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**A cross-modal investigation into the relationship between
bistable perception and a global temporal mechanism**

by Amanda Louise Parker

A thesis submitted in total fulfilment of the requirements of a
Doctor of Philosophy

in

Science

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Organisation of the thesis

This thesis is presented in a thesis-by-publication format. Chapter 1 contains a general introduction to the topic of bistable perception and binocular rivalry as well as justification for the proceeding experimental chapters 2-5. Chapters 2-4 contain peer reviewed, published journal articles, which have been reformatted to fit the thesis format. Chapter 5 contains an article which has been accepted for publication pending revisions. Overview and chapter summary sections have been added to the chapters in order to integrate the findings with the overall thesis structure. Chapters 3 and 5 contain work in which the thesis author is the primary author, having sole responsibility for the work aside from minor stylistic edits conducted by the second author (the thesis supervisor) after the work was completed. Chapters 2 and 4 are papers in which the thesis author was a second and third author respectively.

A discussion of the significance of the experimental papers presented in Chapters 2-5 to the field is contained in the concluding Chapter 6. This discussion includes a more detailed examination of the published literature relevant to the hypothesis and experimental chapters, and ties the findings presented in each chapter together. Appendices 1 and 2 contain additional unpublished data and analysis supplementary to Chapter 5.

Publications included in the thesis

O'Shea, R. P., Parker, A. L., La Rooy, D., & Alais, D. (2009). Monocular rivalry exhibits three hallmarks of binocular rivalry. *Vision Research*, 49(7), 671-81.

Parker, A. L., & Alais, D. (2007). A bias for looming stimuli to predominate in binocular rivalry. *Vision Research*, 47(20), 2661-74.

van Ee, R., van Boxtel, J. J., Parker, A. L., & Alais, D. (2009). Multisensory congruency as a mechanism for attentional control over perceptual selection. *Journal of Neuroscience*, 29(37), 11641-9.

Parker, A. L., & Alais, D. (2013). Temporal auditory information speeds visual selection for consciousness during binocular rivalry. *Frontiers in Consciousness Research*, in press

Abstract

When the two eyes are presented with sufficiently different images, Binocular Rivalry (BR) occurs. BR is a form of bistable perception involving stochastic alternations in awareness between distinct images shown to each eye. It has been suggested that the dynamics of BR are due to the activity of a central temporal process and are linked to involuntary mechanisms of selective attention (aka exogenous attention). To test these ideas, stimuli designed to evoke exogenous attention and central temporal processes were employed during BR observation. These stimuli included auditory and visual looming motion and streams of transient events of varied temporal rate and pattern. Although these stimuli exerted a strong impact over some aspects of BR, they were unable to override its characteristic stochastic pattern of alternations completely. It is concluded that BR is subject to distributed influences, but ultimately, is achieved in neural processing areas specific to the binocular conflict.

Chapter 1

General introduction

What we see is not just a product of what is out there in the world, it is not just light reflecting off objects, striking our retinas and being sent to the visual areas of the brain. What we see is, of course, in part based on this external stimulation; but it is also a product of much more. It is a result of our perceptual history, our experiences as individuals and many complex neural and cognitive processes of which we are largely unaware. What we see – and, more importantly, *how* we see – is as much a matter of cognition as it is a function of the mechanics of our visual systems.

The realisation of this astonishing fact has developed over many years of study into the nature of visual perception. However, one particular phenomenon of perception reveals this more directly than any other: a phenomenon known as ‘perceptual bistability’. Perceptual bistability is any stable visual input that can be perceived in two or more ways by the visual system. If our visual perceptions were solely a product of external stimulation, given a stable input, we would correspondingly experience a stable perception; but this is not the case. When presented with these particular kinds of stimuli, our perception flips between multiple interpretations of the stable input. This is because such stimuli are designed to be ambiguous, and offer more than one perceptual interpretation. Such stimuli, above all other kinds, show us that visual perception is not a matter of computing external input, but rather is a process of interpretation, one that relies on what we have seen before as our visual systems develop, and also one based on the psychological, emotional and motivational states of the perceiver.

Human fascination with bistable perception is not new. Many ancient Roman mosaics demonstrate bistable properties (Ling, 1998), which were surely recognised as such by savvy admirers and the artisans themselves. Since then, the relevance of these unstable image configurations to our understanding of visual perception and the mind was furthered by artists, scholars and curious minds such as Ptolemy, Porta, Wheatstone, Necker and many others. An overview of historical observations of bistable phenomena will be presented later in this chapter. The point being made is that bistable perception is

of enduring interest due to its simplicity and utility in revealing a most fundamental aspect of human existence: that our perceptions of the world, and all within it, are not an objective truth, but are in fact a product of the inner workings of our own minds.

The best way to fully comprehend 'perceptual bistability', if you are unfamiliar with the concept, is to experience it yourself. This does not require complex apparatus (although some forms do require one). You can experience it simply by viewing one of its most popular incarnations; the Necker cube shown in Figure 1. A. The Necker cube is a two dimensional image depicting a cube projected in space; it was first reported by its namesake, Swiss crystallographer Louis Albert Necker in 1832 (Necker, 1832). Due to a lack of depth cues – other than the projections of the lines – the cube can be seen as protruding in one of two directions. These two depth interpretations can be experienced exclusively; and alternately; but never at the same time.

Figure 1. The Necker cube and depth cues

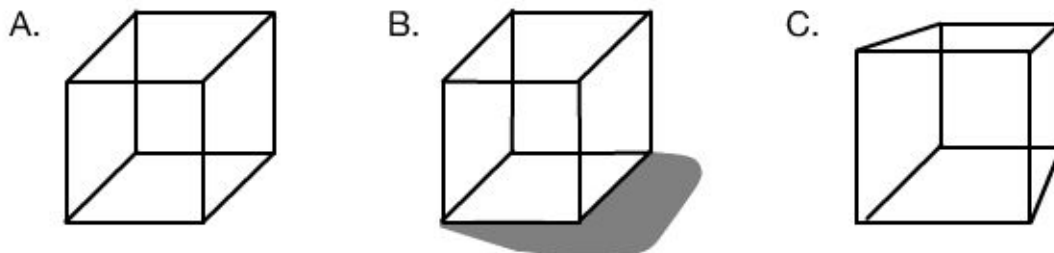


Figure 1 shows examples of the Necker cube, with and without additional depth cues. A) Viewing of the original wire-frame Necker cube results in two distinct depth interpretations; one where the bottom-left face is closest and the other where the top-right face appears closest to the observer. B) The addition of a shadow adds a depth cue that biases an interpretation of the bottom-left face of the cube as closest. C) Relative size, where objects closest to us appear larger is another depth cue that can bias our interpretation of the Necker cube.

Look at Figure 1 A. and focus on the upper right face of the cube: it should appear to be extended outwards and toward you in depth. Now focus on the lower left face: you should now be able to see this as the closest plane of the cube. Free viewing of the Necker cube results in spontaneous reversals between the two depth interpretations.

These reversals are precisely what is meant by the term 'perceptual bistability'. The reversals experienced when viewing bistable images are why these figures are sometimes called 'reversible figures'.

The reversals of depth experienced when viewing the Necker cube are possible because the wire-frame cube is 'depth ambiguous'. The ambiguity arises because there are no additional cues that support one depth interpretation over the other. The extension of the lines of the cube provide some depth information, but not enough to make one interpretation more likely than the other. Figure 1. B. demonstrates the effect of an additional depth cue; an object's shadow. Although the location of a light source needs to be known before a shadow cue can accurately disambiguate an object's extension in depth, the human visual system generally assumes that light comes from above, and the cube in Figure 1. B – with the addition of the shadow – biases an interpretation of the bottom left plane as closest. Another depth cue is relative size. Objects closest to us appear bigger and those farther away appear smaller. When the bottom left face of the cube is enlarged (relative to the top right face), this again biases our perceptual interpretation of the depth of the cube. The cues added to the Necker cubes presented in Figure B and C are examples of only two additional cues for depth that the visual system uses to interpret depth in two dimensional images. There are other depth cues that can be used, the essential point being that bistable illusions of depth arise due to a lack of additional cues that can help disambiguate the depth order in the image.

The Necker cube is only one example of perceptual bistability, there are many more that may be familiar. One of these is the 'young woman/old woman reversible figure shown in Figure 2. A, whose original creator is unknown. In the picture shown in Figure 2 A, either an old or young woman can be seen at any one time. Another example is of the face-vase illusion created by Edgar Rubin (Rubin, 1915) and shown in Figure 2. B. In this figure, either two faces – or one vase – can be seen, depending on which part of the image is interpreted as the foreground and which is the background. Another example is shown in Figure 2. C. of a shape that can be interpreted as either a duck or a rabbit. There are many more examples of perceptually bistable images and stimuli. The key feature of these

images is that they are ambiguous, and offer two or more perceptual interpretations. Of the examples here, many derivatives or entirely new examples are possible given that they satisfy this criteria.

Figure 2. Examples of perceptual bistability involving object interpretations

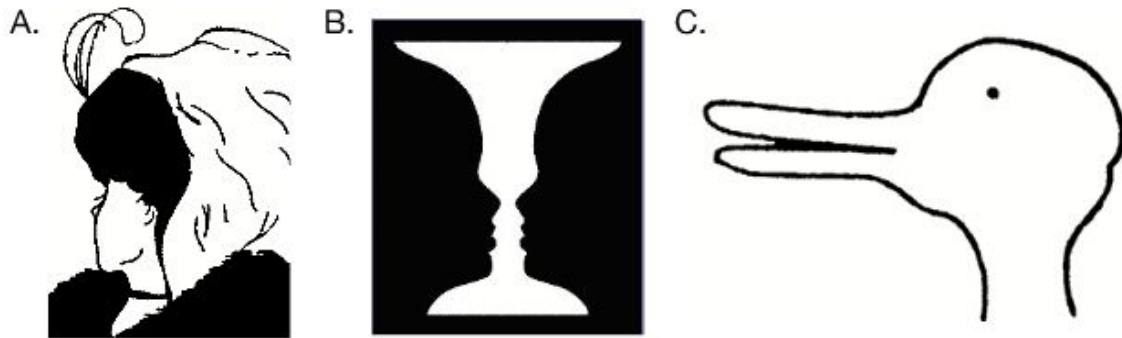


Figure 2 contains three examples of perceptual bistability that involve object interpretations. A) shows the 'old woman-young woman' reversible figure. B) The face-vase illusion, popularised by Rubin (1915) is an example of figure-ground reversals. C) The duck rabbit reversible figure.

The importance of perceptual bistability to modern research is not only due to its ability to reveal the subjective nature of our perceptual experiences. It is also relevant because it allows us to explore the often hidden mechanisms underlying perceptual selection, attention and cognition. By manipulating certain elements of bistable perceptual stimuli, investigators can ascertain what is most salient or important to an individual's perceptual system. Often, what is deemed to have perceptual salience, or importance, is shared among human beings as we all have very similar visual systems and biological motivations. However bistable perception can also be used to explore how an individual's visual processes may differ from others, especially in cases where that individual may have unique life experiences, physiological conditions or motivations. For example, people with high levels of generalised anxiety (Nagamine et al., 2007) or conditions such as bipolar disorder (Miller et al., 2003) can experience a different pattern or speed of perceptual reversals to those without these conditions.

As a tool of inquiry, perceptual bistability offers a way of exploring the biases and expectations we hold as observers as we interpret our external environment and how perceptual selection, awareness and attention operates generally. Modern researchers have recognised this, and as such, research in perceptual bistability is abundant and continues to grow. Before exploring the relationship between perceptual bistability and perceptual selection further, a brief history of bistable perception is presented.

Early observations of perceptual bistability

Observations of perceptual bistability stem far back in human history. One of the oldest recorded was by the mathematician and astronomer Ptolemy (100-170 AD) on the appearance of the sails on boats (Piccolino & Wade, 2006). If viewed at a far enough distance, at any one time the sails could appear either concave or convex, and these interpretations would alternate. The bistable perception of the sails was dependent on a far enough viewing distance to make the smaller details that would reveal the true protrusion of the sails difficult to pick up with the naked eye. As discussed in Figure 1, impoverished depth cues are an essential element to all bistable phenomena involving depth reversals, which are also stronger and more convincing with monocular viewing. This is because binocular vision provides the richest source of information about depth and, when removed from the equation, further diminishes the depth information available.

Ancient mosaics from Roman and Islamic architecture show awareness of perceptual bistability. One example was discovered in the Megiddo prison in Israel in November 2005 and contains reversible elements similar to the Necker cube (*Nature News*, v.440); seen in the image in Figure 3 D. Most of these ancient mosaic patterns use geometric forms, similar to Necker's cube, that contain ambiguity in depth interpretations, and can be seen as one or another depth at any one time: a clear example is a mosaic from Pompeii in Figure 3 B. Other mosaics display bistable properties in the way patterns appear to be grouped together, such as the mosaic in Figure 4 A and C.

Figure 3. Ancient mosaics displaying bistable properties

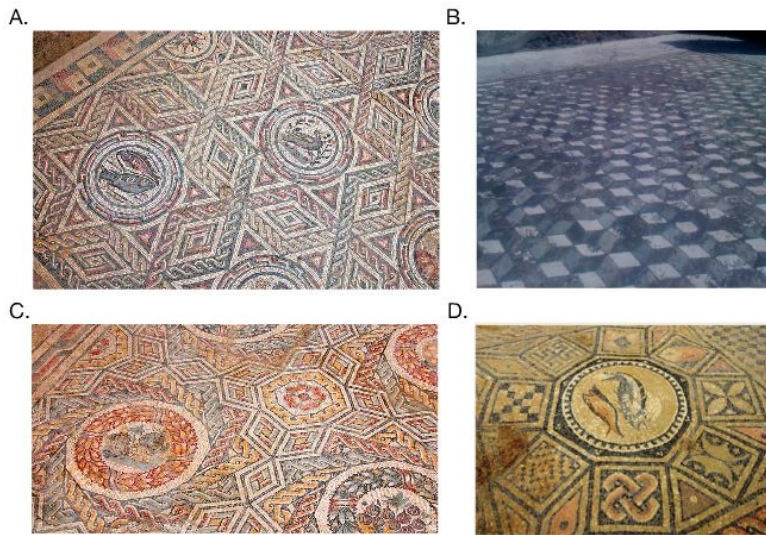


Figure 3. Ancient mosaics displaying bistable properties. A & C show a mosaic from the Villa Romana del Casale, in central Sicily, Southern Italy. A) shows multistability in the way the patterns group together. C) Shows some bistable depth effects similar to the Necker cube. B) A bistable mosaic found in Pompeii similar to the Necker cube. D) Another ancient mosaic containing bistable properties recently

revealed in the Mediggo Prison, Israel (from Nature News 440, 2007) (Image source: URL: <http://www.opticalillusion.net/ambiguous-images/mosaic-illusions/>)

Distinct groupings of the shapes can be seen at any one time, but can suddenly flip to an alternative grouping. Reversals of grouping, and reversals of depth, are the two main categories of perceptual bistability arising from two-dimensional images, and both have been used in art long before they were studied scientifically. These two types of perceptual bistability do sometimes co-exist, with illusions of grouping also giving rise to illusory depth orders of the grouped patterns, where the dominant pattern is seen to hover above the non-dominant pattern.

Another observation of depth reversals was made by English mathematician Robert Smith (Smith, 1738; as cited by Wade, 2005) and later in 1890 by Wilhelm Josef Sinsteden (Wade, 2005), who both described what is now commonly referred to as the ‘silhouette illusion’. It was observed by both on a windmill, where the arms of the mechanism would appear to alternate in direction when viewed at a distance or as a silhouette. This illusion can be recreated in many ways, such as with a walking person or a spinning dancer (by Nobuyuki Kayahara in 2003). An example appears below in the drawing shown in Figure 4 of a horseback rider.

Figure 4. The silhouette illusion

Figure 4. When certain objects are presented in silhouette, their orientation in depth can become ambiguous. Figure 4 shows an example of the bistable silhouette illusion in a drawing found online. The man on the horse can be seen as either approaching the observer, or riding away. Source: Drawing by Kelly Pounds (from www.kellscreations.com), retrieved 14th May 2011.



The astronomer David Rittenhouse (1732-1796) observed depth reversals similar to Ptolemy's observation of boat sails (Rittenhouse, 1786). Rittenhouse noted that when looking at the craters of the moon with only one eye, that they could curiously appear as either indents (craters) or protrusions on the surface of the moon. Again, this bistable phenomenon was primarily due to the lack of additional depth cues and was dependent on monocular viewing. Other reversals of depth were also noted by Albrecht von Haller (1708-1777) in the wax seals used on envelopes (von Haller, 1786). These reversals depended on different angles of illumination relative to the wax seals, specifically whether or not the shadows cast were above or below the bevelled seal. This illusion depends on an internalised norm of visual experience, namely that shadows are cast below objects, and tend not to appear above them, given that illumination most commonly comes from sunlight above us. Similar reversals arising from reliefs were also demonstrated by David Brewster (1781-1868), who is attributed the discovery of the hollow mask illusion. This occurs when changes in the source of illumination result in the mask appearing hollow and in relief; or, alternately, as a convex facial profile – it also depends on the internalised assumption that the source of illumination comes from above (Hill & Johnson, 2007).

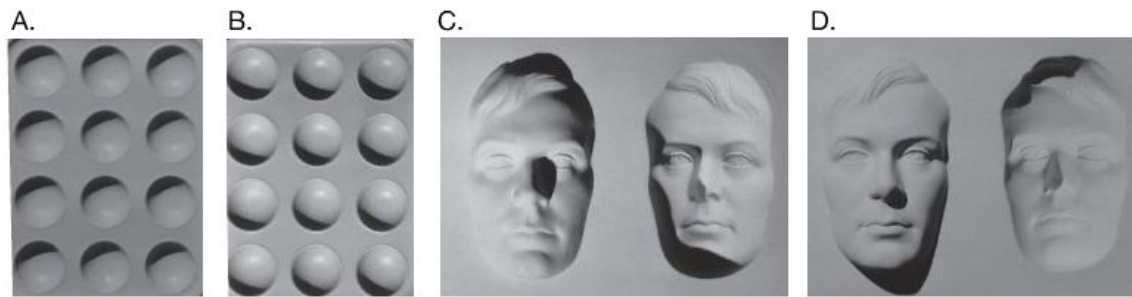
Figure 5. Illumination source can bias interpretation of relief or extension.

Figure 5. One assumption in visual perception is that illumination comes from above. Our interpretation of the images in Figure 5 include this assumption, even if it is inaccurate. A) The circles presented could be convex and illuminated from below, however they are commonly perceived as concave and illuminated from above. B) Similarly, the circles here are seen as convex and illuminated from above but they could just as likely be concave and illuminated from below. C) When illuminated from below, the convex mask on the right side appears convex, as does the actual concave face on the left. D) When the light source matches our internal assumption, and is from above, the face on the right appears accurately, as concave and in relief. Image source: unknown.

Vision science historian Nicholas Wade (in Alais & Blake, 2005) discusses another observation of depth reversals made by the philosopher and mathematician Schröder, who published a reversible figure of a staircase (see Figure 6 A), which can still be seen in popular culture. The staircase can be seen as either of normal orientation or upside-down, although the latter tends to be less readily seen due to its rare appearance in normal visual experience. As with the illumination of the wax seals, the likelihood of one perceptual interpretation over another is biased by what we expect to see based on our perceptual history.

Louis-Albert Necker (1786-1861) documented how the apparent extension of some crystal patterns would appear to reverse between two depth orders. He based his simple drawing of the now famous Necker cube (see Figure 1 A) on these crystal formations (Necker, 1832). Necker's cube appears to be the distillation of the more elaborate illusion using a staircase created by Ernst Schröder. It is one of the most enduring examples of perceptual bistability due of its elegance and simplicity; it has also been useful in

allowing researchers to explore how eye movements and focusing on particular areas of the cube can influence reversals, since the scarcity of the image features allows the experimental variables to be reduced to controllable numbers.

Figure 6. Reversible staircases

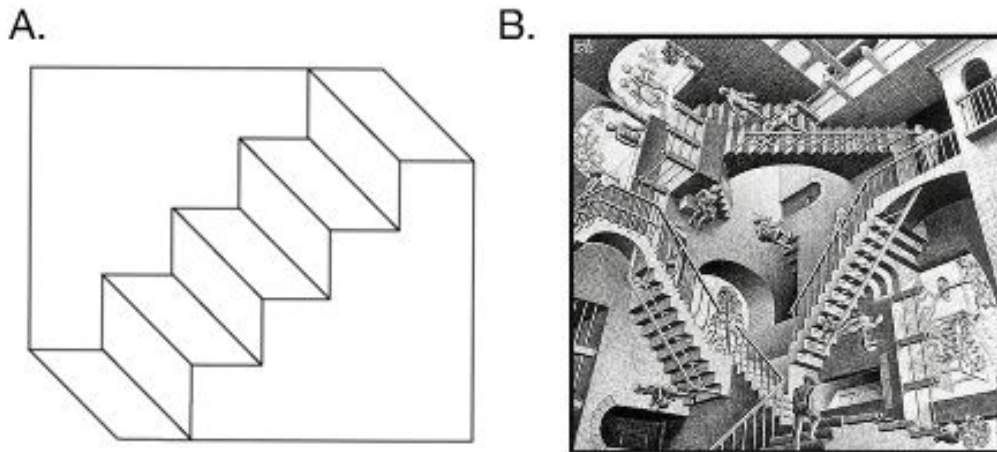


Figure 6. A) Ernst Schröder's original staircase illusion is reminiscent of the Necker cube. B) Dutch artist M.C. Escher was inspired by Schröder's illusion in his illustrations.

Of all these bistable phenomena, reversals are more convincing when viewed with a single eye, or monocularly, as they rely on impoverished depth information. In lieu of cues to distinguish the true depth or projection of an object, the alternate interpretations possible are seen for discrete periods of time. Essentially, this is the common feature of all 2D bistable illusions of depth order; that the depth cues to disambiguate the object's true depth are unavailable. Given such impoverished input, the visual system is unable to resolve true depth, and our perception fluctuates between the possible interpretations.

There are exceptions that do not rely on ambiguous, or impoverished, depth information: these include grouping reversals in ancient mosaics discussed earlier, and in drawings where two disparate objects are depicted within the same figure, such as the old woman/young woman illusion or the rabbit/duck figure shown in Figure 2. There is another much studied form of bistability that depends on discrepant images being presented to the two eyes triggering a perceptual state known as 'binocular rivalry'.

In normal viewing the images both eyes receive are very similar to each other. The slight discrepancies between them arising from the eyes' lateral displacement on the head are used by the visual system to compute stereoscopic depth information. Our visual system is unaccustomed to receiving completely different inputs from the two eyes and when this occurs, rather than attempt to fuse the two eyes' inputs we see one or the other for a short period of time before flipping to the other eye's image. These alternations between the two eyes' inputs constitute a unique form of perceptual bistability arising from a violation of the spatial rules of binocular vision. Both binocular rivalry and bistable patterns constitute a spatial conflict that violates our internalisation of a physical law; that two objects cannot exist in the same place at the same time.

Early observations of conflicting, or discrepant, binocular stimulation were made by Ptolemy, who placed different coloured rods in each eye's axis (Wade, 2005). Another was Giambattista della Porta (1535-1615), who used a septum to separate each eye's view and observed rivalry alternations (Wade, 1998). Other observations of rivalry were made by Jean Theophile Desaguliers (1683-1744) who used apertures to separate the two eyes' views. However, it was not until the invention of the stereoscope by Charles Wheatstone (1802-1875) that binocular rivalry's relationship to stereopsis was understood.

Wheatstone is attributed with the invention of the mirror stereoscope and the first accurate descriptions of stereopsis. He was the first to note that binocular viewing lead to greater depth information than monocular sight, and that the discrepancies between the two eyes' views were used by the visual system to calculate depth. He displayed two different letters, one to each eye, to show how sufficiently discrepant binocular stimulation leads to binocular rivalry alternations. Binocular rivalry, although demonstrating the same reversible properties of all perceptual bistable phenomena, constitutes a unique example and will be dealt with in more detail in the following chapters.

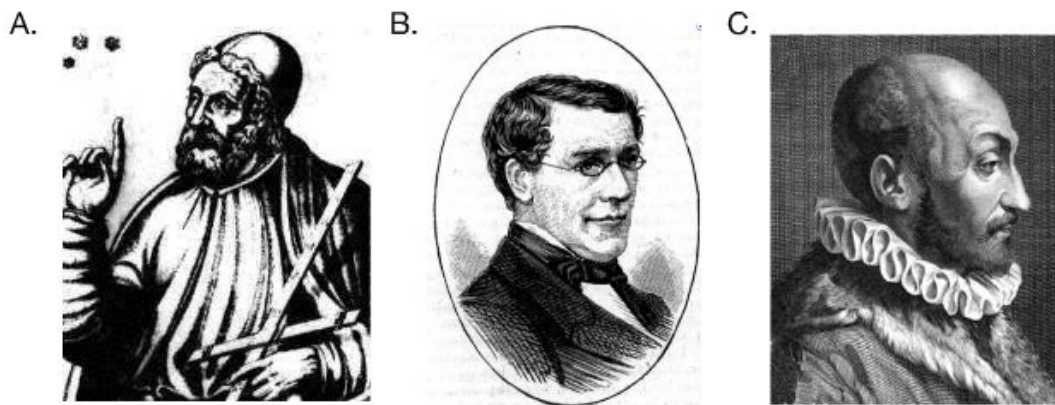
Figure 7. Historical figures who observed perceptual bistability

Figure 7. A) A portrait of Ptolemy who made the first known observations of perceptual bistability. B) A portrait of Charles Wheatstone, who invented the mirror stereoscope and was the first to methodically document binocular rivalry as it relates to stereopsis. C) De Porta, one of the very first people to recognise the importance of binocular rivalry alternations to studies of vision.

In more recent times, perceptual bistability has been examined in the context of psychology and neuroscience as a means of unveiling the hidden perceptual processes of the mind and brain that contribute to our perceptual awareness. Although interesting in its own right, recent investigations of perceptual bistability have focused more on what it can tell us about the underlying nature of visual perception and, in turn, the cognitive and neurophysiological processes that contribute to our conscious experience of the world (Baker, 2010).

The gestaltists used perceptual ambiguity as evidence for their particular theory of the mind (Kohler, 1947). Gestalt psychology arose from a German philosophical tradition that viewed the brain as a holistic, parallel processor, with self organising tendencies. Although a somewhat flawed scientific approach, criticised for being merely descriptive rather than explanatory, Gestaltism did bring to the fore many interesting principles of perception and psychology, such as emergence, perceptual bistability and amodal completion (Lehar, 1999). Their tenant, that “the whole is greater than the sum of its parts” is still a useful statement when applied to the workings of the brain and, indeed,

visual perception. They argued that bistable images demonstrated the ‘all-or-nothing’ nature of a mental representation, and the mind’s ability to interpret perceptual stimuli as a unified whole, rather than just processing the components that appear in front of the viewer.

Figure 8. Perceptual stimuli demonstrating Gestalt principles

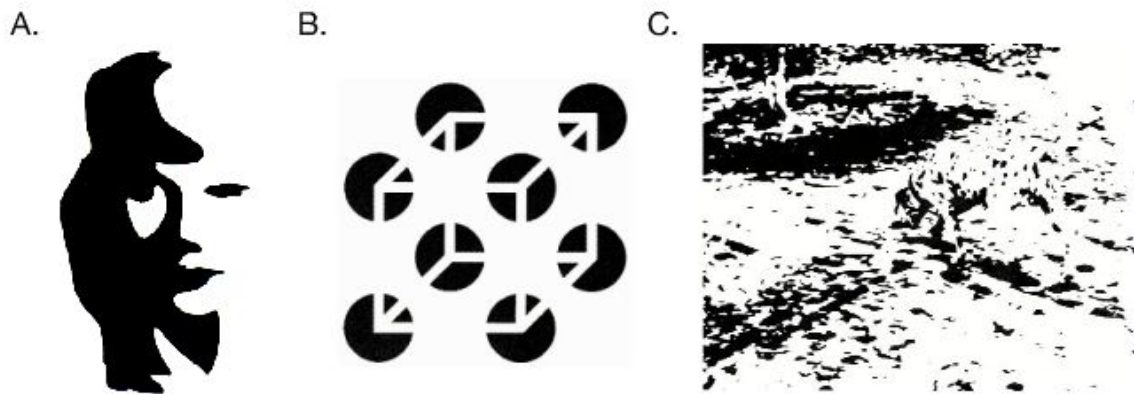


Figure 8. A) A Mooney face. B) Perceptual Completion of the Necker cube occurs despite missing contours. C) An image demonstrating the holistic nature of perception, the Dalmatian dog can only be seen as a whole, our perception of the dog is not achieved in discrete steps.

The Gestalt psychologists proposed that many of the processes underlying the perceptual and mental examples they put forward were due to a unified mechanism of perception and cognition; that is, the mind’s self-organising and interpretive ability. What the Gestaltists called ‘reification’ – more commonly known as amodal completion – does indeed share some features with bistable perception. Kanizsa figures – shapes that are completed perceptually even though their full forms are not depicted in the stimulus – can also engage in bistable reversals under certain conditions (Grossberg, 1997). An example of this is shown in Figure 8 B; the amodally completed Necker cube can appear either on top of the circles, or lying behind the black circles as if they were apertures. The idea that perceptual bistability is a result of a common perceptual mechanism is also supported by more recent experimental evidence, some of which is presented later in this Chapter and in the experiments presented in Chapter 2 of this thesis.

In the later half of the 20th century, perceptual bistability was proposed as a possible means of measuring the neural correlates of consciousness (Crick & Koch, 1990). The utility of this approach is that if the sensory stimulus remains stable, yet the perceptual experience of it fluctuates, then a neural analogue of perceptual awareness, or consciousness, could be recorded using available neuroimaging techniques. This method has been pursued with vigour (Baker, 2010) and has revealed some wonderful and exciting aspects of how visual awareness is achieved in the brain.

The utility of such methods, however, is limited to the technology available and may also be limited by our philosophical definitions and understanding of the term ‘consciousness’. Being able to state where or how a process involved in visual awareness is achieved in the brain is somewhat different to understanding how consciousness arises. This is because the awareness of an object or image, although it can be established as an objective fact, cannot be grouped with the subjective experience of that object or, indeed, our personal awareness of it. Consciousness as such is somewhat different to our awareness of the presence or absence of physical objects; it is above and beyond these sensory processes and cannot necessarily be defined by them. While it is true that perceptual bistability can help shed light on the neural mechanisms of perceptual awareness, this awareness is arguably distinct from what we understand to be human consciousness.

Even so, bistable perception can tell us a lot about the workings of awareness and cognition and how sensory stimuli is processed. It certainly can be used to help identify what aspects of an external stimulus most readily arise to visual awareness. It can also help further explain the precise workings of awareness and attention, if not the elephant in the room: consciousness. In addition, perceptual bistability can also be used to study what kinds of perceptual stimuli are most salient to individuals and to humans generally. Some studies, such as the one included in Chapter 3 of this thesis, compare the relative salience of emotive or arousing stimuli by pairing two stimuli in a perceptually bistable array, then measuring which one is seen first, or which is seen most often, or for the greatest amount of time, during the viewing period.

Figure 9. Examples of binocular rivalry stimuli

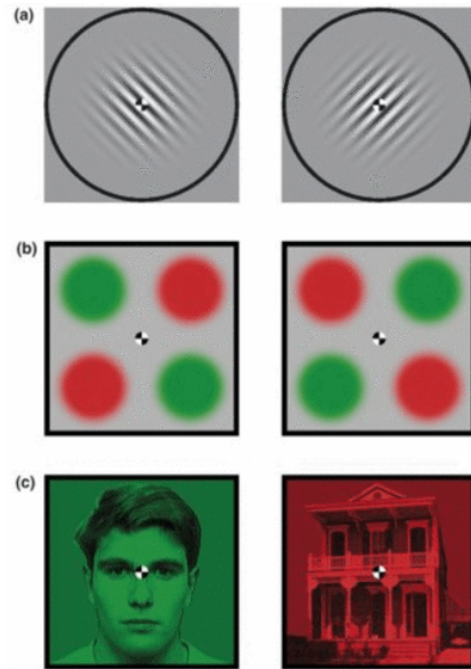
Figure 9. Many different images can be used to elicit binocular rivalry reversals.

A) Sine wave gratings are a popular stimuli, here shown filtered with Gaussian profiles that fade the edges.

B) Simple patches of colour effectively provoke rivalry alternations when presented separately to each of the eyes.

C) Complex images, such as those of a face and house shown here can also be used as rivalry stimuli.

Image credit: Tong et al. 2006.



Unfortunately, many forms of perceptual bistability are not amenable to large image changes. They are reversible because they contain impoverished information about depth or object identity, and because of this cannot be significantly altered to suit experimental demands. Fortunately there is one form of perceptual bistability that is fairly robust in the face of changing stimulus configurations and that is binocular rivalry. Since binocular rivalry is a conflict between the each eye's inputs – and not between the two images used *per se* – these two images can be almost anything that the experimenter wishes; so long as they are distinct enough to generate inter-ocular conflict and not be fused together stereoscopically (Blake & Wilson, 2011). This feature of binocular rivalry makes it the perfect form of perceptual bistability to explore questions about what is salient to the visual system, such as what features and objects rise to awareness most readily and which ones do not. The next section explores the history of binocular rivalry research and also describes its properties in more detail.

Binocular rivalry: a unique type of perceptual bistability

Unlike the examples of perceptual bistability discussed, binocular rivalry is primarily a laboratory-based phenomenon that cannot readily be experienced in everyday life without an apparatus to separate each eye's view (for instructions on how to experience binocular rivalry, see Clifford, 2009). Prior to a full understanding of stereopsis and binocular vision, the suppression theory of binocular vision did include a role for binocular rivalry in everyday sight. Suppression theory dates as far back as Porta in the 1500's and posits that we only see out of one eye at a time (Howard, 1995; page 338) even when the inputs are identical. This theory has consequently been disproved (see O'Shea, 1987). One might think that dissimilar binocular inputs in everyday viewing would give rise to binocular rivalry alternations; however, the conditions under which rivalry occurs are somewhat constrained. The two eyes' inputs must be dissimilar enough to engage in rivalry, but must also be physically alike in terms of stimulus strength; otherwise the stronger eye's image will persistently dominate awareness to the exclusion of the weaker one. An example of this is when one eye is covered with the hand. Although one eye receives a normal view of what is ahead, and the other eye is receiving a completely different image (of the hand), binocular rivalry does not occur. This is because the two images must be equated in luminance and contrast in order for rivalry alternations to take place. The hand covering the eye is both low in luminance and deprived of contrast information and, as a consequence, is never perceptually dominant.

Figure 10. A child peeking

Figure 10. The child in this photograph is not likely to experience binocular rivalry reversals in this situation, even though each eye is receiving markedly different retinal stimulation.

The inability of the obscuring hand to engage in binocular rivalry makes sense in terms of environmental considerations (Arnold, Grove & Wallis, 2007). When peering through a hole in a fence, we are not interested in the surface of the wall that the one eye is presented with, but in what appears through the hole. Likewise, if vision to one eye is impaired due to blindness or a refractive error of the lens causing a blurry retinal image, it makes sense that that eye's darkened or blurry view would be discounted in favour of the other, clearer eye's view. This is exactly what occurs in people born with a lazy eye, or strabismus: the weaker eye's input is discounted in favour of the stronger eye's. If not caught early in development, the muscle weakness underlying lazy eye can impair the development of stereoscopic vision (O'Neal, 1977), which is known to develop rapidly during the first five years of life with optimal corresponding binocular stimulation (Laws, 1964).

The proper development of stereoscopic vision is a crucial factor in the possibility of experiencing binocular alternations. Binocular rivalry depends on the regular functioning of the binocular system, which has learned that the two eyes' inputs correspond to each other and represent a singular scene in the external world. If normal binocular stereopsis fails to develop, as in the case of individuals with uncorrected strabismus, binocular rivalry is generally not experienced as a series of perceptual fluctuations but is a constant condition of one eye (Herzau, 1998). Although estimates vary, the number of people with impaired stereoscopic vision who are unable to experience binocular rivalry alternations is roughly 3-10% of the population (Pai & Mitchell, 2010)

That binocular rivalry is primarily a laboratory artefact does not exclude it from being used as a way to study and understand normal visual perception. Often, it is the manner in which failures occur in a system that can be most helpful in providing insights into how the system normally functions. For this reason, studies of binocular rivalry have been helpful in furthering our understanding of normal binocular vision and stereopsis (for example Wolfe, 1986; Blake, Yang & Wilson, 1991; and Harrad et al., 1994). In addition, binocular rivalry can be used to study the dynamics of perceptual selection and attention that operate under normal viewing conditions.

Binocular rivalry shares many properties with other forms of perceptual bistability, and can be classed as one instance of the same general phenomena (O'Shea et al., 2009). Although the average duration of each eye's perceptual dominance depends on the relative strength (i.e., luminance, contrast or other perceptual salience) of the images (Levelt, 1965), the pattern of reversals is similar among the different forms of bistable phenomena (Zhou et al., 2004; Brascamp et al., 2005; and Klink, van Ee & van Wezel, 2008). The particular pattern of reversals experienced during viewing of perceptually bistable stimuli is best characterised by a gamma distribution (Zhou et al., 2004 and others) with a stochastic probability of alternations (Murata et al., 2003). The ubiquity of this pattern of reversals is one line of evidence that a general perceptual mechanism underlies different forms of perceptual bistability (Carter & Pettigrew, 2003).

Figure 11. Distribution of perceptual dominance durations during rivalry

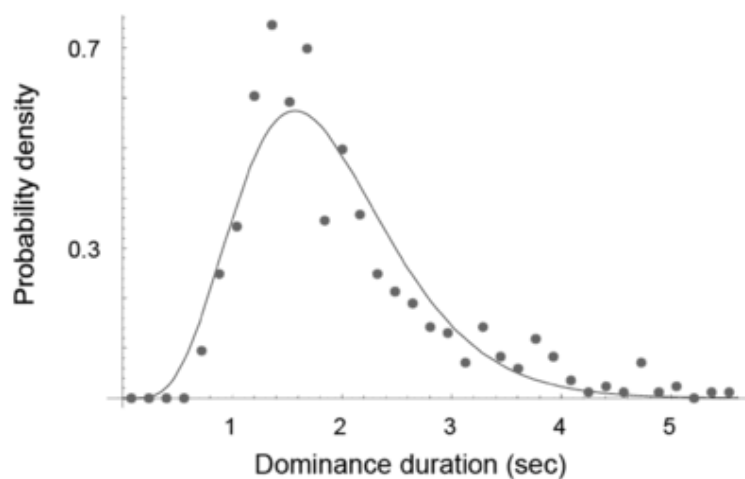


Figure 11. The distribution of durations for which each eye's image is seen is usually best described by a gamma distribution. The y-axis represents the probability of a particular dominance duration (x-axis) during perceptual bistability.

The stochastic pattern of alternations common to binocular rivalry and other forms of perceptual bistability tends to vary in rate between individuals (Miller et al., 2003). The rate of alternations can vary depending on age (Ukai, Ando & Kuze, 2003) and is also correlated to other factors such as generalised anxiety (Nagamine et al., 2007). An individual's bistable reversal rates are even linked to their genetic make-up (Shannon et

al., 2011), which demonstrates that more global factors than those determined by the physical stimulus or the visual system are involved in determining the overall temporal rate of reversals.

Although alternation rates vary among people, an individual's rate of reversal tends to stay consistent across time. Alternation rates can, however, differ depending on the nature of the bistable stimulus viewed. Binocular rivalry rates can depend on the overall brightness, or luminance of the images; alternations with high luminance image pairs result in more rapid perceptual alternations than low luminance ones (Levelt, 1965).

Despite the constrained conditions under which binocular rivalry can occur, its similarity with other forms of perceptual bistability, as well as its ability to be used more flexibly in terms of stimulus modifications, make it an excellent tool for exploring what kinds of stimuli are perceptually or cognitively salient. For this to be an effective endeavour, however, the properties of binocular rivalry alternations need to be fully understood. There are three main properties of binocular rivalry inputs that modify the amount of time one image is seen relative to the other that must be equated and accounted for before trying to compare experimental variations of rival images. These are stimulus luminance, contrast and spatial frequency (as established by Levelt, 1965).

Levelt demonstrated that the amount of time one rival image is seen relative to the other can vary depending on its brightness (luminance), contrast and/or spatial frequency content. If one eye is presented with a low luminance image and the other eye a bright, high luminance one, the bright image will be seen for a greater proportion of the viewing time than the dull one. This is also true for two images that differ in contrast. Contrast is the average luminance difference between the lightest and darkest areas of an image, when this difference is great, the image is said to have high contrast. Take an image with very light, and correspondingly very dark parts with a high contrast value. If presented in binocular rivalry with a low contrast image with light and dark areas that are not as extreme, the high contrast image will dominate perceptual awareness for a larger part of the binocular rivalry viewing period.

Spatial frequency is another property of images that can alter the relative dominance of two rival images. This refers to the periodic cycles between the line components of an image: an image with high spatial frequency is one where the image components are very close together, and are best described as the parts of the image that convey fine detail. Low spatial frequency refers to the line and image segments that are more widely spaced, and can be characterised by the coarse image detail, such as the larger outlines of the head and profile that make up an image such as a face.

Fine details such as the eyelashes, or creases or wrinkles of the skin correspond to the high spatial frequency components in the image. Images that contain a broad range of spatial frequency information, ranging from both high and low extremes, tend to dominate during binocular rivalry over images with less spatial frequency content, such as an image that has had its high or low spatial frequency components filtered out. Interestingly, images containing only extremely low spatial frequency information tend not to rival well with images containing only very high spatial frequency information (Yang, Rose & Blake, 1992). In fact, two rival images of this sort will more often fuse instead of engage in rivalry alternations. One possible explanation for this is that a broad range of spatial frequencies is contained in natural scenes. The binocular system may attempt to integrate two distinct narrow-band inputs because they do not necessarily represent two different scenes, but can be interpreted as two different components, or layers of a singular scene.

Binocular rivalry in relation to stereopsis

Binocular rivalry is a failure of binocular fusion, or stereopsis. As mentioned previously, the first methodological and scientific account of the phenomenon of binocular rivalry was made by Charles Wheatstone (Wheatstone, 1838). Prior to his invention of the mirror stereoscope, methodological studies of binocular vision were limited. The stereoscope allowed the presentation of binocular stimuli in a controlled fashion, not available with apertures or other makeshift methods (such as the use of a septum). This is because the precise location of the binocular images could be controlled and stabilised with the stereoscope. This allowed precise measurements and configurations of the binocular

image discrepancies that resulted in stereoscopic fusion and the perception of depth or the failure of this fusion: binocular rivalry alternations.

In Wheatstone's seminal treatise, he clearly outlines the way in which discrepancies between the two eyes' views result in the perception of depth. This can be achieved by both monocular or binocular image information, but it is only the latter that provides accurate information about the relative distances between objects perceived (Palmer, 1999). Monocular depth cues are only qualitative at best, and can provide information about whether or not two objects are closer or further away relative to one another. Binocular depth information provides information about the precise distance between two objects, and how far away the objects are relative to the observer.

Figure 12. Wheatstone's mirror stereoscope

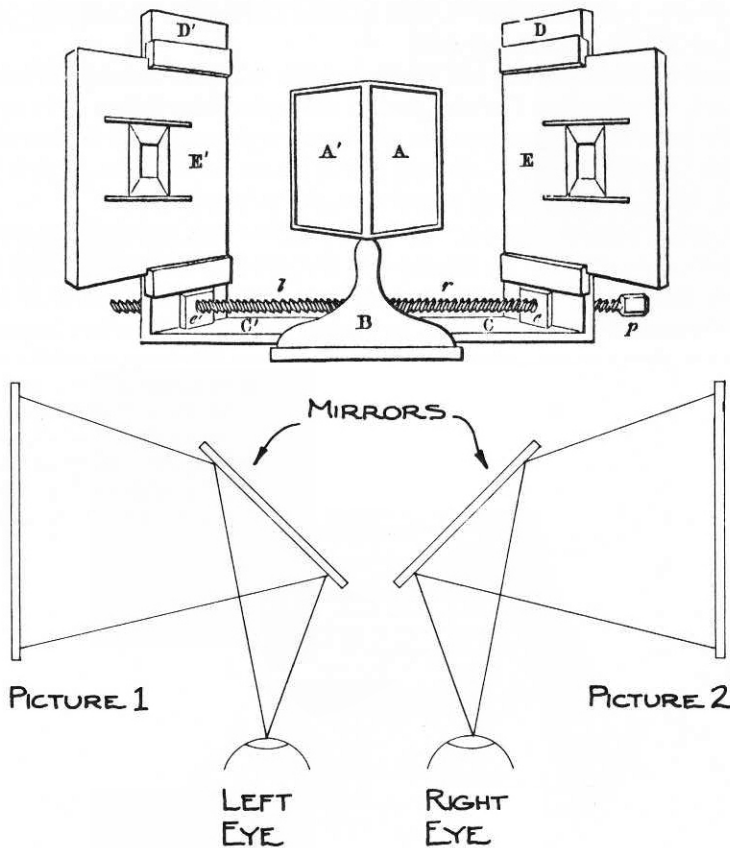


Figure 12. Wheatstone's drawing of his mirror stereoscope. Distinct images can be presented separately to each of the eyes by virtue of the angled mirrors. Image source: Wheatstone 1838.

The lower image is an illustration of how the two eyes views are displaced by the mirror stereoscope (source unknown).

How the visual system computes binocular depth information is still an active area of research (Blake & Wilson, 2010). We do, however, know *what* information is used by the visual system to compute depth: it arises from the slight discrepancies present between the two eyes' inputs, the discrepancies created by their slightly different placement on the head. The small separation between the two eyes of usually a few centimetres or so ensures that objects at different depths are displaced leftward or rightward in one eye's view relative to the other. This relative displacement of the object in the two eyes' views is what the visual system uses to calculate an impression of their depth in space.

The ability of the visual system to calculate stereoscopic depth depends on the objects appearing in the two eyes being the same: we need to be viewing a singular object or scene in space. Since in humans, both eyes face forwards, this is the normal experience we have. The assumption the visual system is making each time we combine the two eyes' retinal images and perceive a scene with binocular depth is that of a singular or cyclopean worldview. Most of our visual experience from birth onward fortifies this assumption. So does the information about our external world collected from the other senses, specifically touch (Bushnell & Bourdreau, 1993). Through the co-operation of explorative touch and visual input, we can ascertain that the apple we see before us is indeed one apple; despite the small differences in view we are experiencing from each of our eyes. The coordination of information gleaned through different senses in the calibration of binocular vision implies that binocular rivalry, too, may be susceptible to sources of information from non-visual senses. This possibility is explored later in this chapter and also in the experiments presented in Chapters 4 and 5. Development of a cyclopean worldview is a necessary condition for binocular combination to occur.

The neurophysiology of vision

In order to discuss neural theories of binocular rivalry, a quick overview of the neurology of the visual system is needed. Broadly speaking, the visual system comprises the eyes, the optic nerve, the lateral geniculate nucleus (LGN) and the visual cortex, which is located at the back of the brain in the occipital lobe. Light hits receptor cells in the retina in the back of the eye. Via a process of chemical transduction, these receptors convert

light energy into an electrical impulse, which is sent down the optic nerve to the visual cortex. The visual system can be described in a feed-forward fashion as a hierarchy of processing areas. The first cortical processing area is called V1, or visual area 1, which is shown in Figure 13 by the light yellow section of the cortex. Neurons located in V1 respond to the particular features of a visual array, such as orientation, contrast and colour and do so within small receptive fields. The activity of V1 neurons is spatially dependent; they only fire when stimuli are presented in their preferred location of the visual field; or rather, to the corresponding section of the retina that represents that area of the visual field (Hubel & Weisel, 1968). The activity of this visual area is therefore thought to constitute a spatially representative map of the visual field (Wandell, Dumoulin & Brewer, 2007).

Figure 13. The anatomy of the visual system

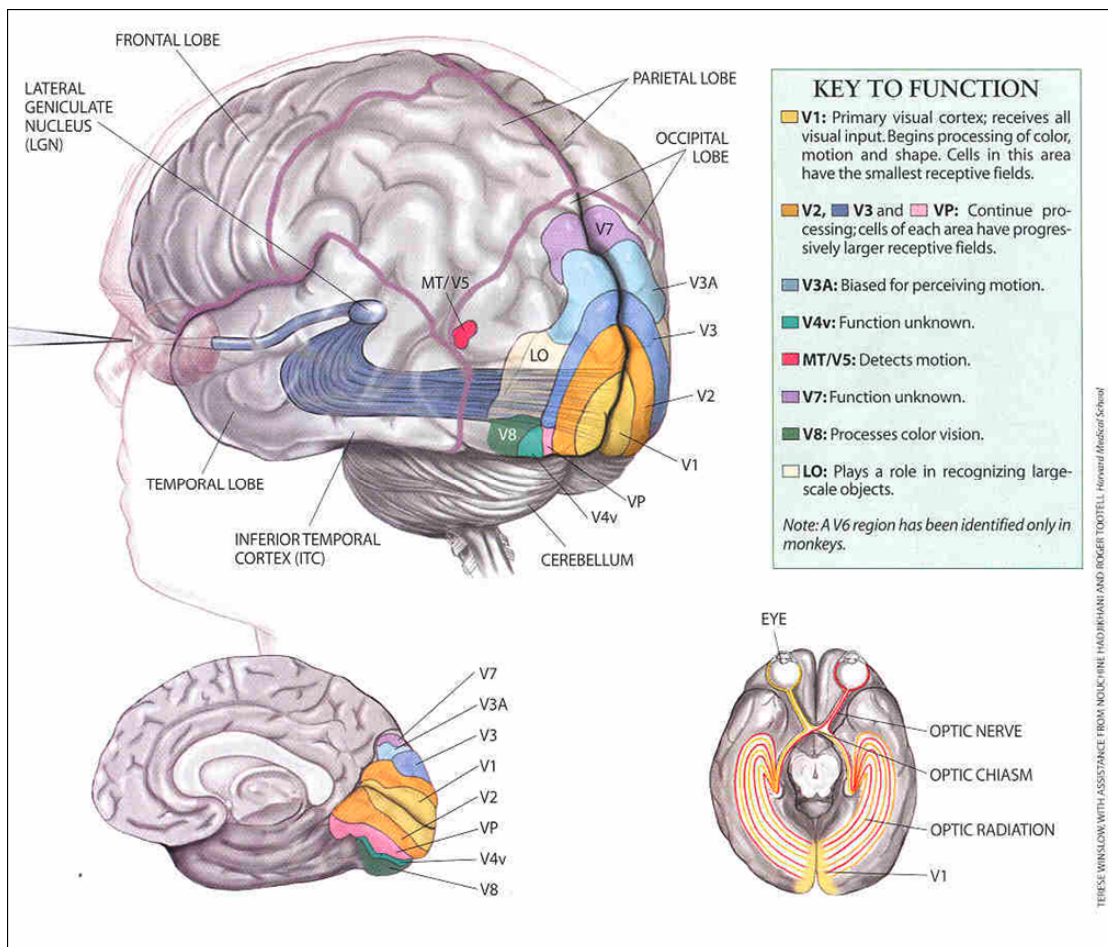


Figure 13. The anatomy of the visual system. Image credit: Terese Winslow.

After V1, visual signals are processed at further stages of the visual processing hierarchy. Later areas, such as V2, contain binocular neurons that are activated regardless of which eye is stimulated. V1 neurons, on the other hand, are monocular and respond to input from their preferred eye (Hubel & Wiesel, 1968). Later in the visual processing stream, more specialised visual areas are found that respond to more holistic stimulus properties, such as visual objects (Epstein & Kanwisher, 1998), faces (Kanwisher, McDermott & Chun, 1997) and movement (Braddick et al., 2001), although it should be noted that cortical area MT/V5, like V1 has a topographical organisation and can respond to motion signals at a similar latency to V1 due to a direct connection with the lateral geniculate nucleus in the optic chiasm. Aside from the topographical nature of complex motion processing, the later visual areas are generally not concerned with the location of the stimuli in the visual field; they respond to their favoured stimuli irrespective of its location in the visual field (Melcher, 2005; Graziano, Andersen & Snowden, 1994).

Information from the visual cortex is processed further by other parts of the brain involved in more complex interpretation, such as the parietal and temporal lobes that are labelled in Figure 13. The parietal lobe is dedicated to representing space and our location within it, and is involved in our physical interactions with the environment (Andersen 1995). The temporal lobe is concerned with the processing of objects; their identity and meaning (Lueschow, Miller & Desimone, 1994) and is involved in memory formation and retrieval (St Jacques, Kragel & Rubin, 2011). The visual pathways terminating in these two cortices are called the dorsal and ventral streams respectively. The dorsal stream is involved in spatial visual processing, and the ventral is concerned with the labelling or identification of what we experience (Goodale & Milner, 1992).

Despite the descriptive convenience the concept of a linear visual processing hierarchy provides, visual areas are highly interconnected (Felleman & van Essen, 1991). The reciprocal pathways between the visual areas of the macaque monkey cortex are shown in Figure 14. The interconnectedness of visual areas mean that information is not simply relayed through the visual cortex in a linear manner: visual signals are processed in parallel in different visual areas that are subject to feedback from each other *and* from

non-visual cortical areas. Once a visual signal is processed, the activity it generates in early visual areas such as V1 can be subject to modulation from higher cortical visual processing areas (Angelucci & Bressloff, 2006). Hence, no single area of the visual cortex acts independently in representing a visual stimulus or feature. Even responses to the most basic of visual elements can be modulated by the simultaneous processing of other features present, or the larger context, background or meaning of the image.

Figure 14. Connections between visual cortical areas of the macaque monkey.

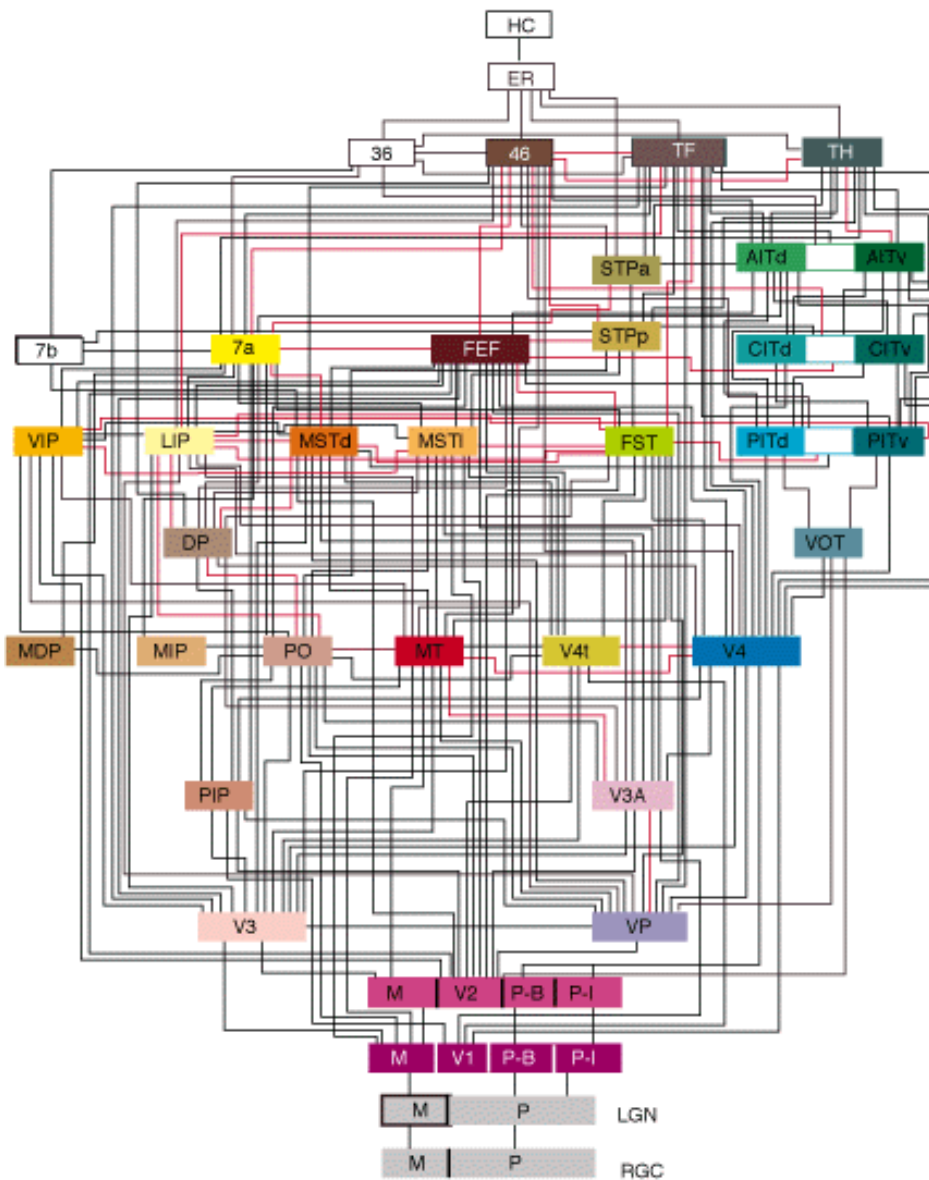


Figure 14. *“Hierarchy of visual areas in the Macaque monkey. This hierarchy shows 32 visual cortical areas. These areas are connected by 187 linkages, most of which have been demonstrated to be reciprocal pathways”. Figure and description from Felleman & Van Essen, 1991.*

The interconnectedness of neural visual processing complicates its study. However, the fact that there does appear to be a certain extent of modular, feature-specific processing occurring is helpful. The way these modules interact in forming a complete perceptual experience is the new frontier for research in visual neuroscience.

Neural theories of binocular rivalry

Investigations into binocular rivalry directly after Wheatstone’s discovery were based mainly on its relationship to stereopsis. During the later 18th and early 19th centuries, visual scientists explored the basic properties of binocular rivalry as a visual phenomena, and established the general requirements for it to occur. This included the stimulus properties that alter the temporal course of binocular rivalry alternations over the viewing period. The understanding of binocular rivalry alternations as a violation of the norm of a cyclopean worldview assumes quite a high-level cognitive appraisal of the non-matching binocular inputs; specifically that they violate an internalised cognitive worldview. There arose quite an active debate, which is still in part ongoing, over whether binocular rivalry depends on a higher-order cognitive process of interpretation; or, rather, on binocular conflict in the earliest stages of the visual processing hierarchy (V1) representing each eye’s input. As it turns out, neither low- nor high-level accounts of rivalry, or indeed stereopsis itself, are sufficient. Most percepts involve both preliminary computations of retinal input – as well as higher-order cognitive processing – in order to be achieved. How the visual system responds to perceptual ambiguity is no different. The question of which type of processing (low-level or high-level) is most involved in a particular perceptual process is still a valid question, and can be used to characterise how feedback from visually peripheral brain areas can impact early visual processing.

In order to comprehend the inter-connectedness of low- and high-level visual processes in binocular rivalry, it is helpful to first characterise how each stage of processing

contributes to our perceptions. In respect to binocular rivalry, low-level theories state that it is a conflict between the two eyes at a monocular neuron level (V1) which results in binocular rivalry. As was briefly touched upon in the last section, the visual system can be characterised by a hierarchy of visual processing stages. Information from each eye's retina travels down the optic nerve and reaches the primary areas of the visual cortex, also called the striate cortex, and area V1. The striate cortex is the only part of the visual system that contains neurons that respond exclusively to monocular stimulation.

Monocular neurons in the striate cortex are those that only respond when a particular area of the retina of one eye is stimulated. Binocular neurons are those which respond to retinal stimulation of either eye. If one part of the retina is stimulated in the left eye, a binocular neuron might respond to this; but it will also respond if the corresponding area of the right eye's retina is stimulated. On the other hand, a monocular neuron will only respond if the retina of the one eye to which it is connected is stimulated.

Low-level theories of binocular rivalry state that it is competition between these monocular neurons that result in rivalry alternations (for example Blake, 1989). High-level theories of rivalry on the other hand, state that it is the conflict between the two image representations at later stages of visual processing that produce rivalry alternations (Leopold & Logothetis, 1999). As the retinal signal progresses to higher levels in the visual processing hierarchy, neural responses become more complex and global. At the earliest stages, visual neurons respond to small or specific image properties such as line orientation, the eye of origin (monocular neurons) and other properties such as colour and spatial frequency content. At higher levels of processing in the extra-striate cortex, the areas of the visual cortex further downstream to the striate cortex, neural responses to images are less feature based. The higher level properties to which extra-striate neurons respond can include object identity and the environmental context of the viewed image. For example, some neurons in the extra-striate cortex fire only when presented with faces; and some only when presented with places. The visual area containing neurons that respond to faces is called the Fusiform Gyrus, or the fusiform face area; the area that responds to places is called the parahippocampal place area. Other visual areas that respond to specific visual priorities, such as motion, have also been identified. High-level

theories of binocular rivalry consider these higher-level processing areas that are involved in representing images holistically to be the neural locus of rivalry alternations.

Interestingly, both high- and low-level theories of binocular rivalry have gathered empirical support, which can be interpreted as reflecting the inseparable nature of low and high level visual processing. Going back to the incomplete, but influential ideas of the Gestalt psychologists, visual processing is a holistic process where discrete physiological functions are performed in parallel to produce the overall perceptual experience. That the whole is greater than the sum of the parts also rings true, as our experience of binocular rivalry, or any other definable perceptual consequence, cannot be explained solely by an isolated area or mechanism in the brain because they are achieved by a distributed network of neural areas related to memory and spatial attention.

Evidence for low-level theories of rivalry come from functional image studies that demonstrate fluctuations between monocular neurons in the striate visual cortex/area V1 (Polonsky et al. 2000). There is also evidence that activity of the lateral geniculate nucleus, a visual processing area even earlier than V1 in the visual hierarchy that contains only monocular neurons, also fluctuates in synchrony with the perceptual alternations accompanying binocular rivalry (Haynes, Deichmann & Rees, 2005; Wunderlich, Schneider & Kastner, 2005). This is interesting, as the thalamus is the source of delta brain wave activity that arises during slow wave sleep; and delta waves and binocular rivalry share a similar frequency range of 0.5-4 Hz. Perhaps an even lower, sub-cortical theory of binocular rivalry is warranted, as suggested by Einhäuser, Stout, Koch and Carter (2008) and explored further in the General Discussion (chapter 6). This possibility is countered by an absence of binocular rivalry related activity in LGN as recorded with single cell electrodes in animals (Lehky & Maunsell 1996) and requires further empirical exploration in human observers.

These studies clearly show that monocular neurons are actively engaged in the image conflict involved in binocular rivalry. However, other neurophysiological research has shown that activity in area V1 is also modulated by 'feedback' from later processing

areas in the extra-striate cortex (Felleman & Van Essen, 1991). It is conceivable that the more complex properties of images undergoing rivalry, processed at later stages of the visual processing hierarchy can influence these V1 responses. It is also possible that monocular neurons in V1, and perhaps even pre-cortical dynamics, are acting as a gatekeeper to the progression of image processing to higher cortical areas.

High-level or ‘stimulus’ theories of binocular rivalry are supported by experiments showing that when early monocular responses in V1 neurons are overridden by certain flickering stimulus presentation, binocular rivalry can still occur. Called “flicker and swap” rivalry, this particular stimulus presentation involves two rival gratings of orthogonal orientation: one coloured red and the other green. As in conventional binocular rivalry presentations, the two different gratings are at first presented one to each eye. Instead of a static presentation however, each grating is flickered on/off at a rate of between 18 and 20 Hz, or cycles per second. In addition, about three times a second (at a 3 Hz cycle), the two gratings are swapped between the two eyes.

When experimental subjects view the flicker and swap stimulus, they experience rivalry alternations; that is, the perceptual dominance of a particular grating, be it red or green, extends over periods where the grating is switched between the two eyes. If rivalry were only between the two eyes’ inputs, and not between the images presented, a physical swap occurring during each eye’s period of perceptual dominance should be seen. That the current dominant perception of one of the gratings is maintained *after* that grating is swapped to the other eye shows that rivalry alternations are not just a matter of which eye is dominant at any one time, but also what stimulus is currently dominant.

The flicker and swap experiments, although a convincing demonstration of the importance of stimulus representations to binocular rivalry alternations, are unusual because they rely on a narrow window of flicker rates. When the rival gratings are simply swapped between the two eyes, the effect all but disappears (Bhardwaj, O’Shea, Alais & Parker, 2008). This has been explained in part by a computational model of binocular rivalry that accounts for the flicker and swap effect (Wilson 2003). Wilson presents

evidence that the particular cycle rate of flicker required for flicker and swap rivalry to occur involves discreet stimulus presentations that are too short to engage monocular processing in V1. A 20 Hz rate of on/off flicker involves discrete stimulus presentations of 50 milliseconds (ms), which is insufficient: for an adequate and sustained response, stimulus presentations of 100 ms or above are required. The flicker is, in effect, disabling the monocular responses necessary for eye-based rivalry to occur, and instead generates stimulus-based rivalry.

Other evidence for stimulus rivalry comes from experiments that show that discrepant image parts presented across the two eyes can group together during binocular rivalry. If two different images are taken apart, like a puzzle, and then each puzzle piece is distributed between the two eyes, rivalry alternations can occur between completed image representations (Kovacs, Papathomas, Yang & Feher, 1996). The piecemeal stimulus used by Kovacs's et al. is shown in Figure 15. Participants can still view the completed images undergoing rivalry, even though the image components have been scattered between the two eyes. Again, this demonstrates that it is the stimulus representation, not the conflicting information at purely a monocular level, that generates rivalry alternations. Functional imaging studies have also been carried out that support the idea that stimulus-based neural representations are involved in binocular rivalry. One of these studies showed activity in specialised processing areas – the extra-striate cortex, the fusiform face area and the parahippocampal place area – fluctuate in activity corresponding to a participant's perceptual experience of binocular rivalry between faces and houses (Tong, Nakayama, Vaughan & Kanwisher, 1998).

Figure 15. Piecemeal binocular rivalry stimuli

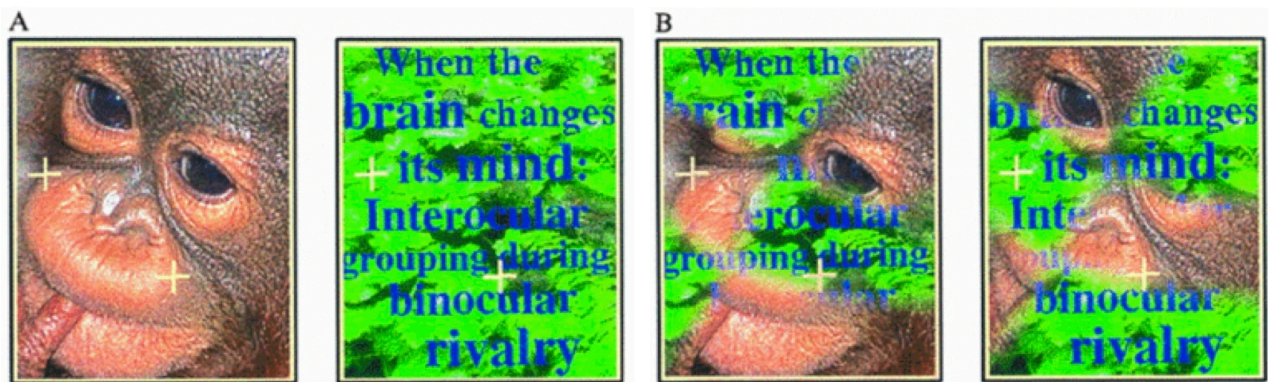


Figure 15 contains the stimuli used by Kovacs et al. (1996). A) The two rival images, as presented to each eye. B) The piecemeal versions of the two images.

Although the evidence for a stimulus-based account of binocular rivalry is convincing, there are some disclaimers to be made about the generality of the findings. Flicker and swap rivalry tends to occur only with a narrow range of stimulus parameters that encourage this form of pattern rivalry. Also, there are periods in which perceptual experience does actually correspond to eye-based accounts of rivalry. For some of the viewing period, especially in the preliminary stages, perceptual dominance is based on the dominant eye's input and does not follow the perceptually dominant grating to the other eye. Similarly, when viewing the 'puzzle-piece' rivalry stimuli used in Kovacs et al. (1996), there are periods in which the piecemeal presentation received by one of the eyes is the dominant one perceived, and not the combined stimulus representation of the unified image between the two eyes' inputs. Also, fluctuations of neural activity in extra-striate areas corresponding to rivalry alternations are not necessarily their source. They could be due to the processing of the currently dominant percept after it has been selected for awareness in earlier processing stages. The evidence indicates that both eye-based and stimulus-based rivalry are possible. Both may be operating concurrently when viewing conventional binocular rivalry displays.

Aside from the evidence that neural processing at the level of stimulus representations can influence binocular rivalry, there is also an active field of research exploring how cognition and attention relate to rivalry dynamics. This thesis explores the idea that binocular rivalry dynamics are due to a less conscious, more hardwired component of attention; one that is associated with general physiological arousal. Before exploring the relationship between attention and perceptual bistability, it would be helpful to briefly cover the relevant aspects of research into the psychology of attention.

Psychological investigations of attention

How human beings allocate attention to the external environment, and what events or objects present in the environment can capture our attention without wilful control, have been subject to much investigation in the field of psychology. Attention can be separated into two broad categories. One, where we purposefully attend to a particular subject or object in front of us, originates from within and is consequently referred to as

‘endogenous’ attention. The other, where external events or objects can capture our attention against our will, is termed ‘exogenous’ attention, or attention that is allocated to stimuli external to ourselves by virtue of their ‘attention grabbing’ properties. Both endogenous and exogenous attention have been subject of much study, with the latter being more amenable to certain types of experimental methodology, given that the subjective nature of endogenous attention is more difficult to define and measure. What motivates us to attend to objects that might otherwise not be salient is governed by a host of internal and unobservable variables, whereas the physical properties of an external stimulus that can capture our attention are more easily identified and controlled. Even so, both are of great interest to psychologists and scientists of the mind, and to some extent both must be considered when contemplating the unified perceptual outcomes of attention.

Psychological investigation into the type of exogenous perceptual stimuli that capture our attention has its origins in the 1980s, although observations of orienting responses in both humans and other animals had been made previously in the areas of biology, neuroscience and other fields. One of the pioneers in the psychology of attentional capture was Anne Triesman, who popularised the experimental paradigm of ‘visual search’ tasks, which involve searching a visual array of features for a target feature that has been defined prior to the trial or by virtue of its uniqueness in respect to the other elements of the array. The time taken to detect the target feature can be used as a measure of the salience of that feature, given the context in which it is presented. Context is a very important aspect of visual search, and is established by the nature of all the other elements in the search array. These non-target elements are referred to as ‘distractors’.

Triesman’s research revealed that particular targets are more salient than others, and are more readily detected because of their uniqueness relative to the distractor elements in an array (Treisman, 1988). For example, if a circular target is present amongst cross distractors, as seen in Figure 16 A, the uniqueness of the target makes it instantaneously recognisable and perceptually salient. This type of target is referred to as a ‘pop-out’, or singleton. Triesman’s research also examined ‘conjunctions’, where a target’s uniqueness

is due to a conjunction of two or more features also present in the distractor elements. This type of visual search is less automatic than ‘pop-out’ displays, and requires serial processing of the elements of the visual array before the target can be located. An example of a pop-out (A) and a conjunction (B) stimulus array are shown in Figure 16 below.

Figure 16. Visual search arrays

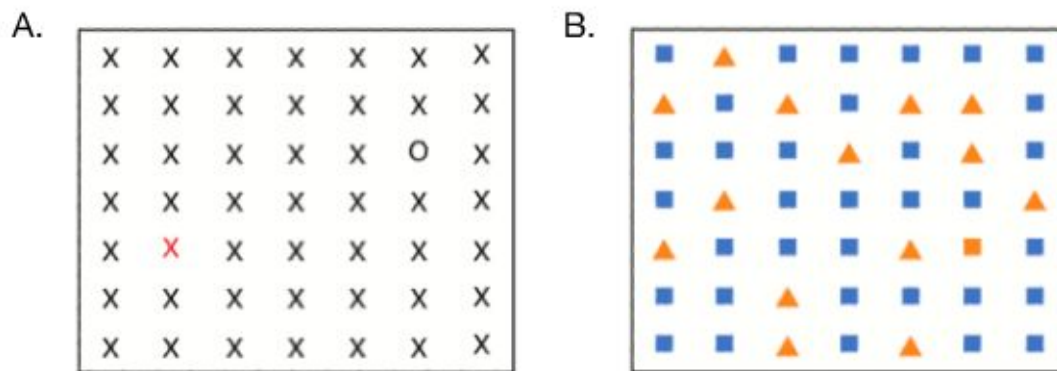


Figure 16. Examples of visual search arrays. A) Includes two singletons; the circle and the red cross which each contain properties not shared with the distractors and consequently ‘pop-out’. B) Shows a conjunction search array, where the unique target shares both of its distinguishing characteristics (colour and shape) with distractor items.

Detection of pop-outs and conjunction targets in visual arrays involve two types of visual search which Treisman thought were dealt with by two different types of attention. Pop-out detection is fast and almost automatic, whereas conjunction searches are slower and more methodical. These differences were used to support her Feature Integration Theory of visual attention (Treisman & Gelade, 1980). The theory states that different maps of visual features are used to consciously integrate visual features into a perceptual whole. She coined the terms ‘bottom-up’ and ‘top-down’ attention, which to this day are still present in psychological and neuroscience vernacular. These terms can be considered as the same two forms of attention described previously; exogenous and endogenous attention, respectively.

The main purpose of the Feature Integration Theory was to describe and explain how features are bound together to form conscious perceptual experiences. The theory stated that different features of a complex visual stimulus are processed in separate stages, represented as ‘feature maps’. A schematic depiction of how feature maps represent the visual environment is shown in Figure 17 below. Also introduced was the idea of a ‘saliency map’, which contains information about the most salient features of the visual scene before us. Although details of Treisman’s theory have been largely discounted by more recent research, the idea of a saliency map is still popular, and in fact the behaviour of area V1 is considered by some as constituting a neurological substrate for the mapping of salient visual features. Whether saliency is a property of the visual stimulus, or the mindset of the observer, is an interesting question; it is, in part, answered in the affirmative on both sides. There is evidence to suggest that the physical properties of certain types of stimulus are the primary determinant of perceptual saliency. However, it is also possible that the tuning of a saliency map in area V1 could be influenced by non-visual feedback about what is perceptually important or salient.

Figure 17. Feature Integration Theory

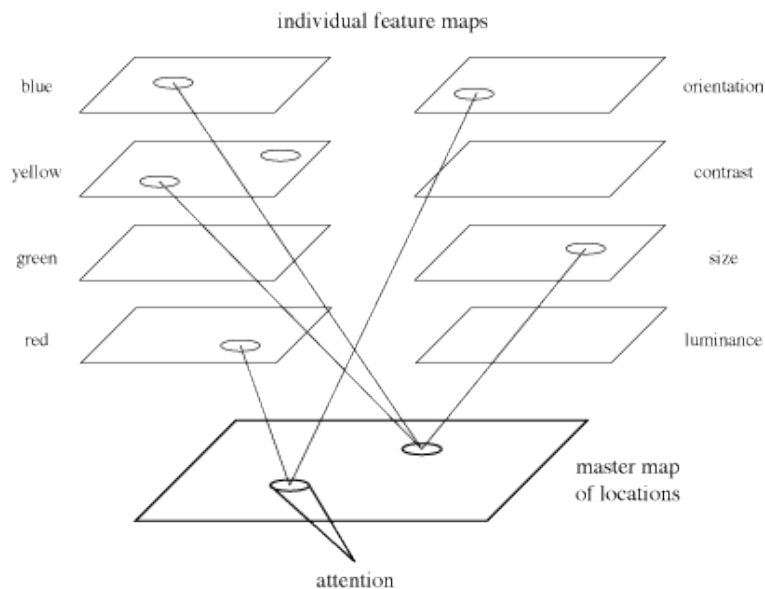


Figure 17. A schematic representation of feature maps. Each ‘map’ is dedicated to a particular feature in the visual stimulus such as colour, orientation, size and others. Image credit: Christopher G. Healey

Studies by Yantis and Jonides in the 1980s and 1990s were conducted to discover which visual elements, events or objects are intrinsically salient, and therefore activate bottom-up, or exogenous attention. They conducted visual search experiments in an attempt to ascertain whether or not any particular stimulus captured attention intrinsically and automatically – irrespective of the number of distractors included in the search arrays (Yantis & Jonides, 1984; Yantis, 1993). In order to determine whether attentional capture was automatic, they employed numerous parameters in the visual search tasks that tested an assumption of automatic attentional capture. This assumption was that if an object captures attention automatically, it should do so *regardless* of the number of distractor elements presented. Of the multitude of target types tested, Yantis found that one particular stimulus – above all others – consistently and automatically captured attention, irrespective of the number of distractor items: the ‘sudden onset’ of a target; i.e., one that appears suddenly during the search trial in a previously unoccupied area of the visual search array. An example of a sudden onset target array is shown in Figure 18 below.

Figure 18. An example of a sudden onset visual search trial

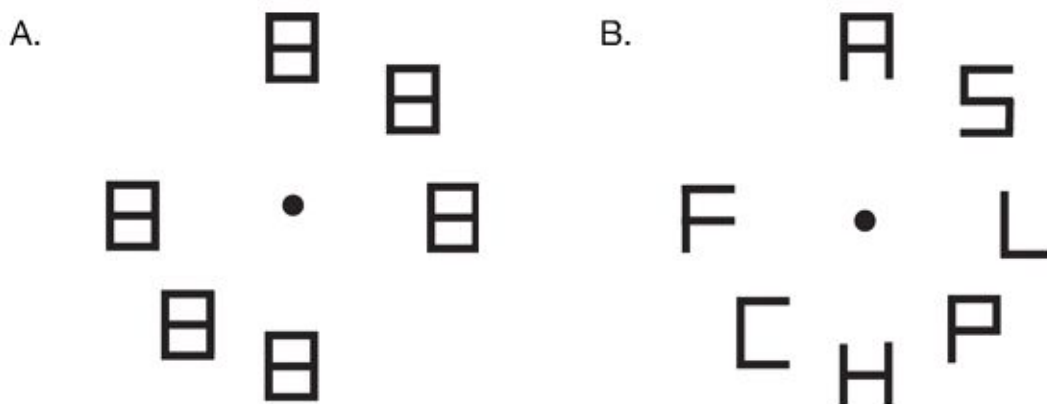


Figure 18. An example of stimuli used in a sudden onset trial. A) The first stage of the trial involves the presentation of six placeholders. B) When the trial letters are revealed in the next stage, a new letter (P) appears where no placeholder was before, constituting a ‘sudden onset’. Image from: Cole et al. *Journal of Vision* January 1, 2003 vol. 3 no. 1 article 3.

The common characteristic of stimuli that capture our attention is that they indicate the appearance or approach of something new in the visual scene. Visual processing is a physiologically energy-intensive task, especially in complex sensory environments. Over time, the visual system tends to reduce its response to constant elements in a scene, a phenomenon known as adaptation. It is only when a new element appears, or a significant change in a pre-existing element occurs, that full processing is again engaged. The visual system possesses specialised neurons and receptors for detecting transient changes and events such as these. The visual pathway responsible, called the magnocellular pathway, begins with magnocellular neurons in the lateral geniculate nucleus a part of the thalamus, a subcortical brain area close to the chiasm of the optic nerve. Magnocellular responses are predominantly linked to retinal receptors in the periphery of our visual field. The more sustained elements of visual processing are attributed to parvocellular pathway responses, which are related to receptors located in the fovea of the retina comprising our central vision. This organisation is biologically adaptive, as the appearance of new, but presently unattended objects or events in a visual scene is most likely to occur in the perimeter of our visual field. Salient objects appearing in our periphery have the ability to orient our sustained or foveal attention to their source. This orienting response is achieved both physically and cognitively, and is a relatively hardwired and automatic response present in nearly all organisms with a complex nervous system. The orienting response can be elicited by stimuli originating from not only vision, but also other senses such as hearing or touch.

In some reptiles, visual awareness is only possible when moving objects are present. This represents an extreme case of the biological salience of transient stimuli: stimuli in which motion is arguably always a characteristic. The parts of the mammalian brain that respond to stimuli indicative of danger, in an automatic fashion, are thought to be an evolutionary artefact of the more ancient reptilian nervous system, and are casually referred to as 'the reptilian brain'. Human beings have not 'outgrown' this ancient motion-sensitive response because it is – and probably always will be – useful to our survival. In modern times, we need to be aware of cars suddenly approaching, rather than predators chasing us; an involuntary and quick response to impending danger is always

going to be a useful reaction for any life form. In contrast to transient visual responses, sustained attention is more a quality of higher cognitive processes involved in learning and communication. Although unnecessary to a reptile, this form of attention is undoubtedly useful for the everyday tasks required of an average human, resulting presumably in its evolutionary selection and retention.

Sustained and transient attention can be paralleled to the concepts of exogenous and endogenous attention introduced earlier, and also Triesman's terms 'bottom-up' and 'top-down' attention. In most of the research conducted on attention and sensory salience, this dichotomy is made explicit. Regardless of what they are called, there is strong evidence of these two distinct forms of attention. Although the amenity of separating attention into two distinct forms for methodological reasons is appealing, it also seems reasonable to assume that internally- and externally-driven attention often act in cohort.

Once a stimulus captures our attention, we have then to decide what to do about it, if anything. Transient stimulation essentially is a first step toward sustained attention. Even though that sustained attention need not be engaged with transient stimulation first, transient events almost always activate sustained processes that appraise the salient event in order to determine what it is, and what needs to be done in response. In the same way that eye-based and stimulus-based binocular rivalry processes act in conjunction, transient and sustained visual processes do not operate in a vacuum, but rather, act together to update and maintain our perceptual experience through time. Given this cooperation, the two should not be artificially separated in cases when they may interact. They may be two facets of the same holistic process of attention and awareness, but their differences suggest that that they are separable components of a larger process.

Binocular rivalry and attention

Past studies of attention and binocular rivalry have examined whether we can exert conscious control over the perceptual reversals that occur when viewing bistable stimuli with attention. Observers have been instructed to try to hold one or the other perceptual outcome arising from viewing a bistable stimulus (Meng & Tong, 2004; van Ee, 2005), or

attempt to increase or decrease the rate of reversals they experience (Lack, 1978). These studies have consistently found that although willpower can exert some limited control over the predominance of one or the other perceptual state during binocular rivalry viewing, it cannot override the natural progression of the perceptual alternations altogether. The limited extent to which purposeful attention can determine bistable perceptions has been taken as evidence that perceptual bistability is the result of a somewhat hardwired, or involuntary, perceptual mechanism (Leopold & Logothetis, 1999).

Object-based attention to one or the other perceptual interpretation is less effective in controlling perceptual dominance compared to ‘non-object’ based efforts, for example, those that attempt to speed or slow reversal rates (Lack, 1978). Object-based attention can be used to determine the initial dominance of a binocular rivalry target (Mitchell, Stoner & Reynolds, 2004); however, its effect over the full duration of the viewing period is negligible (see Meng & Tong, 2004). Wilful control over the rate of perceptual reversals yields much larger effects and improves with time and practice (Lack, 1970). This type of control does not attempt to alter the proportion of time each perceptual outcome is experienced; instead, it operates on the overall rate of alternations.

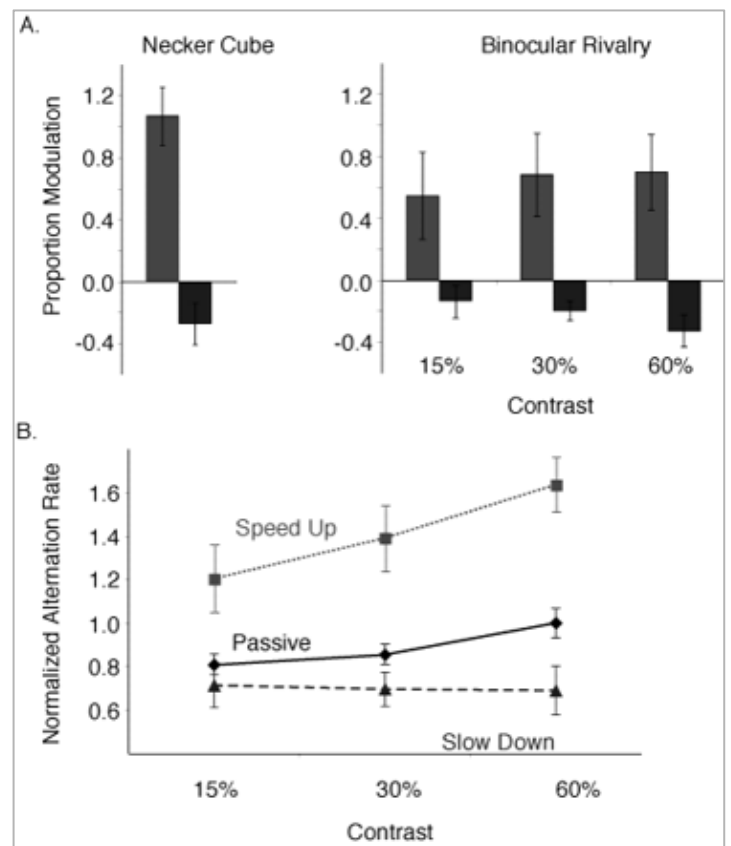
Object-based (or selective) attention is a little more effective in maintaining a particular perception during viewing of other types of bistable stimulus like the Necker cube (Meng & Tong, 2004). This suggests that binocular rivalry may be more hardwired than other forms of perceptual bistability due to its dependence on binocular conflict mediated by early visual area V1. Even so, the effectiveness of non-selective attention over the rate of reversals is clear for both the Necker cube and binocular rivalry, as can be seen in Figure 19 below. Even though these differences show that binocular rivalry is not as open to the influence of endogenous attention, this does not rule out that the other similarities between different forms of perceptual bistability – binocular rivalry included – are at least in part due to the activity of a common mechanism. It is possible that in addition to a centralised process, that each form of bistability is also constrained by the level of

processing engaged by the stimulus. This possibility is explored in more detail in Chapter 2, which contains a systematic comparison between pattern rivalry and binocular rivalry.

Binocular vision is not a visual process that can be overridden by will. We cannot stop combing the two eyes' images in stereopsis— unless we deliberately cross our eyes. However, our perceptions of objects, such as a wire-frame cube, can be altered to some extent: it is possible to view a 2D drawing as a flat piece of paper or alternately as representing a 3D scene by will alone. Even so, Necker cube reversals do involve an involuntary component; even though observers have more success in holding on to one or the other depth interpretation, this cannot be achieved indefinitely, as shown by the results presented by Meng and Tong (2004) as seen in Figure 19.

Figure 19. Results from Meng & Tong, 2004

Figure 19. Graph and figure legend From Meng & Tong 2004: A) Comparison of the proportion of voluntary control over alternation rates for Necker cube reversal and binocular rivalry in Experiment 3. Bar graphs indicate the proportion of modulation in alternation rate for each voluntary control condition relative to passive viewing. Error bars represent ± 1 SEM. Observers showed a strong ability to modulate the alternation rates of both Necker cube reversal and binocular rivalry. B) Normalized rates of alternation across contrast levels for binocular rivalry. Observers showed substantial control of rivalry alternation rates, and could roughly double the rate of fast alternations as compared to slow alternations. Moreover, the amount of control over rivalry alternations significantly increased as a function of stimulus contrast.



Interestingly, given the preceding discussion about the two different modes of attention, there appears to be a dichotomy in the way that attention can modulate perceptual bistability. There is evidence that different types of attention work differently on the perceptually dominant and suppressed images during binocular rivalry alternations. Higher-order visual effects, such as the grouping of subjective contours (Sobel & Blake, 2003) and other contextual influences (Sobel & Blake, 2002) appear to affect rival stimuli only while they are perceptually dominant. Transient effects, using sudden-onset stimuli – such as small flashes (Kanai et al., 2005) or pop-out effects – can operate during the suppression of a rival stimulus to lift that image into perceptual awareness (Ooi & He, 1999), much like the way transient events can direct sustained attention to their source. So called ‘vision for action’ such as attention to certain forms of motion allows for greater control over binocular rivalry than attention to static gratings (Hugrass & Crewther 2012).

Kanai et al.’s 2005 study showed that visual transients – such as flashes of light around rival stimuli – cause perceptual reversals. When a flash of light was presented in proximity to the rival stimuli, the dominant perceptual state quickly swapped to the alternative state. Flashes of light can be considered prime examples of stimuli that activate bottom-up, exogenous attention as they constitute sudden onsets, shown by Yantis and Jonides to be the one perceptual element to reliably and consistently activate automatic visual processing (Yantis & Jonides, 1984; and Jonides & Yantis, 1988). That these kinds of transient stimuli can alter rivalry dynamics supports the idea that the mechanism underlying perceptual bistability is linked to exogenous attention.

Periodic and automatic shifts in attention used to monitor our environment are another possible mechanism of the perceptual alternations experienced when viewing bistable stimuli. In support of this idea, the distribution of dominance durations, (the gamma distribution), is common to the temporal pattern of reaction times during visual search tasks and perceptual rivalry (Wolfe, Torralba & Horowitz, 2002). There may be an unconscious perceptual process that is common to both bistable alternations and perceptual sampling of the visual scene around us. Shifts in attention can be reliably

induced by transient stimuli, as sudden onsets in visual search demonstrate. Chapters 4 and 5 of this thesis explore how transient cross-modal stimuli can help clarify the relationship between binocular rivalry and involuntary (i.e. exogenous) attention. Comparison of the relative effect of inter- and intra-sensory transient stimuli also provides a way to gauge whether a common mechanism is involved in the temporal dynamics of binocular rivalry. The existence of perceptual bistability across the senses may reflect a ‘modality-agnostic’ component of all forms of bistable perception, including binocular rivalry.

Perceptual bistability in non-visual sense modalities.

One of the most convincing arguments that perceptual bistability arises from a common mechanism is that it is not exclusive to stimuli presented in the visual sense. As was discussed in the earliest section of this chapter, many different types of stimuli give rise to bistable reversals. These stimuli all share one feature: they are inherently ambiguous and offer two or more perceptual interpretations. This feature can be considered as the one essential requirement for perceptual bistability to occur, and it is a feature that does not limit the type of stimulus needed to elicit bistable phenomena to any one sense. Perceptual bistability can be achieved with stimuli presented in both touch and auditory modalities, and even via olfactory means (Zhou & Chen, 2009).

Presenting a sound-stream that can be grouped in two different ways evokes auditory bistability (Pressnitzer & Hupé, 2006, review by Brancucci & Tomassi, 2011). Such sound streams generally contain discrete sounds (not continuous tones). Usually, two different pitched tone streams are put together. The bistable alternation is not between one or the other pitch, but between hearing the two streams as separate and hearing them grouped together to form one coherent rhythmic sound stream. Tactile bistability can occur with a tactile version of the ambiguous dot motion quartet (Carter, Konkle, Wang, Hayward & Moore, 2008) and even a moving cylinder (Holcombe & Seizova-Cajic, 2008). When a finger is in contact with the moving, textured cylinder, the textured surface touches the finger at intermittent times. If the point of contact is the same location on the finger, these discrete contacts contain some degree of ambiguity; they could

correspond to the cylinder rotating left or right. Perception of the cylinder's direction of rotation can therefore be bistable.

An interesting question to arise in this area is whether or not information from one sense can influence another engaged in bistable alternations. Another question of interest is how two sense modalities, both engaged in bistable alternations, might behave – and this is addressed in detail in the General Discussion (Chapter 6). Some previous studies have found a small influence of stimuli from one sense modality on the dominance durations or pattern of bistable reversals in another sense (Blake, 2005). Given that object-based and endogenous attention have little impact on the overall predominance of one interpretation during bistable alternations, it is not surprising to find these effects have been small. This is because the cross-modal pairings used enhance the depiction of one or the other rival stimulus, in much the same way that wilful attention might.

In contrast, stimuli that activate exogenous attention are expected to yield a substantial cross-modal influence over perceptual bistability, which is the subject of Chapters 4 and 5. Before concluding that cross-modal effects on bistability are limited, these effects need to be investigated using certain forms of attention-grabbing stimuli already known to exert an influence over perceptual bistability (for example Kanai et al., 2005). These stimuli might also need to be suited to how each of our senses interact with each other in normal perceptual experience, such as auditory temporal driving of vision (Shipley, 1964). Given the evidence that bistable alternations are susceptible to modification by exogenous stimuli, these types of stimuli are used to investigate cross-modal influences during perceptual bistability in Chapters 4 and 5.

Hypothesis

This thesis addresses two questions. The first has already been covered adequately in previous literature, but is extended by research presented in Chapter 2. The second question, although suggested previously (for example by Carter et al., 2007), is approached in a unique way by incorporating novel stimuli into the binocular rivalry experimental paradigm.

1. Is there a common mechanism underlying perceptual bistability, and what evidence is there for the existence of this mechanism?

Although the type of bistable stimulus may differ, the question regarding a ‘common mechanism’ is an attempt to explore if there are neural and cognitive processes of perceptual interpretation that are common to all forms of perceptual bistability. A singular brain area or network need not necessarily underlie this mechanism.

Commonality might be achieved by a singular, centralised network; but it might also arise from isomorphic patterns of neural responding in the areas dedicated to processing the particular qualities of the bistable stimulus. The extent that stimulus-specific processes do or do not determine bistable alternations can be used to estimate the involvement of a common mechanism.

Chapter 2 of this thesis explores the types of evidence that can be used to demonstrate that a shared perceptual process underlies different forms of perceptual bistability by comparing binocular rivalry with a form of bistability between two patterns called monocular rivalry. Although binocular rivalry involves conflict between binocular inputs, it has also been shown to share many perceptual similarities to monocular rivalry, which is a conflict between stimulus patterns, not the two eyes. Despite the similarities, there does appear to be a stimulus-specific component of binocular rivalry alternations as evidenced by differences in suppression. This could support the idea that the commonalities between different forms of perceptual bistability are due to similar patterns of conflict resolution in sensory-specific processing. In addition, these processes appear to be modulated by a centralised neural process related to perceptual awareness and attention rather than being determined by it.

2. Is this common mechanism related to exogenous perceptual selection?

As discussed earlier, endogenous – or wilful – attention is limited in its ability to determine perceptual dominance during binocular rivalry. This has been taken as evidence that bistable reversals are a product of a hardwired mechanism not susceptible to conscious control (Leopold & Logothetis, 1999). This thesis asks if this mechanism is

the same one that underlies exogenous perceptual selection and attention. Whether exogenous attention can alter the overall dominance of one perceptual state during binocular rivalry has not been sufficiently established due to the transient nature of the stimuli required to elicit it. If an appropriate sustained stimulus is used, it is predicted that exogenous attention will determine perceptual state during binocular rivalry more effectively than endogenous attention. This prediction was tested in Chapters 3, 4 and 5. For the experiments presented in Chapter 3, a visual stimulus was designed to elicit exogenous attention indefinitely throughout binocular rivalry trials. This ‘looming’, or approaching, motion stimulus – unlike singular flashes or events – is steady across the trial period while still evoking strong stimulus-driven attention. In the absence of observers’ attempts to wilfully control their perceptual state, this stimulus predominated over a rival motion stimulus of the opposite direction with equal image and motion signal strength. These experiments support the prediction that stimulus-driven, or exogenous, attention is a more effective determinant of perceptual state during binocular rivalry than endogenous attention.

Exogenous perceptual selection operates across all sensory domains. It needs to be open and automatic in order to operate effectively. If it is centrally involved in bistable perceptual dynamics, cross-modal stimuli designed to activate exogenous attention should affect rivalry dynamics in comparable ways. This hypothesis is explored in Chapters 4 and 5. Chapter 4 explores how visually-congruent ‘looming’ sound cycles alter the results reported in Chapter 3. Temporal synchrony between the motion pulses was found to be a critical factor, which motivated the experiments in Chapter 5. Chapter 5 examines the phenomenon of auditory driving and binocular rivalry, showing that task-irrelevant sound and flicker streams can alter binocular rivalry rates. Chapter 5 also examines how these stimulus streams can alter other perceptual and motor processes, including the eye movements and the perception of interval duration.

The results, together with the theoretical and empirical similarities between exogenous selection and the dynamics of perceptual bistability are argued in the final General Discussion Chapter 6 to support the theory that some component of binocular rivalry

dynamics is a product of a distributed mechanism involved in attention and vigilance. Strong auditory effects were found in Chapters 4 and 5 in partial support of the hypothesis that perceptual bistability dynamics are influenced by the activity of distributed processing. Despite these significant cross-modal effects, auditory-driven exogenous attention did not determine binocular rivalry alternations completely. As with the results of Chapter 2, this points to the involvement of a stimulus-specific component of binocular rivalry that is separate from generalised processes underlying attention. Nonetheless, non-visual processes can affect some part of the temporal dynamics of binocular rivalry. The present results suggest that this process may be the same as those governing exogenous perceptual selection and arousal that gives rise to conscious attention

*Chapter 2***Monocular rivalry exhibits three hallmarks of binocular rivalry: Evidence for common processes**

The work in this chapter is published as:

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Overview

The first set of experiments presented in this thesis explores the theory that all forms of perceptual bistability arise from common processes. It extends studies comparing different types of bistable stimuli by comparing binocular and monocular rivalry.

Abstract

Binocular rivalry occurs when different images are presented one to each eye: the images are visible only alternately. Monocular rivalry occurs when different images are presented both to the same eye: the clarity of the images fluctuates alternately. Could both sorts of rivalry reflect the operation of a general visual mechanism for dealing with perceptual ambiguity? We report four experiments showing similarities between the two phenomena. First, we show that monocular rivalry can occur with complex images, as with binocular rivalry, and that the two phenomena are affected similarly by the size (Experiment 1) and colour (Experiment 2) of the images. Second, we show that the distribution of dominance periods during monocular rivalry has a gamma shape and is stochastic (Experiment 3). Third, we show that during periods of monocular rivalry suppression, the threshold to detect a probe (a contrast pulse to the suppressed stimulus) is raised compared with during periods of dominance (Experiment 4). The threshold elevation is much weaker than during binocular rivalry, consistent with monocular rivalry's weak appearance. We discuss other similarities between monocular and binocular rivalry, and also some differences, concluding that part of the processing underlying both phenomena is a general visual mechanism for dealing with perceptual ambiguity. 2009 Elsevier Ltd. All rights reserved.

Introduction

We experience the visual world in astounding richness and detail, yet our knowledge of how our conscious percepts arise is still quite poor (cf. Chalmers, 1995). One way to learn more about these processes is to study phenomena in which visual consciousness changes without any change in the stimuli being viewed (Crick & Koch, 1995). Such phenomena are known as perceptually multistable and include binocular rivalry (Porta, 1593, cited in Wade, 1996), reversals of the Necker cube (Necker, 1832), of the Rubin face-vase figure (Rubin, 1915), and of the kinetic depth effect (Wallach & O'Connell, 1953), and motion-induced blindness (Bonneh, Cooperman, & Sagi, 2001). Binocular rivalry is a particularly fascinating example, in which visual consciousness fluctuates randomly between two different images presented one to each eye. It has been studied extensively (for reviews see Alais & Blake, 2005; Blake & O'Shea, 2009) and has gone some way to shedding light on how visual awareness arises: conscious visual experience in binocular rivalry is thought to arise from activation, and suppression, of neurons at a succession of stages in the visual system via feed-forward and feedback connections (e.g., Blake & Logothetis, 2002).

Our interest in this paper is in the relationship between binocular rivalry and another phenomenon of perceptual multistability, monocular rivalry. Monocular rivalry was discovered by Breese (1899) in the course of his foundational observations and experiments on binocular rivalry. He found that binocular rivalry-like behaviour also occurred when a red and a green grating were optically superimposed by a prism and presented to a single eye. Breese called it monocular rivalry to distinguish it from binocular rivalry. He reported that monocular rivalry alternations tended to occur at a slower rate than binocular rivalry alternations and that the perceptual alternations were less vivid: “Neither [stimulus] disappeared completely: but at times the red would appear very distinctly while the green would fade; then the red would fade and the green appear distinctly” (p. 43).

One of the unresolved questions in the literature on perceptual multistability is whether common neural mechanisms underlie binocular and monocular rivalry. Rubin (2003),

Leopold and Logothetis (1999), and Maier, Logothetis, and Leopold (2005) have proposed that all examples of perceptual multistability represent operations of a single, high-level mechanism. If so, this would tie together diverse multistability phenomena including perception of ambiguous auditory stimuli (e.g., Einhäuser, Stout, Koch, & Carter, 2008), perception of traditional visual ambiguous figures such as the Necker cube (e.g., Meng & Tong, 2004), perception of illusory organisation such as Marroquin patterns (Wilson, Krupa, & Wilkinson, 2000), monocular rivalry, and binocular rivalry.

There are at least three general similarities between monocular rivalry and binocular rivalry that suggest commonality. The basic phenomenology is similar in that both involve periods of alternating dominance. Both forms of rivalry become more vigorous as stimuli are made more different in colour (e.g., Wade, 1975), or in orientation and spatial frequency (e.g., Atkinson, Fiorentini, Campbell, & Maffei, 1973; Campbell, Gilinsky, Howell, Riggs, & Atkinson, 1973; O'Shea, 1998). The two forms of rivalry can influence each other, tending to synchronise their alternations in adjacent regions of the visual field (Andrews & Purves, 1997; Pearson & Clifford, 2005).

Although monocular and binocular rivalry are similar in these three respects, this is by no means an exhaustive list of possible comparisons. Here we test whether monocular rivalry shares three other hallmarks of binocular rivalry. First, binocular rivalry can occur between any two images, providing they are sufficiently different. For example, Porta (1593, cited in Wade, 1996) observed rivalry between two different pages of text. Wheatstone (1838) observed rivalry between two different alphabetic letters. Galton (1907) observed rivalry between pictures of different faces. Yet monocular rivalry has always been shown between simple repetitive stimuli such as gratings, leading some to suppose that such stimuli are necessary for monocular rivalry (e.g., Furchner & Ginsburg, 1978; Georgeson, 1984; Georgeson & Phillips, 1980; Maier et al., 2005). In Experiments 1 and 2, we show that monocular rivalry occurs between complex pictures of faces and houses. We demonstrate this in Figure 1.

Figure 1. Monocular rivalry between complex pictures

Figure 1. Illustration of one of the monocular rivalry stimuli from Experiment 2: a red face and a green house. To experience monocular rivalry stare approximately at the centre of the image, say at the bridge of the face's glasses. Be patient! Monocular rivalry takes a while to develop. But after a time, 10–30 s or so, you will notice fluctuations in the relative clarity of the two images. You may even see one of the two images become exclusively visible briefly, along with brief composites in which different parts of the images appear in different parts of the visual field. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



Second, binocular rivalry has a characteristic distribution of dominance times, a gamma distribution, and the duration of one episode of dominance cannot be predicted by any of the preceding ones (e.g., Fox & Herrmann, 1967; Levelt, 1967). Yet the distribution and predictability of episodes of monocular rivalry dominance are unknown. In Experiment 3, we show that the temporal periods of monocular rivalry are similar to those of binocular rivalry: gamma distributed and stochastic.

Third, binocular rivalry suppression is accompanied by a characteristic loss of visual sensitivity. When a stimulus is suppressed during binocular rivalry and becomes invisible, stimuli presented to the same retinal region are also invisible, provided the new stimuli are not so abrupt or so bright as to break suppression (e.g., Fox & McIntyre, 1967; Nguyen, Freeman, & Alais, 2003; Norman, Norman, & Bilotta, 2000; Wales & Fox, 1970). This is usually demonstrated by showing a loss of sensitivity during periods of suppression relative to periods of dominance, however it is unknown whether monocular

rivalry also shows such suppression effects. In Experiment 4, we show that monocular rivalry does indeed produce threshold elevations during suppression, although the effect is weaker than in binocular rivalry.

The experiments in this paper have been published individually in abstract form (O'Shea, Alais, & Parker, 2005, 2006; O'Shea and La Rooy, 2004). Here we draw these experiments together and give their details to provide evidence for similarities between monocular rivalry and binocular rivalry.

Experiment 1

Maier et al. (2005) reviewed studies of monocular rivalry, and concluded that monocular rivalry occurs only between simple, faint, repetitive images, such as low-contrast gratings. They observed, however, that alternations in clarity could occur between complex images, such as the surface of a pond and a reflection on it of a tree, although they did not measure rivalry with such stimuli. Boutet and Chaudhuri (2001) optically superimposed two faces that differed in orientation by 90°. They reported that the two faces alternated in clarity in a rivalry-like way, but they did not measure rivalry conventionally. They forced observer's choices about whether one or two faces was seen after brief stimulus presentations of 1–3 s. Monocular rivalry, however, usually takes several seconds, or even tens of seconds, before oscillations become evident (e.g., Breese, 1899). We decided to measure monocular rivalry with complex images in a conventional way, by showing observers optically superimposed images for 1-min trials, and asking them to track their perceptual alternations using key presses. We used images of a face and a house. Moreover, we explicitly compared monocular rivalry with binocular rivalry for identical stimuli over a range of stimulus sizes. We chose to manipulate size because, at least with gratings, it has powerful effects on binocular rivalry (e.g., Blake, Fox, & Westendorf, 1974; Breese, 1899, 1909; O'Shea, Sims, & Govan, 1997).

Method

Observers

One female and three males volunteered for this experiment after giving informed consent: HF (age 23), DLR (age 33), and RS (age 24) had some experience as observers; ROS (age 50) was a highly trained observer. All had normal or corrected-to-normal vision. All observers were right handed. HF and RS were naive as to the purpose of the experiment.

Stimuli and apparatus

Stimuli were digitized photographs of ROS's face and part of his house on plain backgrounds, similar to that shown in Figure 1 except that they were greyscale. Stimuli were 0.77, 1.54, 3.08, 6.16, and 12.32 of visual angle square. The smaller images were all scaled-down versions of largest image (800x800 pixels) and scaling was done using NIH Image software. (Scaling from large to small minimises spatial frequency distortions that can arise when scaling from small to large). They were surrounded by two bright vertical bars, each 0.5 wide, as tall as the stimulus, and separated from the edge of the stimulus by 0.5; these were to help observers align the stimuli binocularly. Stimuli were displayed on two identical Sony Trinitron, 19-in., colour monitors with a spatial resolution of 1152 870 pixels and a frame rate of 75 Hz. Each eye of the observer viewed only one monitor from a distance of 1 m through a mirror stereoscope. The experiment was controlled by a Power Macintosh 8600 computer running specially written software (Handley, Bevin, & O'Shea, 2005).

The room was entirely dark, with the monitors as the sole light source. Presenting superimposed images of the face and house to both eyes created monocular rivalry. Presenting the image of the face and house separately to each eye created binocular rivalry. The luminance of the stimuli on each screen was 10 cd/m², and that of the vertical bars was 30 cd/m². Otherwise the screens were dark (0.2 cd/m²). The standard deviation of the luminances in the two images was 2.45 cd/m² for the face and 3.44 cd/m² for the house.

Procedure

There were two sessions each containing a block of 10 binocular rivalry trials and a block of 10 monocular rivalry trials. In each block, observers received two presentations of the images at each of the five image sizes. During binocular rivalry trials, one presentation of each stimulus size was of the face to the left eye and the house to the right eye, and the other was of the opposite arrangement. Order of trials was random within blocks. Order of blocks was counterbalanced over observers and over sessions. Each trial lasted for 60 s and was followed by an inter-trial interval of at least 45 s. Observers reported their perception of either the face or house by pressing the ‘Z’ or ‘?’ keys, respectively. They pressed a key whenever, and for as long as, a particular stimulus exceeded a criterion level of visibility. For binocular rivalry, this criterion was that an image was exclusively visible over at least 95% of the field. For monocular rivalry, this criterion was that an image appeared to be at least twice as clear as the other, or was exclusively visible over at least two-thirds of the field (we call this a 66% visibility criterion).

The experimental sessions were preceded by sufficient practice trials to enable each observer to respond consistently to both sorts of rivalry.

Results and discussion

All observers found it easy to press keys to signal their perception of the two images in both monocular and binocular rivalry. They also commented on some of their unusual perceptions. During binocular rivalry, they sometimes described composites, in which one image would replace the other over a few moments. For example, one might briefly see the left half of the face on the left side of the screen and the right half of the house on the right side of the screen before the face would then wipe out the remaining image of the house. More amusingly, one might briefly see the face with one eye replaced by the house’s window. Such composites are a common property of binocular rivalry, and have been studied by Wilson, Blake, and Lee (2001). Observers reported similar composites during monocular rivalry.

We quantified rivalry in three ways. First, we counted the number of times each key was pressed to obtain a rate measure of rivalry. Second, we counted the cumulative time each key was pressed to obtain a measure of dominance time. Third, we averaged the time of each individual key press to obtain a measure we call *period*.

We analysed these data with three-factor, within-subjects ANOVAs (the factors were type of rivalry, size, and image reported). There was a significant effect of size on rate, $F(4,12) = 12.29$, $p < .001$, such that rate increased with size of the images (see Figure 2). All observers showed this pattern of results. An increasing alternation rate with image size is opposite to the usual finding with simple stimuli such as gratings (e.g., Breese, 1899; O'Shea et al., 1997). Critically, there was no difference between monocular and binocular rivalry in the shape of the function relating size to rate.

There was also one significant effect for dominance time: the face was seen for longer than the house, $F(1,3) = 10.64$, $p < .05$. The mean dominance time for the face was 12.44 s (SD = 9.95 s) and that for the house was 6.90 s (SD = 5.47 s). This could have arisen from a general preference for faces over other stimuli in rivalry (e.g., Beloff & Beloff, 1959; Engel, 1956) or from some preference for the spatial frequencies of the face image over the house image (cf. Lumer, Friston, & Rees, 1998; Tong, Nakayama, Vaughan, & Kanwisher, 1998). But it is not important for our purposes, because there were no other significant effects or interactions for this measure, showing that this advantage for the face was consistent over size and over type of rivalry.

There were no significant effects for period. These were similar over stimuli, over sizes, and over the two sorts of rivalry. The increase in the rate of alternations with size for both sorts of rivalries is consistent with the idea that rivalry between complex stimuli is mediated by interactions among neurons in higher-level visual areas such as the inferotemporal cortex (Alais & Melcher, 2007; Sheinberg & Logothetis, 1997). Not only are such neurons responsive to coherent visual objects, such as the house and face stimuli used here, their receptive fields are far larger than those at earlier levels of the visual

system (Gross, Bender, & Rocha-Miranda, 1969; Yoshor, Bosking, Ghose, & Maunsell, 2007) and would therefore be preferentially activated by the larger rival stimuli.

Figure 2. Binocular and monocular rivalry alternation rate

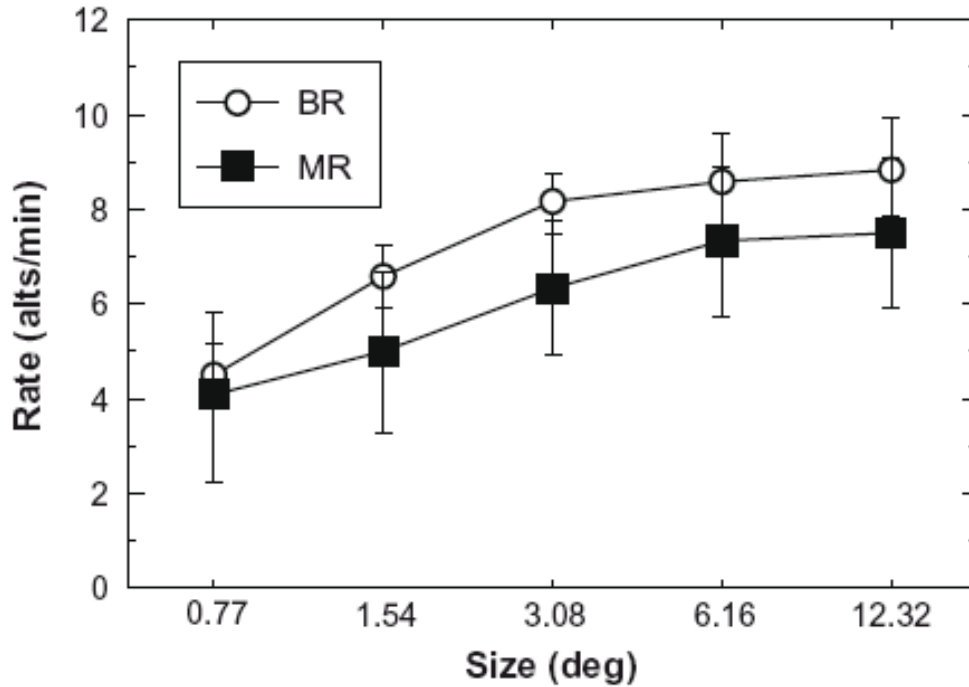


Figure 2. Plot of binocular rivalry (BR) and monocular rivalry (MR) rate (the number of episodes of dominance of each image per minute) against size of the images. The vertical bars show ± 1 standard error of the mean.

One possible alternative explanation is that image size is correlated with spatial-frequency content. This might seem plausible because with grating stimuli, monocular rivalry is usually strongest at low spatial frequencies (Kitterle & Thomas, 1980; Mapperson & Lovegrove, 1984; O’Shea, 1998). But grating stimuli contain only a single spatial frequency, whereas our images are complex with a very broad spatial frequency spectrum that follows a fractal ($1/f$) amplitude profile. Such images are scale invariant (e.g., Field, 1994; Ruderman & Bialek, 1994) Complex images therefore show the same complex mix of spatial frequencies at all sizes of images.

Of more central importance for our purposes is that both monocular rivalry and binocular rivalry, which is robust over a very large range of spatial frequencies (O'Shea et al., 1997), exhibited the same trend of increasing alternation rate with increasing image size. Given this, the similar trends shown in Figure 2 may be indicative of common mechanisms in monocular and binocular rivalry. We further test this idea in the next experiment by assessing the effects on the two sorts of rivalries of adding colour differences to the two rivalling images.

Experiment 2

Monocular rivalry does not require coloured stimuli (e.g., Experiment 1), but its alternation rate is faster when stimuli have complementary colours (Campbell & Howell, 1972; Rauschecker, Campbell, & Atkinson, 1973; Wade, 1975). Similarly, binocular rivalry does not require coloured stimuli, but its alternation rate is also faster when the rival stimuli have complementary colours (Hollins & Leung, 1978; Thomas, 1978; Wade, 1975). The only studies we are aware of in which the effects of colour on monocular and binocular rivalry were compared in the same experiment with the same observers' viewing grating stimuli came to different conclusions. Kitterle and Thomas (1980) found that colour affected monocular but not binocular rivalry whereas Knapen, Kanai, Brascamp, van Boxtel, and van Ee (2007) found that colour affected monocular and binocular rivalry similarly. In Experiment 2, we also examine the role of colour on binocular and monocular rivalry but extend it to include complex broadband images.

Method

The Method of Experiment 2 was very similar to that of Experiment 1. The differences were that a second set of stimuli, that used by Tong et al. (1998) was added, and one of the male observers (RS) from Experiment 1 did not participate. All stimuli were 6.16 square. Tong et al.'s stimuli were similar to those of Experiment 1, except that they comprised a different male face (younger, clean-shaven, and without glasses) and a different house (older, of a Georgian style, and showing more elaborate architectural details). Pixel luminances in Tong et al.'s face and house had standard deviations of 3.22 cd/m² and 4.98 cd/m², respectively. There were 12 binocular rivalry and 12 monocular

rivalry trials in which observers again tracked their rivalry alternations. In four repetitions of each pair of stimuli the images were achromatic, in four the face was red (CIE $x = .315$, $y = .321$) and the house green (CIE $x = .270$, $y = .347$), and in four the face was green and the house red. Mean luminances of all stimuli (colour and greyscale) were the same as that in Experiment 1. See Figure 1 for an illustration of one of the monocular rivalry stimuli.

Results and discussion

Again observers had no trouble recording perceptual alternations in monocular and binocular rivalry, and again they reported episodes of composites for both types of rivalry.

We analysed the same three measures of rivalry with four-factor, within-subjects ANOVAs (the factors were type of rivalry, colour, stimulus set, and image reported). The only significant effect was colour on rivalry rate, $F(1,2) = 19.87$, $p < .05$, such that the alternation rate was greater with coloured images than with achromatic images (see Figure 3). All observers showed this pattern of results. The difference between the rates for monocular and binocular rivalry was not significant, $F(1,2) = 5.19$, $p > .15$.

Figure 3. Colour and binocular and monocular rivalry alternation rates

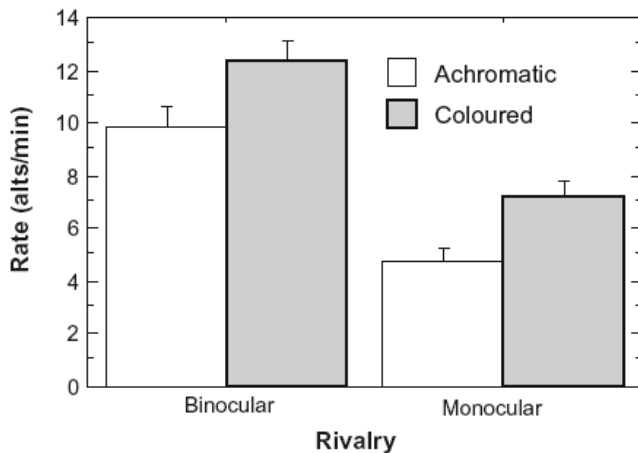


Figure 3. Plot of binocular rivalry and monocular rivalry rate (the number of episodes of dominance of each image per minute) for achromatic and for coloured images. The vertical bars show ± 1 standard error of the mean.

Figure 3 shows that adding colour differences to two complex rivaling images increases the rate of both monocular and binocular rivalry (the interaction between type of rivalry and colour was not significant, $F(1,2) = 0.03$) without consistently affecting the other measures of rivalry. This is different from the result of Kitterle and Thomas (1980) who found that colour enhanced monocular rivalry between gratings, but did not enhance binocular rivalry. Although it is possible that this indicates a difference between simple and complex stimuli, we suspect that there is some other explanation, especially because others did find that colour differences enhanced binocular rivalry rates with gratings (Hollins & Leung, 1978; Thomas, 1978; Wade, 1975). For example, Kitterle and Thomas's binocular rivalry rates for achromatic stimuli were about four times greater than their monocular rivalry rates. Possibly, then, a ceiling effect limited the scope for binocular rivalry to be enhanced by coloured stimuli.

In any case, we are confident that with complex stimuli, adding different colours to different complex images does enhance both binocular and monocular rivalry. This is consistent with some general rivalry mechanism that assesses the degree of difference between representations of two images and instigates rivalry accordingly. Adding different colour to different images adds another dimension along which the stimuli differ, which would be expected to lead to more vigorous rivalry. In a related vein, adding colour to rival images also tends to reduce piecemeal rivalry, because it adds a unifying attribute to each image and tends to lead to more coherent alternations.

By concentrating on overall rivalry alternation rates in the first two experiments, we have ignored the finer-grained temporal dynamics of rivalry. In Experiment 3, we will conduct a comparison of monocular and binocular rivalry on a finer temporal scale.

Experiment 3

The temporal dynamics of binocular rivalry have been well studied. For example, Levelt (1968) showed that the distribution of dominance times approximates a gamma function. Moreover, Levelt demonstrated that the duration of one episode of dominance of one image cannot be predicted from the duration of any of the previous episodes, meaning

that each dominance episode is a statistically independent sample from an underlying population distribution of dominance times. We set out to determine whether monocular rivalry also conforms to these principles, comparing it with binocular rivalry dynamics measured on identical binocular rivalry stimuli. In this we were following the example of van Boxtel, van Ee, and Erkelens (2007) who used similar comparisons to argue that binocular rivalry and dichoptic masking share similar processing.

Essentially all of the studies of the temporal properties of binocular rivalry have used simple repetitive stimuli such as gratings. For comparability with these studies, we use grating stimuli for both monocular and binocular rivalry.

Method

Observers

Three of the authors acted as observers, along with four inexperienced observers who were unaware of the aims of the experiment. All observers had normal vision.

Apparatus

The computer controlling this experiment was a Macintosh G5, running Matlab 7.0.4 scripts that used the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). Stimuli were displayed on a 14-in. DiamondPro monitor showing 800 x 600 pixels at a 90 Hz vertical refresh rate (75 Hz for observers DL, ROS, SM, SS). Stimuli were shown one on each side of the screen and viewed via a mirror stereoscope at a viewing distance of 57 cm.

Stimuli

Stimuli were two orthogonal square-wave gratings, one red and the other green, oriented ± 45 to vertical. The gratings had a spatial frequency of 2.2 cycles/deg with a Michelson contrast of 8% and were placed in a circular aperture subtending 4.6°. Gratings had a mean luminance of 31.30 cd/m²; the background had the same luminance. The gratings were superimposed and visible to both eyes for monocular rivalry conditions; the gratings were presented one to each eye for binocular rivalry conditions.

Procedure

For both binocular and monocular rivalry, the observer's task was similar to that in Experiments 1 and 2: to track episodes of perceptual dominance of one and the other stimuli by pressing keys on the computer keyboard. There were two trials lasting up to 5 min for each viewing condition. Viewing condition was alternated for each observer over trials; each observer started with a different condition.

Results and discussion

We analysed the records of rivalry in two ways. First, we plotted distributions of dominance periods to which we fitted a gamma distribution. However, we also tried fitting a gamma distribution to the reciprocal of dominance duration (alternation rate), following Brascamp, van Ee, Pestman, and van den Berg's (2005) recommendation that the gamma distribution provides a better fit to alternation rates than to the more commonly used dominance durations. When we compared fits to both types of data using the Kolmogorov–Smirnov goodness-of-fit test (the cumulative functions for this test were calculated without binning the data), we found they fitted equally well. Using a critical p-value of 0.10 (as in Brascamp et al., 2005), we found that three out of 14 distributions of duration data were significantly different from the best fitting gamma distribution. For the same analysis based on the rate data, the outcome was the same: three out of 14 distributions differed significantly from the best fit. Although Brascamp et al. did find rate-based fits to be better (based on nearly 200 distributions), there was no difference in our small sample. For this reason, and to make it easier to relate our findings to the previous literature (where duration-based fits have been the standard), we show distributions of dominance periods together with best fitting gamma distributions of the following form:

$$f(t|k, \lambda, a) = a \frac{1}{\lambda^k \Gamma(k)} t^{k-1} e^{-\frac{t}{\lambda}}$$

where k is the “scale” parameter, k is the “shape” parameter, and a scales the height (amplitude) of the distribution.

Figure 4 shows the distributions of dominance periods separately for monocular and binocular rivalry for four observers (the results of the other three observers were similar). We show the fitted gamma functions with their parameters. The parameters of all fits are remarkably similar, showing that monocular and binocular rivalry exhibit globally similar alternation dynamics.

Second, we computed autocorrelations between the recorded dominance sequence and the same sequence offset by various time lags in order to test the sequential independence of rivalry dominance times. Figure 5 shows the autocorrelation analyses from the same four observers for binocular and monocular rivalry. The correlation is arbitrarily 1.0 when there is no lag, and the error bars show 95% confidence intervals (computed from 1000 iterations of a bootstrapping procedure). Similar to binocular rivalry (Levelt, 1968) there is no systematic tendency in monocular rivalry for a given dominance duration to be related to the previous dominance duration, or to dominance durations several phases earlier. Over the seven observers tested at 12 phase lags for monocular and binocular rivalry (a total of 168 points), there are only nine significant deviations from zero – about what would be expected from type I errors with our 95% confidence intervals ($9/168 = 0.053$).

In summary, the results of this experiment show that monocular rivalry possesses the characteristic temporal dynamics of binocular rivalry. The remaining hallmark of binocular rivalry is that there is an objectively measurable suppression of vision of one or the other images. In Experiment 4, we will search for the same suppression in monocular rivalry.

Figure 4. Distributions of perceptual dominance durations

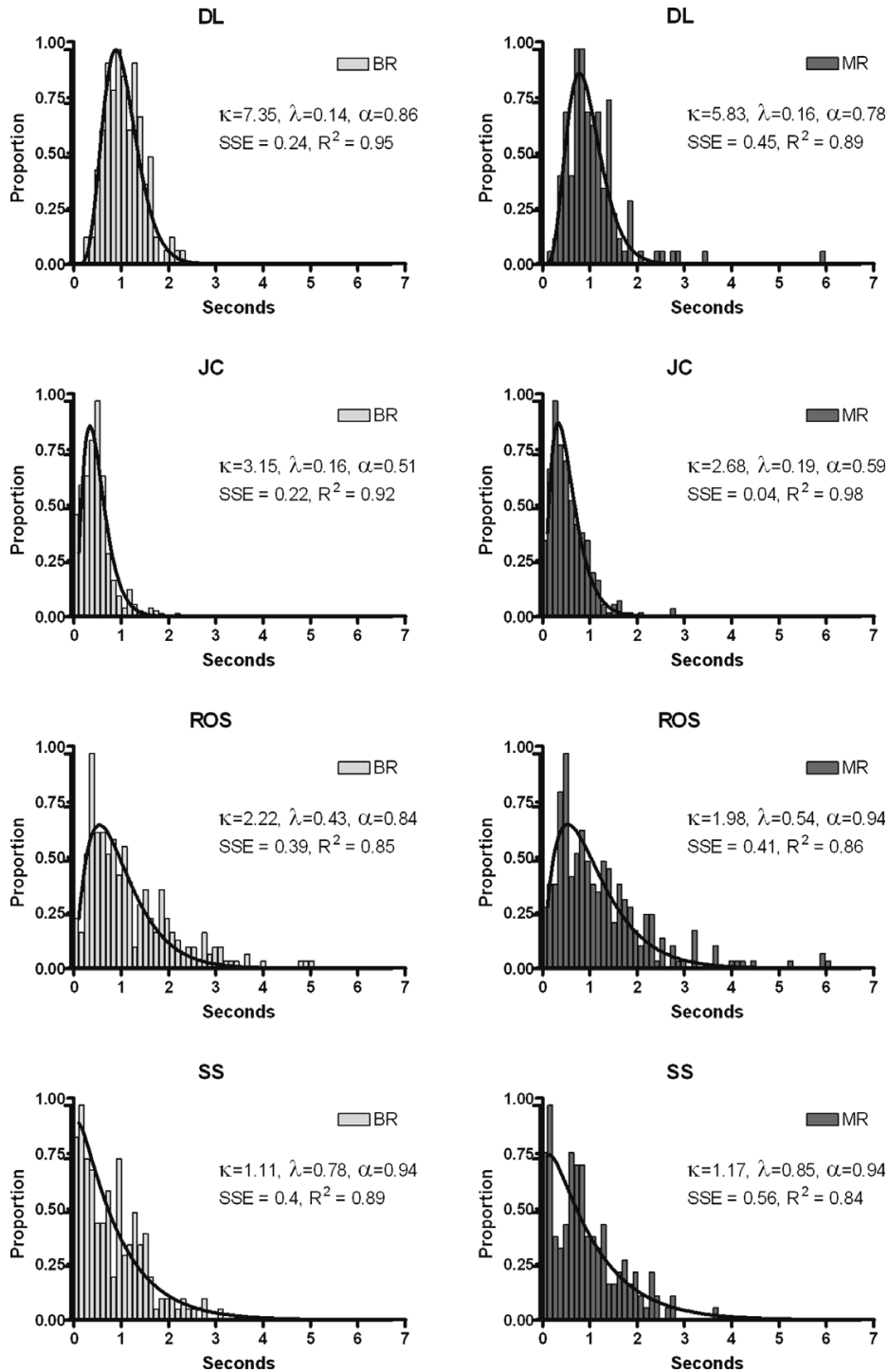


Figure 4. Distributions of dominance durations for four observers for binocular rivalry (left panels) and for monocular rivalry (right panels). The continuous plot shows that best-fitting Gamma distribution fitted to the data. The periods were binned into 125 ms intervals.

Experiment 4

One technique commonly used to study binocular rivalry has been to measure the depth of suppression. This is done by measuring the detection threshold for a probe stimulus presented to an eye during suppression, and comparing it against the threshold for the same probe measured during dominance (Blake & Camisa, 1979; Blake & Fox, 1974; Fox & Check, 1972; Wales & Fox, 1970). Generally, for simple stimuli such as gratings and contours, probe sensitivity is reduced during suppression to about 60% of the level measured during dominance (Fox & McIntyre, 1967; Nguyen et al., 2003; Norman et al., 1999; Wales & Fox, 1970).

Surprisingly, the probe technique has never been used to assess the depth of monocular rivalry suppression. We set out to do so. Of course, it is not possible to use monocular probes (as done in binocular rivalry probe experiments) for monocular rivalry because the rivaling stimuli are both present in the same eye. Instead, our approach was to use a contrast increment of one of the monocular- rivalry stimuli as a probe. Again, for comparability with previous research, we used orthogonal gratings as rivalry stimuli. Gratings were red or green, oriented $\pm 45^\circ$ to vertical. We briefly and smoothly pulsed the contrast of the red grating according to a temporal Gaussian profile, varying the amplitude of the pulse to find the threshold. These thresholds were measured during dominance and suppression to quantify suppression depth for monocular rivalry. As a comparison, we also measured suppression depth for the same stimuli under binocular rivalry conditions.

Method

The Method was similar to that of Experiment 3 with the following exceptions. Observers were the three authors who participated in Experiment 3 and JC, who also participated in Experiment 3. Instead of tracking monocular or binocular rivalry, observers pressed a key either whenever the red or the green grating was dominant, using similar response criteria: at least 95% visibility for binocular rivalry and at least 66% visibility for monocular rivalry. Randomly on 50% of trials this caused a probe, a contrast increment, to appear briefly on the red grating. Observers then made another key press to say

whether the probe appeared or not. Feedback was given for correct and incorrect responses. The probe followed the first key press by 150 Ms, and had a Gaussian profile over time (with a half-width of 67 Ms) to ensure the probe was smooth and free of transients. The Gaussian amplitude had a variable peak that was controlled by an adaptive QUEST procedure (Watson & Pelli, 1983) involving two randomly interleaved staircases to find the contrast increment threshold for the probe. Each QUEST was preceded by four practice trials and comprised 40 trials. Observers responded to at least four QUESTs in each of four conditions (probe presented during dominance vs. suppression and monocular vs. binocular rivalry). Observers alternated between dominance and suppression conditions, and alternated between monocular and binocular rivalry. Starting condition was counterbalanced over sessions and over observers.

Results and discussion

Before discussing the thresholds, it is important to note that the phenomenology of probe detection in the two sorts of rivalry differed in the same way as the rivalries differed. The essential character of binocular rivalry is that its perceptual alternations are of visibility, whereas those of monocular rivalry are of clarity. During binocular rivalry, a suppressed stimulus is invisible. Observers agreed there were three basic experiences when such a stimulus was probed. For low-contrast probes, the probe was invisible too. Observers pressed the key to say that no probe was presented, and were surprised when the feedback told them of their error. For intermediate-contrast probes, the probe would sometimes cause the rival stimulus to break suppression partially, so that the pulse could be seen on the parts of the previously suppressed grating. For high-contrast probes, the probe would cause the rival stimulus to break suppression, so that the contrast pulse could be seen on the previously suppressed grating.

During monocular rivalry a suppressed stimulus is still visible but its visibility is reduced. This means the experience of the probe was necessarily different from that in binocular rivalry. Observers could not agree on different qualitative experiences of the probe; all felt that there was no phenomenal suppression at all! It was only when the results were collated that the small but significant effect of suppression emerged (see below). That is

not to say detection of the probe during monocular rivalry suppression or dominance was easy; it was hard. The probe resembled the naturally occurring fluctuations in the visibility of the suppressed stimulus.

Figure 5. Autocorrelation analysis

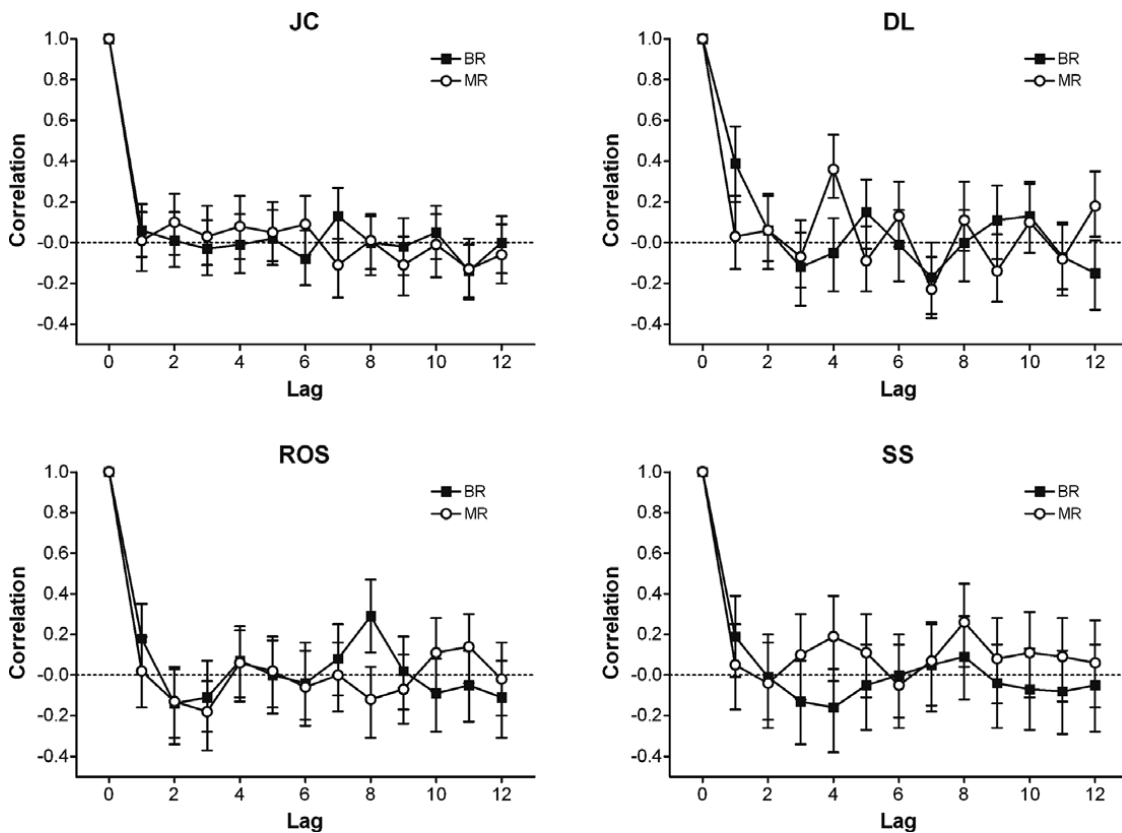


Figure 5. Results of the autocorrelation analysis for four observers for binocular rivalry (open circles) and for monocular rivalry (filled squares). Apart from the arbitrarily perfect autocorrelation when the signal was not lagged, there were no statistically significant deviations from zero. 95% confidence intervals, calculated using Fisher's *r-to-Z*' method, were erected around the correlation at each non-zero lag. All included a correlation of zero.

We analysed the mean thresholds for the four observers using a two-way, within-subjects ANOVA. This found both main effects (rivalry type: monocular vs. binocular; and rivalry phase: dominance vs. suppression) to be significant, but critically there was an interaction between them, $F(1,3) = 21.12$, $p < .05$. The thresholds are shown in the upper panel of Figure 6. Suppression depths are shown in the lower panel of Figure 6. Suppression depth

is calculated by subtracting from unity the ratio of the dominance threshold to the suppression threshold. A suppression depth of zero (i.e., the complete absence of suppression) would occur if suppression and dominance thresholds were equal. Suppression depths approach unity (i.e., very strong suppression) when suppression thresholds are much greater than dominance thresholds. For binocular rivalry, typical suppression depths are around 0.40 (e.g., Fox & McIntyre, 1967; Nguyen et al., 2003; Norman et al., 2000; Wales & Fox, 1970); the lower panel of Figure 6 shows that the suppression depth we measured for binocular rivalry is consistent with this value. Suppression depth for monocular rivalry is much weaker at around 0.10. Nevertheless, this value is significantly greater than zero, $t(3) = 4.67, p < .05$.

Figure 6. Depth of visual suppression

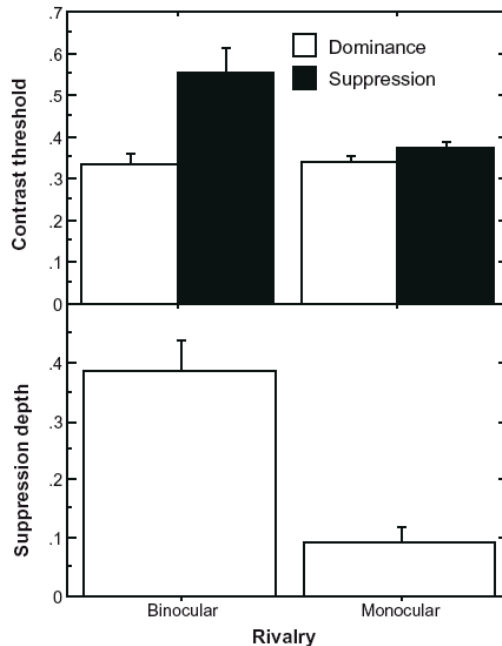


Figure 6. Upper panel. Average thresholds for the four observers for detecting the contrast increment during dominance and during suppression, for both binocular rivalry and monocular rivalry. Lower panel. The dominance and suppression thresholds from the upper panel expressed as suppression depth (i.e., one minus the dominance-to-suppression ratio). Error bars show 1 standard error of the mean.

It could be argued that the weaker suppression depth of monocular rivalry than binocular rivalry is because observers used a more liberal criterion of invisibility for the former. We used this criterion to equate, as far as possible, the number and durations of rivalry

periods. The results of Experiments 1 and 2 show that we were largely successful. The essential character of monocular rivalry is that episodes of suppression are seen as reductions in the clarity of the suppressed stimulus. It is possible that if we had asked our observers to wait for the rare instances of monocular rivalry that reached a 95% criterion of visibility, we would have measured deeper suppression. Nevertheless, we conclude that the thresholds we have measured are an accurate indication of the depth of suppression during typical monocular rivalry.

General discussion

Our main question was whether similar neural mechanisms underlie monocular and binocular rivalry. Our experiments showed that the two phenomena do exhibit important similarities. In Experiments 1 and 2, we demonstrated that both kinds of rivalry can occur between complex images, and that they are affected similarly by the size of the rivalling images, as well as by their colours in quantitatively similar ways. In Experiment 3, we illustrated the similar temporal dynamics of the two sorts of rivalry, showing that both exhibit a gamma distribution of dominance durations with comparable parameters and that neither shows any temporal correlation of one episode of visibility with any of the preceding episodes. In Experiment 4 we demonstrated that both sorts of rivalry involve suppression of visual sensitivity to the non-dominant stimulus, albeit to a very different degree. These qualitative and quantitative (with the exception of suppression depth) similarities between monocular and binocular rivalry are consistent with the idea that their underlying processes involve common neural mechanisms (cf. Leopold & Logothetis, 1999; O'Shea, 1998; Papathomas, Kovács, Fehér, & Julesz, 1999).

There are other similarities between monocular and binocular rivalry. For example, rivalry rate grows with orientation and spatial-frequency differences between the rivalling images (e.g., Atkinson et al., 1973; Campbell et al., 1973; O'Shea, 1998). It has been long known that binocular rivalry is difficult to control voluntarily (Breese, 1899); monocular rivalry is equally difficult to control voluntarily, both for gratings and for complex images (O'Shea, 2006). Moreover, the temporal limits over which rivalry will survive asynchronous flicker are similar for the two forms of rivalry, at around 350 ms

(van Boxtel, Knapen, van Ee, & Erkelens, 2006). And as we pointed out earlier, alternations of one sort of rivalry in one region of the visual field synchronise with alternations of the other from an adjacent region (Andrews & Purves, 1997; Pearson & Clifford, 2005).

Although the conclusion that monocular rivalry shares common processes with binocular rivalry has appeal, there are alternative explanations of monocular rivalry that need to be considered, as well as certain notable differences between the two phenomena that must be addressed. One of the competing explanations of monocular rivalry is that it is not strictly a perceptual alternation but an epiphenomenon produced by a combination of eye movements and afterimages. This line of argument was proposed by Furchner and Ginsburg (1978), by Georgeson and Phillips (1980), and by Georgeson (1984). They maintained that in the case of two superimposed orthogonal gratings, for example, steady fixation would build up afterimages that would tend to cancel visibility of both. If an eye movement were made parallel to one of the gratings, with a magnitude of half the spatial period of the other grating, it would leave the visibility of the first grating impaired but superimpose the negative afterimage of the second grating onto its own real image, causing that grating suddenly to become visible, as if it had just appeared after an episode of suppression. According to this explanation, if eye movements were made randomly, they would produce random distributions of dominance times such as we observed in Experiment 3, and they would also produce the dependencies of monocular rivalry on orientation differences such that it would be most pronounced for orthogonal gratings (O'Shea, 1998).

We argue that eye movements and afterimages cannot be a complete explanation of monocular rivalry for at least four reasons. First, monocular rivalry occurs between afterimages themselves (Crassini & Broerse, 1982), which are fixed on the retina and therefore cannot combine with eye movements as required by the explanation. Second, observers report monocular rivalry composites, patches of the visual field in which one image is seen and adjacent patches in which the other is seen (Sindermann & Lüddecke, 1972). Our observers also reported composites in all our experiments. Such composites

would require eye movements that move the retina in different directions in different regions, which is quite impossible. Third, Bradley and Schor (1988) measured eye movements during monocular rivalry of gratings. They found some disappearances in monocular rivalry that did follow the predicted eye movements, but they also found a proportion of disappearances that followed an incorrect eye movement. Fourth, the explanation requires that the images be simple, repetitive stimuli such as gratings, so that an afterimage can be displaced but still provide a matching overlay of the stimulus that generated it. Experiments 1 and 2 showed clearly that monocular rivalry is possible between complex images for which no eye movement can superimpose a matching afterimage.¹

Given the shortcomings of this alternative account of monocular rivalry, we conclude that monocular rivalry is indeed a genuine perceptual alternation, similar to binocular rivalry, and not an artefact of eye movements or afterimages. Nonetheless, despite the striking similarities between monocular and binocular rivalry, we elaborate below on three differences between the phenomena. We propose that these differences arise because binocular rivalry involves a distributed cortical network entailing both low-level and high-level processes (Blake & Logothetis, 2002; Freeman, Nguyen, & Alais, 2005; Nguyen et al., 2003) whereas monocular rivalry involves interactions only at higher levels. We agree with Maier et al. (2005) that monocular rivalry is likely to reflect a higher-level process because it involves global interpretations of the probable nature of the stimulus. Therefore, we propose that monocular and binocular rivalry share common high-level processing which can be characterised as interpretative processes (e.g., Alais, O'Shea, Mesana-Alais, & Wilson, 2000; Kovács, Pápathomas, Yang, & Fehér, 1996).

¹ The same explanation could also apply to binocular rivalry of gratings. Indeed, van Dam and van Ee (2006) found that saccades changing fixation from one luminance to the opposite luminance (e.g., from a bright bar to a dark bar) were more likely to be followed by a binocular rivalry alternation to that grating than saccades changing fixation from one luminance to the same luminance (e.g., from a dark bar to a dark bar). This is not to say that binocular rivalry is an epiphenomenon of eye movements and afterimages. There is an abundance of evidence similar to that for monocular rivalry, including binocular rivalry with afterimages, binocular rivalry with complex images, and visibility of composites of the two rival stimuli, showing that eye movements and afterimages are not necessary for binocular rivalry.

The key distinction, then, between the two types of rivalry is that binocular rivalry involves additional inter-ocular interactions at early levels of the visual system.²

The first difference between monocular and binocular rivalry was observed by Breese (1899) in his seminal study. He recorded that although binocular rivalry's episodes of dominance involved alternations in visibility, monocular rivalry was weaker and usually involved alternations in clarity. Consistent with this, we showed in Experiment 4 that the magnitude of suppression during monocular rivalry is much less than in binocular rivalry. We propose that the marked difference in suppression depth is due to the different extents of the monocular and binocular rivalry networks rather than to fundamentally different processes. A model similar to that by Wilson (2003) or by Nguyen et al. (2003) or Freeman (2005) could serve here. Specifically, the same inhibitory mechanisms exist at monocular and at binocular levels: these sum their effects in binocular rivalry, but the monocular part does not participate in monocular rivalry, weakening the suppression. The idea of additive suppression components is consistent with recent findings that exclusive visibility during rivalry increases as more dimensions of stimulus conflict are combined (Knapen et al., 2007).

An important consequence of the notion that monocular rivalry involves neural interactions common to the high-level part of the binocular rivalry network is that monocular rivalry should resemble other higher-level rivalries. Here, we review only one: stimulus rivalry, or flicker-and-swap rivalry. Devised by Logothetis, Leopold, and Sheinberg (1996), stimulus rivalry occurs when two rival images are swapped between the eyes at around 1.5 Hz, while also flickering on and off at around 18 Hz. The key observation is that observers report episodes of stable visibility of one of the images that endure for long enough to incorporate several interocular stimulus swaps. Each swap, however, is noticeable as a pulse of some sort during a single episode of visibility,

² Although the term "monocular rivalry" suggests a low-level process, it is simply because it has been misleadingly labelled, prompting Maier et al. (2005) to propose that monocular rivalry would be more appropriately called "pattern rivalry".

showing a similar phenomenal absence of complete suppression in this sort of rivalry as in monocular rivalry. Logothetis et al. proposed that rivalry process acts on representations of images at a high level of the visual system where eye-of-origin information (a low-level property) has been discarded. Recent corroborative evidence for this comes from Pearson, Tadin, and Blake (2007) who showed that transcranial magnetic stimulation of V1 disrupts conventional binocular rivalry but has no effect on flicker-and-swap rivalry.

We argue that with eye-of-origin information removed, flicker-and-swap rivalry should be very similar to monocular rivalry. Supporting this, we recently found that suppression depth in this form of rivalry is also shallow (Bhardwaj, O'Shea, Alais, & Parker, 2008), similar to that of monocular rivalry. There are at least three other similarities between monocular rivalry and flicker-and-swap rivalry phenomena that support our proposal. First, monocular rivalry and flicker-and-swap rivalry do not require that eye-of-origin information be retained (unlike conventional binocular rivalry). Second, flicker-and-swap rivalry is promoted by interspersing monocular rivalry stimuli between the swapping stimuli (Kang & Blake, 2006). Third, flicker-and-swap rivalry and monocular rivalry share some interesting parametric similarities. Both are enhanced at low contrast (Lee & Blake, 1999) and by making the images different colours (Bonneh, Sagi, & Karni, 2001; Logothetis et al., 1996). Moreover, Knapen et al. (2007) found that exclusive visibility in monocular rivalry is similar to that from flicker-and-swap rivalry over a range of colour differences. These similarities between monocular rivalry and flicker-and-swap rivalry are, of course, consistent with our overall conclusion that all forms of rivalry involve a similar, high-level mechanism. Indeed, Pearson and Clifford (2005) showed that all three types of rivalry, monocular, binocular, and flicker-and-swap, synchronise their alternations when all are presented together in adjacent regions of the visual field.

The second major difference between monocular and binocular rivalry, and the hardest to reconcile, is that they are affected oppositely by contrast (O'Shea and Wishart, 2007). Binocular rivalry alternation rate increases with increasing contrast of the rival images whereas monocular rivalry alternation rate decreases with increasing contrast. Evidence

from imaging and transcranial magnetic stimulation support the claim that early visual processes are critical in eliciting binocular rivalry (Lee & Blake, 2002; Pearson et al., 2007; Polonsky, Blake, Braun, & Heeger, 2000). Because early visual responses depend strongly on the level of stimulus contrast, exhibiting a graded monotonic response to contrast, it makes sense that binocular rivalry would be strongly modulated by contrast. Specifically, because increases in stimulus contrast would increase the V1 response to the rival stimuli, it is as expected that binocular rivalry should be more vigorous at high contrast.

What is less obvious is why monocular rivalry would be more vigorous at low contrast. One reason may be that the global interpretative processes implied by Maier et al.'s (2005) work on monocular rivalry, and more generally by Leopold and Logothetis's (1999) review, may be less stable at low contrast. That is, reduced signal-to-noise ratios and stochastic fluctuations would add considerable uncertainty to whether a monocular rivalry stimulus should be interpreted as one or two objects, and possibly to the depth ordering if two objects were signalled. To take Maier et al.'s (2005) real-world example, the bottom of a pond might be visible transparently even though the water's surface may reflect the image of a tree. In this case, with both aspects of the visual scene imaged at the same retinal location, high contrast would facilitate a transparency interpretation and the correct depth order because both images would be reliably signalled with little ambiguity. Low contrast, however, would render the problem more difficult as both interpretations would be potentially valid but the correct transparency and order relationship would be hard to make with poorly visible cues. Under these conditions, an interpretative process with bistable behaviour appears to assume more prominence and perceptual alternations result.

The lack of vigorous monocular rivalry at high contrast may be because there are robust cues for interpreting the image as stable, such as the visibility of the intersections of contours. It may also be because high-level neurons tend to be contrast invariant. That is, their contrast-response functions are much steeper initially with a longer saturated plateau (e.g., Sclar, Maunsell, & Lennie, 1990). A magnetic resonance imaging study (Avidan et

al., 2002) showed steeper contrast-response functions in human subjects along the ventral visual pathway from V1 through V2, V4/V8, and LO. Because of this tendency towards early saturating contrast-response curves, there is no reason to expect that a high-level monocular rivalry process should behave more vigorously at high contrast. Indeed, it would be mainly at low contrast, before reliable responses are elicited, that a high-level interpretive process would be least stable.

The third major difference between monocular and binocular rivalry is that they are potentially affected oppositely by disparity. Knapen et al. (2007) have shown that monocular rivalry increases as two monocular rivalry gratings are given different disparities to make them appear to be at different depths. Shimojo and Nakayama (1994) and have shown that binocular rivalry decreases by adding disparities. Knapen et al. argued from their results that monocular rivalry and binocular rivalry are nevertheless similar, in that the strength of rivalry is determined by the difference between two stimuli in their component features: adding disparity to monocular rivalry stimuli increases their difference whereas adding disparity to binocular rivalry stimuli decreases the amount of interocular conflict between them. Knapen et al.'s approach, although from a different direction to ours, comes to a similar conclusion: that monocular rivalry and binocular rivalry are similar processes aimed at resolving ambiguity in visual inputs.

Conclusion

In summary, we have shown several qualitative and quantitative similarities between monocular and binocular rivalry. Both occur between complex images, both are similarly affected by the images' size and colour, both involve fluctuations in image visibility that are random and sequentially independent, and both involve suppression of visual sensitivity to the non-dominant image. We propose that both sorts of rivalry are mediated by a common high-level mechanism for resolving ambiguity (Alais, O'Shea, Mesana-Alais, & Wilson, 2000; Kovács et al., 1996; Leopold & Logothetis, 1999; Maier et al., 2005), although this process cannot be the primary driver in the case of binocular rivalry, which must be initiated by mutually inhibitory interactions between neurons retaining eye-of-origin information in early cortex. This high level process for ambiguity resolution

probably exerts a modulatory influence on binocular rivalry, exerting its influence via feedback for such things as coordinating local rivalry processes into coherently rivalling global images (Alais & Melcher, 2007), whereas it is more likely to be the primary driver of monocular rivalry.

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Chapter summary

The current chapter has shown that monocular and binocular rivalry share many hallmarks. The differences between these two forms of perceptual bistability are a result of the processing specific to the different ways in which they are presented. This and other research comparing bistable stimuli establish the feasibility of the involvement of a common mechanism in perceptual rivalries. Whether this mechanism is also shared with exogenous perceptual selection is addressed in the following chapters.

Chapter 3

A bias for looming stimuli to predominate during binocular rivalry

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Overview

In the introductory Chapter 1, the limited effect of purposeful attention over the overall predominance of one or the other image undergoing binocular rivalry was discussed (i.e. the results of Meng & Tong 2004). The experiments in this chapter demonstrate that exogenous, or stimulus-driven attention can cause one image to be seen for significantly longer periods during binocular rivalry. These results provide evidence that perceptual bistability may be related to general mechanisms involved in exogenous perceptual selection, in support of Hypothesis 2.

Abstract

Concentric gratings that expand outwards are seen for a greater period of time relative to contracting gratings when engaged in binocular rivalry. During binocular rivalry (BR), which is a fluctuation in visual awareness between different images presented separately to each eye, equivalent images tend to be seen in equal proportion over the observation period. When one eye's image is particularly salient, brighter, or moving, this equality is curtailed, and the stronger image predominates. Here a specific direction of motion is found to predominate over another of equal speed. This tendency is consistent with the ability of looming objects to orient attention, coupled with previous accounts of the role of stimulus-driven attention in binocular rivalry.

Introduction

Binocular rivalry is an unusual perceptual phenomenon that occurs when each eye is presented with one of two distinct images (Blake & Logothetis, 2002; Alais & Blake, 2005). Rather than see the two different images fused or superimposed, a temporal

alternation occurs in which one eye's input is seen to the exclusion of the other's in an independent, stochastic series (Fox & Herrmann, 1967). Binocular rivalry is a widely studied area of vision science, in part because it provides a dissociation between the physical stimulus and perceptual awareness of it, an aspect which has made it a suitable experimental paradigm for studies of visual awareness. A more fundamental point of interest is the underlying mechanism of rivalry which is not yet completely understood. One major debate has concerned whether rivalry is caused by early and low-level interactions between monocular channels or by competing visual object representations at a later stage (Blake & Logothetis, 2002 NRN). More recently it has been suggested that rivalry may be a distributed process, capable of occurring at several levels of the visual pathway (Freeman, 2005; Nguyen, Freeman, & Alais, 2003; Ooi & He, 2003; Wilson, 2003).

It has been proposed that binocular rivalry results from competition between populations of monocular neurons responding to each eye's input at some relatively early point in the visual cortex (Tong & Engel, 2001; Blake, 1989). Such a process would need to happen early in the visual hierarchy where neurons still carry eye-of-origin information. In contrast, single-cell studies in awake monkeys show that neural fluctuations correlating with perceptual alternations during rivalry are rather weak in early cortex but increase at successive stages along the visual processing hierarchy (Leopold & Logothetis, 1996; Logothetis & Schall, 1989; Sheinberg & Logothetis, 1997). Very recently, however, human fMRI studies have refocused the discussion regarding the origins of rivalry on early visual areas by showing that fluctuations corresponding to rivalry perception occur in visual area V1 (Polonsky, Blake, Braun, & Heeger, 2000) and even in the lateral geniculate nucleus (LGN) (Haynes, Deichmann, & Rees, 2005; Wunderlich, Schneider, & Kastner, 2005). This suggests an important role for lateral interactivity between neurons as well as feedback from higher areas in rivalry (Lee & Blake, 2004) because if rivalry were limited to early local competition there would be no rivalry between global stimuli (e.g., faces, global motions) represented in areas beyond LGN and V1 (Alais & Melcher, 2007; Alais & Parker, 2006).

It is well known that when the stimulus given to one eye is brighter, higher in contrast or contains motion, it has a stronger tendency to be seen than a duller or stationary rival stimulus (Blake, Yu, Lokey, & Norman, 1998; Levelt, 1965; Wade & de Weert, 1986). This overall ‘predominance’ of one target over a rival is usually achieved by a reduction in the average suppression duration of the dominant target, rather than an actual increase in its dominance duration. This is known as Levelt’s second proposition (Levelt, 1965) and it has been confirmed in a wide range of rivalry conditions, although it does not hold for motion stimuli and for certain contrast relationships (Bossink, Stalmeier, & de Weert, 1993; Brascamp, van Ee, Noest, Jacobs, & van den Berg, 2006). In this paper, we examine predominance using rivalling global motion stimuli (expansion vs. contraction) and demonstrate a qualitative rather than a quantitative effect in predominance which indicates greater strength for expansion.

Expanding patterns of movement indicating the approach of an object may be more perceptually important than receding motion because they can signal collision and may require an immediate, defensive response. There is some debate concerning whether approaching but not receding motion can capture attention (Abrams & Christ, 2005; Abrams & Christ, 2006; Franconeri & Simons, 2003; Franconeri & Simons, 2005). It seems that both these types of motion can capture attention in visual search tasks, however the possibility that approaching objects are more effective than receding ones, especially when motion onsets are omitted, was not directly addressed. Franconeri and Simon’s initial finding suggests that this may be the case. Neurophysiological evidence indicates that areas of the visual cortex sensitive to optic flow patterns of motion respond more strongly to expanding than to receding motion. A single-cell study of monkey MSTd found a greater preponderance of neurons sensitive to expanding optic flow as opposed to receding (Graziano, Andersen, & Snowden, 1994). This may arise due to the prevalence of expansion in normal experience; forward self-movement is the norm hence a stronger neural response to this direction would be developed. In the behavioural component of one functional MRI study, subjects did not report seeing any motion aftereffect for receding concentric grating stimuli, but strong motion after effects from expanding motion were reported (Berman & Colby, 2002). Given these asynchronies

between expansion and contraction it seems likely that they might manifest in binocular rivalry when pitted against each other. Here, continuous versions of these two directions of motion will be compared under conditions of binocular rivalry. If expanding motion is a more salient stimulus in terms of behaviour or neural response it will predominate over a receding motion of the same speed.

We find that looming/expanding stimuli do predominate over receding/contracting stimuli, even though the rival motions have equal but reversed speed profiles and are thus locally identical. Rivalry predominance in this case therefore appears to be determined qualitatively, rather than in quantitative terms of ‘stimulus strength’ (Levelt, 1965). This effect appears to be very robust as it persists even when the receding motion has a higher temporal frequency than the looming motion.

Experiment 1: Rivalry between looming and receding motion

The first experiment looked at binocular rivalry between looming and receding concentric gratings. Looming is a salient visual cue for survival as it may indicate approaching danger or collision. Quickly approaching objects capture our attention involuntarily in order for us to respond quickly, demonstrated in visual search paradigms (Franconeri & Simons, 2003). This kind of stimulus driven or exogenous attention can be viewed as a different kind of process from endogenous attention deployed voluntarily by an observer. Both types of attention have been shown to affect binocular rivalry (Ooi & He, 1999). Selectively attending to one of the rival targets can moderately extend its average dominance period relative to its rival stimulus (Lack, 1978; Ooi & He, 1999), and overall, attention appears to speed up rivalry alternation rate (Paffen, Alais, & Verstraten, 2006). The effects of attention have been found to be stronger for other types of perceptual bistability which involve no inter-ocular conflict such as reversible figures like the Necker cube (Meng & Tong, 2004). Attending either endogenously or exogenously to a target just prior to rivalrous presentation will usually cause that target to predominate in the first phase of rivalry (Chong & Blake, 2006; Mitchell, Stoner, & Reynolds, 2004). Unlike voluntary attention, the exogenous kind can affect a rival image during perceptual suppression. Transient events presented to a suppressed eye tend to produce a swap to

that eye's stimulus. The 'pop-out' of an odd target in visual search achieves a similar result, even when transients are removed from the presentation (Ooi & He, 1999).

Experiment 1 examines rivalry between looming and receding concentric gratings. Because looming visual objects are an effective stimulus for activating stimulus-driven attention, we expect there to be a bias in predominance favouring looming rather than receding stimuli.

Method

Subjects

Fourteen subjects participated in Experiment 1. All had normal or corrected-to-normal vision. One subject was the primary author. Ten participated for course credit in an introductory psychology course and 4 were experienced in perceptual observation. Ten were female, the other 4 male. All but the author were naïve as to the purpose of the experiment.

Stimuli

Two concentric sine wave gratings were used as rival stimuli. They subtended 2° of visual angle at the viewing distance of 57 cm, had 25% Michelson contrast, a mean luminance of 31 Cd/m², and a spatial frequency of 3 cpd. They were presented in a Gaussian envelope in the same manner as a Gabor patch. The concentric gratings were phase shifted to appear to either expand or contract. The magnitude of the phase shift was increased exponentially over a 1 second period from a baseline increment of 1 cycle per second to a maximum of 4 cycles per second, after which the increase was rapidly tapered off (see Figure 1a). These phase shifts were used in order to make the concentric grating appear to loom in an ecologically valid way, with an accelerating size/speed change. This speed profile was reversed to produce the receding stimuli. Continuous motion was created by repeating these profiles in a loop. The looming/receding gratings were presented one on each side of a CRT monitor and viewed through a mirror stereoscope to produce binocular rivalry. In condition A (n = 4), both rival gratings were

looped at 1 Hz. In condition B ($n = 5$), the looming grating was looped at 1 Hz and the receding at 3 Hz. In the last condition C ($n = 5$), the looming grating was looped at 3 Hz and the receding 1 Hz. These last two conditions were included to enable examination of the alternation patterns for each direction relative to the onset of the motion (not possible when both rival stimuli are pulsed in phase).

Procedure

Before each trial two black apertures were presented on each side of the screen. The mirror stereoscope was adjusted for each subject to achieve comfortable fusion. When ready a trial was initiated by pressing any key. In 2 minute trials, the five observers recorded their alternating dominance periods by holding down one of two keys. A total of four trials were collected for each of the three rival conditions (a total of 8 minutes each). Between trials the stimuli were interchanged between the eyes. After each trial the screen went blank and the observer could rest for a self determined period before resuming. During recording, observers were instructed to maintain fixation on the centre of the rival gratings. They were also instructed to hold down both keys to record instances of mixed or 'piecemeal' rivalry where neither direction was exclusively dominant. All participants were given ample experience observing and recording their rivalry perceptions prior to testing.

Figure 1. Results of Experiment 1

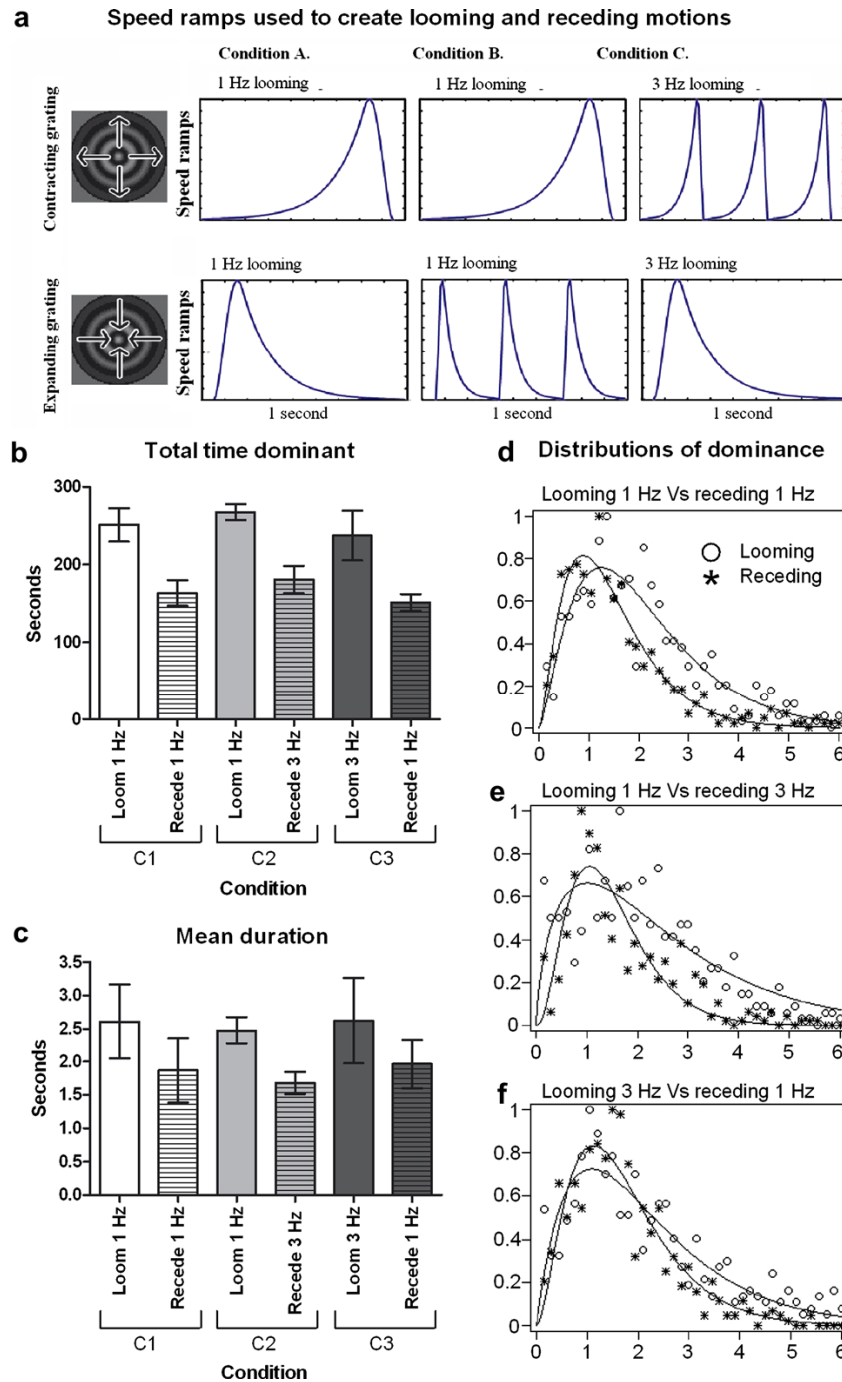


Figure 1. Results of Experiment 1. (a) The speed ramps used for each binocular rivalry pair in Experiment 1. (b) The sum of dominance durations for each rival stimulus. (c) Mean duration of perceptual dominance for each rival stimulus. (d–f) Frequency distributions of dominance durations plotted for each stimulus for conditions 1, 2 and 3 respectively. Distributions were normalised in order to highlight differences between the shapes of the distributions rather than the area.

Results and discussion

The data from Experiment 1 are shown in Figure 1. In panel b it can be seen that over the combined 8 min of rivalry dominance tracking, looming motion predominated significantly longer than receding motion in all conditions on paired t-tests (condition A: $t = 5.601$, $p < .01$, condition B: $t = 4.723$, $p < .01$, condition C: $t = 2.673$, $p < .01$). In each condition, the difference between the two dominance totals and the total observation period of 480 seconds represents total piecemeal duration. We also tested whether there was any difference between the total dominance times for each motion direction pulsed at different rates. There were no significant differences between the looming conditions ($t = 1.115$, $p > .05$), nor the receding conditions ($t = 1.09$, $p > .05$) using Bonferroni's Multiple Comparison test.

The advantage of looming motion over receding can also be seen in the mean dominance periods shown in Figure 1c. Looming predominance persisted even when receding motions were pulsed in faster 3 Hz cycles and was significant for all conditions on paired t-tests except condition C, where the 3 Hz looming cycle was used (A: $t = 5.345$ $df = 3$, $p = .0064$; B: $t = 3.549$, $df = 4$, $p = .0119$; C: $t = 1.528$, $df = 4$, $p = .1006$). Across the three conditions, the mean dominances were very similar, and not surprisingly we observed no significant differences between conditions for alternation rate, mean number of swaps, nor proportion of coherent (non-piecemeal) rivalry.

Figure 1d–f shows the distributions of dominance durations for the three conditions tested, fitted with a Gamma distribution. The fits to the looming stimuli all have a lower peak and broader upper tail than those for receding motion. To test the significance of these apparent differences we represented the same data in cumulative form (e.g., Figure 4) and analysed it using the Kolmogorov–Smirnov (KS) statistic. The KS statistic is a sensitive non-parametric test that can be used to test whether the distance between two cumulative distributions is significant. As such it is ideal for examining differences between distributions of binocular rivalry dominance durations, providing more information than a test of mean duration alone. For all conditions, the looming vs. receding difference was found to be significant (condition A: $d = 0.38$, $p < .01$; condition

B: $d = 0.26$, $p < .01$; condition C: $d = 0.22$, $p < .01$, see Figure 4a–c). There is a possibility that reporting bias may have influenced our results by, for example, faster responding to a change to a looming motion from its receding rival or a piecemeal state. However this seems unlikely for two reasons; the majority of the subjects were naïve as to the hypothesis of the experiment and had no reason to favour one stimulus over the other. Secondly, the importance of accurately recording their perception was heavily emphasised.

Finally, we checked to see whether there was any tendency for the predominance of looming over receding stimuli to vary over the observation period. In particular, since looming stimuli are attentionally salient and attention has been shown to bias the early phase of rivalry to the attended target (Chong & Blake, 2006; Mitchell et al., 2004), we wished to know whether this might account for the predominance of looming. Overall, we found no tendency for the looming predominance to change over the observation period, although all subjects reported beginning their rivalry alternation with looming as dominant.

Experiment 2: Rivalry between linearly expanding and contracting motions

In order to further clarify the predominance findings for looming motion found in Experiment 1, binocular rivalry between continuous linear expansion and contraction was examined. This was done using the same expanding/contracting concentric gratings used in Experiment 1, with the difference that the speed profiles were linear expansions/contractions rather than non-linear accelerations/decelerations. This stimulus (condition A) was intended to determine whether it is the exponentially increasing speed/size that is needed to elevate looming predominance in rivalry. In addition, we measured rivalry for two other kinds of stimuli: expanding/contracting coherent random dot motions (condition B), and expanding/contracting filtered noise images (condition C, See Figure 2). The reason for these conditions is that the bias found in Experiment 1 for looming gratings may be specific to coherent contours that expand consistently with an approaching visual object. If so, then we may not observe the same looming bias for random dots or filtered noise since the discontinuous features in these stimuli, despite

expanding and contracting like a retinal flow field, do not contain coherent and spatially continuous objects. Because of this, although the two random stimuli resemble patterns of expansion/contraction perceived during self-motion, only the concentric contours would expand coherently like an approaching visual object. If the salience of expansion in rivalry is confined to spatially coherent stimuli, it would indicate that this bias is tied to object processing.

Method

Subjects

Eight subjects participated in Experiment 2, 5 female and 3 male. All had normal or corrected-to-normal vision. Seven of these were new subjects who participated in return for credit in an introductory psychology course. Three of the naïve subjects participated in all three conditions. The other four participated in only one condition each. The primary author also participated in condition 2.

Visual stimuli

Three different kinds of visual stimuli were used and are illustrated in Figure 2. Condition A: The same two concentric grating stimuli (with a RMS contrast of 10%) used in Experiment 1, but without the accelerating/decelerating speed ramps. Instead an intermediate and constant (linear) speed of 2 cycles per second was used. Condition B: Expanding and contracting coherent random dot motion arrays were presented in circular apertures 80 pixels wide (2° of visual angle). The background luminance was 0.3 cd/m² with dots of 8% RMS contrast. There were 150 dots, each 3 pixels wide and moving 2 pixels per frame at 85 Hz screen refresh rate yielding an overall speed of 2.25 cp/s. Condition C: Four band-pass filtered (minimum SF 1 cycle p/deg maximum: 20 cycles p/deg) random intensity noise patterns (RMS contrast of 13%) that drifted either toward or away (approx. 1.86 deg visual angle per second) from the centre of the stimulus array were used as the rival stimuli. Although the incidence of coherent (complete) visual dominance of the two eyes' inputs will likely be reduced by quartering the image into independent sectors, the periods in which the whole stimulus is perceived to expand or

contract can still be compared.

Procedure

For all three conditions of Experiment 2 the procedure was the same as that used in Experiment 1. Five observers participated in condition A (concentric gratings). Four subjects (including author AP) participated in condition B (random dots) and four in condition C (filtered random intensity noise). The task was to monitor periods of exclusive visibility of expansion and contraction, as in Experiment 1.

Results

The data from Experiment 2 are shown in Figure 2. In condition A, expanding concentric gratings predominated over contracting ones, similar to what was reported in the first experiment. The difference was significant for both the total dominance durations (Figure 2a: one-tailed t-test $t = 3.994$, $df = 4$, $p < .01$) and mean dominance durations (Figure 2b: $t = 3.995$, $p < .01$). For four of the five subjects, expansion was the initially dominant phase of rivalry, in each of the four 2-min recording blocks.

The distributions of dominance durations for expansion and contraction are shown in Figure 2d. They follow the same pattern as those obtained in Experiment 1 (where the stimulus was a repeating series of accelerations/decelerations) in that the gamma distribution fit to the looming data has a lower peak and a broader upper tail than the receding data. The distributions were significantly different on the Kolmogorov-Smirnov test ($K-S d = 0.58$, $p < .0001$, see Figure 4d).

In conditions B (random-dot motion) and C (filtered random noise), interestingly, there was no tendency for expansion to predominate over contraction. For the random-dot motion, both the total dominance time (Figure 2a: $t = 0.6451$, $df = 4$, $p > .05$) and the average dominance duration (Figure 2b: $t = 0.7610$, $df = 4$, $p > .05$) were similar for both types of motion. The equality of dominance between the two random-dot motions is evident in Figure 2a and b and the gamma distributions in Figure 2e, which were not significantly different on the Kolmogorov-Smirnov test ($K-S d = 0.17$, $p > .05$, Figure

4e). Similarly, using filtered random noise, there was no dominance bias for expansion. This was true for both total dominance time (Figure 2a: $t = 0.3261$, $df = 3$, $p > .05$) and mean dominance duration (Figure 2b: $t = 2.043$, $df = 3$, $p > .05$), and for the Kolmogorov-Smirnov test on the distributions of dominance times in Figure 2f ($K-S d = 0.07$, $p > .05$, Figure 4f). This suggests that the bias documented in Experiment 1 and in condition A of Experiment 2 is not due to a fundamental bias for a certain direction of motion but is specific to the expanding size of a coherent object defined by continuous contours.

Finally, the proportion of the total observation time that coherent rivalry alternations were perceived (Figure 2c) differed between the three conditions ($F = 7.624$, $p < .01$, with the following condition means: A = 0.83, B = 0.65, C = 0.53). As anticipated, this was mainly due to significantly lower rivalry coherence in condition C, filtered random noise, and is borne out by the contrasts between the means involving condition C (A vs. B: $t = 2.436$, $p > .05$; A vs. C: $t = 3.840$, $p < .01$; B vs. C: $t = 1.543$, $p > .05$). The reason for this is most likely that the filtered noise stimulus was spatially quartered, with each quarter drifting towards (or away from) the centre of the display along diagonal axes, instead of undergoing a global expansion/contraction like the other two conditions. Overall, however, mean alternation rates across conditions did not differ significantly between conditions ($F = 0.4712$, $p > .05$).

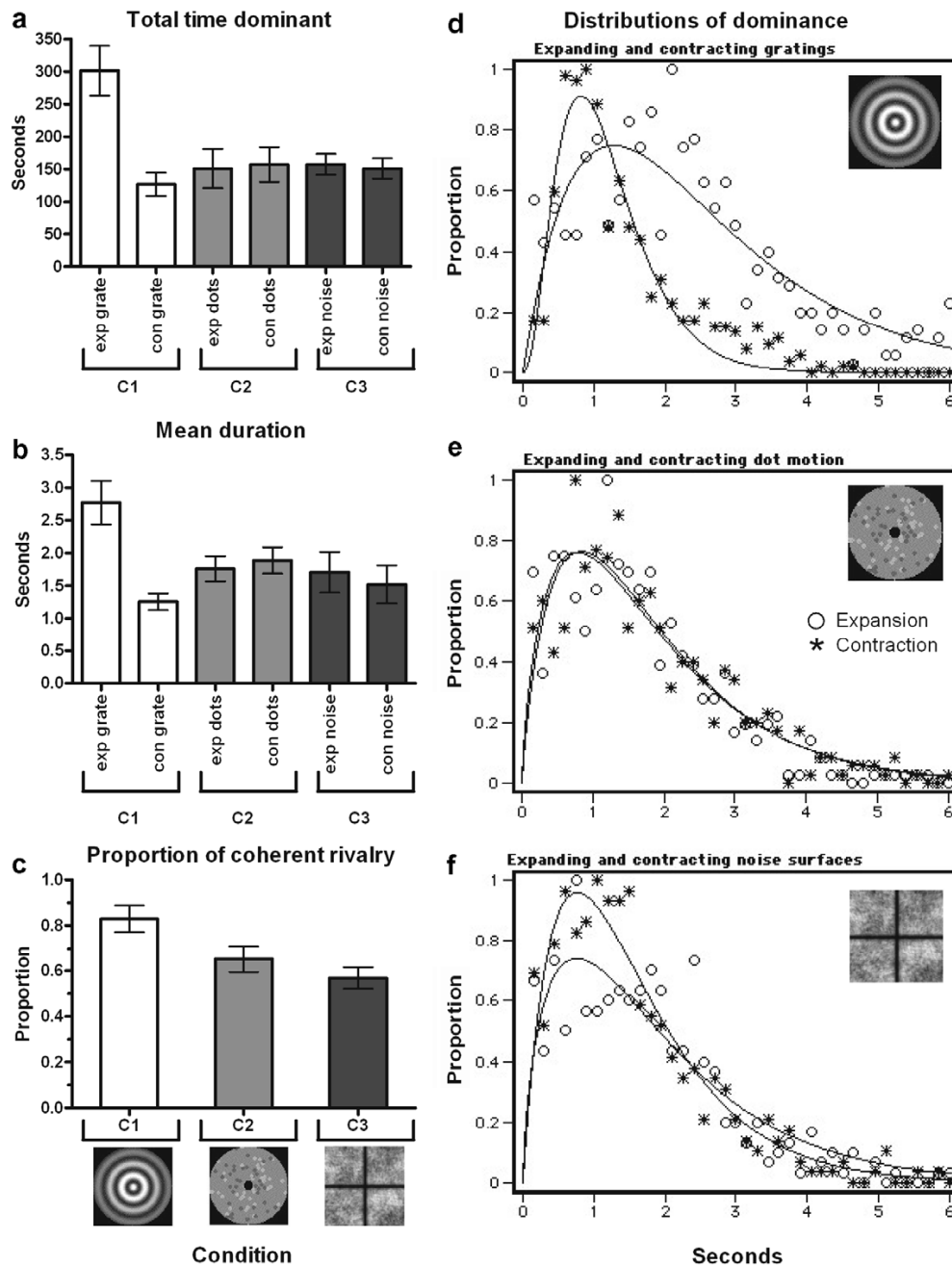
Figure 2. Results of Experiment 2

Figure 2. Results of Experiment 2. (a) The total time each direction was reported perceptually dominant during binocular rivalry between the three rival pairs examined in Experiment 2. (b) The average duration of rivalry dominance for each stimulus. (c) Proportion of coherent rivalry (non-piecemeal) for each of the three conditions. (d–e) The normalised frequency distributions of the binocular rivalry dominance durations. A gamma function was the best fit for these distributions. Only the rivalry between expanding and contracting concentric grating stimuli show a marked difference in the fit parameters.

Discussion

The results with respect to the dominance bias and the type of motion profile (accelerating vs. linear) are very clear. In condition A, where the same stimulus as in Experiment 1 was used (i.e., concentric sine-wave gratings), a dominance bias favouring expanding over contracting stimuli was still observed. Clearly then, whether the motion profile was accelerating or linear was of no consequence for the dominance bias as in both cases a strong advantage to looming/expanding to dominate was observed. It is possible that the reason for this is the rather small size of the stimuli, since larger stimuli would exhibit more pronounced local speed differences between the outer and inner portions of the stimulus. This is really a moot point since in most circumstances binocular rivalry targets are deliberately small in area to minimise the likelihood of piecemeal rivalry. However, it is noteworthy that neurons responsive to global expansions are found beyond V1 in areas where receptive fields are quite large (Duffy & Wurtz, 1991; Komatsu & Wurtz, 1988) and greater perceptual salience of accelerating approaching movement might therefore be achieved with stimuli subtending larger viewing angles. In any event, for the stimulus size we employed (2 visual angle in diameter) there was no difference between accelerating and linear speed profiles.

The most interesting outcome of Experiment 2 was that no dominance bias was observed for the two stimuli with random spatial structure: the random-dot motion and the filtered visual noise. This therefore qualifies the first conclusion from this experiment in that expansion alone is not sufficient to produce a dominance bias over contraction; it must be expansion of spatially coherent contours. The basis for this is probably attentional. The random motion and random noise stimuli created percepts of expanding or contracting surfaces, but not of approaching/looming objects. Only the concentric grating created this impression, with the coherent size change of the circular rings as the stimulus expanded from the centre. It is for this reason that we favour an attentional interpretation, since looming objects are salient for grabbing attention in a stimulus-driven manner, as noted in Section 2.

Experiment 3: Rivalry between static radial gratings and expanding/contracting concentric gratings

To learn more about the predominance found in the previous two experiments, we pitted expansion and contraction (separately) against a static radial grating. Binocular rivalry between static radial gratings and expanding/contracting concentric gratings has been examined previously by Wade and de Weert (1986), although their concentric grating stimulus alternated continuously between expansion and contraction. For this reason, it is not possible to determine from their data whether there was any bias for expansion to predominate over contraction. Experiment 3 compares separately rivalry between static and expanding gratings, and rivalry between static and contracting gratings.

Subjects

Five subjects participated in Experiment 3 across all conditions. Of these, four were naïve as to the purpose of the experiment and participated in return for credit in an introductory psychology course and had not participated in either Experiments 1 or 2. The other was the primary author. All had normal or corrected-to-normal vision.

Method

The same concentric gratings described in condition A of Experiment 2 were used. The static radial gratings were the same dimensions and contrast as the concentric gratings and had a radial spatial frequency of 8 cycles/rev. Following the same procedure used in the previous experiments, 5 observers tracked alternations in dominance between a static radial grating rivaling with: a static concentric grating (condition A), an expanding concentric grating (condition B), or a contracting concentric grating (condition C).

Results

The results of Experiment 3 are shown in Figure 3. The mean durations (Figure 3a) and total dominance times (Figure 3b) of the radial and concentric gratings across the three conditions were significantly different (one-way repeated measures ANOVA, mean duration $F = 5.878$, $df = 9$, $p < .05$, total time $F = 33.39$, $df = 9$, $p < .01$). When both rival

stimuli were static (condition A), the concentric grating appears to predominate slightly over the static radial grating, a point also noted by Wade and De Weert (1986). However, this tendency did not reach statistical significance as neither total time dominant across the combined 8-min observation period (Bonferroni post test contrasts; $t = 2.397$, $df = 9$, $p > .05$) nor the mean dominance duration ($t = 1.416$, $p > .05$) were significantly different between the two static gratings. However, the distance between the normalised dominance distributions was significantly different when converted into cumulative form and compared with the Kolmogorov-Smirnov test (K-S $d = 0.3$, $p < .01$, see Figure 4g).

Not surprisingly, once the concentric stimulus was set in motion (conditions B & C) the patterns of dominance changed dramatically. For expanding concentric gratings, both total dominance time (Figure 3a: $t = 10.65$, $df = 3$, $p < .01$) and mean dominance duration (Figure 3b: $t = 3.864$, $df = 3$, $p < .01$) were significantly higher than was observed for the static radial grating. Contracting concentric gratings followed a similar pattern, but only reached significance where total time is considered (Figure 3a, total dominance time: $t = 6.711$, $df = 3$, $p < .05$). No difference was found between the mean duration of the static rival and contracting grating (Figure 3b, mean dominance duration: $t = 2.408$, $df = 3$, $p > .05$). The dominance distributions for each condition are plotted in Figure 3c–e, and all were significantly different on the Kolmogorov-Smirnov distance test (A: K-S $d = 0.3$, $p < .01$; B: K-S $d = 0.53$, $p < .01$, C: K-S $d = 0.32$, $p < .01$, see Figure 4h and i).

Finally, the proportion of observation time in which piecemeal rivalry was observed was not significantly different between the conditions ($F = 0.8322$, $p > .05$), and neither did alternation rate differ between conditions ($F = 0.5619$, $p > .05$).

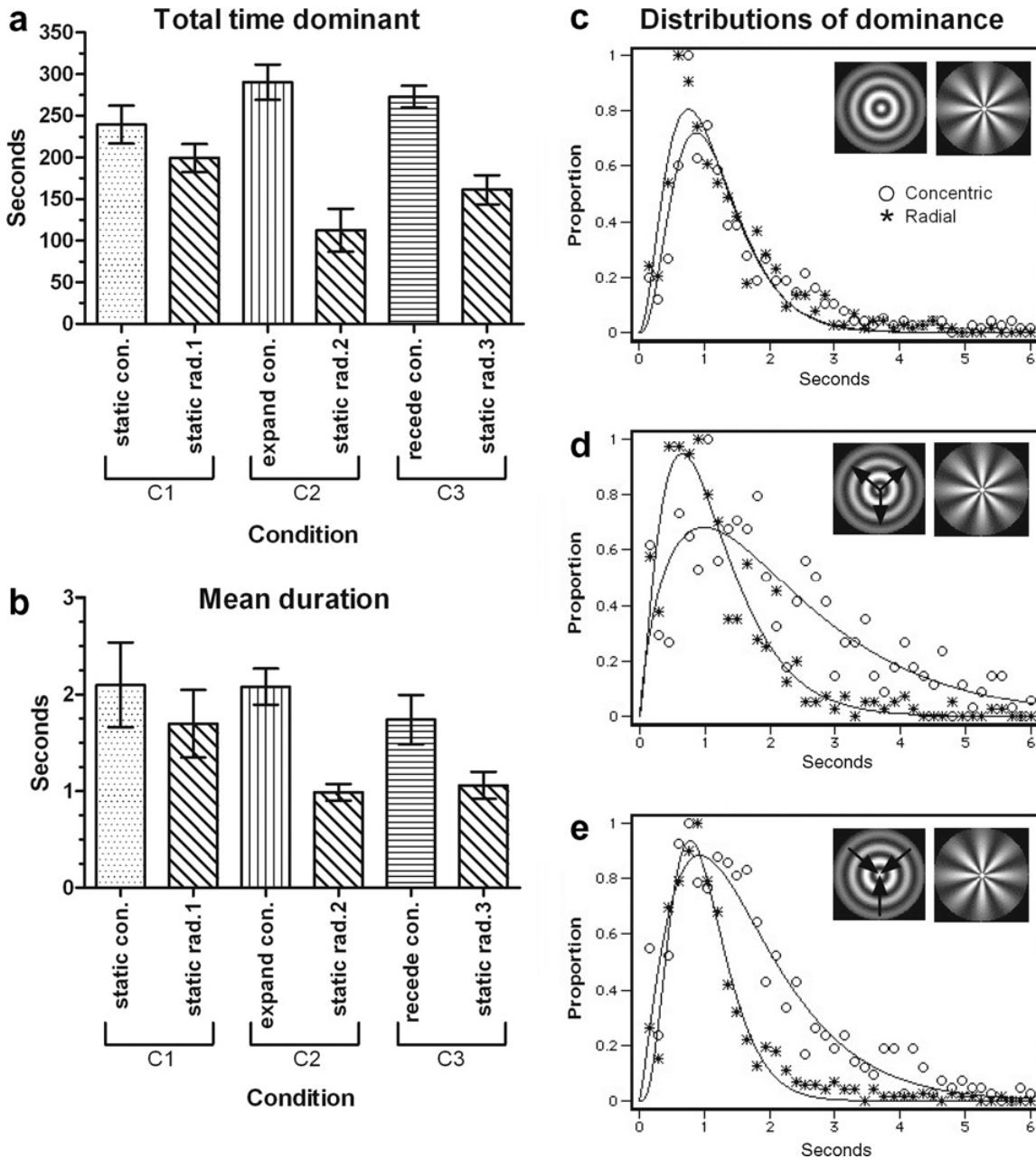
Figure 3. Results of Experiment 3

Figure 3. Results of Experiment 3. (a) The sum total of dominance durations across the observation period is shown for the three rivalry pairs examined in Experiment 3. (b) The mean dominance durations for these rival pairs. (c–e) The distributions of dominance; between the static gratings (c), expanding and static gratings (d) and contracting and static gratings (e). Adding motion appears to be the primary determinant of increased predominance when considering the sum and distribution of dominance of an image relative to a static rival. However, only the expanding grating mean duration differed significantly from its static rival.

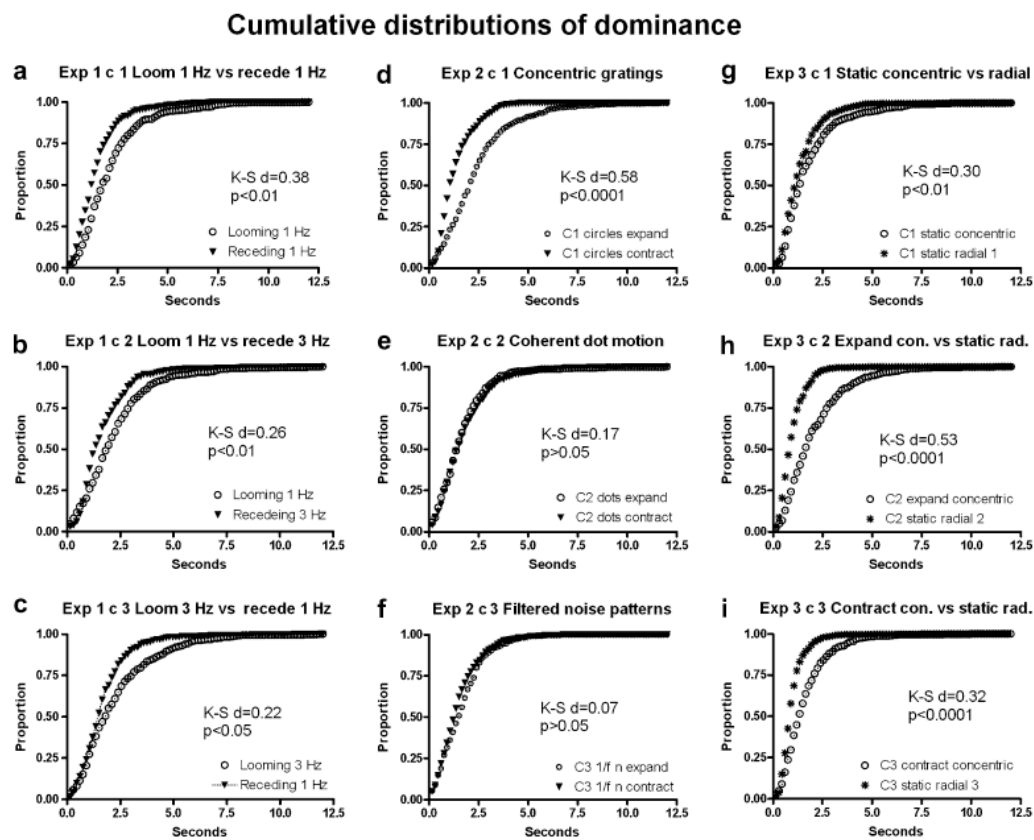
Figure 4. Cumulative distributions of perceptual dominance durations

Figure 4. Cumulative distributions of binocular rivalry dominance durations. Dominance durations are binned then plotted cumulatively. These functions are compared using the KS statistical test for cumulative distributions. (a–c) The results of Experiment 1. (d–f) The results of Experiment 2 and (g–i) the results of Experiment 3. Looming and expanding concentric gratings produce a greater proportion of longer dominance durations when paired with receding gratings. The same asynchrony occurs when motion is added to one of the rival stimuli in Experiment 3 (h and i). The d (distance between functions) statistic and corresponding p value for each rival pair is displayed in each plot.

Discussion

Adding an expanding motion component to the concentric grating decreased the total amount of time it was suppressed, as well as increasing its sum dominance compared to the static rival. In contrast, adding contracting motion did not affect the mean of the dominance nor suppression durations, but did affect the overall time the stimulus was dominant and the distribution of dominance durations relative to the static rival. These

observations are consistent with previous reports showing that when one rival stimulus is moving it tends to predominate over another static one (Blake et al., 1998; Breese, 1909; Wade & de Weert, 1986). Interestingly, these observations also show a qualitative asynchrony between two directions of motion that are otherwise equal in strength.

The most intuitive interpretation of the general predominance of motion is that by adding motion to one of the stimuli, we add a non-contested dimension to one of the rival stimuli that therefore confers an advantage on it. That is, from the point of view that binocular rivalry is mutually suppressive competition between low-level inputs, adding motion to one stimulus may boost its predominance because there is no competing motion in the other stimulus. In other dimensions, the two rival stimuli would compete on more or less an equal footing in terms of contrast, contour density, mean luminance, etc. However, adding motion to one of the stimuli, whether expansion or contraction, would give a competitive advantage to the motion stimulus because its motion dimension would not be subject to inhibition from the other competing stimulus.

At the simplest level the predominance of moving rival stimuli over static ones may be due to a reduction in contrast adaptation early in the visual system. Locally, the moving stimulus produces a continuous oscillation of contrast levels, which will effectively reduce contrast adaptation. For the static stimulus, there is a constant input which will inevitably lead to contrast adaptation. This is significant because models based on mutual inhibition between inputs all predict that as one channel adapts it weakens its suppressive influence on the other channel which ultimately leads to a switch in dominance (Blake, 1989; Wilson, 2003). If a moving stimulus resists contrast adaptation, but not the static stimulus, it will exert a stronger suppression over its rival.

Consistent with the preceding experiments, the effect of expansion was stronger than for contraction, with the increase in mean dominance duration over the static rival being significant for expansion, but not for contraction. This asynchrony may be due to an enhanced neural response to expanding motion, as indicated in monkey (areaMSTd) physiology (Graziano et al., 1994) and human behavioural data on the motion after effect

(MAE) (Berman & Colby, 2002). The Berman and Colby study found that no MAE was perceptible when a contracting concentric grating was adapted. Other findings support the idea of specialised processing of expansion; for example that neural populations of the superior temporal sulcus (STS) preferentially respond to looming visual stimuli (Maier, Neuhoff, Logothetis, & Ghazanfar, 2004) and that human observers are biased to perceiving approaching motion in a three-dimensional apparent motion task (Lewis & McBeath, 2004). An asynchrony between expansion and contraction is not completely surprising given that the majority of our experience of optic flow arises because of forward motion and the likely consequence of this during development would be a greater neural response to process this direction.

A second factor that may lie behind the increased predominance of the expanding motion stimulus is attention. Attention to one rival stimulus makes it less likely to become suppressed (Ooi & He, 1999) and alternation rates can be altered by attention (Lack, 1978). Although the effects of attention in determining predominance of a stimulus are relatively modest in binocular rivalry compared to other bistable contexts (Meng & Tong, 2004), moving objects are salient targets that can engage attention automatically, and in the absence of other stimuli of interest may continue to engage attention. Therefore, the finding that expansion is to an extent more effective than contracting motion may indicate that attention, rather than simply the strength of the motion signals, is determining its comparably elevated predominance.

Experiment 4: Flash suppression between expansion and contraction, and moving and static stimuli

Experiment 4 uses ‘flash suppression’ in an attempt to quantify more precisely the relative strength of the two moving concentric grating stimuli used in condition A of Experiment 2. Flash suppression (Wolfe, 1984) is a brief variant of binocular conflict in which one eye’s image is presented before the other for a short lead time. After this monocular lead period - or stimulus onset asynchrony (SOA) - a second rival image is presented to the other eye. The typical result, given a lead time of a second or so before the dichoptic phase begins, is the instant suppression of the lead stimulus. There are at

least two advantages of flash suppression. The first is that it can be used to determine the initial phase of binocular rivalry, without employing the attentional strategies of Mitchell et al. (2004) and Chong and Blake (2006). Second, the likelihood of a perceptual switch to the later stimulus can be measured as a function of lead time to compute a psychometric function, which is otherwise difficult in traditional binocular rivalry. In Experiment 4, we measure the threshold SOA required for a perceptual switch from the lead stimulus to the second stimulus, and we do this for different pairs of rival stimuli to clarify the biases found in the preceding rivalry experiments.

Method

The stimuli were exactly the same as used above in Experiment 2 condition 1, (the linearly expanding and contracting concentric gratings) and the static radial gratings used in Experiment 3. Only the paradigm (i.e., flash suppression) was different in Experiment 4. Four observers participated (both authors, 2 naïve). All subjects had normal or corrected-to-normal visual acuity. The two naïve observers were experienced in perceptual observation and did not participate in any of the previous experiments.

Condition 1: Flash suppression between expanding and contracting gratings

Either an expanding or a contracting concentric grating was used as the lead stimulus. Linear expansions and contractions were used to ensure a consistent speed in the lead stimulus regardless of the moment at which the second ‘flash’ stimulus was delivered. The average latency required for complete flash suppression to occur was measured across a minimum of 75 trials using the QUEST adaptive staircase procedure (Watson & Pelli, 1983) for each of the two possible stimulus presentation orders (expanding lead with contracting flash, and contracting lead with expanding flash). Before each trial, subjects binocularly fused two black circular apertures presented on each side of the monitor. Upon initiating a trial by key press, the lead stimulus was presented to one of the eyes. The other eye remained exposed to the binocularly presented circular aperture filled with the mean background luminance. After a variable period of time determined by the staircase procedure, the flash stimulus was presented to this eye. After the second eye received the flash, both moving gratings remained on the screen for a further 500 ms after

which the screen returned to uniform grey. Subjects were then required to judge whether the swap to the flashed stimulus was complete or not by pressing one of two keys on the keyboard. The criterion for a complete swap was determined to be when the flashed motion instantly and completely suppressed the lead motion. If the dominance of the flash stimulus occurred nearer to the removal of both stimuli at the end of a trial, subjects were able to discern this alternation from instantaneous suppression and report it as an incomplete swap. After the subject's response the empty black apertures reappeared for the next trial. The eye given the lead stimulus was alternated on each trial to counter any effects of eye dominance and adaptation, as was done in Experiments 1, 2 and 3.

Condition 2: Flash suppression between static and contracting gratings

The same method as condition 1 except that contracting concentric gratings were paired with static radial gratings.

Condition 3: Flash suppression between static and expanding gratings

Again, the same method as condition 1 is used except now expanding concentric gratings were paired with static radial gratings.

Results and discussion

Results for the expanding vs. contracting and moving vs. stationary data are shown in Figure 5. Figure 5a-c shows the raw data plotted as the likelihood of complete suppression (expressed as a percentage) as a function of a particular lead time for each subject across the three conditions shown in Figure 5 (5a: C1, 5b: C2 and 5c: C3). From these psychometric functions, we defined the lead time corresponding to 75% probability of a switch to the flashed stimulus as the 'critical switch duration'. The average of these 'critical switch durations' are graphed in Figure 5d-f. Figure 5d shows how flash suppression latencies vary according to the type of lead stimulus (stationary radial grating, expanding concentric grating, or contracting concentric grating) with data pooled across all the conditions employing that stimulus as a lead. Stationary lead stimuli required very short lead periods to be suppressed by either expanding or contracting motion in contrast

to moving leads which required much longer lead times before being suppressed by stationary or other moving stimuli. When the flash stimuli are plotted in the same fashion (Figure 5e) a complementary pattern emerges whereby moving flash stimuli more readily suppress a lead than stationary stimuli. The average critical switch duration for each stimulus alone and for each condition are shown in Figure 5f.

Figure 5. Flash suppression thresholds

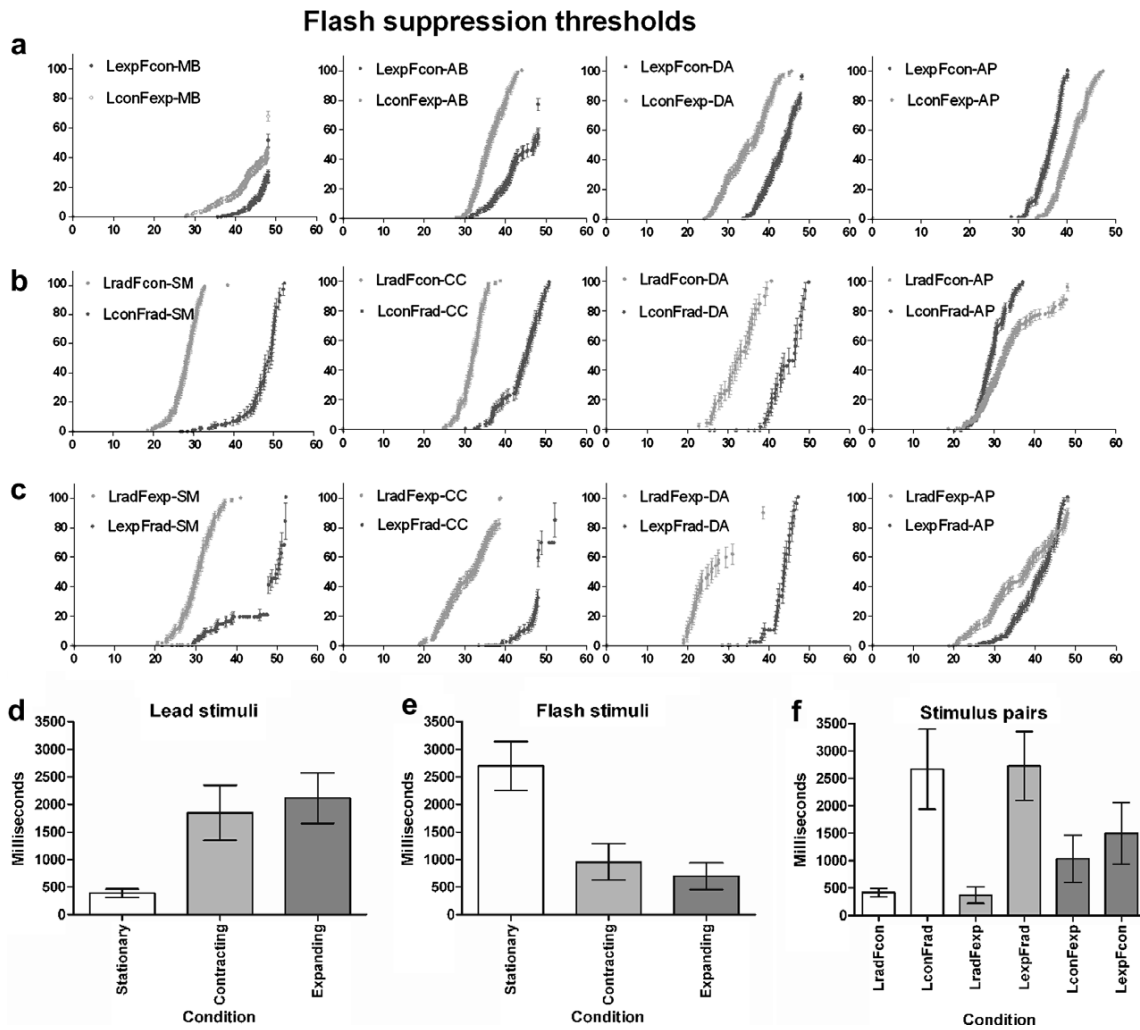


Figure 5. Flash suppression thresholds. (a–c) Threshold probabilities for complete flash suppression (FS) expressed as a percentage. The x-axis shows lead time in number of refresh frames (each 11.76 ms at 85 Hz vertical refresh rate) in decibel scale. Moving stimuli require longer lead times in order to be suppressed by static rivals. Mean SOA's required for FS are shown in parts d, e and f.

For condition 1 (expansion vs. contraction), all but one subject needed significantly less lead time to effect a complete perceptual switch when the lead stimulus was a contracting grating and the flashed stimulus an expanding grating (Figure 5a). The mean critical switch duration for expanding leads was 1.5 s in condition 1 (Figure 5f, dark gray bars), about one third longer than that required to produce a perceptual switch for contracting lead stimuli (1 s). This difference however was not statistically significant ($t = 1.382$, $p > .05$. One-tailed paired t-test).

Data for the static radial grating pitted against a contracting (white bars) or expanding (gray bars) concentric grating are shown in Figure 5f which plots mean critical switch durations for four observers. A clear trend for moving lead gratings to resist suppression can be seen for both the contracting ($t = 3.144$, $p < .05$) and expanding directions ($t = 3.359$, $p < .05$). The absence of any direction specific effect when each direction is paired with a static radial grating may be attributable to the transients associated with the onset of the ‘flash’ stimulus. Transients in the suppressed stimulus are highly salient at promoting the suppressed stimulus into dominance in binocular rivalry (Walker & Powell, 1979) and it may well be that the transients associated with the flash are strong enough to promote a switch regardless of whether the lead stimulus is an expansion or contraction. In regular rivalry, by contrast, these transients are not present and the expansion bias emerges. Also, flash suppression itself is dependent upon stimulus onsets, the presence of motion, regardless of direction appears to have the most influence over its time scale.

Discussion

Overall, the mean of the critical switch durations for the two ‘motion lead’ thresholds (contracting 1.8 seconds and expanding 2.1 seconds, Figure 5d) are more than four times greater than the mean of the static lead conditions (0.39 seconds). The longer threshold lead times for moving stimuli mean that motion stimuli better resist a perceptual switch to the new flashed static stimuli. Static lead stimuli, on the other hand, will readily switch to a new flashed motion stimulus after only half-a-second of lead time. Likewise, moving flash stimuli more readily suppress lead stimuli (Figure 5e). This points to the general

salience of moving stimuli over static stimuli, which has been previously well established in regular binocular rivalry (Blake et al., 1998; Breese, 1909; Wade & de Weert, 1986). We can now conclude that the salience of motion over static stimuli holds equally well in the context of flash suppression. The role of the lead time in the flash suppression paradigm is presumably to adapt those neurons responsive to the lead stimulus, making a switch to the second stimulus more likely when it is presented, similar to the role of adaptation postulated in models of binocular rivalry (Freeman, 2005; Wilson, 2003). Moving stimuli resist this adaptation resulting in longer critical switch durations.

Turning to the comparison of expanding and contracting stimuli, we note that the lead time for the contracting stimulus to suppress an expanding lead was not significantly longer than that for the reversed stimulus order although a trend in this direction emerged. The difference between this result and the predominance of expansion found in the previous experiments is probably due to the increased sensitivity of the flash suppression paradigm to visual transients compared to regular binocular rivalry. Flash suppression is dependent upon a transient event, a lead or flash stimulus high in transients, such as moving gratings, can either interfere (as lead) or enhance (as flash) this process, irrespective of direction.

General discussion

The preceding experiments investigated the behaviour of expanding versus contracting stimuli, and moving versus stationary stimuli, in binocular rivalry and in flash suppression. The two main findings are that there is a consistent bias to favour expansion over contraction, and that moving stimuli strongly resist suppression in the paradigm of flash suppression, just as they are known to do in conventional binocular rivalry. Both of these observations can be understood within current accounts of binocular rivalry and known properties of visual motion-sensitive neurons and attentional factors.

A bias in favour of expansion was documented for binocular rivalry in Experiments 1, 2 and 3. This bias did not depend on whether the motions expanded linearly, or nonlinearly in an accelerating fashion as they would during typical optic flow. Interestingly, in

Experiment 2, we found that the expansion bias for dominance did not occur with the two stimuli with random spatial structure; the random-dot motion and the filtered visual noise. Only the stimulus that was both expanding and had spatially coherent contours showed the expansion bias. We suggest this is probably due to object processing and attentional factors. The expanding random dots and filtered-noise stimuli created percepts of surfaces undergoing expansion within a fronto-parallel plane, but not of approaching or looming objects. Only when there was a coherent size change (as in the expanding concentric gratings) did an impression of looming and expanding objects arise. For this reason we favour an interpretation in terms of attention to a visual object, since it is known that looming objects are salient for grabbing attention in a stimulus-driven manner. When a looming object is perceived, attentional orienting to the exact location and trajectory of this object becomes of primary importance and may activate preparatory or defensive movements mediated by a subcortical network involving the superior colliculus and amygdala or by a cortical network involving the ventral intraparietal area and a polysensory zone in the precentral gyrus (Graziano & Cooke, 2006).

We believe the predominance bias in favour of expansion is not likely to be explained by early motion-sensitive neurons. Early cortical neurons respond to local features, and locally, the expanding and contracting motions in each eye were equal in magnitude but simply opposite in direction. In terms of global stimulus properties, it is known that global motions such as expansions are processed by neurons beyond primary visual cortex, for example in MST and STS (Duffy & Wurtz, 1991; Maier et al., 2004). Therefore, if rivalry is an early process, then any bias for global expansion must be the result of feedback from extrastriate areas signalling looming motion and/or visual objects on a collision path with the observer. Such feedback would presumably coordinate early and local binocular rivalry processes into a globally coherent ensemble.

Another factor that may lie behind the increased dominance of the motion stimulus is attention. Moving objects are salient targets that can engage attention automatically, and in the absence of other stimuli of interest may continue to engage attention. Attention toward or away from both rival stimuli produces variance in alternation rates (Lack,

1978; Paffen et al., 2006) and attention to one stimulus has been shown to boost its predominance in rivalry (Lack, 1978; Ooi & He, 1999), although the effects are relatively modest in binocular rivalry compared to other bistable contexts (Meng & Tong, 2004). As noted before, attention is known to boost the response of neurons in the early part of the visual system that represent an attended feature (Alais & Blake, 1999; O'Craven, Rosen, Kwong, Treisman, & Savoy, 1997; Somers, Dale, Seiffert, & Tootell, 1999), particularly for basic attributes such as orientation and motion (McAdams & Maunsell, 1999; Treue & Martinez-Trujillo, 1999; Treue & Maunsell, 1996). Thus attended rival stimuli are expected to be more resilient to suppression from unattended stimuli as they will be higher in effective contrast and therefore stimulus strength.

There is also reason to suspect that the looming motion may retain some salience even when suppressed. It has been shown in an fMRI study that a fearful face undergoing a period of rivalry suppression still produces a response in the amygdala (Pasley, Mayes, & Schultz, 2004) despite not being in perceptual awareness, indicating that this subcortical mechanism still has access to suppressed stimuli. This does not occur for neutral expressions, perhaps because fearful faces are indicative of impending danger. It is worthwhile considering that the looming objects are also salient for attention and may too indicate impending danger and therefore activate alternative pathways to consciousness such as via the amygdala. This suggestion could be easily tested in an fMRI study. Interestingly, the visual pathway to the amygdala is via the superior colliculus where neurons respond to looming movement in all modalities. Therefore, the presence of a perceptually suppressed 'looming' object could still be present via this subcortical loop, and from there be fed into the visual areas which presumably underlie the rivalry suppression process. This additional source of looming response could potentially boost the total response to the looming stimulus when it is dominant, causing the increased predominance noted in Experiment 1, and curtailing suppression phases for looming stimuli.

In conclusion, these experiments have demonstrated a robust tendency for expanding and looming contours to predominate over receding ones during binocular rivalry. This

occurs despite the fact the two motions are equal in motion energy and differ only in direction. We suggest that the inhibitory interactions that are essential to rivalry probably occur early in visual processing (Alais & Melcher, 2007; Blake, 1989; Tong & Engel, 2001) and that subsequent neural processes such as attention and global motion processing feedback to influence and coordinate these early rivalry processes.

Chapter summary

The experiments presented in this chapter clearly show a bias for looming motion during binocular rivalry. The predominance of the looming motion suggests that binocular rivalry may be related to mechanisms governing exogenous attention. Although a stronger neural representation of expanding motions can explain the results, it is also possible that attentively salient stimuli are represented more strongly in visual cortical areas. That stimulus driven attention yields a stronger influence over binocular rivalry dominance than endogenous, or purposeful, attention might, supports the idea that perceptual bistability is achieved by an unconscious process of perceptual selection. Although it cannot be concluded that this is the same process that mediates exogenous perceptual selection in normal viewing, it is strongly suggestive of that possibility.

Chapter 4

Multisensory congruency as a mechanism for attentional control over perceptual selection

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Overview

The following experiments explore whether sounds and tactile stimuli congruent with one or the other rival stimulus can enhance that stimuli's dominance duration during binocular rivalry. The experiments show that temporally congruent sound and tactile stimuli can further enhance the predominance of looming motion during binocular rivalry that was reported in Chapter 3, but only when subjects are actively attending to the cross-modal pairing. Facilitation of wilful control with sound and touch significantly exceeds the effect of wilful control without cross-modal input. These findings suggest that cross-modal stimulation facilitates processes involved in perceptual awareness and selection. The following experiments clearly demonstrate sensory neural processing that is extraneous to the site of binocular rivalry competition can modulate perceptual bistability.

Abstract

The neural mechanisms underlying attentional selection of competing neural signals for awareness remains an unresolved issue. We studied attentional selection, using perceptually ambiguous stimuli in a novel multisensory paradigm that combined competing auditory and competing visual stimuli. We demonstrate that the ability to select, and attentively hold, one of the competing alternatives in either sensory modality is greatly enhanced when there is a matching cross-modal stimulus. Intriguingly, this multimodal enhancement of attentional selection seems to require a conscious act of attention, as passively experiencing the multisensory stimuli did not enhance control over the stimulus. We also demonstrate that congruent auditory or tactile information, and combined auditory-tactile information, aids attentional control over competing visual

stimuli and visa versa. Our data suggest a functional role for recently found neurons that combine voluntarily initiated attentional functions across sensory modalities. We argue that these units provide a mechanism for structuring multisensory inputs that are then used to selectively modulate early (unimodal) cortical processing, boosting the gain of task-relevant features for willful control over perceptual awareness.

Introduction

Although lower organisms possess a direct coupling between sensory input and behavioral output, humans are able to intervene during this sequence and influence their output (Gilbert and Sigman, 2007), not only with respect to our motor actions but, intriguingly, also for our awareness. Although we are still learning about the precise mechanisms of this voluntary control and its necessary and sufficient conditions, we do know that it operates in a top-down manner through attention. For visual stimuli there is mounting evidence (Reynolds and Chelazzi, 2004) that attention to features and spatial locations can influence neural activity at early levels of cortical processing. It is unclear, however, how attention influences perceptual selection when multisensory signals are involved. A promising way to study awareness and voluntary attentional control over perception is to expose the sensory system to an ambiguous stimulus that generates bistable perception. This provides the opportunity to study multisensory processing related to the percepts rather than to the stimulus (Leopold and Logothetis, 1999; Blake and Logothetis, 2002; Tong, 2003).

Here, we used perceptually ambiguous stimuli in a novel multimodal paradigm that combined competing auditory stimuli and competing visual stimuli. We studied whether multisensory congruency facilitates voluntary control over perceptual selection, reasoning that this would open a novel window on multisensory aspects of perceptual control and shed light on the level at which it occurs. For unisensory stimuli, quite a few reports have shown a role for attention in voluntarily selecting one perceptual interpretation in perceptually bistable stimuli. These have shown that observers can lengthen the duration that the selected percept is dominant, but they cannot exert full control over the selection process and spontaneous perceptual alternations still occur (Lack, 1978; Meng and Tong,

2004; van Ee et al., 2005). Very recently, a degree of unisensory attentional control has also been demonstrated over ambiguous stimuli in the auditory domain (Pressnitzer and Hupé, 2006). Different senses interact with each other, and it is known from audiovisual experiments that a stimulus in one modality can change perception in the other (Sekuler et al., 1997; Shimojo and Shams, 2001; Alais and Burr, 2004; Witten and Knudsen, 2005; Ichikawa and Masakura, 2006). We combine these findings to study attentional control over perceptually ambiguous stimuli in a multisensory context, focusing on the role of cross-modal congruency. Congruency may facilitate multimodal mechanisms of voluntary control, since there is more support for one of the two competing percepts when there is information from another sensory modality that is congruent with it.

Many neurons in human posterior parietal and superior prefrontal cortices are involved in voluntary attentional shifts between vision and audition (Shomstein and Yantis, 2004), and attention to audiovisual feature combinations produces stronger activity in the superior temporal cortices than does attention to only auditory or visual features (Degerman et al., 2007). It has also been shown that the auditory cortex can be profoundly engaged in processing nonauditory signals, particularly when those signals are being attended (for review, see Shinn-Cunningham, 2008). What is the role of these multimodal attention-modulated neurons? None of the existing studies used competing cross-modal stimuli.

We studied whether the ability to voluntarily select one interpretation from an ambiguous visual or auditory stimulus would be enhanced when it was combined with auditory, visual, tactile, or auditory-tactile information that was congruent with that interpretation.

Materials and method

We presented subjects with a binocular rivalry (Levelt, 1965) stimulus consisting of a looming concentric pattern in one eye and a rotating radial pattern in the other eye (Figure 1a) and a pair of auditory stimuli consisting of a looming sound and a spatially separated stationary tone triad (Figure 1b). The auditory stimuli were binaurally presented over headphones (Pressnitzer and Hupé, 2006; Bidet-Caulet et al., 2007). The

looming stimuli were rate matched (same frequency) in both the visual and auditory modalities. The rotating radial pattern was chosen to rival with the looming visual pattern, because it is orthogonal to the concentric looming stimulus and is symmetrical so that small eye movements in any direction would not unduly favor the visibility of one pattern over the other (Wade and de Weert, 1986; Parker and Alais, 2007). We deliberately designed the rotation rate to be different from the looming sound rate so that their changes over time did not match. Following previous attentional studies of unisensory ambiguous perception, we examined voluntary control over visual rivalry by comparing “active” and “passive” conditions (Helmholtz, 1866; Lack, 1978; Peterson and Hochberg, 1983; Leopold and Logothetis, 1999; Suzuki and Peterson, 2000; Hol et al., 2003; Toppino, 2003; Meng and Tong, 2004; Chong et al., 2005; Slotnick and Yantis, 2005; van Ee et al., 2005, 2006; Brouwer and van Ee, 2006; Chong and Blake, 2006; Hancock and Andrews, 2007). In the passive condition, no attentional control was exerted in favor of either visual pattern. There were two types of active condition. In one, observers were instructed to “hold” the visual looming pattern dominant, and in the other they were instructed to hold the visual radial pattern. All three conditions were tested with and without the sound stimuli present, amounting to six conditions in total.

Visual stimuli

The competing binocular rivalry stimuli were a rotating radial sine wave pattern in one eye and a concentric sine wave pattern looming at 1 Hz in the other (Wade and de Weert, 1986; Parker and Alais, 2007). The visual stimuli had a mean luminance of 30 cd/m², a contrast of 25%, and were presented in a Gaussian envelope (SD 0.6°) (Figure 1a). The radial pattern consisted of seven cycles (propeller blades), rotating at 30.7°/s, producing a repetition frequency of 0.6 Hz at each visual location. The looming pattern had a spatial frequency of 3 c/degree, its motion being induced by a phase-shift that increased exponentially over a 1 s period from a baseline of 1 c/s to a maximum of 4 c/s, after which the increase was rapidly tapered off by a cosine profile. Continuous looming motion was created by repeating these profiles in a loop with 1Hz so that it matched the looming sound rate and mismatched the rotation of the radial pattern. The stimuli were presented one on either side of a cathode ray tube monitor and viewed through a mirror

stereoscope (viewing distance, 57 cm) to produce binocular rivalry. Stimuli were presented on a black square of 5.5° , with a white border; the rest of the screen had a luminance of 30 cd/m².

The visual stimulus used to disambiguate the ambiguous sound (Experiment 6) consisted of a white flickering disk (diameter, 7.5° ; viewing distance, 57 cm) with a static frame around it. The disk flickered with on and off periods of 120 ms, equating the presentation sequence of the low tone in the ambiguous auditory stimulus.

Auditory stimuli

We used headphones to present competing stationary and looming sounds, meaning that attention needed to be used to follow the looming sound. The stationary sound was a constant, unmodulated tone triad (an “E major” chord) (Figure 1b), with maximum amplitude of 76 dB sound pressure level (SPL) on average. The competing tone triad was present in all experiments in which we used competing sound to resolve ambiguity in the visual domain (thus, in all experiments, except in Experiment 6). The looming sound was produced by modulating the amplitude of a pure tone (200 Hz) incremented from an amplitude of zero to a maximum amplitude designated by each subject to be comfortable (average, 74 dB SPL). The amplitude envelope had a profile identical to the phase-shift profile of the visual stimulus (1 Hz in Experiment 1 (Figure 1b); note that it was different, 0.82 Hz in Experiment 2 (Figure 1c)) and was precisely phase synchronous with the carrier sinusoid (200 Hz) to prevent readily detectable anomalies. To assign different spatial directions to the two sounds, they were both presented binaurally, with the looming sound having an interaural time difference of 200 μ s so that it was heard to originate from a location 20° to the right (with respect to straight ahead) and the constant tone triad having an opposite phase difference of 200 μ s so that it was heard to originate from a location 20° to the left. The “tone pips” that we presented in Experiment 3 had a frequency of 1 Hz (i.e., at the visual looming frequency) (Figure 1d), a duration of 280 ms, and an average maximum amplitude of 76 dB SPL.

In the experiment where we examined whether a visual stimulus can disambiguate an ambiguous sound stream (Experiment 6), we followed a recent study on attentional control over auditory ambiguity (Pressnitzer and Hupé, 2006). We presented a high-frequency pure tone H alternating with a low-frequency pure tone L, in an LHL_ pattern (van Noorden, 1975). The frequency of H was 587 Hz and that of L was 440 Hz. The duration of each tone was 120 ms. The silence “_” that completed the LHL_ pattern was also 120 ms long. The sequence is perceived either as one stream (LHL-LHL, i.e., grouped galloping rhythm) or as two streams (H-H-H-H and -L—L-, i.e., segregated Morse tones). The loudness of the tones was adjusted to a comfortable level (on average 75 dB SPL), which was kept constant during the experiment.

Figure 1. Speed profiles of the binocular rivalry and sound stimuli

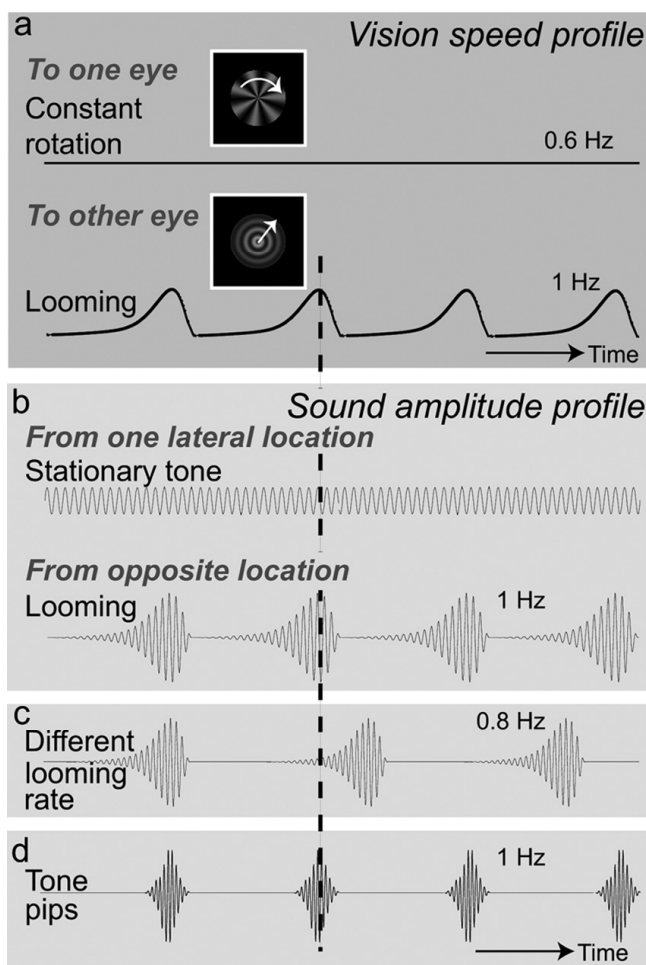


Figure 1. A) The vision speed profiles. The binocularly rivaling visual images consisted of a constantly rotating radial pattern and a looming concentric circle pattern. We deliberately designed the rotation rate (0.6 Hz) to be different from the looming rate (1 Hz) so that their changes over time did not match. B) The sound amplitude profiles. The two sounds that competed for attention consisted of a stationary tone triad (E chord) and a 1 Hz looming sound coming from opposite lateral locations (20 and 20° relative to straight ahead). Auditory and visual looming were rate matched and in phase (dashed vertical line). C) To examine whether it is either looming as such, or its rate, that caused the multimodal attentional control effects of the looming sound, we presented the looming sound with 0.8 Hz. D) To examine the role of sound rate, we presented tone pips with the same frequency (1 Hz) and phase as the looming visual pattern. Ramp and damp times were equal.

Tactile stimuli

To produce stationary and looming tactile stimuli, we detached a loudspeaker from its sound box (commercially available Logitech R-10 computer speakers). The vibrating speaker membrane was lightly attached to the skin of the dorsal side of the left hand by an elastic band (supplemental Figure 6a, Appendix 3). The hand was placed on the left knee underneath the stereoscope. By playing the looming sound exactly the same as in the basic experiment, the observer felt a “looming” pattern (although this was perceived as increasing pressure) that was matched to the visual looming pattern. In the no-sound conditions, observers wore earmuffs so that the sound of the vibrating membrane on the hand was not heard.

Procedure

Subjects were instructed to maintain fixation on the center of the visual pattern which is easily possible for a monocular looming pattern with a fixed reference around it and with the small size used at the distance presented (Erkelens and Regan, 1986). They pressed one of two keys when the visual looming stimulus was dominant and the other when the radial pattern was dominant. They were instructed to release both keys during instances of superimposed and piecemeal pattern perception (which averaged 13.7%), where neither pattern was exclusively dominant. We consistently compared passive and active conditions. In the passive condition, no attentional control was exerted. In one of the active attention conditions, observers were instructed to hold the visual looming pattern; in the other, observers were instructed to hold the visual radial pattern. Stimulus presentation series lasted 2 min. Between series, the stimuli were counterbalanced between the eyes, comprising sessions of 4 min per condition. All three conditions were tested with and without the sound stimuli present, amounting to six conditions in total and a duration of 24 min per experiment. Six subjects did three 24 min experiments. We established that there was no clear dependence on order and that fluctuations in mean predominance between repeated sessions were such that it was sufficient to ask the other subjects to do only one 4 min session per condition. We discarded the first 30 s of each series list for data analysis to ensure rivalry alternations had stabilized.

In the experiment where we examined whether a visual stimulus can disambiguate an ambiguous sound stream (Experiment 6), the procedure was very similar. The experiment, again lasting 24 min, consisted of three 4 min sound-only and three 4 min sound plus vision sessions. In addition to the passive baseline condition, observers were instructed to hold the grouped sound (galloping) or the segregated sound stream (high and low Morse tones). The stimuli were presented using four 1 min series per condition. In the no-vision conditions, a small marker was fixated. In the vision conditions, subjects fixated the center of the flickering disk.

In the experiment where we examined the role of congruent tactile “looming” (Experiment 7), we compared the attentional gains for the sound-only, the tactile-only, and the tactile plus sound conditions. Observers were instructed to hold the visual looming pattern or to passively view the stimuli. Stimulus presentation sessions lasted again 4 min consisting of two 2 min series with stimuli counterbalanced between the eyes. Informed written consent was obtained after the nature and possible consequences of the study were explained.

Results

Experiment 1: Quantifying the influence of sound on attentional control

We first determined the baseline level of attentional control in unimodal, vision-only conditions by comparing hold versus passive conditions. Subjects ($n = 22$; 14 male, 8 female) tracked perceptual alternations in binocular rivalry. The mean perceptual durations for the looming visual pattern and the radial visual pattern (Figure 2) are lengthened in the hold relative to the passive conditions (from 2.6 ± 0.2 s to 3.6 ± 0.3 s for looming, and from 2.3 ± 0.2 s to 3.0 ± 0.3 s for radial patterns, both $p < 0.001$, paired t-test), replicating previous work (Lack, 1978; Toppino, 2003; Meng and Tong, 2004; Chong et al., 2005; Slotnick and Yantis, 2005; van Ee et al., 2005). In total, superimposed or piecemeal pattern perception averaged 13.7% of the observation period. Further details of the influence of attentional control over perception in unimodal conditions are presented in supplemental Results (supplemental Figure 1; supplemental text, Appendix 3).

Interestingly, in the sound present conditions, the data suggest that the presence of an attended and matched sound enhances a subject's ability to select and hold a looming visual pattern (4.5 vs 3.6 s, in sound and no-sound conditions, respectively) (Figure 2) but slightly impairs their ability to select and hold an unmatched (radial) visual pattern (2.9 vs 3.0 s). To quantify this multimodal attentional effect, we calculated the increase in perceptual duration for the hold task relative to the passive task and compared these values between sound-present condition and the no-sound condition. We defined the gain of multimodal attentional control as “hold-dependent increase in sound condition”/“hold-dependent increase in no-sound condition.” These gains implicitly normalize differences in attentional control across subjects and isolate the multimodal aspects of attentional control. They are plotted in rank order for all subjects in supplemental Figure 1b, in Appendix 3.

For the hold-looming condition, the mean multimodal attentional gain amounted to 29.35.8% ($p < 0.001$, t-test) (Figure 3a), indicating that subjects were more successful in holding the visual looming pattern when the matched looming sound was present than when it was absent. (Alternatively, this gain can be denoted as a ratio of 1.293; we will use the ratio and percentage notations interchangeably for ease of discussion. Since the metric for the statistic analysis is a linear transformation of the ratio used to denote multimodal attentional gain, it has no bearing on the results.) The same attention-related change in perceptual duration was calculated for the rotating radial pattern. The effect of voluntarily holding the visual radial pattern with the unmatched looming sound present was on average 3.83.8% (Figure 3a), indicating that the presence of the looming sound decreased the ability to attentionally hold the radial visual pattern, although not significantly ($p > 0.3$, t-test) (supplemental Figure 1b, Appendix 3). The attentional gains for the looming and radial patterns were uncorrelated (supplemental Figure 1c, Appendix 3) (linear regression: $r = -0.055$, $p = 0.29$). This suggests that response bias did not cause the pattern of results, as there is no reason for the subject to assume that sound would facilitate holding the looming pattern but not the radial pattern. Results from the next experiment also add evidence against response bias.

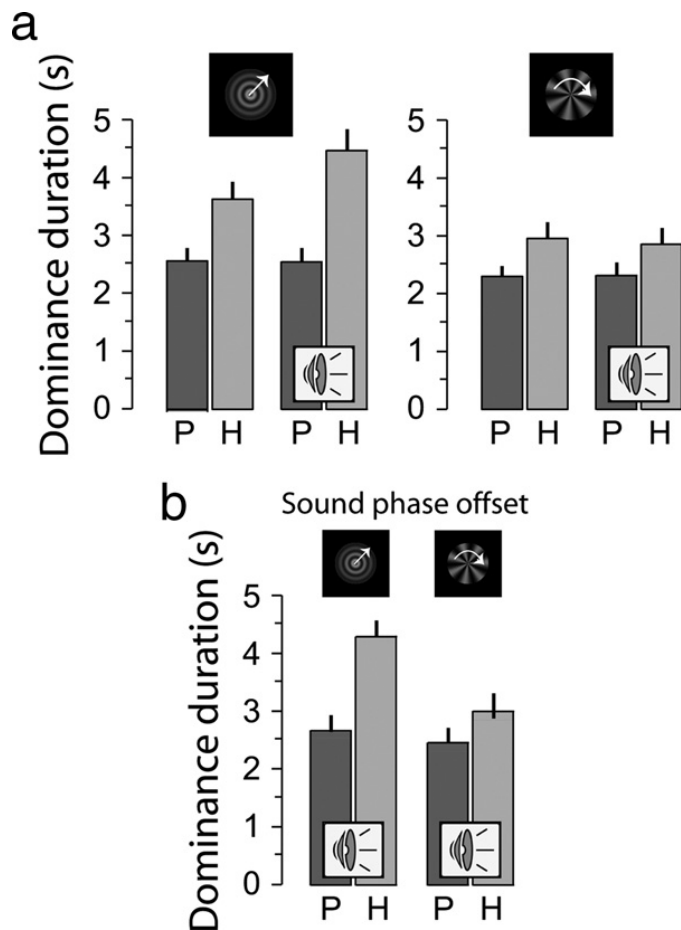
Figure 2. Average durations of perceptual dominance

Figure 2. a, The mean duration for the looming (left) and the radial (right) visual patterns. Subjects were able to hold (light gray bars) the looming pattern for the no-sound condition (relative to the dark passive bar) and even more so with looming sound present (for right pair denoted with “speaker icons”). Error bars denote 1 SE. **b**, To test for the influence of a phase offset, five observers (the ones who participated in all 7 experiments) repeated experiment 1 but now with a sustained phase offset (a quarter of a period) of the sound stimulus relative to the visual stimulus. The data are essentially the same, as we found without phase offset.

It is worth noting that on average we did not find an influence of sound on mean percept durations for passive viewing. It has, nevertheless, been reported that concurrently presented looming sounds can increase perceptual dominance of a looming image in binocular rivalry even in passive viewing (Alais and Parker, 2006). However, this 2006 study was different in two ways: First, it did not include a comparison between attention and no-attention conditions. Including a passive “no-attention” condition in the current experiments may have mitigated the effect of involuntary automatic attention. Second, the previous report involved only a single auditory stimulus (a looming sound), whereas our study involved a looming sound and a second competing sound in the form of a constant tone triad. Even though the looming sound was clearly audible over the tone triad, it is possible that the requirement of attention for the cross-modal effect only applies when the critical sound is accompanied by a competing sound. That is, in cases

where there are competing auditory stimuli, selectively attending to the relevant sound may be necessary. The absence of a competing stimulus could then explain why Parker and Alais (2006) got their cross-modal effect in the passive condition. Therefore, in all the following experiments, we present competing information in each of the sensory modalities. This, in turn, enables us to study multisensory processing related to the attentively selected percepts.

In sum, congruent sound aids attentional control over visual ambiguity. In this experiment, we started with a high level of congruency between auditory and visual information. In the next experiments, we systematically manipulate the congruency to determine the importance of aspects of congruency for multimodal attentional control. Our experiments capitalize on congruence in frequency (rhythm). Pilot experiments indicated that changing the phase (offset in time) of the sound relative to the visual pattern did not significantly affect the influence of sound. As experimenters, we noted during the programming of our stimuli that without objective measures it was hard to validate the phase offset in any of our conditions; even a phase offset of 1/4 of a period between the looming sound and the looming visual pattern went subjectively unnoticed. Our observers confirmed this, as they could readily match the perceived offset in timing between the two patterns, particularly when attention to the two sensory modalities was involved (Kanai et al., 2007). This happens in the real world, as when experiencing the periodicity of pile driving at a close distance or at a farther distance: the different transmission times for visual and auditory stimuli produce different offsets. The brain is able to deal with this by constantly calibrating the point of synchrony, as shown by adaptation to artificial temporal delays (Fujisaki et al., 2004). Figure 2b depicts objective data of the five subjects (who all participated in all experiments yet to be presented), showing that the mean percept durations for a 1/4 period phase offset (between looming sound and vision) was very similar to the mean percept durations with zero phase offset. Although it is possible that there may be a systematic temporal offset effect (such as in the recently reported enhanced perception of visual change by a coincident auditory tone pip) (van der Burg et al., 2008), from our pilot work we expect that in our setting it must

be much smaller in magnitude than the frequency effect. Thus, the next set of experiments capitalizes on congruency in frequency (rhythm).

Figure 3. Results of Experiment 1

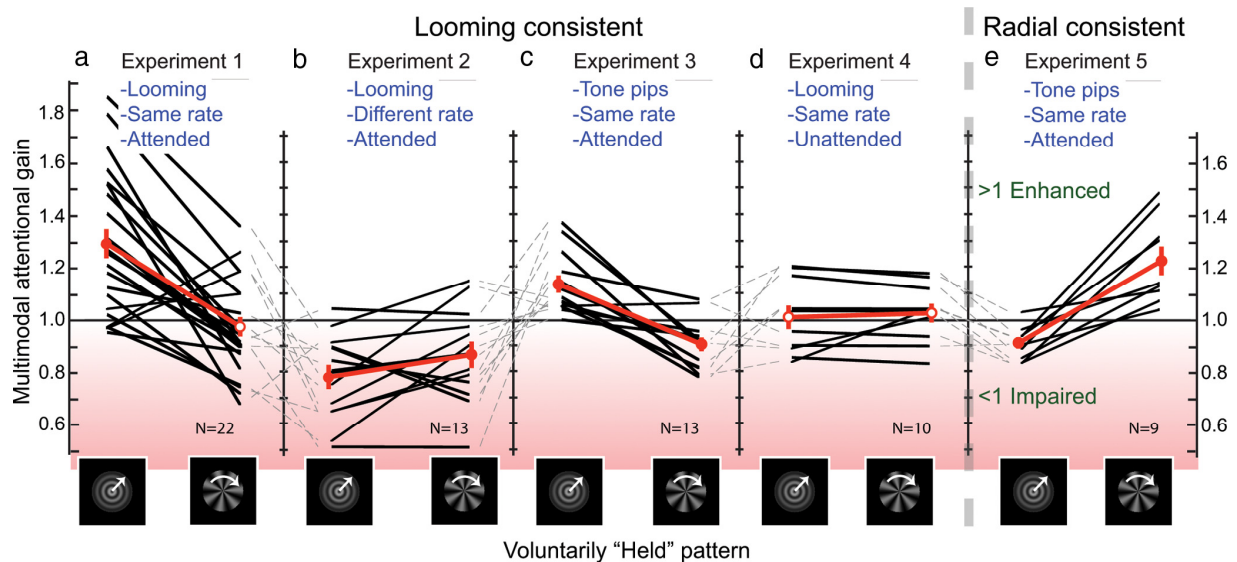


Figure 3. *a*, Results from Experiment 1. Black lines connect the data of a particular subject. *b*, A different rate of the looming sound impairs the multimodal attentional gain (Experiment 2). *c*, Tone pips with the same rate as the looming visual pattern enhance multimodal attentional control over the looming pattern, indicating that rate (or rhythm) is important (Experiment 3). *d*, Paying attention to the congruent looming sound is required to enhance holding the visual looming pattern (Experiment 4). *e*, The benefit of congruent sound also holds for the radial pattern and is not specific to the looming pattern (Experiment 5). The dashed lines between the panels connect data of identical subjects. Filled circles indicate significance (*t*-test, see Results); error bars denote 1 SE.

Experiment 2: The rate (rhythm) of the sound is key to enhance attentional control

We asked whether the synchronized periodicity in Experiment 1 was necessary or whether non-synchronized looming sounds would be equally effective in promoting multimodal attentional control. We slightly changed the rate of the looming sound envelope to 0.82 Hz (Figure 1c) and repeated the measurements with 13 subjects (9 male, 4 female) from Experiment 1. In Figure 3b, we show individual subjects' multimodal attentional gain. The slight change in auditory looming rate dramatically changed the effect of sound from one of enhancing attentional control of bistable visual perception to one of

impairing attentional control, as shown by the impaired multimodal attentional gain (Figure 3b, left) ($20.3 \pm 4.4\%$; $p < 0.001$, t-test) (see supplemental Figure 2a, available in Appendix 3 as supplemental material, for percept durations). Thus, subjects were less able to hold the looming visual pattern when it was accompanied by a looming sound of a different rate than when sound was absent. After debriefing, observers reported that the mismatched looming sound was annoying and distracting, which may explain part of the impairing effects and might point to an automatic and obligatory component in cross-modal integration (Guttman et al., 2005; van der Burg et al., 2008). In turn, this might mean that the cross-modal effect obtained may have been partly motivational; subjects might have made more effort to control bistability when the sound matched the to-be-held visual motion, whereas they might have been less motivated when the sound “annoyingly” mismatched the to-be-held visual motion. However, that would likely only cause the disappearance of the attentional effect measured in Experiment 1, not the observed decrease in dominance durations. Supporting an automatic component is the reported presence of cortical activity specifically related to coincident visual and auditory looming stimuli (Maier and Ghazanfar, 2007) and points to the functional significance of looming (approaching) stimuli (Neuhoff, 2001; Parker and Alais, 2007).

This experiment underscores the importance of temporal congruency, versus the looming character of the sound, in enhancing attentional control. Because subjects were still explicitly instructed to pay attention to the looming sound, this finding supports the conclusion that the results of Experiment 1 were not a bias in response to instructions. Also, consistent with the findings of Experiment 1, the ability to voluntarily hold the visual radial pattern was impaired (relative to no sound) when a looming sound was present ($12.2 \pm 4.8\%$; $p < 0.03$) (Figure 3b, right; supplemental Figure 2a, Appendix 3).

Experiment 3: Rhythmic tone pips also enhance attentional control

If congruent rate is the key factor as indicated by Experiment 2, would another sound with a rate identical to the visual looming stimulus be sufficient to enhance attentional control? We tested this on the same 13 subjects (9 male, 4 female) using discrete tone pips presented at 1 Hz (i.e., at the visual looming frequency) (Figure 1d) and found

significant multimodal gain in holding the looming pattern dominant (13.8 ± 3.2%, $p = 0.001$) (Figure 3c; see supplemental Figure 2b, available in Appendix 3, for percept durations). Although there is a significant decrease in effect compared with Experiment 1 ($p = 0.05$, t-test), this difference disappears when comparing only the subjects that participated in both experiments ($p = 0.2$, paired t-test), suggesting again that the looming character of the sound was not a cardinal factor of congruency. Furthermore, there was a small impairment in the ability to hold the radial pattern relative to the no-sound condition of 8.4 ± 2.5% ($p = 0.006$) (Figure 3c; supplemental Figure 2b, Appendix 3). Therefore, the rate of the auditory signal is the factor that governs multimodal control of visual ambiguity, rather than the sound's looming-like envelope.

Experiment 4: Paying attention to the sound is essential to enhance attentional control

In the experiments above, subjects were explicitly instructed to pay attention to the sound. We wished to determine whether paying attention to the sound was essential for multimodal control to occur. A group of 10 subjects (7 male, 3 female) who had not participated in any of the previous conditions performed an additional experiment before Experiment 1. They were given the instruction that the sound was not relevant to their task, although no explicit instruction was given to attend or to disregard the sound. Interestingly, we found for this group that multimodal gain was not significantly different from zero (1.6 ± 4.3%, $p = 0.70$; and 3.1 ± 3.4%, $p = 0.40$, for the looming and radial visual patterns, respectively (Figure 3d); and see supplemental Figure 3a, Appendix 3, for percept durations), meaning that the mere presence of a matched looming sound did not automatically trigger the ability to select and hold the looming visual stimulus. Instead, control over the visual stimulus requires an explicit act of attention to the sound stimulus. We then let this group of subjects do the previously described experiments, for which they showed average behavior (other panels, Figure 3). Supplemental Figure 3b in Appendix 3, directly compares the data of Experiments 1 and 4 for each individual of this group of subjects and emphasizes that the subjects' ability to hold the visual stimulus was profoundly enhanced once the sound was attended. One could argue that the absence of an effect for these subjects could be attributable to being unpracticed at the task.

However, when comparing these subjects' results in Experiment 1 (their second experiment) to the subjects whose first experiment was Experiment 1, there was no significant difference ($p = 0.8$, t-test) (supplemental Figure 3c, Appendix 3).

Experiment 5: Generalization to other visual patterns—rhythmic tone pips enhance attentional control over the radial pattern

Does ambiguity resolution hold for the radial pattern as well? Discrete tone pips (the same as used above in Experiment 3) were presented at 0.6 Hz to match the rotational frequency of the radial pattern. The tone pips were timed to occur each time a spoke pointed exactly downward, and this was explicitly indicated to the subjects ($n = 9$, 6 male, 3 female; participated in all previous experiments). We found significant multimodal gain in holding the radial pattern dominant (22.4 5.3%, $p = 0.006$) (Figure 3e; see supplemental Figure 4, Appendix 3, for percept durations) when this train of congruent tone pips was present and attended. Conversely, the ability to voluntarily hold the looming pattern was impaired (relative to the no-sound condition) when attending the tone pips ($-7.8 -2.1%$, $p = 0.003$) (Figure 3e; supplemental Figure 4, Appendix 3).

Together with Experiments 1 and 3, these results reveal that the resolution of visual ambiguity by congruent sound is not specific to looming visual stimuli as it also occurs when the auditory stimulus is temporally congruent with radial visual stimuli.

Experiment 6: A congruent visual pattern aids in control over ambiguous sounds

Thus far, our experiments have involved the resolution of ambiguity in the visual domain by a congruent auditory stimulus. Would congruent vision also facilitate control of ambiguous auditory signals? To test this, we presented subjects with alternating high and low tones (van Noorden, 1975), where observers either hear segregated tone streams (Morse) or a grouped (galloping) pattern (supplemental Figure 5a, Appendix 3). This stimulus has become a standard way to study auditory scene analysis, and in the only extant study that addressed attentional control of this ambiguous auditory stimulus, observers were able to lengthen the duration of the dominance of one of the alternatives (Pressnitzer and Hupé, 2006). Interestingly, there is evidence that perception of

ambiguous stimuli in the auditory domain can be biased by a visual stimulus (O'Leary and Rhodes, 1984), but this study did not specifically address the role of attentional control. As an unambiguous visual stimulus, we used a disk (diameter, 7.5° ; see Materials and Methods) flickering at the low tone frequency. As a competing visual stimulus, we presented a static frame around the disk. We tested seven subjects (4 male, 3 female) who had all participated in the other experiments. We explicitly asked observers to pay attention to the flicker frequency of the disk, as pilot experiments made it readily obvious that without actively viewing the disk there is no effect of the presence of the disk (see supplemental Figure 5d, Appendix 3, for pilot data). Thus, even though subjects had already participated in experiments one to five in which they matched the frequency of a sound stimulus to a visual stimulus, in this experiment they did not automatically match the frequency of the visual stimulus to the sound stimulus. Interestingly, this was even the case when we presented the disk (and the frame) on a large projector screen with a diameter subtending a visual angle of 80° horizontal by 60° vertical. It must be said though that these pilot experiments using the whole field projection were ran for 1 min only. It could be the case that prolonged subjection to a whole field visual stimulus with the same frequency as the auditory stimulus might lead to automatic cross-modal effects.

The results, using the 7.5° disk, showed a significant multimodal gain in holding the segregated Morse-like percept dominant ($23.9 \pm 9.1\%$, $p = 0.039$) when the flickering visual disk was present and attended (supplemental Figure 5c, Appendix 3; Figure 4, fourth bar). Conversely, there was an insignificant impairment in the ability to voluntarily hold the grouped (galloping) percept dominant when attending to the visual pattern ($3.4 \pm 9.9\%$, $p = 0.7$) (supplemental Figure 5c, Appendix 3). These results reveal that the resolution of ambiguous perceptual signals by congruent stimuli is not limited to an auditory influence on visual processing but can also operate in the reverse direction with vision disambiguating sound.

Experiment 7: Generalisation to touch—a tactile pattern aids in disambiguating vision

To this point, our experiments have involved vision and audition. Here, we introduce a tactile stimulus to test the prediction that trimodal congruency aids in attentional control over the visual looming pattern. To make a temporally congruent tactile signal, we attached a vibrating loudspeaker membrane to the skin on the back of the hand (supplemental Figure 6a, Appendix 3) and played the same competing sounds as we used in Experiment 1, being the looming and the tone triad. The looming sound was felt as a pulsing pattern that was temporally matched to the looming visual pattern. The tone triad was felt as tactile noise. Again, we explicitly asked observers to pay attention to looming feeling as pilot experiments made it readily obvious that without actively attending to the tactile looming there was no effect of the presence of the tactile stimulus.

Five subjects (3 male, 2 female) participated, all of whom had participated in all other experiments. First, we tested the bimodal visuo-tactile condition. With only the congruent tactile stimulus accompanying the ambiguous visual stimuli, there was a significant multimodal gain in the ability to hold the visual looming pattern dominant ($19.1 \pm 8.4\%$, $p < 0.05$, one-tailed t-test) (supplemental Figure 6c, Appendix 3; Figure 4, fifth bar). In the trimodal condition, when congruent stimuli were present in both the auditory and the tactile domain, an even stronger effect was observed, with multimodal gain in holding the visual looming pattern dominant increasing to $39.7 \pm 14.3\%$ ($p < 0.05$) (supplemental Figure 6c, Appendix 3; Figure 4, sixth bar), which was significantly higher than the tactile condition ($p < 0.05$, one-sided paired t-test). Importantly, and as found above, the ability to hold the radial pattern was not facilitated by tactile stimuli ($18.6 \pm 12.4\%$; $p < 0.2$), nor by combined audio-tactile stimuli ($3.5 \pm 4.0\%$, $p < 0.4$). Individual subject data are provided in supplemental Figure 6, Appendix 3.

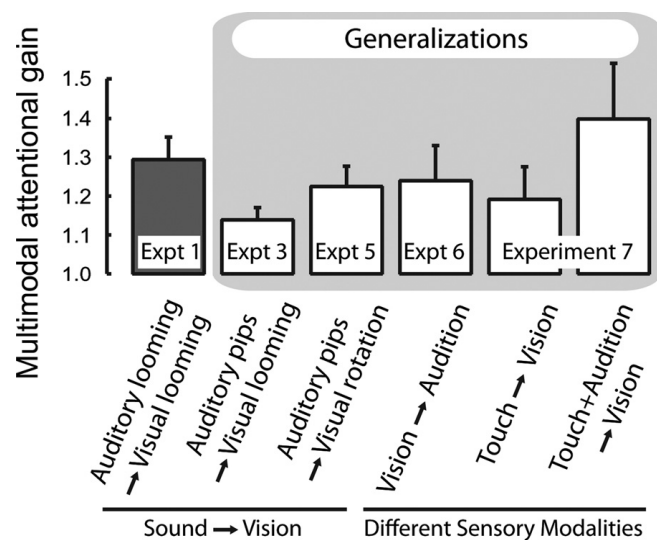
Discussion

The primary finding is that the presence of an attended sound matching the temporal rate of one of a pair of competing ambiguous visual stimuli allows subjects much more control over voluntarily holding that stimulus dominant. Attentional control over the

other, temporally mismatched, visual pattern was also influenced by the sound but in the opposite manner. The size of this effect is remarkably large, given that attentional control over binocular rivalry is usually found to be quite weak (Meng and Tong, 2004; Chong et al., 2005; van Ee et al., 2005; Paffen et al., 2006). Importantly, we also showed that active attention to both the sound and the visual stimulus promoted enhanced voluntary control. Below, we argue that this may help to explain why other researchers in psychophysics have failed to find such intimate links between auditory and visual attentional control. We also demonstrated a facilitatory relationship in the opposite direction in that attentional control over audio ambiguity is markedly aided by a matching visual stimulus. Extending this generalisation, we demonstrated that a matching tactile stimulus enhanced attentional control in perceptually selecting competing visual stimuli and that this control was further strengthened in a trimodal condition that combined congruent audio-tactile stimuli with the bistable visual stimulus. Figure 4 summarises the generalisation of results across different visual patterns, sound patterns, and sensory modalities.

Figure 4. Results of the cross-modal conditions

Figure 4. The first bar from the left shows the basic finding (Figure 3a, Experiment 1). The second bar depicts a generalisation across attended sound patterns: tone pips provided significant multimodal attentional gain in holding the visual looming pattern dominant (Figure 3c, Experiment 3). Next, the third bar shows that congruent tone pips aided the visual radial pattern as well, generalising our findings to visual stimuli other than looming patterns (Figure 3e, Experiment 5). The three right most bars show generalisations to other sensory domains. The fourth bar shows the role of vision on the dominance of competing sounds (supplemental Figure 5, Appendix 3, Experiment 6). The fifth bar shows the influence of touch on active visual ambiguity resolution, and the sixth bar depicts the combined effect of touch and audition on the ability to actively control visual ambiguity resolution (supplemental Figure 6, Appendix 3, Experiment 7). Error bars denote 1 SE.



When the sound was temporally delayed, subjects still sensed that vision and sound were linked because of their constant phase relationship (Figure 2b). In addition, although we have only provided formal evidence for a mandatory involvement of directed attention in the sound-on-vision experiments (Figure 3d), our pilot work (supplemental Figure 5d, Appendix 3) and the available literature suggest that attention must be engaged to promote cross-modal interactions (Calvert et al., 1997; Gutfreund et al., 2002; Degerman et al., 2007; Mozolic et al., 2008; for review, see Shinn-Cunningham, 2008).

Nevertheless, although a systematic investigation of temporal offset and automation for the cross-modal effects goes beyond the scope of the present paper, it is interesting to note that the underlying rhythm mechanism for our rhythm-based effect may be different from the mechanism underlying automatically occurring coincidence-based auditory-visual interactions (such as in the reported enhanced perception of visual change by a coincident auditory tone pip) (van der Burg et al., 2008).

Our study is unique in that it uses competing bistable visual and bistable auditory stimuli, providing the opportunity to study how competing sensory processing in two modalities (related to percepts rather than physical stimuli) are influenced by signals from other modalities. How do our findings shed light on the mechanisms underlying the resolution of perceptual ambiguity? We suggest that the enhanced capacity for attentional selection of the congruent stimulus results from a boost of its perceptual gain, which is attributable to top-down feedback from multisensory attentional processes that select the congruent feature of the input signal. In support of this, for vision, it has been shown previously that the effect of top-down attention on extending dominance durations for perceptually competing stimuli is equivalent to a boost in stimulus contrast (Chong et al., 2005; Chong and Blake, 2006; Paffen et al., 2006). This is in line with recent studies on visual spatial and feature attention in psychophysics (Blaser et al., 1999; Carrasco et al., 2004; Boynton, 2005) and neurophysiology (Reynolds and Chelazzi, 2004) which demonstrate that the neural mechanism underlying attentional selection involves boosting the gain of the relevant neural population. This is observed in the early cortical stages of both visual (Treue and Maunsell, 1996; Treue and Martínez Trujillo, 1999; Lamme and Roelfsema, 2000; Womelsdorf et al., 2006; Wannig et al., 2007) and auditory processing (Bidet-

Caulet et al., 2007). From the present results, we can conclude that the scope of this feedback process can be extended to incorporate relevant multimodal signals. Thus, it appears that voluntary control over ambiguity resolution can be modeled as an increase in effective contrast (perceptual gain) of stimulus elements involving feature attention, as opposed to spatial attention. Dovetailing with this, voluntary control in perceptual bistability depends multiplicatively on stimulus features (Suzuki and Peterson, 2000), and an equivalence between stimulus parameter effects and attentional control is evident even at the level of fit parameters to distributions of perceptual duration data (Brouwer and van Ee, 2006; van Ee et al., 2006). It can also be demonstrated quantitatively, as in a recently developed theoretical neural model (Noest et al., 2007), that attentional gain modulation at early cortical stages is sufficient to explain all reported data on attentional control of bistable visual stimuli (Klink et al., 2008). Thus, there is converging evidence that an early gain mechanism is involved in attentional control of perceptual resolution of ambiguous stimuli, although it is too early to entirely rule out high-level modification.

Although there is support for the idea that auditory and visual attention are processed separately (Shiffrin and Grantham, 1974; Bonnel and Hafter, 1998; Soto-Faraco et al., 2005; Alais et al., 2006; Pressnitzer and Hupé, 2006; Hupé et al., 2008), our findings support the neurophysiological literature (Calvert et al., 1997; Gutfreund et al., 2002; Shomstein and Yantis, 2004; Amedi et al., 2005; Brosch et al., 2005; Budinger et al., 2006; Degerman et al., 2007; Lakatos et al., 2007, 2008; Shinn-Cunningham, 2008) that the mechanisms mediating multisensory attentional control are intimately linked. To understand these seemingly disparate results, note first that psychophysical studies finding separate processing, focused on spatial attention, as opposed to our study. Our findings concern feature attention and agree with recent findings that feature attention can more profoundly influence processing of stimuli than spatial attention (Melcher et al., 2005; Kanai et al., 2006). Note further that we presented the matched audio and visual stimuli simultaneously. The only other study on attentional control of ambiguous auditory and visual stimuli (Pressnitzer and Hupé, 2006) presented the stimuli from the two modalities separately in time, finding that results from the two modalities were unrelated. Although there are studies reporting that audiovisual stimulus combination is mandatory

(Driver and Spence, 1998; Guttman et al., 2005), this is not a general view (Shiffrin and Grantham, 1974; Bonnel and Hafter, 1998; Soto-Faraco et al., 2005; Alais et al., 2006; Hupé et al., 2008). Our experiments address this by using perceptually ambiguous competing auditory and visual stimuli, thereby dissociating attention and stimulation to reveal that active attention to both modalities promotes audiovisual combination, in line with other recent studies (Calvert et al., 1997; Gutfreund et al., 2002; Degerman et al., 2007; Mozolic et al., 2008).

Our data suggest a functional role for neurons recently found in human posterior parietal, superior prefrontal, and superior temporal cortices that combine voluntarily initiated attentional functions across sensory modalities (Gutfreund et al., 2002; Shomstein and Yantis, 2004; Degerman et al., 2007). We suggest that when the brain can detect a rhythm in a task, attention feeds back to unisensory cortex to enforce coherent and amplified output of the matching perceptual interpretation. Recently, neurophysiologists were able to demonstrate that an attended rhythm in a task enforced the entrainment of low-level neuronal excitability oscillations across different sensory modalities (Lakatos et al., 2008). The fact that oscillations in V1 entrain to attended auditory stimuli just as well as to attended visual stimuli reinforces the view that the primary cortices are not the exclusive domain of a single modality input (Foxy and Schroeder, 2005; Macaluso and Driver, 2005; Ghazanfar and Schroeder, 2006; Kayser and Logothetis, 2007; Lakatos et al., 2007) and confirms the role of attention in coordinating heteromodal stimuli in the primary cortices (Brosch et al., 2005; Budinger et al., 2006; Lakatos et al., 2007, 2008; Shinn-Cunningham, 2008). We suggest that the same populations of neurons may control multimodal sensory integration and attentional control, suggesting that the neural network that creates multimodal sensory integration may also provide the interface for top-down perceptual selection. However, our understanding of multisensory neural architecture is still developing (Driver and Noesselt, 2008; Senkowski et al., 2008) and a competing view, rather than focusing on feedback from multisensory to unisensory areas, proposes that multisensory interactions can occur because of direct feed-forward convergence at very early cortical areas previously thought to be exclusively unisensory (Foxy and Schroeder, 2005; Ghazanfar and Schroeder, 2006). Testing competing views will require

further studies, possibly using neuroimaging techniques with high temporal resolution or neurodisruption techniques to temporarily lesion the putative higher-level area.

Conclusion

In sum, our novel paradigm involving ambiguous stimuli (either visual or auditory) enabled us to demonstrate that active attention to both the auditory and the visual pattern was necessary for enhanced voluntary control in perceptual selection. The audiovisual coupling that served awareness was therefore not fully automatic, not even when they had the same rate and phase. This suggests a functional role for neurons that combine voluntarily initiated attentional functions across different sensory modalities (Calvert et al., 1997; Gutfreund et al., 2002; Shomstein and Yantis, 2004; Amedi et al., 2005; Brosch et al., 2005; Budinger et al., 2006; Degerman et al., 2007; Lakatos et al., 2007, 2008), because in most of these studies congruency effects were not seen unless attention was actively used. This squares with psychophysics and neurophysiology showing intimate links between active attention and cross-modal integration (Spence et al., 2001; Kanai et al., 2007; Lakatos et al., 2007; Mozolic et al., 2008; Shinn-Cunningham, 2008). Thus, these attention-dependent multisensory mechanisms provide structure for attentional control of perceptual selection in two ways. First, in responding to intermodal congruency, they may boost the baseline response of the congruent alternative (as there is more “proof” for a perceptual interpretation when it is supported by two converging modality sources). Second, they may increase attentional control over perceptual selection because a multiplicative gain will be more significant when acting on a higher baseline, therefore allowing more attentional control.

Chapter summary

Although the experiments in the current chapter are designed to test whether non-visual stimuli can aid *wilful* attentional control over binocular rivalry, it is important to qualify what this means in terms of the type of stimulus used. Looming sounds and transient tactile and sound events, such as the sound pips used in this chapter, are all types of stimuli that engage exogenous, stimulus-driven attention. That these types of stimuli can assist *wilful* control over rivalry predominance where others do not (Meng & Tong,

2004) is congruent with the current hypothesis concerning the interconnectedness of exogenous perceptual selection and perceptual bistability.

The type of attention producing the effects reported could be characterised as ‘exogenous-based’ attention, in that purposeful control is first engaged by stimulus-driven attention. Whether purposeful or not, the effect of attention is dependent upon the intrinsically salient nature of the stimulus used as the object of attention. As discussed in the introductory chapter, once transient attention is engaged, sustained attention is allocated to its source in order to decide what to do with that event or object. In this way, stimulus-driven attention works in concert with sustained attention. This results of these experiments clearly demonstrate the potential for this interconnection and is presented in support of the overall thesis hypothesis.

Chapter 5

Temporal auditory information speeds visual selection for consciousness during binocular rivalry

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Overview

The findings of Chapter 4 pave the way for further exploration of how auditory stimulus-driven attention might affect rivalry alternations, which is the subject of Chapter 5. It is clear that sound pips presented at the same temporal rate of one of the visual stimulus undergoing rivalry influence its predominance. In this Chapter, whether or not sound streams unrelated to the visual stimuli can affect rivalry dynamics is explored. The experiments presented in Chapter 5 are motivated by the finding that visual transients unrelated to the rivalry stimulus can provoke dominance reversals (Kanai et al., 2005) and asks: will the same occur when the transient stimuli are presented in the auditory sense modality? If this is the case, it would strongly support the idea that exogenous attention and perceptual rivalry share a common, distributed process.

Abstract

Binocular rivalry occurs when discrepant images are presented to corresponding retinal regions of the two eyes resulting in continuous fluctuations in awareness between each eye's image. Experiments are presented showing that rapid, perceptually salient sound streams increase the overall alternation rate during binocular rivalry viewing. These increases in alternation rate are not accompanied by changes in the stochastic pattern of alternations, nor precise entraining of alternations to the sound events, and occur most strongly with audio-temporal streams in the EEG beta-wave band frequency, indicating that increased physiological arousal underlies the result. Eye movements do not account for the magnitude of the increased binocular rivalry alternation rate, nor do key press errors contingent with the sounds. A duration discrimination task using the same sound streams resulted in expanded duration estimates for rapid auditory streams, adding

support to the role of a general mechanism. These results demonstrate that temporal information in the auditory modality can have a significant impact over the rate of visual processing during binocular rivalry and constitute further evidence that a general timing mechanism is involved in the perceptual fluctuations that occur during bistable perception.

Introduction

At any one time we are consciously aware of only a fraction of the environmental information that surrounds us. Which sensory information rises to conscious awareness depends on both the motivational state of the observer and the physical properties of the stimulus, such as loudness, temporal frequency or brightness. ‘Pre-attentive’ selection for consciousness is mediated by an evolutionarily old, neural substrate that moderates alertness and is not modality specific (Sturm & Willmes, 2001). It has been suggested that this substrate is also involved in the fluctuations in awareness that arise during bistable perceptual phenomena such as binocular rivalry. In order to clarify this link the present research examines how temporal auditory information affects visual selection for consciousness during binocular rivalry.

Binocular rivalry involves fluctuations in awareness between monocular images that are sufficiently distinct to prevent binocular fusion. An illustration of how binocular rivalry is elicited is shown in Figure 1. During viewing of binocular rivalry stimuli, one eye’s image occupies conscious awareness briefly before swapping to the other eye’s image. These alternations continue indefinitely and involuntarily during the presentation period in a stochastic temporal pattern. Similar stochastic patterns of alternations are found for many types of bistable stimuli, including the Necker cube, the kinetic depth illusion and binocular rivalry (Zhou et al., 2004; van Ee & Klink, 2005; van Ee & van Wezel, 2008), monocular and binocular rivalry (O’Shea, Parker, La Rooy & Alais, 2008) and even between auditory and visual bistable phenomena (Pressnitzer & Hupé, 2006). The pervasiveness of these dynamics suggests that although processing specific to the bistable stimulus takes place, the process determining overall temporal dynamics is shared. Suggestions of a shared temporal mechanism or oscillator underlying different forms of

bistable perception (Carter & Pettigrew, 2003; Leopold & Logothetis, 1999) are supported by links between bistable dynamics and physiological states such as neuropharmacology (Carter et al., 2005 and 2007), mood (Nagamine et al., 2007) and age (Ukai, Ando & Kuze, 2003). Further, two physiological markers of increased alertness and arousal; pupil diameter (Einhauser, Stout, Koch & Carter, 2008) and beta-wave EEG amplitude (Piantoni, Kline & Eagleman, 2010) predict the onset of binocular rivalry alternations.

To further probe the idea that binocular rivalry fluctuations arise from a common temporal oscillator, we examined the affect of auditory temporal streams on binocular rivalry and other perceptual processes such as eye movements, perceptual-motor responding and duration discrimination. Auditory information is weighted heavily in our awareness of temporal frequency and onset, as demonstrated by auditory driving of flicker perception (Ogilvie, 1956 and Shipley, 1964) and the double flash illusion (Shams, Kamitani & Shimojo, 2002). Congruent sounds can moderately increase one visual interpretation over the other during binocular rivalry (Kang & Blake, 2005; Conrad et al, 2010; Chen, Yeah & Spence, 2011), especially with an effort of will (van Ee et al., 2009). In contrast, diverting auditory attention away from gratings undergoing rivalry fluctuations reduces the perceptual alternation rate (Alais et al., 2010) as do diversions of attention to a visual task (Paffen, Alais & Verstraten, 2006), showing that cognitive resources involved in binocular rivalry are shared across modalities. However, no studies as yet have examined the temporal dynamics of binocular rivalry in the presence of auditory temporal information. To this end, seven participants recorded binocular rivalry fluctuations during exposure to streams of perceptually salient (72 dB) auditory tone pips or white-noise bursts unrelated to the visual stimuli undergoing rivalry. Given the evidence that a modality non-specific general mechanism involved in generalised arousal influences binocular rivalry, it was expected that binocular rivalry fluctuations would ‘entrain’ to the temporal auditory information presented during the trials.

Experiment 1: Binocular rivalry dynamics under ambient auditory temporal streams

In the first experiment, streams of auditory and visual transient events were presented during observation of standard binocular rivalry stimuli (orthogonally oriented gratings). Single transient visual events (flashes of light) presented in close spatial proximity to a bistable stimulus reliably induce a switch from the dominant percept to its alternative (Kanai, Moradi, Shimojo & Verstraten, 2005). Given this and the cross-modal interactions discussed previously, if the mechanism determining bistable dynamics during binocular rivalry integrates information across modalities it is expected that a stream of similar attention-grabbing auditory events, will induce or entrain binocular rivalry alternations. Four types of perceptually salient temporal streams were used to test for this effect, over a range of ambient temporal frequencies. Two auditory (tone pips and white-noise bursts), one visual (contrast increment) and one audiovisual (AV: tone and contrast) conditions were compared at temporal frequencies of (0.5, 1, 2, 3.9, 8.1 & 15 Hz). We also compared several patterns of temporal streaming: periodic, low random jitter, high random jitter. Since visual transients can trigger alternations in bistable stimuli (Kanai, Moradi, Shimojo & Verstraten, 2005) and auditory events can drive perception of visual temporal rate (Oglivie, 1956 and Shipley, 1964) it is expected that streams of auditory events will entrain or speed the pattern of binocular rivalry alternations.

Figure 1. Alternating visual awareness during binocular rivalry

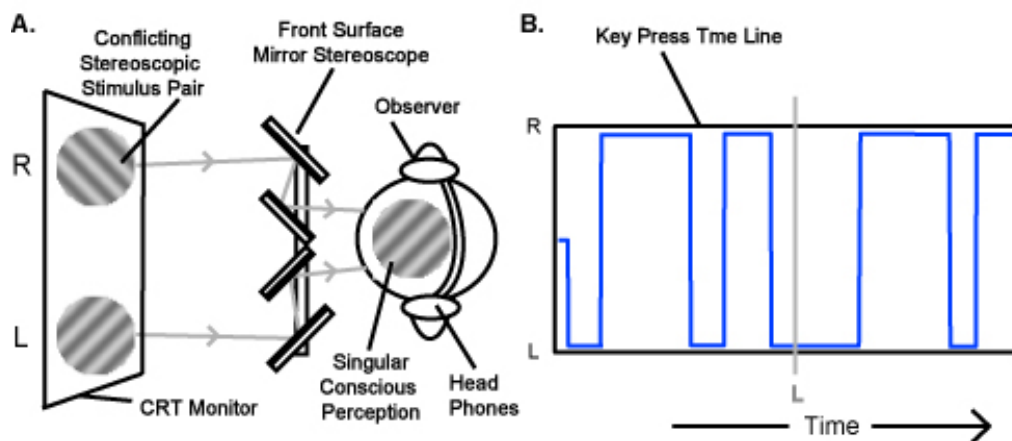


Figure 1: A) A conflicting stereoscopic image pair is presented to corresponding retinal regions of the two eyes by displacing each image on a CRT monitor and fusing the two images with a mirror stereoscope (shown by the light grey arrowed lines in A). Observers see only one of the images at any one time as binocular rivalry alternations occur between the two conflicting images. Observers wore headphones so auditory stimuli could be presented. B) An example time-line of binocular rivalry alternation key presses recorded during trials.

Materials and method

Visual stimuli: Two orthogonal sine-wave gratings oriented $\pm 45^\circ$ with a spatial frequency of 5.5 cycles per degree and subtending 1.5° visual angle were used to induce binocular rivalry. The gratings were horizontally displaced on a gamma-corrected, Diamond View 17" CRT monitor with a 90 Hz vertical refresh rate and 800 x 600 pixel screen resolution. The grating pair were binocularly fused via a front-surface mirror stereoscope positioned 57 cm from the monitor. Michelson contrast of the gratings was 12%, 24% or 48% depending on the condition being tested. During visual temporal stream conditions, visual transients were created by increasing the contrast of the gratings two-fold, keeping mean luminance constant, for approximately 20 ms for each event in the temporal stream.

Auditory stimuli: Two types of transient auditory events were used in the auditory temporal stream conditions: tone pips (20 ms duration, 800 Hz, 72 dB SPL, with a raised cosine on/off ramp) and white-noise bursts (20 ms 72 dB SPL cosine ramped). The AV condition combined the tone and contrast increments with the tones presented at a 10 ms latency to the visual events to help create perceptual synchrony.

Procedure: All trials were conducted in a sound-attenuated room using a G4 Macintosh PC, CRT monitor, headphones and a front surface mirror stereoscope adjusted for each subject prior to testing. Before testing commenced in the AV condition, the timing of the tone pips and contrast increments was verified with an oscilloscope, microphone and a photosensitive light emitting diode. Stimulus presentation and response recording were controlled with Matlab (version r2007a) with Psychophysics Toolbox (Brainard, 1997) and Statistics and Image Processing Toolbox functions. Participants recorded binocular

rivalry alternations by pressing and holding down one of two keys corresponding to the perceptual dominance of the left and right gratings or both keys during times when a blend of each eye's image was seen. Testing included 126 1-minute trials measuring binocular rivalry alternations between a 12%, 24% or 48% contrast grating pair during auditory or visual temporal streams. Four types of transient event (contrast increments, tone pips, white noise and AV) were tested at six temporal frequencies; 0.5, 1, 2, 3.9, 8.1 and 15 cycles per second (Hz). Trials were run in blocks according to transient type, conducted over sequential days. Trials were run in a randomised order within each block. Two additional conditions tested the 48% binocular rivalry gratings with tone pip and contrast increment streams that had been randomly perturbed to have a high (HTU) or low (LTU) temporal uncertainty. In the HTU condition, events were randomised across the 60 second trial. The LTU pattern randomised the timing of the event only within the cycle period being tested, e.g. within a 1 second window for the 1 Hz streams.

Subjects: Seven adults aged between 24-48 (4 female, 3 male) all with normal or corrected-to-normal visual acuity and binocular depth perception acted as subjects. One subject did not complete the two random jitter conditions and a further two did not participate in the AV condition.

Results

The key press data corresponding to observers' perceptual alternations were converted to alternation rates (cycles per second) for each 60-second trial. Analysis of variance (ANOVA) of the alternation rates across conditions (within subjects factors: stream type (4) x binocular rivalry grating contrast (3) x stream rate (7)) resulted in significant main effects of stream type ($F(3,9.92)$, $p < .01$), binocular rivalry contrast ($F(2,10.44)$, $p < .05$) and stream rate ($F(1.28, 9.228)$, $p < .05$, Greenhouse-Geisser correction for violation of sphericity). Binocular rivalry alternation rates were significantly sped in the presence of high-frequency 8.1 and 15 Hz streams auditory streams tested (simple contrasts 8.1 Hz: $F=12.13$, $p < .05$, 15 Hz: $F=13.916$, $p < .01$). All auditory event conditions resulted in a speeding of binocular rivalry at these two frequencies, as can be seen in Figure 2. The effect is similar for all the sounds used, including the white noise and AV stimuli, but

Figure 2. Binocular rivalry alternation rates during auditory and visual temporal streams

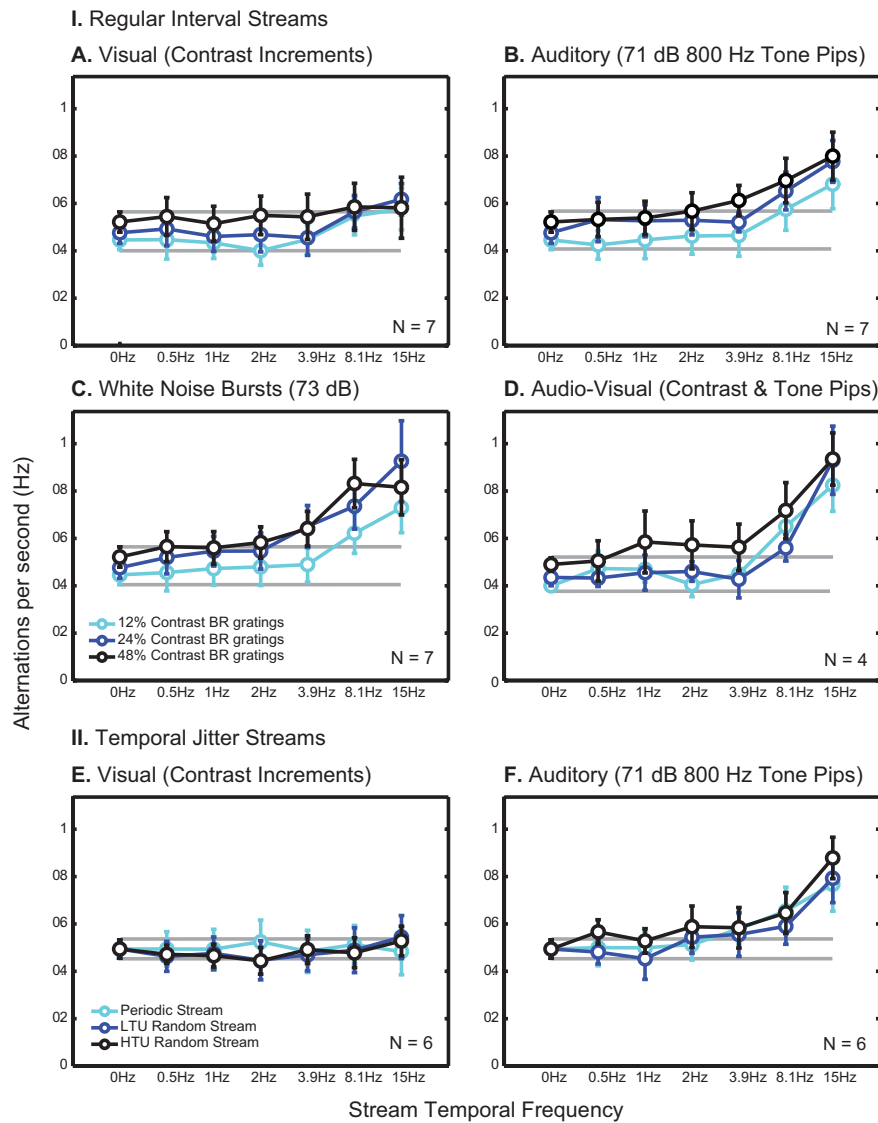


Figure 2: Average binocular rivalry alternation rates in Hz (y axis) is plotted for conditions where observers experienced auditory or visual temporal streams at one of six different temporal frequencies; 0.5, 1, 2, 3.9, 8.1 and 15 Hz (x axis) and a baseline no-stream 0 Hz condition (grey vertical lines $\pm 1SE$). Six transient stimulus types were tested including regular streams of contrast increments (A), tone pips (B), white noise bursts (C) and auditory-visual events (D) as well as randomized streams of contrast increments (E) and tone pips (F). Fast 8.1 and 15 Hz temporal streams in the auditory modality significantly increased binocular rivalry alternation rates above the 0 Hz control condition whereas visual contrast increments had no significant effect. Changes in the contrast of the binocular rivalry gratings did not impact the effect of auditory streams (A-D, coloured lines), neither does adding random jitter to the temporal streams (E-F, blue and black lines).

does not occur with the visual contrast increments alone ($F=0.13$, $p > .05$). A separate ANOVA on the random temporal stream conditions replicated the same results for the regular tone pip and contrast increments streams, with no further elevation of binocular rivalry rates with randomly jittered temporal streams. The contrast of the binocular rivalry gratings did not interact with the main effect of the sound streams ($F=0.74$, $p > .05$) or the frequency at which they were presented ($df=2.33$, $F=2.37$, $p > .05$ Greenhouse-Geisser correction). The proportion of piecemeal rivalry did not differ as a function of any of the conditions tested ($F(2.34, 2.66)$ $p > .05$ Greenhouse-Geisser correction), as the small rival stimuli used (1.5° diameter) limit piecemeal rivalry (Blake, O'Shea & Mueller, 1992).

To test whether the periodic audio-streams were entraining binocular rivalry alternations, an autocorrelation analysis was performed on the key press durations recorded. The probability of each eye's dominance duration during binocular rivalry is stochastic (Levelt, 1968, Fox and Hermann 1967). If the regular event streams presented here were entraining binocular rivalry alternations, alternations should become more periodic and less stochastic. For trials data, the dominance durations were correlated with each other over 12 lags, with the first correlation (of no lag) giving a correlation coefficient of 1. Individual dominance periods in binocular rivalry remain stochastically independent of each other in all the conditions tested here. Although there were occasional instances of significant correlations, these did not occur more than would be expected from chance (less than 5% of the time) and no systematic differences across any condition were found (ANOVA: event rate main effect $F(6, 1.178)$ $p > .05$ and event type $F(2.41)$, $p > .05$). The underlying stochastic nature of rivalry alternations is preserved during the presentation of auditory temporal streams, indicating that such streams do not override or 'capture' the temporal pattern of binocular rivalry fluctuations.

In a further test of entraining of the random stream patterns, time-lines of the binocular rivalry alternations and temporal streams were correlated with each other across 90 lags (corresponding to a one second lag at a sample rate of 90 Hz). A slight modulation in the correlation coefficients mirroring the periodic event streams could be seen, however none

of the correlations was significant when tested against 5% P values obtained from randomly shuffling and bootstrapping the data sets 1000 times. The cross-correlogram for one subject is shown in Appendix 2, Figure 5. The blue line shows the pattern expected from a perfect correlation between the streams of temporal events and binocular rivalry alternations. The red line shows the performed cross correlations, which were all non-significant. This result is consistent with the lack of periodicity found between the dominance durations in the autocorrelation analysis, and the preservation of the stochastic properties of rivalry dynamics despite the temporal streams in the present experiment. Auditory temporal streams therefore do not entrain binocular rivalry alternations. Lack of entraining is also supported by informal subject interviews: observers noted that only occasionally did binocular rivalry alternations coincide with sounds or visual events in the temporal streams. Observers revealed that they found the white-noise transient events at the higher rates (8.1 & 15 Hz) irritating, but did not report irritation at lower cycle rates or for the pure tone pips. This provides qualitative support for the interpretation that the speeding of rivalry alternations accompanied by rapid transient event sequences is due to increased arousal. If the effect of transient events is due to a startle effect that adapts or diminishes over the trial, there should be a negative correlation or slope between alternation rate and time elapsed during the trial. A few significant correlations were found between alternation rate and time, but these were below 5% of the data points tested and had no particular pattern. Binocular rivalry alternation rates did not consistently change across the duration of the 60-second trials. Together with the lack of entraining, this suggests that the effect of sound events on binocular rivalry is not due to a quickly adapting orienting, or startle response but rather to an increase in general alertness.

Discussion

The results of Experiment 1 demonstrate a clear auditory temporal influence over binocular rivalry alternation rate. Fast auditory event streams significantly increase the temporal rate of binocular rivalry alternations with no concomitant change to the stochastic pattern of alternations. It is possible that auditory events presented in isolation invoke a single binocular rivalry swap, however the continuous sound streams used here

did not entrain the temporal pattern of binocular rivalry alternations over a lengthy period. This raised the possibility that response inhibition affects perceived salience of the temporal stream across the course of the trial. This was not supported by the non-significant correlation between binocular rivalry alternation rates and elapsed trial time and an additional cross-correlation analysis between binocular rivalry alternations and the temporal streams performed on only the first 10 seconds of each trial. Rather than directly impacting binocular rivalry switches, the overall pace of alternations is being affected. This increase can be interpreted as the addition of ambient neural activity or noise to the binocular rivalry (BR) process. Neural noise refers to the activity of background neurons not directly involved in the neural process at hand but indirectly influencing it. Random background noise is included in models of binocular rivalry to account for the stochastic properties of the alternation periods (Wilson, 2003; Freeman, 2005) and the addition of visual noise modulates binocular rivalry periods according to the principles of stochastic resonance (Kim, Grabowecky & Suzuki, 2006). Sounds have been shown to act as a source of resonating noise during a visual detection task (Lugo, Doti & Faubert, 2008), and it follows that the effect of sound reported here may be due to the addition of noise to neural oscillations underlying binocular rivalry alternations, a possibility considered further in the General Discussion.

Experiment 2: Binocular rivalry key press tracking accuracy during auditory temporal streams

Even though the startle response does not appear to cause the increased binocular rivalry rates reported here, potential motor errors caused by the sounds need to be ruled out. To see if the auditory streams were affecting the accuracy of participants' binocular rivalry tracking, their ability to track "pseudo-rivalry" was tested. Pseudo-rivalry is a form of simulated rivalry where two identical binocular gratings change orientation according to a shuffled version of an observer's real binocular rivalry alternations. Differences in key press data and the pattern of pseudo-rivalry alternations are a measure of motor error. This procedure is carried out in Experiment 2, using the same transient event streams shown to speed rivalry previously (8.1 and 15 Hz). If the auditory streams resulted in key press responses related to the transient events that were not responses to real changes in

perceptual state during binocular rivalry there should be elevated errors during the 8.1 and 15 Hz sound stream conditions, but not other temporal frequencies.

Materials and method

Stimuli: The visual and auditory stimuli were the same as those used in Experiment 1, however the pseudo-rivalry grating pairs were always the same orientation at any one time during the trials and changed orientation in a temporal pattern determined by each observers baseline binocular rivalry recordings from Experiment 1.

Procedure: The procedure was identical to that used in Experiment 1, except that instead of tracking real binocular rivalry alternations participants (N=6) tracked physical alternations in orientation between two binocularly identical gratings that were switched according to a random shuffling of each subject's own baseline alternations for the 48% contrast grating. Pseudo-rivalry alternations were tracked by observers in the presence of the contrast increment, tone and white noise streams as during the real binocular rivalry conditions tested in Experiment 1.

Results and discussion

Accuracy was quantified as the number of erroneous key presses that did not correspond to an actual change in grating orientation during each trial. Small elevations in error key presses were found for the contrast increment condition at the 0.5 Hz event cycle (difference contrast for rate by event type interaction comparing contrast increment and tones at 0.5 Hz $F=9.731$ $p < .05$) but not any other conditions. Some significant decreases in error rate were found for the tone pip and white noise conditions however a decrease in motor errors does not bear on the results of Experiment 1. Errors were not increased during the auditory conditions, indicating that erroneous key presses are not responsible for the effects reported in Experiment 1.

Figure 3. Key-press motor errors during binocular rivalry and auditory and visual temporal streams

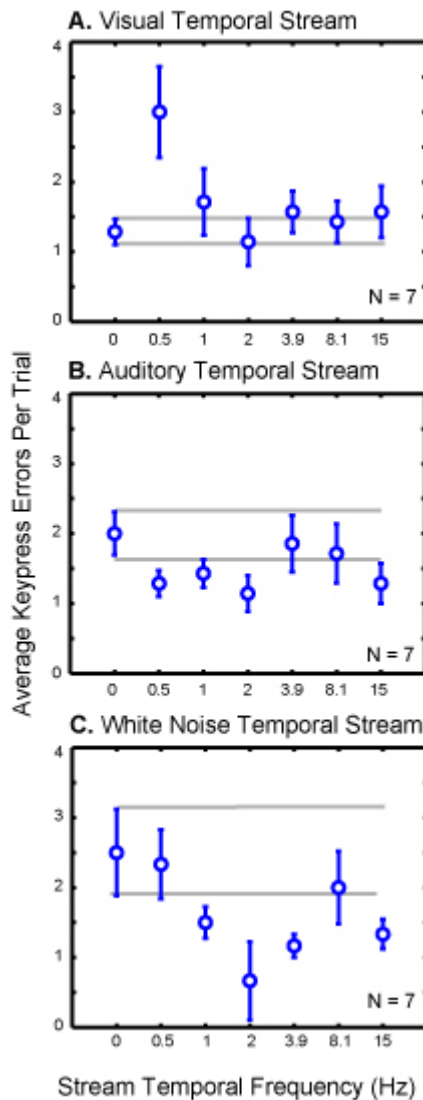


Figure 3: Key press errors made during the 0.5 to 15 Hz temporal contrast increment (A), tone pip (B) and white noise burst (C) streams tested. Participant's errors ranged between 0 and 4 unnecessary key presses per 30 second trial. Average error rates in some conditions were significantly lower (B, 0.5, 1, 2 & 15 Hz, C: 1, 4 & 15 Hz) or higher (A: 0.5 Hz) than the no-stream control trial. Error rates tended to decrease during the temporal streams and showed no tendency to increase at 8.1 and 15 Hz, against a motor-error explanation for the results of Experiment 1.

Experiment 3: Eye movements during binocular rivalry and auditory temporal streams

Loud, perceptually salient sounds could potentially provoke an orienting response including eye movements and/or blinks. Voluntary saccades can increase binocular rivalry alternation rate (van Dam & van Ee, 2006). It is possible therefore that increased eye movements contributed to the effects reported in Experiment 1. In order to test whether an increase in eye movements accompanies the speeding of binocular rivalry in the presence of transient auditory streams, pupil velocity and blinks were measured

during the conditions tested in Experiment 1 for streams of tones and white-noise bursts. For comparison, contrast increments and the audio-visual condition were also tested.

Materials and method

Stimuli: The four types of transient event streams used in Experiment 1 were again tested: contrast increments, tones, white noise bursts and an audio-visual condition combining the contrast increments and tones. To better reveal differences between these conditions, only periodic 15 Hz temporal streams were tested as this rate produced the most effective increase in binocular rivalry alternation rate.

Procedure: Binocular rivalry between the orthogonal sine wave gratings was recorded during a baseline condition that included no transient events as well as the four 15 Hz temporal stream conditions. The five conditions were tested in a sequence of 1-minute trials while observers wore head-mounted eye tracking goggles. The procedure was otherwise identical to that reported in Experiment 1, except for the eye-tracking goggles and calibration of the eye tracking system prior to each trial.

Apparatus: The eye tracking hardware and software was the same used and reported in Macdougall & Moore (2005) with the exception that only positional eye movements were recorded, not head movements. The goggles were constructed using commercially available materials including lightweight swimming goggles (Aquasphere Seal, Genova, Italy) and two firewire (IEEE 1394) digital cameras (Firefly; Point Gray Research, BC, Canada). Weighing 146 g, these goggles are lighter than standard headmounted eye tracking devices making them optimal for recordings in the field. An IR light-emitting diode (HSDL-4220; Hewlett-Packard, Houston, TX) illuminated the left eye. An image of the left eye was projected to the camera via a dichroic mirror placed in front of the eye (Wideband Hot Mirror, OCLI, CA). This mirror allowed visible light to pass through but reflected the IR band light illuminating the eye to the camera above. The cameras were connected to a PCMIA firewire card (IEEE-1394 CardBus PC Card CBFW3U; Ratic Systems International, San Jose, CA) inserted into the PC slot of a second desktop PC.

Eye movements were calibrated with the aid of a 10 cm diameter fixation cross presented on the CRT monitor. The cross bisected the rival stimuli at its origin.

Software and Calibration: A program written in Labview G (National Instruments, Austin, TX) was used to record the eye movement data at a sampling rate of 200 Hz. Images of the eyes were recorded at a visual refresh rate of 30 Hz. A “center-of-mass” algorithm was used to determine the center of the pupil. Using a spherical model of the eye, Fick coordinates were used to calculate horizontal and vertical eye position. The radius of these coordinates was determined by the measurements taken during calibration to the 10 cm fixation cross at the start of each trial. Central fixation was specified by the center of gaze relative to the eye tracker, not to a fixed point on the monitor. This point was calibrated while the subject fixated on the center of a binocular cross with horizontal and vertical arms subtending 10 degrees visual angle. Calibration of the cardinal axes was made when subjects fixated the outer edges of the cross and diversions of the eyes +/- 5 degrees visual angle from the center of the binocular rivalry gratings.

Subjects: Six subjects participated; five of which participated in Experiment 1, and an additional naïve subject who had not participated in any of the previous experiments.

Results

Replicating the binocular rivalry data from Experiment 1, alternation rates significantly increased while 8.1 and 15 Hz auditory streams played ($F(4, 4.02)$, $p < .05$).

For each trial, eye movement magnitude was calculated by dividing each distance by the maximum distance recorded in the trial to give a proportion between 0 and 1. This was done on the horizontal and vertical eye movements separately which are plotted as a magnitude between +/- 5 degrees visual angle in Figure 4. A threshold analysis was performed on combined horizontal and vertical data sets giving the total number of deviations from central fixation 75% above background noise. The total eye movements divided by the trial period yields the frequency of eye movements during each trial. A within-subjects one-way ANOVA was performed to detect any significant changes in eye movement frequency across the different conditions tested.

Figure 4. Eye movements during binocular rivalry during auditory and visual temporal streams

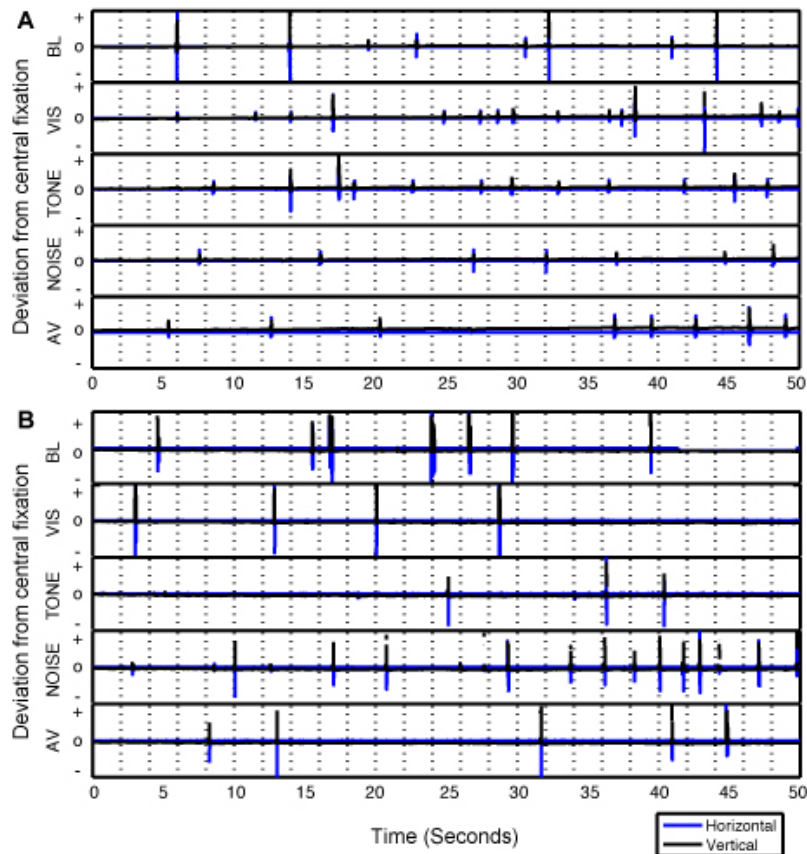


Figure 4: Horizontal and vertical eye movements are shown for 2 of the 7 participants (A & B). Five binocular rivalry conditions were tested: binocular rivalry accompanied by contrast, tone pip, white noise and audio-visual temporal streams, all with a 15 Hz cycle rate, as well as a control, no-stream binocular rivalry condition. Increases in eye movements occurred for some observers in some conditions, but no systematic pattern was found across conditions.

Eye movement counts did not significantly differ across conditions ($F(4,1.61)$, $p > .05$); although, as can be seen in Figure 4, there is a tendency for increased eye movement frequencies during tone pip and audio-visual conditions for some subjects. Inspection of the individual data suggests that a small fraction of subjects experience increased eye movements during some sound conditions but not others. These increases were not statistically significant.

Discussion

Eye movements due to an anxiogenic stimulus such the repetitive 72 dB sounds used in the current experiments are expected, however only slight, non-significant increases were found. Eye movements therefore do not underlie the increases in binocular rivalry rates during auditory temporal streams. This result, together with the results of Experiment 1 and 2, point away from a role of the startle or orienting reflex in boosting binocular rivalry alternation rates at 8.1 and 15 Hz. The succession of sounds used was effective at priming against the reflex, as has previously been reported; pre-pulse presentations attenuate the startle reflex (Blumenthal & Goode, 1991). Startle-induced key press errors and eye movements do not account for the affect of auditory temporal information in speeding binocular rivalry.

Although evidence of the startle reflex is missing, another way to measure its influence is with observers in altered states of consciousness. People with schizophrenia experience impaired habituation of startle responses (Braff, Grillon & Geyer, 1992), particularly to auditory stimuli. They also experience a markedly different pattern of binocular rivalry alternations that do not conform to parameters established in control groups. This is also true for individuals under the influence of psilocybin, a hallucinogenic drug (Carter et al., 2005, 2007). If the speeding were due to the startle response repeating the current experiments on these participants is expected to show enhanced or unique effects. It is still possible that eye movements are related to the speeded binocular rivalry alternation effects reported in Experiment 1 but are not the primary cause of it. The slight increase in eye movements in the tone event stream conditions may be a parallel consequence of a shared, general source of the rivalry speeding: increased physiological arousal. Elevated general arousal might account for both the slight eye-movement increases and the rivalry speeding and any interaction of the two may be peripheral in the effect of sound over binocular rivalry. The lack of increased eye movements in the temporal stream conditions does not rule out the possibility that other eye movements not measured here, such as micro-saccades, contribute to the results of Experiment 1. This would need to be clarified with more sensitive eye movement recording. Although a limited data set prevents any firm conclusions from being made, it suggests that temporal

sound streams might affect eye movements, but are not the primary cause of increased binocular rivalry alternation rates found under the 15 Hz auditory streams. If increased general physiological arousal is a more likely cause, the auditory streams tested are expected to affect more distributed perceptual processes, such as our experience of time, which is the subject of the next experiment.

Experiment 4: Perception of duration during auditory and visual temporal streams

The results of the preceding experiments support previous evidence that distributed neural processes affect the overall rate of binocular rivalry fluctuations (Carter et al., 2005, 2007 and Nagamine et al., 2007). The source of these processes lie beyond those specific to vision, as the significant auditory influence on binocular rivalry rates reported here shows. However, the auditory influence reported in the previous experiment also exhibited a strong temporal-frequency dependency, with higher frequencies producing the greatest effects. The aim of Experiment 4 is to explore other aspects of audio-visual temporal processing to further elucidate the basis of the effect of fast auditory streams on binocular rivalry rate. To test whether the sound events used alter subjective perception of duration, a duration discrimination task was carried out using visual and auditory stimuli identical to those used in Experiment 1.

It has previously been reported that intervals containing high frequencies of auditory or visual events are perceived as lasting longer than intervals equivalent in duration containing fewer or no events (Treisman, Faulkner, Naish & Brogan, 1990; Johnston & Nishida, 2001; and Johnson, Arnold & Nishida, 2006). This experiment attempts to test these effects using the auditory stream and binocular rivalry stimuli used in Experiment 1. If the processes involved in time perception and bistable dynamics are shared, auditory temporal streams are expected to distort perceived duration in a similar way to binocular rivalry reversal rates

Materials and method

Stimuli: A duration discrimination task was carried out using the same visual and auditory stimuli as used in Experiment 2. Each grating was presented separately in two

intervals, with or without accompanying contrast increments or auditory streams. A 1 cm fixation cross was present at all times during trials and white Arial font 14 point text ('Interval 1' and 'Interval 2') were used between the intervals to warn subjects that an interval was beginning. The temporal stream stimuli tested were the tone pips and contrast increments and both periodic and the low temporal uncertainty (LTU) random jitter streams tested in Experiment 1.

Procedure: In the two-interval duration discrimination task, a horizontally oriented grating of 48% contrast was presented that was identical in all other respects to those used before to induce binocular rivalry. One interval always contained a grating with a standard 2 Hz periodic event cycle. The 2 Hz interval was either visual or auditory depending on the condition and was used as a standard to which the faster test interval was compared. The duration of the 2 Hz intervals was 2 seconds, with a random duration in the range of 0-500 MS added or subtracted (to prevent event counting strategies). The comparison interval contained a grating at faster temporal streams of 3.9, 8.1 or 15 Hz depending on the condition (either tone pips or contrast increments, as used in Experiment 1). The subject's task was to indicate which interval seemed longer. Using an adaptive staircase procedure (QUEST) with a minimum of 75 trials per session, the duration ratio between the standard and comparison intervals was varied above or below equivalence (a ratio of 1). Incorrect responses drove the duration ratio further from unity, while correct responses reduced the ratio towards unity and closer to physical equivalence. The QUEST procedure varied the duration ratio and converged on the point of subjective equality (PSE) where the intervals were perceived as being of equal duration. Each temporal frequency was compared to the 2 Hz standard in separate sessions.

Subjects: Five observers participated in the experiment (aged 26-43, 3 female, 2 male). All but one participated in Experiment 1, including the author (AP) and subjects 1, 3 and 7. Apart from the author, all were naïve as to the hypothesis of the experiment and both S1 and the new subject (S8) were unaware of both the pilot data and the results of Experiments 1 and 2. Observers were instructed to judge only the duration of the visual

stimulus when making their comparisons and not to use any conscious strategy (such as counting, tapping, etc.).

Figure 5. Subjective duration of auditory and visual temporal stream intervals

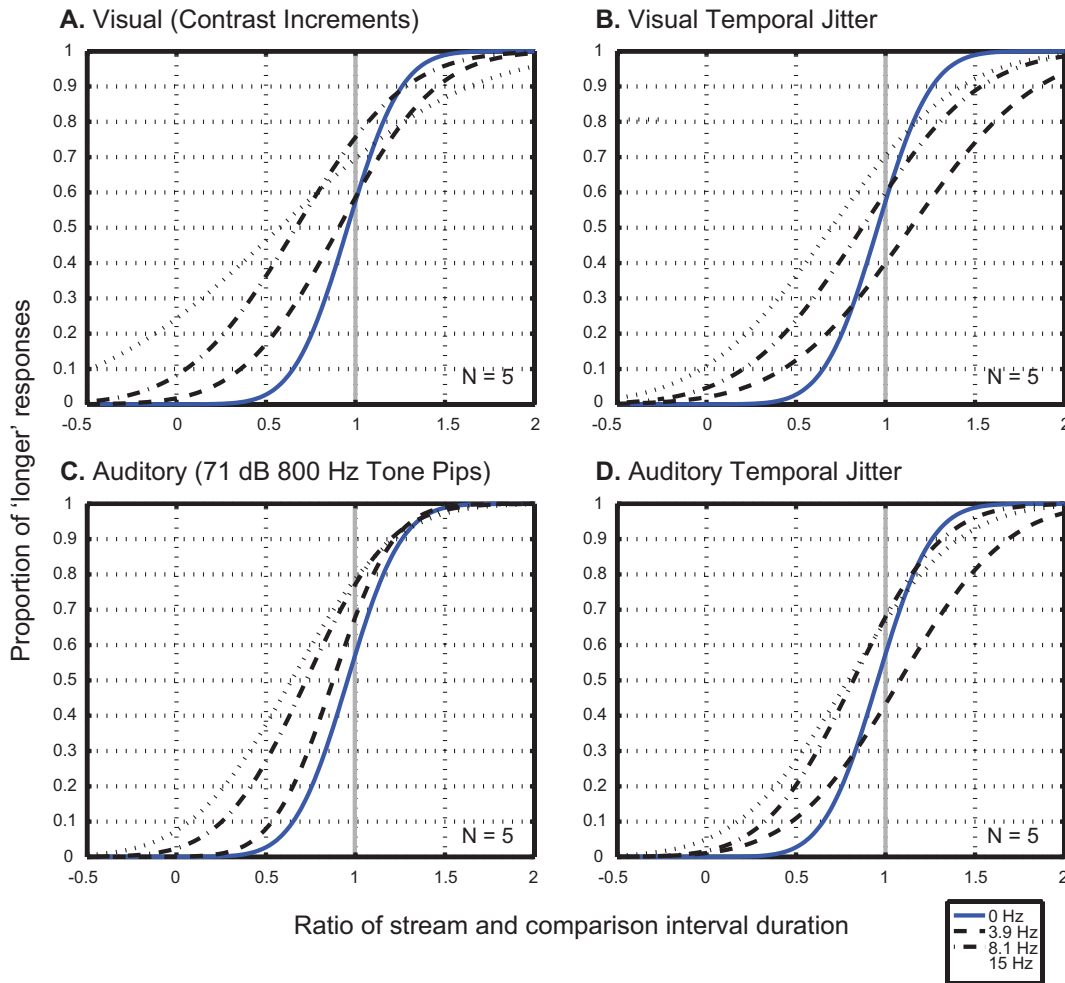


Figure 5: Psychometric functions from Experiment 4 showing performance on the duration discrimination task (5 observers pooled, minimum 75 trials per observer and condition). The x-axis shows the ratio of the standard to the comparison durations. The point of subjective equality shifts to the left as the temporal frequency of the event streams increases, indicating an expansion of perceived duration of the comparison interval relative to the standard. The blue solid lines show performance for two static-grating intervals, where no distortion was expected. Intervals containing 15 Hz temporal streams were perceived as equivalent in duration to a 2 Hz stream interval when they were objectively 60-75% shorter than it. Similarly, 8.1 Hz stream intervals needed to be around 30-50% shorter than the 2 Hz comparison intervals to be perceived as equal in duration.

Results

Figure 5 plots the thresholds for subjective equality between the duration of the standard and comparison intervals at the 3.9, 8.1 and 15 Hz temporal streams tested; streams (A) contrast increments (B) tone pips with (C) periodic and (D) LTU randomly jittered temporal cycles. Frequencies of 3.9, 8.1 and 15 Hz event streams are effective at dilating the perceived duration of the comparison intervals relative to the 2 Hz standard. The point at which 15 and 2 Hz intervals are perceived as equal in length is when the faster 15 Hz interval is 30-50% shorter, as can be seen in Figure 5 where the 15 Hz dotted line intersects with 0.5 proportion of longer responses. This distortion also occurred for the 3.9 and 8.1 Hz streams, and for all temporal stream stimuli, including the contrast increments. This pattern occurred in all of the individual observers.

The dilation effect observed means that intervals containing increasingly faster cycles of events required significantly shorter presentations of the 2 Hz standard in order to be perceived as equivalent in duration (main effect of cycle rate $F(3,11.79)$, $p < .05$). There was no significant difference between the tone-pip and contrast-increment events in their ability to dilate perceived duration (main effect $F(1,1.26)$, $p > .05$), showing that auditory and visual event streams distort temporal judgments to the same extent. Dilation occurred with all comparison temporal frequencies tested (Helmert contrasts comparing control versus 3.9 Hz: $F(1,15.74)$, $p < .05$, 3.9 Hz versus 8.1 Hz: $F(1,23.28)$, $p < .01$, 8.1 Hz versus 15 Hz: $F(1,4.49)$, $p > .05$).

The randomly jittered (LTU) 3.9 Hz cycles were not as effective as the periodic 3.9 Hz cycles in distorting duration judgments, but at all higher event rates both cycle patterns (periodic and LTU) were equivalent (main effect of cycle pattern: $F(1,12.514)$, $p < .05$; interaction with event rate: $F(2,6.48)$, $p < .01$. Helmert contrasts on interaction effect: 2 Hz standard versus 3.9 Hz: $F(1,12.51)$, $p < .05$; 3.9 Hz versus 8 Hz: $F(1,6.67)$, $p > .05$; 8.1 Hz versus 15 Hz: $F(1,0.63)$, $p > .05$). The reason for the difference between cyclic and random patterns only emerging at 3.9 Hz is not clear, but may be due to the longer cycle period at 3.9 Hz, relative to 8.1 and 15 Hz. Since the LTU randomisation involved jittering the temporal position of each event within its event cycle period, there is larger

scope for uncertainty with the slower 3.9 Hz event rates than the higher ones. Also, the broadening of the temporal frequency spectrum that occurs with the LTU events reduced the overall temporal frequency in this condition. These results are consistent with the equivalence of randomised and periodic event streams tested in Experiment 1. Overall it is the temporal frequency of events, not the pattern of events, that influences binocular rivalry rate and duration discrimination.

Discussion

Adaptation to visual temporal rate can dilate perceived visual duration in a spatially local manner (Johnson, Arnold & Nishida, 2006), evidence for a specifically visual component in perceived visual duration of the kind measured in the current experiment. The discrepant ability for visual streams to affect duration discrimination, but not binocular rivalry dynamics, indicates that local visual adaptation contributes to the effects reported here. However since non-visual (auditory) temporal information replicates Johnson, Arnold & Nishida's results, a cross-modal timing process must also be at work. Binocular rivalry is also strongly tied to local visual processes in the primary visual cortex and adaptation at that level is thought to play a significant role in determining alternation rate (Lehky, 1988; Blake, Sobel & Gilroy, 2003; Wilson, Blake & Lee, 2001; and Alais et al., 2010). With this in mind, the effects of sound in the current experiments might be due to auditory-elicited visual potentials. Sounds can elicit evoked potentials from cortical electrodes normally associated with visual evoked responses and might do so during rivalry and other visual processes, which could be tested in the future with an EEG experiment.

Auditory event streams have been shown to distort temporal judgements previously (Treisman, Faulkner, Naish & Brogan, 1990) as have links between temporal judgements and binocular rivalry effects also been reported. The magnitude of change in the subjective perception of speed accounts for contextual effects of a motion surround on binocular rivalry (Baker & Graf, 2008). Parallels exist between this and the present results; both temporal duration judgements and binocular rivalry rate are modified by temporal information. The results of Experiment 4 mirror those of Experiment 1 with the

exception that significant time dilation did occur for the contrast increments and the lowest comparison event rate of 3.9 Hz (although only for the periodic cycle, not the randomised LTU cycle) that was not effective at altering rivalry rates in Experiment 1. The difference in the influence of the 3.9 Hz streams and the contrast increments is possibly due to the shorter time intervals used in the duration discrimination task. In conclusion, auditory temporal streams alter the temporal dynamics of binocular rivalry alternations as well as perceived visual duration, and arguably do so by acting on distributed physiological processes involved in alertness and attention.

General discussion

In summary, temporal auditory information can alter the pace of binocular rivalry when presented with fast streams of events (8 and 15 Hz) but not slower ones between 0.5-4 Hz (Experiment 1). None of the auditory streams entrained binocular rivalry alternations or significantly increased eye movements during the binocular rivalry trials (Experiment 3) and neither did they provoke significantly more motor-response errors compared to normal binocular rivalry tracking (Experiment 2). It appears that fast auditory streams affect a timing process in binocular rivalry alternations not involved in determining individual swaps, but rather the overall temporal frequency of alternations during 1-minute periods. They also affect a timing mechanism involved in the subjective experience of duration (Experiment 4), pointing to the role of elevated general arousal rather than auditory driving of vision or the startle reflex in the present results. Auditory event streams have been shown to distort temporal judgements before (Treisman, Faulkner, Naish & Brogan, 1990), that they can consistently distort timing processes involved in binocular rivalry is a new finding. These results follow from previous studies showing that sound strongly influences visual processing in the temporal dimension (Recanzone, 2003 and Recanzone & Sutter, 2008) and that cognitive resources involved in binocular rivalry interact cross-modally (van Ee et al., 2009; Alais et al., 2010). Together the results of the four experiments - the superiority of fast streams, lack of entraining and no evidence of the startle reflex - point to increased general arousal induced by auditory temporal streams that persists in the presence of the stream. The sounds used were salient (72 dB SPL) and although they appear not to produce startle

blink responses they were informally reported as mildly irritating by subjects after some auditory conditions.

The scope for temporal auditory information to alter binocular rivalry alternations is likely to be limited by processes specific to the inter-ocular conflict. Although reliably increasing alternation rate at fast cycles, the presence of sound streams did not entrain the pattern of perceptual alternations - no trend toward periodicity in the alternations emerged. Stochastic independence between each eye's percept durations was preserved in these experiments. Forcing a state change with a visual transient has been examined before. Transient visual events initially disturb the inhibitory-adaptive balance by forcing awareness to a particular eye but a return to stochastic alternations eventually returns (Blake, Westendorf & Fox, 1990). That the periodic sound streams used here did not entrain the temporal pattern of rivalry into a more rhythmic state points to a limit in the ability of higher-order influences to alter rivalry dynamics. These results support other evidence that rivalry dynamics are constrained by inhibitory-adaptive links between monocular neurons present in early visual cortical areas (e.g. Wilson, 2003; Alais et al., 2010). The temporal dynamics of other forms of bistable visual phenomena without early hard-wired competitive mechanisms, e.g. the Necker cube, are expected to be more susceptible to auditory entraining given the increased sensitivity of other forms of bistable stimuli to the higher-order effects of voluntary control compared to binocular rivalry (Meng & Tong, 2004).

The source of higher-order effects in this research appear similar to the influence of generalised anxiety disorder on binocular rivalry rates reported by Nagamine et al. (2007). It is possible that auditory streams affect distributed brain wave activity corresponding to states of increased alertness that are enhanced in anxiety disorder. Periodic auditory signals can entrain brain waves recorded with EEG (Will & Berg, 2007). The most effective temporal cycles used in the current Experiments (15 Hz) are in the beta brain wave frequency range of 13-40 Hz which is associated with increased levels of alertness and even states of panic (Sanei & Chambers, 2007). Beta frequencies have also been linked to the timing of binocular rivalry alternations; large changes in

power in the beta range (14-30 Hz) occur at the time of perceptual alternations (Piantoni, Kline & Eagleman. 2010), Given a stochastic resonance model of bistable dynamics (Kim, Grabowecky & Suzuki, 2006), even modest amplification of activity in the beta frequency range could account for the present results, as an increase in the overall power of beta-wave oscillations would lower the threshold for binocular rivalry alternations to occur.

Conclusion

The results of the experiments presented in this manuscript demonstrate a clear but circumscribed effect of rapid, 15 Hz auditory streams on overall binocular rivalry alternation rate. The effects are consistent with both local and global contributions to the temporal dynamics of bistable perception, as temporal markers of local adaptation such as the stochastic independence of each alternation period were preserved during the auditory conditions. As direct audio-visual entraining was not found, it is believed that the fast sound streams impacted binocular rivalry rates via elevations of general physiological arousal. This mechanism does not appear to be mediated by increased eye movements or motor response errors however it is also present during a duration discrimination task, contributing to other evidence of the involvement of a general timing mechanism in bistable perception.

Acknowledgements

Thanks to Hamish McDougal for providing the head mounted eye tracker and recording software.

*Chapter 6***General discussion**

The hypothesis stated in Chapter 1 of this thesis asks whether binocular rivalry is a product of a distributed neurological mechanism; and, if so, is this the same mechanism that underlies exogenous selection-for-attention? The research presented addresses the possibility of a common mechanism underlying all bistable perception and examines its nature using psychophysical paradigms such as tracking of bistable alternations, probing sensitivity during suppression and measuring flash suppression thresholds. The distributed processes under consideration in the current thesis include temporal processing, orienting of attention and cross-modal sensory interactions – all of which are modality agnostic and, therefore, suitable for inferring the extent of distributed activity over the resolution of binocular conflict.

The current experimental chapters add to what is known about the mechanism behind binocular rivalry; specifically, how it behaves with respect to exogenous attention and cross-modal interactions. The experiments contained herein were designed to test the idea that a general mechanism underlies the temporal dynamics of binocular rivalry. The possibility of a general mechanism arises from the fact that bistable alternations are ubiquitous across the senses. The ubiquity of bistable perceptual phenomena is such that it even occurs in the olfactory sense between two different smells presented separately to each nostril (Zhou & Chen, 2009). It has been demonstrated with auditory stimuli, which Brancucci and Tomassi review (2011), as well as tactile stimuli (Holcombe & Seizova-Cajic, 2008; Carter, Konkle, Wang, Hayward & Moore, 2008). Not only are bistable alternations ‘modality-agnostic’, the temporal pattern of alternations is remarkably similar for an individual observer across bistable stimuli of different modalities (Holcombe & Seizova-Cajic, 2008; Pressnitzer & Hu, 2006). This is also the case for the many different forms of visual bistable stimuli (Brascamp, van Ee, Pestman & van den Berg, 2005; Klink, van Ee & van Wezel, 2008), many of which were discussed in the introductory chapter of this thesis. Additional psychophysical and physiological evidence also points to the possibility that some form of general mechanism underlies all forms of

perceptual bistability, and will be discussed below in relation to the results contained in this thesis.

Brief, temporal stimuli - designed to engage subconscious arousal systems responsible for selection for attention - feature strongly in many of the experiments. The strong temporal signals used in Chapters 3, 4 and 5 all demonstrate a strong influence of transient events over rivalry alternations, even when they had little or nothing to do with the binocular conflict, such as the tone and white noise streams used in Chapter 5. Together with the results of Chapter 2, on the similarities and differences between binocular rivalry and pattern rivalry; and Chapter 3 and 4, on the effect of exogenous and endogenous attention; this research contributes to previous evidence that binocular rivalry is influenced by distributed neural processes. Whether or not the distributed processes in question are the same as those networks underlying selection for attention in normal viewing circumstances cannot be conclusively settled by the current results. The results point, rather, to local (or stimulus specific) mediation of binocular rivalry that is under the influence of distributed processing, as opposed to centrally caused by it.

Nonetheless, this interpretation does not exclude the possibility that identical patterns of activity within sensory specific processing areas cause the similarity in bistable temporal dynamics across its different forms. These patterns may arise from a similar temporal course of inhibition and adaptation in sensory neurons found across the brain in visual, auditory, tactile and olfactory areas. Unfortunately, testing this possibility is out of the scope of this thesis, but it is a feasible theory for future exploration.

Local and distributed processes in binocular rivalry

Visual processing in the brain is both modular and distributed. Although particular areas of the occipital lobe respond best to specific visual attributes – such as colour, orientation or motion (listed in Zeki & Bartels, 1998) – the activity of these areas is influenced by what is happening in other visual processing areas, as well as other non-visual areas of the brain. A review by Kayser and Logothetis (2007) of the cross-modal influences on early sensory areas, such as area V1 of the visual cortex, attests to this and that these

early intersensory interactions are far more widely present than was previously thought. How these interactions give rise to cognition and perception is a complex problem that requires continued experimental work. A useful paradigm for this work is binocular rivalry because it provides an excellent means to infer how disparate neural events contribute to visual awareness and the physical stimulus used to induce rivalry can be highly controlled, and the subsequent perceptual outcome reliably tracked (both with psychophysical and physiological methods).

In order to examine the extent of stimulus specific (i.e. local or modular) versus distributed processing during bistable perception, the first experimental chapter (Chapter 2) explored the similarities between binocular rivalry and another form of perceptual bistability called monocular rivalry. Perceptual alternations in monocular rivalry arise between conflicting patterns overlaid and presented similarly to both eyes, rather than conflict between two different images presented separately to each eye, as is the case with binocular rivalry. During monocular rivalry observation, perception of the two fused patterns does occur, which does not happen with binocular rivalry stimuli. The fact that monocular rivalry does not require binocular conflict to occur confers its name, although it is also known simply as ‘pattern’ rivalry. The comparisons made between binocular rivalry and pattern rivalry in Chapter 2 revealed many similarities. These can be interpreted as evidence for the involvement of a common bistable mechanism, as has also been inferred from previous similar studies (Brascamp, van Ee, Pestman & van den Berg, 2005; Klink, van Ee & van Wezel, 2008). There was also evidence from the experiments of Chapter 2 comparing monocular and binocular rivalry that not all processing is common, such as the large difference in depth of suppression between the two bistable phenomena.

Supporting the other studies showing similarities between different forms of bistability (Zhou et al., 2004; Brascamp et al., 2005; and Klink, van Ee & van Wezel, 2008), the pattern of results in Chapter 2 again show that there are indeed similar dynamics between these different forms of perceptual bistability. However the extent that a common mechanism determines bistable perceptual alternations is limited by the involvement of

processing specific to the physical nature of the bistable stimulus; in the case of binocular rivalry, inter-ocular processing occurring in early visual cortical areas V1. For instance, computation modeling evidence (Wilson, 2003) suggests the particular time course of binocular rivalry alternations is linked to the time-course by which monocular and binocular neurons in the early striate cortex (area VI) adapt and interact with each other. However, both the computational modeling and other psychophysical experiments utilising measures of the depth of binocular rivalry suppression (such as Alais & Parker, 2006) show that the nature of the stimulus used, beyond simple binocular competition, can also contribute to the depth of binocular rivalry suppression. More complex stimuli activating extrastriate visual areas are more deeply suppressed (Nguyen, et al. 2003).

Stimulus- versus eye-based suppression

The distinction between binocular competition and the contribution of the type of stimulus used to elicit binocular rivalry can be characterized, respectively, in terms of ‘eye-based’ and ‘stimulus-based’ competition. Eye-based competition refers to the inhibitory competition between monocular neurons involved in binocular vision; and stimulus-based competition refers to the higher-order properties of the visual stimulus, such as motion or type of object depicted. These terms are another way of referring to the relative contribution of what is previously called local and distributed processing in this work. Although a standard binocular rivalry stimulus always involves some component of eye-based processing, stimulus features can exert an additional influence over the alternating perception. Flicker-and-swap rivalry, where the dominance of one image persists when it is swapped between the eyes, seemingly isolates the stimulus-based component of binocular rivalry suppression (Leopold & Logothetis, 1996). However, this type of rivalry stimulus is only effective when it is flickered on and off at 18 Hz or so, a flicker rate thought to override inhibitory binocular interactions (Wilson, 2003). Despite this, there is other evidence that stimulus-based rivalry occurs during binocular rivalry.

Bartels and Logothetis (2010) demonstrated that the likelihood that eye or stimulus dominance would persist after a physical swap is dependent on the time lag in the

binocular rivalry cycle, showing that eye and stimulus competition have different relative contributions to binocular rivalry depending on how long ago the last perceptual reversal occurred. This variability may be linked to fluctuations in suppression depth that correspond to the current level of stimulus inhibition in the rivalry cycle, as measured by Alais, Cass, O'Shea and Blake (2010). Despite the reason, Bartels and Logothetis' results show that stimulus-based dominance can occur without fast flicker (also reported by Bhardwaj, O'Shea, Alais & Parker, 2008); the fluctuation between stimulus and eye based suppression across the viewing period demonstrates that there is both local and higher-order suppression occurring during observation of standard binocular rivalry stimuli.

The general consensus among the body of research is that there are both local, or eye-based, and high-level, or stimulus-based, components of binocular rivalry suppression. The study of the role of stimulus-based processing during binocular rivalry overlaps somewhat with the role of stimulus-based attention. A lot of the evidence for the role of stimulus-based processing during binocular rivalry comes from examining the role attention to stimulus features has over binocular rivalry dynamics.

Attention as a distributed process operating on binocular rivalry

Some aspect of the temporal pattern of binocular rivalry will always be confined to the underlying neurophysiology of binocular combination. The temporal course by which binocular signals are resolved and integrated with each other appears to limit the degree to which binocular rivalry can be modulated by distributed processes, such as willful attention or stimulus-congruent cross-modal signals. No amount of attention or trying can hold one binocular rivalry percept over the other indefinitely, although there appears to be an exception to this; studies using Tibetan monks as observers have found incredibly long dominance periods for one stimulus – up to 20 minutes (Carter et al., 2005).

Buddhist monks are quite an unusual population; they spend a great deal of time with their eyes closed in meditation as well as honing their ability to see things 'as they are' rather than how they are 'constructed' by previous experience or presumption. This

unusual perceptual existence could impair stereoscopic (and other visual) functioning as it exists in the majority of people that lead less reclusive, less contemplative lives than the monks, rather than produce an enhanced ability to control rivalry alternations with attention. If this were the case, the monks' anomalous binocular rivalry results can not be generalised to normative models of visual processing. Another explanation is that the monks are experiencing extremely low levels of physiological activity, which substantially reduces their binocular rivalry rate. Physiological measures of meditating monks have shown reduced somatic activity (Dillbeck & Orme-Johnson, 1987). Monks also demonstrate moderated EEG responses to negative stimuli (Aftanas & Golosheykin, 2005). If general physiological arousal underlies the overall temporal rate during binocular rivalry, as is argued in Chapter 5 and discussed later in this chapter, it makes sense that these 'almost hibernating' monks would be experiencing extremely slow binocular rivalry cycles due to their underactive arousal systems. This explanation might also account for the slower rivalry alternations experienced by observers with bipolar disorder (Miller et al 2003).

Aside from data taken among unusual populations, research has shown that wilful attention is less effective over binocular rivalry dominance durations than other forms of bistable perception that do not involve binocular conflict (Meng & Tong, 2004). Electrophysiological data also suggests that the influence of endogenous control is reduced during binocular rivalry viewing compared to pattern rivalry (Mishra & Hillyard, 2009). This difference can be explained by the involvement of relatively non-conscious neural circuitry in binocular processing, as opposed to the more conscious aspects of perceiving colour, shapes and forms. Bistable stimuli that rely on conflict between object interpretations (such as the face/vase illusion) or orientation (as with monocular rivalry) feature visual components open to conscious visual appraisal under normal viewing conditions.

Although the effect of endogenous, or wilful, attention is somewhat limited during binocular rivalry (Meng & Tong, 2004), susceptibility to the influence of exogenous or stimulus-driven attention should be considerable if bistable perception relies on the same

subconscious neurological mechanism as that underlying automatic visual selection for attention. The possibility that binocular rivalry and visual selection for attention share the same neural hardware is reasonable given that binocular rivalry (and all bistable phenomena for that matter) is an attempt to resolve ambiguous sensory input, and involves deciding what should be attended to at any one instance. In everyday sensory experience, these selection decisions are made all of the time. The difference with binocular rivalry is that a final, stable decision cannot be reached due to the equivalence of the two possible interpretations. If this relationship to visual selection exists, it is expected that salient stimuli that orient attention – such as loud noises or objects on an impending collision course with the observer – would impact on binocular rivalry much more strongly than has been demonstrated with endogenous attention.

The role of exogenous attention during binocular rivalry

The preponderance of research on the role of attention during binocular rivalry has been largely restricted to self-directed, wilful or ‘endogenous’ attention; i.e. ‘purposeful attention’ generated from within. Less research has focused on the role of exogenous attention (some examples being Ooi & He, 1999 and Paffen & Van der Stigchel, 2010). Even so, there is enough to indicate that exogenous attention has a very strong impact on binocular rivalry, even when exogenous attention *per se* is not specifically under examination.

Stimuli that intrinsically capture our attention, when presented to one of the eyes during binocular rivalry, can predominate over stimuli that do not command such attention (Sheth & Pham, 2008). These stimuli include things like faces showing marked emotions (Alpers & Gerdes, 2007). Stimuli that are accompanied with an exogenous cue are also likely to be the first seen at the start of a binocular rivalry observation session (Mitchell, Stoner & Reynolds, 2004; Chong & Blake, 2006). Not only do exogenous stimuli prolong predominance when consciously available, they also appear to be able to penetrate through suppression (Ooi & He, 1999) and produce an alternation (Paffen & Van der Stigchel, 2010). If exogenous attention can influence binocular rivalry through suppression, it is unlikely that feedback from higher-order visual processing areas is the

only distributed influence over rivalry. It seems reasonable to invoke a role for unconscious (perhaps subcortical) neural networks in the disruption of binocular rivalry suppression. Whether or not this role is ongoing and underlies suppression dynamics continuously during regular binocular rivalry observation sessions – or whether it only occurs when a relevant stimulus is present – is open to additional inquiry.

The hypothesis that exogenous attention is more effective at modulating binocular rivalry predominance than internally driven, or endogenous, attention was the subject of Chapters 3 and 4. In Chapter 3, looming motion – a strong cue for exogenous attention – was expected to predominate during binocular rivalry. Given the limited effects over binocular rivalry reported with endogenous attention, and the possible relationship between binocular rivalry and visual selection mentioned, this kind of exogenous attention was expected to influence binocular rivalry predominance in the absence of endogenous attention. This was found to be the case, as there was a large bias for looming motion stimuli to be seen during binocular rivalry compared to an equivalent (and even faster) motion of the opposite direction presented to the competing eye.

In using a ‘looming’ motion stimulus, balanced by an equivalent motion signal of an opposite motion direction in the other eye (contracting motion), the tendency for motion strength to predominate was dissociated from motion direction. The strong predominance for the forward, looming motion during binocular rivalry supports connections between bistable perceptual selection and selection for attention in normal, non-binocular rivalry viewing. Rapidly approaching motion is perceptually salient, and processed by neurons in the superior colliculus of the brainstem – an area responsible for quickly orienting to environmentally important objects and events (Wurtz & Albano, 1980), as well as in cortical areas responsive to motion stimuli (e.g., MST). It was so salient during binocular rivalry that slower 1 Hz cycles of looming motion predominated over the faster 3 Hz contractions. It should be noted that the realism of the looming cycle is potentially reduced at the faster cycle stream, which explains the superiority of the slower cycle over the fast one without diluting the interpretation that exogenous attention is at play.

The effect of looming stimuli reported in Chapter 3 was strongest for motions presented with concentric gratings, and weaker for dot motion arrays. This difference presumably occurs because dot motion arrays correspond to optic flow fields corresponding to passage through the environment – such as walking or running (a neutral environmental experience) – whereas the contours of a concentric grating correspond to objects that approach an observer independently of their own movement (posing a possible threat to bodily integrity). Expanding motion arrays are afforded a greater neural representation than contracting motion in the visual areas of the brain (Graziano et al., 1994; Berman & Colby, 2002) presumably due to the greater perceptual experience of expansion during self motion across the lifespan and greater processing need. However, given the different results obtained with dot-motion arrays and concentric gratings, it is not simply a greater neural representation of expanding optic flow that accounts for the increased predominance of looming gratings during binocular rivalry. The difference points to a specific influence of exogenous attention: it must be an object approaching – not just expanding motion that is associated with optic flow – in order to engage exogenous attention and have an impact over binocular rivalry predominance durations. A recent study supplements this interpretation by demonstrating a high degree of attention control over rivalry with motion stimuli that engage ‘vision for action’ (Hugrass & Crewther, 2012).

The neural area responsible for achieving the orienting or startle response displays cross-modal summation (Yeomans, Li, Scott & Frankland, 2002) whereby a looming signal presented in more than one sensory modality – for instance both visual and auditory senses – will produce a greater neural response than either the visual or auditory responses alone. The possibility of cross-modal summation of the effect of looming found in Chapter 3 was explored in Chapter 4, which examined the effect of looming *sounds* on the predominance of looming visual motion in binocular rivalry. Chapter 4 examined how sounds congruent with binocular rivalry stimuli affect predominance. The experiments explored how a matching looming sound might be able to boost the effect of attention in raising one of the binocular rivalry targets to perceptual dominance. It was concluded that sounds do assist in boosting elevations in the predominance of the

matching binocular rivalry target; but they do not elevate the target's predominance in the absence of effort. That is, passive viewing of binocular rivalry in the presence of the sounds did not elevate predominance of the visual stimuli that matched the sound.

A study matching motion sounds to motion targets during binocular rivalry found that the effects of the sounds were comparable to context effects (Conrad, Bartels, Kleiner & Noppeney, 2010). In Conrad et al.'s study, directional sounds were able to extend periods of rivalry predominance, when the congruent visual motion was consciously available. The sounds did not attenuate suppression periods, unless they were directionally opposite the currently dominant visual motion. This result parallels the influence endogenous attention has over dominance periods during binocular rivalry, but not over suppression phases. This suggests that cross-modal influences on binocular rivalry act in a similar fashion to endogenous attention, by providing a boost to a dominant percept via feedback mechanisms. This goes against the expectation that looming sounds might influence rivalry via mechanisms related to exogenous attention. An automatic orienting mechanism, by definition, should be able to operate on sensory information not in the current scope of conscious awareness in order to bring it into awareness (Yin, Murray & Boynton, 2009), including suppressed binocular rivalry stimuli. Although the lack of auditory influence in the passive viewing conditions in Chapter 4 suggests that cross-modal influences over rivalry are high-level, the experimental purpose (to specifically examine how cross-modal information might boost attentional control) limit extrapolation of the results to exogenous attention.

Experiments conducted by Chong, Tadin and Blake (2005) mirror the paradigm used in Chapter 4 in that they tested whether the effect of endogenous attention over rivalry can be increased with the use of temporally salient cues. Their study used transient stimuli – such as flicker and spatial frequency changes – to elicit endogenous attention. Even though these transient stimuli did not achieve an equivalent extension of dominance during the unattended condition as compared to the purposeful attention one, nonetheless, the unattended condition produced significant extensions of binocular rivalry dominance periods (see Figure 1). This inconsistency with the results presented in this thesis are

probably due to the presence of dual sound streams in Chapter 4, which masked the effectiveness of the looming sound stream when it was not being actively attended to. Additionally, instructions *not* to attend could have been interpreted as instructions to explicitly direct attention *away* from the sound stimuli.

The component of endogenous attention allocated to a transient stimulus in the data from Chong et al. and Chapter 4 cannot be wholly separated from the survival-based attention mechanism activated by the exogenous cues that were used. It is doubtful whether wilful attention conditions that are anchored on the highly attention-grabbing stimuli used – known to be a strong trigger for exogenous attention (Franconeri & Simons, 2003) – can rightly be attributed to endogenous attention alone. The type of attention producing the effects reported could be called ‘transient-based’ attention; whether purposeful or not, the effect is dependent upon the intrinsically salient nature of the stimulus used as the object of attention. The tone pips, looming sounds and even periodic tactile vibrations used in Chapter 4 can all be classed as attention-orienting stimuli. Further, the flicker and spatial frequency changes used by Chong et al. are not ‘objects’ *per se*, but events such as changes to a feature. The idea that object-based attention is relatively ineffective at controlling dominance durations, compared to event-based attention, deserves further exploration. This can be achieved with experiments explicitly designed to pit object-based attention against event-based attention during binocular rivalry and other bistable phenomena.

Figure 1. Results from Chong, Tadin and Blake 2005

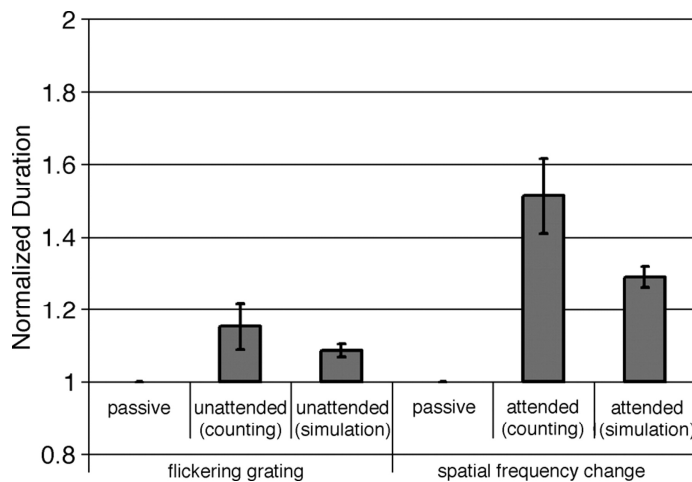


Figure 1. Results from Chong, Tadin & Blake, (2005) showing that both unattended and attended transient events increase binocular rivalry dominance durations.

The results contained in Chapter 4 – that the effect of sound over binocular rivalry predominance requires willful attention – differs from results collected using the same stimulus where instructions concerning attention were not given (Parker & Alais, 2005). In the 2005 study, subjects were simply instructed to record the visual fluctuations experienced during binocular rivalry and were given no instruction concerning the sounds (other than a non-specific warning that they might be present in any given trial). As mentioned, an explanation for this difference with the results in Chapter 4 is that the auditory stimulus used in Chapter 4 was not presented independently. Both a constant chord and the looming sound wave were presented through ear phones, requiring the participants to pay attention to one or the other sound selectively. Not only does the presence of an additional sound, competing for auditory attention, diminish the salience of the looming sound, headphone presentations also diminish its salience. In the Parker and Alais experiment, the tones were presented from two speakers on either side of the monitor. In this way the sounds appeared to emanate from a distance and simulated a realistic approach. When sounds are played via headphones they are typically experienced as emanating from within the head. This important distinction likely underlies the lack of auditory enhancement of rivalry predominance in the passive viewing conditions tested in Chapter 4. A comparison of the relative salience of headphone and speaker presented looming tones would confirm this explanation.

Rhythmic versus directional auditory influences

Control conditions carried out in Chapter 4 indicate that temporal congruency, rather than motion direction is the important factor in auditory-visual integration during binocular rivalry. The conditions comparing a non-directional auditory stimulus with an auditory temporal modulation that was phase-locked to the visual target produced equivalent results; showing that temporal consistency is a major factor in the effect of sound over binocular rivalry in the tested conditions. In fact, it appears to be the primary factor; if motion direction had an independent effect, it is expected that the conditions with both temporal and motion direction sounds would yield a greater influence over predominance. On the other hand, there could be a cap on the extent to which binocular rivalry predominance periods can be modulated, which would rule out the potential for a superior effect with directional stimuli.

Although temporal rate appears to be the determining factor in the subject's ability to use the sounds as an aid to holding one binocular rivalry target perceptually dominant, the fact that the sound consistent with the radial grating's motion did not show comparable effects means that rate is not the sole factor: motion direction, or meaning, does indeed play a role in the cross-modal influence over binocular rivalry predominance. The sound pulses used can be considered representative of some kind of object onset. Disentangling the influence of auditory motion type, or meaning, and auditory temporal rate over binocular rivalry deserves more exploration. The interpretation of the data from Chapter 4 – that temporal rate is of primary importance in auditory affects over binocular rivalry – leads into the next series of experiments contained in Chapter 5. This chapter explored the impact of temporal auditory information over the overall rate and pattern of binocular rivalry alternations, not just the predominance of one binocular rivalry target over another. These experiments were conducted to isolate the effect of temporal information (both visual and auditory) over binocular rivalry dynamics.

Given past research showing that temporal auditory information can heavily bias visual temporal perception – more so than spatial auditory information can bias visual spatial perception (Shipley, 1964; Recanzone, 2003) – Chapter 5 explored how temporal

auditory information affects the temporal dynamics of binocular rivalry. The auditory sense has a much better temporal resolution than vision. Vision, on the other hand, is superior to hearing in spatial resolution (Alais & Burr, 2006). Hearing, being a better temporal sense, lends its advantage to vision during congruent cross-modal stimulation and vice versa (Recanzone, 2003; Alais & Burr, 2004). Recent unpublished evidence (conducted in the same lab as this thesis) suggests that temporal perception is modality agnostic; that is, occurs in a centralised and distributed manner not dependent upon any one sensory modality. This ties in with the possibility that the temporal element of bistable perception is, likewise, subject to a distributed temporal mechanism or oscillator. Chapter 5 sought to address the question of whether the temporal element of binocular rivalry is determined in a modality-agnostic fashion by a centralised temporal process.

In the experiments contained in Chapter 5, streams of flashes, tone pips or white noise bursts were presented while participants experienced and recorded their perceptual alternations to the binocular rivalry stimulus. At the fastest 8 and 15 Hz presentation frequencies, binocular rivalry alternations were significantly sped up for all participants, without changing the underlying stochastic independence of the alternation periods, nor by entraining each alternation to the timing of the auditory stimuli. This generalised elevation of binocular rivalry rates was not tied to the specific temporal pattern of the sounds. Due to this, it appears that the effect of sounds over binocular rivalry is achieved via a secondary elevation in generalised arousal (or perhaps even anxiety) produced by the sounds, rather than by temporal driving of the alternations with audition.

A series of control experiments measuring the effect of the auditory stimuli on motor control, eye movements and the perception of interval duration indicate that the effect of sound was not due to errors in key press responding or an increase in eye movements, but rather, was affecting a centralised timing mechanism also involved in the perception of duration. In consideration of other results published in the literature concerning individual variability in binocular rivalry rates as a function of age (Ukai, Ando & Kuze, 2003), mental health (Miller et al., 2003), and anxiety (Nagamine et al., 2007), the pattern of results appears consistent with the idea that individual variance in binocular rivalry

temporal rate is influenced by the overall activity of the nervous system, which can in turn be modified by the presence of anxiogenic stimuli, such as a fast auditory tempo (Dillman-Carpentier & Potter, 2007).

Neurophysiological evidence for this connection can be found in a study by Einhauser et al. (2008); pupil diameter reliably predicted both a perceptual reversal and the duration of subsequent binocular rivalry dominance period. Pupil dilation is an indicator of visual interest, but also occurs when a new visual object is presented to a viewer (Loewenfeld, 1993). It is aligned with activity of norepinephrine (also known as noradrenaline) in the locus coeruleus (Koss, 1986), a part of the brainstem whose major purpose is regulation of the sympathetic nervous system and the physiological response to stress, i.e. arousal (Samuels & Szabadi, 2008). It is theorised that the overarching purpose of this network is to enable recalibration of sensory organisation; that is, to mediate shifts in attention (Bouret & Sara, 2005). This connection is consistent with the interpretation put forward regarding the results of Chapter 5 as being due to physiological arousal; if binocular rivalry and other bistable alternations are achieved by networks mediating stress and arousal responses, it is feasible that elevations of arousal will correspondingly elevate overall binocular rivalry alternation rate.

In order to confirm an arousal interpretation of the speeding of binocular rivalry reported in Chapter 5, clarification is needed on the effect that the particular transient event streams used have on physiological arousal. This can be achieved with skin conductance response or heart rate monitoring during stimulus presentation. Skin conductance response is an ideal measurement being a fairly robust measure of physiological arousal and activity of the sympathetic nervous system (Martini & Bartholomew, 2003). In lieu of the results of these future experiments, past measurements of skin conductance response during the presentation of slow and fast music scores suggest that an elevation of arousal is likely. Skin conductance response was shown to be greater for fast tempo music than slow tempos, which in turn produced greater skin conductance response than silence (Dillman-Carpentier & Potter, 2007). This increase in arousal to increased tempo is very likely to be replicated with the transient sound streams used during the binocular

rivalry trials described in Chapter 5. Whether or not this increase in turn causally increases binocular rivalry switching rate remains to be proven; yet, at this stage, it appears to be the most fitting explanation of the effect, given the pattern of results reported such as the lack of alternations time-locked to individual transient events.

An alternative interpretation of the results of Chapter 5 can be made in terms of the addition of neural noise to the rivalry mechanism. Neural noise refers to the activity of background neurons not directly involved in a specific neural process, that can still have an impact on it. It is a feature of computational models of binocular rivalry, included to account for the stochastic properties of the alternation periods (Wilson, 2003; Freeman, 2005). Evidence that principles of stochastic resonance are involved in binocular rivalry have been reported previously (Kim, Grabowecky & Suzuki, 2006), as have the ability of sounds to act as a source of resonating noise to a visual detection task (Lugo, Doti & Faubert, 2008). Together, these findings suggest the effects reported in the present work could be due to additional neural noise created by the transient event streams, rather than an increase in general arousal. This alternative interpretation requires validation, perhaps using computational and physiological methods and to quantify the amount of neural noise produced by the sounds streams and to model the subsequent influence on rivalry dynamics.

Appendix 1 and 2 present experiments and data analysis supplementary to Chapter 5. Appendix 1 presents experimental data examining the effect of brief sounds on the likelihood of inter-ocular suppression in a 1-cycle version of binocular rivalry called flash suppression (Wolfe, 1984). In these experiments, conflicting inter-ocular stimuli were not presented for an extended viewing period as in binocular rivalry. This is because flash suppression involves presenting one of the binocular rivalry stimuli to one eye first. Then after a period of time (usually around 1 second) – when the second image is presented (or flashed) to the other eye – the first stimulus becomes instantly suppressed. Instant suppression only occurs when the second stimulus is presented with enough of a latency after the first stimulus. This latency is called the stimulus onset asynchrony and allows for sufficient adaptation to the first image to occur. Thresholds for the required stimulus

onset asynchrony for complete and instant flash suppression can be measured across numerous trials by altering the asynchrony (e.g. in a staircase procedure) and recording the consequent perceptual outcome to find the asynchrony required for flash suppression.

Flash suppression thresholds were measured for the same grating stimuli that were used in Chapter 5 – with and without the presence of sounds at, or around, the time of the second stimulus's onset. It was found that the presentation of a tone just before (or synchronous to) the flashed stimulus significantly decreased the required stimulus onset asynchrony for complete flash suppression to occur. This result agrees with those reported in Chapter 5, where temporal auditory information was found to speed up temporal processes in vision. Specifically, auditory events seem to be speeding up the baseline cycle period of inter-ocular suppression. The effect of sounds on shortening the threshold time required for inter-ocular flash suppression appears to be different to the speeding effect of sounds over long-duration binocular rivalry trials. The attentional boost from the singular sound bursts might 'tip' the balance of inhibition and adaptation in favour of a perceptual switch, especially later in cycle when a swap is more probable. That this is not happening for individual alternations during binocular rivalry with continuous sound streams (as evidenced by a lack of auditory entraining) indicates that two different mechanisms are at work. The distinction lies in the difference between a persistent increase in physiological arousal with continuous sound streams and the instantaneous capture of attention achieved by isolated sounds and is discussed in more detail later in this chapter.

Is temporal rate during binocular rivalry determined by a generalised, whole-brain mechanism?

In the introductory chapter of this thesis, two interlinked hypotheses were posed. The first was concerned with whether a common mechanism underlies perceptual bistability, specifically; "*Is there a common mechanism underlying perceptual bistability; what evidence is there for the existence of this mechanism?*" The experimental chapters contained herein point to the conclusion that temporal rate during binocular rivalry is at least in part determined by a generalised mechanism. The fact that temporal rate but not

predominance in binocular rivalry can be altered by factors not relevant to the visual conflict, such as the sound streams used in Chapter 5, partially supports the first hypothesis. Physiological data also supports the role of distributed brain activity in bistable perception; activity in non-visual processing areas correlates with perceptual alternations (for example Britz, Pitts & Michel, 2011) and there are measurable whole-brain oscillatory networks that coincide with binocular rivalry fluctuations (Doesburg et al., 2009), although there is conflicting evidence, such as MEG frequency tagging data (Kamphuisen, Bauer & van Ee, 2008) showing synchronised neural activity is confined to exclusively visual areas during rivalry.

The temporal rate of binocular rivalry alternations is more open to the influence of attention than the predominance of one binocular rivalry target over the other. Attention toward or away from both rival stimuli produces variance in alternation rates (Lack, 1978; Paffen et al., 2006). It seems that there is a dissociation between the effects of attention on the spatial versus the temporal aspects of binocular rivalry – ‘spatial’ referring to the ability to bias perception of one binocular input over the other.

The temporal rate of binocular rivalry is plastic over time. Binocular rivalry settles into a stable rate for individuals after experiencing the phenomena a few times; however, alternation rate is slower and more sporadic in the first few experiences (Suzuki & Grabowecky, 2007). Binocular rivalry rate also varies between individuals and is correlated with age (Ukai, Ando & Kuze, 2003) and other variables that modulate overall somatic physiology (Nagamine et al., 2007). This flexibility suggests that the determinant of temporal rate is not intrinsic to the visual processes underlying binocular rivalry but is provided by other, shared mechanisms that govern the speed of other perceptual processes. This interpretation is supported by the data collected in Chapter 5 that rivalry temporal rate is changeable. In conclusion, it appears that the temporal rate of binocular rivalry, but not dynamics or alternation pattern, is at least partially governed by a common mechanism across different forms of perceptual bistability.

Neurophysiological evidence of distributed processing during binocular rivalry

Neurophysiological measurements can be used to infer the locus of bistable activity, especially when cause and correlation can be accounted for. Particular physiological markers have been shown to predict perceptual alternations during binocular rivalry, such as pupil dilation (Einhauser, Stout, Koch & Carter, 2008) and activity in non-visual areas of the brain responsible for sensory integration (Lumer & Rees, 1998; Britz, Pitts & Michel, 2011). There have also been studies showing that widespread, synchronised oscillations correlate with perceptual fluctuations arising from bistable stimulation (Doesburg et al., 2009). The above, and other examples, suggest that a modality-agnostic and distributed neural mechanism is involved in binocular rivalry. It is suggested that this mechanism is focused on the overall task of resolving ambiguity and in selecting objects for conscious attention, irrespective of the particular form of ambiguity encountered. Another complementary possibility is that bistable perception reflects the malfunction (or state of permanent flux) of a subconscious system responsible for selecting objects in the environment for conscious attention. A role for the subconscious system of attentional selection in bistability is supported by the behavior of the pupil response during binocular rivalry (Einhäuser et al., 2008).

It is difficult to distinguish whether activity occurring in particular areas of the brain are the locus of bistable alternations or are simply activated due to an awareness of the currently dominant image. Activity that corresponds to the conscious perceptual experience of an observer, but has little to do with achieving the actual bistable alternations, could be separated by comparing its similarity to normal, non-bistable sensory experience. Unfortunately, there may be some component of the conscious bistable percept that, although not involved in the resolution of rivalry fluctuations, produces a unique neurological trace due to the bistable presentation. Another way to determine whether specific neural activity is involved in bistable alternations is to test whether or not the activity appears causally related to alternations, for example, by appearing just prior to an alternation, or when disruption of the neural event (as with transcranial magnetic stimulation) disrupts the alternation.

Right parietal lobe activity has been found to precede perceptual reversals during binocular rivalry (Britz, Pitts & Michel, 2011). The same result was reported for bistable stimuli that did not involve binocular conflict (Britz, Landis & Michel, 2009) – implying that activity in this parietal area is common to all bistable phenomena, at least in the visual modality. Whether or not it is involved in bistable phenomena arising from the other senses remains to be examined. This possibility is not unreasonable given that the parietal lobes are involved in sensory integration across all of the senses, not just vision. The right parietal lobe is also aligned with spatially-based aspects of higher-order sensory processing, which is consistent with the view of bistable phenomena as the attempted resolution of a spatial conflict (i.e. the impossibility of two objects appearing in the same space at the same time).

A complementary investigation conducted by Zaretskaya et al. in 2010 supports a causative role for parietal activity in binocular rivalry. Transcranial magnetic stimulation (TMS) was used to disrupt parietal function during viewing of a binocular rivalry stimulus. This disruption had the effect of prolonging binocular rivalry dominance periods; that is, preventing a perceptual reversal during the TMS disruption. It would be further confirmation of the role of the parietal areas to obtain data from individuals who have experienced damage to this area of the brain; if the parietal areas are essential for perceptual alternations, it is possible that such individuals may not experience perceptual alternations at all. Measurements of parietal involvement were made with TMS and via electroencephalogram (EEG), which can not target brain areas much deeper than the cortical surface. It is possible that areas deeper in the brain are activated preceding a perceptual alternation, particularly brainstem areas involved in shifts of attention and selecting which objects should be attended to in the environment.

That activity in brain regions involved in cross-modal sensory integration is linked to binocular rivalry alternations provides evidence that it is not solely uni-sensory areas specific to the particular bistable stimulus that are responsible for alternations; there may be a more general locus of bistable alternations. There is the alternative possibility that these cross-modal areas are active consequent to a resolution of the conflict by activity in

the local brain areas responsible for processing the bistable stimulus. Even though the response in the parietal lobe is recorded before the perceptual alternation is experienced, it is possible that this activity is triggered from feed-forward activity in early visual cortical areas that have reached a ‘decision’ – that is, the adaptation threshold required to produce a switch to the non-dominant percept, before it is consciously experienced and recorded by the observer.

Psychophysical studies of cross-modal influences

Examining the influence of information arising from a sensory modality not involved in the primary bistable conflict is a way to gauge if, and how, distributed processes are involved in determining alternations during bistable perception. Since the auditory information is not necessary to the specific local processes involved in resolving the conflicting visual stimuli, it can be inferred that the extent that sound affects binocular rivalry is an indicator of its susceptibility to distributed processing in the brain. Non-visual sensory signals that are congruent with one or the other binocular rivalry inputs increase the amount of time that input is perceptually predominant. Congruent cross-modal signals do not, however, attenuate suppression periods (Conrad et al., 2010) – which indicates that the effect of sound over binocular rivalry is achieved via feedback mechanisms that require observers to be conscious of the visual input to which the sound coheres. This reasoning also applies to the effects of contextual surrounds (Sobel & Blake, 2002) and willful attention (Meng & Tong, 2004) over the predominance (but not suppression) of the targeted stimulus involved in binocular rivalry. These influences can be considered ‘higher-order’, requiring full conscious awareness of the targeted stimuli in order to have an impact on the temporal course of binocular rivalry. They are achieved by feed-back mechanisms originating from processing sites downstream of the local visual processes that handle binocular input.

Some evidence points away from a unified mechanism for different bistable phenomena. Experiments conducted by Hupé, Joffo and Pressnitzer (2008) are inconsistent with the idea that the switching mechanism in bistable perception is mediated by a supra-modal process. Participants in their experiments measured perceptual reversals to auditory

bistability, visual bistability and a condition where both forms of bistable stimuli were presented together. In the conditions where auditory and visual stimuli were meaningfully paired, greater periods of co-predominance were found for the bi-modally congruent interpretations. However, no coincidence between auditory and visual bistable switches was found; the reversals experienced for the visual bistable stimulus did not coincide with the reversals experienced for the auditory stimulus. Due to this, the authors argued that the switching mechanism underlying bistable phenomena is based on stimulus-specific processing areas and is not achieved by a supra-modal or global mechanism. The increased coincidence of congruent auditory and visual dominance periods was accounted for by the influence of higher-order feed-back, such as that operating during the effects of context and attention. This is consistent with the boost to endogenous attentional control over rivalry with auditory (and tactile) stimuli reported in Chapter 4. The lack of synchronised switching does not support a central oscillator account of bistable perception.

The absence of synchronous switching in Hupé et al.'s (2008) study supports the idea that local processing determines the dynamics of bistable alternations. The similarities in the temporal pattern of alternations across different modalities of bistable perception could be due to the action of a common (but not central) mechanism reproduced in the local processing specific to each sensory modality and the qualities of the bistable stimulus. The inability of the temporal sound streams used in Chapter 5 to precisely determine bistable dynamics is consistent with this interpretation. The dynamics of binocular rivalry were not vulnerable to a strong auditory temporal cue, as might be expected for other forms of temporally ambiguous visual stimulation (Shipley, 1964; Alais & Burr, 2004). It is more reasonable to attribute the moderate speeding of binocular rivalry by the high tempo sound streams to a general increase in whole-brain physiological processing; i.e. an increased level of general arousal. Increased arousal has been previously demonstrated to correlate with an increased speed of binocular rivalry alternations (e.g. in subjects with generalised anxiety), and is likely the same underlying cause of the pattern of results reported here.

Although Hupé et al.'s study showed no coincidence between auditory and visual bistable switching, auditory cues can impact on bistable perception in the visual modality in ways independent of higher-order effects. The way they do so constitutes evidence that sounds can tap into unconscious perceptual processes occurring during binocular rivalry.

Takahashi and Wantanabe (2010) compared the influence of auditory cues on a bistable visual motion stimulus. The bistable visual motion was accompanied by a non-bistable auditory stimulus that was congruent with one of the visual motion interpretations, similar to how looming visual and auditory motions were paired in Chapter 4. Takahashi and Wantanabe (2010) found that auditory cues can bias visual bistable perception even when the auditory signal is below conscious threshold. This result argues against contextual cross-modal influences based on awareness of the stimuli, and suggests that unconscious audio-visual integration can and does play a role in the resolution of ambiguous sensory inputs. The ability of subconscious auditory-visual integration to influence bistable perception implicates the involvement of the subcortical neural pathways in the superior colliculus responsible for orienting responses.

There is also evidence that auditory cues can affect bistable suppression by triggering a perceptual switch. Takahashi and Wantanabe (2011) published an examination of how auditory and visual transients impact on bistable motion in the visual modality. The visual stimulus was a bistable apparent motion dot quartet (see Figure 2 below). Although they did not manipulate the temporal frequency and pattern of transient events in their study, they did demonstrate an equivalent influence in the ability of visual and auditory transients to trigger visual alternations. The trial periods in their experiment were as long as 240 seconds per trial, which is comparable with the length of the binocular rivalry trials in Chapter 5. Their results cohere with the flash suppression results contained in Appendix 1 in that transient events triggered an alternation, but this was not the case for the longer binocular rivalry trials of Chapter 5.

Figure 2. Stimulus presentation used by Takahashi & Wantanabe 2011

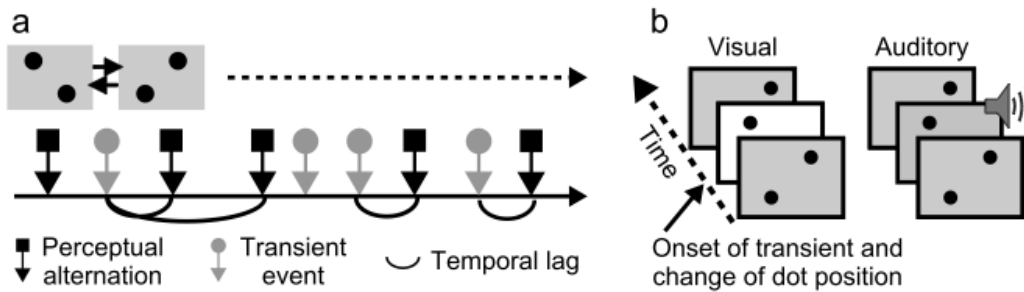


Figure 2. Perceptual alternations in a bistable apparent motion stimulus were induced by the presentation of visual and auditory transients. The effects of auditory transients were equivalent to the effect of visual transients in their ability to provoke a change in the current perceptual state.

The finding that transient events evoked time-locked visual alternations for the bistable motion used in Takahashi and Wantanabe's (2011) study was not replicated in the prolonged binocular rivalry trials with continuous transient streams conducted in Chapter 5. Participants observed binocular rivalry in trials of 1 minute per duration – much longer than the flash suppression presentations. During the binocular rivalry trials, transient visual or auditory events were presented in a continuous stream, not in isolation. There are a few reasons why these continuous streams of transients did not produce time-locked alternations in the binocular rivalry stimulus. One reason for this is the dependence of binocular rivalry on competition between monocular neurons, as well as the relative imperviousness of binocular rivalry to top-down effects of attention compared to other forms of visual bistability such as the Necker cube (Meng & Tong, 2004) or the ambiguous motion used by Takashi and Wantanabe. However, this explanation does not account for the preservation of the transient effect with the flash suppression stimulus used in Appendix 1. Flash suppression is a form of bistable phenomena dependent on binocular adaptation – ruling out the imperviousness of monocular neurons to the influence of cross-modal transients. The difference between long periods of binocular rivalry and short, one-cycle binocular rivalry (i.e. flash suppression presentations) is less likely to be the reason behind the difference between Takahashi and Wantanabe's results and Chapter 5 – it is more likely to do with the continuous presentation of the transient

events used in Chapter 5 versus singular sounds: continuous presentation of the transient events could have resulted in an adaptation of the startle-orienting response.

The transients used by Takahashi and Wantanabe (2011) were apparently distanced enough to keep the orienting response alive, whereas the regularity of those used in Chapter 5 were not. Future experiments comparing the point at which repetition leads to a loss of the orienting response during bistable perception should be carried out to confirm the source of this difference. Another possibility is that ambiguous motion, which is already engaging transient-based perceptual processes, is more susceptible to transient disruptions. Whether this is also the case with motion used in a binocular rivalry paradigm should be tested. In any case, if binocular rivalry between conflicting motion stimuli are equally susceptible to transient events as the bistable motion array, this would imply a dependency on stimulus-specific processes, rather than a blanket openness to the orienting response during binocular rivalry.

The orienting response versus general physiological arousal

Although there is evidence that the orienting response does impact on binocular rivalry alternations, the overall speeding effect due to transients (in the absence of transient-locked switching) implies that discreet, repeated orienting responses are not at play in the results of Chapter 5. To disentangle whether or not an attention-based orienting response, or an increase in general arousal, was responsible for the speeding of binocular rivalry reported in Chapter 5, further experiments comparing single transients and transient streams during binocular rivalry viewing will need to be conducted. These experiments can clarify the difference in the ability of transient auditory events to cause time-locked alternations in binocular rivalry compared to flash suppression by asking whether single transient events during prolonged binocular rivalry viewing will cause time-locked alternations.

To determine whether general arousal underlies the current results, simple physiological measurements can be made while repeating the primary conditions of Chapter 5. For example (and as mentioned previously) the arousal hypothesis would be supported if

simple heart rate and skin conductance monitoring (which are robust measures of levels of physiological arousal) measures increased physiological activity to the transient stimuli that produced speeded binocular rivalry rates. Other experiments could be conducted on two different sample groups: one with high levels of susceptibility to anxiogenic stimuli, and another low-susceptibility group. Differences between these two groups in the size of the effects reported in the current research would support the arousal hypothesis. Overall, it is feasible that the transient induced individual switches reported in Appendix 1 and elsewhere and the binocular rivalry speeding reported in Chapter 5, reflect the immediate and sustained responses of the one arousal network.

Many processes that contribute to our conscious awareness occur unconsciously. It is possible that, since the exogenous stimuli used in the present experimental chapters were all created and presented in a laboratory environment, that true exogenous attention was not activated. The artificiality of the stimulus may have precluded its being treated as a true threat that needed to be oriented to. This possibility points to the need to conduct research in increasingly realistic stimuli and environments, a future direction made available with advances in the equipment and technology needed to simulate realistic environments and to collect data in the field.

Conclusions

The results of the present experimental chapters compliment previous literature on binocular rivalry, concluding that binocular rivalry involves a specifically visual component of competition; some part of the conflict is mediated by neural areas dedicated to stimulus-specific processing. This is because binocular rivalry alternations cannot be fully taken over by auditory cues, as other visual temporal information can (e.g. Shipley, 1964). Distributed influences over binocular rivalry exist but are limited in their ability to modulate the temporal dynamics of the perceptual alternations.

Exogenous attention cues, such as looming motion targets, cannot completely determine perceptual dominance during binocular rivalry. Likewise, extremely salient attention-grabbing sound streams cannot trigger perceptual alternations in binocular rivalry to match the auditory temporal pattern and rate. The binocular rivalry mechanism cannot be concluded to be the same as that underlying exogenous attention, or attention generally; but it is, to some extent, influenced by it. The temporal dynamics of binocular rivalry are more likely tied to unconscious mechanisms of visual selection, such as the resolution of binocular signals with and without ambiguity, that are functionally related to selection for conscious awareness. Resolution of ambiguity appears to be a response to modality-specific inputs in modality-specific processing sites that is in turn assisted by concurrent processing in areas responsible for sensory integration.

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Appendix 1: Flash Suppression and sound

In order to more objectively characterise the likelihood of an alternation with transient sounds and flashes during binocular rivalry the flash suppression paradigm was used to measure stimulus onset asynchrony adaptation thresholds required for 75% probability of an alternation. Flash suppression (FS) involves presenting a rival image to one eye first, then waiting a short stimulus onset asynchrony (SOA) before presenting the second rival image to the other eye. The likelihood that this second image completely suppresses the first (provoke an alternation) increases with increasing SOAs. In this way the SOA can be varied across numerous FS trials (using an adaptive staircase procedure) to measure the threshold adaptation period required for suppression of 75% of trials. In the following experiments this method is used to measure the likelihood of alternations during trials with or without singular auditory transients accompanying the second flash stimulus. In the first experiment, flash suppression thresholds are obtained across three conditions; 1) without sound (control), 2) with an 800 Hz pure tone accompanying the second ‘flash’ stimulus and 3) with a white-noise burst accompanying the flash. In the following experiment, the audio-visual synchrony between the pure tones and the second ‘flash’ stimulus was shifted plus or minus 300 ms in two further conditions.

Figure 1. An illustration of the time course of a flash suppression trial

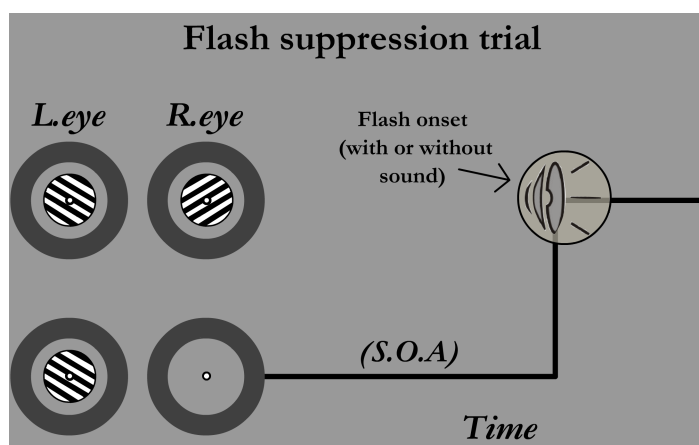


Figure 1. The time course of a flash suppression trial. For the first part of the trial, only one grating is presented to one of the eyes. After a stimulus onset asynchrony (SOA) the second grating is presented to the other eye. This onset was accompanied by a sound in the active conditions and without a sound in the control condition.

Method

Subjects: Six subjects participated in Experiment 1, 2 female, 4 male with ages ranging between 25-43 years. All had normal or corrected-to-normal acuity as in the previous experiments. Three of the subjects including the authors AP and DA participated in previous experiments. The other three were new subjects and naïve as to the hypothesis of the Experiment.

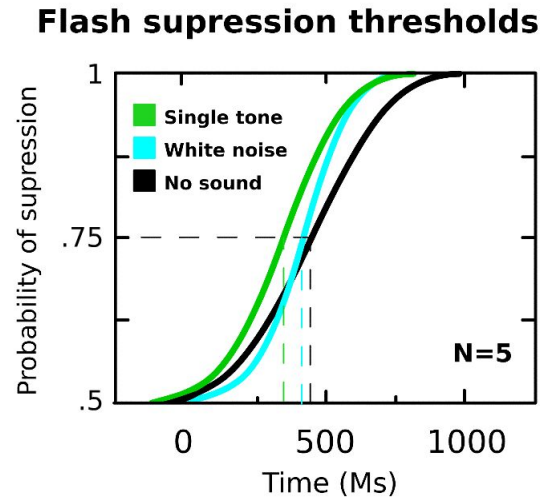
Stimuli: The two sine-wave gratings used in the previous experiments were again used as the flash suppression stimuli with one difference; in this experiment the gratings were full contrast. The orientation of the gratings presented to each eye differed trial to trial in a random order, as did the presentation order of the two gratings. In order to stabilise fusion of the binocular stimuli a narrow binocular annulus was added to each eye's view, as was a central white fixation dot with a 1 pixel width black border, similar to that shown in Figure 1.

Procedure: Subjects adjusted the mirror stereoscope to comfortably fuse the binocularly presented fixation spot and annulus. Each trial was initiated by pressing any key, which started with the presentation of the first rival stimulus to one of the eyes. The eye receiving the first stimulus was randomly determined trial to trial. This was also done for the orientation of the first and second grating to decrease adaptation effects. After a certain SOA determined by an adaptive staircase method, the second rival stimulus (the flash stimulus) was presented to the other eye, which until then had only been exposed to the annulus and fixation spot against the grey background. The two rival stimuli remained on the monitor a further 500 ms after which a random-noise patch cycled at 60 Hz to produce a spatially and temporally broadband mask. The mask remained on the screen for 1000 ms. A further pause of 500 ms was imposed between trials in an attempt to counter ongoing adaptation. After each trial subjects were required to judge whether or not the second 'flash' stimulus completely suppressed the first by responding either 1 (yes) or 2 (no) on the keyboard. Each session consisted of either two interleaved staircases, each testing a control and a sound condition in interleaved trials (subjects 1-3) or as a

continuous block of either control or sound trials (subjects 4-6). A minimum of 100 trials was used to calculate thresholds of suppression for each subject and condition.

Figure 2. Averaged threshold for flash suppression with and without sound

Figure 2. Single tones significantly decreased the stimulus onset asynchrony (SOA) required for complete flash suppression compared to trials where no sounds were presented. This effect was greatest for pure tones, with white-noise bursts resulting in a very small, non-significant decrease in the required SOA.



Results and discussion

During trials with pure tones accompanying the flash, the likelihood of suppression was significantly increased relative to the no-sound control trials ($t=2.484$, $df=5$ one tailed t-test $p < .05$). This was not the case with white-noise bursts which did not affect the likelihood of alternations ($t=0.411$, $df=5$ one-tailed t-test, $p > 0.05$). It should be noted that during a great number of white-noise sessions (each session consisted of 25 trials) thresholds for suppression could not be obtained/fitted. White-noise appeared to be disrupting inter-ocular inhibition rather than assisting suppression.

Parametric studies mapping out these effects with sounds of various stimulus intensities may shed light on the difference between broad-spectrum white-noise and singular pure tones in producing transient-induced alternations. Importantly, the results of Experiment 1 show that the speeding of rivalry found in Chapter 5 is not an artefact of transient events affecting motor responses, because responses were required after the trial stimulus was presented.

The discrepancy between white-noise and pure tones may be due to the naturalistic (or lack thereof) quality of the auditory stimuli used. The white-noise stimulus did not appear to sound like anything that is encountered in the normal environment (the random phase of the components makes it very unlike natural sounds, with synchronised onset of frequency components and co-modulation of harmonics). Pure tones on the other hand are similar to a variety of auditory cues used in everyday scenarios such as email and text message alert systems, alarms, sirens and indicators on electronic appliances to name a few. These may have a stronger influence over processes underlying visual selection than sounds we rarely encounter, especially due to the attention grabbing nature of their functional associations.

Experiment 2: Flash Suppression and audio-visual synchrony

The second flash suppression experiment carried out examines how robust the effect of pure tones is in increasing the likelihood of suppression when they are presented with a 300 ms asynchrony to the flash onset. Many auditory influences over visual perception, such as the sliding/bouncing ball effect (Sekuler, Sekuler & Lau 1997) are robust at audiovisual asynchronies up to 300 ms. If the effect of sound over flash suppression documented in Experiment 2 is similarly robust the processes involved in the auditory effects over rivalry described here adhere to the same principals involved in cross-modal integration more generally. This outcome would also support the pattern of results found in the previous experiments; that the effects of sound over binocular rivalry are mediated by a system more global than vision.

Method

Subjects: Three subjects from Experiment 1 participated in Experiment 2 ages ranging from 27 to 43 years and including the authors AP and DA.

Stimuli and procedure: The stimuli and procedure were the same as that used in Experiment 1 during the pure-tone conditions. The pure tone was however not presented in synchrony with the flash onset but either 300 ms prior to, or after it. Here the control

thresholds (no sounds appeared during the trial) were measured with trials interleaved with the sounds trials.

Figure 3. Audio-visual asynchrony and the effect of sound on flash suppression

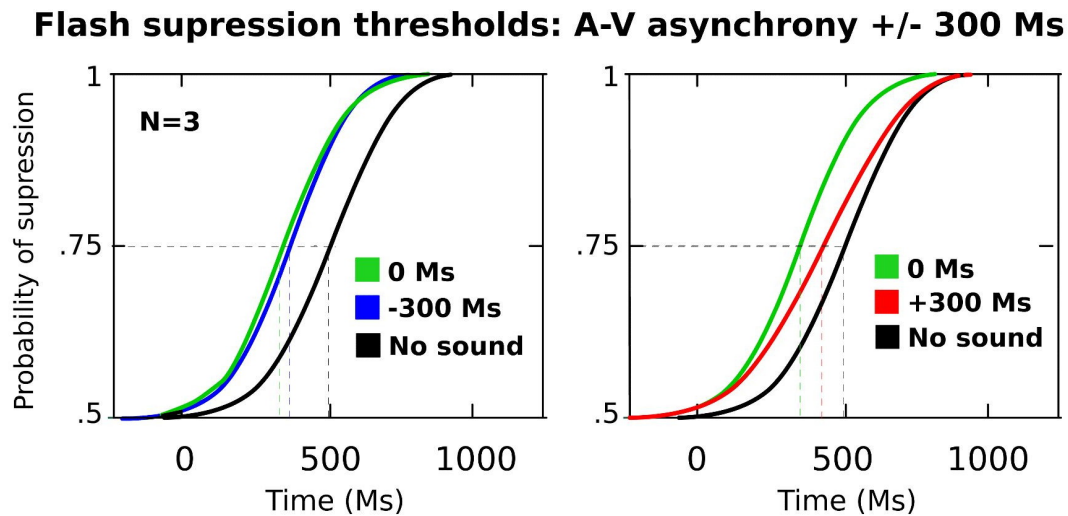


Figure 3. A) Sounds presented before the flash onset still reduced the SOA required for complete flash suppression to occur. B) Sounds presented after the flash onset were not as effective.

Results and discussion

When sounds are presented 300 ms before the flash onset, the effect remains the same as reported in Experiment 1; these sounds significantly increase the likelihood that a complete swap to the new, flashed image occurs ($F=8.63$, $df=3$, $p < 0.05$). If sounds are presented 300 ms after the flash however, they have no significant impact on this likelihood, although a small trend is observed (see Figure 3 B). This result is consistent with the finding that audiovisual interactions can persist with small asynchronies (Sekuler, Sekuler & Lau 1997).

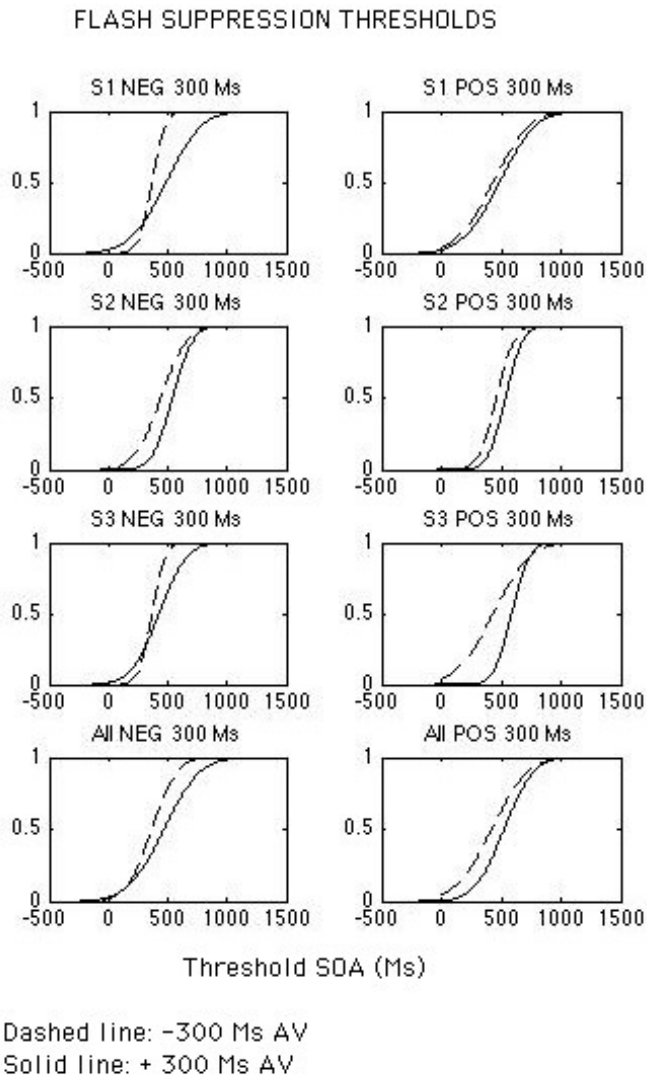
Figure 4. Individual data

Figure 4. A positive or negative 300 ms asynchrony between the sound and flash stimulus did not eradicate the effect of pure tones on reducing FS latencies, although it is diminished.

Appendix 2: Data analysis supplementary to Chapter 5

Results and discussion supplementary to Chapter 5 Experiment 1

Binocular rivalry key press responses during each 60-second trial were recorded as a series of key press states (1, -1 and 0 for piecemeal) and their corresponding durations. These data are plotted for one subject in Figure 1, which shows the key presses for 6 of the 87 trials. The particular 6 trials shown in Figure 1 involved pure-tone event streams at the 6 different temporal frequencies tested during binocular rivalry between 48% contrast gratings.

Figure 1. Binocular rivalry key press data

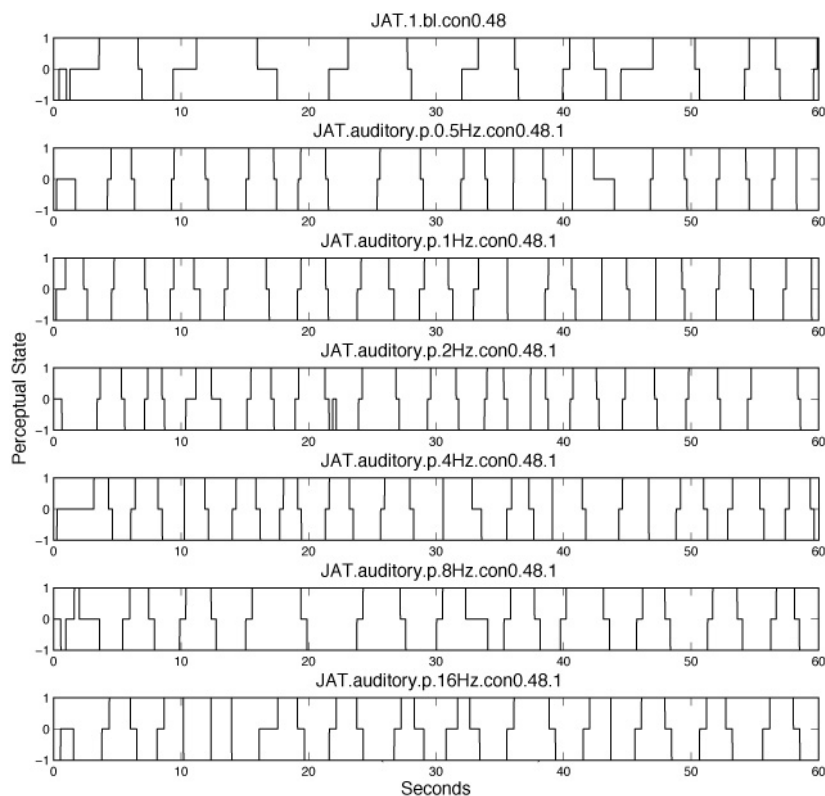


Figure 1. Key press recordings from one of the subjects in Experiment 1. The recordings from 7 trials are shown, including a baseline trial (the first row). These particular data were recorded during rivalry between orthogonal 48% contrast gratings. Rows 2 to 7 show binocular rivalry key-presses during the presentation of the sound streams. The sound streams tested ranged from 0.5 to 15 Hz.

The key press data indicating the observers' perceptual alternations over time were converted to alternation rates (alternations per second). Binocular rivalry alternation rates were significantly sped up in the presence of high-frequency event streams, specifically the 8.1 and 15 Hz streams tested. The effect appears to be similar for all the types of transient events used, including the sound events. Analysis of variance of the alternation rates across conditions (within subjects factors: event type (4) x contrast (3) x event rate (7)) resulted in significant main effects of event type ($F(3,9.92)$, $p < .01$), contrast ($F(2,10.44)$, $p < .05$) and event rate ($F(1.28, 9.228)$, $p < .05$ Greenhouse-Geisser correction for violation of sphericity). All auditory event types, including the audiovisual condition, were as effective as the contrast increments in speeding rivalry, as can be seen in Figure 2.

Figure 2. Binocular rivalry alternation rates

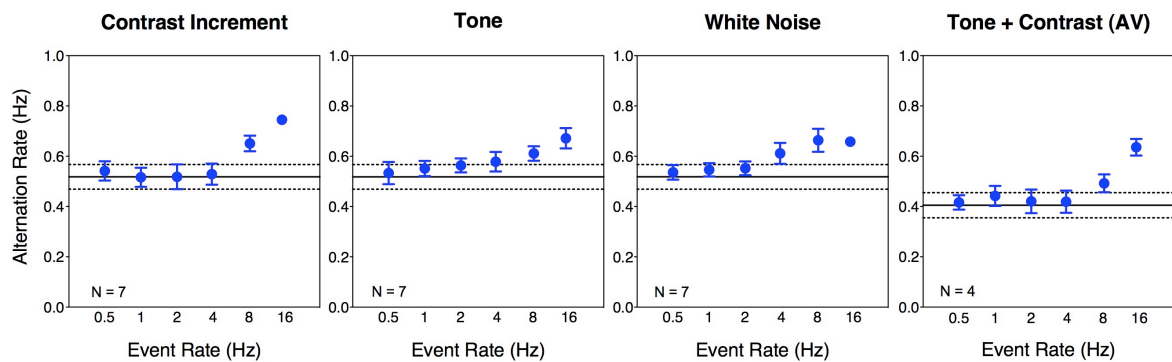


Figure 2. Average alternation rate during each of the experimental conditions across all subjects. The black solid line shows the alternation rate for the baseline binocular rivalry condition. The corresponding black dashed lines represent the standard error of measurement for the baseline average. The blue circular data points show averages during conditions with transient event streams. Each plot shows the data collected for the four different types of transient events, visual, auditory (including tones and white-noise bursts) and audiovisual. Six event cycle frequencies were compared, shown on the x-axis.

Helmert contrasts showed no difference between the different transient event conditions; sounds such as the tones and white-noise bursts used can affect rivalry as much as transient contrast increments. The equivalence of sounds and contrast increments in these experiments is at first surprising. Visual transient responses are more sluggish than

auditory ones, with a latency of up to 100 ms. This is because the conversion of light energy into a neural signal involves chemical transduction, whereas hearing involves a more immediate mechanical process. It is possible that the 22 ms contrast increments used were not long enough to produce a robust transient visual response. Pilot experiments replicating some of the conditions from Experiment 1 suggest elevated speeding effects for combined contrast and luminance increments (compared with contrast only increments, as tested here). The possibility that the speeding of rivalry alternations with visual transients depends on their salience deserves future exploration. Although sounds here show equivalent effects, the salience of visual and auditory events should be properly equated before concluding that they are truly equal in their ability to speed binocular rivalry.

Rivalry alternation rates are known to increase with visual contrast. Confirming this, the main effect of contrast was significant ($df=2$, $F=10.44$, $p < .05$), although it did not interact with event type ($F=0.74$, $p > .05$) or event rate ($df=2.33$, $F=2.37$, $p > .05$ Greenhouse-Geisser correction) meaning that the elevation of rivalry rate was the same for each contrast tested. Only the 8.1 and 15 Hz event cycles significantly sped alternation rate (see Figure 2 which shows the baseline rate as a solid line) compared to the 0 Hz trials (simple contrasts 8.1 Hz: $F=12.13$, $p < .05$, 15 Hz: $F=13.916$, $p < .01$). From inspection of the probability of particular dominance durations plotted in Figure 3, it appears that this is due to reduced likelihood of long, outlier dominance durations, rather than a shift in the most frequent dominance durations. This can be seen by comparing the peak with the range in the frequency histograms shown in Figure 3. Compared to the histogram peak, range becomes markedly narrower in the two fastest event streams (8 & 16 Hz).

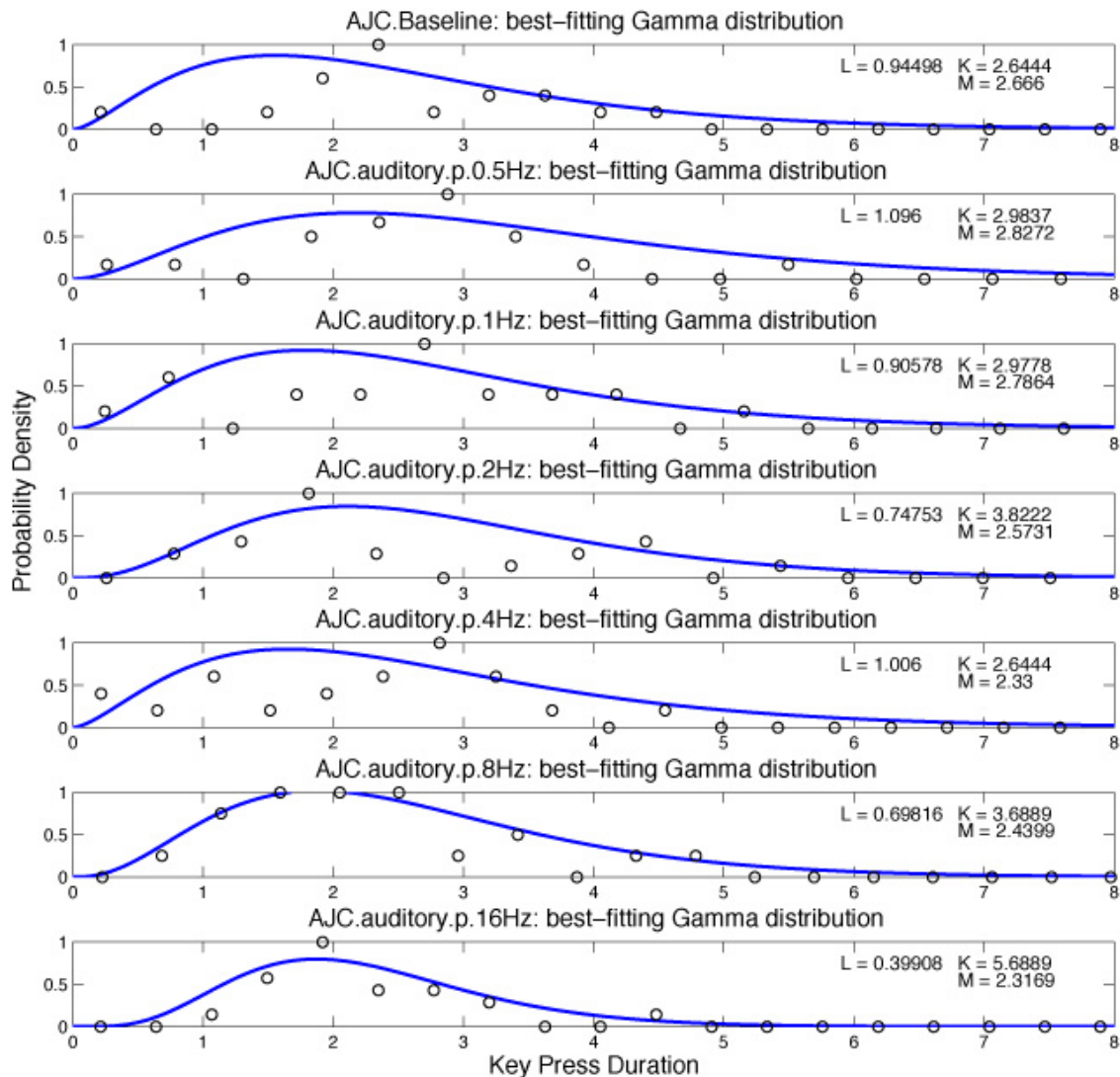
Figure 3. Distribution of dominance durations

Figure 3. Frequency histograms of the binocular rivalry perceptual durations. The key press durations have been binned and then the frequency tallies normalised to the maximum. The probability density of these dominance durations (y-axis) is plotted for each key press duration (x-axis). Data from one of the subjects is shown for the same conditions presented in Figure 1. The probability of longer key press durations in the fast, 15 Hz sound stream condition is reduced.

Because visual transients can trigger alternations in bistable stimuli (Kanai, Moradi, Shimojo & Verstraten 2005) and auditory events can drive perception of visual temporal rate (Shipley 1964) it is reasonable to ask whether the stream of visual or auditory events are entraining binocular rivalry alternations. A hallmark of discreet binocular rivalry

durations is that they are independent from each other; the probability of each eye's dominance duration is stochastic (Levelt, 1968, Fox and Hermann 1967). If the regular event streams presented here are entraining binocular rivalry alternations, alternations should become more periodic and less stochastic. To test this, an autocorrelation analysis was performed on the key press durations recorded. For each subject and condition, the dominance durations were correlated with each other over 12 lags, with the first correlation (of no lag) giving a correlation coefficient of 1.

As has been mentioned, individual dominance periods in binocular rivalry show stochastic independence with each other (Levelt, 1968, Fox and Hermann 1967). This holds true for the conditions tested here, showing that periodic event streams do not increase the periodicity of rivalry alternations. Although there were occasional instances of significant correlations, these did not occur more than would be expected from random error (less than 5% of the time) and no systematic differences across any condition were found (AVOVA: event rate main effect $F(6, 1.178)$ $p > .05$ and event type $F(2.41, p > .05)$). This indicates that the underlying stochastic nature of rivalry alternations is preserved during the presentation of periodic transient events across the trial period. In other words, transient events do not override or 'capture' the temporal pattern of binocular rivalry fluctuations.

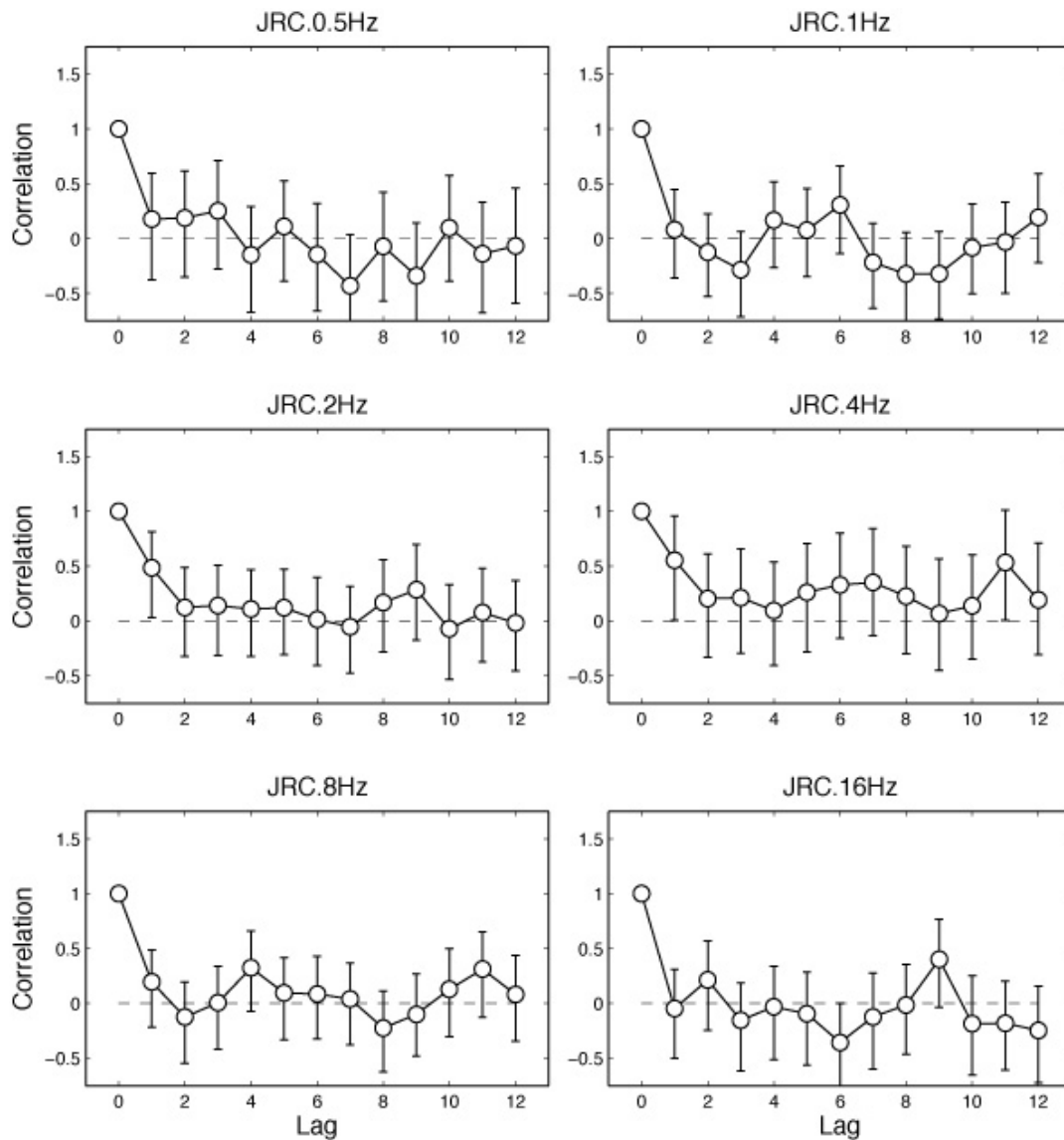
Figure 4. Autocorrelation of binocular rivalry dominance durations

Figure 4. Autocorrelations of key press durations recorded by one of the experimental subjects. Key press durations were not correlated with one another, except at the zero lag step, where identical key press series are compared. This independence is a feature of regular binocular rivalry alternations and shows that the event streams do not alter the stochastic dynamic involved.

In addition to the autocorrelation analysis, a cross-correlation analysis was performed between the transient events and the key presses. Key press and event data were transformed into periodic sawtooth waveforms, seen in bottom panels of Figure 5 A

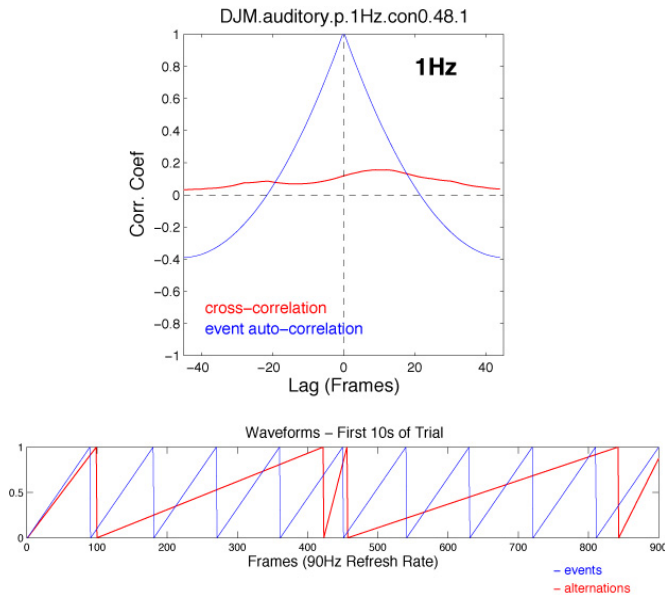
& B for one subject for the 1 and 2 Hz sound-stream conditions. These waveforms captured the occurrence of a key press swap or a transient event across the 60-second trial (although the plots in Figure 5 show only the first 10 seconds of the trial due to space constraints). The waveform peak of 1 denotes a swap or a transient event, the value of y giving the time to next swap or event : $y = 1 - (1/t)$ (t = time to next event/swap).

The two waveforms were correlated with each other across 90 lags (corresponding to one second at a sample rate of 90 Hz). A slight modulation in the correlation coefficients mirroring the periodic event streams was found, however none of the correlations was significant, when tested against P values obtained from randomly shuffling them and bootstrapping the data sets 1000 times. The cross-correlogram for one subject is shown in Figure 5. The blue line shows the pattern expected from a perfect correlation between the events themselves. The red line shows the actual cross-correlations, which were all non-significant. This result is consistent with the lack of periodicity found between the dominance durations in the autocorrelation analysis, and preservation of the stochastic properties of rivalry dynamics.

Lack of any specific entraining is also supported by informal subject interviews; observers noted that there were only occasional instances where alternations appeared to coincide with the accompanying sounds or visual events. Qualitative post-experiment reports from observers revealed that they found the white-noise transient events at the higher rates (8.1 & 15 Hz) irritating, but did not report irritation at lower cycle rates or for the pure-tone pips. This provides qualitative support for the interpretation that the speeding of rivalry alternations accompanied by rapid transient event sequences is due to increased arousal. In order to explore this further an additional analysis was performed on the speed of rivalry alternation across the duration of each trial. If the effect of transient events is due to a startle effect that adapts or diminishes over the trial, there should be a negative correlation or slope of alternation rate across time.

Figure 5. Cross-correlation between events and binocular rivalry alternations

A.



B.

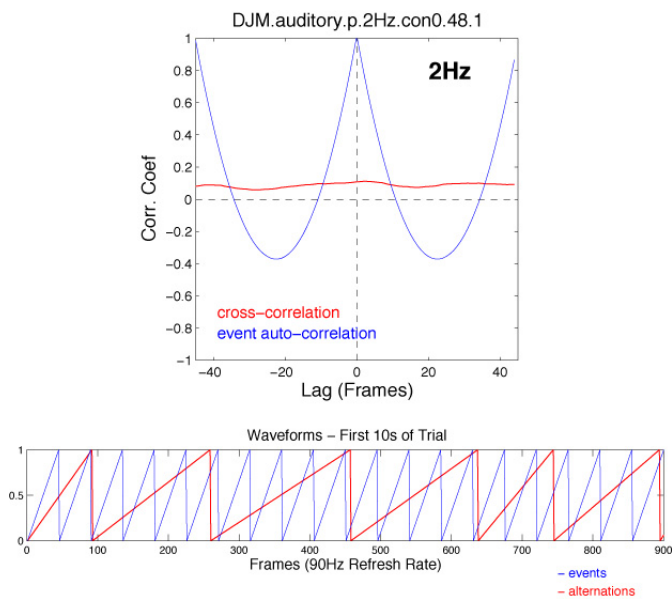


Figure 5. Cross-correlograms of events and key presses, here shown for one subject for the 1 and 2 Hz sound event stream conditions.

Rivalry alternation rates did not change across the duration of the 60-second trials in any of the conditions tested. A few significant correlations were found, but these were below

5% of the data points tested and had no particular pattern. This suggests that the effect of sound events on binocular rivalry is not due to a quickly adapting startle response.

Figure 6. Alternation rate across time

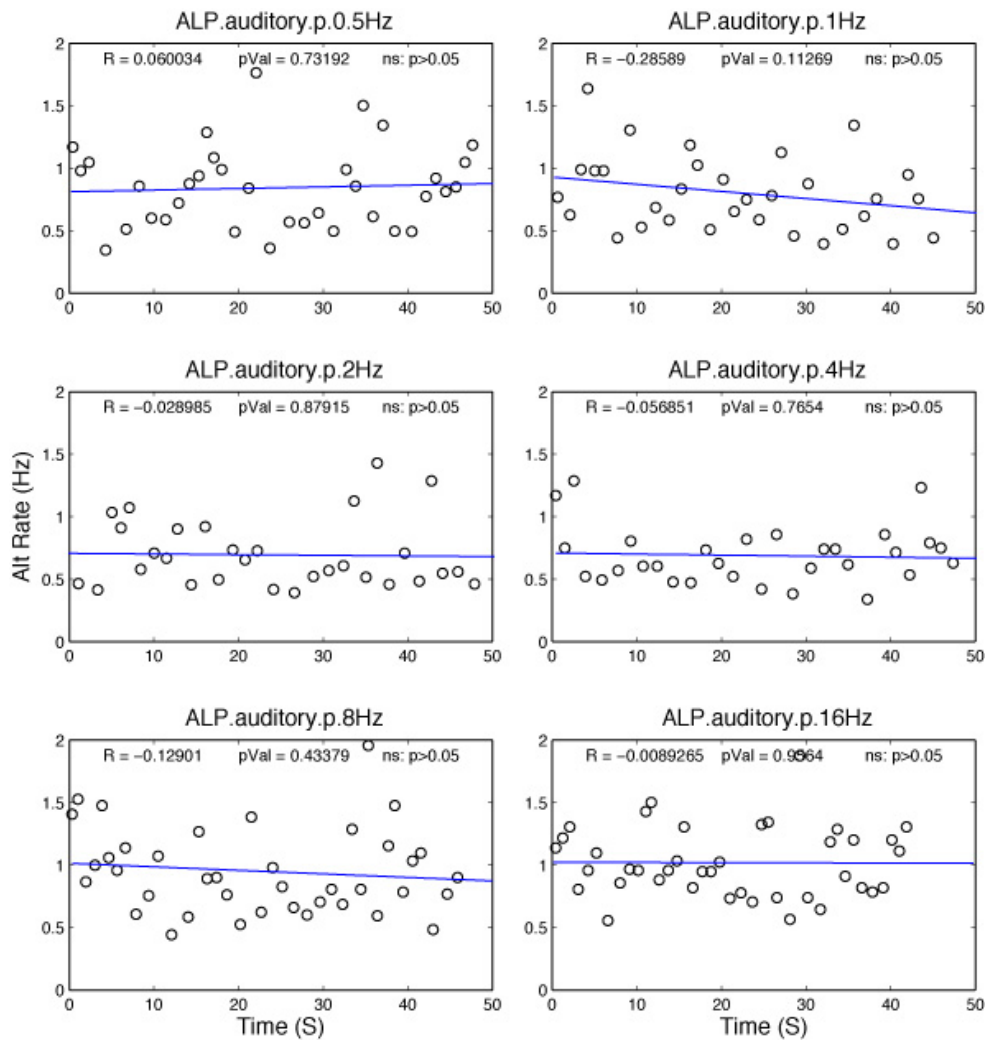


Figure 6. The alternation rate did not change across the trial durations tested (60 seconds). The data plotted here include only the left and right eye key press recordings, and not the shorter instances of piecemeal rivalry.

The effect of contrast on speeding rivalry alternations is well documented; rivalry alternation rates increase linearly with log increases in the contrast of the rival stimuli (Levelt, 1968). The contrast increments constituted an overall increase in the binocular rivalry stimuli across the trial. Interestingly, the overall increased contrast accounts for the magnitude of the speeding effects found. The effect of visual transients in changing

rivalry alternation rates can be explained by changes in this average contrast when compared to the speeding-effect of contrast measured in the 12, 24, 48 and 96% contrast grating baseline conditions. Figure 7 shows the rivalry alternation rates in the flicker conditions as a function of time-averaged rivalry contrast.

Since the contrast transients in Experiment 1 involved adding a 50% increment to the base contrast, this was proportionately a greater contrast increase for the 12% base contrast than for 24% and 48% contrasts. In addition, as the number of contrast increments increased (i.e., at higher event rates), the time-averaged contrast would be even further enhanced. Together, this would mean that alternation rates for the lower rival contrasts at higher event rates should be most accelerated by the visual transients, just as was observed (see Figure 1, top-left panel). The similarity in the pattern of results for sounds and visual transients suggests that sounds may contribute to contrast gain during rivalry, in the same way that sound is thought to boost visual contrast responses in the early visual cortex.

Figure 7: Binocular rivalry rates as a function of averaged stimulus contrast

Figure 7. Alternation rates during binocular rivalry from Expt 1 and 2 are shown as a function of stimulus contrast averaged across the 1-minute trial periods for the visual transient condition tested in Experiment 1. The black data points show rivalry switching rates for four different visual contrasts, 12, 24, 48 and 96 % in the absence of any transient events. The increasingly darker grey data points show mean alternation rates (N=7) for the 12, 24 and 48% contrast pedestals respectively. Each event rate condition is expressed as the average visual contrast across the 1-minute trial, rather than event frequency for comparison with the effect of visual contrast alone on rivalry switching rates.

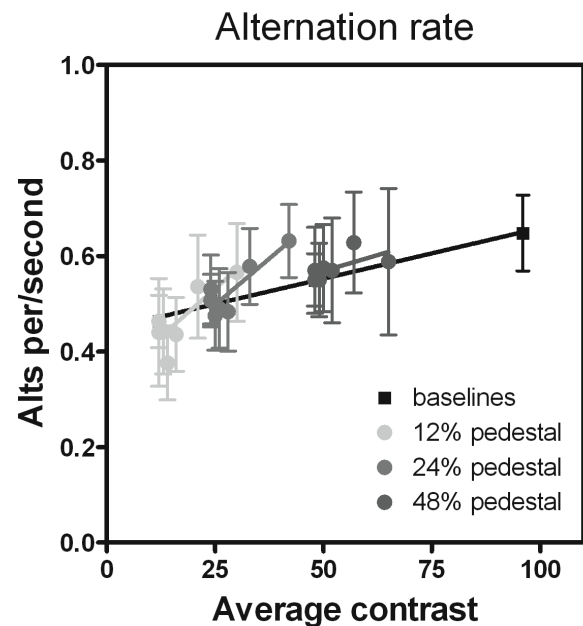


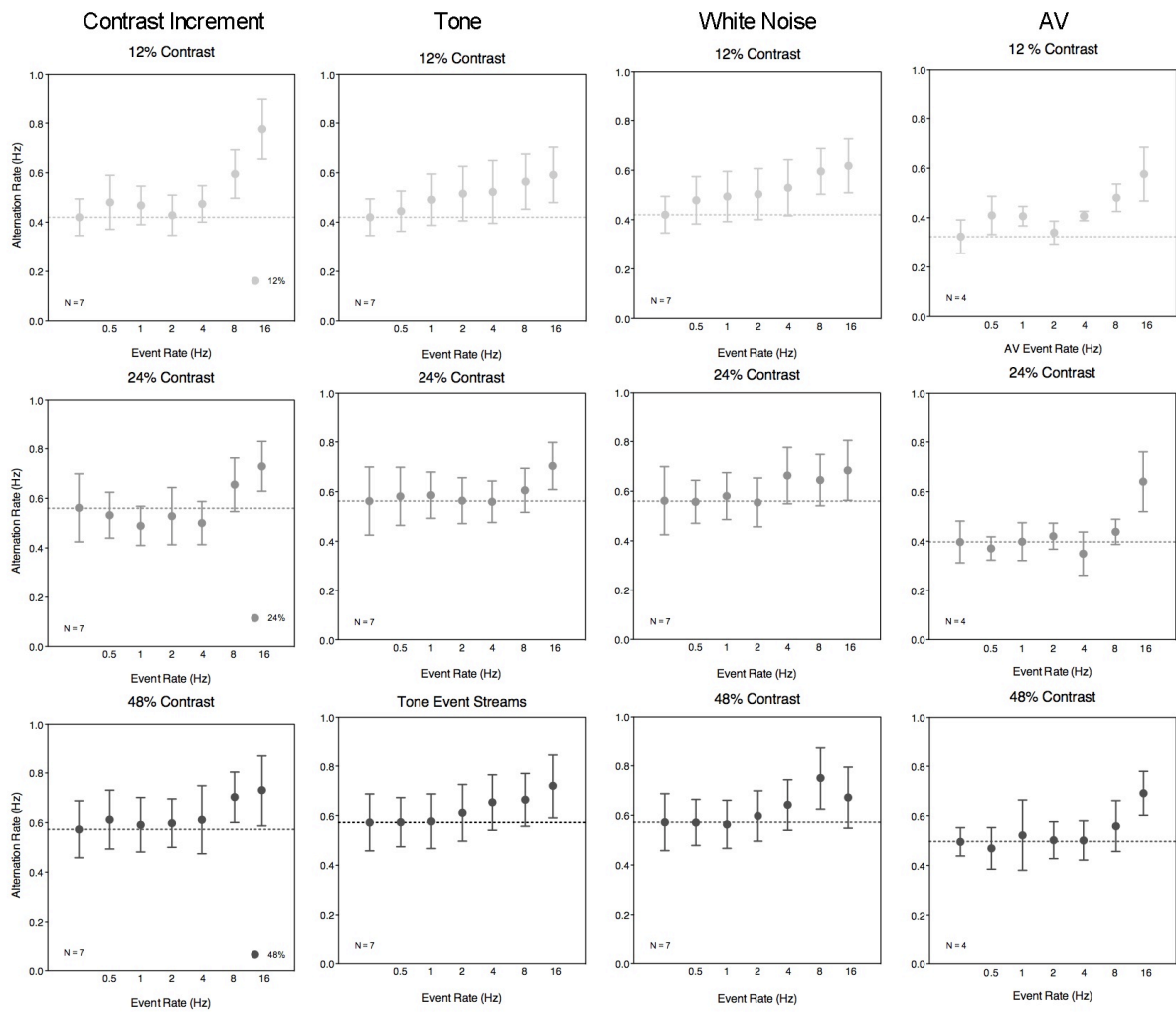
Figure 8. Alternation Rate and rivalry contrast

Figure 8. Binocular rivalry alternation rates as a function of stimulus contrast. Increasing stimulus contrast produced corresponding increases in rivalry rates, as has been demonstrated previously.

An additional analysis was performed on the proportion of piecemeal rivalry during the event conditions. The proportion of piecemeal rivalry did not differ as a function of any of the conditions tested ($F(2.34, 2.66) p > .05$ Greenhouse-Geisser correction), although this may be due in part to our small rival stimuli (1.5° diameter), as this is known to limit piecemeal rivalry (Blake, O'Shea & Mueller 1992). The possibility that transient contrast increments and sounds can affect the completeness of binocular rivalry alternations could be tested with larger images in the future.

The results of Experiment 1 demonstrate an auditory influence over binocular rivalry dynamics. For a range of auditory event rates tested, there is a significant increase in the temporal rate of rivalry alternations with no concomitant change to the stochastic properties of the rivalry dynamics. Although it is conceivable that an auditory event presented in isolation may invoke singular alternations during rivalry, the continuous sound streams we used did not entrain the temporal pattern of binocular rivalry alternations raising the possibility that response inhibition affects perceived salience across the course of the observation trial. This is not supported by the correlation analysis, but event-dependent alternations did seem to occur in the first few seconds of each trial. Whether sounds can increase the likelihood of one swap is the subject of Experiments 1 and 2 of Appendix 1. A replication of Kanai et al.'s 2005 study with auditory transient stimuli would also address this question.

Appendix 3: Material supplementary to Chapter 4

Figure 1

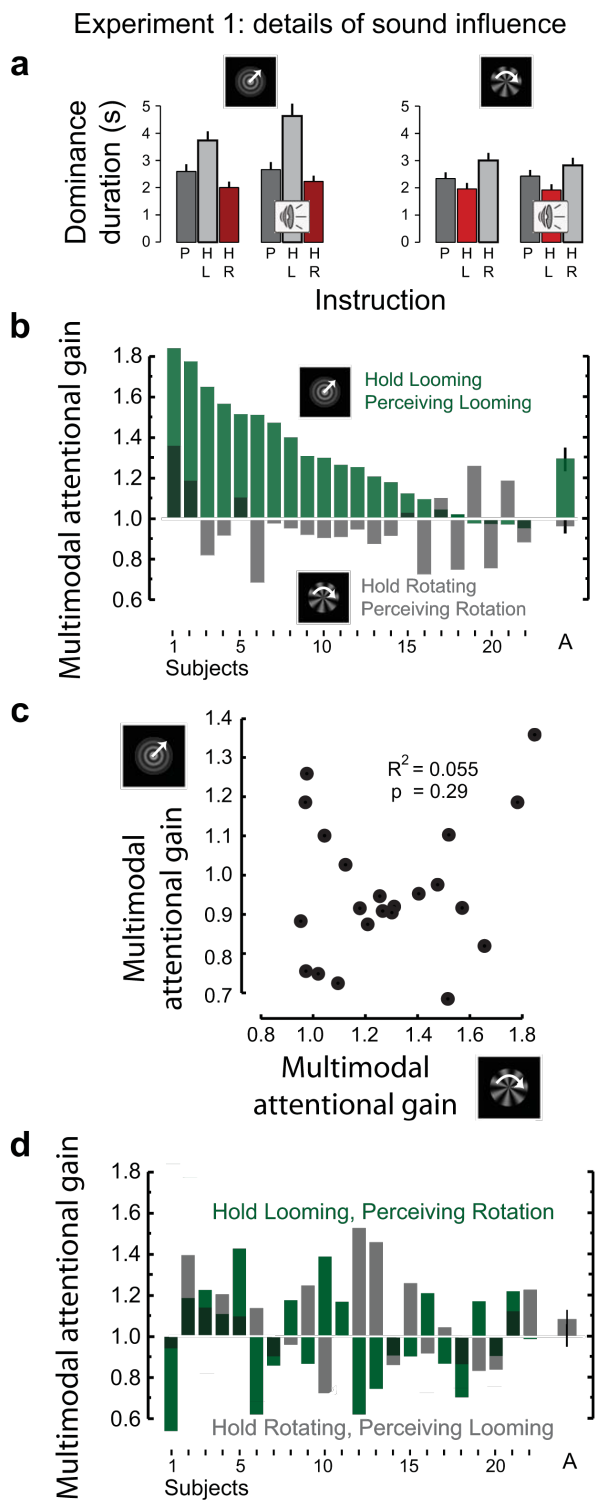


Figure 2

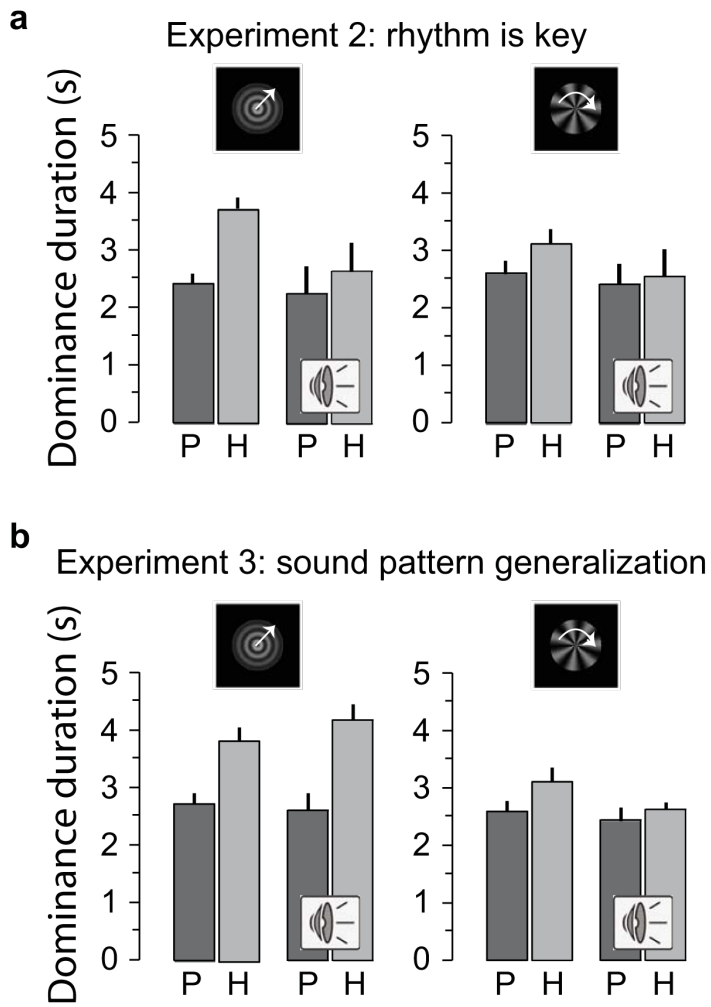


Figure 3

Experiment 4: role of attention

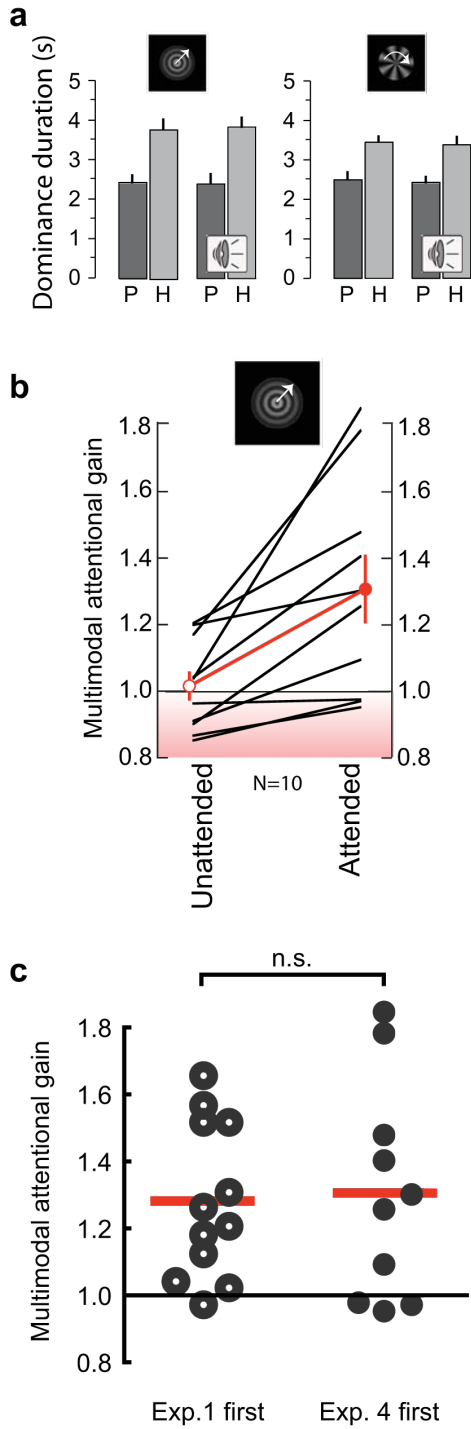


Figure 4

Experiment 5: visual pattern generalization

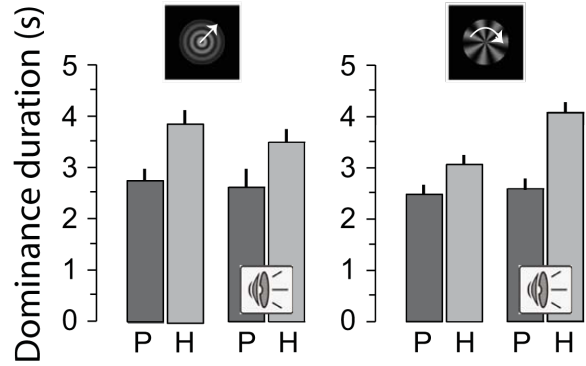


Figure 5

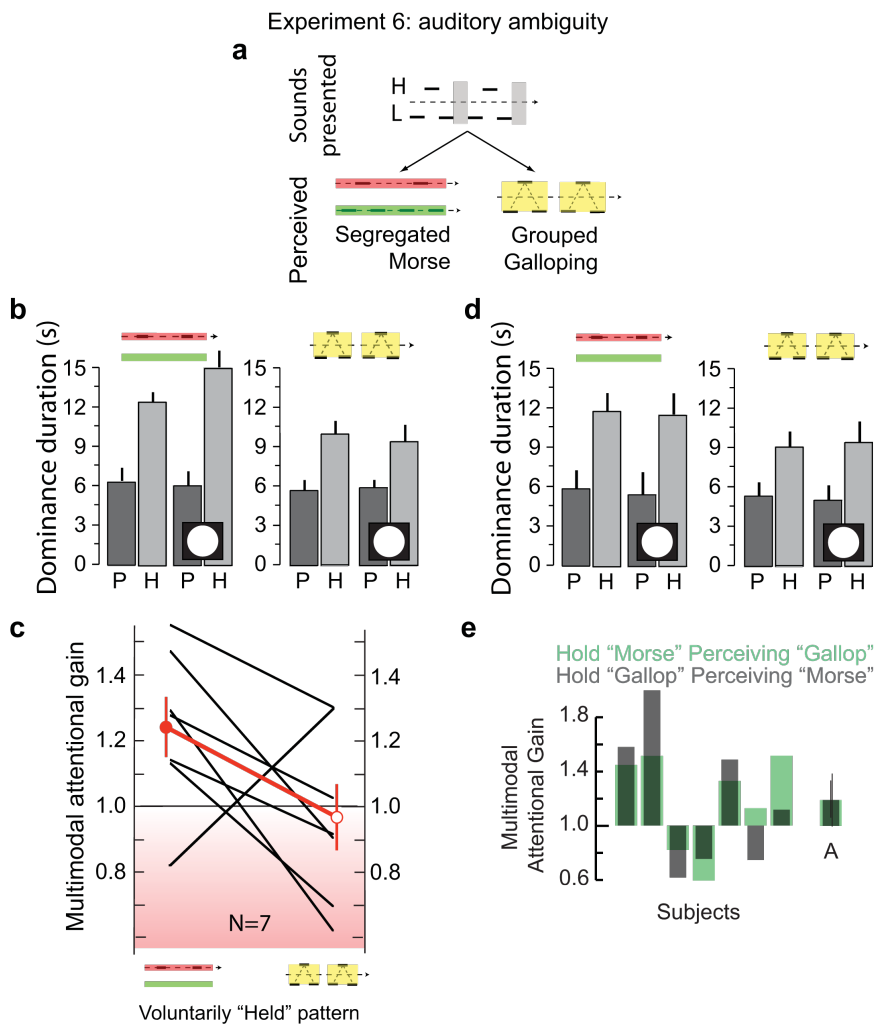


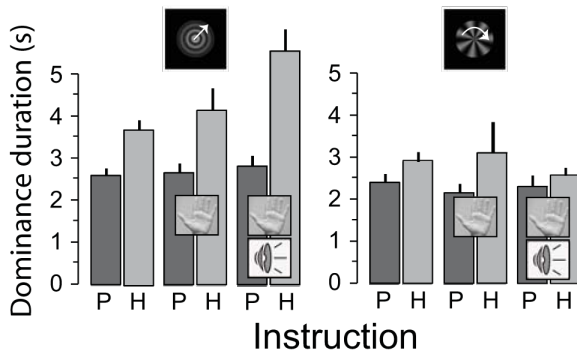
Figure 6

Experiment 7: touch and sound

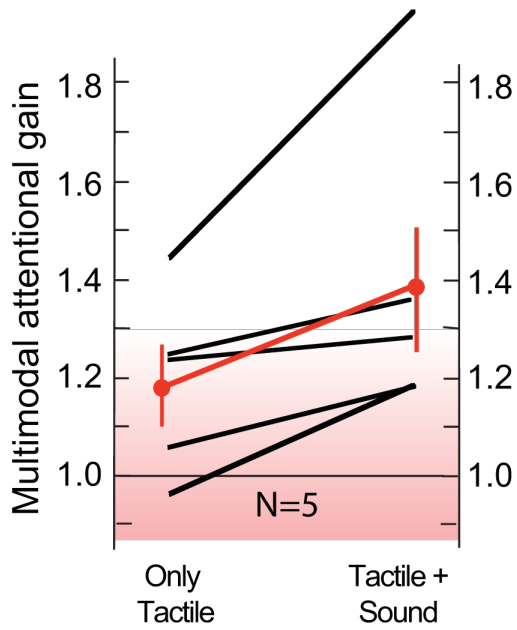
a



b



c



Supplement: Results in detail

Binocular rivalry tracking data for a total of 816 mins ($n = 22$) were collected to quantify the baseline influence of sound on attentional control of rivalry dominance. There were 6 conditions, with 16 subjects doing 4 min blocks and 6 subjects (who did three repetitions of the experiment) doing 12 min blocks. The mean perceptual durations for the passive and the two active ‘hold’ conditions are plotted in Figure Suppl1a (part of these data were presented in Fig 2), shown separately for the looming visual pattern (left-hand panel) and the radial visual pattern (right-hand panel). For the raw dominance durations of the looming pattern, the mean dominance duration without sound (first pair of columns) was 2.6 ± 0.2 s in the passive condition, and subjects were able to increase dominance to 3.6 ± 0.3 s by attentively holding it ($p < 0.001$, paired t-test). For the radial pattern, mean dominance duration without sound (right panel, first pair of columns) was 2.3 ± 0.2 s in the passive condition, increasing to 3.0 ± 0.3 s when subjects attentively held it ($p < 0.001$, paired t-test). These findings from the no-sound conditions replicate earlier reports showing a degree of voluntary attentional control in selecting the dominant percept in perceptual bistability. These findings also replicate earlier reports showing that not only the dominance periods for the held pattern change, but also those for the other pattern. When subjects held the looming pattern the dominance duration of the radial pattern changed slightly from 2.3 ± 0.2 s to 1.9 ± 0.2 s ($p < 0.001$). When subjects held the radial pattern the dominance duration of the looming pattern changed from 2.6 ± 0.2 s to 2.0 ± 0.2 s ($p < 0.001$). There were brief periods of superimposed or piecemeal pattern perception scattered throughout the observation period where neither pattern was exclusively dominant. In total, they averaged 13.7% of the observation period.

Next we turn to the multimodal conditions (see also Fig Suppl1a), in which the visual stimuli and attentional selection tasks were identical to those just described above, but there was a looming sound matched to the visual looming pattern. During passive viewing, mean dominance duration for the looming pattern was identical ($p > 0.85$, paired t-test) to the passive-no-sound condition (2.5 ± 0.3 s), but subjects were able to nearly double mean dominance duration to 4.5 ± 0.4 s in the active sound condition by attentively holding it ($p < 10^{-4}$). The absence of a change in dominance durations in the passive

condition shows that presenting sound with the visual stimuli did not automatically change dominance durations. These findings were corroborated by a two-way repeated-measures ANOVA (sound (present/absent) x hold (yes/no)), revealing significant main effects for sound ($F_{1,21}=10.4$, $p < 0.005$) and hold ($F_{1,21}=55.2$, $p < 0.005$). Importantly, there was a significant interaction between these factors ($F_{1,21}=22.1$, $p < 0.001$), indicating that subjects were better able to hold the looming pattern with the sound present than with the sound absent.

For the radial pattern, similarly, the mean dominance duration in the passive condition was virtually unchanged by the presence of sound (2.3 ± 0.2 s vs 2.3 ± 0.2 s without sound; $p > 0.80$, paired t-test), and subjects were able to increase it to 2.9 ± 0.3 s by attentively holding it ($p < 0.001$, paired t-test). A similar two-way ANOVA for the radial pattern revealed no effect of sound ($F_{1,21}=0.35$, $p > 0.7$), but a significant increase of dominance durations when subjects attempted to influence dominance ($F_{1,21}=20.4$, $p < 0.0001$). The interaction was not significant ($F_{1,21}=1.2$, $p=0.27$), although it showed a trend in the opposite direction to the looming pattern, suggesting that subjects were worse at holding the radial pattern when the looming sound was present. We also examined predominance of the looming and radial patterns and ruled out that sound had a non-specific enhancing effect: the non-held pattern duration did not increase with sound present (all $p > 0.3$; paired t-test). In these multimodal conditions, the dominance duration of the radial pattern changed from 2.3 ± 0.2 s (for passive) to 1.9 ± 0.2 s (hold looming). When subjects held the radial pattern the dominance duration of the looming pattern changed from 2.5 ± 0.3 s (passive) to 2.1 ± 0.2 s (hold radial pattern). Again a two-way ANOVA for the non-held patterns showed only significant effects of the hold-condition ($p < 0.0001$). Detailed results of the other experiments are given in the figures.

Captions of Supplementary Figures

Fig Suppl1: Detailed data from Experiment 1 (part of the data were presented in Figs. 2a and 3a of the main paper). **a.** The mean duration for the looming (left) and the radial (right) visual patterns. P denotes passive; HL and HR denote hold the looming pattern and rotating pattern, respectively. The ‘speaker icon’ denotes the sound conditions. **b.**

The proportion of the gain with the sound present over the gain without sound quantifies how much the looming sound enhances attentional control over the visual pattern. Those proportions for each individual subject (horizontally) are presented as multimodal attentional gain for the looming (green) and the radial (grey) patterns. The average value across the 22 subjects is denoted by A. **c.** The lack of correlation between the multimodal attentional gains for the two patterns demonstrates that a subject who is successful in holding the looming pattern is not necessarily successful in holding the radial pattern. **d.** Same as panel b, but now for the non-held patterns. Neither of them produces data significantly greater than 1 ($p's > 0.1$). Error bars, ± 1 standard error.

Fig Suppl2: The mean duration for the looming (left) and the radial (right) visual patterns in Experiment 2 (**a**) and Experiment 3 (**b**). P denotes passive; H denotes hold. Error bars, ± 1 standard error.

Fig Suppl3: **a.** The mean duration for the looming (left) and the radial (right) visual patterns in Experiment 4. Error bars, ± 1 standard error. **b.** Direct comparison of the data from Experiment 1 (Fig. 3a of main text) and Experiment 4 (Fig. 3d) for each individual who ran both the attended and unattended conditions, demonstrating that paying attention to the congruent looming sound is required to enhance holding of the visual looming pattern. The dashed lines connect data of identical subjects. The filled red circle indicates significance (t-test, see text), and error bars are ± 1 standard error. **c.** Multimodal attentional gain in Experiment 1, comparing subjects who started with Experiment 1 (open circles) with those who first completed Experiment 4 (closed circles). These data show that there is no significant difference between the two groups ($p > 0.8$), while both groups show multimodal attentional gains larger than 1 ($p < 0.002$, and $p < 0.02$, respectively), implying that there is no effect of practice. These results show that the absence of multimodal attentional gain in Experiment 4 is unlikely to be due to inexperience of the subjects.

Fig Suppl4: The mean duration for the looming (left) and the radial (right) visual patterns in Experiment 5. Error bars, ± 1 standard error.

Fig Suppl5: **a.** We presented a high-frequency pure tone (H) alternating with a low-frequency pure tone (L) in an LHL pattern. This sequence can be perceived either as one stream (LHL-LHL, i.e., grouped ‘galloping’ rhythm) or as two streams (H-H-H and L-L-L, i.e., segregated ‘Morse’ tones). **b.** The mean duration for the Morse (left) and the galloping (right) auditory patterns. Note that the scale is different as in the other mean durations data figures. The disk icon denotes the visual flickering disk that supported the Morse pattern. **c.** There was significant multimodal gain in holding the percept of segregated Morse tones dominant over the galloping tones when the flickering visual disk (matching the Morse) was viewed, but there was no significant change when holding the galloping pattern. **d.** Same as panel b but here subjects were given the instruction that the flickering disk was not relevant to their task, although no explicit instruction was given to attend or to disregard the disk. These data concern a preliminary pilot experiment whose conditions were exactly identical to those used to collect the data for panel b but it involved only four out of the seven subjects who participated in this experiment (note that those four subjects participated in all experiments presented in this paper). The duration of a pilot series was 2 minutes. They did this attention task before they participated in Expt 6. **e.** Same as panel d of Fig. Suppl1 but now for the 7 subjects whose data are plotted in panel c of this figure: changes in “multimodal attentional gain” for the non-held patterns. Neither of the two multimodal attentional gains is significantly greater than 1 ($p's > 0.2$). The average value across the 7 subjects is denoted by A. Error bars show ± 1 standard error.

Fig Suppl6: **a.** A sound speaker was attached to the dorsal side of the hand to produce a tactile looming stimulus matched to both the visual and the auditory looming stimuli. **b.** The mean duration for the looming (left) and the radial (right) visual patterns in tactile condition (middle pair of bars) and the tactile+sound condition (right pair of bars). The ‘hand icon’ denotes the tactile conditions. **c.** The individual subject data for both the tactile and the tactile+sound conditions. Error bars, ± 1 standard error.

Appendix 4: Statements of co-author contributions

Statement of co-authors contributions: Chapter 2

The thesis entitled “A cross-modal investigation into the relationship between bistable perception and a global temporal mechanism”, submitted by Amanda Louise Parker in fulfillment of the degree of Doctor of Philosophy at the University of Sydney, contains four papers either published or in press. The work contained in Chapter 2, entitled “Monocular rivalry exhibits three hallmarks of binocular rivalry: evidence for common processes”, was co-authored with Robert O’Shea, David La Rooy and David Alais. As co-authors, we agree that the authors’ contributions to the paper are as listed below:

Robert O’Shea

Study conception
Data collection
Data analysis
Graphical presentation of results
Manuscript preparation

Amanda Parker

Protocol and stimulus programming
Data collection
Data analysis
Graphical presentation of results
Manuscript preparation

David Alais:

Protocol and stimulus programming
Manuscript preparation
Guidance on initial design aspects of the project

David La Rooy

Data collection
Data analysis

Statement of co-authors contributions: Chapter 3

The thesis entitled “A cross-modal investigation into the relationship between bistable perception and a global temporal mechanism”, submitted by Amanda Louise Parker in fulfillment of the degree of Doctor of Philosophy at the University of Sydney, contains four papers either published or in press. The work contained in Chapter 3, entitled “A Bias for Looming Objects to Predominate During Binocular Rivalry”, was co-authored with David Alais. As co-authors, we agree that the authors’ contributions to the paper are as listed below:

Amanda Parker

Study conception
Protocol and stimulus programming
Subject recruitment
Data collection
Data analysis
Graphical presentation of results
Manuscript preparation

David Alais

Manuscript advice and editing

Statement of co-authors contributions: Chapter 4

The thesis entitled “A cross-modal investigation into the relationship between bistable perception and a global temporal mechanism”, submitted by Amanda Louise Parker in fulfillment of the degree of Doctor of Philosophy at the University of Sydney, contains four papers either published or in press. The work contained in Chapter 4, entitled “Multimodal congruency as a mechanism for wilful control over perceptual awareness”, was co-authored with Raymond Van Ee, Jeroen van Boxtel and David Alais. As co-authors, we agree that the authors’ contributions to the paper are as listed below:

Raymond van Ee

Study conception
Data collection
Data analysis
Graphical presentation of results
Manuscript preparation

Amanda Parker

Study conception
Protocol and stimulus programming
Data analysis
Manuscript advice

Jeroen van Boxtel

Protocol and stimulus programming
Data collection
Data analysis
Graphical presentation of results

David Alais:

Manuscript advice and editing
Guidance on initial design aspects of the project

Statement of co-authors contributions: Chapter 5

The thesis entitled “A cross-modal investigation into the relationship between bistable perception and a global temporal mechanism”, submitted by Amanda Louise Parker in fulfillment of the degree of Doctor of Philosophy at the University of Sydney, contains four papers either published or in press. The work contained in Chapter 5, entitled “Temporal auditory information speeds visual selection for consciousness during binocular rivalry”, was co-authored with David Alais. As co-authors, we agree that the authors’ contributions to the paper are as listed below:

Amanda Parker

Study conception
Protocol and stimulus programming
Subject recruitment
Data collection
Data analysis
Graphical presentation of results
Manuscript preparation

David Alais

Manuscript advice and editing