



## Attending to auditory signals slows visual alternations in binocular rivalry

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### ABSTRACT

A previous study has shown that diverting attention from binocular rivalry to a visual distractor task results in a slowing of rivalry alternation rate between simple orthogonal orientations. Here, we investigate whether the slowing of visual perceptual alternations will occur when attention is diverted to an auditory distractor task, and we extend the investigation by testing this for two kinds of binocular rivalry stimuli and for the Necker cube. Our results show that doing the auditory attention task does indeed slow visual perceptual alternations, that the slowing effect is a graded function of attentional load, and that the attentional slowing effect is less pronounced for grating rivalry than for house/face rivalry and for the Necker cube. These results are explained in terms of supramodal attentional resources modulating a high-level interpretative process in perceptual ambiguity, together with a role for feedback to early visual processes in the case of binocular rivalry.

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### 1. Introduction

When the eyes are presented with very different stimuli in corresponding locations a phenomenon known as binocular rivalry occurs (von Helmholtz (1924), for reviews see Alais and Blake (2005); Blake and Logothetis (2002)). Rather than seeing both stimuli at once, perhaps transparently or as a summed image, a stochastic alternation takes places whereby each monocular image is seen exclusively for a second or so before a switch to the other eye occurs (as shown in Fig. 1b). Much of the work on rivalry until the recent decade or so was conducted with simple contoured stimuli and focused on low-level stimulus properties and how factors such as spatial frequency and contrast affected rivalry alternation rates and relative dominance of one image over another (Blake, 1989; Levelt, 1965). More recent research has moved away from a low-level focus by using more complex images (Alais & Melcher, 2007; Alais & Parker, 2006; Baker & Graf, 2009; Tong, Nakayama, Vaughan, & Kanwisher, 1998) and adopting a multi-level approach to rivalry that includes a role for global organisation and feedback to earlier levels? (Alais & Blake, 1998; Carlson & He, 2004; Tong, Meng, & Blake, 2006; van Boxtel, Alais, & van Ee, 2008a; van der Zwan, Wenderoth, & Alais, 1993; Watson, Pearson, & Clifford, 2004). Current theories of rivalry have therefore evolved to include competition at multiple levels of the visual system and feedback between levels (Freeman, 2005; Lee, Blake, & Heeger,

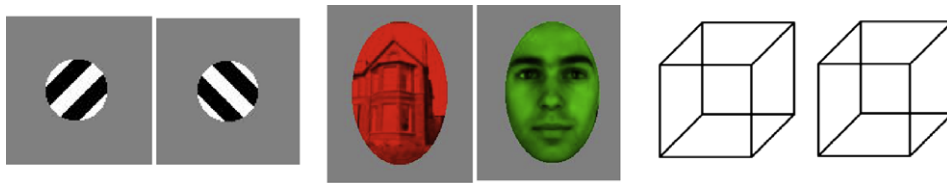
2007; Leopold & Logothetis, 1999; Nguyen, Freeman, & Alais, 2003; Tong, 2001; Wilson, 2003).

The swing away from a low-level focus has revived a long-standing question regarding whether binocular rivalry can be brought under attentional control or not (Chong & Blake, 2006; Chong, Tadin, & Blake, 2005; Lack, 1978; Mitchell, Stoner, & Reynolds, 2004; Paffen, Alais, & Verstraten, 2006; van Ee, van Boxtel, Parker, & Alais, 2009; van Ee, van Dam, & Brouwer, 2005). There are obvious parallels between rivalry and attention in that both are processes of selection. More than a century ago, Helmholtz suggested that attention played a role in governing binocular rivalry in that attending to one of the images led to a modest lengthening of its dominance duration (von Helmholtz, 1924). Against this, however, it is also true that no amount of attentional effort can stop rivalry alternations entirely, and rivalry will continue independently of attentional switches between the competing stimuli, demonstrating that rivalry entails more than just a process of attentional selection. An important distinction is that rivalry is initiated at early levels of the visual system, the default outcome when the binocular matching process fails (Blake & Boothroyd, 1985), whereas attention is regarded as a top-down process originating at higher levels (for useful discussion of terms such as “bottom-up/top-down”, “early/late” in the context of perceptual ambiguity, see Kornmeier, Hein, & Bach, 2009). As a feedback process, it appears that attention can feed back to early stages of the visual system to modulate existing activity – which may include rivalry-related activity – at those levels (Chong et al., 2005; Desimone & Duncan, 1995; Klink et al., 2008; Treue, 2001).

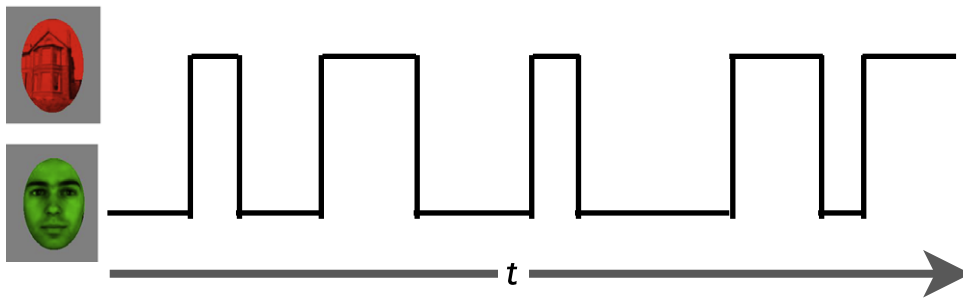
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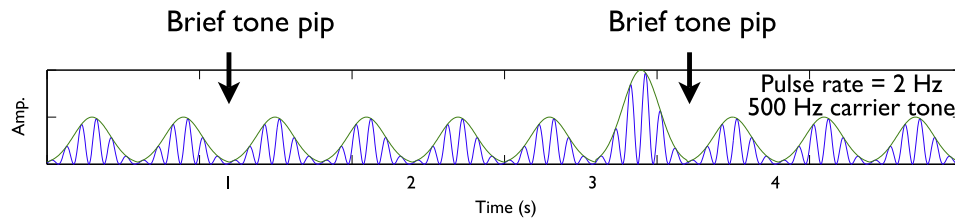
(a) Stimuli



(b) Task 1: Track perceptual alternations over time



(c) Task 2: Was the tone pulse preceding each pip a loud one or not?

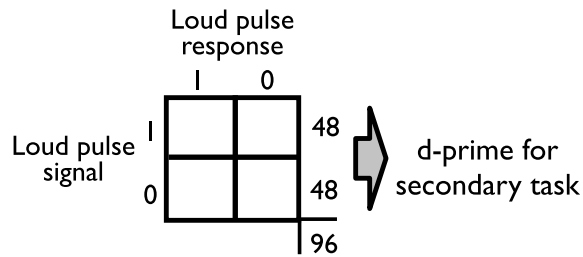


(d) Dependent variables:

- 1) Perceptual alternation rate
- 2) Sensitivity to loud-tone detection ( $d'$ )

- Alternations averaged over 3 x 2 min tracking trials.

- 3 conditions:
  - (i) easy distractor,  $d' \approx 1$
  - (ii) hard distractor,  $d' \approx 2$
  - (iii) baseline (no 2nd task, sound present at 'hard' level)



**Fig. 1.** Stimuli and procedures. (a) Examples of the three kinds of perceptually ambiguous stimuli used in these experiments. The first two pairs of images were dichoptically viewed so as to induce binocular rivalry. The last pair shows a Necker cube that was binocularly viewed. (b) The primary task in all conditions was to track continuously perceptual alternations over three 2 min observation periods. From these data a mean alternation rate was calculated. These alternation time series were also used to produce 'pseudo-rivalry' conditions where for any observer/condition alternating sequences of monocular images were replayed that were shuffled versions of a subject's own tracking sequences for a given condition. Pseudo-rivalry conditions provide an important control by mimicking the perceptual alternations of real binocular rivalry, with the advantage that the observer's tracking behaviour can be objectively measured against a known sequence. (c) The secondary 'distractor' task was to detect odd-ball loud-tone pulses in a series of standard tone pulses presented at rate of 2 Hz. At 32 points randomly inserted in the 2 min tracking period a brief tone pip was presented. This served as a cue for the subject to respond (within a 1 s limit) whether the tone pulse just preceding the pip was a loud one or not. For half of the cues, randomly distributed, there was a loud-tone immediately preceding the cue, and for the other half of cues there was not. (d) From these responses, task sensitivity ( $d'$ ) could be calculated and task difficulty could be controlled as a function of the loudness increment magnitude. For the 'easy' distractor task, the loudness increment was set to a value giving performance at approximately  $d' = 2$ . For the 'hard' distractor, the loudness increment was reduced to produce performance at approximately  $d' = 1$ .  $D$ -prime values were calculated on a total of 96 responses (32 per 2 min tracking trial).

Because attention is a feedback process that can alter early visual responses, it should not be surprising that attention can modulate rivalry. Attentionally selecting and holding one of the stimuli biases predominance in favour of the selected stimulus in free running rivalry (Lack, 1978; Meng & Tong, 2004; van Ee et al., 2005), similar to Helmholtz's original observation. Although this bias is not especially strong, it is somewhat stronger for ambiguous stimuli such as the Necker cube which, in contrast to binocular rivalry, do not involve interocular conflict (Meng & Tong, 2004; van Ee et al., 2005). Attentional orienting to one of the stimuli can have strong acute effects on rivalry, as stimulus cueing paradigms have shown. For example, exogenously cueing a non-rivalrous image just prior to rivalry onset ensures that the cued image will appear as the initially dominant percept (Mitchell et al., 2004). Endogenous cueing has been shown to produce a similar effect (Chong & Blake, 2006; Klink et al., 2008), although in both cases the influence is restricted to the early phase of rivalry. Studies with other kinds of perceptually bistable stimuli show similar modulatory effects of attention (Meng & Tong, 2004; Toppino, 2003; van Ee et al., 2005) in that attention can bias which percept tends to dominate. Together, these studies demonstrate that attention can influence binocular rivalry (and bistable perception in general) but not particularly powerfully, although with training observers can learn to increase their attentional control over binocular rivalry (Lack, 1978).

The studies reviewed above have generally studied attention by having observers focus their attention on one of the perceptual alternatives, an approach which can bias predominance in favour of the selected stimulus but cannot freeze the rivalry process. Here, we adopt a complementary approach similar to that used by Paffen, Alais and Verstraten (Paffen et al., 2006) which involves directing attention away from the rival stimuli towards a peripheral distractor task. Paffen et al. study demonstrated that removing attention from the stimuli causes rival alternations to slow by an amount related to the difficulty of the distractor task. A similar approach was later used by Pastukhov and Braun (Pastukhov & Braun, 2007) to show that perceptual alternations in bistable motion perception were slowed by a difficult attentional distractor, although they continued to occur even in the near-absence of attention. Both studies show that withdrawing attention from bistable stimuli causes a slowing of perceptual alternations. In the present study, we extend these earlier studies in two ways. First, we will use an auditory task as an attentional distractor (see Fig. 1c) to see whether the attentional resources involved in binocular rivalry are specifically visual or are modality independent. Attention is known to act crossmodally between the senses (Alais, Newell, & Mamassian, 2010; Driver & Spence, 1998), and recent work has shown specifically that attention can act crossmodally from touch and audition to influence alternation rates in binocular rivalry, or from vision to influence auditory ambiguity (van Ee et al., 2009). This implies that there are supramodal attentional resources involved in resolving perceptual ambiguity and we therefore predict that an auditory distractor should slow alternations in binocular rivalry.

The present study will also compare the effects of attentional distraction across several types of visually ambiguous stimuli (see Fig. 1a): grating rivalry, house/face rivalry, and the Necker cube. The aim of this comparison is to determine whether attentional modulation depends on the complexity of the rival stimuli, and in particular to test whether ambiguous stimuli without interocular conflict are more prone to attentional effects. Given the results of earlier attentional studies using Necker cubes and grating rivalry (Meng & Tong, 2004; van Ee et al., 2005), we predict that auditory attentional modulation will be greater for the Necker cube than for the binocular rivalry between gratings.

## 2. Methods

### 2.1. Observers

Nine subjects, the four authors plus five naïve observers, performed in all conditions of these experiments. All had normal hearing, and normal or corrected-to-normal vision.

### 2.2. Stimuli

Three kinds of perceptually ambiguous visual stimuli were compared. As shown in Fig. 1a, two of these were binocular rivalry stimuli (grating rivalry, and house/face rivalry) and were presented dichoptically, while the third was a Necker cube which was presented binocularly. The grating stimuli were orthogonally oriented square-waves  $\pm 45^\circ$  from vertical with a spatial frequency of 1.25 cpd and were  $1.6^\circ$  in diameter. The gratings and the Necker cube had maximum contrast (black and white), with the Necker cube composed of thin black lines 9 arc min wide and the front face of the cube being a square subtending  $2.5^\circ$  on a side. The house and face images were matched at the maximum possible RMS contrast (.17) with equal mean luminance. The house and face were also tinted red and green respectively, as in Alais and Parker (2006), as this facilitates rivalry tracking by making instances of piecemeal rivalry more obvious (which may sometimes go unnoticed in complex achromatic images). The house/face stimuli were presented in an oval aperture  $4.4^\circ$  wide and  $6.6^\circ$  high. All stimuli were presented on a CRT monitor with the background set to the mean luminance grey value ( $29.2 \text{ cd/m}^2$ ). Monitor resolution was  $1024 \text{w} \times 768 \text{h} \times 75 \text{ Hz}$ .

The auditory signal which provided the stimulus for the attentional task was a series of tone pulses digitized at rate of 32 kHz. A 500 Hz carrier tone was windowed by a series of Gaussian profiles ( $\text{SD} = 80 \text{ ms}$ , truncated at  $\pm 3.125 \text{ SD}$ ) to create a regular sequence of smooth pulses. The Gaussian peaks were separated by 500 ms so that the tones pulsed continually at a rate of 2 Hz. The tones had a maximum sound pressure level of 74 dB A as measured through the presentation device (headphones) at the listening position.

### 2.3. Procedure

The primary dependent measure in these experiments was the alternation rate of the perceptual reversals. To determine this, the visual stimuli were presented for 2 min at a time (using a mirror stereoscope) and subjects continuously tracked their perceptual alternations using two keys on the computer keyboard (and pressing neither for percepts of mixed dominance). A total of 6 min of tracking ( $3 \times 2 \text{ min trials}$ ) was measured for each condition and the alternation rates were averaged over the trials into a single estimate of perceptual alternation rate.

Alternation rates were measured under three different attentional conditions: (i) attend to difficult distractor, (ii) attend to easy distractor, (iii) no attention baseline. The attentional task involved monitoring the series of tone pulses in order to detect an odd-ball tone pulse that was louder than the others (which observers indicated by pressing the keyboard space bar). The loudness increments for the odd-ball were calibrated for each individual observer in pilot experiments to be either easy to detect ( $d' = \sim 2.0$ ) or difficult to detect ( $d' = \sim 1.0$ ). There were a total of 240 tone pulses in each 2 min trial, and at the offset of 32 of them (randomly selected on each trial) a brief tone pip was played. This pip signaled to the subject to respond in a yes/no manner whether or not the tone pulse just preceding the pip had been an odd-ball (i.e., a loud pulse). On a given 2 min trial, 16 of the pulses that

preceded the pips were odd-balls and 16 were not, and from the subjects' responses we used signal detection theory to compute hit rates and false-alarm rates in order to measure their sensitivity ( $d'$ ) for detecting the odd-ball loud pulse. Whether the attentional condition was easy, difficult or baseline, the tone pulses were always present (at the difficult level in the case of baseline conditions), together with the 32 randomly inserted tone pips. Baseline alternation rates were recorded first, followed by the 'easy' and then 'hard' conditions. By doing the hard task last, subjects were already familiar with the attentional task they had to perform (from the preceding 'easy' condition), meaning that any performance decrement could be attributed to the task being more demanding rather than to unfamiliarity with it.

For the grating rivalry and house/face rivalry conditions we also ran pseudo-rivalry conditions that were carefully calibrated so that tracking the pseudorivalry alternations did not alter sensitivity to the attentional task. Three 2 min pseudo-rivalry tracking trials were completed for each attentional condition: easy distractor, difficult distractor, and baseline. Pseudo-rivalry mimics the perceptual alternations of binocular rivalry by presenting the two binocular rivalry stimuli in an alternating sequence according to a shuffled version of an observer's own rivalry alternations (this is not possible for the Necker cube, as it is a single binocularly viewed stimulus). Pseudo-rivalry can be trivially easy to track if image transitions are abrupt and transient, which would allow more attention to be allocated to the second task than was the case in real rivalry. To minimize transients, we smoothed image changes over a 0.15 s interval according to a cumulative Gaussian cross-fade technique. This smoothing interval was chosen after pilot experiments showed it produced performance on the attentional task that was equivalent to real binocular rivalry (see Fig. 2b). Shorter smoothing intervals produced better performance on the attentional task, presumably because the tracking task required little or no attention and resources could be allocated to the second task. With equivalent performance on the second task, we can conclude that the tracking task in both the real and pseudo-rivalry conditions were equivalently demanding.

### 3. Results

Mean alternation rates for the three stimuli are plotted in Fig. 2a under each of the three attentional conditions: no attention baseline, attend to easy distractor, attend to difficult distractor. It is clear that perceptual alternations declined with the increasing attentional load of the loudness increment detection task for all three stimulus types. Confirming this, a two-way (stimulus type vs. attentional load) repeated-measures analysis of variance produced a significant main effect of attentional load ( $F(2, 16) = 26.72, p < .001$ ), and a trend analysis showed the attentional effect to be a significant linear ( $F(1, 8) = 32.01, p < 0.001$ ) but not quadratic ( $F(1, 8) = 1.96, p = 0.200$ ) trend, showing that the effect of attention increases monotonically with distractor task difficulty. The main effect across stimulus types was also significant ( $F(2, 16) = 11.47, p < 0.001$ ), and there was no significant interaction between the main factors ( $F(4, 32) = 1.48, p = 0.232$ ).

Pseudo-rivalry conditions were run to verify that the reduction in perceptual alternation rate apparently due to the attentional distractor task was not simply due to poor vigilance and "missed" alternations. Mean performance on the loudness increment detection task under rivalry and pseudo-rivalry conditions is plotted in Fig. 2b in terms of sensitivity ( $d'$ ), for the 'easy' and 'difficult' levels. Mean  $d'$  was 1.28 for the 'easy' task and 2.15 for the 'hard' task and performance was comparable whether observers were tracking rivalry alternations or pseudo-rivalry alternations. For grating rivalry, task sensitivity was not significantly different between rivalry and pseudo-rivalry for the 'easy' condition ( $t_8 = 0.626; p = 0.549$ )

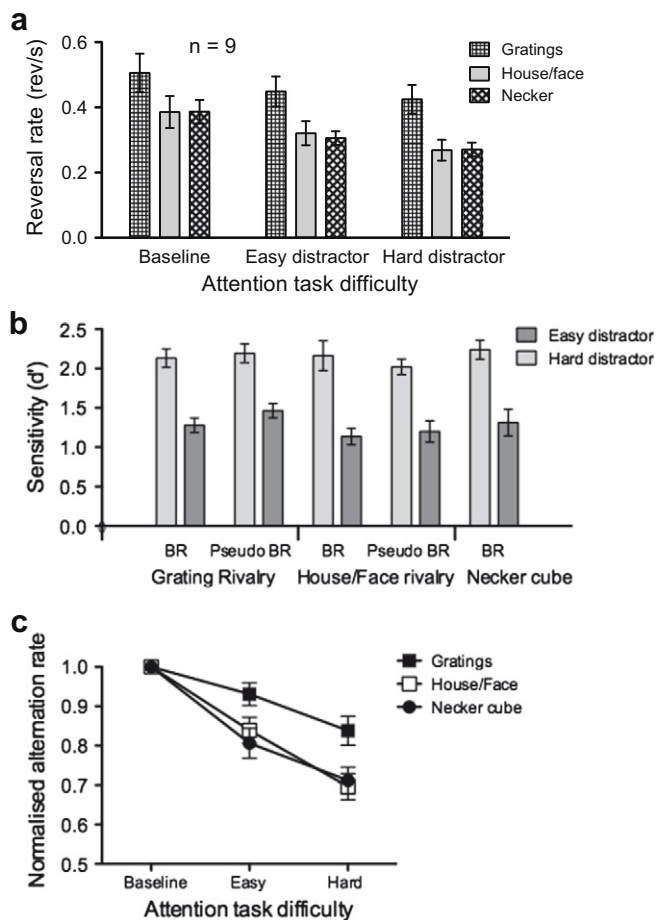
or the 'hard' condition ( $t_8 = 1.791; p = 0.111$ ). Similarly, there were no significant differences for the same tests in the house/face rivalry conditions ('easy':  $t_8 = 0.966; p = 0.359$ , 'hard':  $t_8 = 0.422; p = 0.683$ ). Note that the right panel of Fig. 2b (Necker cube) only shows task sensitivity for perceptual alternations because pseudo-alternations are not possible with this stimulus.

Overall, it is clear that performance on the attentional task was similar across rivalry and pseudo-rivalry and was reliably harder when the loudness increment was small. How accurate were observers at tracking pseudo-rivalry alternations under these conditions? Averaged over all attentional conditions, 80% of alternations were responded to within 1 s, a rate similar to the pseudo-tracking performance reported by Paffen et al. (2006) using the same time limit. Typically, those alternations that were missed were nearly always the briefest ones. Confirming this, when dominance durations of  $<0.4$  s were excluded, the percentage of successfully tracked alternations increased to 92%. Note that if tracking had been trivially easy in pseudo-rivalry (as when abrupt transitions are used), tracking performance would have been higher as detecting the changes would have demanded little or no attention. However, here we chose to match performance on the attentional task across real and pseudo-rivalry conditions, implying equivalent resources remain for tracking changes in those conditions. Despite real and pseudo-rivalry conditions being matched in this way, the fact that performance is  $<100\%$  accurate in pseudo-rivalry implies some alternations may also be missed by observers in real rivalry, although being a subjective measure there is no way to verify this.

It was noted above that there was no overall interaction between attention and stimulus type in the ANOVA, which would suggest that all three stimulus types were equally affected by the attentional manipulation. However, we hypothesized in the Introduction that alternation rates for the Necker cube might be more subject to the attentional effect than alternations between rivaling gratings. Fig. 2c suggests that this may indeed be so. The figure shows alternation rates after normalization to the value of the baseline condition, so that the effect of attention on all three stimuli can be compared in a standardized way as a proportionate change from baseline. It appears that the decrease in alternation rate as a result of doing the attentional distractor task is weakest for grating rivalry, and is about equally strong for the house/face stimuli and the Necker cube. We tested our prediction with one-tailed Bonferroni-corrected pairwise comparisons using the normalised data. Confirming what is apparent in Fig. 2c, attentional slowing of alternation rate for the Necker cube was significantly stronger than for grating rivalry, in both the 'easy' condition ( $t_8 = 4.24, p < 0.005$ ) and 'hard' condition ( $t_8 = 3.98, p < 0.005$ ). This demonstrates that grating rivalry is less susceptible to attentional slowing than the Necker cube. Interestingly, attentional slowing of alternations in house/face rivalry was not significantly different from the Necker cube condition ('easy' condition:  $t_8 = 0.83, p = 0.214$ ; 'hard' condition ( $t_8 = -0.27, p < 0.602$ ), which largely explains the lack of significant interaction among all conditions in the overall ANOVA.

### 4. Discussion

The results reported here show that perceptually bistable visual stimuli alternate more slowly when attentional resources are deployed on a concurrent task in the auditory domain. The study extends findings from a recent paradigm developed by Paffen et al. (Paffen et al., 2006) in which diverting attention away from a pair of rivaling gratings to a visual distractor task caused the rate of rivalry alternations to slow. We confirmed Paffen et al. result that rivalry slows when performing a concurrent secondary task, and that the slowing is a graded function of the secondary task's difficulty.



**Fig. 2.** Data showing mean alternation rates and sensitivities to the secondary task. (a) Mean alternation rates in reversals per second across the three levels of attentional task difficulty (where 'baseline' refers to the "no attention" or "passive viewing" condition), with the type of bistable stimulus as a parameter. There is a significant effect of attentional task load, with alternations for all stimuli slowing relative to the baseline rate. The attentional slowing is greater for the more demanding distractor task. These data also show slower overall alternations for the Necker cube and house/face rivalry relative to grating rivalry. (b) Mean sensitivities ( $d'$ ) to the loud-tone detection task (see Fig. 1c) that served as the secondary (attentional distractor) task, at 'easy' and 'hard' levels. The size of the loudness increment was calibrated to each observer during pilot experiments to ensure that the 'easy' level produced a  $d'$  value of  $\sim 2$ , and the 'hard' level a  $d'$  of  $\sim 1$ . The plot shows data from the tracking experiments quantifying how well subjects did the secondary task (see Fig. 1d) while simultaneously tracking perceptual alternations. Apart from confirming that the difficulty levels were in the intended range, these data show that secondary difficulty was independent of the type of bistable stimulus, and more importantly that the secondary task was just as difficult in the pseudo-rivalry conditions. (c) To facilitate comparison between the stimulus types, the raw alternation rates for each stimulus in panel A are re-plotted here as normalized rates relative to baseline rate. This comparison clearly shows that attentional modulation for the Necker cube and house/face rivalry is greater than for rivalry between gratings. In all panels, error bars show  $\pm 1$  standard error, calculated over the group of nine observers.

More interestingly, however, we extend Paffen et al. study in two ways. First, we demonstrate that the slowing of perceptual alternations due to attentional diversion is greater for more complex rival stimuli and for a non-rivalrous bistable stimulus (Necker cube). Second, we show that attention-related slowing of visual perceptual alternations can be elicited just as effectively by diversion of resources to an auditory distractor task, demonstrating that the effect does not depend specifically on visual attentional resources.

Concerning the first point, this study adds to a growing literature showing that binocular rivalry and other forms of perceptual rivalry are modulated by attention (Chong & Blake, 2006; Lack,

1978; Meng & Tong, 2004; Mitchell et al., 2004; Ooi & He, 1999; Paffen et al., 2006; Pastukhov & Braun, 2007; Toppino, 2003; van Ee et al., 2005, 2009). Commonly in these studies the attentional task is specifically to select one of the rival stimuli (or perceptual interpretations) or to willfully control the alternation rate (Lack, 1978; Meng & Tong, 2004; van Ee et al., 2005) and they have generally shown limited effects of attention. Our study confirms the viability of an alternative approach in which the observer's attention is diverted to a secondary task, and alternations are observed to slow (Paffen et al., 2006). The clear implication of this is that the dynamics of binocular rivalry and other forms of bistable perception are partially attentionally dependent. This is broadly consistent with top-down 'interpretative' theories of binocular rivalry and bistable perception (Carter & Pettigrew, 2003; Leopold & Logothetis, 1999; Lumer, Friston, & Rees, 1998; Pressnitzer & Hupe, 2006), which will be discussed in detail further below. According to these theories, high-level executive processes such as found in frontoparietal brain regions interpret the visual input and initiate perceptual alternations by feeding back signals to early visual areas to select one interpretation or the other. When attentional resources are free to be allocated entirely to the ambiguous visual input, the interpretative process would become more active and produce more vigorous switching, similar to the response increase seen in feature-selective neurons when attention is actively deployed to those features (Treue, 2001). However, when resources are directed to a distractor task, rivalry alternations would slow.

Concerning the second conclusion, our finding that distractor tasks in the auditory domain slow perceptual alternations in the visual domain implicates attentional processes that are not sensory specific. While there is evidence suggesting that separate attentional resources exist for the visual and auditory modalities (Alais, Morrone, & Burr, 2006; Bonnel & Hafer, 1998), this appears to be confined to basic discrimination and detection tasks with simple stimuli. The more general finding is that a single pool of attentional resources exists that is supramodal and therefore dividing resources between two tasks of any kind leads to an attentional cost (Pashler, 1998). There is considerable evidence for strong crossmodal links in attention (Beer & Roder, 2005), including data showing that a location cued in one modality is effective at priming responses at that location in another modality (Driver & Spence, 2004). Our results show that the attentional processes contributing to the dynamics of binocular rivalry and the Necker cube are of this supramodal kind, implying more central processes than the visual processes engaged by the rival stimuli and the Necker cube.

Consistent with this 'common attentional resources' view, the magnitude of rivalry slowing we report here for auditory distractor tasks is similar to that reported by Paffen et al. (Paffen et al., 2006) for visual distractors. The rivaling gratings used in both studies were very similar (square-wave gratings of similar size and spatial frequency), and the 'easy' and 'hard' conditions were of comparable difficulty (respectively,  $d' = 1.1$  and  $1.6$  [Paffen et al.] and  $d' = 1.2$  and  $2.1$  [current study]). Normalising Paffen et al. data shows that their visual distractor task slowed rivalry alternations across 'easy' and 'hard' conditions to  $0.90$  and  $0.81$  of the baseline alternation rate, respectively. Our auditory task slowed rivalry alternations very similarly to  $0.89$  and  $0.84$ , consistent with the conclusion that common resources underlie this attentional modulation. More broadly, this is consistent with claims that there is a high-level component to binocular rivalry (Leopold & Logothetis, 1999; Lumer et al., 1998) which involves a general form of competitive pattern competition process that is also revealed in the dynamics of many other kinds of perceptual ambiguity (Klink et al., 2008) which do not involve interocular conflict, such as the Necker cube or Vase-Face illusion (Diaz-Caneja, 1928; Hupé, Joffo, & Pressnitzer, 2008; Leopold & Logothetis, 1999) or monocular (or "pattern") rivalry (O'Shea et al., 2009; Tong, 2001; van Boxtel, Knapen, Erkelens, & van Ee, 2008b).

The proposal that all forms of bistable perception share at least some common processes, perhaps a high-level pattern competition process, is supported by findings showing that all perceptual ambiguities share similar bistable Gamma-distributed dynamics (Brascamp, van Ee, Pestman, & van den Berg, 2005; Fox & Herrmann, 1967; Logothetis, Leopold, & Sheinberg, 1996; O'Shea et al., 2009; van Boxtel et al., 2008b). There are, however, important differences that point to the contribution of other distinct processes, especially for binocular rivalry. Binocular rivalry is less able to be brought under attentional control than ambiguous figures such as the Necker cube or Face/Vase illusion (Meng & Tong, 2004; van Ee et al., 2005). Binocular rivalry is also the only form of ambiguity that involves interocular conflict, which ties it (although not exclusively) to early visual processes, unlike other perceptual ambiguities. This appears to have important consequences because binocular rivalry is the perceptual ambiguity most likely to undergo alternations of complete suppression rather than simply changes in vividness of percept. In addition, binocular rivalry dynamics are affected by a host of low-level stimulus parameters, such as spatial frequency and contrast, that do not obviously follow from a high-level theory. In addition, piecemeal rivalry tends to occur with large rival stimuli (but not ambiguous figures) which is a problem because high-level selection should be a choice between one or the other interpretation, and not a conflated mixture of both. Overall, top-down 'interpretative' theories are not likely to provide a complete explanation of bistable perception.

Paffen et al. (2006) explained their result in terms of low-level consequences of attention. They reasoned that alternations were faster without the distractor task because all attentional resources were free to be allocated to the rivaling gratings, leading to a boost in effective stimulus contrast. A boost in response gain due to attention has been shown neurophysiologically and psychophysically (Alais & Blake, 1999; Treue, 2001), and since higher contrast does lead to faster rivalry alternations (especially for grating stimuli), this provided a reasonable account of their data. Expressed in more general terms, this 'gain' explanation could extend to explain our observations with house/face rivalry and the Necker cube, even though Necker cube alternation rates are not greatly affected by contrast change (Cornwell 1976). The reason is that the 'contrast gain' proposal is part of a broader notion that attentionally selected stimuli enjoy greater salience than other competing objects, which then biases neural competition in their favour (Desimone & Duncan, 1995). Our finding that all stimuli, whether gratings, house/face, or Necker cube, showed an attentional modulation of alternation rate is consistent with this broader notion of attentional gain as a boost in stimulus salience, and squares with a related proposal outlined by Hupé et al. (2008) (see also Long & Toppino, 2004).

In a related vein, another way to explain our results would be in terms of an attention-dependent interpretative process capable of feeding back to modulate early visual processes. A number of observations support the top-down 'interpretative' account of bistable perception. For one, significant correlations are observed between the dynamics of different types of rivalry presented simultaneously (Pearson & Clifford, 2005), and more broadly the dynamics of very different forms of ambiguous visual stimuli tend to be correlated (Brascamp et al., 2005; Leopold & Logothetis, 1999; Pearson & Clifford, 2005; van Ee, 2005). Also, idiosyncratic alternation dynamics within observers tend to be conserved across a variety of ambiguous stimuli (Carter & Pettigrew, 2003; Hupe & Rubin, 2003; Sheppard & Pettigrew, 2006), and even ambiguous auditory streaming stimuli show similar alternation dynamics to ambiguous visual stimuli (Pressnitzer & Hupe, 2006). All of this is consistent with a single interpretative network, possibly supramodal as suggested by the recent findings of van Ee et al. (2009), governing bistable perceptual dynamics, although against it is Pressnitzer and Hupe's observation that idiosyncratic alternation

dynamics in one modality were not seen in the other. Our findings add to evidence for a supramodal interpretative process by showing that attentional slowing effects are not modality specific, with auditory as well as visual tasks being similarly effective at producing a slowing of perceptual alternations.

In summary, our results show that attention plays a role in the dynamics of perceptual ambiguity for rivalrous and non-rivalrous visual stimuli. Deploying attention on a competing task slows perceptual alternations as a graded function of task difficulty, and the resources underlying this effect appear to be modality independent. The attentional slowing affect here is weaker for rivaling gratings than for ambiguous figures and complex rivalry patterns, although this could be due to different levels of processing in the visual system or to stimulus differences (size, spatial frequency, contrast etc). We propose that these attentional modulations of bistable dynamics can be attributed to an attention-dependent interpretative process that feeds back to modulate specifically visual processes to resolve perceptual ambiguity.

## References

- Alais, D., & Blake, R. (1998). Interactions between global motion and local binocular rivalry. *Vision Research*, 38, 637–644.
- Alais, D., & Blake, R. (1999). Neural strength of visual attention gauged by motion adaptation. *Nature Neuroscience*, 2, 1015–1018.
- Alais, D., & Blake, R. (Eds.). (2005). *Binocular rivalry*. Cambridge, MA: MIT Press.
- Alais, D., & Melcher, D. (2007). Strength and coherence of binocular rivalry depends on shared stimulus complexity. *Vision Research*, 47, 269–279.
- Alais, D., Morrone, C., & Burr, D. (2006). Separate attentional resources for vision and audition. *Proceedings of the Royal Society, Series B*, 273, 1339–1345.
- Alais, D., Newell, F. N., & Mamassian, P. (2010). Multisensory processing in review: From physiology to behaviour. *Seeing and Perceiving*, 23, 3–38.
- Alais, D., & Parker, A. (2006). Independent binocular rivalry processes for motion and form. *Neuron*, 52, 911–920.
- Baker, D. H., & Graf, E. W. (2009). Natural images dominate in binocular rivalry. *Proceedings of the National Academic Science USA*, 106, 5436–5441.
- Beer, A. L., & Roder, B. (2005). Attending to visual or auditory motion affects perception within and across modalities: An event-related potential study. *European Journal of Neuroscience*, 21, 1116–1130.
- Blake, R. (1989). A neural theory of binocular rivalry. *Psychological Review*, 96, 145–167.
- Blake, R., & Boothroyd, K. (1985). The precedence of binocular fusion over binocular rivalry. *Perception & Psychophysics*, 37, 114–124.
- Blake, R., & Logothetis, N. K. (2002). Visual competition. *Nature Reviews Neuroscience*, 3, 13–21.
- Bonnell, A. M., & Hafter, E. R. (1998). Divided attention between simultaneous auditory and visual signals. *Perception & Psychophysics*, 60, 179–190.
- Brascamp, J. W., van Ee, R., Pestman, W. R., & van den Berg, A. V. (2005). Distributions of alternation rates in various forms of bistable perception. *Journal of Vision*, 5, 287–298.
- Carlson, T. A., & He, S. (2004). Competing global representations fail to initiate binocular rivalry. *Neuron*, 43, 907–914.
- Carter, O. L., & Pettigrew, J. D. (2003). A common oscillator for perceptual rivalries? *Perception*, 32, 295–305.
- Chong, S. C., & Blake, R. (2006). Exogenous attention and endogenous attention influence initial dominance in binocular rivalry. *Vision Research*, 46, 1794–1803.
- Chong, S. C., Tadin, D., & Blake, R. (2005). Endogenous attention prolongs dominance durations in binocular rivalry. *Journal of Vision*, 5, 1004–1012.
- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, 18, 193–222.
- Diaz-Caneja, E. (1928). Sur l'alternance binoculaire. *Annales d'Oculistique*, 165, 721–731.
- Driver, J., & Spence, C. (1998). Crossmodal attention. *Current Opinion in Neurobiology*, 8, 245–253.
- Driver, J., & Spence, C. (2004). Crossmodal spatial attention: Evidence from human performance. In C. Spence & J. Driver (Eds.), *Crossmodal space and crossmodal attention* (pp. 179–220). Oxford, UK: Oxford University Press.
- Fox, R., & Herrmann, J. (1967). Stochastic properties of binocular rivalry alternations. *Perception & Psychophysics*, 2, 432–436.
- Freeman, A. W. (2005). Multistage model for binocular rivalry. *Journal of Neurophysiology*, 94, 4412–4420.
- Hupé, J.-M., Joffo, L.-M., & Pressnitzer, D. (2008). Bistability for audiovisual stimuli: Perceptual decision is modality specific. *Journal of Vision*, 8(7), 1–15.
- Hupé, J. M., & Rubin, N. (2003). The dynamics of bi-stable alternation in ambiguous motion displays: A fresh look at plaids. *Vision Research*, 43, 531–548.
- Klink, C., van Ee, R., Nijs, M. M., Brouwer, G. J., Noest, A. J., & van Wessel, R. J. A. (2008). Early interactions between neuronal adaptation and voluntary control determine perceptual choices in bistable vision. *Journal of Vision*, 8(5), 1–18.
- Kornmeier, J., Hein, C. M., & Bach, M. (2009). Multistable perception: When bottom-up and top-down coincide. *Brain and Cognition*, 69, 138–147.

- Lack, L. C. (1978). *Selective attention and the control of binocular rivalry*. The Hague, The Netherlands: Mouton.
- Lee, S. H., Blake, R., & Heeger, D. J. (2007). Hierarchy of cortical responses underlying binocular rivalry. *Nature Neuroscience*, *10*, 1048–1054.
- Leopold, D. A., & Logothetis, N. K. (1999). Multistable phenomena: Changing views in perception. *Trends in Cognitive Sciences*, *3*, 254–264.
- Levelt, W. J. M. (1965). *On Binocular Rivalry*. Soesterberg: Mouton & Co.
- Logothetis, N. K., Leopold, D. A., & Sheinberg, D. L. (1996). What is rivaling during binocular rivalry? *Nature*, *380*, 621–624.
- Long, G. M., & Toppino, T. C. (2004). Enduring interest in perceptual ambiguity: Alternating views of reversible figures. *Psychological Bulletin*, *130*, 748–768.
- Lumer, E. D., Friston, K. J., & Rees, G. (1998). Neural correlates of perceptual rivalry in the human brain. *Science*, *280*, 1930–1934.
- Meng, M., & Tong, F. (2004). Can attention selectively bias bistable perception. Differences between binocular rivalry and ambiguous figures. *Journal of Vision*, *4*, 539–551.
- Mitchell, J. F., Stoner, G. R., & Reynolds, J. H. (2004). Object-based attention determines dominance in binocular rivalry. *Nature*, *429*, 410–413.
- Nguyen, V. A., Freeman, A. W., & Alais, D. (2003). Increasing depth of binocular rivalry suppression along two visual pathways. *Vision Research*, *43*, 2003–2008.
- Ooi, T. L., & He, Z. J. (1999). Binocular rivalry and visual awareness: The role of attention. *Perception*, *28*, 551–574.
- O'Shea, R. P., Parker, A., La Rooy, D., & Alais, D. (2009). Monocular rivalry exhibits three hallmarks of binocular rivalry: Evidence for common processes. *Vision Research*, *49*, 671–681.
- Paffen, C. L., Alais, D., & Verstraten, F. A. (2006). Attention speeds binocular rivalry. *Psychological Science*, *17*, 752–756.
- Pashler, H. E. (1998). *The Psychology of Attention*. Cambridge, MA: MIT Press.
- Pastukhov, A., & Braun, J. (2007). Perceptual reversals need no prompting by attention. *Journal of Vision*, *7*, 5 1–17.
- Pearson, J., & Clifford, C. W. (2005). When your brain decides what you see: Grouping across monocular, binocular, and stimulus rivalry. *Psychological Science*, *16*, 516–519.
- Pressnitzer, D., & Hupe, J. M. (2006). Temporal dynamics of auditory and visual bistability reveal common principles of perceptual organization. *Current Biology*, *16*, 1351–1357.
- Sheppard, B. M., & Pettigrew, J. D. (2006). Plaid motion rivalry: Correlates with binocular rivalry and positive mood state. *Perception*, *35*, 157–169.
- Tong, F. (2001). Competing theories of binocular rivalry: A possible resolution. *Brain and Mind*, *2*, 55–83.
- Tong, F., Meng, M., & Blake, R. (2006). Neural bases of binocular rivalry. *Trends in Cognitive Sciences*, *10*, 502–511.
- Tong, F., Nakayama, K., Vaughan, J. T., & Kanwisher, N. (1998). Binocular rivalry and visual awareness in human extrastriate cortex. *Neuron*, *21*, 753–759.
- Toppino, T. C. (2003). Reversible-figure perception: Mechanisms of intentional control. *Perception & Psychophysics*, *65*, 1285–1295.
- Treue, S. (2001). Neural correlates of attention in primate visual cortex. *Trends in Neuroscience*, *24*, 295–300.
- van Boxtel, J. J., Alais, D., & van Ee, R. (2008a). Retinotopic and non-retinotopic stimulus encoding in binocular rivalry and the involvement of feedback. *Journal of Vision*, *8*(17), 1–10.
- van Boxtel, J. J., Knapen, T., Erkelens, C. J., & van Ee, R. (2008b). Removal of monocular interactions equates rivalry behavior for monocular, binocular, and stimulus rivalries. *Journal of Vision*, *8*(13), 1–17.
- van der Zwan, R., Wenderoth, P., & Alais, D. (1993). Reduction of a pattern-induced motion aftereffect by binocular rivalry suggests the involvement of extrastriate mechanisms. *Visual Neuroscience*, *10*, 703–709.
- van Ee, R. (2005). Dynamics of perceptual bi-stability for stereoscopic slant rivalry and a comparison with grating, house-face, and Necker cube rivalry. *Vision Research*, *45*, 29–40.
- 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*, 11641–11649.
- van Ee, R., van Dam, L. C., & Brouwer, G. J. (2005). Voluntary control and the dynamics of perceptual bi-stability. *Vision Research*, *45*, 41–55.
- von Helmholtz, H. (1924). *Treatise on physiological optics* (J.P.C. Southall, Trans.). Rochester, New York: The Optical Society of America.
- Watson, T. L., Pearson, J., & Clifford, C. W. (2004). Perceptual grouping of biological motion promotes binocular rivalry. *Current Biology*, *14*, 1670–1674.
- Wilson, H. R. (2003). Computational evidence for a rivalry hierarchy in vision. *Proceedings of the National Academic Science USA*, *100*, 14499–14503.