The dynamics of perceptual rivalry in bistable and tristable perception

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Human observers are extremely adept at correctly interpreting the visual input that they receive despite its inherent ambiguity. There are, however, situations in which no single, valid interpretation exists and perception oscillates. Such situations offer insight into the processes underlying perception, as they reveal the conditions under which our percept can alter in the presence of an unchanging physical stimulus. Many studies have focused on perceptual switching during binocular and monocular rivalry, or when viewing ambiguous figures. The majority of these studies have focused on bistable phenomena. In this paper we report the study of a range of ambiguous stimuli that provoke tristable perception, thereby providing a more exacting test bed for current models. We find that subjects spontaneously move from periods of bistable to tristable perception and that this results in a characteristic change in the rate of perceptual switching. In contrast to reports for bistable stimuli, we find only weak evidence for consistency in the relative switch rates of individuals across our test stimuli and explain why our results are inconsistent with the theory of interhemispheric switching. We go on to describe how the results are, instead, largely consistent with models of rivalry based on mutual inhibition and adaptation.

Introduction

Background

One of the great challenges to human perception is that there is no simple relationship between the image received by our eyes and the objects and events in the world that produced that image. Although we are usually able to build a single, correct impression of an external stimulus, there are situations in which inherent stimulus ambiguity or visual conflict makes this impossible. The perceptual vacillation that results in these cases is particularly evident when viewing ambiguous figures such as the Necker Cube (Necker, 1832), or during binocular, monocular, and stimulus rivalry (Breese, 1899; Campbell & Howell, 1972; Helmholtz, 1867; Levelt, 1967, 1968; Logothetis, Leopold, & Sheinberg, 1996). In all four cases, the appearance of a visual stimulus alters spontaneously and often completely, despite the stimulus not undergoing any physical change. Hence it is possible for a single, unchanging stimulus to produce quite different perceptual experiences in an observer from one moment to the next. Quite apart from questions surrounding the basic processes underlying switching behavior, stimuli capable of perceptual rivalry have become important tools for behavioral scientists because of their ability to elicit perceptual change in the brain without altering the physical stimulus. This, it is hoped, will provide insights into where perceptual decisions take place and beyond that, the neural basis of consciousness (see e.g., Blake & Logothetis, 2002).

Although ambiguous and rivalrous stimuli generally induce bistable perception (with percepts oscillating between two possibilities), they can, in a few instances, also produce three or more. Figures 1 and 2 provide examples of visual stimuli that provoke tristable perception, with the latter based on monocular rivalry. Other examples of visual stimuli evoking multistable perception include the combination of interocular fusion with binocular rivalry (Suzuki & Grabowecky, 2002) and the motion-induced disappearance of dots (Bonneh, Cooperman, & Sagi, 2001). Apart from visual stimuli, it is also possible to experience multistability for auditory cues (Warren, 1961; Warren & Gregory, 1958). Although intrinsically more complicated than bistable phenomena, tristable and multistable rivalry is
Figure 1. Example of a depth-related tristable stimulus. (a) The original version of the stimulus, adapted from a paper by Poston and Stewart (1978). We tried this stimulus but many subjects failed to report the third possible percept (of a cube in front of a larger cube), and so it was not used in the experiments described here. (b) We have since created a new version that accentuates the third percept by making this interpretation correct in terms of visual perspective. It nonetheless remains possible to see the other two more obvious interpretations: a large cube with one corner cut away, or a misshapen room with a cube sitting in the corner. Note that there is, in theory, a valid fourth interpretation (of an inverted room within a larger room), but for the observers we tested, this interpretation turned out to be too improbable for it to ever win the perceptual tug-of-war.

Figure 2. Example of a tristable, monocular rivalry stimulus similar to that used in Naber et al. (2010). (a) The stimulus consists of three superimposed sinusoidal gratings, each offset from the others by 120° and each with a unique hue (corresponding to red, green, and blue in this case). In our case we also chose to ensure than none of the gratings were oriented more closely than 15° to a cardinal axis. With a little tinkering in a dark room, it is possible for most observers to experience reliable rivalry, such that perception spontaneously shifts between the three constituent gratings b, c, and d. In practice we were unable to obtain stable switching across all of our subjects. Switching tended to be rapid and therefore hard for them to track, and all subjects described periods of mixed percepts or traveling waves of the type described by Wilson, Blake, and Lee (2001) in binocular rivalry. We therefore chose not to use this stimulus in the experiments described here.
of especial interest because it offers a more exacting test of models of switching behavior, as we demonstrate in this paper.

**Searching for commonalities**

One key to understanding the various forms of perceptual rivalry is to understand commonalities and differences. On the face of it, binocular, stimulus, and monocular rivalry do share a number of similarities. All involve periods of disappearance of one or another part of the stimulus, and all are capable of producing intermediate/hybrid percepts. On the other hand, there are differences. The longstanding debate about the neural locus of binocular rivalry (Blake & Logothetis, 2002) has revealed differences between stimulus and binocular rivalry (Bonneh, Sagi, & Karni, 2001; Lee & Blake, 1999), which has, in turn, led to conjecture that they occur at different levels of the visual hierarchy (Freeman, 2005; Wilson, 2003). Nonetheless, detailed studies of suppression and the effects of stimulus properties including color have confirmed that many of the similarities run deep (Andrews & Purves, 1997; O’Shea, Parker, La Rooy, & Alais, 2009) and may well reveal functional linkages between these three types of rivalry (Pearson & Clifford, 2005).

Despite these commonalities it is less clear to what extent ambiguous figures are related to the other three phenomena. Ambiguous patterns do not, for example, generally involve perceptual disappearance of all or part of the stimulus. On further reflection, however, some similarities do exist. The switching from one percept to another appears to defy fully conscious control, and this paper considers one example, at least, for which changes in interpretation do lead to the appearance or disappearance of parts of the stimulus, albeit of illusory occluders (see Hidden Square in Figure 4). Recent years have seen a growing number of attempts to unite all four types of multistable perception in the hope of identifying a common mechanism behind perceptual switching. One commonly cited piece of evidence for such a link is that the relative rate of perceptual switching in an individual is consistent across a range of stimuli—i.e., someone who experiences rapid switching for one type of stimulus usually experiences rapid switching for other stimuli as well. High correlations have been reported between switch rates in binocular rivalry, multistable motion induced blindness, and bistable plaids (Carter & Pettigrew, 2003; Sheppard & Pettigrew, 2006). By way of clarification one should add that the link is only correlational and describes switch rates of individuals relative to other observers. Hence, the precise rate at which interpretations switch can and does vary from stimulus to stimulus (Andrews & Purves, 1997; Carter & Pettigrew, 2003; Sheppard & Pettigrew, 2006). Although first brought to the vision science community’s attention by Carter and Pettigrew (2003), the result has since been investigated by many groups across uni- and multimodal domains. The results appear largely consistent within certain modalities such as vision and audition, but not consistently across multimodal domains, such as visuo-haptic (Carter, Konkle, Wang, Hayward, & Moore, 2008; see also Schwartz, Grimault, Hupé, Moore, & Pressnitzer, 2012, for a brief review). In a recent study which included a large number of subjects and genetic markers in its analysis, Kondo, Kitagawa, Kitamura, Nomura, and Kashino (2012) reported evidence for consistencies across numerous stimuli, with evidence of a link between switch rate and serotonin (for visual shape) and dopamine (for sound). This result mirrors earlier work by Carter and colleagues who described a link between switch rates and activation of 5HT receptors, a receptor family closely linked to the role of serotonin in regulating neural activity (Carter et al., 2005; Carter et al., 2007). The picture is, however, not as clear when one considers the possible role of attention. Studies of attentional control suggest that there are differences in the effect of attention on different types of ambiguous figure (Taddei-Ferretti et al., 2008). Some authors have argued that ambiguous figures are much more amenable to personal control than binocularly rivaling stimuli (Meng & Tong, 2004). On the other hand, other studies have revealed that attention can have a sizeable effect on switch rates and stimulus dominance in binocular rivalry (Chong, Tadin, & Blake, 2005). Overall, it seems that all stimuli are amenable to a degree of personal control, but the precise level of control and effects of attending are specific to both the stimulus and stimulus type (van Ee, van Dam, & Brouwer, 2005). Attempts to alter normal switching behavior using transcranial magnetic stimulation have shown that it can affect binocular rivalry (Miller et al., 2000; Pearson, Tadin, & Blake, 2007) and although this was not reported for ambiguous-figure rivalry, caloric stimulation did work for both (Miller et al., 2000).

**Models of switching**

Despite the tantalizing links across the different types of ambiguous stimuli, few researchers have attempted to trace all of the effects to a single underlying source. One notable exception has been Pettigrew and colleagues (Carter & Pettigrew, 2003; Sheppard & Pettigrew, 2006; Miller et al., 2000) who have proposed that switching is driven by a single, external oscillator. The basis for this oscillator, they argue, is a subcortical signal that cyclically promotes rival interpretations across the two cortical hemi-
spheres (Carter & Pettigrew, 2003; Miller et al., 2000; Miller et al., 2010). More mainstream models attempt to reconcile evidence of higher-level, object-based rivalry (Leopold & Logothetis, 1999) with lower-level, eye-based effects (Tong, 2001), leading theoreticians to postulate the presence of numerous competitive neural processes extending through a hierarchy of stages (Blake & Logothetis, 2002; Crewther et al., 2005; Dayan, 1998; Freeman, 2005; Gomez, Argandona, Solier, Angulo, & Vazquez, 1995; Hupé & Rubin, 2003; Laing & Chow, 2002; Leopold & Logothetis, 1996; Wilson, 2003). That said, many authors argue that binocular rivalry may reflect the actions of a quite separate system to those underlying other forms of rivalry (Meng & Tong, 2004; Polonsky, Blake, Braun, & Heeger, 2000). To some extent, what is unusual about binocular rivalry is that it is something we experience throughout our everyday lives, and hence the visual system may well have evolved a specific mechanism for automatically suppressing diplopic regions (Arnold, Grove, & Wallis, 2007; Shimojo & Nakayama, 1990, 1994).

**Multistability**

Models of perceptual rivalry have traditionally focused on trying to explain the switching process in binocular rivalry or other bistable phenomena. In practice, the oscillatory behavior of bistable systems can be simulated via a myriad of flip-flop oscillatory networks, making it difficult to isolate the most appropriate model. Suzuki and Grabowecky (2002) sought a more complex stimulus that might provide deeper insights into the mechanisms involved in perceptual rivalry. They adopted stimuli that involve the simultaneous combination of monocular and binocular rivalry (see Diaz-Caneja, 1970; Kovacs, Papathomas, Yang, & Feher, 1996), providing four possible percepts. The authors described long periods of bistable switching interleaved with a sudden recombination of the monocular cues, a phenomena they referred to as “perceptual trapping.” One means of explaining this effect, based on neural adaptation, is that disappearance of part of the stimulus promotes its later, complete reappearance after the complimentary form has experienced a period of dominance and subsequent adaptation. Indeed, the authors were able to provide a general model of this behavior based along these lines. Unfortunately, what is not clear is the extent to which trapping is a peculiarity of stimuli in which elements cyclically appear and disappear. More recently, two groups presented preliminary results from studies looking at tristable perceptual phenomena (Naber, Gruenhage, & Einhäuser, 2009; Wallis & Ringelhan, 2009). This paper describes the Wallis and Ringelhan (2009) data in more detail, providing results from the study of several stimuli that offer a more powerful and yet tractable data set for investigating the explanatory and predictive power of various models.

As a motivation for what follows, it is instructive to consider how various models of rivalry might accommodate tristable perception. The interhemispheric switching model can, in a broad sense, explain bistable switching, but the question occurs as to what happens when there are three possible interpretations. One possibility is that one hemisphere represents one interpretation and the other hemisphere the other two. That immediately offers a strong and testable prediction: Switching between two of the percepts will occur rarely, if at all, and one percept will dominate on as many occasions as the sum of the other two. For adaptation the story is more complex. It has been known for some time that if a rivaling stimulus is interrupted (e.g., by blinking), the previously perceived stimulus tends to dominate again (Leopold, Wilke, Maier, & Logothetis, 2002; Orbach, Zucker, & Olson, 1966). It is conceivable that switching away from percept A to B (for example) would serve the purpose of an interruption of percept A and hence promote its reoccurrence after B—suggesting that ABA or bistable switches would be more common than ABC or tristable ones. On the other hand, a model in which the neural population associated with percept A had not yet fully recovered from initial adaptation at the moment percept B wanes would promote takeover by percept C, suggesting that ABC type switches would be more likely—see Figure 3. If this doesn’t happen, it constrains the recovery of neurons to be practically complete within the period of dominance of a subsequent perceptual state.

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**Experiment**

**Methods**

**Participants**

Twenty-four participants with corrected-to-normal vision were tested. All participants were recruited through the School of Psychology’s paid participant register at the University of Queensland. The experiment was conducted in accordance with University of Queensland Ethics guidelines and with approval of the University’s Behavioural and Social Sciences Ethical Review Committee. Informed consent was obtained from all participants. One additional participant was dropped from the experiment for failing to achieve the required stimulus selection criteria (see Procedure).
A quick survey of the literature on rivalry and multistable perception suggests that there are relatively few stimuli that evoke tristable perception. We uncovered five and selected three for further testing. The other two were not used here for reasons given in the figure legends (see Figures 1 and 2).

**Stimuli**

A quick survey of the literature on rivalry and multistable perception suggests that there are relatively few stimuli that evoke tristable perception. We uncovered five and selected three for further testing. The other two were not used here for reasons given in the figure legends (see Figures 1 and 2).

**Adelson-Movshon grid**

Adelson and Movshen (1986) described a stimulus as part of their investigations into the aperture problem and border ownership (Adelson & Movshon, 1982, 1986; Fennema & Thompson, 1979; Stumpf, 1911). For the purposes of this investigation we will refer to this as the “Adelson-Movshon grid” (AMGrid). This stimulus consists of three sets of lines moving at $120^\circ$ to one another (see Figure 4a). Although the three sets of lines move in separate directions, the percept is of one set of lines moving in one direction and diamonds moving in the opposite direction. In the case of our stimulus the three interpretations were: (a) Line motion down and right at $15^\circ$ to vertical, (b) line motion right and up at $45^\circ$, and (c) line motion up and left at $15^\circ$ to the horizontal. The impression then swaps to one of the other three directions as time progresses. (Stimulus parameters: aperture $10^\circ$, stripe speed $0.8^\circ/s$, stripe spacing $2.0^\circ$, stripe width $0.4^\circ$.) The whole stimulus was rotated by $15^\circ$ clockwise from vertical to avoid an innate preference observers have demonstrated for perceiving motion along the cardinal axes (see Andrews & Schuppeck, 2000).

**Hidden square**

Another stimulus used here has been investigated by several authors looking at illusory contours and edge integration (Lorenceau & Shiffrar, 1992; Shiffrar & Pavel, 1991; Figure 4b). The stimulus has been described as bistable in the past; however, with training it is possible to see three distinct arrangements of the four moving lines: (a) All four lines can be grouped to form a diamond oscillating left and right behind illusory occluding bars; (b) Neighboring pairs on each side can be grouped, resulting in the impression that they are moving up and down; and (c)

![Figure 3. Tristable switching patterns. Tristable switching permits more complex switching dynamics to emerge than for bistable phenomena. (a) A neural adaptation model might suggest that cyclical switching (ABC) is more likely than sequences involving a backward switch (ABA). (b) Likewise, interhemispheric switching might predict that switches between the two states preferred by one hemisphere (B and C) are only possible after perceiving the state preferred by the opposite hemisphere (A), resulting in hub-based switching, characterized by very lopsided transition probabilities.](image1)

![Figure 4. Static renderings of the four stimuli used in these experiments. The first induced tristable perception in our subjects, and the fourth induced bistable perception. (a) The Adelson-Movshon grid (AMGrid). (b) The hidden square (HS). (c) The triangle array (Tri). (d) A bistable plaid motion pattern (Plaid).](image2)
Opposite pairs can be grouped, resulting in the sense that they slide back and forth in depth. As with all of our stimuli, we used training with disambiguated forms of the stimulus to ensure subjects were aware of all three percepts. For the purposes of this paper the stimulus will be referred to as the Hidden Square (HS) illusion. (Stimulus parameters: stripe length 2.0°, stripe width 0.4°, amplitude of stripe motion 2.0°, stripe speed 2°/s.)

**Triangular array**

If tristable perception is mentioned at all, authors usually refer to a stimulus consisting of an array of equilateral triangles (e.g., Attneave, 1971), usually arranged at regular intervals to form a larger triangle (see Figure 4c). Observers tend to group the triangles, describing them as all pointing upward or at an angle of ±120° to the vertical. The perceived direction then alternates over time. In our stimulus the choices corresponded to (a) up and left, (b) right, or (c) down and left.

**Plaid**

As well as the three stimuli described above, we also tested one stimulus that provoked bistable perception in our observers, to act as a reference to literature on bistable perception. A modern take on the two-orientation version of the AMGrid stimulus involves

Movies 1–11. Animated versions of the dynamic stimuli used (Movies 1, 5, and 9), along with various disambiguated versions used during training to highlight the possible alternative interpretations.
use of transparent lines which enhances the duration of two competing percepts (Hupé & Rubin, 2003; see Figure 4d). In our case the two percepts were (a) diamonds with a single, coherent direction of motion, or (b) transparent lines moving in two distinct directions. Of particular relevance to the issues being studied in this paper, the stimulus has been used in previous studies of relative switch rate (Sheppard & Pettigrew, 2006). (Stimulus parameters: aperture 10°, stripe speed 0.8°/s, stripe spacing 2.4°, stripe width 0.6°.)

The parameters given above represent those used and for which our subjects were best able to perceive all of the potential interpretations without periods of uncertainty or hybrid percepts emerging.

Animated versions of the stimuli are supplied as movies for the three dynamic stimuli (Movies 1–11). As one of the reviewers of this paper pointed out, another stimulus capable of eliciting tristable perception is the Necker Cube. Although generally regarded as producing bistable perception, in its static form the cube can appear to be composed of an array of abutting or overlapping flat, outlined shapes (triangles, diamonds, or rhomboids), especially when viewed from specific angles (Taddei-Ferretti, Musio, & Santillo, 1995). A second reviewer also brought our attention to the fact that the plaid motion rivalry stimulus used as our bistable reference can also produce tristable rivalry since the depth order of the separate lines can swap (Hupé & Pressnitzer, 2012). That said, our subjects were instructed to only report whether they saw coherent motion or separate lines and received appropriate training to that effect (see supplementary materials). Also they enhanced the effect by coloring their two sets of gratings in opposite colors (red and green) rather than using a single colour as we did. More to the point, the stimulus has been successfully used in the past in studies matching bistable switching behavior across multiple visual stimuli and forms of rivalry, and hence remains a useful baseline to which switching behavior can be compared (e.g., Sheppard & Pettigrew, 2006).

Display

Participants sat 60 cm from a 24” Sony Trinitron monitor (Sony Corporation, Tokyo, Japan) observing the stimulus which subtending an angle of approximately 10° × 10°. The moving stimuli were rendered at a frame rate of 24 Hz, which was sufficient to give the impression of smooth motion of the three moving stimuli.

Procedure

The four stimuli were tested for 24 min each over two sessions split over 2 days. The order of testing was counterbalanced across subjects. Each 24-min test session was broken down into four 6-min blocks with a 2-min pause between blocks. Each session was preceded by a period of subject familiarization using a disambiguated version of the relevant stimulus (Movies 1–11). The familiarization process included a period of training using the up, down, and left arrow response keys on a standard QWERTY keyboard to indicate which of the three possible interpretations was currently being perceived. To ensure rapid and accurate responses, training included a 5-min response selection test, during which unambiguous versions of the stimulus were displayed in a rapidly and unpredictably alternating stream of images (stimulus duration 3000 ± 500 ms). Subjects were only allowed to proceed to the main part of the experiment if they were able to select the appropriate arrow key quickly enough to match their selection to the stimulus displayed for 85% of the total time the stimulus appeared. This proved to be a demanding task, as much of the 15% error can be attributed to reaction time. Many subjects required multiple attempts to reach criteria. One subject failed to reach criteria after four attempts and so was dropped from the experiment.

Results

Basic switching patterns

The first two predictions to test are those of hub-based and cyclical switching. Figure 5 plots the probability of cyclical switching. In order to estimate the significance of these results, it is important to try to estimate what one would expect by chance. Given innate preferences or biases in the subjects towards particular interpretations, one would actually predict an imbalance between the proportion of ABA and ABC switches on the basis of this bias alone. In order to compensate for this effect, we calculated the probability of a nonrepeating sequence of three states (ABC, BAC, CBA, etc.) based on the assumption of quasi-independence of states (see the Appendix). Figure 5 includes these expected levels estimated on the basis of random sequences generated to match the first-order and length characteristics of each individual. In practice the majority of subjects do show a preference for cyclical switching. This is consistent with a neural adaptation model in which neural recovery after a period of dominance is of a similar duration to the duration of the current percept. In other words, neurons corresponding to percept A are still recovering by the time activity associated with percept B declines, tending to promote percept C next, rather than A.

Figure 6 provides summary data for how often a particular interpretation was reported. The hub-based switching model would predict that one percept should dominate as often as the sum of the other two percepts.
There is no evidence for this. Figure 7 reports the period of dominance duration across subjects, ranked by switch rate. The durations are clearly quite variable across subjects, but one positive consequence of this is that no single percept appears to dominate across all subjects. What also emerges from the data is that subjects who saw all three percepts equally often also experienced the fastest switch rates, a result consistent with work on stimuli evoking bistable perception (Moreno-Bote, Shapiro, Rinzel, & Rubin, 2010).

Results from the two graphs are combined in Figure 9, which shows the link between the duration of a percept and the probability of it occurring (i.e., the proportion of switches to that state). All three stimuli reveal a degree of correlation between the two measures, suggesting that subjects often had a preferred interpretation of the stimulus (switched to more often) that was also stable for longer periods or, equally, a less preferred interpretation (switched to less often) that was only briefly perceived: AMGrid ($r^2 = 0.44$, $p$-slope < 0.01**), HS ($r^2 = 0.17$, $p$-slope < 0.01**), and Triangle ($r^2 = 0.42$, $p$-slope < 0.01**). One consequence of this relationship is that the duration of ABA switches should, on average, be longer than ABC switches.

To investigate this prediction further, Figure 8 reports the duration of an ABA versus ABC switch for all 24 subjects and all three stimuli. There is a clear tendency for ABA switches to take longer than ABC switches in any one individual. A paired $t$-test analysis confirmed that the differences were statistically significant for all three stimuli: AMGrid $t_{23} = -5.03$, $p < 0.01**$; HS $t_{23} = -2.22$, $p < 0.05*$; Tri $t_{23} = -2.37$, $p < 0.05*$. As described above, this link is predicted by the relationship between preference for a state and its average duration, established in Figure 9. It is conceivable that other effects are at work too, but this appears to be a sufficient explanation for the effect. Irrespective of its source, this relation is a testable prediction of any model of switching behavior. Note we also carried out extensive analyses of switch rate durations. For those interested, please see the supplementary materials section entitled: “Analysis of switch-rate distribution.”

**Stochastic process analysis of transitions**

With bistable perception, the study of state transitions during prolonged, uninterrupted viewing is (computed as the number of visits, not percept duration). There is no evidence for this. Figure 7 reports the period of dominance duration across subjects, ranked by switch rate. The durations are clearly quite variable across subjects, but one positive consequence of this is that no single percept appears to dominate across all subjects. What also emerges from the data is that subjects who saw all three percepts equally often also experienced the fastest switch rates, a result consistent with work on stimuli evoking bistable perception (Moreno-Bote, Shapiro, Rinzel, & Rubin, 2010).

Figure 5. Probabilities of tristable versus bistable switching. The probability of each subject producing a forward (ABC), as opposed to reverse switch (ABA), is recorded for the three tristable stimuli. The green lines indicate the probability of such a switch pattern based on a quasi-independent model derived from an individual’s perceptual state probabilities. The dotted lines are confidence intervals derived from simulations of the model matched in length to the sequence lengths of the subjects. Overall there is a tendency for subjects to produce more ABC type switches than would be expected by chance. This is largely consistent with an adaptation model that promotes tristable over bistable switching.
Figure 7. Relative duration of perceptual dominance of the three states for all 24 subjects. For a description of the individual states see the description of the test stimuli in the Methods section (the colors correspond to states A [blue], B [green], and C [purple], respectively). Subjects are ranked by switch rate along the horizontal axis lowest to highest for each of the three tristable percepts. Interesting to note is that as switch rate increases (left to right), dominance duration for all three percepts becomes more similar.

Figure 6. Ratios of the total number of visits to each perceptual state for each stimulus. The colored bars correspond to each of the three perceptual states. For a description of the individual states, see the description of the test stimuli in the Methods section (the colors correspond to states A [blue], B [green], and C [purple], respectively). A possible prediction of the interhemispheric switching hypothesis is that the number of transitions to one state is will be equal to the sum of transitions to the other two. There is no evidence for this.
limited to their timing. With the inclusion of a third perceptual state, a range of new questions emerge. For example, one can ask about transition probabilities, i.e., the extent to which the choice of subsequent states is predicted by the current state. It is possible that there are preferences to move from one state to another or that a state will be revisited after a set number of intermediate states. Any patterning may reveal details of the underlying mechanisms involved.

Following the example of Attneave (1959), Gottman and Roy (1990) offer an approach for assessing determinacy in sequences based on information theory in which one can gain an estimate of the “surprise” associated with the distribution of observed occurrences of sequences of progressively increasing length. As Attneave (1959) points out, this approach is only asymptotically equivalent to the chi-squared approach that it is imitating, and with the advent of fast computers, simulations and explicit calculations are now tractable, obviating the need for these forms of approximation. Unfortunately, neither approach is really valid for what is being asked in this case. All sequential analysis based on chi-squared contingency tables relies on the fact that the expected values at all points in the table are nonzero, but this is not true in our case because state repetitions cannot occur. In other words, AA or BB is not possible since we are only considering transitions from state to state. Bishop, Fienberg, and Holland (1975) review methods for analyzing incomplete contingency tables, but it turns out that for the special case that only the leading diagonal entries are missing/zero, an exact model exists (Goodman, 1968, see his table 11). An appropriate modification to the information theory approach is also described by Chatfield and Lemon (1970), but as they point out, for small samples the approximations involved may be violated. Given that many of the sequences in the experiments described here were around 100 steps long, the approach is probably not suitable; hence we adopted the Goodman (1968) approach to search for first-order relations. Figure 10 displays the results of the analysis. There does appear to be evidence for first-order determinacy for the Triangle stimulus, but not for the other two.

But what about higher-order relationships? The Goodman (1968) approach is only useful for testing first order relations. Naber, Gruenhage, and Einhäuser (2010) describe a method for determining whether second- or higher-order relations in the switch sequences exist. Modern techniques based on maximum-likelihood estimation are another alternative and have the advantage that they can pick apart the details of any relations. Buhlmann and Wyner (1999) describe the basis for an approach they call Variable-Length Markov Chain modelling. According to Mächler (2009, personal communication), variable length markov chains (VLMC) has the advantage that it does not rely on the assumption of independence of the perceptual states (c.f. Bishop et al., 1975). For the relatively short sequences produced by subjects in these experiments, it is debatable whether there is sufficient power to identify patterns definitively. To control for this, random
sequences of states were generated matched to the state probabilities of the subjects and the sequence lengths they produced. Preliminary investigations using an implementation of VLMC, written by Mächler and Bühlmann (2004) in the statistics language “R,” are reported here. The first step of the analysis involves determining a criterion level of a sequence order limit parameter that they refer to as “K.” In their paper the authors provide a method for estimating this parameter based on Aikaike’s C (AIC), which was the method employed here. The procedure was applied to each of the 24 subjects’ individual switch patterns for the three types of stimuli and formed a minimum at a cutoff criterion centred around K = 4 (see Mächler and Bühlmann, 2004). Using this value the analysis was run for each individual’s data for each of the three stimuli. The results appear in Figure 11. Note that the new analysis takes a different approach to that offered by the Goodman. His analysis is looking for discrepancies from a nonrepeating sequence, whereas this analysis is looking for discrepancies from a repeating sequence, which is why first order relations almost always emerge. One means of testing the significance of any higher-order relations is to compare them with what one would expect by chance. For that reason, the figure also provides 95% confidence intervals derived from simulation of random sequences whose lengths were matched to the lengths of sequences generated by the subjects. Note that one might expect the order of a random sequence should be zero, but as described above, because the “random” sequences in this case do not repeat (AA, BB, or CC), the states are not independent. The sequences are also of limited length, which has the potential to generate spurious low-order dependencies.

Because the VLMC approach looks for discrepancies from true randomness, it is not possible to decide the significance of the first order relations, since similar length nonrepeating random sequences also contain significant first order relationships. The Goodman analysis is best suited for that purpose. Although first-order relationships are part and parcel of any non-repeating sequence, higher-order relationships are not. The VLMC analysis indicates that some subjects exhibit higher-order relations that deviate significantly from chance. Looking across subjects and stimuli, the pattern is not very consistent. The only slight consistency is a tendency for subjects with higher switch rates to produce higher-order patterns. Unfortunately, this may simply be due to the fact that these subjects produced longer sequences of switches for the analysis to search through. In the end, the sequences are probably too short to tell us definitively when higher-order relations do not exist. Instead they should be seen as a lower bound on the order which, for some subjects at least, is already significantly higher than one.

Periodicity of bistable and tristable switching

Another question one can ask about the pattern of switching is whether there are blocks of time during which subjects experience tristable switching followed
by periods in which they experience bistable switching. In some sense this is related to the stochastic process analysis, but not trivially so because the precise order of states is less important than whether they resulted in a bistable or tristable switch. To test for periodicity of two-step switches, the switch types of each individual were reduced to a stream of switch types $1 = \text{tristable (ABC)}$ and $-1 = \text{bistable (ABA)}$. The stream of events was then analyzed using autocorrelation. An appropriate baseline for the autocorrelation might be thought to be 0.0, but this is not the case because the probabilities of a bistable versus tristable switch are not equal and they vary across subject. In order to estimate a baseline, the probabilities of each transition type were used to generate 1,000 sequences of a length matched to each individual and their specific probabilities of ABC versus ABA switching. The values at each state transition lag from the average of the simulated sequences were then used to normalize the values from the real data generated for each individual by subtracting the simulated data mean from the actual autocorrelation figure calculated. The results appear in Figures 12 and 13.

As an alternative to the cross-correlation approach, one can also simply estimate the probability of a switch of the same type as the current one (be it bistable or tristable) at differing time lags. To ensure that the cross-correlation approach was not introducing any spurious effects, we also ran the analysis in this manner, using simulation to predict the probability of a same transition type (be it bistable or tristable) one would expect by chance for each individual. The difference between the chance value and that obtained from each subject was then used as dependent measure for a group-level $t$-test and nonparametric (Wilcoxon) equivalent. The results were basically indistinguishable to those obtained using the cross-correlation approach. The only minor difference was that the significant effects became marginal at lags of 1 and 3 for the Tri stimulus on $t$ test (lag 3, $p = 0.057$) or nonparametric (Wilcoxon) test (lag 1, $p = 0.052$). In the forerunning analysis, the effects of bistable and tristable repetitions are combined. To identify the source of these effects in terms of the two types of repetition, a further analysis was conducted on the two types of repetition independently. Analysis using both $t$ tests and the Wilcoxon test singled out the same lags as the cross-correlation analysis as being the only lags at which repetitions of both bistable and tristable switches were significantly above chance.

To summarize these effects, it seems that whichever type of switch observers have just experienced (be it tristable or bistable), they are likely to experience the same type of switch in the following two transitions.
Beyond that point, the transitions appear largely random. One interpretation of this result is that, on average, subjects experienced brief periods in which the states were seen approximately equally often, leading to consistent tristable switching, followed by periods over which one stimulus became suppressed, resulting in consistent bistable switching. This is, in turn, consistent with a periodic (presumably internally generated) signal cyclically promoting tri- and bistable switching. It should be added at this point however, that we cannot say for certain whether there are any specific patterns of switching (e.g., ABC rather than BCA, or ABA rather than CBC etc.) underlying the results, or if the patterning is generic to any type of tristable and bistable switch. Future research should consider this in more detail by gathering a larger number of switch events.

Figure 12. Autocorrelation analysis for concurrent ABA or ABC type switches (individuals). The purpose of the analysis is to see if the likelihood of performing an ABA or ABC switch is affected by switching at previous time steps (lags) from the current switch. Significant deviations from zero indicate deviations from correlations predicted by chance. The Normalized Autocorrelation measure is derived from the autocorrelation values for a particular subject minus the value one would expect by chance given the relative probabilities of ABA and ABC type switches for that individual. For all three stimuli the first two lags produced higher than expected correlations.

Figure 13. Autocorrelation analysis for concurrent ABA or ABC type switches (population). The graph summarizes the same data presented for individuals in the previous figure. For all three stimuli the first two lags produced higher than expected correlations, suggesting that the current type of switch (ABA or ABC) predicts the type of switch that will be seen next and the one subsequent to that (or equally the two previous switches). Beyond two switches the links are more sporadic. Error bars represent the 95% confidence intervals, and asterisks indicate significant deviation from chance for both t test and the Wilcoxon test at \( p < 0.05 \).

**Stimulus onset effects**

The response of any oscillatory system to an external stimulus is a function of both the input and its current state. For example, if the system is assumed to be initially inactive, stimulus onset will produce a period of increasing system activity that may well result in different patterns of switching from those seen during steady-state switching. Switching patterns peculiar to stimulus onset have indeed been reported for bistable perception (Hupé & Rubin, 2003). In the particular case of binocular rivalry featuring an in-built contrast bias, Mamassian and Goutcher (2005) were able to show an initial preference for the high-contrast image that waned over time. Of more direct relevance to the stimuli used here, Hupé and Pressnitzer (2012) detected...
onset transients for the Plaid stimulus used here. In their study, the authors reported an increased duration of the first stable percept relative to subsequent durations, an effect they refer to as the “inertia of the first percept.” Their subsequent analysis was based on this finding as all measures were related back to this “maximum.” In order to test whether an equivalent form of perceptual “inertia” was detectable in our data, we simply plotted the difference in log-transformed duration of the percept immediately subsequent to the current percept (see Figure 14). We obtained a consistent pattern, but it was actually in the opposite direction to that described by Hupé and Pressnitzer (2012). The reason for the discrepancy is not clear. We are using slightly different parameter values for the Plaid (e.g., a single color for both sets of lines). We also did not attempt to equate the long-term perceptual dominance of the two percepts as those authors did, and we included data from all trials, not just those in which subjects reported the coherent percept first. Nonetheless, it seems unlikely that minor alterations to the stimulus or analysis would reverse this highly consistent effect. It is also striking that the effect is consistent across all four of the stimuli and all four blocks of trials. One potential problem with asking subjects to report state changes as and when they saw them is that we cannot be sure if their responses are correct. Some subjects took several seconds to make their first response, and so we cannot rule out the possibility that their first response was different to the first percept they had. Nonetheless, the training session (with strict timing criteria) trained them to respond as quickly and accurately as possible, and the consistency of behavior across stimuli and subjects suggests that even slow subjects were behaving in a manner consistent with those subjects who responded more rapidly. More work will be required, but suffice it to say that there is evidence for unusual dynamics at the moment of stimulus onset. In our case the effect is for the first percept to be shorter than the subsequent percept, a result that is consistent with preliminary simulations of a tristable oscillator in our lab (Wallis & Ringelhan, 2009). The reason for this appears to be that all states accumulate activity initially due to a lack of adaptation in any of the populations. This then allows the first dominant state to be usurped sooner than during steady-state activity when recovery from adaptation prevents a second state from rising too quickly, and the dominant state is firing fully—thereby inhibiting the other neural populations more strongly.

In their paper on bistable and tristable stimuli, Hupé and Pressnitzer (2012) report a strong preference in their subjects to see the coherent version of the Plaid at stimulus onset. For sake of comparison we analyzed our own data for all four stimuli across all four blocks and found similar biases. In order of the description of each of their perceptual states in the Methods section above: AMGrid (62.5%, 10%, 27%), HS (67%, 16.5%, 16.5%), Tri (46.5%, 7%, 46.5%), and Plaid (89.5%, 10.5%). The latter pattern is largely consistent with the bias reported by Hupé and Pressnitzer (2012). Note, however, that these figures are only a first indicator of the full story. A full analysis would need to take

Figure 14. Relative duration of pairs of consecutive percepts. To check for onset transient behaviour the first five perceptual states were analyzed in terms of their duration relative to one another. Relative duration was measured as the difference between the log-transformed durations of the two percepts in seconds. The horizontal axis lists the pair of perceptual durations being compared (“1–2” indicates the first stable percept versus the second, etc.). Negative numbers indicate that the earlier percept was shorter in duration than the later percept, and positive numbers that they were longer. Note that there was a strong tendency across all subjects and stimuli for the first percept to be shorter in duration than the second percept. There was also a slight tendency for the second percept to last longer than the third, but beyond that point no obvious pattern emerges. This appears to provide some evidence for transient stimulus onset behavior. Each bar corresponds to a single subject with their data averaged across the four blocks of trials.
account of inherent perceptual biases for each stimulus and each individual.

We also checked for evidence of increased variability in perceptual duration at onset. A test across subjects of the duration variability over four switches (measured as standard deviation of the log-transformed durations averaged across all four switches and all four blocks) yielded no significant change from the first four switches to the next four for any of the stimuli.

**Effects of transition order on percept duration**

In their paper on tristability, Naber et al. (2010) described links between perceptual duration and preceding or subsequent perceptual state. We repeated the analysis they conducted on median-normalized dominance durations (see figure 4 of their paper) to look for evidence that the durations are influenced by the preceding state. Results from our analysis appear in Figure 15. As is clear from the figure, we did indeed find evidence for an increased duration of percept A when transitioning from C, as well as an increased duration of percept C when transitioning from A, as compared to transitions from B to A or B to C. However, this asymmetry was only apparent for the AMGrid.

One of the things to note about the AMGrid is that it is closely allied to the two stimuli used by Naber et al. (2010), both of which involved two sets of rotationally offset parallel lines. As a result, both of their stimuli produced the impression of lines oriented upwards, leftwards and/or rightwards, leaving open the possibility that the types of asymmetry reported in their paper and for the AMGrid here, are limited to this family of stimuli. One reason for thinking this might be the case is that we know from Andrews and Schluppeck’s (2000) study that observers have a preference for seeing the AMGrid moving vertically or horizontally rather than at an oblique orientation—possibly due to eye movements, the oblique-effect (Andrews & Schluppeck, 2000), or the oblique plaid effect (Hupé & Rubin, 2004). We deliberately oriented our stimulus such that no perceived motion ran exactly vertically or horizontally, but this still resulted in two percepts (A and C) being closer to the ordinal axes than the third (B). Looking at dominance durations for the AMGrid in Figure 7, the vast majority of subjects spent less time seeing percept B than the other two. Similarly, looking at Figure 6, they also transitioned to it less frequently, all of which points to an orientation-specific effect. The fact that the link between previous state and duration fails to occur for the other two stimuli tested here provides further grounds for thinking that the link may be unique to those patterns containing oriented lines.

**Switch rate correlations**

One of the main driving forces behind attempts to unite all switching phenomena into one model is the consistency of relative switch rates for individuals across stimuli. Some studies have reported $r^2$ values as high as 0.7 between switch rates for binocular and plaid rivalry stimuli (Sheppard & Pettigrew, 2006). Correlational analysis was conducted between the four stimuli...
Correlations were relatively low (switches alone, and for tristable switches alone. the data are reported for all switches, for bistable under investigation. Results appear in Table 1, in which the data are reported for all switches, for bistable switches alone, and for tristable switches alone. Correlations were relatively low ($r^2 \leq 0.2$) except for the two stimuli which were the most similar in appearance: the Plaid and AMGrid ($r^2 = 0.6$). Asterisks indicate a significant value of slope of above zero magnitude ($p < 0.05$). The analysis revealed weak but significant correlations in switching for three of the four stimuli (all except the HS stimulus).

In earlier studies by Carter and Pettigrew (2003) and Sheppard and Pettigrew (2006), the high correlations reported were obtained with larger numbers of subjects (up to two or three times the number tested here). It is quite possible that higher correlations would have been obtained by testing larger numbers of subjects, although current evidence suggests that correlations would not have been as high as in their studies even with the addition of more subjects.

Another important consideration to bear in mind when interpreting these correlations in switch rate is the fact that the relative dominance of the percepts varied across subject and stimulus. As mentioned above, both our results and those of Moreno-Bote et al. (2010) have shown that switch rate is affected by the degree of perceptual “balance” between the percepts, and it may well be the case that failure to balance the relative duration of the three percepts affects individuals differently across stimuli, leading to the reported loss of correlation (Schwartz et al., 2012). In future experiments one option might be to tailor the parameters of the stimuli to each subject so as to obtain matched dominance durations, as proposed by Schwartz et al. (2012). That said, in the Sheppard and Pettigrew (2006) paper, the authors also chose not to balance the dominance durations of their stimuli (see their figure 3) and were nonetheless able to report highly correlated switch rates across stimuli.

**Modelling tristable switching**

It has been evident for many years that one way to simulate multistable perceptual switching would be through some form of simple oscillatory circuit (e.g., Attneave, 1971). One of the earliest models to capture the “all-or-nothing” nature of the perceptual experience in binocular rivalry was Matsuoka (1984). While his work continues to be cited today, it is often used as an example of a naive forerunner of more sophisticated models which integrate eye- and object-based influences. Nonetheless, a recent model by Noest, van Ee, Nijs, & Wezel, (2007) has had success in simulating numerous aspects of rivalry, including the effects of interruption (Leopold et al., 2002; Orbach et al., 1966), based closely on Matsuoka’s models.

Of relevance to the work on tristable perception described here, and something many researchers in perceptual rivalry might not know, Matsuoka went on to study more general situations in which more than two states interact. In a pair of papers he described several higher-order models including a fully connected three-way oscillator (Matsuoka, 1985, 1987). In our own preliminary studies based on his model, we have discovered evidence for a number of interesting phenomena (Wallis & Ringelhan, 2009). For example, when the system enters a period of bistable switching (e.g., ABAB), the overall duration of each percept lengthens (i.e., switch rate drops) relative to that seen during tristable switching. We also find that activation of the population associated with the interpretation no longer perceived (e.g., C), synchronises (phase-locks) with that of one of the dominant percepts (e.g., A), resulting in a lengthened predominance of that state relative to the other perceived state (e.g., B), but at a lower level of activation. These results are only preliminary, but point to other ways in which the study of tristable stimuli can produce a range of complex, testable predictions.

**Conclusions**

Although much progress has been made, the processes and neural substrates underlying perceptual rivalry remain poorly understood. This paper has studied switching behavior for a family of stimuli that evoke tristable perceptual rivalry in observers. We have argued that such stimuli can help discriminate competing theories of rivalry but also unravel what the
underlying mechanisms might be. Compared to bistable perception, tristable perception possesses complex and yet tractable dynamics which yield bolder and, in some cases, contradictory predictions from competing models of perceptual rivalry.

One of the initial findings was that in contrast to predictions of interhemispheric switching, there was no evidence for hub-based switching, in which one transition (e.g., B to C) never occurs, or in which the sum of visits to one state is equal to the sum of visits to the other two. Although not an insurmountable objection to the hypothesis, it does appear to demand more complex dynamics than the current characterization of the model would permit. On a more positive note for this and other hypotheses, there was some evidence for carry-over of relative switch rates between stimuli. However, the effects were surprisingly weak.

A more mainstream alternative to the interhemispheric switching combined with mutual inhibition. The results described in this paper are broadly consistent with such a model in so far as cyclical switching was seen to occur more often that chance in all subjects across all stimuli. What this result also tells us is that the recovery period for a neural population immediately after a period of dominance is of the same order as the dominance duration of the subsequent state—since this imparts an advantage for the third state to dominate when the second state wanes. Given that stimulus interruption promotes reoccurrence of the previous state (Leopold et al., 2002; Orbach et al., 1966) it was conceivable that the opposite might be true—there would be a preference for reverse ABA type switching. That this does not happen places constraints on the decay time of a previously dominant state and its recovery time, both relative to the dominance of the immediately subsequent percept. It may also indicate that neural states associated with the oscillator do not cut off as cleanly or suddenly as the perceptual experience—suggesting a higher-level thresholding decision process at work.

Regarding previous studies of tri and quadri-stable perception, we were unable to replicate the findings of Naber et al. (2010) regarding links between dominance duration and subsequent state choice, except in the special case of a stimulus very similar in appearance to those which they used. We would argue that more work needs to be done before one can feel confident that the types of relationship they describe apply to patterns other than oriented parallel lines. We would likewise argue that the perceptual trapping described by Suzuki and Grabowecky (2002) is likely a function of the combined monocular/binocular stimuli they used. Given the absence of higher order patterns in the stochastic process analysis conducted here, we would argue that no discernible long-term perceptual trapping emerged for the stimuli we tested, although on a shorter timescale we did find evidence for being ‘trapped’ into cycles of tristable and then bistable switching.

Despite their long history and appeal, adaptation models of perceptual rivalry have received criticism over a number of years. For one, they predict that the time for which a percept is suppressed should correlate with the time for which it is subsequently active following reversal. In fact, periods of dominance and suppression of a particular percept are uncorrelated (Taylor & Aldridge, 1974; Walker, 1975). Modern models accommodate this issue by applying liberal amounts of randomizing (decorrelating) “noise” at the input or internal stages. This may seem a little fishy, but it currently remains the best means available for capturing the complexities of attentional and memory based top-down influences and bottom-up influences of fixation location and eye-movements (if only during pursuit).

Another prediction of adaptation models to cause problems in the past is the idea that if neural adaptation is taking place, a concurrent stimulus detection task that is reliant on the same neural population should also adapt. To test this, detection thresholds have been measured for briefly interjected stimuli presented to either the dominant or nondominant eye during binocular rivalry. Inconveniently for adaptation models, no evidence for changes in threshold was found (Fox & Check, 1972; Norman, Norman, & Bilotta, 2000). That was, until very recently, when Alais, Cass, O’Shea, & Blake (2010) took a different approach, normalizing adaptation times to the duration of the percept, rather than predicting thresholds on the basis of time since the last perceptual switch. With the help of these recent discoveries, all current evidence seems to be pointing inexorably to a model based on mutual inhibition and adaptation. The power of these models was further emphasized by Noest et al.’s (2007) elegant wrinkle on the models of Matsuoka and others. As mentioned earlier, they were able to explain how a number of well-established peculiarities of perceptual rivalry can be encapsulated in the model itself, without recourse to external memory or other processes. Indeed it may well be the case that the shunting inhibition model that they introduced can explain why time relative to dominance duration is the controlling variable in Alais et al.’s (2010) study, rather than time itself.

Whatever the mechanisms are that underlie perceptual rivalry in humans; tristable perception appears to present an exciting and exacting situation in which to test actual neural behavior. The model described here also offers concrete predictions in terms of increased variability at stimulus onset, rate changes between periods of tristable and bistable switching, and phase locking of a dominant and nondominant population
during periods of bistable perception. Hence tri and quadristable perception, and adaptive models of the type described in this paper, appear well placed to help neuroscientists identify both the mechanisms and neural substrates of perceptual rivalry in all its guises.

Keywords: rivalry, multistable perception, bistable perception, tristable perception

Acknowledgments

We are grateful to two anonymous reviewers for detailed and expert comments that helped improve many aspects of the manuscript. GW was supported by QEII and Future Fellowships from the Australian Research Council (DP0343522, FT100100020), and SR was supported by a Program Grant from the Human Frontier Science Program held by GW (HFSP-Grant RGP 03/2006).

Commercial relationships: none.
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References


Necker, L. A. (1832). Observations on some remarkable phenomena seen in Switzerland; and an optical phenomenon which occurs on viewing a crystal or geometrical solid. *London and Edinburgh Philosophical Magazine and Journal of Science, 1*, 329–337.


**Appendix**

In order to assess the effects of inherent biases in subject perceptual preferences, it is necessary to establish a measure of expectation associated with the switch sequences they produced. The method employed here involved creating random sequences matched in terms of length and overall state probability to each individual. Because we know a priori that the states cannot repeat, the calculations for this are not trivial, but they are relatively straightforward to derive. If the probabilities for the three states (A, B, or C) are denoted $p(A)$, $p(B)$ and $p(C)$, for a switch sequence of length $n$ with state given by $s_i$ for the $i^{th}$ state, the formula for any particular state is simply:

$$p(A) = \frac{1}{n} \sum_{i=1}^{n} (s_i = A)$$

To determine the probability of a particular three state sequence $s_s, s_{s+1}$, and $s_{s+2}$, we need to calculate the appropriate conditional probabilities. Taking the example sequence ABC, the probability of the sequence occurring $p(ABC)$ is given by

$$p(ABC) = p(A)p(B|A)p(C|B)$$

where $p(B | A)$ denotes $p(s_{i+1} = B | s_i = A)$.

The formulae for the conditional probabilities need to take account of the quasi-independence of the sequences (no same-state transitions). To do this we need to establish selection probabilities $p(x)$, $p(\beta)$, and $p(y)$, which correspond to the states A, B, and C. When generating a sequence, if state A is selected, the probability that it is a same-state transition is $p(x)$, $p(x) = p(x)^2$, representing a measure of state transitions “lost” due to the constraint that same-state transitions are not possible. These corrected selection rates are in exact proportion to the state probabilities $p(A)$, $p(B)$, and $p(C)$:

$$p(A) = k_b p(B) = k_a p(C)$$

$$p(x) = p(x)^2 = k_b (p(\beta) - p(\beta)^2)$$

$$= k_b \left(p(y) - p(y)^2\right)$$

Hence we can derive expressions of the form

$$p(B) \left( p(x) - p(x)^2 \right) = p(A) \left( p(\beta) - p(\beta)^2 \right)$$

Since $p(A) + p(B) + p(C) = 1$, we can derive exact expressions for the selection probabilities:

$$p(x) = \frac{4p(A)p(B) - 4p(A) - 2p(A) + 4p(B)^2 + 1}{4p(A)^2 + 4p(A)p(B) - 4p(A) + 4p(B)^2 - 4p(B) + 1}$$

$$p(\beta) = \frac{4p(A)p(B) - 4p(B) - 2p(A) + 4p(A)^2 + 1}{4p(A)^2 + 4p(A)p(B) - 4p(A) + 4p(B)^2 - 4p(B) + 1}$$

$$p(y) = 1 - p(x) - p(\beta)$$

These selection probabilities are used to govern selection of states in the data simulation, providing random sequences which match the empirically derived state probabilities $p(A)$, $p(B)$ and $p(C)$ under the constraint that $p(A | A), p(B | B)$ and $p(C | C) = 0$.

The corrected conditional probabilities can also be derived, producing equations of the form:

$$p(B | A) = \frac{p(\beta)}{p(\beta) + p(y)}$$

$$p(C | B) = \frac{p(y)}{p(x) + p(y)}$$

Hence from the expression given above for $p(ABC)$:

$$p(ABC) = \frac{p(A)p(y)p(\beta)}{(p(x) + p(y))(p(\beta) + p(y))}$$