Tri-stable stimuli reveal interactions among subsequent percepts: rivalry is biased by perceptual history

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Abstract

In rivalry, constant stimuli allow several interpretations ("percepts"). Percepts are characterized by their probability to occur and by the duration of their dominance. During continuous presentation of bi-stable stimuli, both percept probabilities are trivially 50%. To disentangle the processes triggering a percept from those stabilizing it, we introduce tri-stable stimuli having three percepts. We find the probability and dominance duration of a percept independently adjustable. Percept probabilities and dominance durations show mutual dependencies across several perceptual switches. Consequently, the current perceptual experience depends on perceptual history; therefore, rivalry - even for continuous presentation - is not a memory-less process.

1 Introduction

Signals arriving at our sensory system typically contain incomplete or ambiguous information about their sources in the real world. The system is then faced with the challenge to infer a unique and consistent interpretation. If several interpretations are equally probable, the perceptual experience tends to switch between several alternatives over time, while at any given time point one interpretation dominates. This phenomenon, termed rivalry, is observed for a huge variety of stimuli (Blake & Logothetis, 2002 for review), ranging from geometrical figures (Necker, 1832; Schröder, 1858), faces (Boring, 1930), structure from motion (Ullman, 1979), binocular (Wheatstone, 1838), tactile (Carter, Konkle, Wang, Hayward, & Moore, 2008), auditory (Warren & Gregory, 1958; Van Noorden, 1975), and olfactory stimuli (Zhou & Chen, 2009). Although these stimuli differ substantially across features and modalities, they induce a strikingly similar rivalry process: continuous and stochastic perceptual alternations between two interpretations of an ambiguous sensory stimulus (e.g., Brascamp, van Ee, Pestman, & van den Berg, 2005; Rubin & Hupé, 2003; Sheppard & Pettigrew, 2006; Pressnitzer & Hupé, 2006; Naber, Carter, & Verstraten, 2009; O'Shea, Parker, Rooy, & Alais, 2009).

In rivalry, successive dominance durations (i.e., the time period a certain percept is visible) are generally considered as independent and the exact timing of rivalry switches as unpredictable (Fox & Hermann, 1967; Levelt, 1967; Blake, Fox, & McIntyre, 1971; Borsellino, De Marco, Allazetta, Rinesi, & Bartolini, 1972; Walker, 1975). However, several outwardly accessible physiological measures, such as eye position, saccades, eye-blinks, and pupil size have been found to relate to rivalry states (Wundt, 1898; Becher, 1910; Glen, 1940; Eure, Hamilton, & Pheiffer, 1956; Ito, Nikolaev, Luman, Aukes, Nakatani, & van Leeuwen, 2003; Einhäuser, Martin, & König, 2004; van Dam & van Ee, 2005, 2006; Einhäuser, Stout, Carter, & Koch, 2008; Hupé, Lamirel, & Lorenceau, 2009) and may potentially serve as predictors for dominance durations and switch times.

Even without the use of physiological markers, independence and unpredictability of perceptual states have received considerable challenge. By carefully accounting for noise effects in reporting the perceptual state, van Ee (2009) has recently reported a non-zero correlation between successive dominance durations in rivalry. On long and on very brief time-scales, perceptual history also is known to affect the speed of rivalry switching: Suzuki & Grabowecky (2007) find a brief initial

decrease of dominance durations during the first 6 trials of 20-s rivalry presentations and a feature-specific long-lasting effect of daily exposure to a rivalry stimulus. Most evidence against the stochasticity of rivalry, however, has resulted from studies using interrupted presentations of rivalry stimuli. In such a setting the order of percepts and their dominance durations also contain information about subsequent percepts (e.g., Maloney, Martello, Sahm, & Spillmann, 2005; Brascamp, Knapen, Kanai, Noest, van Ee, & van den Berg, 2008; Pastukhov & Braun, 2008). More specifically, if a bi-stable stimulus presentation is interrupted by a blank presentation period, the chance that the preceding percept returns after the blank is related to the length of its previous dominance duration. Some of the resulting theories and models of multi-stable perception that take into account these facts, have denoted a significant role of an internal bias and memory (Leopold, Wilke, Maier, & Logothetis, 2002; Maier, Wilke, Logothetis, & Leopold, 2003; Kanai, Knapen, van Ee, & Verstraten, 2007; Brascamp et al., 2008; Pastukhov & Braun, 2008; Brascamp, Pearson, Blake, & van den Berg, 2009). These studies generally imply that a perceptual bias cumulatively builds up during the dominance periods of a percept and the larger the bias for this percept (i.e., the longer its preceding dominance durations), the higher the probability to turn dominant again after interruption. An exogenously controlled factor, such as blanking the stimulus, however, may itself affect rivalry dynamics. Indeed, during discontinuous presentation of bi-stimuli, the process of alternations can, depending on the duration of blank interruptions, either be sped up (Orbach, Ehrlich, & Heath, 1963) or slowed down (Leopold, et al., 2002). In addition, the effect of an intermittently presented stimulus depends on whether the interrupting stimulus itself is ambiguous and on its similarity to the interrupted stimulus. If an ambiguous stimulus interrupts a percept, this percept is less likely to survive as compared to an unambiguous interrupting stimulus (Pearson & Clifford, 2005). If the interrupting and the interrupted are dissimilar, the interruption has effects comparable to a blank; increasing similarity between the features of the rivalry stimulus and the interrupter, however, decreases the survival probability of the percept preceding the interruption (Pearson & Clifford, 2005; Kanai et al., 2007). The probability of a percept to survive an interruption furthermore depends on the contrast of the rivalry stimulus (Brascamp, Knapen, Kanai, van Ee, & van den Berg, 2007). These studies show that intermittent presentation of a rivalry stimulus reveals important features about the process of rivalry. However,

here we are interested in the dynamics of rivalry without any exogenous events (such as interruptions). Hence we here aim at studying effects of perceptual history on the current perceptual experience by using the continuous presentation of an uninterrupted stimulus.

Most stimuli used in rivalry research are bi-stable, that is, they allow exactly two distinct percepts. For continuously presented bi-stable stimuli, the probability to experience one of the two percepts at an arbitrary point in time is proportional to the average dominance duration of this percept. Only considering the percept sequence, both percepts occur equally often (provided the sequence is sufficiently long to neglect edge effects from start and end of the sequence). If we refer to the percentage of occasions in which a percept becomes dominant as percept probability, percept probability will thus be exactly 50% for any uninterrupted bi-stable stimulus by definition. (Note that the average TIME a percept is dominant, i.e. the dominance duration, is distinct and can be substantially different between the two percepts of a bi-stable stimulus). Hence, the factors underlying the stabilization of a given percept and those subserving its (re-) occurrence cannot be disentangled in bi-stable stimuli, unless perceptual states are exogenously interrupted. To keep presentation continuous, while nevertheless dissociating dominance durations from the probability of entering a percept, we here use tri-stable stimuli (i.e., figures that induce three distinct interpretations of a constant stimulus).

Stimuli with more than two interpretations have been studied before. Burton (2002) used a quad- (or tetra-)stable perceptual rivalry stimulus and showed an effect of instructions on the percept sequences, but did not report relations between dominance durations and switches. Other studies on multi-stable stimuli combined binocular rivalry with other forms of rivalry. O'Shea, Tep, Roeber, & Schröger (2008) showed different perceptual rivalry stimuli to each eye to achieve a tri- (to hex-)stable percept ("trinocular rivalry"). Suzuki & Grabowecky (2002) asked subjects to report four different dominance states during bi-stable rivalry in which the percept could have exclusive dominance (i.e., one eye was fully dominant) or was intermixed with its rival to achieve 4 different percepts through instruction. Despite several similarities between perceptual and binocular rivalry (Andrews & Purves, 1997), both might differ from each other in other respects, in particular with regard to the dependence on perceptual history (van Ee, 2009). Hence it is well conceivable that using binocular rivalry or a combination of binocular and perceptual rivalry stimuli, may yield substantially different results as

compared to using a rivalry stimulus without binocular conflict. To assess whether multi-stable perception without binocular conflict reveals similar dependencies between dominance durations and transition probabilities, we use different tri-stable stimuli without inducing binocular rivalry.

With our stimuli, rivalry is either induced in the motion (Experiments 1 and 2) or in the color domain (Experiments 3 and 4). Within each domain, slight modifications of the stimulus allow us to bias the stimulus such that either one of the three percepts dominates (experiments 1 and 3) or all are about equally strong (experiments 2 and 4). Hence we can measure the relation between dominance duration and percept probabilities and check whether any perceptual history effect is contingent on a specific parameter choice. In addition to analyzing the sequence of percepts, we measure dependencies between dominance durations and percept probabilities, and identify a new relation between these measurements. Our data support the view that, even under continuous viewing conditions and without binocular conflict, rivalry is not a memory-less process, but biased by perceptual history.

2 Methods

2.1 Observers

Author M.N. and 7 naive observers (age 18-31) participated in each experiment. Observers had normal or corrected to normal vision. Each observer gave written informed consent to participation; all procedures adhered to national standards on experiments with human observers and with the Declaration of Helsinki.

2.2 Stimuli

We used four different tri-stable stimuli in four separate experiments. In Experiment 1 and 2, the stimulus was a moving plaid consisting of two superimposed gratings (Wallach, 1935; Adelson & Movshon, 1983) (Fig. 1A). These plaid stimuli allowed three distinct alternating percepts: coherent upward motion (U), incoherent transparent motion in which the leftward motion is perceived on top (L), and incoherent transparent motion with rightward motion on top (R). In Experiment 1 the gratings were tilted ±120 degrees against the vertical midline. In Experiment 2 the tilt was increased to ±140 degrees. The latter parameter change generally increased the relative stimulus strength of the incoherent sideward motion percepts. In both experiments, gratings were square-waves, had a spatial frequency of 0.73 cycles per degree, a peak luminance (white) of 84.2 cd/m^2, a minimum luminance (gray) of 23.3 cd/m^2, a 5 degree circular aperture, and drifted outwards at a speed of 1.73 deg/s.

Stimuli in Experiments 3 and 4 consisted of three stationary overlapping color gratings (for bi-stable version: Breese, 1899) in a 5-degree circular aperture (Fig. 1B). Despite the fact that luminance remained physically constant throughout the experiment, the stimulus induced alternating shifts in perceived luminance per color, with one of the 3 colored gratings clearly dominating (i.e., appearing brightest) at any given point in time. Each grating's color was produced by a single gun of the screen only. For Experiment 3 the gratings had CIE coordinates (x, y, Y) of (0.623, 0.332, 17.7 cd/m^2), (0.298, 0.598, 60.6 cd/m^2), and (0.153, 0.068, 8.99 cd/m^2), respectively. In Experiment 4 the luminance (Y) of the green grating was lowered to 25.1 cd/m^2 with otherwise identical settings. This made the perceived luminance of the green grating closer to that of the other gratings and therefore increased the relative stimulus strength of the red and blue gratings. Gratings were square-

waves and had a spatial frequency of 1 cycle/degree. Orientations relative to the vertical midline were -120 degrees (red grating), 0 degrees (green), and +120 degrees (blue). For consistency of notation with Experiments 1 and 2, we referred to the red, green and blue gratings by their tilt to the midline, i.e. by L (red), U (green) and R (blue), respectively.

2.3 Setup

Stimuli were generated using Matlab (Mathworks, Natick, MA) with its Psychophysics toolbox extension (Brainard, 1997; Pelli, 1997; http://psychtoolbox.org) running on an Optiplex Dell computer and presented with a 21 inch EIZO Flexscan monitor on a gray background with 1280x1024 pixels at a refresh rate of 100 Hz. Mean luminance of the background was 23.3 cd/m^2, minimum luminance (black) of the screen as well as ambient light levels were negligible. Head position was stabilized using a chin and forehead rest that assured a steady viewing distance of 82cm.

2.4 Procedure

Observers were instructed to indicate the percept by holding down one of three arrow keys of a USB-gamepad (Left, Up, or Right) per percept. Observers were asked to always press one button even if their perceptual dominance was weak. Since during transitions the button for the preceding percept had to be released, while the button for the new percept had to be pressed, in the transition period either two or none of the buttons were pressed. In 30% of the cases this transition was below the resolution of the input device (36 ms). In the remaining cases, the overlap periods lasted on average (medians) 80ms (two buttons, 31% of cases) and 130ms (no button, 39% of cases), which is very short compared to the overall dominance durations (median: 2750ms). This indicates that the transitions between percepts were experienced as sharp. In both cases, the period with two or no button were allotted to the second percept. Only very rarely (3% of all transitions) did observers release a button and press the same one again. For the reported data, we aggregated the periods if the release lasted less than 10s and excluded the whole period otherwise. Neither exclusion nor inclusion of all these periods, however, changes any of the reported results or conclusions (data not shown).

Each experiment consisted of three 5-minute blocks. Experiments were taken on separate days and observers were allowed to take breaks between blocks. Before the actual experiment observers were familiarized with the stimuli and apparatus.

2.5 Notation

We denote the sequence of perceptual states ("percepts") by S_1, S_2 ..... S_N where $S_i \in \{L, U, R\}$. The dominance duration corresponding to the i-th state is denoted by d_i. To enable analysis across observers, we normalized distributions of dominance durations by dividing them through the median dominance duration within blocks and observers. These **normalized dominance durations** are denoted as d_i^*. We also analyzed relative dominance durations; i.e. how much longer was percept d_{i-2} relative to d_{i-1}. Hence we defined **relative dominance duration** as $(d_{i-2}-d_{i-1})/(d_{i-2}+d_{i-1})$. The experimental setting only allows transitions between different states (as same-state transitions, if existent, would not be reported as "switch"), that is $S_i \neq S_{i-1}$. Consequently, given S_{i-2} there are only two alternatives for S_i. If $S_{i-2} = S_i$, we will refer to a (S_{i-2}, S_{i-1}, S_i) triplet as **"switch back" (SB)**, otherwise we refer to $(S_{i-2} \neq S_i)$ as **"switch forward" (SF**, Fig. 1C).

2.6 Test for Markov property

If rivalry were a memory-less process, the probability to transit from a current state to another should be independent of any preceding state other than the current one. In other words, the sequence of perceptual states would have the so-called Markov property. In the Appendix, we devised a test of the null-hypothesis that a given finite sequence fulfills the Markov property; p-values in Results section 3.4 (denoted as p_{Markov} to avoid confusion with the transition probabilities) refer to this test. A low p_{Markov} implied that the null-hypothesis, and thus the hypothesis of a memory-less process, is likely to be refuted.

3 Results

3.1 Tri-stable stimuli show the same dominance-duration statistics as bi-stable stimuli

We investigated tri-stable rivalry with four different stimuli in four separate experiments. First we assessed, per experiment, whether general properties of tri-stable stimuli, in particular the distribution of dominance durations, match those typically observed for bi-stable stimuli. At visual inspection, the sequence of perceptual states and associated dominance durations appears irregular and random (Fig. 2A), similar to the typical observation for bi-stable stimuli. To facilitate comparison and pooling across observers, we consider normalized dominance durations d_i^* (see 2.5; Table 1 for raw durations). As for bi-stable stimuli the distribution of dominance durations has a leptokurtic (i.e., heavy-tailed) distribution, which can be approximated well by a Gamma or a Log-normal distribution (Fig. 2B). Hence the 0th order properties of all our tri-stable stimuli, namely the distribution of dominance durations, are similar to the bi-stable case.

3.2 Dominance durations and percept probabilities are independently adjustable

In bi-stable stimuli the probability of both percepts to occur in the sequence is exactly 50% (neglecting initial / final percept). In tri-stable stimuli, however, percept probabilities may range from near 0 (only the other two percepts are observed) to 50% (the percept re-occurs after every other switch). Dominance durations, in turn, need not be coupled to these percept probabilities (consider for illustration a case, where the sequence of percepts is ABACABACA, but B's and C's duration is twice that of A's). If the processes underlying stabilization and (re-)occurrence of a percept, however, would be the same, we would predict percept probabilities and dominance durations to be proportional to each other. To test this hypothesis, we analyze whether stimulus parameters can adjust percept probability independently from average dominance duration. First, we compare the two drifting plaid stimuli (Experiment 1 and 2). In Experiment 1, both the mean dominance duration of the up percept (Fig. 2C) and its probability (Fig. 2D) are higher than the other two percepts. Note that compared to Experiment 1, the motion direction of the gratings was deliberately changed to "weaken" the U percept in Experiment 2. In Experiment 2, however, the up-percept still has (marginally) the highest average dominance duration, while it occurs substantially less frequent than the left and right percept.

Consequently - although we cannot exclude some coupling between dominance duration and percept probability; the relation that trivially holds in the bi-stable case, does indeed not hold for tri-stable rivalry. We observe a similar result for the color stimuli of Experiment 3 and 4. The U percept is dominant in both mean dominance duration and percept probability in Experiment 3. In contrast, the U percept still has significantly higher dominance durations in Experiment 4, but is only second to the L percept in terms of percept probability. Again, percept probability and dominance duration are not proportional. In conclusion, the processes determining the probability of a percept to occur and the processes subserving the persistence of its dominance are – at least partly – distinct.

3.3 First-order transition probabilities

For all experiments, we analyzed the first-order transition probabilities between the 3 percepts (Fig. 3). No comparable measure exists for continuously presented bi-stable stimuli, as the probability to switch to the other percept is always 1 if only two percepts exist. In the tri-stable case, however it is relevant to see whether certain transitions are preferred. As illustrative example, consider a case in which all percepts had equal occurrence probability. With this example all transition probabilities could be 0.5, but, on the other extreme, could also be 1 for L→R, R→U, U→L and 0 for the other (L→U, U→R, R→L). In the former case, switch back and switch forward would be equally likely, while in the later case only switches-forward would exist.

In Experiment 1 (Fig. 3, left), it is more likely to switch from an incoherent percept (L or R) to the coherent percept (U) than between the incoherent percepts. This is not surprising, given that the U percept is most probable to occur (Fig. 2D). Conversely, in Experiment 2 the transition from incoherent to coherent is less likely than between incoherent percepts, although there is a slight asymmetry in favor of the R to L transition (Fig. 3, 2nd from left). In Experiment 3 there is a bias to switch from U to L (rather than to R), while in Experiment 1 and 2 the incoherent to coherent transition probability is independent of whether the incoherent percept was L or R (Fig. 3, 3rd from left). The preference to go from U to L is preserved in Experiment 4 (Fig. 3, right). In both cases this is consistent with the overall more likely occurrence of L as compared to R (Fig. 2D). In sum, there is an effect of stimulus properties on first-order transition probabilities. However, this effect is mostly

accounted for by the effects on the (0th order) percept probabilities and beyond this, there is no evident preference for any specific first-order transition.

3.4 The sequence of percepts is non-Markovian

If rivalry were a memory-less process, percept sequences induced by the tri-stable stimuli should have the Markov property (cf. Methods). To test this, we calculated for each possible triplet (see Appendix) the probability that a particular sequence is Markovian (p_{markov}). When calculating p_{markov} for all observers and experiments, we find that in Experiment 1, the null-hypothesis of the sequence being Markovian can be refuted (at $p_{markov} < 0.05$) in 4 out of 8 observers (Fig. 4, top-left). In Experiment 2 even 6 out of 8 observers violate the Markov assumption (Fig. 4, top-right). With the exception of observer KG in Experiment 1, the violation consistently occurs when U is the intermediate percept (S_{i-1}) in a triplet sequence (S_{i-2}, S_{i-1}, S_i) and is symmetrical with respect to the two possibilities for S_{i-2}. In all significant cases (at $p < 0.05$) the switch forward is more likely than the switch back. Again for 3/8 observers in Experiment 3 (Fig. 4, bottom-left) and 4/8 observers in Experiment 4 (Fig. 4, bottom-right) the Markov property is violated. Since we perform 192 individual comparisons, (4 experiments * 8 observers * 6 transitions), an adjustment of the alpha-level of the test is needed. When adjusting the expected false discovery rate (FDR) to 0.05 by using the Benjamini & Hochberg (1995) method, the corrected level across all experiments is 0.006. Using this corrected level, we still find significant preferences for the switch forward in 3/8 observers in each experiment.

It should be noted that the lack of significant Markov violation in the remaining observers does not imply that their sequences are indeed Markovian. First, we only checked violations of the Markov property in the transitions up to S_{i-2}. Second, for particularly short sequences, like in observer SG with only 66 switches, the statistical power to reject the Markov assumption is low. In sum, we find the Markov property to be violated in all experiments, which is clear evidence against a memory-less process in continuous rivalry.

3.5 Dominance durations are influenced by the preceding percept

Next we address whether the dominance duration of a given percept depends on which percept preceded it. Again, this question cannot be posed for continuous presentation of a bi-stable stimulus,

as there is only one possible preceding percept. Separately for each experiment and each percept (L, U, R), we compared the median dominance durations between the two different preceding percepts (Fig. 5). Since the distributions of dominance-durations are non-Gaussian, the non-parametric Wilcoxon test for the comparison of medians is used. In all experiments, we find a significant effect of the preceding percept on median dominance duration for at least one of the percepts. In experiments 1, the incoherent percepts (L or R) are significantly longer when preceded by the coherent (U) percept than when preceded by the other incoherent (R or L) percept (Fig. 5 left panel; $p=7.65*10^{-4}$ for $S_i=L$, $p = 0.04$ for $S_i=R$). The same and even stronger pattern is observed for Experiment 2 (Fig. 5, 2nd panel from left; $p=1.99*10^{-5}$ for $S_i=L$, $p=9.81*10^{-11}$ for $S_i=R$). In experiments 3 and 4, when there is no obvious hierarchy of the percepts (coherent vs. incoherent), we nonetheless observe a similar dependence of the dominance duration on the preceding percept for some percepts (Fig. 5 right panels; Experiment 3: $p=8.79*10^{-3}$ for $S_i=U$; Experiment 4: $p=4.90*10^{-3}$ for $S_i=L$: $p=7.31*10^{-3}$ for $S_i=U$). Note that while the reported p-values are uncorrected, all but one of the significant effects survive an individual Bonferoni-adjustment within each experiment ($0.05/3=0.0016$) and most of the significant effects survive an adjustment to an expected FDR of 5% across all experiments (adjusted alpha level: 0.0088). In sum, there is a significant dependence of dominance duration on the preceding percept.

3.6 Subsequent percept depends on preceding dominance durations

We have demonstrated that dominance durations depend on the preceding percept. Does in turn the probability to switch to a certain percept depend on the dominance durations of the preceding percepts? To answer this question, we consider the effect of preceding dominance durations on the subsequent switch probability in triplets of percepts: for an identical pair of S_{i-2} and S_{i-1} (i.e., identical 2nd order history) does S_i depend on d_{i-1} and/or d_{i-2}? As before, we compare two distinct cases (Fig. 1C): the switch-back (SB, $S_i=S_{i-2}$) and the switch forward (SF, $S_i\neq S_{i-2}$) across all experiments and all (S_{i-2}, S_{i-1}) pairs ($4x6=24$ data points). To achieve sufficient amounts of data, we pool across all observers and consider normalized dominance durations d^*_i. If switch probabilities were associated with the duration of preceding percepts, then we would expect that the median dominance duration per condition is different between the switch back triplets and switch forward triplets. Data show that for switches back the dominance duration d^*_{i-1} is longer than for switches forward in 18/24 cases (points

-13-

below diagonal in Fig. 6, left panel). This fraction is significantly larger than expected by chance, even when the absolute size of the durations is neglected (p=0.02, sign-test). Conversely, d^*_{i-2} is shorter if $S_{i-1} \rightarrow S_i$ is a switch back than if it is a switch forward (22/24 cases, Fig. 6 middle, p=3.6x10^{-5}). The relative dominance duration $(d_{i-2}-d_{i-1})/(d_{i-2}+d_{i-1})$, which was computed individually at each switch and thus not affected by normalization, confirms this result (Fig. 6, right): in 21/24 cases, a longer d_{i-2} (as compared to the following d_{i-1}) is observed for switches back than for switches forward. In sum, this shows that the shorter a percept has lasted and the more time has elapsed since it disappeared, the more likely it is to reappear. This result is consistent with a slowly adapting bias that persists across several percepts and is not reset by a perceptual switch.

4 Discussion

To dissociate the probability of a certain percept to occur from the duration of its dominance, we introduced tri-stable stimuli. Indeed, dominance duration and occurrence probability can – at least to some extent – be adjusted independently of each other. Furthermore, the sequence of percepts is non-Markovian. This implies that the perceptual history of at least two percepts back influence the current perceptual experience. Further analysis revealed that also dominance durations and percept probabilities are coupled across subsequent perceptual states, extending previous work on multi-stable percepts. These effects were independent from stimulus domain (motion or color) or specific stimulus features (i.e., motion direction and color luminance), and insensitive to one percept being dominant. In sum, we find that perceptual state and dominance durations are related to more than just the current and immediately preceding state. Hence, we demonstrate – for the first time during continuous presentation of an unchanged stimulus without binocular conflict – that neither the sequence of percepts nor their dominance durations are generated by memory-less processes; instead both are biased by perceptual history.

In our experiments 1 and 2, dominance durations of the incoherent percepts (L, R) were significantly shorter if preceded by the other incoherent percept (R, L) as compared to being preceded by the coherent percept (U). One possible interpretation of this finding is that switches between percepts of different quality (here: coherent versus incoherent) prolong the subsequent dominance duration. Such an interpretation would be in line with a high-level "fatigue" (adaptation) account of rivalry (Attneave, 1971; Taylor & Aldridge, 1974; Lehky, 1988; Blake, 1989): stimuli with more similar properties fatigue overlapping neuronal populations. It should be noted, however, that adaptation in a single population of neurons with simple direction preferences ("component cells") would generate the opposite prediction: by itself upward motion is more similar to left- and rightward motion than the two side-wards directions are to each other. Neurons reflecting the percept (rather than only the stimulus) with– say – a left-ward motion preference would also partially encode the U percept. They should therefore be adapted more by U than by R, and thus an L percept following a U percept should be comparably shorter. Instead our findings require distinct populations for encoding U, L and R. Higher areas in the dorsal stream of visual cortex (such as MT) indeed tend to code

coherent pattern motion separately from component motion, while lower areas such as V1 almost exclusively encode the components (Movshon, Adelson, Gizzi & Newsome, 1985; Gizzi, Katz, Schumer, & Movshon, 1990). A fatigue account of rivalry thus – at least for the plaid stimulus –would need to involve not only early visual areas but also higher areas. This argues in favor of rivalry originating at more than one level of the visual hierarchy (Blake & Logothetis, 2002).

In rivalry, the function of interruptions is an ongoing puzzle. It is known that interruptions tend to stabilize the percept (Leopold et al., 2002), although this effect reverses when interruptions are sufficiently short (Orbach et al., 1963). In the present context it is tempting to speculate that the middle percept of each triplet acts as endogenous analogue to the exogenous interruption with respect to the other two percepts. At first glance our results support this interpretation: a longer d_{i-1} (equivalent to the interruption) makes switches back more likely (Figures 4, 6). However, some recent studies have found a positive correlation between the probability of a percept to "survive" after an interruption and the preceding duration of its dominance (Brascamp et al., 2008; Pastukhov & Braun, 2008). In the "middle percept (S_{i-1}) equals interruption" interpretation, this would predict a positive relation between the duration of d_{i-2} and the probability to switch back, contrary to our actual findings. Nonetheless, the present results might provide some hint on the role of interruptions. In the view that prolonged experience of a percept makes it less likely to return to a percept without actively destabilizing it, a short blank would render a switch more likely (one cannot return to the percept after the blank), while a long blank allows for recovery. In any case, our results are in line with the general finding of Brascamp et al. (2008) and Pastukhov & Braun (2008) in that perceptual history modulates percept probabilities. Our stimuli in Experiment 1 and 2 as well as in Experiment 3 and 4 differ only in one feature value (the relative direction of the drifting gratings and the luminance of the green grating). These subtle differences mainly reduce the relative bias towards one dominant percept. However, we also observe that the coupling between state and subsequent dominance duration becomes somewhat more pronounced (Fig. 5). Since the feature change affects both the interrupting and the interrupted percept, this effect might be related to the findings that survival probabilities are modulated by stimulus features (Brascamp et al., 2007) and by the similarity between interrupted and interrupting percept (Pearson & Clifford, 2005; Kanai et al., 2007). To assess the role of feature similarity and to

fully uncover the role of the interruptions as compared to intervening ("middle") percepts, a combination of tri-stable rivalry and independently varied interruptions seem a promising approach, which is, however, beyond the scope of the present study.

The dissociation of percept probabilities and dominance durations suggests that at least partially distinct processes are responsible for either. In other words, there is a different mechanism determining whether a percept is (initially) chosen as compared to those controlling its persistency. Interestingly, this qualitative distinction has been predicted by a theoretical account of rivalry (Noest, van Ee, Nijs, & van Wezel, 2007) that models initial choice of percept and later switches without the necessity for a high-level decision stage. Although this model aims primarily at explaining the effect of stimulus interruptions, an extension to the tri-stable case is well conceivable.

Multi-stable stimuli with more than two percepts have been described earlier (Burton, 2002; Suzuki & Grabowecky 2002; O'Shea, Tep, Roeber, & Schröger, 2008), but either included binocular rivalry or were designed for different analyses. Closely related to the current study is the phenomenon of "trapping" described by Suzuki & Grabowecky (2002). In a tetra-stable (4 percepts) condition, these authors find a violation of the Markov property ("path dependence" in their terms). In addition, they report an increased probability to stay within a pair of percepts. The probability to stay in this "trap" decreases with the length of the "trapped" sequence, while dominance durations tended to increase within the trapped sequence. This result argued in favor of a long-term ("post-selection") adaptation, but against an adaption of the currently available stimulus. The method employed by Suzuki & Grabowecky (2002) is different from the one used here in various respects. Most importantly, these authors used binocular conflict, while in our paradigm rivalry is purely perceptual. Furthermore, they separated "exclusive" from "intermixed" percepts by instruction, thus combining binocular rivalry with binding features into objects. Our stimuli, in turn, operate in distinct feature domains (motion or color). Despite obvious commonalities, it is unclear, to what extent binocular rivalry and perceptual rivalry are comparable; these potential differences particularly pertain to the dependence on perceptual history (van Ee, 2009) and to the transition between dominant states, which in binocular rivalry often spreads in wave-like manner (Wilson, Blake, & Lee, 2001) and is feature-dependent (Knapen, van Ee, & Blake, 2007; Naber, Carter, & Verstraten, 2009). In the light of these differences it is remarkable

that Suzuki & Grabowecky (2002) arrive at similar conclusions. First, both studies observe a violation of the Markov property ("path dependence" in Suzuki & Grabowecky's terms, Fig. 4). Second, we find a dependence of the switch probability on dominance durations of preceding percepts (Fig. 6), which is well in line with Suzuki & Grabowecky's finding of "post-selection" adaptation. In conjunction with Suzuki & Grabowecky's (2002) results, our data suggest the following interpretation: experiencing a certain percept does not per se destabilize it (simple adaptation); instead, prolonged experiencing of a percept reduces the probability to return to this percept once it has been left (thus the dependence on d_{i-2}. in Fig. 6). This reduction in probability then relaxes over time (thus the converse dependence on d_{i-1} in Fig. 6). In the case of trapping, the reduction in the probability to switch back to the preceding percept is most evident for transition between closely related percepts, which - after a while in the trap - can drop below the between-trap transition probability and thereby release trapping (Fig. 6 in Suzuki & Grabowecky's study). Our results both confirm and generalize these earlier results for multi-stable stimuli without binocular conflict.

The trapping phenomenon depends on the similarity between percepts and can be affected dramatically by comparably subtle changes of instruction (Burton, 2002). Consequently, it is important to show that the effect of perceptual history on the current percept does not need a particular trapping pattern. By varying stimulus parameters, we here modulate several of the parameters affected by trapping: dominance durations, percept probabilities and first-order transition probabilities. Since results on perceptual history, in particular the coupling between dominance durations and percept probability, are qualitatively similar across all our experiments, our findings also generalize beyond the trapping stimuli.

In sum, we find effects of perceptual history on the current perceptual experience. This history dependence is reflected in percept probabilities, dominance durations and the coupling between the two across subsequent percepts. This general finding is neither contingent on binocular conflict nor on trapping. Taken together with the aforementioned studies, our results therefore demonstrate that the dependence of the present perceptual experience on perceptual history is a general property of rivalry, which is independent of whether rivalry is induced through binocular conflict, motion, shape or color. This is further support for the view that rivalry is to some extent predictable by perceptual history,

occurs at multiple levels of perception with similar properties, and that the encoding and eventual resolution of rivalry might be as ubiquitous in the sensory systems as ambiguity is in real-world stimuli.

Appendix – Test for Markov property

To consider a process memory-less, the sequence of perceptual states $S_1, S_2, ... S_N$ would need to fulfill the Markov property. That is, the conditional probability of a state S_i may only depend on the directly preceding state S_{i-1} but not on any other preceding state S_j ($j \neq i$, $j \neq i-1$), that is $p(S_i|S_{i-1}) = p(S_i|S_0,...S_{i-1})$. In other words, if the Markov property is fulfilled, this conditional probability would be the same independent of preceding sequences. In the present context, we considered triplets of sequences which could only either constitute an SB - (C,B,C) - or an SF - (A,B,C) with $C \neq A$ (Fig. 1C). If the Markov property holds, it follows that

$$p(S_i=C|S_{i-1}=B,S_{i-2}=C) = p(S_i=C|S_{i-1}=B,S_{i-2}=A) \ [C \neq A].$$

By the definition of the conditional probability this can be rewritten (under the assumption that $p(S_{i-1}=B,S_{i-2}=A) \neq 0$ and $p(S_{i-1}=B,S_{i-2}=C) \neq 0$):

$$\frac{p(S_i = C, S_{i-1} = B, S_{i-2} = C)}{p(S_{i-1} = B, S_{i-2} = C)} = \frac{p(S_i = C, S_{i-1} = B, S_{i-2} = A)}{p(S_{i-1} = B, S_{i-2} = A)} \quad (1)$$

or for the counts of the respective triplets and pairs in the sequence:

$$\frac{\#(S_i = C, S_{i-1} = B, S_{i-2} = C)}{\#(S_{i-1} = B, S_{i-2} = C)} = \frac{\#(S_i = C, S_{i-1} = B, S_{i-2} = A)}{\#(S_{i-1} = B, S_{i-2} = A)} \quad (2)$$

The discrepancy between the left-hand side (LHS) and right-hand side (RHS) of equation (2) provides a measure as to what extent a sequence of perceptual states violates the Markov property. Even if a Markov process underlies the generation of state sequences, only infinite sequences will be guaranteed to fulfill equations (1) and (2) perfectly. For finite sequences deviations from equation (1) and (2) are to be expected due to random fluctuations. Since the length of an observed sequence is necessarily finite, we thus need a baseline to estimate which discrepancy from equation (2) can be expected for a finite sequence by chance. Accordingly, we tested the Markov property by computing the discrepancy between the conditional probability $p(S_i|S_{i-1},S_{i-2})$ of SB and SF triplets of subsequent states (S_{i-2}, S_{i-1}, S_i).

We exemplify this procedure for observer KL in Experiment 2 for the pair $(S_{i-1},S_i)=(U,R)$. This analysis shows that the switch back is less likely than the switch forward (Fig. 7A, dot), that is $p(S_i=R|S_{i-1}=U,S_{i-2}=R) < p(S_i=R|S_{i-1}=U,S_{i-2}=L)$. Consequently, in this example the Markov property is clearly violated. To assert the significance of this discrepancy, we compared it with a baseline, that is

the same discrepancy computed on simulated sequences. To compute this baseline, we performed 10^5 simulations for each observer and experiment to create surrogate sequences under the Markov assumption, whose first-order transition probabilities $p(S_i|S_{i-1})$ and sequence lengths were matched to the actual data. When testing for the Markov assumption, the data for most of these simulated chains falls closer to the diagonal than the actual data (histogram represented as heat map in Fig. 7). In the example of observer KL 99934 of 100000 simulated chains fall closer to the diagonal than the actual data, yielding an estimate for the probability of $p=1-99934/100000=6.6*10^{-4}$ that the actual data can occur under a Markov assumption. In contrast, when comparing a switch back and a switch forward for the data for $(S_{i-1},S_i)=(R,U)$ in the same observer (Fig. 7B, dot), there is no evidence against the Markov assumption, as estimating the p-value from the respective simulations yields $p=1-13644/100000=0.86$. These p-values provided an estimate of the probability to obtain the actual sequence from a Markov process. Hence the fraction will be referred to as p_{markov} and indicates the significance level for the null-hypothesis that the state sequence has the Markov property. These data are given for all observers, transitions and experiments in figure 4 of the Results section.

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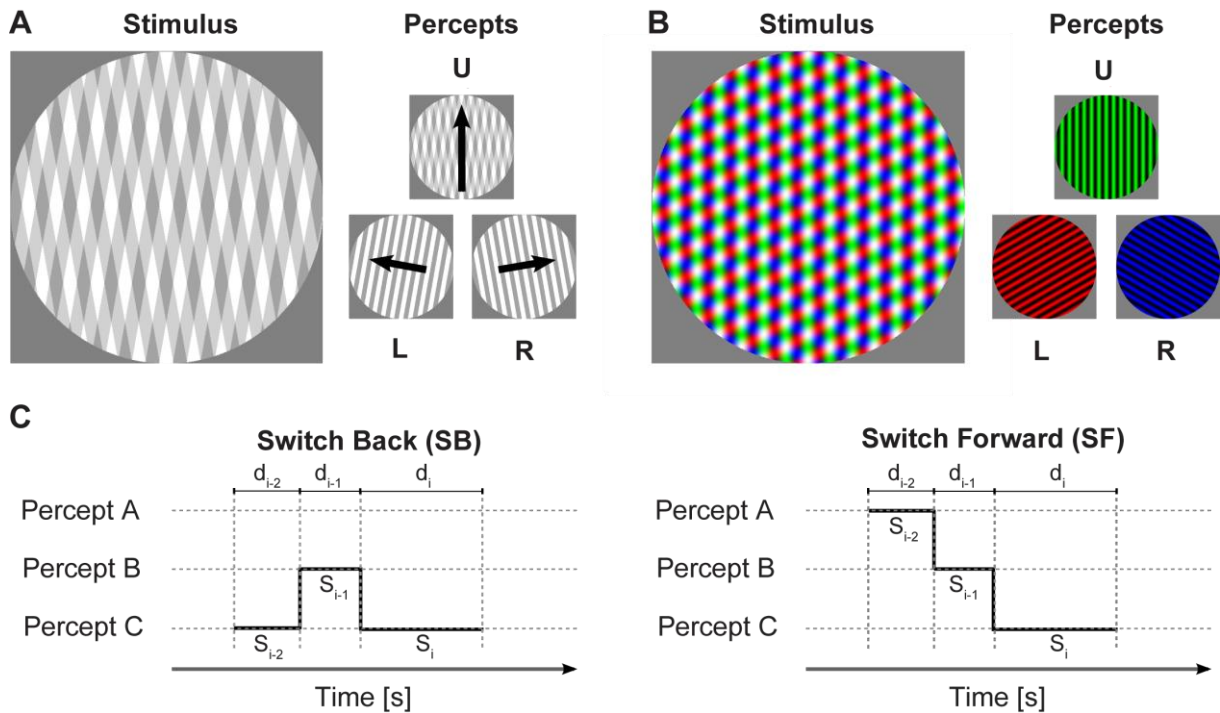
Acknowledgements

Figure Captions

Figure 1

(A) Moving plaid stimulus used in experiments 1 and 2. Two superimposed gratings move sideward, inducing three possible percepts: coherent upward motion (U), transparent (incoherent) motion with leftward moving grating in front (L), or transparent motion with rightward-moving grating in front (R).

(B) Static color grating stimulus used in experiments 3 and 4. Perceptually one color grating of the stimulus dominates at any given point in time (red=L, U=green, R=blue). Note that the figure's color and luminance values might differ dramatically from the actual presentation and that it takes several seconds before rivalry initiates.

(C) Considering triplets of percepts, two sequence types can be observed: "switch forward" (S_i is different from S_{i-2}) and "switch back" (S_i is the same as S_{i-2}). S_i denotes the state (percept), d_i denotes the corresponding duration of the percept being dominant (dominance duration), and i denotes the index of the percept in the sequence.
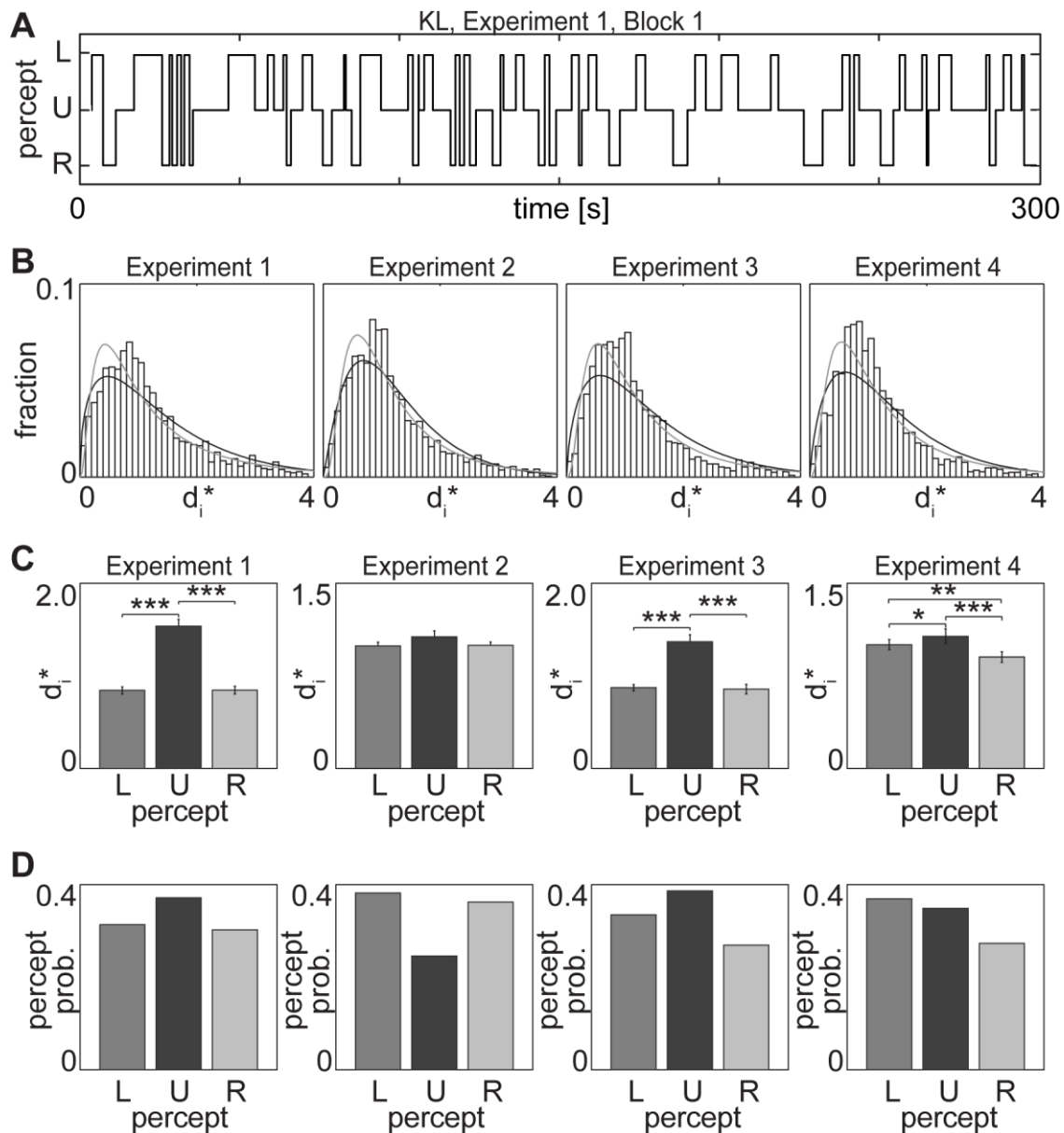
Figure 2

(A) Example sequence of reported percepts over time (observer KL in first block of Experiment 1), illustrating the seemingly stochastic nature of rivalry.

(B) Distribution of normalized dominance durations, pooled across observers and normalized to unit integral (probability densities). Gamma (black) and log-normal (gray) distributions are shown with the same mean and variance as empirical data.

(C) Median and standard error of pooled normalized dominance durations per percept. Since dominance duration distributions are non-Gaussian (panel B), significance markers refer to a non-parametric Wilcoxon test on equality of medians.

(D) Probabilities for each percept to occur, data pooled across observes.
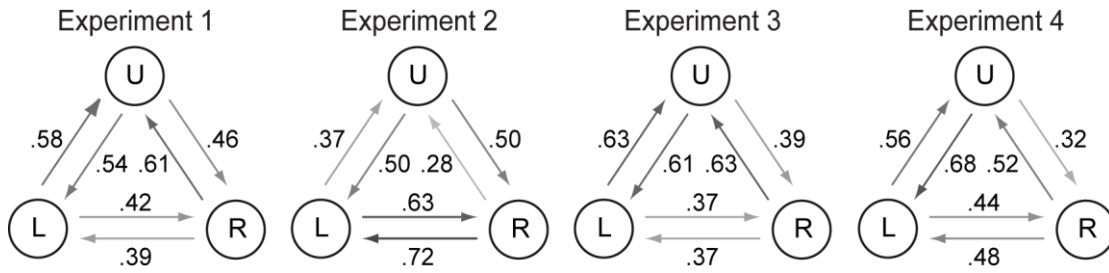
Figure 3

First-order transition probabilities between the different percepts for the 4 different experiments, data pooled across all observers. Gray value of arrows is negatively related to the size of probabilities.
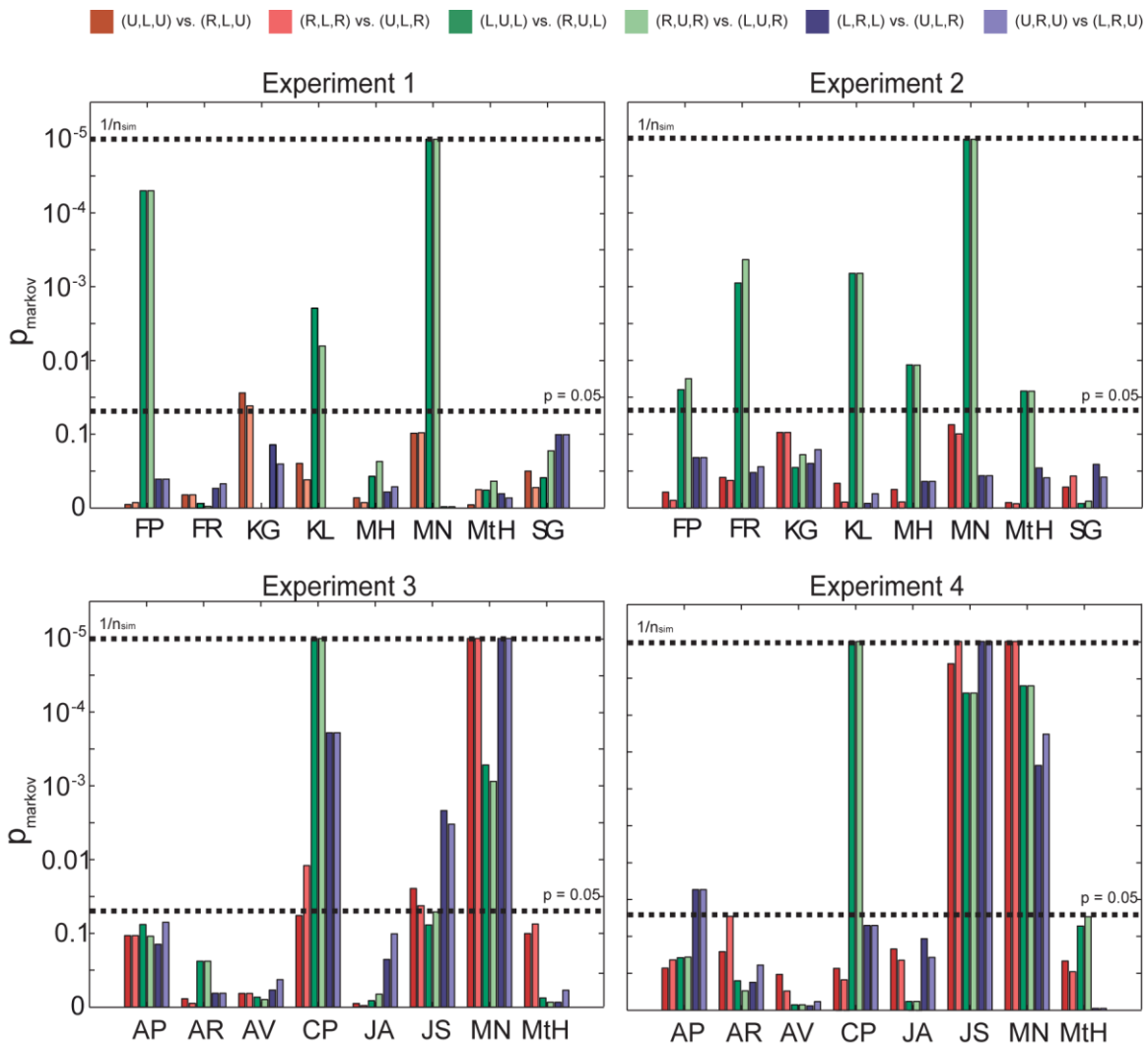

Figure 4

Estimated p-values for the null-hypothesis that a sequence of perceptual states has the Markov property (i.e., is memory-less). Each bar represents the data of one particular transition per experiment and observer. A bar exceeding the p=.05 line indicates that for this particular sequence, the Markov assumption is violated and the probability to switch from the current percept (S_{i-1}) to the next percept

(S_i) depends on the preceding percept (S_{i-2}). The y-scale is logarithmic and significance increases towards the top (-$\log_{10}$ p represented).
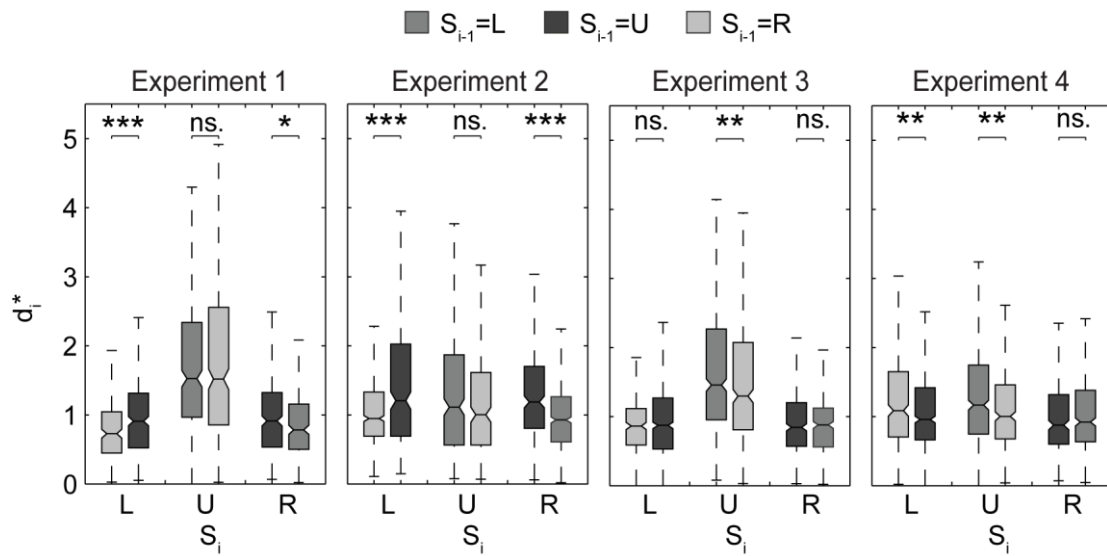

Figure 5

Boxplots of median normalized dominance durations (d^*_i) per experiment. Any difference within a pair of bars indicates that the median dominance duration (d^*_i) of the current percept (S_i) depends on the preceding percept (S_{i-1}). Current percept is labeled on x-axis, the preceding percept (S_{i-1}) is encoded by gray values (legend on top). Boxes represent the lower quartile, median, and upper quartile of the data, whiskers the extent of the data. Significance markers refer to uncorrected results of two-sided Wilcoxon-test on equality of the medians.
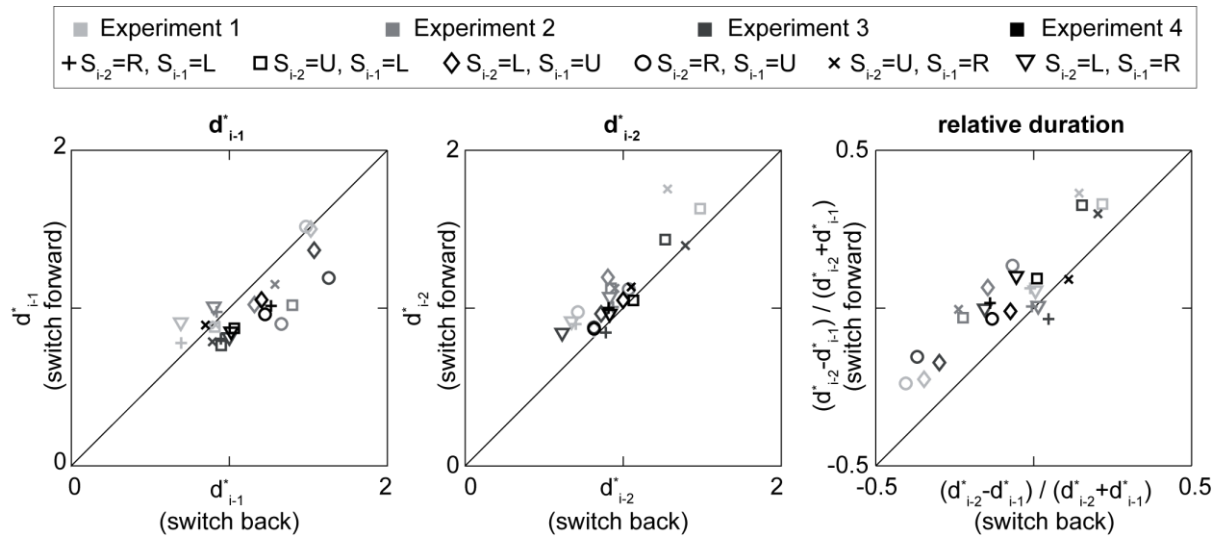
Figure 6

Effect of preceding dominance durations on transition from preceding state (S_{i-1}) to current state (S_i).

Median values for d^*_{i-1} (left), d^*_{i-2} (middle), and relative duration (right) on y-axes for switches forward

($S_{i-2} \neq S_i$), on x-axis for switches back ($S_{i-2} = S_i$), cf. Fig. 1C. Gray values denote experiment, markers

denote pairs of subsequent states (S_{i-2}, S_{i-1}) as given in the legend on top. Points above the diagonal

imply higher durations for switches forward. Note that for each data point the two preceding percepts,

whose dominance durations are considered (S_{i-2}, S_{i-1}), are identical on both axes, only the current state

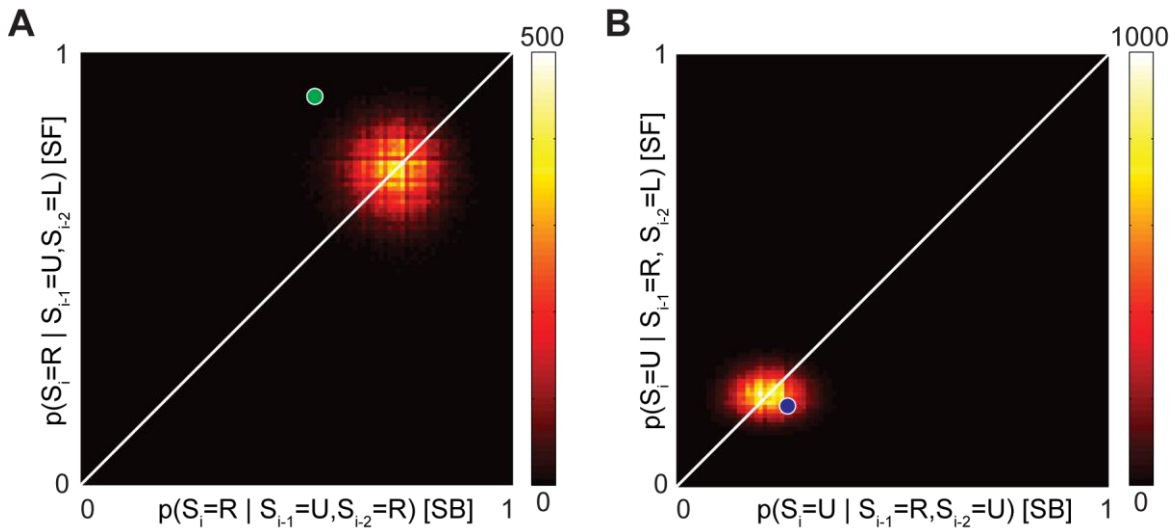(S_i) differs between the axes.

Figure 7

Example to illustrate the test for Markov property in Experiment 2, data from observer KL. Colored

dots show the actual data for the conditional switch probabilities; heat maps represent a histogram of

the results for 10^5 simulated surrogate sequences that share length (N=456) and first-order transition probabilities with the actual data. Left: S_i=R, S_{i-1}=U; Right: S_i=U, S_{i-1}=R. The maximum significance of rejecting the null-hypothesis, that a sequence has the Markov property, is reached when all 10^5 simulations fall closer to the diagonal than the actual data (dashed line).

Table

Exp. 1	FP	FR	KG	KL	MH	MN	MtH	SG
L	3.89±2.24 (061)	1.94±1.14 (067)	1.76±1.92 (096)	2.17±1.22 (079)	3.27±1.88 (084)	1.91±0.91 (101)	1.06±3.81 (056)	4.09±12.0 (025)
U	3.34±6.53 (084)	6.43±5.11 (077)	3.29±3.05 (099)	3.62±2.67 (115)	4.71±4.75 (072)	3.93±2.14 (108)	3.19±6.75 (092)	19.6±15.2 (025)
R	3.32±2.67 (055)	1.82±1.30 (077)	2.04±1.83 (097)	2.19±1.63 (083)	2.41±1.72 (063)	2.38±1.12 (092)	0.99±3.59 (066)	5.38±3.44 (018)
Exp. 2	**FP**	**FR**	**KG**	**KL**	**MH**	**MN**	**MtH**	**SG**
L	4.83±3.78 (079)	1.34±0.80 (177)	1.68±1.86 (136)	1.94±2.25 (123)	3.36±3.22 (096)	2.57±1.36 (118)	2.93±2.68 (104)	6.20±10.7 (027)
U	1.62±2.55 (054)	3.17±1.78 (085)	2.78±2.59 (083)	2.77±2.22 (078)	4.40±2.64 (028)	2.18±1.25 (102)	1.10±2.07 (094)	14.2±13.3 (024)
R	3.63±2.88 (063)	1.39±0.85 (197)	1.78±1.95 (122)	1.85±1.85 (116)	2.45±3.35 (093)	3.07±1.31 (107)	3.00±2.07 (097)	5.74±9.15 (020)
Exp. 3	**AP**	**AR**	**AV**	**CP**	**JA**	**JS**	**MN**	**MtH**
L	2.66±2.09 (084)	2.66±4.11 (037)	1.43±11.54 (036)	2.12±1.15 (102)	2.55±1.94 (081)	1.11±1.54 (184)	0.94±0.48 (223)	1.54±2.70 (099)
U	3.38±2.64 (112)	9.31±9.77 (039)	3.48±14.12 (042)	3.48±1.84 (115)	5.06±3.78 (090)	1.57±1.69 (199)	1.52±0.97 (252)	3.19±4.33 (117)
R	1.81±2.13 (075)	6.25±6.61 (018)	1.41±13.58 (045)	2.46±1.20 (077)	2.01±1.66 (038)	1.01±1.81 (152)	1.02±0.56 (219)	0.94±2.33 (062)
Exp. 4	**AP**	**AR**	**AV**	**CP**	**JA**	**JS**	**MN**	**MtH**
L	3.33±2.93 (117)	5.10±8.91 (039)	1.84±3.53 (052)	2.34±0.93 (111)	2.31±3.60 (114)	1.31±3.59 (156)	1.22±0.83 (218)	1.90±1.97 (130)
U	1.45±0.94 (076)	6.92±13.17 (041)	3.71±11.55 (062)	2.89±1.45 (143)	2.90±2.43 (117)	1.51±1.90 (108)	1.28±0.80 (205)	2.13±3.93 (130)
R	2.33±1.81 (108)	3.10±3.81 (026)	1.61±6.05 (042)	2.19±0.90 (086)	1.44±1.97 (032)	1.22±2.11 (154)	1.38±0.74 (187)	1.19±2.18 (057)

Table 1 Median and standard deviation of dominance durations for individuals and number of occurrences.