaid is moving in their preferred direction but not when the individual components of the plaid are so disposed (Movshon, et al. 1985, Maunsell and Newsome 1987). Movshon and his colleagues attempted to explain these results by arguing that orientation- and direction-selective neurones in area V1 respond to one-dimensional component gratings of the plaid. Under conditions of coherence, these cells feed via an AND-gate to pattern selective neurones in area MT which inhibit area MT component selective cells. This would account for the inability to see component gratings in a coherent plaid. Under non-coherent conditions the AND-gate does not function, and the area V1 neurones feed directly into similar component selective cells in area MT, which conversely inhibit the pattern selective cells. Thus transparent motion is perceived. More recently, Stoner and Albright (1992) have found cells in area MT respond to either the pattern direction or the component direction, depending upon whether the conditions favour transparency or coherence. This suggests a more complicated mechanism. Even more recently, psychophysical data has been reported which supports notions of more complex processing (Alais, Wenderoth and Burke 1994). Particularly, those workers report a pattern of results indicative of both local and global contributions to the final perception. Whether these can be assimilated with prestriate, striate, and extrastriate mechanisms in an unambiguous way remains to be seen.

Regardless of the actual mechanism by which it is achieved, it is still the case that prior to area MT, cells have not been found which are pattern rather than component selective. Wiesenfelder and Blake (1990) used both methods of varying plaid speed described above to examine the patterns of binocular rivalry associated with such variations. As described earlier, they studied predominance during rivalry of a variable speed plaid pattern and a stationary, high-contrast noise pattern and found that when increases in plaid speed were accomplished by varying component angular separation, time for which the plaid was exclusively visible increased but suppression of the stationary rivalrous pattern did not increase. In other words, piecemeal rivalry decreased. On the other hand, when plaid speed increases were accomplished by increasing component speed, plaid predominance increased while the predominance of the rival pattern decreased. For a number of reasons, Wiesenfelder and Blake (1990) concluded that this pattern of results was evidence for the site of rivalry suppression lying beyond area V1 but prior to area MT, with feedback from area MT to the site of rivalry. The soundness of this conclusion has already been discussed.

In a second experiment Wiesenfelder and Blake (1990) examined the effect of rivalry on the spiral motion aftereffect. Several neurophysiological studies have described neurones which responded selectively to radial and/or rotational motion, the two components of rotating spiral motion, but never in lower cortical areas like area V1. Rather, such cells were located in area MST (medial superior temporal area) or area PG (the posterior parietal association area), which receives input from area MST (Sakata, Shibutani, Ito and Tsurgai 1986, Tanaka and Saito 1989). Because psychophysical evidence also suggests the spiral motion aftereffect involves global rather than local processes (Cavanagh and Favreau 1980, Hershenson 1984) and since global interactions are characteristic of extrastriate mechanisms (Allman et al. 1985), Wiesenfelder and Blake (1990) postulated that if rivalry occurs after area V1 but before or at area MT, which inputs to area MST, then rivalry might disrupt the spiral motion aftereffect even though it does not disrupt the linear motion aftereffect. Not only did they obtain this result, but for six of seven observers, the correlation between the duration of the spiral predominance and the magnitude of the motion aftereffect was between 0.8 and 0.9. As already mentioned, they concluded that the site of rivalry suppression lies at or prior to area MT because the spiral motion aftereffect occurs at or beyond area MT, a result consistent with physiological reports (Logothetis and Schall 1989).

The question arises as to why Wiesenfelder and Blake chose to study the effect of rivalry on the spiral motion aftereffect rather than the plaid motion aftereffect, partly because they had used plaids in their lead up work, and partly because there already exists evidence that there is an extrastriate contribution to plaid induced motion aftereffects (Wenderoth, Bray and Johnstone 1988, Alais, et al. 1994). Obviously they were unaware of the results described here, but testing the impact of rivalry on plaid motion aftereffects would have enabled them to examine the relationship between area MT and rivalry. If the site of rivalry suppression is earlier than area MT or if it occurs at area MT and feeds back, Wiesenfelder and Blake should have predicted observable changes in plaid motion aftereffects induced with rivalry. That spiral motion aftereffects show decrements in magnitude under such conditions, and arise no earlier in the visual system than plaids, further suggests this to be the case. Clearly the impact on plaid motion aftereffects of binocular rivalry is a test of the arguments developed here.

Area MT is generally assigned to the so called magno-cellular pathway, and is considered to be a specialised motion processing area (Zeki 1988). It receives a substantial input from area V2 and is primarily binocular (DeYoe and Van Essen 1988, Van Essen et al. 1992). Together these characteristics suggest area MT could behave similarly to area V2 in response to appropriate rivalrous input, or alternatively, reflect the effects of rivalry arising in area V2 from which much of its information comes. Area MT is dissimilar to both areas V2 and area V1 in that its neurones are functionally more homogeneous, most being selective for direction of motion (Zeki 1990). Indeed, cells in area MT exhibit what appear to be axis-of-motion columns and hypercolumns almost analogous to orientation columns observed in earlier visual cortical areas (Albright, Desimone and Gross 1984, Albright and Desimone 1987). This does not discount area MT as a site for rivalry, rather it points to being involved only in rivalry involving motion. Orientation and direction tuning are more coarse in area MT than in area V1 (Albright 1984) and while area MT has receptive fields much larger than those observed in earlier areas, it has a small cortical magnification factor. This results in a stimulus activating roughly equivalent numbers of modules in areas MT and area V1 (Albright and Desimone 1987). The implications of this have already been described, the effect of the cortical magnification factor may be sufficient to provide the perception of small units of predominance or suppression characteristic of piecemeal rivalry that some workers (eg. Blake 1989) argue reflect small receptive fields.

It seems that there is sufficient evidence to implicate area MT in rivalry, either as a recipient of input affected by rivalrous interactions, or as a cortical location where such interactions can independently occur, and these areas are thought to be predominantly binocular. It was predicted, therefore, that instances of binocular rivalry during the induction of plaid motion aftereffects, which can be attributed either partially or wholly to area MT, will reduce the plaid motion aftereffect. Since plaid motion aftereffects can be induced by adapting to alternating components (Wenderoth, et al. 1988), it is interesting to ask whether rivalry will similarly disrupt aftereffects thus induced. While there is evidence of two processes giving rise to such effects (Alais, et al. 1994), the neural substrate of such mechanisms are undetermined, and may have a significant monocular component from area V1 (Alais, et al. 1994). With this in mind, plaid motion aftereffects induced by alternating components, with and without rivalry, were also examined. If there is an extrastriate component to such aftereffects then rivalry during induction may disrupt it, causing a reduction in the aftereffect. This and the next experiment were designed to test these hypotheses.

Methods

The use of moving stimuli required a number of changes to the apparatus and methods. Only relevant changes to procedures and the apparatus are described here.

Subjects: Unlike previous experiments the subjects used for this study included trained psychophysical observers (n = 5) in addition to untrained, naive volunteers (n = 6). These separate groups were used because few volunteers were available at the time of testing. The data for the two groups was treated separately.

Apparatus: Polaroid filters were arranged in the tachistoscope so that adapting and test stimuli were viewed only by the subjects right eye while the rivalrous pattern was viewed only by the left eye. The left eye stimulus was a Moire screen saver generated on a Macintosh Classic (Apple Computers, Sydney, Austalia) screen. The pattern consisted of random shapes composed of one pixel wide lines of random orientation, size, and drift direction whose density and speed could be selected from a menu. Pilot work had previously established that various combinations, in number and speed, of these elements could be used to systematically vary the amount of time for which each of the rivalrous stimuli, either the Moire pattern or a drifting plaid or grating, would predominate during an adaptation period. Similarly, it was found that the Moire pattern did not itself generate any motion aftereffect on a stationary plaid or grating (van der Zwan et al. 1993).

Plaid stimuli were generated by a Macintosh IIci computer and displayed on a single 33cm AppleColor High Resolution RGB Monitor. Drifting plaid stimuli were created by allocating alternate pixels on each raster scan line to one or other of the component gratings by assigning one 127 gray-level colour lookup table (CLUT) to the even pixels and a second, independent CLUT to the odd pixels. Alternate horizontal scan lines of pixels were shifted one pixel out-of-phase so that the two gratings were effectively assigned to pixels arranged in the pattern of either the light or dark squares of a checkerboard.

The maximum light bar luminance (L_{max}) and the minimum dark bar luminance (L_{min}) were 104.6cdm^{-2} and 0.7cdm^{-2} respectively. This provided a Michelson contrast of 0.98 (Note: Plaid luminances were strictly not double-grating luminances because the two gratings of the plaid occupied spatially descrete pixels. However, given that each pixel subtended less than 0.027 visual angle, spatial summation of luminance would have effectively made plaid contrast double that of the grating contrast.). Spatial frequency of the component sine-wave gratings was 0.46 cyc/deg and the test stimulus was the same, stationary plaid composed of both adapting components. Using a convention such that left horizontal is 0, the component drift directions (and drift separation) used were 225 and 315 (90). The component gratings both had velocities of 2.15s^{-1}, so the drift direction of the plaids was always straight down (270), the bisector of the component directions.

Procedure: Subjects were instructed to report cessation of the motion aftereffect only when no trace whatsoever of apparent motion remained. This was stressed because it has been found previously that such instructions minimise variability (Wenderoth et al. 1988, van der Zwan et al. 1993). Also emphasised was the requirement that subjects attempt to use a constant criterion for motion cessation throughout the experiment, to avoid the possibility that subjects might change their criterion during the course of the experiment.

Every subject was given three practice trials, two in which no rivalrous stimulus was presented and one in which the subject was asked to report the relative dominance of the plaid or the rivalrous Moire pattern. Subjects were required to fixate a small black dot in the centre of the screen at all time during adaptation and test to avoid any aftereffects due just to eye movements (eg. Chadhuri 1991).

With stimuli of the size used here it is rare for complete predominance of either of two patterns involved in rivalry to occur, unless one is a very much more energetic stimulus than the other. The parameters selected for each of the displays ensured that this was not the case, and so during rivalry trials subjects were required to report which ever of the two fields, "mostly plaid" or "mostly Moire", were currently visible. Whenever predominance shifted from Moire to plaid the subject indicated this by saying "yes", or from plaid to Moire by saying "no". When subjects understood the instructions, practice trials using 30s adaptation periods were given, one without rivalry and two with rivalry. Instructions were further clarified as required during the ensuing five minute rest period. The Moire pattern was chosen to produce about 50% predominance for each eye. At the commencement of a trial four manual timers were started. Two timers measured predominance time as signalled by subjects during rivalry trials and two measured the total duration of a trial from the start of adaptation until cessation of the motion aftereffect, with the motion aftereffect duration calculated as the total time minus the adaptation duration. Manual timing, while not optimal, was chosen as a means of controlling the experiment. During design and development of the experiment it was found that most naive, untrained subjects had some difficulty in keeping track of what they were signalling if given a set of switches. This could be overcome if subjects were given extensive practice, but this was not a viable option. It is interesting that this occurred for motion stimuli but not for the stationary stimuli used in the previous experiments. It is perhaps linked to the task requirements upon completion of the adapting phase of the experiment. Instead, verbal signalling with manual timing by the experimenter and research assistants was found to be more reliable. Considerable practice by the experimenter and assistants ensured that measurments never differed between recorded times by more than 0.1s. Timers recorded times independently, with results for each subject combined only at the completion of the experiment. An arbitrary criterion of 0.1s was set, and any time differences greater than this would lead to exclusion of that subject. No subjects were excluded in this way.

Eight measures of the motion aftereffect were taken, two under each of four adapting conditions: 60s plaid without rivalry, 60s plaid with rivalry, 120s alternating components (60s each with a 10s alternation rate) without rivalry, and 120salternating components with rivalry. These are represented schematically in Fig. 25. The naive observers also completed another condition in which they adapted to the drifting plaid stimulus for 30s. Although this condition was not a rivalry mimic condition, since adaptation was continuous, it did give a measure of the motion aftereffect duration with half the adaptation period used in the plaid conditions. Wiesenfelder and Blake (1990) reported strong correlations between predominance time and motion aftereffect magnitude, and the stimuli used in this experiment were set up to produce approximately 50% predominance for the adapting stimulus. It was used also to ensure that motion aftereffect had not peaked after only half the adaptation period. Between trials, there was a 150s rest period and the order of the trials was always completely random.

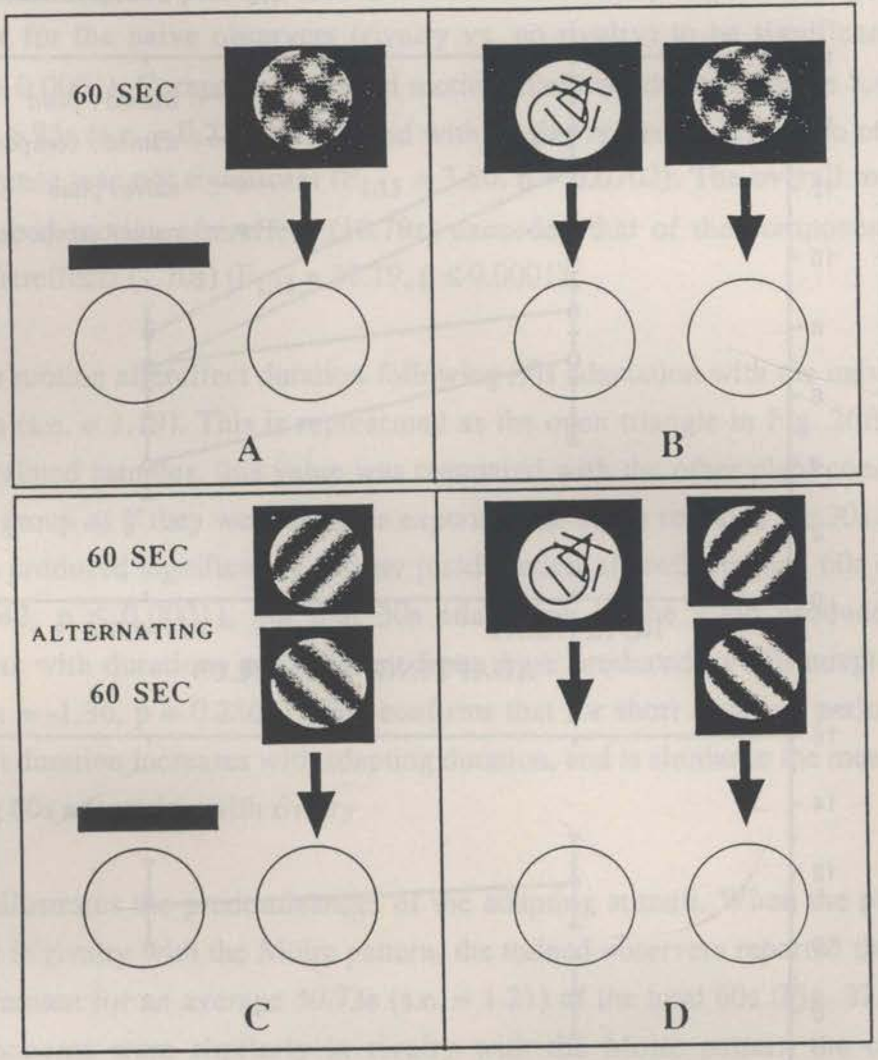


Fig. 25. A schematic representation of the four conditions examined in Experiment Nine. A: 60s adapting plaid with no rivalry to the other eye. B: As in A., but with a rivalrous pattern in the other eye. C: Alternating plaid components for 120s (10s cycle) without rivalry. D: As in C., but with rivalry. Naive subjects did a fifth condition, not depicted here, which was similar to A., but with only 30s adaptation.

Results

Means and standard errors of the aftereffect durations induced with drifting plaids and alternating components are shown in Fig. 26A. For the trained observers the plaid-induced motion aftereffect duration was 12.61s (s.e. = 2.64) without rivalry and 6.76s (s.e. = 1.42) with rivalry, yeilding a rivalry/non-rivalry duration ratio of 0.54 (s.e. = 0.023). A simple repeated measures analysis of variance with planned orthogonal contrasts revealed this mean difference to be significant ($F_{1,12} = 19.64$, $p = 0.0008$). The component-induced motion aftereffect durations without and with rivalry were 7.07s (s.e. = 2.51) and 3.96s (s.e. = 1.00) respectively. The rivalry/non-rivalry duration ratio was this time 0.64 (s.e. = 0.11), and the difference between these durations was also significant ($F_{1,12} = 5.55$, $p = 0.036$). Overall, plaid induced motion aftereffect durations exceeded significantly the component induced durations ($F_{1,12} = 20.005$, $p = 0.0008$).

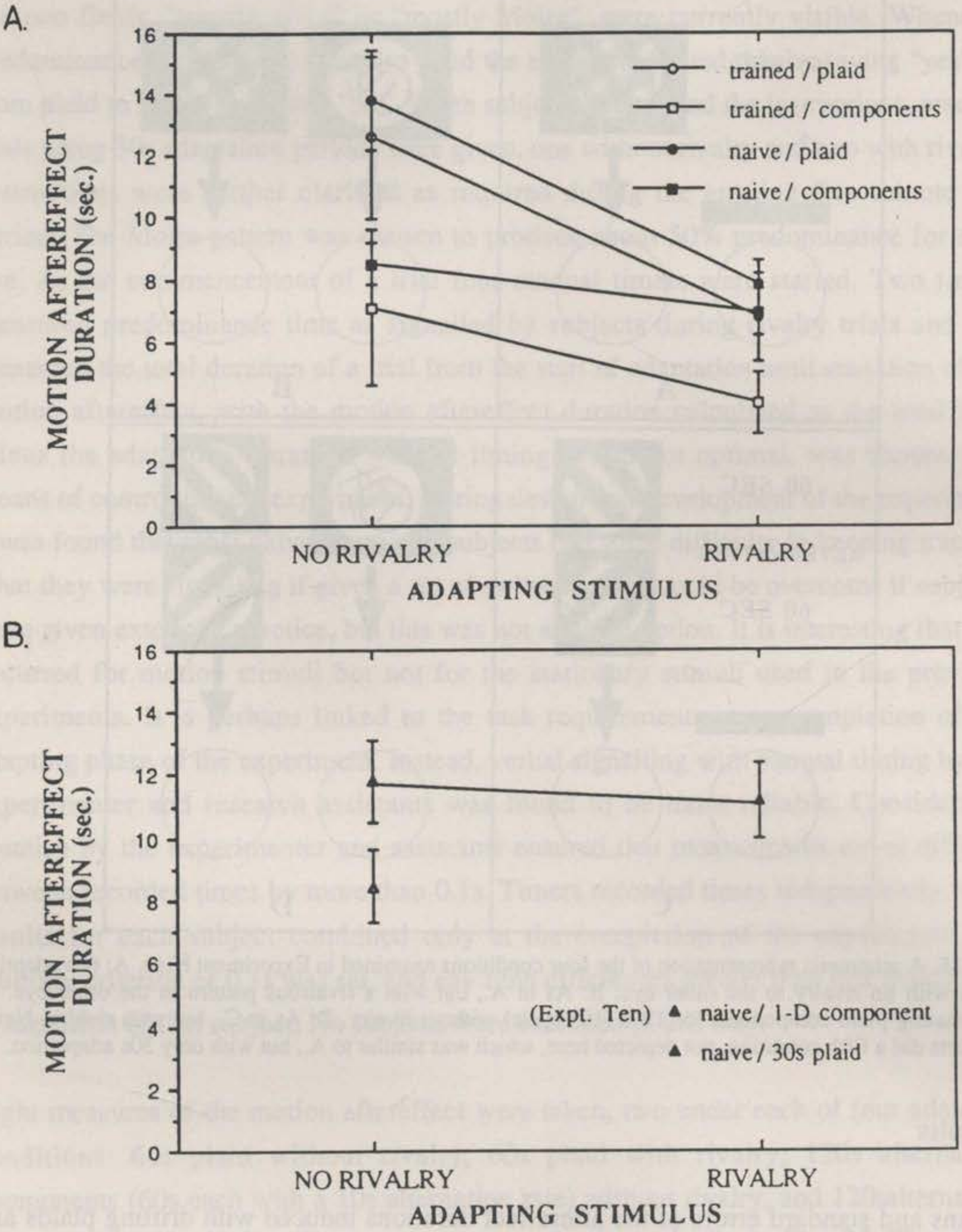


Fig. 26. A: Motion aftereffect durations under conditions of rivalry and no rivalry for trained and naive observers after adapting to coherent plaids (circles) or alternating components (squares). For both naive and trained observers, the duration of the plaid motion aftereffect was reduced by rivalry. The effect is less clear for alternating components, with a significant reduction observed only for trained observers. B: Naive subjects, adapting to a plaid without rivalry for 30s exhibited motion aftereffects comparable with those produced by adapting to a plaid with rivalry for 60s, open triangle. The results of Experiment Ten, a control experiment, are represented by solid triangles. They show that under the conditions used in these experiments, the linear motion aftereffect is not diminished by periods of rivalry. Error bars show ± 1 standard error.

For the naive observers, plaid-induced motion aftereffect durations were 13.78s (s.e. = 1.63) (non-rivalry) and 7.80s (s.e. = 0.78) (rivalry), producing a rivalry/non-rivalry duration ratio of 0.57 (s.e. = 0.023). A one way analysis of variance, again with repeated measures and planned contrasts showed the difference between the 60s plaid conditions for the naive observers (rivalry vs. no rivalry) to be significant ($F_{1,15}$ = 56.70, $p \leq 0.0001$). Component induced motion afterefect durations were 8.48s (s.e. = 0.66) and 6.93s (s.e. = 0.72) without and with rivalry respectively, a ratio of 0.81, but this difference was not significant ($F_{1,15}$ = 3.80, p = 0.0702). The overall mean of the plaid-induced motion aftereffect (10.79s) exceeded that of the component-induced motion aftereffects (7.70s) ($F_{1,15} = 30.19$, $p \leq 0.0001$).

The mean motion aftereffect duration following 30s adaptation with the naive subjects was 8.45s (s.e. = 1.19). This is represented as the open triangle in Fig. 26B. Using t-tests for related samples, this value was compared with the other plaid conditions for the naive group *as if* they were separate experiments. These revealed the 30s adaptation condition produced significantly shorter plaid motion aftereffects than 60s adaptation (t_5 = 11.42, $p \leq 0.0001$), but that 30s adaptation to the plaid produced motion aftereffects with durations not different from those produced by 60s adaptation with rivalry (t_5 = -1.36, p = 0.2307). This confirms that for short adapting periods motion aftereffect duration increases with adapting duration, and is similar to the mean duration following 60s adaptation with rivalry

Fig. 27. illustrates the predominances of the adapting stimuli. When the plaids were presented in rivalry with the Moire pattern, the trained observers reported the plaids to be predominant for an average 30.73s (s.e. = 1.21) of the total 60s (Fig. 27A.). When the components were similarly in rivalry with the Moire pattern the component predominance averaged 59.11s (s.e. = 1.27) of the 120s (Fig. 27B.). The corresponding means for the naive observers were 30.76s (s.e. = 2.72) and 59.92s (s.e. = 2.29). For both groups, rivalry resulted in about 50% predominance of each eye's stimulus.

Finally, there was no evidence that there was any buildup of motion aftereffects from the first to the second trial. Over all observers, the mean first- and second-trial motion aftereffects were 13.17s (s.e. = 1.29) and 13.34s (s.e. = 1.66), respectively, for plaids; and 7.45s (s.e. = 1.12) and 7.96s (s.e. = 1.26), respectively, for alternating components. Neither of these differences proved to be significant when tested with a t-test for related samples (plaids: $t_{10} = 0.19$, $p > 0.05$; components: $t_{10} = 0.61$, $p > 0.05$).

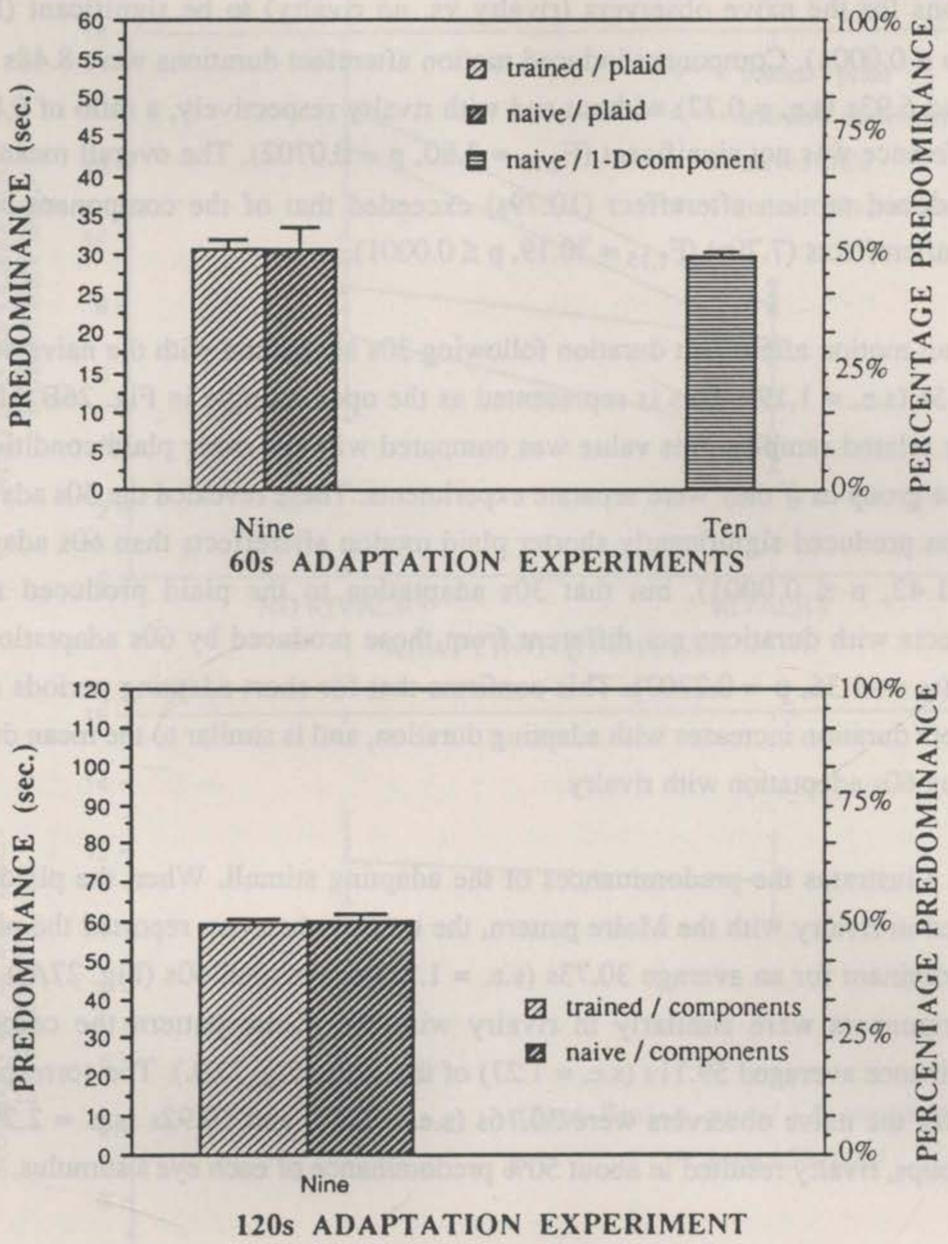


Fig. 27. Reported predominances of the plaid under all rivalry conditions for Experiments Nine and Thirteen. Under both 60s adaptation (plaids) and 120s adaptation (components), the adapting stimulus was perceived to predominate over the rivalrous stimulus for approximately half the adaptation period. As described above, rivalry generally reduced the aftereffect durations also by approximately 50%. Error bars are ± 1 standard error.

Discussion

Experiment Nine has demonstrated that binocular rivalry does reduce the duration of plaid-induced motion aftereffects; a result true for both trained and naive observers.

The picture is less clear for component induced effects because while a significant reduction was obtained with trained observers, the reduction was not significant with naive subjects. There is some evidence to suggest that both pattern tracking processes and intersection of constraint mechanisms are involved in the perception of plaids (Burke and Wenderoth 1992, Alais, et al. 1994), so some reduction might be expected. Similarly, as with real contour orientation aftereffects, motion perceptions with strong area V1 contributions seem little affected by rivalry, unless binocular processes alone are examined (Experiment Eight), and component induced aftereffects fall into this category. It may be that cortical areas other than area MT contain binocular neurones involved in the perception of two-dimensional moving stimuli beyond that suggested by the cells known to be sensitive for the components of that stimuli. If this were the case, rivalry may have an impact on the processing occurring in this group of neurones, altering what ever contribution they make. It would, therefore, be an interesting manipulation to test the component induced aftereffects interocularly. Several experiments more relevant to the hypotheses are required first, however. These results present a clear picture of plaid motion aftereffects, attributable to processing in area MT, as being similar to processes attributed to area V2, in that they too are disrupted by periods of rivalrous suppression during their induction. They provide psychophysical evidence in support of the findings of Logothetis and Schall (1989), and reinforce the evidence suggesting that all binocular cells exhibit interactions like those which give rise to the perception of rivalry.

In some aspects, this result is more intriging than that reported by Wiesenfelder and Blake (1990). They reported disruption to an aftereffect clearly attibutable to extrastriate mechanisms. There is no striate cortex neurone tuned for any type of motion like spiral motion, it is an emergent property of global mechansims. This is not to say that low level mechanisms are not involved, just that there are no simple motions like spiral motion. The plaid motion aftereffect used here is a two dimensional equivalent of one-dimensional linear motion, which has been shown previously to be independent of the mechanisms giving rise to binocular rivalry (eg. Lehmkuhle and Fox 1975). As discussed, plaid motion can be described in terms of its components motions, or in terms of its motion as a coherent pattern, and neurophysiological encoding of both occurs, but at different levels. While there is some reason to believe that the behaviour of the pattern sensitive cells depends on the behaviour of the component sensitive neurones, it is the former which must be suspected of being influenced by the rivalrous suppression. The decrement in aftereffect duration can be attributed to the extrastriate component of plaid perception, and indeed it may be the neuronal structures responsible for solving the aperture problem which are subject to the interactions described for the binocular neural array. Alternatively, the pattern selective cells described by Maunsell and Newsome (1987) and Stoner and Albright (1992) may interact in such a fashion themselves. Such speculation is true, of course, only if the procedures used in this experiment have not disrupted the component selective processes.

Thus, before formalising any conclusions, it seemed critical to run a control experiment using a single adapting grating to demonstrate that under the experimental conditions used in Experiment Nine, the simple linear motion aftereffect is not significantly reduced by binocular rivalry. That was the purpose of Experiment Ten.

EXPERIMENT TEN

Experiment Nine demonstrated that like purely subjective contour tilt aftereffects and spiral motion aftereffects (Wiesenfelder and Blake 1990), acquisition of plaid motion aftereffects is disrupted by binocular rivalry during induction. Whether rivalry also disrupts component-induced effects is ambiguous. That the linear motion aftereffect is not disrupted by rivalry, that is, that its duration is unaffected by rivalry, has been discussed (cf. Lehmkuhle and Fox 1975, Blake 1989). So for the above result to be meaningful it will be necessary to replicate that observation under the same conditions used in the previous experiment, particularly as it has been shown that there are conditions under which area V1 effects might show perturbation in response to rivalry. The aim of Experiment Ten was to test the prediction that the duration of the motion aftereffect induced with a single adapting grating drifting in a single direction is not reduced by binocular rivalry.

Method

All details of the method and procedures were as described for Experiment Nine, except that the adapting stimulus was a single horizontal grating which drifted straight down (270°) with a velocity of $2.51^{\circ}s^{-1}$. The test stimulus was a stationary version of the same grating.

Subjects: These were six naive volunteers from an Introductory Psychology course.

Results

The mean predominance time for the grating under the rivalry adapting condition was 29.62s (s.e. = 0.63), shown in Fig. 27A. The mean motion aftereffect durations were 11.80s (s.e. = 1.29) and 11.18s (s.e. = 1.20) under the no rivalry and rivalry conditions respectively. The difference between these was not significant ($t_5 = 2.36$, $p = 0.0641$). These data points are represented on Fig. 26B as solid triangles.

Discussion

These data indicate that simple linear motion aftereffect durations show no impact of rivalry, a result that has been previously reported (Lehmkuhle and Fox 1975, O'Shea and Crassini 1981). Since there was no effect of rivalry on the duration of motion aftereffects induced by a single drifting grating under the same conditions that reduced the duration of the plaid motion aftereffect, the latter result can be taken as evidence that the site of rivalry, or its effect via feedback, lies between the site of grating adaptation and that of plaid adaptation, putatively between area V1 and area MT or at area MT, which fits nicely with the results of Experiment Eight. It is interesting to note that like area V2, area MT receives a direct projection from layer 4B of area V1, and just as monocular input is converted to binocular information in area V2, so it is converted to binocular input in area MT (Burkhalter, et al. 1986, DeYoe and Van Essen 1988). Whether the combination of monocular inputs into binocular information is significant in understanding the mechanism of rivalry is unknown. More investigation of the coincidence of these processes must be carried out before firm conclusions can be drawn.

The suppression induced decrement in aftereffect magnitude observed in Expeiment Nine can now be considered. The nature of suppression, in terms of binocular neural arrays, has already been discussed, and there is no reason to believe that such interactions are not responsible for the neural processing underlying these effects. There is nothing about the structure of area MT, or even hierarchically higher areas, which suggests that neural interactions fundamentally different from those thought to occur in lower areas operate in there. Thus, when the non-adapting stimulus (moire) is predominant, there is less activity in the neurones tuned for the adapting stimulus. The neurones involved are probably those area MT cells described above as being pattern selective, although they could well be from higher areas with feedback connections to area MT, and as highlighted by Logothetis and Schall (1989), there is every reason to suspect that the tuning characteristics of these neurones change during rivalry. This factor has not been built into the binocular model and is obviously a limitation. Equally, the decrement observed could arise earlier than area MT, in binocular neurones somewhere between the component selective neurones of area V1 and the pattern selective neurones of area MT. Such neurones would then be implicated in the neural solution for the problem of ambiguous one-dimensional motion. While these two experiments do not distinguish between these alternatives, they suggest that rivalrous suppression probably occurs also at or prior to area MT, where plaids are encoded, and certainly after area V1. As already discussed, there is no logical nor parsimonious reason to expect rivalry is implemented by feedback from higher areas.

In these last experiments, aftereffect duration was decremented by rivalry, which points to the degree of adaptation induced in motion sensitive extrastriate neurones being less than without rivalry. Indeed, a reduction in predominance of around 49% led to a reduction in aftereffect duration of between 43%-46% in Experiment Nine. For experiments Five and Seven, which measured aftereffect magnitude, the equivalent reductions were roughly similar; about a 55% reduction in predominance led to a reduction in the tilt aftereffect magnitude of around 65%. The explanation of rivalry offered here implies a relationship between activity and fatigue: The most active cells are those perceived and are also those becoming fatigued at the greatest rate. This suggests a relationship should exist between predominance and the size of the subsequent aftereffect. The more time during adaptation for which a plaid is visible, he longer the aftereffect duration.

In terms of the processes operating, if the amount of motion is varied in the rivalrous stimulus, predominance of the plaid stimulus should concurrently vary also (assuming, reasonably, that motion channels are determining the strongest stimulus), but in an inverse relationship. As the rivalrous stimulus decreases in motion information (ie. moves slower), the strength of the inhibition, etc. generated by neurones tuned for it would similarly decrease, and so the cells tuned for the plaid would be adapted more, because their activity increases at this time. Remember, that this is true only for binocular neurones involved in both rivalrous activity and plaid perception. Neurones in area V1 are little affected by dissimilar dichoptic input. So conceivably, even if the moire was completely predominant for the entire adapting period, area V1 neurones tuned for the components of the plaid would still be adapted, and may generate some residual aftereffect. The component aftereffect results in Experiment Nine suggest, although equivocally, that this would be the case. This prediction was the basis for Experiment Eleven.

predominance in the aftereffect magnitude of around 65%. The explanation of rivalry effects now implies a relationship between rivalry and fatigue; The more active cells are the more predominant and yet also those becoming fatigued to the greatest extent. This suggests a relationship should exist between predominance and the extent of the subsequent aftereffect. The more time during adaptation for which a grating is visible, the longer the aftereffect duration.

In terms of the processes operating, if the amount of motion is [illegible] the grating stimulus, predominance of the plaid stimulus should concurrently vary also (assuming, reasonably, that motion channels are determining the strongest stimulus), but in an inverse relationship. As the rivalrous stimulus decreases in motion information (ie. moves slower), the strength of the inhibitions exerted by neurones tuned for it would similarly decrease, and so the cells tuned for the plaid would be adapted more because their activity increases at this time. Remember, that this is true only for binocular neurones involved in both rivalry and plaid perception. Neurones in area V1 are little affected by binocular rivalry as input is monocular. So conversely, if the motion was completely predominant for the entire adapting period, area V1 neurones tuned to the components of the plaid would still have adapted, and may generate some residual aftereffect. The component aftereffect results in Experiment Nine suggest, although not conclusively, that this would be the case. This prediction forms the basis for Experiment Eleven.

EXPERIMENT ELEVEN

The aim of this experiment was to test the second hypothesis outlined in Experiment Nine: that predominance and neural activity may be correlated. Recall Wiesenfelder and Blake (1990) not only demonstrated that binocular rivalry reduced the magnitude of the spiral motion aftereffect but they went on to show that when spiral predominance was varied, motion aftereffect duration was highly linearly correlated with duration of spiral visibility, psychophysical evidence that some direct relationship between predominance and amount of adaptation exists. This is not to suggest that there is a simple *linear* relationship between the time for which an adapting stimulus is perceived to be suppressed, and the amount of inhibition to which it is subject; the relationships described by equations (1) and (2) in Fig. 3. show a much more complicated interaction is likely. Instead, it can be taken as evidence that some proportional relationship exists, and that a linear description can describe a large amount of the variation.

In this experiment, speed of the rivalrous stimulus was varied in order to manipulate the predominance of the adapting plaid, in an attempt to examine the correlation between motion aftereffect duration and plaid visibility during adaptation. It was predicted that as predominance increased, motion aftereffect duration would also increase.

Methods

Most details of the methods for this experiment are like those described for the previous two. Four conditions were examined, one of which was a no-rivalry treatment. In the other three, the rivalrous pattern was modified so the adapting plaid predominated for approximately 25%, 50% and 75% of the adaptation period; Table 11. 1.

Table 11. 1. Correlation between predominance and aftereffect duration.

Plaid Speed	Constant			
Moire Speed	Variable Between Conditions			
Adaptation Duration	60s			
Plaid Predominance	~15s (25%)	~30s (50%)	~45s (75%)	60s (100%)

Subjects: Four volunteers from the naive population of first year students were used for this study.

Procedure: Stereopsis was verified for each subject, and none was rejected on this criterion. After instructions and practice trials had been given, each subject completed the four conditions ; no rivalry, ~25%-, ~50%-, ~75%-plaid predominance, in random order. The plaid was that used in Experiment Nine. Adaptation was for 60s, with 3 minutes between trials, and a 5 minute break between the first two and last two conditions. Again, this protocol was adopted to prevent a buildup of the plaid motion aftereffect over the course of the experiment. Within each rivalry treatment, three measures of predominance and three measures of motion aftereffect duration were taken, and the values for each subject were calculated as the means of these measures. Just as for the previous experiments, subjects signalled which of the two patterns was currently most predominant. For the reasons detailed above, an experimenter and an assistant timed plaid predominance, and the measure for that trial was the mean of the two values thus recorded. The same criteria were applied here as in Experiment Nine. Total testing time per subject was about 85 minutes.

Results

The mean plaid predominance times under the three rivalry conditions, expected to be 25%, 50% and 75%, were in fact 18.48s (s.e. = 0.47), 30.14s (s.e. = 1.80), and 50.50s (s.e. = 1.05), or actually 30.8%, 50.2%, and 83.4% respectively. There is a sufficient spread to allow the correlation between plaid visiblility (ie. predominance) and motion aftereffect duration to be calculated[14]. Fig. 28 plots, for each subject, pattern visibility as a function of motion aftereffect duration.

Pearson product-moment correlations, as can be seen, range between 0.84 and 0.94 (mean = 0.89, s.e. = 0.02), values comparable to those reported by Wiesenfelder and Blake (1990) for their correlations. The graph clearly illustrates the strong relationship between plaid predominance and aftereffect duration.

The mean duration of the aftereffect was calculated for each condition: 4.45s (s.e. = 0.80), 7.99s (s.e. = 0.43), 11.23s (s.e. = 0.82), and 14.10s (s.e. = 0.71), for the shortest to longest predominance (no rivalry) respectively. These means are plotted against the four visibility conditions in Fig. 29. This figure shows the group means as a function of the physical condition used, rather than of the actual reported visibility which varied between subjects (see Fig. 28.) and was thus not appropriate for combining all subjects' data into a single analysis. A one-way analysis of variance for repeated measures, with

---

[14] Planned contrasts and a one-way analysis of variance for repeated measures revealed each of the viewing conditions produced a significantly different time in predominance for the adapting plaid (see Appendix Two).

planned orthogonal contrasts in the form of a trend analysis, revealed a significant linear trend ($F_{1,9} = 204.79$, $p \leq 0.0001$), and non-significant quadratic nor cubic trends; $F_{1,9} = 0.44$, $F_{1,9} = 0.0009$ respectively. Finally, the line-of-best-fit was found, and the correlation between treatment and mean duration for each treatment was calculated. These are shown in Fig. 29., along with a similar linear function, this time calculated for the motion aftereffect duration as a function of the actual predominances (as %) observed. While this second function is included merely for comparison, it does suggest that there is a strong correlation between the perception of the physical stimulus and the motion aftereffect duration (the line-of-best-fit predicts 98.4% of the variance).

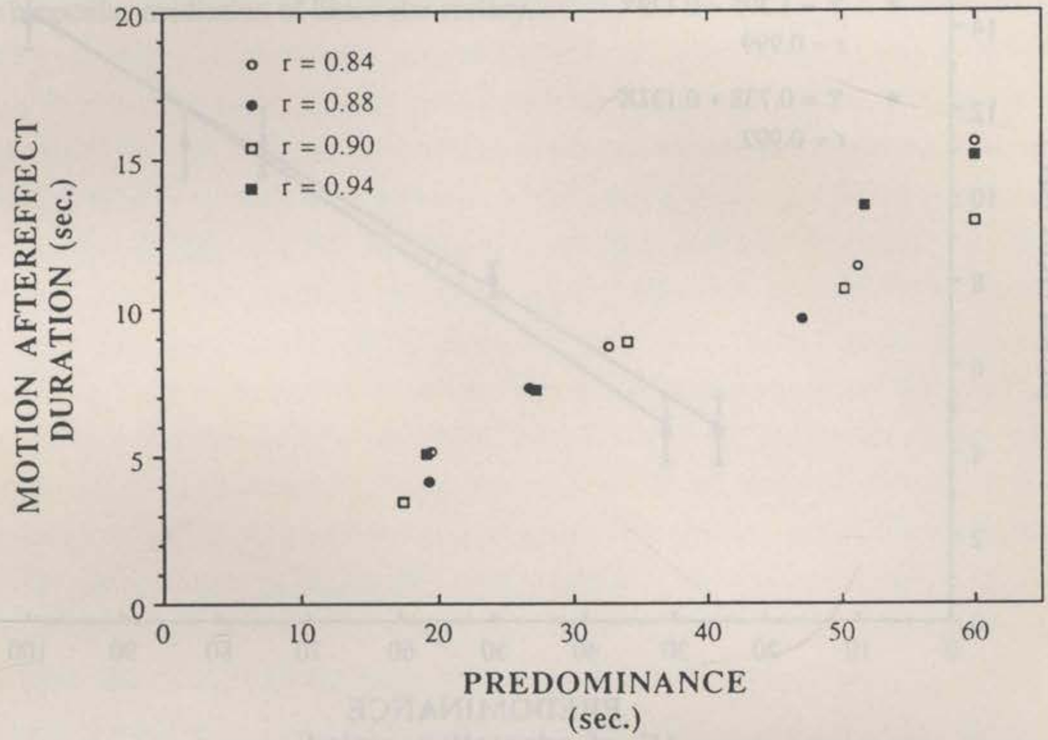


Fig. 28. Motion aftereffect duration as a function of the time for which the adapting pattern predominated during the 60s adaptation period. Note the no-rivalry condition, for which all subjects aftereffects lie at 60s exactly, but also the clustering of the reported predominances for each of the other three conditions. Pearson product-moment correlations between the time the pattern was visible and the motion aftereffect duration are shown for each subject.

Discussion

These last three experiments were designed to test the hypotheses that rivalrous interactions (those described by the model) occur between all groups of binocular neurones, and that activity within such groups can be correlated with predominance.

This they have done. In summary, the results of Experiment Nine demonstrated that plaid motion aftereffects, like purely subjective contour tilt aftereffects (Experiment Five) and spiral motion aftereffects (Wiesenfelder and Blake 1990) can be modulated by periods of rivalry during their induction. It is known that neurones in area MT are almost exclusively binocular, and it seems reasonable to conclude that the interactions occurring during rivalry do so between binocular neurones. An alternative explanation holds that it is possible that earlier monocular interactions mediate rivalry, and that the effects observed with plaid motion aftereffects reflect this. Such an argument is difficult to sustain given that no monocular cells, which occur mainly in area V1, exhibit tuning for plaids, only for their one-dimensional components, and simple linear motion aftereffects induced by such components have been shown to be unaffected by rivalry.

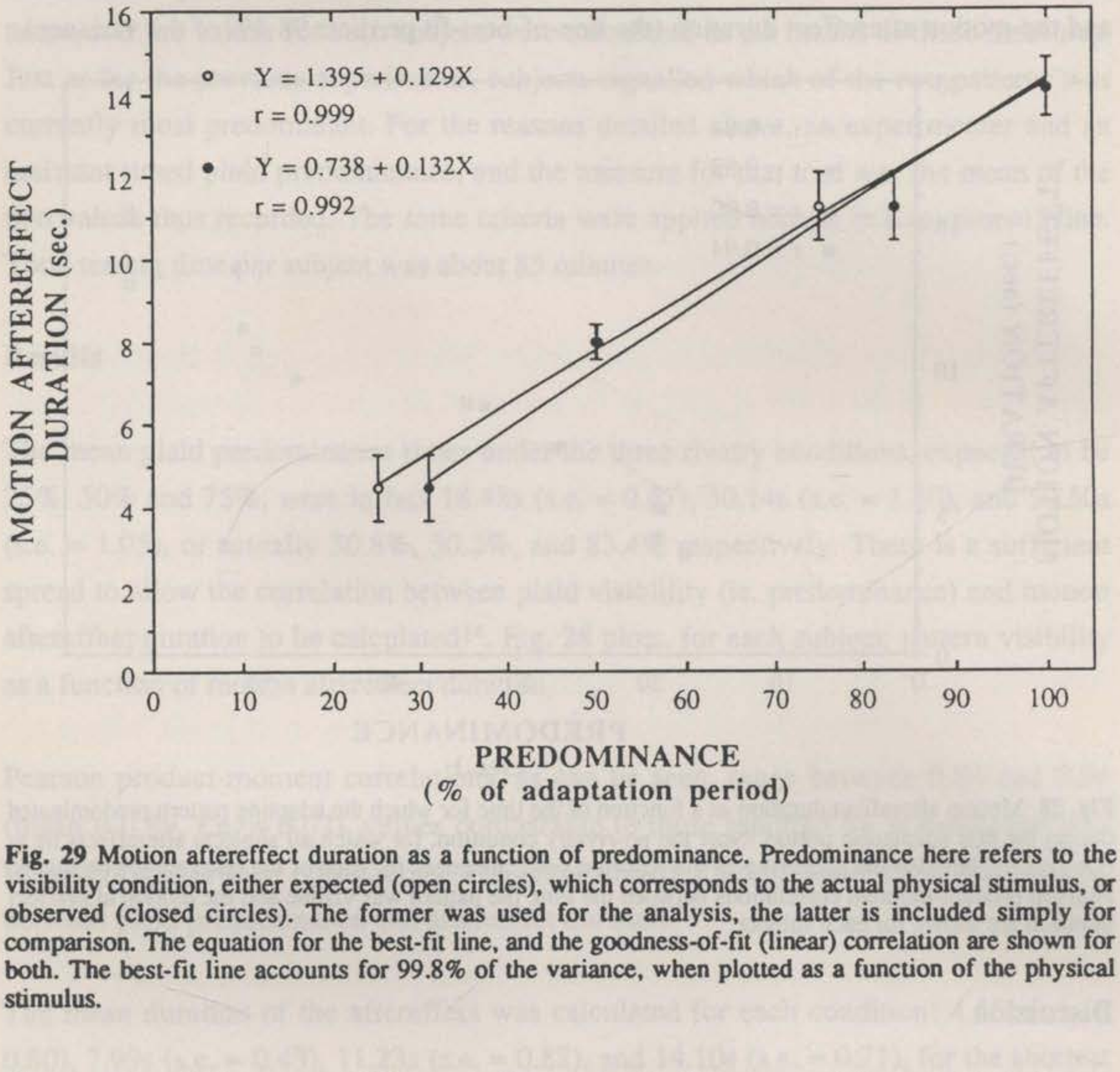


Fig. 29 Motion aftereffect duration as a function of predominance. Predominance here refers to the visibility condition, either expected (open circles), which corresponds to the actual physical stimulus, or observed (closed circles). The former was used for the analysis, the latter is included simply for comparison. The equation for the best-fit line, and the goodness-of-fit (linear) correlation are shown for both. The best-fit line accounts for 99.8% of the variance, when plotted as a function of the physical stimulus.

The results of Experiment Eleven indicate clearly that a correlation exists between predominance during adaptation and aftereffect duration. The binocular model predicts this result on the basis of normal binocular interactions. Predominance of a stimulus during rivalry is related to the activity of cells tuned for that stimulus. Activity, in turn, is related to the aftereffect subsequently generated (it may be related to the number of cells involved also, but this is an issue not addressed here), and so the model predicts a relationship between predominance and the magnitude or duration of an aftereffect. This relationship was demonstrated in this experiment by the strong positive correlation between predominance and aftereffect duration. While correlations themselves demonstrate no causality at all, in the context of these experiments this appears to be evidence for a causal relationship between activity, predominance, and aftereffect. Recall, however, while the correlations described here are linear, this should not be considered strong evidence that the relationships described by the correlation are linear. In fact, if the hypothetical interactions described by the model are in any way realistic they are much more complex. It may be possible to demonstrate, and the model predicts, similar relations between predominance and aftereffect magnitude. This is work for the future, however, as these experiments have provided strong evidence for the binocular mediation of binocular rivlary.

GENERAL DISCUSSION AND CONCLUSIONS

Summary.

A characteristic of binocular rivalry is the compelling perception of competition between the eyes. Monocular views of two different stimuli seem alternately to suppress each other from view. A review and re-analysis of earlier psychophysical and neurophysiological investigations, in terms of currently understood neural interactions, revealed theoretical and empirical evidence which suggested that processing in monocular cell populations is not the substrate of rivalry. Rather, binocular rivalry is described here as arising from binocular interactions. A model, based on the reciprocal inhibition oscillator developed by Mueller (1990), was described. In his model Mueller predicted rivalry on the basis of inhibition between populations of monocular neurones tuned for specific stimulus characteristics. While this aspect of his theory was rejected, the relations described by Mueller's (1990) model accounted for the interactions known to affect activity in a neurone and so his relationships were generalised to binocular neurones and incorporated into a binocular model. This model predicted rivalrous perceptions by assuming most active neurones are those which underlie perception, and that activity is dependent on input (excitation), inhibition (of all types), and fatigue (which causes fluctuations in firing rate even in the presence of constant stimuli). General forms of the inter-relations between these variables was provided, although specific interactions were not formally described. Several predictions about the substrates of rivalry arose from the model. These included the suggestion that rivalry was mediated by binocular neurones in extrastriate cortex.

Processing in extrastriate cortex was utilised to test these predictions. Purely subjective contours are characterised by the perception of edges or lines at locations where they do not exist. An important characteristic of stimuli in which such edges are perceived is that, even in the Fourier domain, there are no components corresponding to the orientation of the perceived subjective edge. In neurophysiological terms, these edges are unique in that no area V1 cells have been found to exhibit tuning for such edges, while some cells area V2 neurones do (von der Heydt and Peterhans 1989). This suggests the tilt aftereffects induced with purely subjective contours (Paradiso, et al. 1989) arise first in area V2. If this is the case, and the mechanisms of purely subjective contour tilt aftereffects can be described, then just as effects ascribed to area V1 have been used to examine the role of that area in rivalry, such effects may be used as a tool for examining the impact of binocular rivalry on processing in extrastriate visual area V2.

Experiments One - Four were aimed at establishing the similarity or differences in the mechanisms of subjective contour and real contour tilt aftereffects, which was necessary if real and subjective contour effects were to be equated. von der Heydt and Peterhans (1989) developed a model which suggested that subjective contour and real contour perceptions arise from similar processes. It follows from their arguments that subjective edges should be processed similarly to real contours. Real contour tilt aftereffects have been shown to arise from two mechanisms; one local which gives rise to direct effects and one global which gives rise to indirect effects (Wenderoth, et al. 1993). Experiment One demonstrated that purely subjective contour tilt aftereffects exhibit angular relations similar to those observed for real contours, and that these can be described in terms of direct and indirect effects. Experiments Two and Three examined the individual mechanisms of subjective contour direct and indirect effects, respectively, and found subjective contour effects behaved similarly to real contour effects. This was taken as evidence that subjective contour direct effects, like real contour direct effects, are generated primarily by lateral inhibitory interactions between orientation selective neurones. The difference between real and subjective contour effects is that the latter can almost certainly be thought of as occurring exclusively beyond area V1. Real contour indirect effects have been ascribed to more global mechanisms (Wenderoth and Johnstone 1988a), possibly involved in orientation constancy, and this seems to be true also of subjective contour indirect effects. Finally, real contour tilt aftereffects and real contour tilt illusions are thought to arise via the same processes (Wenderoth and Johnstone 1987). It follows, therefore, that subjective contours too should elicit tilt illusions comparable to their tilt aftereffects. This was examined in Experiment Four and found to be the case. These experiments established the usefulness of subjective contour tilt aftereffects as a tool for examining the effect of binocular rivalry on extrastriate processing and that conclusions drawn from real contour effects could be extended to subjective contours. They suggest also that subjective contours are processed like real contours, and that equating real and subjective effects has some validity.

Experiment Five examined the impact of periods of binocular rivalry on the magnitude of subjective contour direct and indirect effects. Real contour direct effects are not disrupted by rivalry during their induction (Wade and Wenderoth 1978), and this contributed to the evidence against area V1 cells being involved in generating binocular rivalry. It was found that subjective contour direct effects were diminished by periods of rivalry during their induction. Similarly, so too were subjective contour indirect effects. This was taken as evidence that area V2 neurones are subject to different processing during rivalry than they are otherwise. Referring to the model, and findings reported by Logothetis and Schall (1989), the process by which such disruption occurs was described in terms of the tuning characteristics of area V2 neurones and lessened activity in neurones tuned for the adapting stimulus during rivalry. Binocular neurones can respond to characteristics of both the adapting and rivalrous stimuli, and because such responses will occur across the array of binocular cells, interactions between cells generate dynamic changes in the activity of those cells. Because activity changes, inhibition and fatigue rates will change, disrupting the rate of adaptation to the adapting stimulus. The outcome of these interactions is that after rivalrous adaptation cells are less adapted than they are after adaptation without rivalry. Experiment Six provided a control for Experiment Five, replicating the earlier finding that real contour direct tilt aftereffects are not disrupted by rivalry. This suggested conclusions that rivalry arises beyond area V1 are valid. Importantly, real contour indirect tilt aftereffects were found to be disrupted by rivalry during their induction. This reinforces arguments for their origin being 'higher order' and probably extrastriate (Wenderoth and Johnstone 1987). It reinforces also the suggestion that rivalry too is an extrastriate process.

While the previous experiments provided indirect evidence that binocular rivalry is mediated primarily through binocular interactions, it was possible to more directly address this issue. Burkhalter and Van Essen (1986) and Tootell and Hamilton (1989) described area V2 neurones as being almost completely binocular, but with slight differences in the ocular dominance of those binocular cells. On the basis of this observation it was predicted that complete interocular transfer of subjective contour tilt afterteffects would be observed, if these effects were induced without rivalry. As to such effects induced with rivalry, the question that followed was whether all binocular cells are affected equally by dichoptically dissimilar inputs, or whether ocular dominance is a factor. Experiment Seven was designed to examine these issues, and complete interocular transfer of subjective contour tilt aftereffects induced without rivalry was observed. This was interpreted as evidence that subjective contour tilt aftereffects are mediated only by binocular neurones. The magnitude of the aftereffect measured interocularly after adaptation plus rivalry was slightly reduced compared to the aftereffect measured interocularly after no rivalry. This was taken as evidence that small differences in ocular dominance results in cells adapting at slightly different rates, cells driven more by the eye receiving a monocularly presented stimulus adapt more quickly than cells driven more by the contra-lateral eye. While this difference is not observable for long adaptation times when there is no rivalry, when there is rivalry the effect is such that it is like a shorter adaptation period, that is, there is less adaptation. This results in those cells most strongly driven by the unadapted eye being least adapted and testing interocularly highlights this difference.

The results of this experiment suggested not only that subjective contour tilt aftereffects were binocular in origin, but that binocular rivalry was binocular in origin also. Similarly, it provided some support for the suggestion that rivalry arose from extrastriate interactions. Experiment Eight examined these conclusions by replicating the manipulations made in Experiment Seven, but by using real contour stimuli. The data for this experiment showed that while no monocular neurones were involved in generating the subjective contour tilt aftereffect, they were similarly not involved in mediating binocular rivalry. More than this, they demonstrated also that it is unlikely that any neurones in area V1, monocular or binocular, are involved in binocular rivalry. Thus the second aspect of the model, that rivalry arises via extrastriate interactions, was validated

The final three experiments were included to examine several issues that arose during the investigation. The explanation of rivalry offered by the binocular model suggested that rivalry generating interactions occur between extrastriate binocular neurones. The question arose as to whether such processing was limited to area V2 or could be generalised to any extrastriate location? Data presented by Logothetis and Schall (1989) and Wiesenfelder and Blake (1990) supported the view that rivalry manifests via interactions throughout the extrastriate cortex. The perception of two dimensional plaid motion has been linked with activity in pattern selective cells in area MT (eg. Movshon, et al. 1985), and plaid motion aftereffects are thought to be linked to these cells also (eg. Wenderoth, et al. 1988). Experiment Nine examined the impact of binocular rivalry on the duration of plaid motion aftereffects and found that rivalry during adaptation caused a reduction in the duration of the plaid motion aftereffect. Experiment Ten demonstrated these same reductions were not observed for aftereffects induced with more simple moving stimuli, which are thought to have a significant area V1 component. In addition to providing support for the rationale that generated the conclusions drawn from Experiments Seven and Eight, these experiments provided sufficient evidence to conclude that rivalry probably disrupts all extrastriate processing: plaid motion aftereffects, subjective contour tilt aftereffects and spiral motion aftereffects are all thought to have extrastriate origins. Since no area V1 processes have been shown to be similarly sensitive to rivalry; since area V1 is the only visual area with significant monocular cell populations; and since all extrastriate cortex is thought to be predominantly binocular, this was additional evidence that rivalry is a binocular not a monocular process. While this provides support for a binocular model of rivalry, the model also predicts that the amount of adaptation occurring in cells tuned to the adapting stimulus is proportional to activity in those cells during rivalry, and this in turn is proportional to the time the adapting stimulus predominated during the adapting period. It follows that predominance and the magnitude or duration of the aftereffect will be correlated. This conclusion is supported by the roughly proportional relations observed between predominance and aftereffect magnitude reduction observed in the earlier experiments, and the data described by Wiesenfelder and Blake (1990). Those workers showed the duration of the spiral motion aftereffect was linearly correlated with the predominance of the spiral during adaptation with rivalry. Experiment Eleven examined the correlation between plaid motion aftereffect duration and the predominance of the plaid during adaptation with rivalry. A strong, significant linear correlation was observed, and while correlations are not evidence of causal relations this was interpreted as further support for the binocular model[15].

Conclusions

These experiments have elucidated possible neural correlates for binocular rivalry. They have demonstrated that rivalry can be thought of as the perceptual consequence of normal neural interactions. The binocular model, which proposed that excitation, inhibition and fatigue in groups of binocular neurones is all that is required in order to account for rivalry, was shown to be of some value. Not only can it account for previous findings by other researchers, but it was used successfully to predict the effects described here. On this basis, it is concluded that binocular rivalry arises through interactions between groups of binocular neurones. Monocular neurones appear not to be involved in generating the perception of rivalry, nor are they required for it. Further, the data reported here suggests that in addition to being binocular, rivalry arises through interactions between extrastriate neurones. Processing in area V1 seems not to be involved. In addition to these findings, it was also demonstrated that purely subjective contours, once encoded appear to be treated by the visual system as if they were real. This is in line with models suggesting that subjective contours are the product of the processes involved in real contour perception (von der Heydt and Peterhans 1989).

Some Implications.

The final experiments suggest that any aftereffect attributable to extrastriate processing might reflect the impact of rivalry during their induction in terms of a diminution in their magnitude, or duration, or both. For example, spiral motion is complex and the

---

[15] While they were not considered in the explanation of the results, some comment is required on the possible role of eye movements in generating some of the effects described here. It is certainly the case that eye movements may change perceptions during rivalry, and this has already been discussed. There is no evidence that eye movements could be linked with any of these aftereffects under the experimental conditions employed. In the case of the last experiments, for example, it has been reported that only very small eye movements accompany adaptation with a horizontal drifting grating when the subject fixates and no eye movements accompany the motion aftereffect which is generated, even with a stimulus subtending >30° visual angle and moving at $6\text{-}9^{\circ}s^{-1}$ (Seidman et al. 1992). Thus it seems reasonable to assume that eye movements are not involved in these aftereffects.

spiral motion aftereffect has been shown to be sensitive to rivalry (Wiesenfelder and Blake 1990). Spiral motion can be broken up into more simple component motions; rotary motion and field expansion or contraction, just as plaid motion can be described in terms of its component motions. While aftereffects induced by the individual components of plaid motion are not affected by rivalry, both the 'simpler' motions contributing to spiral motion are themselves thought to be extrastriate in origin. No area V1 cells exhibit tuning characteristics appropriate for unambiguously signalling either rotary motion nor expansion/contraction. On the other hand, Sakata, et al. (1986) found parietal neurones sensitive for rotary motion, while Tanaka and Saito (1989) found neurones in area MST sensitive for field flow (expansion or contraction). On the basis of the work reported here, it must be predicted that aftereffects induced with these motions would be sensitive to rivalry during their induction, and work is currently underway to test this hypothesis. Similarities and differences in the effect of rivalry on effects induced by simple and more complex motions may reveal much about binocular rivalry, but also about how compound motions are 'built up' from more simple motions. However, it is likely that more complicated examinations of the temporal characteristics of rivalry, tuning sensitivities of neurones during rivalry, and of stimulus relations will be required for complete understanding of these interactions.

Finally, there are two issues in binocular rivalry research which have not been addressed previously in this investigation, and they have important implications for the nature of visual processing generally. First is the observation that for very short presentation durations, normally rivalrous stimuli can be perceived as a coherent, single percept (Wolfe 1983, O'Shea and Crassini 1984). These workers have reported that presentation durations of longer than approximately 400ms are required before rivalry manifests. Some workers (eg. Blake 1989) have taken this observation as evidence of the magno-cellular nature of the rivalry mechanism, and it might be possible to couch explanations in terms of the transient nature of the responses of some magno-cellular cells in order to strengthen this position. On the other hand, there is some evidence that colour can generate rivalry (eg. Hollins and Leung 1978), and very recently Nguyen and Freeman (1994) have presented evidence suggesting that rivalry exhibits characteristics of parvocellular mechanisms. The apparent discrepancy between these results reflects what is probably an unnecessary dichotomy in explanations of binocular rivalry. That is, it is not necessary that rivalry must arise via magno- or parvo-cellular mechanisms. The types of interactions described by the binocular model are not restricted to either of these pathways, and if they can occur equally in one, or the other, or in both, it is perhaps not surprising that different studies, each examining different stimulus properties characteristic of one pathway or the other, find evidence that rivalry occurs in one pathway or the other. Stoner and Albright (1993) and Peterhans and von der Heydt (1993) have highlighted ambiguities that can arise in treating the processes of vision as being exclusive to one stream or the other, particularly in terms of their functional significance. It may be the case that in terms of explanation the parvo/magno dichotomy is useful anatomically but this may be less so psychophysically.

Second is the issue of stereopsis, and whether rivalry and stereopsis can co-exist. Again on this issue, different workers have presented conflicting results. A number of workers have argued that rivalry and stereopsis cannot coexist (Blake and Boothroyd 1985, Blake 1989, Shimojo and Nakayama 1990). These workers generally base the rationale for their conclusions on the assumption that rivalry arises as the default outcome of a failure to find a solution to the problem of binocular correspondence (Blake 1989). Other workers have argued that rivalry and stereopsis can occur concurrently. Julesz and Miller (1975) described evidence that suggested stereopsis involves input from spatial frequency tuned channels. They argued also that such channels can operate independently, and while some channels might be involved in rivalry, others simultaneously could support stereopsis. From this position, stereopsis and rivalry can be thought of as exclusive, at least within channels, but can coexist within the visual system. Wolfe (1986) developed a theory of vision in which stereopsis and rivalry occupy parallel, but independent pathways and can coexist without any restrictions, while O'Shea and Blake (1987) developed displays in which depth can be perceived during rivalry. More recently, a more complicated relationship between rivalry and stereopsis has been proposed by Blake, Yang and Wilson (1991). Using random dot stereograms with and without noise added to the right hand side of the stereogram those workers found that stereopsis occurred in the absence of rivalry if noise was low. However, as noise in the right field increased sufficiently to generate piecemeal rivalry between the two random dot fields, local regions were perceived either as engaging in rivalry, or as stable and in depth, but not both at the same spatial locations. At very high noise levels the right field predominated entirely and there was no stereopsis. Blake and his colleagues interpret these results as indicating that stereopsis and rivalry cannot coexist at a given location, but that they can within a visual field. In terms of the binocular model of rivalry, these results are consistent with the argument that localised regions of activity govern perception and if these are involved in rivalry, then that is what is perceived at that location. Rather than rejecting the notion that stereopsis can occur at those locations, however, it is proposed here that qualitative variations in stereopsis occur during rivalry, just as they do for varying degrees of diplopia. If rivalry is linked to activity, and stereopsis depends on activity in cells tuned for disparity (Livingstone and Hubel 1984, Livingstone and Hubel 1987, Tootell and Hamilton 1989), it seems reasonable to conclude that if binocular cells like those tuned for disparity are involved in interactions generating rivalry, then as activity in those cells varies during rivalry, so will their contribution to stereopsis. For example, Blake, et al. (1991) used spatial frequency channels to generate rivalry and found little evidence for stereopsis during rivalry. As pointed out by Peterhans and von der Heydt (1993), in area V2, which these experiments implicate strongly in rivalry, cells tuned for spatial frequency and for disparity are closely linked. Less closely linked are cells tuned for wavelength and disparity, so it might be expected that colour rivalry and stereopsis could coexist, and this is exactly what Ramachandran, et al. (1973) reported. In terms of the results of Julesz and Miller (1975) and of Blake, et al. (1991) it may be necessary to readdress the strength of stereopsis at locations involved in rivalry. At these locations stereopsis may appear to be absent, but this may be a comparative measure made with respect to other regions, visible simultaneously, in which depth is clearly perceived. In this situation, it may not be useful to describe stereopsis as occurring or not occurring during rivalry, but rather to consider the effectiveness of the mechanism for stereopsis, a consideration which perhaps should be generalised to all cortical processes.

REFERENCES

Abadi, R.V. (1976) Induction masking - a study of some inhibitory interactions during dichoptic viewing. Vision Research, 16, 269-275.

Adleson, E.H. & Movshon, J.A. (1982) Phenomenal coherence of moving visual patterns. Nature, 300, 523-525.

Alais, D., Wenderoth, P. & Burke, D. (1994) The contribution of 1-D motion mechanisms to the perceived direction of drifting plaids and their aftereffects. Vision Research, in press.

Albright, T.D. (1984) Direction and orientation selectivity of neurones in visual area MT of the macaque. Journal of Neurophysiology, 52, 1106-1130.

Albright, T.D. & Desimone, R. (1987) Local precision of visuotopic organisation in the middle temporal area (MT) of the macaque. Experimental Brain Research, 65, 582-592.

Albright, T.D., Desimone, R. & Gross, C.G. (1984) Columnar organisation of directionally selective cells in visual area MT of the macaque. Journal of Neurophysiology, 51, 16-31.

Allman, J.M., Miezin, F. & McGuiness, E. (1985a) Stimulus specific responses from beyond the classic receptive field: Neurophysiological mechanisms for local-global comparisons in visual neurones. Annual Review of Neuroscience, 8, 407-430.

Allman, J.M., Miezin, F. & McGuiness, E. (1985b) Direction- and velocity-specific responses from beyond the classic receptive field in the middle temporal visual area (MT). Perception, 14, 105-126.

Baizer, J.S., Robinson, D.L. & Dow, B.M. (1977) Visual responses of area 18 neurones in awake, behaving monkey. Journal of Neurophysiology, 40, 1024-1037.

Barrell, J.J. & Parks, T. (1969) Hemi-retinal attention under conditions of color rivalry. Perception and Psychophysics, 5, 246-248.

Bauer, R., Hoffman, K.P., Huber, H.P. & Mayr, M. (1989) Different anisotropies of movement direction in upper and lower layers of the cat's area 18 and their implications for global optic flow processing. Experimental Brain Research, 74, 395-401.

Bauman, L.A. & Bonds, A.B. (1989) Inhibitory refinement of the spatial frequency bandpass of single cells in the cat striate cortex. Seeing Contour and Colour, ed. Kulikowski, J.J., Dickinson, C.M. & Murray, I.J. Oxford: Pergammon Press.

Berkley, M.A., Debruyn, B. & Orban, G. (1994) Illusory, motion, and luminance-defined contours interact in the human visual system. Vision Research, 34, 209-216.

Blake, R. (1977) Threshold conditions for binocular rivalry. Journal of Experimental Psychology: Human Perception and Performance, 3, 251-257.

Blake, R. (1989) A neural theory of binocular rivalry. Psychological Review, 96, 145-167.

Blake, R. & Boothroyd, K. (1987) The precedence of binocular fusion over binocular rivalry. Perception and Psychophysics, 37, 114-124.

References.

Blake, R. & Fox, R. (1974a) Adaptation to invisible gratings and the site of binocular rivalry suppression. Nature, 249, 488-490.

Blake, R. & Fox, R. (1974b) Binocular rivalry suppression: Insensitive to spatial frequency and orientation change. Vision Research, 14, 687-692.

Blake, R. & Lehmkuhle, S.W. (1976) On the site of strabismic suppression. Investigative Ophthalmology, 15, 660-663.

Blake, R. & O'Shea, R. (1988). Abnormal fusion of stereopsis and binocular rivalry. Psychological Review, 95, 151-154.

Blake, R., O'Shea, R.P. & Mueller, T.J. (1992) Spatial zones of binocular rivalry in central and peripheral vision. Visual Neuroscience, 8, 469-478.

Blake, R. & Overton, R. (1979) The site of binocular rivalry suppression. Perception, 8, 143-152.

Blake, R., Sloane, M. & Fox, R. (1981) Further developments in binocular summation. Perception and Psychophysics, 30, 266-276.

Blake, R., Westendorf, D. & Overton, R. (1980) What is suppressed during binocular rivalry? Perception, 9, 223-231.

Blake, R., Yang, Y. & Wilson, H.R. (1991) On the coexistence of stereopsis and binocular rivalry. Vision Research, 31, 1191-1203.

Blake, R., Zimba, L. & Williams, D. (1985) Visual motion, binocular correspondence and binocular rivalry. Biological Cybernetics, 52, 391-397.

Blakemore, C. (1970) A new kind of stereopsis. Vision Research, 10, 1181-1199.

Blakemore, C., Carpenter, R.H.S. & Georgeson, M.A. (1970) Lateral inhibition between orientation detectors in the human visual system. Nature, 228, 37-39.

Boynton, R.M. (1978) Ten years of research with the minimally distinct border. Visual Psychophysics and Physiology. J.C. Armington, J. Krauskopf, and B.R. Wooten (eds) New York: Academic Press, pp. 193-207.

Braddick, O. (1979) Binocular single vision and perceptual processing. Proceedings of the Royal Society of London, B, 204, 503-512.

Braddick, O., Campbell, F.W. & Atkinson, J. (1978) Channels in vision: Basic aspects. Handbook of Sensory Physiology, VIII. Perception. R. Held, H.W. Leibowitz & H-L Teuber (eds) Heidelberg: Springer-Verlag, pp. 3-38.

Bradley, D.R. (1982) Binocular rivalry of real vs. subjective contours. Perception and Psychophysics, 32, 85-87.

Bradley, D.R. & Dumais, S.T. (1975) Ambiguous cognitive contours. Nature, 257, 582-584.

Bravo, M., Blake, R. & Morrison, S. (1988) Cats see subjective contours. Vision Research, 28, 861-865.

Breese, B.B. (1899) On Inhibition. Psychological Monographs, 3, 1-65.

Breese, B.B. (1909) Binocular rivalry. Psychological Review, 16, 410-415.

Burke, D. & Wenderoth, P. (1989) Cyclopean tilt aftereffects can be induced monocularly: is there a purely binocular process. Perception, 18, 471-482.

Burke, D. & Wenderoth, P. (1993) Determinants of two-dimensional motion aftereffects induced by simultaneous and alternately presented plaid components. Vision Research, 33, 351-359.

Burkhalter, A., Felleman, D.J., Newsome, W.T. & Van Essen, D.C. (1986) Anatomical and physiological asymmetries related to visual areas V3 and VP in macaque extrastriate cortex. Vision Research, 26, 63-80.

Burkhalter, A. & Van Essen, D.C. (1986) Processing of colour, form and disparity information in visual areas VP and V2 of ventral extrastriate cortex in the macaque monkey. Journal of Neuroscience, 6, 2327-2351.

Burr, D.C. & Morrone, M.C. (1987) Inhibitory interactions in the human vision system revealed in pattern-evoked potentials. Journal of Physiology, 389, 1-21.

Carlson, N.R. (1991) Physiology of Behaviour, 4ed. Boston: Allyn and Bacon.

Carpenter, R.H.S. & Blakemore, C. (1973) Interactions between orientations in human vision. Experimental Brain Research, 18, 287-303.

Cavanagh, P. & Favreau, O.E. (1980) Motion aftereffect: A global mechanism for the perception of ratation. Perception, 9, 175-182.

Chaudhuri, A. (1991) Eye movements and the motion aftereffect: Alternatives to the induced motion hypothesis. Vision Research, 31, 1639-1645.

Cogan, A.I. (1987) Human binocular interaction: Towards a neural model. Vision Research, 27, 2152-2139.

Cohen, J. (1988) Statistical Power Analysis For The Behavioural Sciences, Revised ed. Hillsdale: Lawrence Erlbaum.

Creed, R.S. (1935) Observations on binocular fusion and rivalry. Journal of Physiology, 84, 381-392.

Crovitz, H.F. (1964) Retinal locus of tachistoscopic binocular color rivalry. Perceptual and Motor Skills, 19, 808-819.

DeValois, K.K., De Valois, R.L. & Yund, E.W. (1979) Responses of striate cortex cells to grating and checkerboard patterns. Journal of Physiology (London), 291, 483-505.

de Weert, C.M.M. & Wade, N.J. (1988) Compound binocular rivalry. Vision Research, 28, 1031-1040.

DeYoe, E.A. & Van Essen, D.C. (1985) Segregation of efferent connections and receptive field peroperties in visual area V2 of the macaque. Nature, 317, 58-61.

DeYoe, E.A. & Van Essen, D.C. (1988) Concurrent processing streams in monkey visual cortex. Trends in Neuroscience, 11, 451-456.

DuTour, E.F. (1760) Discussion d'unequestion d'optique. Mathematics and Physics Academy of the Royal Society of Paris, 3, 514-530.

Ebenholtz, S. & Utrie, J.W. (1983) Peripheral circulation contours inhibit the visual orientation control system. Aviation, Space and Environmental Medicine, 54, 343-346.

Fahle, M. & Palm, G. (1991) Perceptual rivalry between illusory and real contours. Biological Cybernetics, 66, 1-8.

Felleman, D.J. & Van Essen, D.C. (1987) Receptive field properties of neurons in area V3 of macaque monkey extrastriate cortex. Journal of Neurophysiology, 57, 889-920.

Ferster, D. (1986) Orientation selectivity of synaptic potentials in neurones of cat primary visual cortex. Journal of Neuroscience, 6, 1284-1301.

Ferster, D. (1988) Spatially opponent excitation and inhibition in simple cells of the cat visual cortex. Journal of Neuroscience, 8, 1172-1180.

Foster, K.H., Gaska, J.P., Nagler, M. & Pollen, D.A. (1985) Spatial and temporal frequency selectivity of neurones in visual cortical areas V1 and V2 of the macaque monkey. Journal of Physiology (London), 365, 331-363.

Fox, R. & Rasche, F. (1969) Binocular rivalry and reciprocal inhibition. Perception and Psychophysics, 5, 215-217.

Gattass, R., Gross, C.G. & Sandell, J.H. (1981) Visual topography of V2 in the macaque. Journal of Comparative Neurology, 201, 519-539.

Gibson, J.J. & Radner, M. (1937) Adaptation, aftereffect and contrast in perception of tilted lines. 1: Quantitative studies. Journal of Experimental Psychology, 20, 453-467.

Grosof, D.H. Shapley, R.M. & Hawken, M.J. (1993) Macaque V1 neurones can signal 'illusory' contours. Nature, 365, 550-552.

Grossberg, S. (1987) Cortical dynamics of three dimensional form, colour, and brightness perception: II. Binocular theory. Perception and Psychophysics, 41, 117-158.

Hastorf, A.H. & Myro, G. (1959) The effect of meaning on binocular rivalry. American Journal of Psychology, 72, 393-400.

Hering, E. (1964) Outlines Of A Theory Of The Light Sense (L Hurvich and D. Jameson, Translators) Cambridge: Harvard University Press (Originally Published 1920).

Hershenson, M. (1984) Phantom spiral aftereffect: Evidence for global mechanisms in perception. Bulletin of the Psychonomic Society, 22, 535-537.

Hollins, M. & Leung, E.H.L. (1978) The influence of colour on binocular rivalry. Visual Psychophysics and Physiology, ed. J.C. Armington, J. Krauskopf & B.R. Wooten, New York: Academic Press.

Horridge, G.A., Zhang, S-W. & O'Carrol, D. (1992) Insect perception of illusory contours. Philosophical Transcripts of the Royal Society - London, 335,

Howard, I. (1982) Human Visual Orientation. New York: Wiley.

Hubel, D. & Livingstone, M. (1987) Segregation of form, colour, and stereopsis in primate area 18. Journal of Neuroscience, 7, 3378-3415.

Hubel, D.H. & Wiesel, T.N. (1959) Receptive fields of single neurones in the cat's striate cortex. Journal of Physiology (Lond.), 148, 574-591.

Hubel, D.H. & Wiesel, T.N. (1962) Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. Journal of Physiology (Lond.), 160, 106-154.

Jefferys, D.A. (1977) Evoked potential evidence for contour-abstraction in prestriate cortex. Journal of Physiology (London), 275, 59P.

Johannsen, D.E. (1930) A quantitative study of binocular color vision. Journal of General Psychology, 4, 282-308.

Julesz, B. (1971) Foundations of Cyclopean Perception. Chicago: Chicago University Press.

Julesz, B. & Miller, J.E. (1975) Independent spatial frequency-tuned channels in binocular fusion and rivalry. Perception, 4, 125-143.

Kaiser, P.K. & Boynton, R.M. (1985) Role of the blue mechanism in wavelength discrimination. Vision Research, 25, 523-529.

Kandel, E.R. & Schwartz, J.H. (1985) Principles of Neural Science, 2ed. New York: Raven Press.

Kaufman, L. (1964) Suppression and fusion in viewing complex stereograms. American Journal of Psychology, 77, 193-205.

Kepple, G. (1973) Design and Analysis: A Researchers Handbook. Englewoods Cliffs, New Jersey: Prentice Hall.

Kertesz, A.E. & Jones, R.W. (1970) Human cyclofusional response. Vision Research, 10, 891-896.

Koch, C. & Segev, I. (1989) Methods in Neuronal Modelling: From Synapses to Networks. Cambridge: MIT Press.

Kohler, W. & Wallach, H. (1944) Figural-aftereffects: An investigation of visual processes. Proceedings of the American Philosophical Society, 88, 269-357.

Krubitzer, L. & Kaas, J. (1990) Convergence of processing channles in the extrastriate cortex of monkeys. Visual Neuroscience, 5, 609-613.

Lack, L.C. (1978) Selective Attention And The Control Of Binocular Rivalry. The Hague: Mouton.

Lamme, V.A.F., van Dijk, B.W. & Spekreijse, H. (1993) Contour from motion processing occurs in primary visual cortex. Nature, 363, 541-543.

Lee, B.B., Martin, P.R. & Valberg, A. (1989) Nonlinearity of summation of M- and L- cone inputs to phasic retinal ganglion cells of the macaque. Journal of Neuroscience, 9, 1433-1442.

Lehky, S.R. (1988) An astable multivibrator model of binocular rivalry. Perception, 17, 215-228.

Lehmkuhle, S.W. & Fox, R. (1975) Effect of binocular rivalry suppression on the motion aftereffect. Vision Research, 15, 855-859.

Lesher, G. & Mingolla, E. (1993). The role of edges and line-ends in illusory contour formation. Vision Research, 33, 2253-2270.

Levelt, W.J.M. (1965) Binocular brightness averaging and contour information. British Journal of Psychology, 56, 1-13.

Levelt, W.J.M. (1968) On Binocular Rivalry. The Hague: Mouton.

Levine, M.W. & Shefner, J.M. (1991) Fundamentals of Sensation and Perception, 2ed. Pacific Grove: Brooks/Cole.

Livingstone M. & Hubel D. (1982) Thalamic inputs to cytochrome oxidase-rich regions in monkey visual cortex. Proceedings of the National Academy of Science (USA), 79, 6098-7101.

Livingstone, M.S. & Hubel, D.H. (1984) Anatomy and physiology of a colour system in the primate visual cortex. Journal of Neuroscience, 4, 309-356.

Livingstone M. & Hubel D. (1988) Segregation of form, colour, movement, and depth: Anatomy, physiology, and perception. Science, 240, 740-749.

Logothetis, N.K. & Schall, J.D. (1989). Neural correlates of subjective visual perception. Science, 245, 761-763.

Logothetis, N.K., Schiller, p.H., Charles, E.R. & Hulbert, A.C. (1990) Perceptual deficits and the activity of the color-opponent and broad-band pathways at isoluminance. Science, 247, 214-217.

Marr, D. (1977) Artificial Intelligence - A Personal View. Artificial Intelligence, 9, 37-48.

Matsuoka, K. (1984) The dynamic model of binocular rivalry. Biological Cybernetics, 49, 201-208.

Magnussen, S. & Johnsen, T. (1986) Temporal aspects of spatial adaptation: A study of the tilt aftereffect. Vision Research, 26, 661-671.

Maunsell, J.H.R. & Newsome, W.T. (1987) Visual Processing in Monkey Extrastriate Cortex. Annual Review of Neuroscience, 10, 363-402.

McKenna, T., Davis, J. & Zornetzer, S.F. (1992) Single Neurone Computation. New York: Academic Press.

McIlwain, J.T. (1964) Recpetive fields of optic tract axons and lateral geniculate cells: Peripheral extent and barbituate sensitivity. Journal of Neurophysiology, 27, 1154-1173.

Meenes, M. (1930) A phenomenological description of retinal rivalry. American Journal of Psychology, 42, 260-269.

Merigan, W.H., Nealey, T.A. & Maunsell, J.H.R. (1993) Visual effects of lesions in cortivcal area V2 of macaques. Journal of Neuroscience, 13, 3180-3191.

Morant, R.B. & Harris, J.R. (1965) Two different aftereffects of exposure to visual tilts. American Journal of Psychology, 78, 218-226.

Morgan, M.J. (1989). Watching neurones discriminate. Nature, 341, 20-21

Morrone, M.C., Burr, D.C. & Maffei, L. (1982) Functional implications of cross-orientation inhibition of cortical visual cells. I. Neurophysiological evidence. Proceedings of the Royal Society, London, B216, 335-354.

Movshon, J.A., Adelson, E.H., Gizzi, M.S. & Newsome, W.T. (1985) The analysis of moving visual patterns. Pattern Recognition Mechanisms, ed. Chagas, C., Gattass, R. & Gross, C. Rome: Vatican Press.

Mueller, T.J. (1990) A physiological model of binocular rivalry. Visual Neuroscience, 4, 63-73.

Mueller, T.J. & Blake, R. (1989) A fresh look at the temporal dynamics of binocular rivalry. Biological Cybernetics, 61, 223-232.

Nelson, J.I. (1985) Globality and stereoscopic fusion in binocular vision. Journal of Theoretical Biology, 49, 1-88.

Nguyen, V.A. & Freeman, A.W. (1994) Changes in spatial vision during interocular suppression. Presented at 14th Australian Neuroscience Society Conference.

Oatley, K. (1978) Perceptions and Representations. London: Methuen.

Orban, G. (1984) Neuronal Operations In the Visual Cortex. Berlin: Springer Verlag.

O'Shea, R. & Blake, R. (1987) Depth without disparity in random dot stereograms. Perception and Psychophysics, 42, 205-214.

O'Shea, R. & Crassini, B. (1981) Interocular transfer of the motion aftereffect is not reduced by binocular rivalry. Vision Research, 21, 801-804.

O'Shea, R. & Crassini, B. (1984) Binocular rivalry occurs without simultaneous presentation of rival stimuli. Perception and Psychophysics, 36, 266-276.

O'Toole, B. & Wenderoth, P. (1977) The tilt illusion: Repulsion and attraction effects in the oblique meridian. Vision Research, 17, 367-374.

Over, R. (1971) Comparisons of normalisation theory and neural enhancement explanation of negative aftereffects. Psychological Bulletin, 75, 225-243.

Paradiso MA, Shimojo S & Nakayama K. (1989) Subjective contours, tilt aftereffects, and visual cortical organisation. Vision Research, 29, 1205-1213.

Peterhans, E. & von der Heydt, R. (1987) The role of end-stopped receptive fields in contour perception. New Frontiers in Brain Research (Proceedings of the 15th Gottingen Neurobiology Conference), ed. Elsner, N. & Creutzfeldt, O. Stuttgart: Thieme Verlag.

Peterhans, E. & von der Heydt, R. (1989) Mechanisms of contour in Monkey visual cortex. II. Contours Bridging Gaps. Journal of Neuroscience, 9, 1749-1763.

Peterhans, E. & von der Heydt, R. (1991) Subjective contours - bridging the gap between psychophysics and physiology. Trends in Neurosciences, 14, 112-119.

Peterhans, E. & von der Heydt, R. (1993) Functional organisation of area V2 in the alert Macaque. European Journal of Neuroscience, 5, 509-524.

Pickford, R.W. (1947) Binocular colour combinations. Nature, 159, 268-269.

Reeke, G.N. & Sporns, O. (1993) Behaviourally based modelling and computational approaches to neuroscience. Annual Review of Neuroscience, 16, 597-623.

Ramachandran, V.S. & Sriram, S. (1972) Stereopsis generated with Julesz patterns in spite of rivalry imposed by colour filters. Nature, 237, 347-348.

Ramachandran, V.S., Rao, V.M., Sriram, S. & Vidyasagar, T.R. (1973) The role of colour perception and "pattern" recognition in stereopsis. Vision Research, 13, 505-509.

Rogers, D.C. & Hollins, M. (1982) Is the binocular rivalry mechanism tritanopic? Vision Research, 22, 515-520.

Rose, D. (1980) The binocular: monocular sensitivity ratio for movement detection varies with temporal frequency. Perception, 9, 577-580.

Rose, D., Blake, R. & Haplern, D.L. (1989) The relationship between binocular summation, Fusion, stereopsis and allelotropia. Seeing Contour and Colour, ed. Kulikowski, J.J., Dickinson, C.M. & Murray, I.J. Oxford: Pergammon Press.

Sagawa, K. (1981) Minimum light intensity required for color rivalry. Vision Research, 21, 1467-1474.

Sakata, H. , Shibutani, H., Ito, Y. & Tsurugai, K. (1986) Parietal cortical neurones responding to rotary movement of visual stimulus in space. Experimental Brain Research, 61, 658-663.

Sekuler, R., Pantle, A. & Levinson, E. (1978) Physiological Basis of Motion Perception. Handbook of Sensory Physiology, VIII, Perception. R. Held, H.W. Leibowitz & H-L Teuber (eds) Heidelberg: Springer-Verlag, pp. 67-96.

Seidman, S.H., Leigh, R.J. & Thomas, C.W. (1992) Eye movements during motion aftereffect. Vision Research, 32, 167-171.

Selverston, A.I. (1993) Modelling of neural circuits: What have we learned? Annual Review of Neuroscience, 16, 531-546.

Shimojo, S. & Nakayama, K. (1990) Real world occlusion constraints and binocular rivalry. Vision Research, 30, 69-80.

Shipp, S. & Zeki, S. (1985) Segregation of pathways leading from area V2 to areas V4 and V5 of macaque monkey visual cortex. Nature, 315, 322-325.

Sloane, M.E. (1985) Binocular rivalry: A psychophysics in search of a physiology. Models of Visual Cortex, ed. Rose, D. & Dobson, V. Chichester: Wiley.

Smith, D. (1992) Coherence of plaids comprising components of disparate spatial frequencies. Vision Research, 32, 393-397.

Smith, A.T. & Over, R. (1979) Motion aftereffect with subjective contours. Perception and Psychophysics, 25, 95-98.

Sperling, G. (1970) Binocular vision: A physical and a neural theory. American Journal of Psychology, 83, 461-534.

Stalmeier, P.F.M. & de Weert, C.M.M. (1988) Binocular rivalry with chromatic contours. Perception and Psychophysics, 44, 456-462.

Sterling, W. (1901) An experiment on binocular colour vision with half-penny postage stamps. Journal of Physiology (London), 27, 23.

Stoner, G.R. & Albright, T.D. (1992) Neural correlates of perceptual motion coherence. Nature, 358, 412-414.

Stoner, G.R. & Albright, T.D. (1993) Image segmentation cues in motion processing: Implications for modularity in vision. Journal of Cognitive Neuroscience, 5, 129-149.

Stuart, G.W., Edwards, M. & Cook, M.L. (1991) Colour inputs to random-dot stereopsis. 18th Annual Australian Experimental Psychology Conference.

Sugie, N. (1982) Neural models of brightness perception and retinal rivalry in binocular vision. Biological Cybernetics, 43, 13-21.

Tanaka, K. & Saito, H. (1989) Analysis of motion of the visual field by direction, expansion/contraction, and rotation cells clustered in the dorsal part of the medial superior temporal area of the macaque monkey. Journal of Neurophysiology, 62, 626-641.

Tansley, B.W. & Boynton, R.M. (1976) A line, not a space, represents visual distinctness of borders formed by different colours. Science, 191, 954-957.

Tolhurst, D.J. & Thompson, P.G. (1975) Orientation illusions and aftereffects: inhibition between channels. Vision Research, 15, 967-972.

Tootell, R.B.H., Born, R.T. & Hamilton, S.L. (1988) Studies of primate visual cortex using double-label DG technique and colour autoradiography. Society of Neuroscience Abstracts, 14, 897.

Tootell, R.B.H. & Hamilton, S.L. (1989) Functional anatomy of the second visual area (V2) in the Macaque. Journal of Neuroscience, 9, 2620-2644.

Tootell, R.B.H., Hamilton, S.L., Silverman, M.S. & Switkes, E. (1988a) Functional anatomy of cat striate cortex. I. Ocular dominance, baseline conditions, and binocular interactions. Journal of Neuroscience, 8, 1531-1568.

Tootell, R.B.H., Hamilton, S.L., Silverman, M.S. & Switkes, E. (1988b) Functional anatomy of cat striate cortex. II. Retinotopic organisation. Journal of Neuroscience, 8, 1500-1530.

Tootell, R.B.H., Silverman, M.S., De Valois, R.L. & Jacobs, G.H. (1983) Functional organisation of the second cortical visual area in primates. Science, 220, 737-739.

Ullman, S. (1986) Artificial intelligence and the brain: Computational studies of the visual system. Annual Review of Neuroscience, 9, 1-26.

Van Essen, D.C., Anderson, C.H. & Felleman, D.J. (1992) Information processing in the primate visual system: An integrated systems perspective. Science, 255, 419-423.

van der Zwan, R., Wenderoth, P. & Alais, D. (1993) Reduction of pattern-induced motion aftereffect by binocular rivalry suggests the involvement of extrastriate mechanisms. Visual Neuroscience, 10, 703-709.

Virsu, V. & Taskinen, H. (1975) Central inhibitory interactions in human vision. Experimental Brain Research, 23, 65-74.

Vogels, R. & Orban, G.A. (1985) How finely can we judge the orientation of an illusory contour? Societie Belge de Physiologie et de Pharmacologie. Gent., November, p. 6.

Vogels, R. & Orban, G.A. (1987) Illusory Contour Orientation Descrimination. Vision Research, 27, 453-467.

von der Heydt, R. & Peterhans, E. (1989) Mechanisms of contour perception in Monkey visual cortex. I. Lines of pattern discontinuity. Journal of Neuroscience, 9, 1731-1748.

von Helmholtz, H. (1924) Treatise On Physiological Optics. (J.P.C. Southall, Translator) New York: Dover (Originally Published 1909).

Wade, N. (1975) Monocular and binocular rivalry between contours. Perception, 4, 85-95.

Wade, N.J. (1978) Why do pattterns fluctuate in visibility? Psychological Bulletin, 85, 338-352.

Wade, N., de Weert, C.M.M. & Swanston, M.T. (1984) Binocular rivalry with moving patterns. Perception and Psychophysics, 35, 111-122.

Wade, N. & Wenderoth, P. (1978) The influence of colour and contrast rivalry on the magnitude of the tilt aftereffect. Vision Research, 18, 827-835.

Wallace, G.K. (1969) The critical distance of interaction in the zollner illusion. Perception and Psychophysics, 5, 261-264.

Ward, F. & Boynton, R.M. (1974) Scaling of large chromatic differences. Vision Research, 14, 943-949.

Ware, C. & Mitchell, D.E. (1974) On interocular transfer of various visual aftereffects in normal and stereoblind observers. Vision Research, 14, 731-734.

Weisstein, N., Maguire, W. & Berbaum, K. (1977) A phantom motion aftereffect. Science, 198, 955-957.

Wenderoth, P. (1992) Perceptual illusions. Australian Journal of Psychology, 44, 147-151.

Wenderoth, P. (1994) On the relationship between the psychology of visual perception and the neurophysiology of vision. Australian Journal of Psychology, in press.

Wenderoth, P. & Beh, H. (1977) Component analysis of orientation illusions. Perception, 6, 57-75.

Wenderoth, P., Bray, R. & Johnstone, S. (1988) Psychophysical evidence for an extrastriate contribution to a pattern-selective motion aftereffect. Perception, 17, 81-91.

Wenderoth, P. & Johnson, M. (1985) What is the appropriate control for the tilt illusion? Perception, 14, 275-283.

Wenderoth, P. & Johnstone, S. (1987) Possible neural substrates for orientation analysis and perception. Perception, 16, 693-709.

Wenderoth, P. & Johnstone, S. (1988a) The different mechanisms of the direct and indirect tilt illusion. Vision Research, 28, 301-312.

Wenderoth, P. & Johnstone, S. (1988b) The differential effects of brief exposures and surrounding contours on direct and indirect tilt illusions. Perception, 17, 165-176.

Wenderoth, P. & Latimer, C. (1978) Perception and the neurophysiology of vision. Conceptual Analysis and Method in Psychology., ed. Sutcliffe, P., Sydney: Sydney University Press.

Wenderoth, P., O'Connor, T. & Johnson, M. (1986) The tilt illusion as a function of the relative and absolute lengths of test and inducing lines. Perception and Psychophysics, 39, 339-345.

Wenderoth, P. & van der Zwan, R. (1991) Local and global mechanisms of one- and two-dimensional orientation illusions. Perception and Psychophysics, 50, 321-332.

Wenderoth, P., van der Zwan, R. & Williams, M. (1993) Direct evidence for competition between local and global mechanisms of two-dimensional orientation illusions. Perception, 22, 273-286.

Westendorf, D.H. (1989) Binocular rivalry and dichoptic masking: Suppressed stimuli do not mask stimuli in a dominating eye. Journal of Experimental Psychology, 15, 485-492.

Wheatstone, C. (1838) Contributions to the physiology of vision: 1. On some remarkable and hitherto unobserved phenomena of binocular vision. Philosophical Transactions of the Royal Society of London, 128, 371-394.

Wiesenfelder, H. & Blake, R. (1990) The site of binocular rivalry relative to the analysis of motion in the human visual system. Journal of Neuroscience, 10, 3880-3888.

Winer, B.J., Brown, D.R. & Michels, K.M. (1991) Statistical Principles In Experimental Design. 3ed. New York: McGraw-Hill.

Wolfe, J.M. (1983) Influence of spatial frequency, luminance, and duration on binocular rivalry and abnormal fusion of briefly present, dichoptic stimuli. Perception, 12, 447-456.

Wolfe, J.M. (1986) Influence of spatial frequency, luminance, and duration on binocular rivalry and abnormal fusion of briefly presented, dichoptic stimuli. Perception, 12, 447-456.

Wolfe, J.M. (1986) Stereopsis and binocular rivalry. Psychological Review, 93, 269-282.

Wolfe, J.M. (1988) Parallel ideas about stereopsis and binocular rivalry: A reply to Blake and O'Shea (1988). Psychological Review, 95, 155-158.

Wolfe, J.M. & Held, R. (1983) Shared characteristics of stereopsis and the purely binocular process. Vision Research, 23, 217-227.

Zeki, S. (1988) The motion pathways of the visual cortex. Coding and Efficiency in the Visual System, ed. Blakemore, C. Cambridge: Cambridge University Press.

Zeki, S. (1990) Functional specialisation in the visual cortex: The generation of separate constructs and their multistage integration. Signal and Sense: Local and Global Order in Perceptual Maps, ed. Edelman, G.M., Gall, W.E. & Cowan, W.M. New York: Wiley-Liss.

Zeki, S. & Shipp, S. (1988) The functional logic of cortical connections. Nature, 335, 311-317.

Zeki, S. & Shipp, S. (1989) Functional segregation within area V2 of Macaque Monkey Visual Cortex. Seeing Contour and Colour, ed. Kulikowski, J.J., Dickinson, C.M. & Murray, I.J. Oxford: Pergammon Press.

APPENDICES.

APPENDIX ONE
RAW DATA

Experiment One: Angular function of the purely subjective contour tilt aftereffect.

This was a single factor study with repeated measures on each of the seven levels of the factor. The data is arranged across levels by subjects.

Treatment: Adapting Orientation

Levels: (direction of rotation) 0° (vertical), 15°, 30°, 45°, 60°, 75°, 90° (horizontal)

Dependent variable: Aftereffect magnitude (deg)

CW	1.17	5.00	3.83	0.67	-2.17	-0.17	0.33
CW	-1.00	1.00	3.17	1.17	-0.50	-0.17	0.17
CW	-0.17	2.17	1.00	0.67	-0.50	-1.17	-0.83
CW	0.17	7.00	5.33	2.00	0.00	-1.00	-0.17
CW	0.33	1.00	0.50	-0.33	1.00	0.33	0.17
CW	-1.00	3.00	2.83	1.00	-0.67	-1.67	0.00
CW	0.67	3.67	1.67	0.83	-1.00	-1.83	-0.33
CW	-0.33	3.33	1.00	0.67	-0.33	-1.00	-0.33
CCW	0.17	1.83	0.67	1.17	-0.67	-0.33	-0.17
CCW	0.33	2.83	1.50	-0.83	-0.17	0.00	0.33
CCW	-0.33	4.17	0.83	0.83	0.00	-2.00	-1.00
CCW	-0.17	3.83	3.17	0.83	-1.83	-2.33	0.50
CCW	-0.50	3.67	0.00	1.50	0.00	0.50	0.00
CCW	0.33	1.00	4.17	0.50	-2.66	-1.83	0.83
CCW	1.00	5.17	0.50	-0.83	-0.17	-1.83	-0.17
CCW	-0.50	2.83	0.50	1.83	-0.83	-2.50	-0.66

Experiment Two: Effect of spatial gaps on the magnitude of the purely subjective contour direct and indirect tilt aftereffects.

This experiment employed a one way analysis of variance with repeated measures. The data are listed subjects by condition.

Treatments: Adapting orientation, Spatial relation

Levels: 15° (direct), 75° (indirect); no gap, gap

Dependent variable: aftereffect magnitude (deg)

3.17	-0.66	-0.17	-2.17
5.83	1.67	-1.33	-0.33
3.50	2.33	-2.00	-0.50
0.00	-1.17	-3.00	-1.33
1.50	0.50	-1.67	-1.00
2.33	1.17	1.17	1.50
4.33	0.67	-0.33	-0.83
3.33	4.83	-1.00	-3.33
5.50	1.33	-1.00	-1.00
4.67	-2.83	-0.33	-4.67
5.00	1.33	-4.33	-1.00
3.33	5.67	-0.33	-0.17
3.66	1.17	-1.33	-1.17
3.00	1.00	-1.00	-1.00
3.50	1.17	-2.00	-1.33

Experiment Three: Effect of a frame of reference on the magnitude of purely subjective contour direct and indirect tilt aftereffects.

This experiment employed the same design as the previous experiment. Data are similarly listed.

Treatments: Adapting orientation, Reference frame
Levels: 15° (direct), 75° (indirect); no frame, frame
Dependent variable: aftereffect magnitude (deg)

3.67	4.17	-0.67	1.00
3.67	7.50	-0.33	1.00
2.00	2.33	-2.67	0.50
4.67	5.67	-2.00	-0.67
5.00	3.50	-1.00	0.33
3.00	0.33	0.00	-0.50
1.50	-0.83	-4.50	1.00
2.50	3.00	-1.33	-1.33
2.33	3.00	-0.83	-0.83
4.83	4.17	-1.83	0.67
0.00	0.83	-0.33	1.00
3.67	7.33	0.00	1.00
4.17	3.66	-1.17	-0.17
4.33	4.17	-1.67	-0.33
4.00	2.83	-2.33	0.00

Experiment Four: Angular function of the purely subjective contour tilt illusion.

This experiment, like the previous one, had seven levels of a single factor. The data is shown here across levels by subjects.

Factor: Adapting Orientation
Levels: 0° (vertical), 15°, 30°, 45°, 60°, 75°, 90° (horizontal)
Dependent variable: illusion magnitude (deg)

-1.00	0.17	1.33	0.33	-0.83	-1.33	0.17
0.67	0.67	1.50	0.17	-1.17	-2.50	-0.33
0.50	0.67	1.67	0.67	1.00	-1.00	0.33
-0.17	3.17	1.67	0.83	-0.17	-0.17	0.50
0.17	3.33	1.17	0.00	-2.00	-2.00	-0.17
0.00	1.50	0.67	-0.67	0.67	-1.67	-0.50
-0.33	1.00	-0.33	0.00	-0.33	1.17	0.50
0.50	3.67	0.50	0.17	0.00	0.17	0.50
0.67	2.33	2.33	0.50	-0.67	-1.17	-0.17
-1.00	3.50	1.67	1.17	-0.83	-1.67	-0.33

Experiment Five: Effect of binocular rivalry during induction on the subsequent magnitude of purely subjective contour direct and indirect tilt aftereffects.

This experiment employed a factorial (two factors), repeated measures design for the aftereffect data and a simple linear design for the predominance data. Predominance data for each subject, for each of the four measures, follows the aftereffect data.

Factors: Adapting orientation, Viewing condition
Levels: 15° (direct), 75° (indirect); no rivalry, rivalry
Dependent variable: aftereffect magnitude (deg)
Predominance: Four measures of predominance of adapting pattern (sec)
Orientations: first, 15°, 75°, last

3.17	0.5	-1.17	0.5	32.19	30.23	27.11	26.57
3.5	0.83	-4.33	2.5	16.06	20.1	20.79	28.33
2.5	-1.66	0.83	-1.33	25.7	25.8	24.32	26.43
4.33	-0.33	-0.5	0.17	26.47	25.27	27.27	26.46
2.83	1.33	-1	0	28.91	26.35	24.42	28.21
6.17	2	-0.17	2.33	30.96	28.07	25.43	26.28
4.17	4	-3	-3	30.51	31.89	32.48	31.64
3.83	-2.67	-4	0.17	19.13	15.99	15.15	19
2	-1.83	-1.16	-0.66	26.1	26.19	29.62	27.75
2.17	2	-1.67	-1.67	30.04	27.22	26.03	22.55
0.833	2.33	-1.33	1	22.48	24.47	23.01	22.39
1.67	1.5	1.67	-0.67	32.31	33.39	31.69	32.77
1.17	2.67	-2.33	-0.5	24.5	25.47	24.29	24.5
2.83	1.67	-1	1.83	30.64	31.73	32.34	30.01
3.33	1.83	1.33	4	28.75	29.37	28.41	27

Salience Ratings;

subjective contour no rivalry	subjective contour rivalry	no contour no rivalry	no contour rivalry
10.00	8.67	4.33	5.00
9.00	8.83	0.00	0.00
10.00	8.67	2.00	1.33
9.83	9.83	1.17	0.83
9.67	10.00	0.00	0.00
10.00	10.00	2.33	1.83
6.50	7.33	2.33	2.33
10.00	10.00	0.00	0.00
10.00	10.00	1.33	1.33
10.00	10.00	2.17	1.17

Experiment Six: Effect of binocular rivalry during induction on the subsequent magnitude of real contour direct and indirect tilt aftereffects.

This experiment employed the same design as the previous experiment. Data are similarly listed.

Factors: Adapting orientation, Viewing condition
Levels: 15° (direct), 75° (indirect); no rivalry, rivalry
Dependent variable: aftereffect magnitude (deg)
Predominance: Four measures of predominance of adapting pattern (sec)
Orientations: first, 15°, 75°, last

0.67	1.83	-2.33	-0.33	39.36	34.01	34.22	31.6
2	1.67	-1.33	-2	26.17	25.2	22.39	28.5
2.83	2.33	-1.67	-1.33	28.73	35.17	24.23	30.1
1.83	1.67	-0.67	-0.5	34.24	25.06	38.84	29.3
2.83	3.33	-2	0	32.29	33.01	31.01	28.7
2.5	2.33	-1.67	-0.67	36.39	34.72	33.12	28.9
1.5	1.67	-0.83	-0.67	30.2	29.94	28.99	33.6
1.67	1.83	-0.33	0.17	35.33	39.52	31.27	30.3
1.83	1.67	0	-0.83	26.79	32	34.63	29.8
3.5	3	-0.67	0.5	31.65	31.22	30.16	31.1
0.83	0.67	-1	-0.5	28.5	29.36	27.51	28.8
1.33	2	-0.83	0.33	30.15	32.43	29.38	30.4
1.5	1.83	0	-0.67	33.66	34.11	29.9	29.5
1.67	0.67	-1	-0.33	30.32	27.22	32.61	31.5
3.67	2.17	-1	0	33.04	29.94	29.49	29.2

Experiment Seven: Effect of interocular transfer on subjective contour direct tilt aftereffects induced with, and without binocular rivlary.

This experiment employed a factorial (two factors), repeated measures design for the aftereffect data . Predominance data for each subject, for each of the four measures, follows the aftereffect data, and has been treated as for the previous two experiments.

Factors: Adapting orientation, Viewing condition
Levels: 15° (direct), 75° (indirect); monocular-monocular, interocular transfer
Dependent variable: aftereffect magnitude (deg)
Predominance: Four measures of predominance of adapting pattern (sec)
Orientations: first, 15°, 75°, last

2.50	4.50	2.00	-0.50	29.92	28.62	26.62	26.53
1.83	3.00	0.00	-0.17	29.89	30.69	28.95	30.05
0.33	-0.33	0.50	-0.33	36.39	33.12	34.72	34.24
2.33	2.00	-0.33	-0.17	27.91	24.97	24.86	25.20
6.00	5.67	3.00	2.83	31.83	32.22	30.14	30.45
-1.00	-2.83	-0.50	-0.67	20.38	21.40	28.15	28.34
3.17	4.00	0.50	0.67	34.24	31.01	32.29	33.01
1.00	0.83	0.33	-0.17	26.26	23.06	26.70	23.56
1.83	2.33	-1.00	0.00	28.73	35.17	32.56	28.99
1.83	3.50	1.50	0.00	29.95	27.47	32.51	29.65
1.67	2.33	2.33	-0.50	27.66	30.12	27.89	27.99
2.17	1.00	0.83	0.67	27.26	26.75	26.93	25.90
2.00	-0.33	-1.17	-0.67	25.20	27.33	27.57	26.20
2.67	2.67	1.33	1.67	32.31	29.31	29.99	31.21
2.67	4.00	0.33	0.00	25.45	23.70	25.31	24.19

Experiment Eight: Effect of interocular transfer on subjective contour direct tilt aftereffects induced with, and without binocular rivlary.

This study replicated the previous study, differing only in that real contours replaced the subjective contours of the previous experiment.

Factors: Adapting orientation, Viewing condition
Levels: 15° (direct), 75° (indirect); monocular-monocular, interocular transfer
Dependent variable: aftereffect magnitude (deg)
Predominance: Four measures of predominance of adapting pattern (sec)
Orientations: first, 15°, 75°, last

0.17	1.00	1.17	-0.50	30.88	31.23	31.83	30.05
2.50	1.17	2.00	0.67	32.19	30.12	31.71	33.09
4.33	3.17	3.50	2.33	24.25	24.80	25.70	24.10
2.17	1.50	2.33	1.17	31.86	31.25	33.65	32.50
2.33	1.67	2.33	1.50	28.19	35.59	28.72	30.12
2.17	1.00	2.50	0.67	32.58	29.16	31.58	30.09
3.33	1.67	3.00	0.83	27.22	26.03	30.04	22.55
4.33	2.00	4.17	0.67	29.17	29.33	29.66	29.00
2.50	1.67	3.00	1.00	32.77	31.69	33.39	32.31
2.17	1.00	2.33	0.50	22.48	24.47	23.01	22.39
2.00	1.17	2.00	-1.00	29.23	27.19	28.59	27.58
1.50	1.67	1.00	0.83	31.66	31.56	29.83	30.26
2.17	2.33	1.33	1.17	32.12	29.65	33.33	31.79
2.00	0.67	0.50	0.50	26.99	28.99	29.38	30.55
0.83	1.33	1.00	2.00	33.01	32.10	29.16	29.48

Experiment Nine: Effect of binocular rivalry during induction on the subsequent duration of motion aftereffects induced with drifting plaids and components.

This experiment employed a simple repeated measures design and t-tests for related samples. Shown here are the means for each subject Predominance data for each subject, follows the aftereffect data for each treatment.

Treatments: Inducing stimuli; plaid, components
Levels: no rivalry, rivalry
Dependent variable: aftereffect duration (sec)
Predominance: Predominance (sec), one for each adapting condition
Adaptation: 60s, 30s (naive only) 120s

naive

10.88	7.01	6.72	29.23	8.50	8.00	50.00
21.60	11.70	14.25	35.55	11.63	10.01	65.56
12.23	6.76	7.53	29.50	7.64	6.42	58.30
14.01	6.98	8.10	28.99	8.03	5.94	61.10
11.01	7.01	6.25	32.33	7.09	5.91	59.91
12.97	7.53	7.84	28.29	7.99	5.31	64.70

trained

13.64	6.80		29.98	5.92	3.60	59.83
9.88	4.73		29.17	6.21	3.26	62.73
6.28	3.57		29.92	3.49	2.19	55.63
22.02	11.89		29.08	16.78	7.85	56.94
11.21	6.85		35.51	2.96	3.43	60.43

grouped data for first and second measures (s) (to test for buildup of aftereffect).

11.34	15.94	6.00	5.83
10.73	9.03	5.75	6.66
6.88	5.67	3.78	3.19
19.25	24.79	15.78	17.78
10.50	11.92	3.20	2.72
11.76	10.00	8.05	8.95
22.10	21.10	12.11	11.15
13.28	11.18	6.87	8.41
15.22	12.80	9.07	6.99
11.90	10.12	6.28	7.90
11.86	14.08	8.05	7.93

Experiment Ten: Effect of binocular rivalry during induction on the subsequent duration of motion aftereffects induced with a drifting grating.

This experiment employed a repeated measures design. Shown here are the means for each subject on each of the two conditions Predominance data for each subject follows.

Treatment: Inducing stimulus; drifting grating
Levels: no rivalry, rivalry
Dependent variable: aftereffect duration (sec)
Predominance: Mean predominance (sec) for each subject on rivalry condition
Adaptation: 60s

11.29	10.75	28.09
8.74	8.53	29.63
14.18	12.42	30.47
9.20	9.25	27.46
10.47	9.63	31.12
16.89	16.50	30.97

Experiment Eleven: Correlation of plaid predominance, during rivalrous induction, with motion aftereffect duration.

This experiment employed a simple repeated measures design. Shown here are the scores for each subject on each of the four rivalry conditions. Predominance data for each subject on each condition follows.

Factor: Inducing stimulus; drifting plaid
Levels: no rivalry, ~25% rivalry, ~50% rivalry, ~75% rivalry
Dependent variable: aftereffect duration (sec)
Predominance: Mean predominance (sec) for each subject on each rivalry condition
Adaptation: 60s

14.99	5.20	9.80	12.87	*	*	16.60	30.00	46.29
15.39	5.99	7.83	11.51	*	*	18.94	31.98	54.73
16.17	4.32	8.26	9.55	*	*	23.06	36.00	52.84
14.42	4.93	8.09	11.25	*	*	19.03	23.49	49.83
10.98	4.04	7.11	8.64	*	*	18.78	29.05	42.59
13.26	3.38	6.65	8.82	*	*	20.02	27.66	48.62
13.03	4.35	7.92	11.16	*	*	13.40	35.50	46.17
14.01	3.25	9.25	9.92	*	*	23.01	30.13	51.04
11.55	2.85	9.35	10.69	*	*	16.00	36.17	53.23
16.41	6.82	7.84	12.59	*	*	19.33	20.49	50.01
15.01	4.45	6.80	13.50	*	*	18.02	30.01	49.98
13.94	3.86	6.98	14.22	*	*	19.87	31.24	55.29

APPENDIX TWO

STATISTICAL ANALYSES

Experiment One

Angular function of the purely subjective contour tilt aftereffect.

t-Test for differences between CW and CCW rotations of adapting stimulus

Condition	df	Mean CW-CCW	Hypothesised Mean	Alternative	t-value	probability
0°	7	-0.061	0	≠ 0	-0.188	0.8538
15°	7	0.105	0	≠ 0	0.123	0.9042
30°	7	0.999	0	≠ 0	1.268	0.2253
45°	7	0.210	0	≠ 0	0.502	0.6232
60°	7	0.270	0	≠ 0	0.578	0.5722
75°	7	0.455	0	≠ 0	0.926	0.3701
90°	7	-0.081	0	≠ 0	-0.325	0.7502

Contrast Coefficients

Contrast	Trend	μ1	μ2	μ3	μ4	μ5	μ6	μ7
Ψ1	Linear	-1	-2	-1	0	1	2	3
Ψ2	Quadratic	5	0	-3	-4	-3	0	5
Ψ3	Cubic	-1	1	1	0	-1	-1	1
Ψ4	Quartic	3	-7	1	6	1	-7	3
Ψ5	Quintic	-1	4	-5	0	5	-4	1
Ψ6	Sextic	1	-6	15	-20	15	-6	1

Condition Means

Inducing Orientation	0°	15°	30°	45°	60°	75°	90°
Mean	0.011°	3.219°	1.917°	0.730°	-0.656°	-1.062°	-0.083°
Standard Error	0.158	0.414	0.402	0.204	0.288	0.244	0.121

ANOVA Summary Table

Source	SS	df	MS	F	probability
Subject	19.771	15	1.318		
1	74.483	1	74.483	63.018	≤0.0001
2	9.506	1	9.506	8.043	0.0056
3	121.883	1	121.883	103.121	≤0.0001
4	9.716	1	9.716	8.221	0.0052
5	3.305	1	3.305	2.796	0.0979
6	1.311	1	1.311	1.109	0.2951
Error	106.374	90	1.182		

t-Tests

Condition	df	Mean	Hypothesised Mean	Alternative	t-value	probability
0°	15	0.011	0	≠ 0	0.067	0.4736
15°	15	3.219	0	> 0	7.776	≤0.0001
30°	15	1.917	0	> 0	4.773	≤0.0001
45°	15	0.73	0	> 0	3.583	0.0014
60°	15	-0.656	0	< 0	-2.876	0.0057
75°	15	-1.062	0	< 0	-4.346	0.0003
90°	15	-0.083	0	≠ 0	-0.685	0.2519

Experiment Two

Effect of spatial gaps on the magnitude of the purely subjective contour direct and indirect tilt aftereffects.

Contrast Coefficients

Contrast		$\mu1$	$\mu2$	$\mu3$	$\mu4$
$\Psi1$	Effect of gap direct	1	-1	0	0
$\Psi2$	Effect of gap indirect	0	0	1	-1
$\Psi3$	Orientation	1	1	-1	-1

Effects

Inducing Condition	15° No Gap	15° Gap	75° No Gap	75° Gap
Mean	3.510°	1.212°	-1.243°	-1.222°
Standard Error	0.389	0.538	0.335	0.361

ANOVA Summary Table

Source	SS	df	MS	F	p
Subject	46.202	14	3.3		
1	39.606	1	39.606	17.067	0.0002
2	0.003	1	0.003	0.001	0.9696
3	193.717	1	193.717	83.476	≤0.0001
Error	97.466	42	2.321		

t-Tests

Condition	df	Mean	Hypothesised Mean	Alternative	t-value	probability
15° no gap	14	3.511	0	>0	9.022	≤0.0001
15° gap	14	1.212	0	>0	2.252	0.0205
75° no gap	14	-1.243	0	<0	-3.708	0.0012
75° gap	14	-1.222	0	<0	-3.381	0.0023

Experiment Three

Effect of a frame of reference on the magnitude of purely subjective contour direct and indirect tilt aftereffects.

Contrast Coefficients

Contrast		$\mu1$	$\mu2$	$\mu3$	$\mu4$
$\Psi1$	Effect of Frame direct	1	-1	0	0
$\Psi2$	Effect of Frame indirect	0	0	1	-1
$\Psi3$	Orientation	1	1	-1	-1

Effects

Inducing Condition	15° No Frame	15° Frame	75° No Frame	75° Frame
Mean	3.289°	3.444°	-1.377°	0.178°
Standard Error	0.361	0.597	0.308	0.203

ANOVA Summary Table

Source	SS	df	MS	F	p
Subject	55.562	14	3.969		
1	0.179	1	0.179	0.100	0.7533
2	18.143	1	18.143	10.118	0.0028
3	235.977	1	235.977	131.601	≤0.0001
Error	75.311	42	1.793		

t-Tests

Condition	df	Mean	Hypothesised Mean	Alternative	t-value	probability
15°/no frame	14	3.289	0	>0	9.12	≤0.0001
15°/frame	14	3.445	0	>0	5.766	≤0.0001
75°/no frame	14	-1.377	0	<0	-4.465	0.0002
75°/frame	14	0.178	0	<0	0.878	0.1974

Experiment Four
Angular function of the purely subjective contour tilt illusion.

Contrast Coefficients

Contrast	Trend	μ1	μ2	μ3	μ4	μ5	μ6	μ7
Ψ1	Linear	-1	-2	-1	0	1	2	3
Ψ2	Quadratic	5	0	-3	-4	-3	0	5
Ψ3	Cubic	-1	1	1	0	-1	-1	1
Ψ4	Quartic	3	-7	1	6	1	-7	3
Ψ5	Quintic	-1	4	-5	0	5	-4	1
Ψ6	Sextic	1	-6	15	-20	15	-6	1

Condition Means

Inducing Orientation	0°	15°	30°	45°	60°	75°	90°
Mean	0.001°	2.001°	1.218°	0.317°	-0.433°	-1.017°	-0.050°
Standard Error	0.199	0.427	0.239	0.162	0.277	0.350	0.124

ANOVA Summary Table

Source	SS	df	MS	F	probability
Subject	8.252	9	0.852		
1	20.304	1	20.304	28.402	≤0.0001
2	1.350	1	1.350	1.889	0.1750
3	37.099	1	37.099	51.896	≤0.0001
4	1.064	1	1.064	1.488	0.2278
5	1.779	1	1.779	2.489	0.1205
6	0.002	1	0.002	0.003	0.9592
Error	38.603	54	0.737		

t-Tests

Condition	df	Mean	Hypothesised Mean	Alternative	t-value	probability
0°	9	0.001°	0	≠ 0	0.005	0.9961
15°	9	2.001°	0	> 0	4.684	0.0005
30°	9	1.218°	0	> 0	5.089	0.0003
45°	9	0.317°	0	> 0	1.955	0.0412
60°	9	-0.433°	0	< 0	-1.563	0.0763
75°	9	-1.017°	0	< 0	-2.903	0.0088
90°	9	-0.050°	0	≠ 0	0.403	0.6967

Experiment Five:

Effect of binocular rivalry during induction on the subsequent magnitude of purely subjective contour direct and indirect tilt aftereffects.

Predominance Analysis

Contrast Coefficients

Contrast	Comparison	μ1	μ2	μ3	μ4
Ψ1	First vs. Last	1	0	0	-1
Ψ2	Direct vs. Indirect	0	1	-1	0
Ψ3	Non-adapting vs. Adapting	1	-1	-1	1

Predominance Means

Condition	First	15°	75°	Last
Mean	26.96s	26.77s	26.16s	26.66s
Standard Error	1.25	1.17	1.19	0.92

ANOVA Summary Table

Source	SS	df	MS	F	probability
Subject	896.400	14	64.029		
1	0.678	1	0.678	0.148	0.7024
2	2.809	1	2.809	0.613	0.4380
3	1.799	1	1.799	0.393	0.5342
Error	192.397	42	4.581		

Aftereffect Analysis

Aftereffect Means

Inducing Condition	15° No Riv.	15° Rivalry	75° No Riv.	75° Rivalry
Mean	2.967	0.945	-1.189	0.311
Standard Error	0.252	0.476	0.451	0.466

ANOVA Summary Table

Source	SS	df	MS	F	p
Subject	46.892	14	3.349		
15° vs. 75°	85.992	1	85.992	30.667	≤0.0001
error	39.257	14	2.804		
No Riv. vs. Bin. Riv.	1.022	1	1.022	0.454	0.5112
error	31.478	14	2.248		
NoRiv./Riv. vs. 15°/75°	46.517	1	46.517	14.664	0.0018
Error	44.409	14	3.172		

t-Tests

Condition	df	Mean	Hypothesised Mean	Alternative	t-value	probability
15°/no riv.	14	2.967°	0	≠ 0	8.42	≤0.0001
15°/riv.	14	0.945°	0	≠ 0	1.984	0.0336
75°/no riv.	14	-1.189°	0	≠ 0	-2.635	0.0098
75°/riv.	14	0.311°	0	≠ 0	0.0.668	0.2574

Salience Analysis

Contrast Coefficients

Contrast	Comparison	$\mu1$	$\mu2$	$\mu3$	$\mu4$
$\Psi1$	Sub. Cont. No Riv. vs. Riv.	1	-1	0	0
$\Psi2$	Modified Stim. No Riv. vs. Riv.	0	0	1	-1
$\Psi3$	Subjective vs. Mod.	1	1	-1	-1

Salience Means

Condition	SC+NRiv.	SC+Riv.	Mod+NRiv.	Mod+Riv.
Mean	9.5	9.33	1.57	1.38
Standard Error	0.38	0.29	0.43	0.48

ANOVA Summary Table

Source	SS	df	MS	F	probability
Subject	20.418	9	2.269		
1	0.139	1	0.139	0.107	0.7465
2	0.169	1	0.169	0.130	0.7217
3	630.833	1	630.833	482.647	≤0.0001
Error	35.29	27	1.307		

Experiment Six:
Effect of binocular rivalry during induction on the subsequent magnitude of real contour direct and indirect tilt aftereffects.

Predominance Analysis

Contrast Coefficients

Contrast	Comparison	μ1	μ2	μ3	μ4
Ψ1	First vs. Last	1	0	0	-1
Ψ2	Direct vs. Indirect	0	1	-1	0
Ψ3	Non-adapting vs. Adapting	1	-1	-1	1

Predominance Means

Condition	First	15°	75°	Last
Mean	31.79s	30.52s	30.09s	31.53s
Standard Error	0.94	1.05	0.36	1.01

ANOVA Summary Table

Source	SS	df	MS	F	probability
Subject	277.395	14	19.814		
1	0.510	1	0.510	0.056	0.8139
2	1.387	1	1.387	0.153	0.6980
3	27.581	1	27.581	3.036	0.0888
Error	381.553	42	9.085		

Aftereffect Analysis

Aftereffect Means

Inducing Condition	15° No Riv.	15° Rivalry	75 No Riv.	75° Rivalry
Mean	2.011	1.911	-1.022	-0.455
Standard Error	0.229	0.182	0.176	0.166

ANOVA Summary Table

Source	SS	df	MS	F	p
Subject	11.192	14	0.799		
15° vs. 75°	109.323	1	109.323	142.082	0.0001
error	10.772	14	0.769		
No Riv. vs. Bin. Riv.	0.819	1	0.819	2.228	0.1577
error	5.147	14	0.368		
NoRiv./Riv. vs. 15°/75°	1.633	1	1.633	7.352	0.0169
Error	3.167	14	0.226		

t-Tests

Condition	df	Mean	Hypothesised Mean	Alternative	t-value	probability
15°/no riv.	14	2.011°	0	≠ 0	8.774	≤0.0001
15°/riv.	14	1.911°	0	≠ 0	10.501	≤0.0001
75°/no riv.	14	-1.022°	0	≠ 0	-5.812	≤0.0001
75°/riv.	14	-0.455°	0	≠ 0	-2.74	0.0080

t-Test: subjective contour predominance vs. real contour predominance.

Contour	Sub.	Real
Mean Pred.	26.638s	30.982s
Standard Error	0.171	0.404

Hypothesised Difference	Alternative Difference	df	t-value	probability
0	≤ 0	6	-9.898	≤0.0001

Experiment Seven

Effect of interocular transfer on subjective contour direct tilt aftereffects induced with, and without binocular rivlary.

Predominance Analysis

Contrast Coefficients

Contrast	Comparison	$\mu1$	$\mu2$	$\mu3$	$\mu4$
$\Psi1$	First vs. Last	1	0	0	-1
$\Psi2$	Monocular vs. IOT	0	1	-1	0
$\Psi3$	Non-adapting vs. Adapting	1	-1	-1	1

Predominance Means

Condition	First	Monocular	IOT	Last
Mean	28.89	28.33	29.01	28.367
Standard Error	1.020	1.011	0.758	0.811

ANOVA Summary Table

Source	SS	df	MS	F	probability
Subject	545.240	14	38.946		
1	2.065	1	2.065	0.591	0.4464
2	3.502	1	3.502	1.002	0.3225
3	0.026	1	0.026	0.007	0.9322
Error	146.754	42	3.494		

Aftereffect Analysis

Aftereffect Means

Inducing Condition	15° Mon. No Riv.	15° IOT. No Riv.	15° Mon. Rivalry	15° IOT. Rivalry
Mean	2.067	2.156	0.644	0.178
Standard Error	0.388	0.568	0.312	0.247

ANOVA Summary Table

Source	SS	df	MS	F	p
Subject	90.705	14	6.476		
No Riv. vs. Bin. Riv.	43.394	1	43.394	26.461	0.0001
error	22.959	14	1.640		
Monocular vs. IOT	0.533	1	0.533	1.469	0.2455
error	5.074	14	0.362		
NoRiv./Riv. vs. Mon./IOT.	1.152	1	1.152	1.162	0.2992
Error	13.872	14	0.991		

t-Tests

Condition	df	Mean	Hypothesised Mean	Alternative	t-value	probability
15° Mon. No Riv.	14	2.067	0	> 0	5.333	≤0.0001
15° IOT. No Riv.	14	2.156	0	> 0	3.793	0.001
15° Mon. Rivalry	14	0.644	0	> 0	2.065	0.0289
15° IOT. Rivalry	14	0.178	0	> 0	0.720	0.2416

Experiment Eight

Effect of interocular transfer on real contour direct tilt aftereffects induced with, and without binocular rivlary.

Predominance Analysis

Contrast Coefficients

Contrast	Comparison	μ1	μ2	μ3	μ4
Ψ1	First vs. Last	1	0	0	-1
Ψ2	Monocular vs. IOT	0	1	-1	0
Ψ3	Non-adapting vs. Adapting	1	-1	-1	1

Predominance Means

Condition	First	Monocular	IOT	Last
Mean	29.640	29.544	29.972	29.057
Standard Error	0.841	0.770	0.746	0.891

ANOVA Summary Table

Source	SS	df	MS	F	probability
Subject	447.650	14	31.975		
1	2.546	1	2.546	0.980	0.3279
2	1.374	1	1.374	0.529	0.4712
3	2.513	1	2.513	0.967	0.3311
Error	109.158	42	2.599		

Aftereffect Analysis

Aftereffect Means

Inducing Condition	15° Mon. No Riv.	15° IOT. No Riv.	15° Mon. Rivalry	15° IOT. Rivalry
Mean	2.300	1.535	2.144	0.823
Standard Error	0.284	0.162	0.264	0.215

ANOVA Summary Table

Source	SS	df	MS	F	p
Subject	29.320	14	2.094		
No Riv. vs. Bin. Riv.	2.825	1	2.825	15.029	0.0017
error	2.632	14	0.188		
Monocular vs. IOT	16.328	1	16.328	19.529	0.0006
error	11.705	14	0.836		
NoRiv./Riv. vs. Mon./IOT.	1.159	1	1.159	5.113	0.0402
Error	3.174	14	0.227		

t-Tests

Condition	df	Mean	Hypothesised Mean	Alternative	t-value	probability
15° Mon. No Riv.	14	2.300	0	> 0	8.091	≤0.0001
15° IOT. No Riv.	14	1.535	0	> 0	9.473	≤0.0001
15° Mon. Rivalry	14	2.144	0	> 0	8.128	≤0.0001
15° IOT. Rivalry	14	0.823	0	> 0	3.82	0.0009

Experiment Nine

Effect of binocular rivalry during induction on the subsequent duration of motion aftereffects induced with drifting plaids and components.

Trained Subjects

Contrast Coefficients

Contrast		$\mu1$	$\mu2$	$\mu3$	$\mu4$
$\Psi1$	Rivalry on PMAE	1	-1	0	0
$\Psi2$	Rivalry on Component MAE	0	0	1	-1
$\Psi3$	Inducing Pattern	1	1	-1	-1

Effects

Inducing Condition	Plaid No Riv.	Plaid Riv.	Comp. No Riv.	Comp. Riv.
Mean	12.61s	6.76s	7.07s	3.96s
Standard Error	2.64	1.42	2.51	1.00

ANOVA Summary Table

Source	SS	df	MS	F	p
Subject	273.77	4	68.44		
$\Psi1$	85.32	1	85.32	19.64	0.0008
$\Psi2$	24.09	1	24.09	5.55	0.04
$\Psi3$	86.90	1	86.90	20.01	0.0008
Error	52.13	12	52.13		

t-Tests: buildup of aftereffect

Condition	df	Mean (D)	Hypothesised Mean	Alternative	t-value	probability
plaids	10	0.16	0	>0	0.19	>0.05
components	10	0.23	0	>0	0.61	>0.05

Naive Subjects

Contrast Coefficients

Contrast		$\mu 1$	$\mu 2$	$\mu 3$	$\mu 4$
$\Psi 1$	Rivalry on PMAE	1	-1	0	0
$\Psi 2$	Rivalry on Component MAE	0	0	1	-1
$\Psi 3$	Inducing Pattern	1	1	-1	-1

Effects

Inducing Condition	Plaid No Riv.	Plaid Riv.	Comp. No Riv.	Comp. Riv.
Mean	13.78s	7.80s	8.48s	6.93s
Standard Error	1.64	0.78	0.66	0.72

ANOVA Summary Table

Source	SS	df	MS	F	p
Subject	98.90	5	98.90		
$\Psi 1$	107.34	1	107.34	56.66	≤ 0.0001
$\Psi 2$	7.19	1	7.19	3.80	0.0702
$\Psi 3$	57.17	1	57.17	30.19	≤ 0.0001
Error	28.40	15	28.40		

t-Tests: difference between 30s and 60s plaid adaptation, naive subjects

Condition	df	Mean (D)	Hypothesised Mean	Alternative	t-value	probability
60s no riv. vs. 30s no riv.	5	5.33	0	>0	11.42	≤ 0.0001
60s riv. vs. 30s no riv.	5	-0.64	0	$\neq 0$	-1.36	>0.05

Experiment Ten

Effect of binocular rivalry during induction on the subsequent duration of motion aftereffects induced with a drifting grating.

Effects

Inducing Condition	Grating No Rivalry	Grating Rivalry
Mean	11.80s	11.18s
Standard Error	1.29	1.20

Predominance

Condition	Rivalry
Mean	29.62s
Standard Error	0.63

t-Tests: difference between grating durations (riv. vs. no riv)

Condition	df	Mean (D)	Hypothesised Mean	Alternative	t-value	probability
60s no riv. vs. 60s riv.	5	0.615	0	≠0	2.368	0.0641

Experiment Eleven

Correlation of plaid predominance, during rivalrous induction, with motion aftereffect duration.

Contrast Coefficients

Contrast	Trend	μ1	μ2	μ3	μ4
Ψ1	Linear	-3	-1	+1	+3
Ψ2	Quadratic	+1	-1	-1	+1
Ψ3	Cubic	-1	+3	-3	+1

Effects

Inducing Condition	25% pred.	50% pred.	75% pred.	100% pred.
Mean	4.45s	7.99s	11.23s	14.10s
Standard Error	0.40	0.43	0.82	0.71

ANOVA Summary Table

Source	SS	df	MS	F	p
Subject	9.18	3	3.059		
Ψ1	207.014	1	207.014	204.79	≤0.0001
Ψ2	0.446	1	0.446	0.441	0.5234
Ψ3	0.001	1	0.001	0.001	0.9767
Error	9.098	9	1.011		

Mean Predominances

Predicted Predominance	25%	50%	75%
Observed Predominance	30.8%	50.2%	83.4%
Mean	18.48s	30.14s	50.50s
Standard Error	0.47	1.80	1.05

Contrast Coefficients

Contrast	μ1	μ2	μ3	μ4
Ψ1	+1	-1	0	0
Ψ2	+1	+1	-2	0
Ψ3	+1	+1	+1	-3

ANOVA Summary Table

Source	SS	df	MS	F	p
Subject	15.794	3	5.265		
Ψ1	255.606	1	255.606	55.818	≤0.0001
Ψ2	1742.510	1	1742.510	380.520	≤0.0001
Ψ3	2185.245	1	2185.245	477.202	≤0.0001
Error	41.214	9	4.579		

Individual Correlations: duration with predominance

	μ_x	μ_y	$S_{\mu x-1}$	$S_{\mu y-1}$	est. covariance	r_{xy}
Subject 1	8.37	34.49	2.87	14.17	34.14	0.84
Subject 2	6.99	31.01	2.54	12.67	28.22	0.88
Subject 3	7.63	33.96	3.27	14.40	42.15	0.90
Subject 4	8.56	32.69	3.89	15.12	55.34	0.94

Regression Analysis: duration with percentage predominance

Predominance	Intercept	Gradient	r_{xy}
observed	0.738	0.132	0.992
predicted	1.395	0.129	0.999

APPENDIX THREE

Power Calculations

The interpretation of results for a number of these experiments depends upon the reliability of the data to detect small changes in the magnitudes of effects being observed. These issues are addressed by considering the power of the relevant analyses.

For two hypotheses:

H_o - null hypothesis
H_a - alternative hypothesis,

once H_a has been specified as true it is possible to determine ß, the probability of incorrectly deciding H_a is false. Power, the probability of correctly deciding H_a is true is then defined as

$$\text{Power} = 1 - ß.$$

The power of a test is determined by several factors including variance, which in turn depends on sample size. Variance also determines the smallest reliably detectable treatment effect size.

Several workers have provided treatments for estimating the power of an experiment, and the calculations used here are based on the work of Cohen (1988) and the charts in Appendix D, Tables 11 and 14 of Winer, Brown and Michels (1991, pp. 984-991). For those tables,

$$f = \frac{\sigma_\mu}{\sigma_\varepsilon}$$

and the value

$$Ø = f\sqrt{n}$$

and also

$$Ø = \sqrt{\frac{\lambda}{k}}$$

where k = No. of groups
and λ = the non-centrality parameter

In turn, the non-centrality parameter is defined such that;

$$\lambda = n\sum \tau_j^2/\sigma_\varepsilon^2$$

where n = sample size
and τ = effect size

Finally, it is possible to define Ø such that

$$Ø = Ø'\sqrt{n}$$

where

$$Ø' = \sqrt{\frac{\sum \tau_j^2}{k\sigma_e^2}}$$

Using these relations, it is possible to calculate the power of a test if some estimate of the smallest reliably detectable difference can be made, if the sample size is known, and if an estimate of the mean square error can be obtained from the data. To that end, if the smallest reliably detectable difference is nominated to be 0.40° (see Cohen 1988), and if $n = 15$, and the estimate of the mean square error is such that $MS_e = 1.0$, which is a value at the upper end of the range of such errors reported in these experiments, then

$$Ø' = 0.40$$

and so

$$Ø = 0.40 * \sqrt{15}$$

$$Ø = 1.55$$

Now for a 2x2 design (Experiments Five - Eight), if $Ø = 1.55$, and

f_t = df. for treatments = 1
f_e = df. for error = 16

with

$$\alpha = 0.05$$

then from the tables, power = ~0.60.

If the smallest reliably detectable difference is reduced to 0.2° then

$$Ø' = 0.2$$

and

$$Ø = 0.77$$

which yields a power = ~0.25.

These calculations suggest that while larger changes (ie. those around 0.4°) in the effects described in Experiments Five, Six, Seven and Eight could be reliably detected, the power of these experiments to detect very small changes in effect size was limited. The power for all these experiments could be increased by increasing the sample size, but practical constraints limited the opportunity to do this. Interpretation of the results of these experiments must be constrained by relations described by these calculations.

Similar calculations can be carried out for the experiments using a one-way design. If the same values as those used above are applied, then for

$f_t = 3$
$f_e = 42$

and an effect size of 0.4°, power = ~0.78. For an effect size of 0.2° this is reduced to ~0.33. These values are similar to those for the factorially designed experiments, and must generate similar conclusions.

APPENDIX FOUR

Errata

From p. 42.
The inducing subjective contour did not extend across the entire inner diameter of the black ring which defined the extent of the stimulus. As depicted by Fig. 7., the central region, corresponding to the test field area, was left blank. This blank area had the same diameter as the test field, and accommodated it exactly when the two stimuli were viewed simultaneously (see Experiment Four).

This particular stimulus configuration was chosen for several reasons. Indirect effects, using real contours, are often small and difficult to observe. This type of stimulus structure has produced reliable effects when used by other workers (eg. Wenderoth and Johnstone 1988a), and was employed in order to provide the best chance for observing both direct and indirect effects should they occur. The similarity between this stimulus and those used by other workers provided the second advantage that a number of these experiments (Two and Three) will replicate conditions already examined by those workers (Wenderoth and Johnstone 1988a), but using purely subjective contours rather than real. Further, it has been noted that indirect effects are maximal when inducing contours have a greater extent than test contours, with indirect effect size systematically decreasing as the length of the inducing contour first equals the test contour, and then decreases with respect to it (Wenderoth, O'Toole and Curthoys 1975). It seemed better, therefore, to use a display which had the test stimulus shorter than the inducing stimulus. The configuration used here met this criterion while optimising the available display area. Finally, this type of stimulus configuration had the advantage that it could be applied, without alteration, to both aftereffect and illusion paradigms. Exactly the same stimuli could be used in each case, allowing for more reliable comparisons between effects elicited under both paradigms.

Omissions

Levy, M., & Lawson, R.B. (1978) Stereopsis and binocular rivalry from dichoptic stereograms. Vision Research, 18, 239-246.

Wenderoth, P., O'Toole, B. & Curthoys, I.S. (1975) The effect of inducing-line length on the magnitudes of the tilt illusion and tilt aftereffect. Australian Journal of Psychology, 27, 1-7.