

## When motion is not perceived: Evidence from adaptation and dynamical stability

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**Abstract**—Adaptation was used to probe the perceiver’s activation state when either motion or nonmotion percepts are formed for bistable, single-element apparent motion stimuli. Although adaptation was not observed in every instance, when it was observed its effect was to increase the probability of both motion-to-nonmotion and nonmotion-to-motion switches, the time scale of adaptation corresponding to neurophysiological observations for directionally selective cortical cells (Giaschi *et al.* 1993). This susceptibility to de-stabilizing adaptation effects indicated that the nonmotion percept was not the result of inadequate stimulation producing subthreshold levels of motion detector activation; if that were the case, activation-dependent adaptation would have decreased the nonmotion-to-motion switching rate by reducing activation further below threshold. Above-threshold activation levels are therefore associated with both nonmotion and motion perceptual states, and the failure to perceive motion despite the presence of adequate motion detector stimulation can be attributed to inhibitory competition between detectors activated by motion-specifying stimulus information and detectors activated to similar levels by motion-independent stimulus information, consistent with the dynamical quality of single-element apparent motion.

*Keywords:* Adaptation; motion; dynamics; stability; nonmotion.

### INTRODUCTION

Research in motion perception generally has been concerned with the measurement of motion detection thresholds. The overall message from studies of apparent motion of discrete elements (e.g. Korte, 1915; Kolers, 1972), continuous motion of discrete elements (e.g. Nakayama and Tyler, 1978), and continuously drifting sine gratings (e.g. Kulikowski, 1978; Nakayama and Silverman, 1985) is that when motion is *not* perceived, it is because motion detectors are inadequately stimulated. These results notwithstanding, Hock *et al.* (1997a) have shown that adequate stimulation of motion detectors does not guarantee that motion will be perceived.

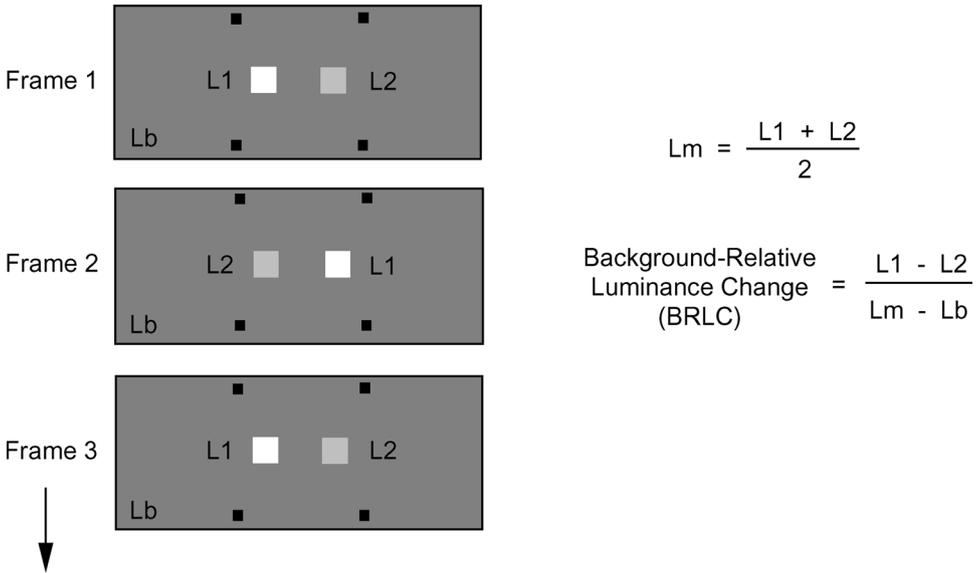
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They found that motion and nonmotion can be perceived equally often for the same bistable, apparent motion stimulus. Even when a stimulus is adequate for perceiving motion, it can just as readily result in the perception of nonmotion.

One possibility is that this bistability reflects only the activation state of motion detectors. On this basis, when nonmotion is perceived, it is because inadequate stimulation has left motion detector activation below the threshold level required for motion to be perceived. If this were true, adaptation caused by prolonged stimulation would *decrease* the likelihood of motion being perceived by reducing activation further below threshold. A second possibility is that motion/nonmotion bistability reflects the joint activation state of detectors responsive to motion-specifying stimulus information and detectors responsive to motion-independent stimulus information. On this basis, nonmotion can be perceived even when there is adequate motion detector stimulation. This would occur if the activation of the motion detectors is suppressed by inhibitory competition from similarly activated detectors that are responsive to motion-independent stimulus information. If this were the case, adaptation would be expected when motion is perceived (because there is above threshold activation of detectors responsive to motion) and also would be expected when nonmotion is perceived (because there is above threshold activation of detectors responsive to motion-independent stimulus information). However, regardless of whether motion or nonmotion is perceived, activation, and therefore adaptation, would be greater for the perceived than the unperceived alternative. This follows from adaptation being activation-dependent; i.e. adaptation effects are greater for higher levels of activation (Pantle and Sekuler, 1969; Levinson and Sekuler, 1975; Vautin and Berkeley, 1977; Saul and Cynader, 1989; Giaschi *et al.*, 1993). The difference in adaptation between perceived and unperceived alternatives would bring the activation levels for the competing detector ensembles closer together, increasing the probability that a noise-induced fluctuation in activation will be large enough to reverse their relative activation and produce a switch between them (a smaller, more probable fluctuation would be sufficient as a result of adaptation). The frequency of both nonmotion-to-motion and motion-to-nonmotion switches therefore would be expected to *increase* as a result of adaptation.

The experiments reported in this article distinguish between inadequate stimulation and motion/nonmotion competition as the basis for the perception of nonmotion by investigating the adaptation of both nonmotion and motion for spatially and temporally discontinuous apparent motion stimuli. Anstis *et al.* (1985, Experiment 1) found that after some period of time viewing an apparent motion stimulus, the perception of motion is replaced by the perception of nonmotion, presumably as a result of adaptation. Two further aspects of their results are relevant to the current study. The first is that both motion and nonmotion were perceived early in each trial, consistent with perception being bistable for these stimuli. The second is that the overall trend was for the probability of perceiving motion to decrease over time, but the probability tended to oscillate. Although there were periods during which



**Figure 1.** Illustration of generalized single-element apparent motion stimulus (not drawn to scale) and the formula for calculating the background-relative luminance change (BRLC).

the perception of nonmotion increased, consistent with greater adaptation of motion than nonmotion, there also were periods during which the perception of motion increased, consistent with greater adaptation of nonmotion than motion.

Anstis *et al.*'s (1985) results are consistent with the motion and nonmotion perceptual states for apparent motion stimuli being similar in adaptability, and therefore similar in activation. We more directly tested this hypothesis with a method that separates the adaptation of the nonmotion percept from the adaptation of the motion percept. The method entails measuring time-dependent changes in the probability of perceptual switches from nonmotion to motion (and *vice versa*) for the bistable, generalized version of single-element apparent motion (Johansson, 1950; Hock *et al.*, 1997). Pairs of elements with different luminance values were simultaneously visible, and the two luminance values were exchanged during successive frames (Fig. 1).<sup>1</sup> The likelihood of motion being perceived for this stimulus increases with each element's increase in background-relative luminance change (BRLC), the frame-to-frame change in luminance divided by the difference between the average luminance and the luminance of the background (Fig. 1). For standard apparent motion, as in Anstis *et al.* (1985), only one element is visible at a time (BRLC = 2.0).

## EXPERIMENT 1

The experimental paradigm for independently measuring the adaptability of the nonmotion and motion perceptual states was developed by Hock *et al.* (1997b).

It measures the probability of a switch *per unit of time* by having participants report whether there was at least one switch anytime during a trial, and varying the duration of the trial. Regardless of whether or not there is an influence of adaptation, the probability of at least one switch occurring during a trial increases as its duration is increased; longer trial durations provide more opportunity for the occurrence of noise-induced fluctuations in activation that are sufficient in size to produce a switch. However, if adaptation decreases the difference in activation between the perceived and unperceived motion/nonmotion alternatives, the probability of a switch per unit of time would increase over the course of a trial.

Whether or not there are time-dependent changes in switching probability was determined by assuming, for trials of a particular duration, that the probability of a switch per unit of time ( $p$ ) remained constant over the entire trial. Assuming such temporal independence, the value of ' $p$ ' was calculated that would account for the empirically measured 'probability of at least one switch' during a trial with  $N$  display cycles. The equation for these calculations defines the probability of there not being a switch during a single display cycle ( $1 - p$ ), extends it to there not being a switch *anytime* during the trial  $(1 - p)^{N-1}$ , where  $N$  is the number of display cycles composing the trial, and subtracts the result from 1. A switch cannot occur during the first display cycle: hence,  $N - 1$  in equation (1).

$$\text{Probability [1 or more switches]} = 1 - (1 - p)^{N-1}. \quad (1)$$

Evidence for adaptation would be obtained if the calculated probability of a switch per display cycle ( $p$ ) changes as a function of trial duration ( $N$ ). If the perception of nonmotion were the result of inadequate motion detector stimulation, adaptation would *decrease*  $p$  with increased trial duration because activation would be reduced further below the threshold required for motion to be perceived. However, if the nonmotion percept were the result of its successful competition with motion, a relatively high level of activation would be associated with the nonmotion percept. Activation-dependent adaptation would *increase*  $p$  with increased trial duration by decreasing the activational advantage of the nonmotion percept.

### Method

A pair of horizontally separated,  $16.2 \times 16.2$  min squares was presented simultaneously (40.4 min apart, center-to-center) in the center of a gray background ( $2.8 \times 2.8$  deg; luminance =  $3.30 \text{ cd/m}^2$ ), which in turn was centered in the darkened screen (luminance  $< 0.001 \text{ cd/m}^2$ ) of a Macintosh II RGB monitor. Viewing distance was maintained at 30 cm by a head restraint. The luminance values for the two squares were different during each 195 ms frame, and were exchanged during successive frames over a series of 2-frame display cycles (either 6, 10, 14, 18, 22, 26 or 30 display cycles per trial). There were 2 blocks of 56 trials (8 order-randomized repetitions of each of the 7 trial durations) in each of 6 testing sessions.

Based on preliminary testing, each participant's BRLC value was chosen so that the motion and nonmotion percepts would be approximately equally likely at the

start of each trial. The BRLC values were 0.60 for DN (luminance alternated between 8.05 and 5.89  $\text{cd/m}^2$ ), 0.54 for JR (luminance values were 7.95 and 5.99  $\text{cd/m}^2$ ), and 0.51 for RK (luminance values were 7.91 and 6.04  $\text{cd/m}^2$ ). When nonmotion was perceived for these BRLC values, the elements appeared to flicker in place. The participants were an author and two volunteer undergraduate students at Florida Atlantic University. The latter were naive with respect to the purpose of the experiment. They were instructed to make two responses at the end of each trial, the first to indicate whether their initial percept was motion or nonmotion, the second to indicate whether there was a switch to the other percept *anytime* during the trial.

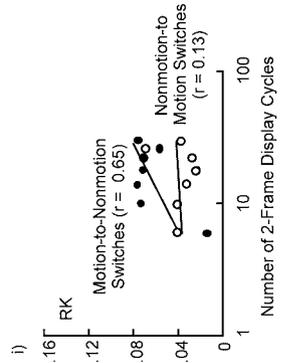
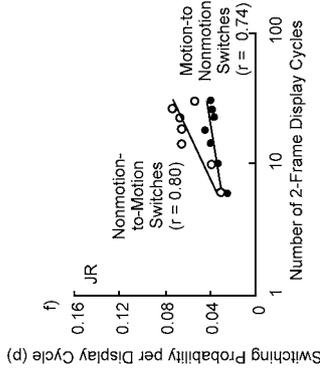
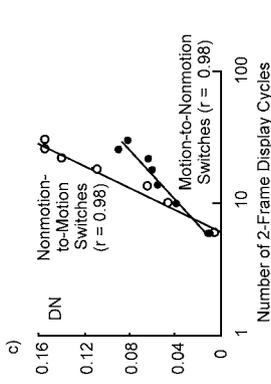
### Results

Motion was the initial percept for 55, 73, and 66% of the trials for DN, JR, and RK, respectively. With switches to motion from the initial percept of nonmotion included, motion was perceived sometime during 84, 87, and 81% of the trials. Although motion was not always perceived, it could be concluded that motion detectors were adequately stimulated.

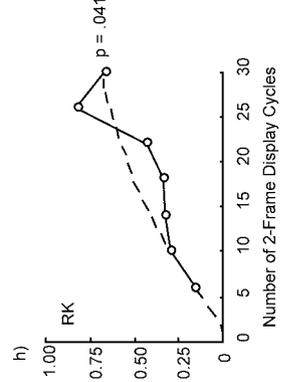
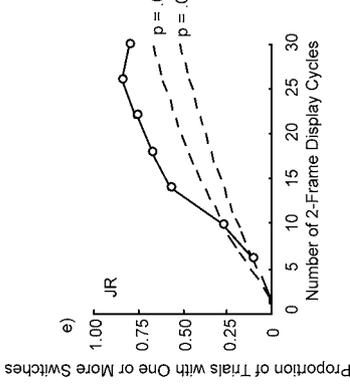
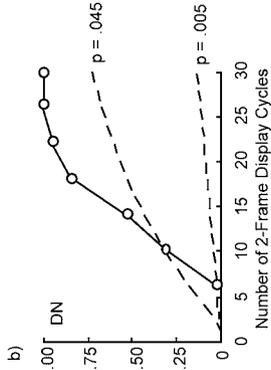
As anticipated, the empirically determined ‘probability of at least one switch’ increased as a function of trial duration for both motion-to-nonmotion switches (Fig. 2a, d, g) and nonmotion-to-motion switches (Fig. 2b, e, h). Included in these graphs are illustrative weighted temporal independence functions (indicated by broken lines) that were calculated for the two briefest trial durations with equation (2), which is derived below. These functions give the probability of a switch per display cycle ( $p$ ) that account for the empirically determined ‘probability of at least one switch’ under the assumption that  $p$  does not change over time. It can be seen, however, that with the exception of RK’s nonmotion-to-motion switches,  $p$  increased for these trial durations, indicative of adaptation increasing the probability of a switch. In order to calculate  $p$ , it was necessary to determine whether the formation of the initial percept and/or its subsequent susceptibility to switching were delayed (the exponent  $N - 1$  in equation (1) assumes that a switch becomes possible during the second display cycle). The two additional experiments that addressed these possibilities are described below.

*Experiment 1a.* To determine the time required for either motion or nonmotion to be perceived at the start of each trial, the participants from the main experiment were asked to indicate whether they had clearly perceived either motion or nonmotion anytime during a trial. There were 1, 2, 3, 4, 5, 6, or 7 display cycles per trial, and 4 blocks of 56 randomly ordered trials during each of 2 testing sessions. Because the results were very similar for the motion and nonmotion percepts, they are combined in Fig. 3a, where it can be seen that a clear percept almost always emerged by the second or third display cycle. This delay was very likely the result of participants’ attention not being sufficiently focused at the start of each trial. Previous results have indicated that when enough time is provided at the start of each

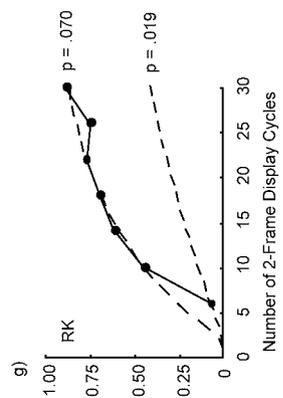
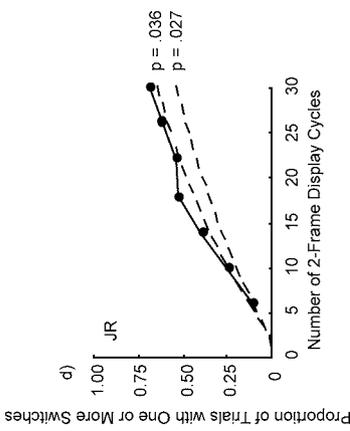
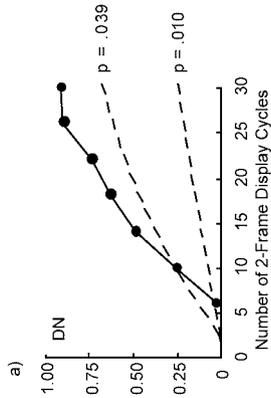
Switching Probability per Display Cycle (p)



Probability of at Least One Nonmotion-to-Motion Switch per Trial

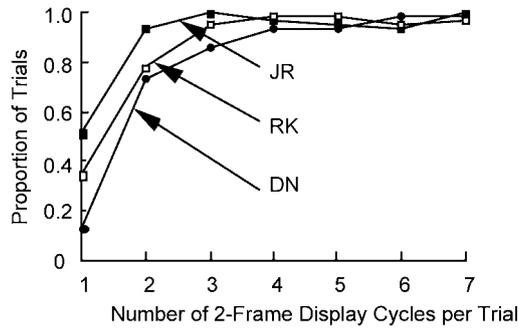


Probability of at Least One Motion-to-Nonmotion Switch per Trial

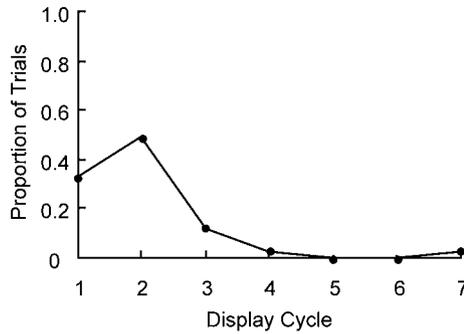


Proportion of Trials with One or More Switches

a) Is Motion or Nonmotion Clearly Perceived Anytime During Trial?



b) When is a Clear Motion or Nonmotion Percept Formed?



**Figure 3.** Experiment 1a: (a) For each participant, the proportion of trials for which either motion or nonmotion was clearly perceived anytime during a trial. The results are combined for the two percepts. (b) The proportion of trials for which a clear motion or nonmotion percept emerged during display cycle. This was determined by subtracting the proportion for trials with  $N - 1$  display cycles from the proportion for trials with  $N$  display cycles (averaged over the three participants).

trial for attention to be focused between the two elements of the generalized apparent motion stimulus, motion and nonmotion are clearly discriminated when there is just a single frame during which the luminance of the two elements are exchanged (Hock *et al.*, 2002).

**Figure 2.** Experiment 1: (a, d, g) For each participant, the effect of trial duration (i.e. the number of 2-frame display cycles) on the proportion of trials for which at least one perceptual switch from motion to nonmotion was perceived anytime during the trial. (b, e, g) For each participant, the effect of trial duration (i.e. the number of 2-frame display cycles) on the proportion of trials for which at least one perceptual switch from nonmotion to motion was perceived anytime during the trial. (c, f, i) Calculated values of the switching probability per display cycle (see text). The broken lines are temporal independence functions calculated on the basis of the assumption that the probability of a switch during a display cycle remains constant over the entire duration of a trial. Filled circles indicate motion-to-nonmotion switches; open circles indicate nonmotion-to-motion switches.

*Experiment 1b.* Is there a kind of refractory period following the formation of a percept during which there is relative immunity to the fluctuations in activation that would produce perceptual switching? It is not possible to determine whether this is the case when the fluctuations are produced by random perturbations because it cannot be known when potential switch-inducing perturbations occur. In this experiment, therefore, a fluctuation in activation was experimentally introduced by changing the BRLC during a single frame. For one stimulus, the BRLC was 0.3 for the first 3 display cycles, increased to 0.8 for a single frame, and then restored to 0.3 for another 3 display cycles. For the second stimulus, the BRLC was 0.8 for the first 3 display cycles, decreased to 0.3 for a single frame, and then restored to 0.8 for another 3 display cycles. In both cases, switches back and forth between motion and nonmotion were easily perceived. There was no evidence for a refractory period during which changes in activation do not produce perceptual switches.

*Weighted temporal independence functions.* Averaging over the three participants, the results of Experiment 1a indicated that a clear percept emerged during the first display cycle for 33% of the trials, during the second display cycle for 49% of the trials, and so on (Fig. 3b). Although the  $N - 1$  exponent in equation (1) was appropriate for many of the trials, an exponent of  $N - 2$  or less would have been more appropriate for the majority. The results in Fig. 3b were the basis for the weighted temporal independence functions in equation (2).

$$\begin{aligned} & \text{Probability [1 or more switches]} \\ & = 0.33 \times [1 - (1 - p)^{N-1}] + 0.49 \times [1 - (1 - p)^{N-2}] \\ & \quad + 0.12 \times [1 - (1 - p)^{N-3}] + 0.06 \times [1 - (1 - p)^{N-4}]. \end{aligned} \quad (2)$$

*Switching probability ( $p$ ) as a function of trial duration.* The switching probability per display cycle ( $p$ ) calculated from the weighted temporal independence functions are presented for each participant in Figs 2d, f, i.<sup>2</sup> Trial duration is log-transformed in these graphs because  $p$  tended to asymptote toward a constant value with increased trial duration. For motion-to-nonmotion switches, the switching probability per display cycle increased as a function of trial duration for all three participants, though the effect was small for JR. Correlation coefficients (presented with each graph) were highly positive, ranging from 0.65 to 0.98. For nonmotion-to-motion switches,  $p$  increased with trial duration for DN and JR (correlation coefficients were 0.98 and 0.80, respectively), but there was no effect of trial duration for RK (correlation coefficient = 0.13). Significance was tested for each participant on the basis of the average of their nonmotion-to-motion and motion-to-nonmotion switching probability at each trial duration. These correlations were statistically significant at the 0.05 level for DN ( $r_{\text{avg}} = 0.99$ ) and JR ( $r_{\text{avg}} = 0.81$ ), but not for RK ( $r_{\text{avg}} = 0.71$ ).<sup>3</sup>

## EXPERIMENT 2

The results for Experiment 1 indicated that the increase in the probability of a nonmotion-to-motion switch per display cycle was approximately asymptotic after 10 display cycles (4.9 s) for JR and 22 display cycles (10.8 s) for DN. The question regarding the nonmotion-to-motion switches was whether 4.9 to 10.8 s represents the time course of adaptation to nonmotion within trials beginning with the perception of nonmotion, or whether it represents the period of time required for the recovery from motion adaptation that occurred when motion was perceived during an immediately preceding trial.

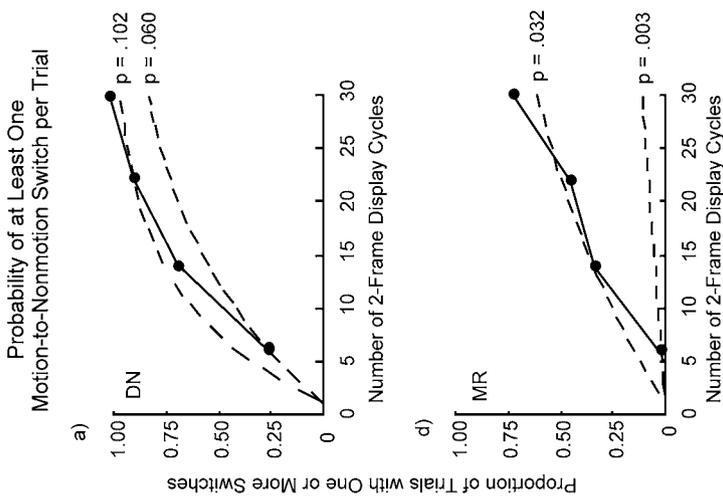
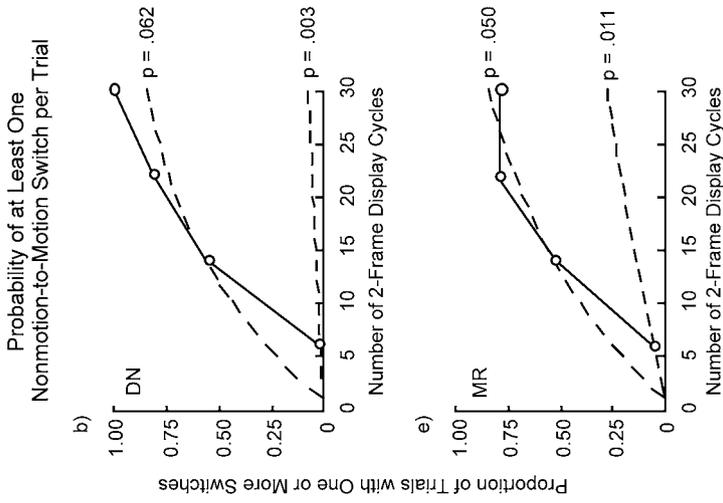
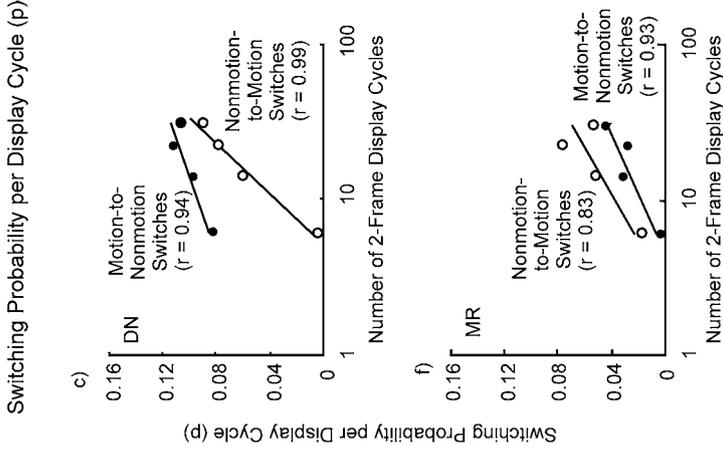
To distinguish between these alternatives, each trial was temporally isolated from its predecessor by a 10.4 s delay between the end of each trial and the beginning of the next trial. This approximated the longest asymptotic value in Experiment 1, sufficient opportunity for recovery from whatever adaptation might have occurred during preceding trials. If the observed nonmotion-to-motion switching functions were the result of recovery from prior motion adaptation, the probability of a nonmotion-to-motion switch per display cycle ( $p$ ) would be expected to be unaffected by trial duration. That is, there would be little if any effect of recovery once the trial began because recovery would have been completed during the inter-trial interval. If, however, the increase in  $p$  is the result of adaptation of the nonmotion perceptual state within trials beginning with the perception of nonmotion, then results similar to those of Experiment 1 would be expected, even with a long inter-trial interval.

### *Method*

The stimuli and procedure were similar to Experiment 1, but now stimuli were presented on a ViewSonic 15GA RGB monitor and controlled by a Macintosh 7300/180 computer. The event sequence for successive trials was as follows: (1) at the end of a trial, the gray background was removed for 9.0 s, (2) the luminance of the background was gradually increased to its final value of 3.3 cd/m<sup>2</sup> over an interval of 1.0 s, (3) the background remained at this value for 0.4 s, and (4) the generalized apparent motion stimulus (BRLC = 0.60) was presented for 6, 14, 22 or 30 display cycles. There were 32 trials per block (8 order-randomized repetitions of the 4 durations), and 2 blocks of trials in each of 4 testing sessions.

### *Results*

Motion was perceived at the start of 29% of the trials for DN and 61% of the trials for MR. Increases with trial duration in the 'probability of at least one switch' again were observed for both participants for both the perception of motion (Fig. 4a, d) and the perception of nonmotion (Fig. 4b, e), and the 'probability of at least one switch' approached asymptotic values for trials with more than 14 display cycles. The switching probabilities per display cycle ( $p$ ), calculated with equation



(2), are presented in Fig 4c, f. It can be seen that  $p$  increased as a function of trial duration for both participants, for nonmotion-to-motion as well as motion-to-nonmotion switches. The correlations between  $p$  and log-transformed trial duration were highly positive, ranging from 0.83 to 0.98. One-tailed tests for correlations based on the average of the motion-to-nonmotion and motion-to-motion switching probabilities at each trial duration were statistically significant at the 0.05 level for DN ( $r_{\text{avg}} = 0.99$ ) and MR ( $r_{\text{avg}} = 0.94$ ). Because each trial in this experiment was preceded by an interval long enough for recovery from adaptation to motion that was perceived during preceding trials, the results indicate that the effect of trial duration on the probability of a nonmotion-to-motion switch per display cycle ( $p$ ) was the result of adaptation to the nonmotion perceptual state within trials beginning with the perception of nonmotion.

## GENERAL DISCUSSION

Adaptation effects were not always observed when nonmotion was perceived (see RK's results in Experiment 1), so the evidence for an adaptable nonmotion state was not conclusive. However, when adaptation effects were observed, switching probabilities increased as a function of trial duration for nonmotion as well as motion percepts. The similarity of these adaptation effects indicated that both motion and nonmotion percepts were stabilized at similar above-threshold levels. This would not have been the case if the nonmotion percept were the result of inadequate stimulation producing subthreshold motion detector activation (adaptation then would have reduced activation further below threshold, decreasing the probability of a switch to the motion percept, the opposite of our experimental results). Experiment 2 provided further evidence for the adaptability of the nonmotion perceptual state while ruling out recovery from adaptation to previously perceived motion.

The probability of a switch per unit of time is increased by activation-dependent adaptation because it brings activation levels for perceived and unperceived alternatives closer together. However, so long as *both* perceived and unperceived alternatives adapt (Hock *et al.*, 1996), activation-dependent adaptation is not sufficient to reverse their relative activation levels. Switching ultimately depends on random

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**Figure 4.** Experiment 2: (a, d) For each participant, the effect of trial duration (i.e. the number of 2-frame display cycles) on the proportion of trials for which at least one perceptual switch from motion to nonmotion was perceived anytime during the trial. (b, e) For each participant, the effect of trial duration (i.e. the number of 2-frame display cycles) on the proportion of trials for which at least one perceptual switch from nonmotion to motion was perceived anytime during the trial. (c, f) Calculated values of the switching probability per display cycle (see text). The broken lines are temporal independence functions calculated on the basis of the assumption that the probability of a switch during a display cycle remains constant over the entire duration of a trial. Filled circles indicate motion-to-nonmotion switches; open circles indicate nonmotion-to-motion switches.

fluctuations in activation. Evidence for this was provided by the satiation of adaptation, which was indicated by the probability of a switch per display cycle approaching an asymptotic value with increasing trial duration. Switching continued to occur, even when there were no further adaptation-induced increases in the likelihood of a switch per display cycle. These switches could only have come from random fluctuations in activation.<sup>4</sup> Thus, adaptation reduces the stability of both motion and nonmotion percepts by increasing their susceptibility to the stochastic fluctuations in activation that would produce a switch to the alternative percept. Smaller, therefore more probable fluctuations became sufficient because adaptation reduced the activation of the percept compared with the unperceived motion/nonmotion alternative.

The satiation of motion adaptation between the 10th and 22nd display cycles (4.9 to 10.8 s) for single element apparent motion was consistent with Giaschi *et al.*'s (1993) neurophysiological evidence that directionally selective cortical cells have a time scale of adaptation to continuously drifting square-wave gratings over a temporal range of 4 to 10 seconds.

The convergence of these results would be expected on the basis of psychophysical studies indicating that continuous and discontinuous motion are based on the same detecting mechanisms (e.g. Burr *et al.*, 1986), as well as evidence that directionally selective neurons in Areas V1 and MT respond to both continuously and discontinuously displaced stimuli (Newsome *et al.*, 1986).

In conclusion, there are certainly many stimuli for which motion detectors are not sufficiently stimulated for motion to be perceived (e.g. the generalized apparent motion stimuli when BRLC values are very low), but motion perception also can fail when detectors are adequately stimulated. Hock *et al.* (1997) have shown that there is a range of luminance changes (BRLC values) for which generalized apparent motion stimuli are bistable with respect to whether motion or nonmotion is perceived. They observed both spontaneous switching and hysteresis for these stimuli, evidence that thresholds for the perception of apparent motion are dynamic. The results of the current study provide further evidence for the motion/nonmotion threshold being dynamic by showing that adaptation affects the stability of the competing motion/nonmotion percepts (by increasing switching rates between the alternative percepts). Evidence that levels of activation for the nonmotion and motion percepts were similar (their adaptation was similar) indicated that the likely source of the dynamics was inhibitory competition between detectors responsive to motion-independent stimulus information and detectors responsive to motion-specifying stimulus information. Substantial evidence for interaction between the perception of motion and position (Breitmeyer *et al.*, 1974; Kulikowski and MacCana, 1980; Banta and Breitmeyer, 1985; Eastman and Hock, 1999; Whitney and Cavanagh, 2000), indicates that motion-independent *spatial* information rather than flicker is the likely basis for the nonmotion percept.

## NOTES

1. These stimuli are homologous with the crossed-phi and cross-over stimuli studied by Watson (1986), Mather and Anstis (1995), and Werkhoven, Sperling and Chubb (1993).

2. For DN's nonmotion-to-motion switches, the 'probability of at least one switch' was at ceiling for the two longest trial durations. To avoid over-estimation, ' $p$ ' was determined for these trials from the weighted temporal independence function that provided the best fit to the three longest trial durations.

3. The effect of trial duration on ' $p$ ' would have been as large, if not larger, if ' $p$ ' was calculated with equation (1).

4. It is likely that random perturbations intrinsic to neural mechanisms (e.g. Koch and Poggio, 1987) contributed to the switches between the perception of motion and nonmotion observed in the current study. It is also possible that switches were produced by perturbations in attention, motion perception being more likely when attention is focused between the two elements of the generalized apparent motion stimulus, and flicker perception being more likely when attention is shifted to one of the elements.

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