Measuring Perceptual Hysteresis with the Modified Method of Limits: Dynamics at the Threshold [*]

Howard S. Hock [1,**] **and Gregor Schöner** [2]

[1] Department of Psychology and Center for Complex Systems and Brain Sciences, Florida Atlantic University, Boca Raton, FL 33431, USA

[2] Institute for Neuroinformatics, Ruhr-University Bochum, Germany

Abstract

This article describes modifications to the psychophysical method of limits that eliminate artifacts associated with the classical method, and thereby indicate whether or not there is perceptual hysteresis. Such hysteresis effects, which are characteristic of dynamical systems, would provide evidence that the near-threshold perception of an attribute is affected by stabilization mechanisms intrinsic to individual neural detectors, and by nonlinear interactions that functionally integrate the detectors when there is sufficient stimulus-initiated activation, thereby stabilizing activation at suprathreshold levels. The article begins with a review of research employing the modified method of limits. It concludes with a model and computational simulations showing how detection instabilities inherent in neural dynamics can create 'activational gaps' between the functionally-integrated and functionally-independent states of neural ensembles, resulting in clear and distinct discrimination between the perception and non-perception of an attribute. The 'self-excitation' threshold for engaging such functionally-integrating detector interactions is differentiated from the traditional 'read-out' threshold (criterion) that determines whether or not the attribute in question can be perceived.
© Koninklijke Brill NV, Leiden, 2010

Keywords

Method of limits, psychophysics, hysteresis, neural dynamics, detection instability, motion quartets, apparent motion

1. The Classical Method of Limits

The method of limits is typically cited as one of the psychophysical methods developed by Fechner (1860), though its antecedents have been traced back as far as 1700 (Boring, 1942). The method, which has been used to measure absolute thresholds (the minimal intensity for detection) as well as difference thresholds (the minimal

---

noticeable difference), entails trials that begin with parameter values that are well above threshold (descending trials) alternating with trials that begin with parameter values that are well below threshold (ascending trials). For both ascending and descending trials, the parameter is gradually changed over a sequence of steps until values are reached for which the observer reports that the attribute in question is now perceived, or it no longer is perceived (see Note 1).

A well-known issue for threshold measurements using the classical method of limits is that the parameter value for the transition from non-perception to perception differs from the parameter value for the transition from perception to non-perception. The artifacts contributing to this difference have been understood for many years (see Woodworth and Schlosberg, 1938, as well as more recent textbooks). Artifactual ascending/descending differences have been attributed to: (1) *response perseveration* (historically called 'habituation'), a tendency to repeat the same response for successive stimuli irrespective of what is perceived; (2) *inferences from trial duration* (historically called 'anticipation'), where perceptual transitions are reported after a long sequence of stimulus steps because the parameter is thought to have reached values for which the percept should have changed; and (3) *judgment uncertainty*, reports of a change are withheld until the transition is perceptually definite. Less frequently discussed are potential artifacts for rapidly changing stimuli, as in the study of motion perception. Differences between ascending and descending trials might then be artifacts of *decision/response time*: the time required for the observer to reach a decision and execute a response would delay the response until after the perceptual transition has occurred.

The assumption in using the method of limits has been that the artifacts described above are symmetrical, so an accurate measure of the threshold would be obtained by averaging the transitional parameter values for the ascending and descending trials. More recently, however, it has been recognized that the difference in transitional parameter values between ascending and descending trials can reflect a meaningful, non-artifactual perceptual effect.

2. Perceptual Hysteresis

Perceptual hysteresis occurs when the percept formed at the start of a descending trial persists despite a parameter changing to values for which the alternative would have been perceived during an ascending trial, and *vice versa* for the percept formed at the start of an ascending trial (e.g., Fender and Julesz, 1967; Williams *et al.*, 1986). Such hysteresis effects are signatures of state-dependent neural dynamics (Hock and Schöner, 2010; Hock *et al.*, 2003; Wilson, 1999). Accordingly, perception at any moment in time depends not only on stimulus-initiated detector activation, but also on the immediately preceding activation state of the ensembles of detectors that are activated by the stimulus.

It is implicit in classical psychophysics that near-threshold perception depends on whether a stimulus adequately activates detectors that are responsive to it. The

threshold indicates the parameter value for which the stimulus is barely adequate; i.e., the value for which the attribute in question can be perceived, but the percept is uncertain and indistinct. The dynamical account is much different. Perceptual hysteresis indicates that in addition to the activation initiated by the stimulus, near-threshold perception depends on whether the stimulus-initiated detector activation is sufficient to create excitatory interactions among the stimulated detectors. When such excitatory interactions are engaged, activation is amplified and stabilized well above the threshold 'read out' level that determines whether or not there is sufficient detector activation for an attribute to be perceived. When excitatory interactions are not engaged, detector activation is stabilized below the read-out threshold. The activational gap between the alternative perceptual states that is created by the presence *vs* the absence of self-excitatory interactions makes the alternatives (whether the attribute is perceived or not) clear and distinct. Moreover, excitation-amplified activation states persist over time, so there is a predisposition for the perception of the attribute to persist, even when there are stimulus changes that would otherwise result in a different percept. This is the basis for perceptual hysteresis.

Classical and dynamical psychophysics also differ with respect to whether near-threshold perception reflects only the feedforward processing of visual information. Activation induced in the feedforward path is largely stimulus determined, the preferential responding of different detectors occurring because different receptive fields respond selectively to different stimulus attributes. Although this would be consistent with the classical perspective, most neuronal activity entails more than feedforward processing. Braitenberg (1978) has estimated that 95% of the input to each cortical neuron comes from its connectivity with other cortical neurons; Felleman and Van Essen (1991) have determined that there are more feedback than feedforward connections between higher- and lower-level areas in the brain; and Movshon and Newsome (1996) and Girard *et al.* (2001) have shown that feedforward and feedback signals are more than fast enough (on the order of several milliseconds) for feedback from higher brain levels to affect percepts established at lower brain levels. It will be shown that it is because of this neural connectivity that percepts can be stabilized at activation levels beyond the minimal level required for perception, so when something is perceived for near-threshold parameter values, the percept is clear and distinct, and persists despite parameter changes that favor a change in perception (as per perceptual hysteresis).

The distinction between classical and dynamical psychophysics thus entails more than a technical question of how best to measure thresholds using the method of limits. Its importance lies in the evidence it provides that detectors that would otherwise function independently (classical psychophysics) are potentially organized into functional units that amplify the differences in activation that determine whether or not a near-threshold attribute is perceived (dynamical psychophysics). Given this theoretical significance of perceptual hysteresis, the classical method of limits was modified in order to eliminate potential artifacts involving response

perseveration, decision/response time, inferences from trial duration, and judgment uncertainty.

3. Response Perseveration and Decision/Response Time

Response perseveration refers to the persistence of a response that is repeated over and over again for each stimulus step in a sequence of ascending or descending parameter changes. If there were no perceptual hysteresis, the parameter value for perceptual transitions would be the same for ascending and descending trials, but response perseveration would result in artifactual hysteresis because the responses indicative of a perceptual transition would not occur for some period of time subsequent to the actual perceptual change.

Decision/response time poses a similar potential for artifact: hysteresis could occur because of the time required for the observer to reach a decision and execute a response. Once again, if there were no perceptual hysteresis the parameter value for the perceptual transition would be the same for ascending and descending trials. However, the time required for a decision and response execution (depending on the extent to which response speed is stressed) would make it appear as though the initial percept had persisted until values were reached that are later in the parameter sequence, after the perceptual transition had actually occurred. Different transition values for ascending and descending trials due to decision and response execution time could result in a hysteresis effect, but it would not be perceptual hysteresis.

The time required for decision and response execution is not a factor when the parameter in the method of limits is changing very slowly, so that the perceiver's response to an ascending or descending parameter step would occur before there is a change to the next parameter value. Even when the parameter changes more quickly, perceptual hysteresis can be inferred by showing that the size of the measured hysteresis effect is larger than an independent estimate of the hysteresis that would be attributable to the time required for decision and response execution time (see, for example, Gori *et al.*, 2008). However, it is possible for true perceptual hysteresis effects to be smaller than estimates of artifactual hysteresis due to decision/response time, perhaps because of stimulus perturbations that reduce the size of the perceptual hysteresis (e.g., Hock and Ploeger, 2006). It is shown next how the modified method of limits eliminates artifacts of response perseveration, decision/response time, and dependence on the rate of parameter change.

4. The Modified Method of Limits

The key to the modified method of limits is that it allows one to determine when perceptual transitions have occurred without requiring the observer to respond during the sequence of ascending or descending steps, and without concern for how quickly the parameter has changed or how quickly or slowly the observer decides that there was a perceptual change and executes an appropriate response. As in

the classical version, the modified method of limits begins ascending and descending trials with parameter values for which only one of two perceptual alternatives is possible. The parameter is then gradually decreased (descending trials) or gradually increased (ascending trials) by a variable number of steps, so the final, end-point parameter value for each trial also is variable.

For trials with just a few parameter steps, it is unlikely that there will be a change in perception. For trials with more steps, the probability of the initial percept persisting for the entire trial will decrease as the number of parameter steps increases. It then can be determined when perceptual transitions were likely to have occurred by comparing reports of perceptual change for ascending and descending trials with different end-point parameter values. Perceptual hysteresis would be indicated if the percept for a particular end-point parameter value is different, depending on whether the end-point is reached via an ascending or descending sequence of parameter changes. Response perseveration, decision/response-time, and the rate of parameter change are not factors because the order of ascending and descending trials is randomized, and because the observer does not respond until the end of each trial (and then, without speed stress).

4.1. Motion Quartets

The modified method of limits was first used to measure perceptual hysteresis with motion quartets (Hock *et al.*, 1993). The motion quartet is an apparent motion stimulus for which two spots of light corresponding to the opposite corners of an imaginary rectangle are presented during odd numbered frames, and two spots of light corresponding to the other, opposite corners of the imaginary rectangle are presented during even numbered frames. Either parallel-path horizontal motion or parallel-path vertical motion can be perceived for the same stimulus, but both are never perceived at the same time (Fig. 1(a)). The control parameter for the motion quartet is its aspect ratio, the vertical divided by the horizontal distance between the spots of light composing the quartet. Large aspect ratios favor the perception of horizontal motion (vertical motion is perceived less often than horizontal motion), as in Fig. 1(b). Small aspect ratios favor the perception of vertical motion (horizontal motion is perceived less often than vertical motion), as in Fig. 1(c).

Ascending trials in Hock *et al.* (1993) all began with an aspect ratio of 0.5, which strongly favored the perception of vertical motion. Descending trials all began with an aspect ratio of 2.0, which strongly favored the perception of horizontal motion. The aspect ratio changed in steps of 0.25 for both ascending and descending trials. As indicated in Table 1, there were six kinds of ascending trials that varied with respect to the number of steps by which the aspect ratio was increased, and six kinds of descending trials that varied with respect to the number of steps by which the aspect ratio was decreased. The twelve ascending and descending trials were presented in random order, with observers indicating at the end of each trial whether or not they perceived a change from the initially perceived to the alternative motion pattern *at any time* during the trial. (In other experiments observers first indicated
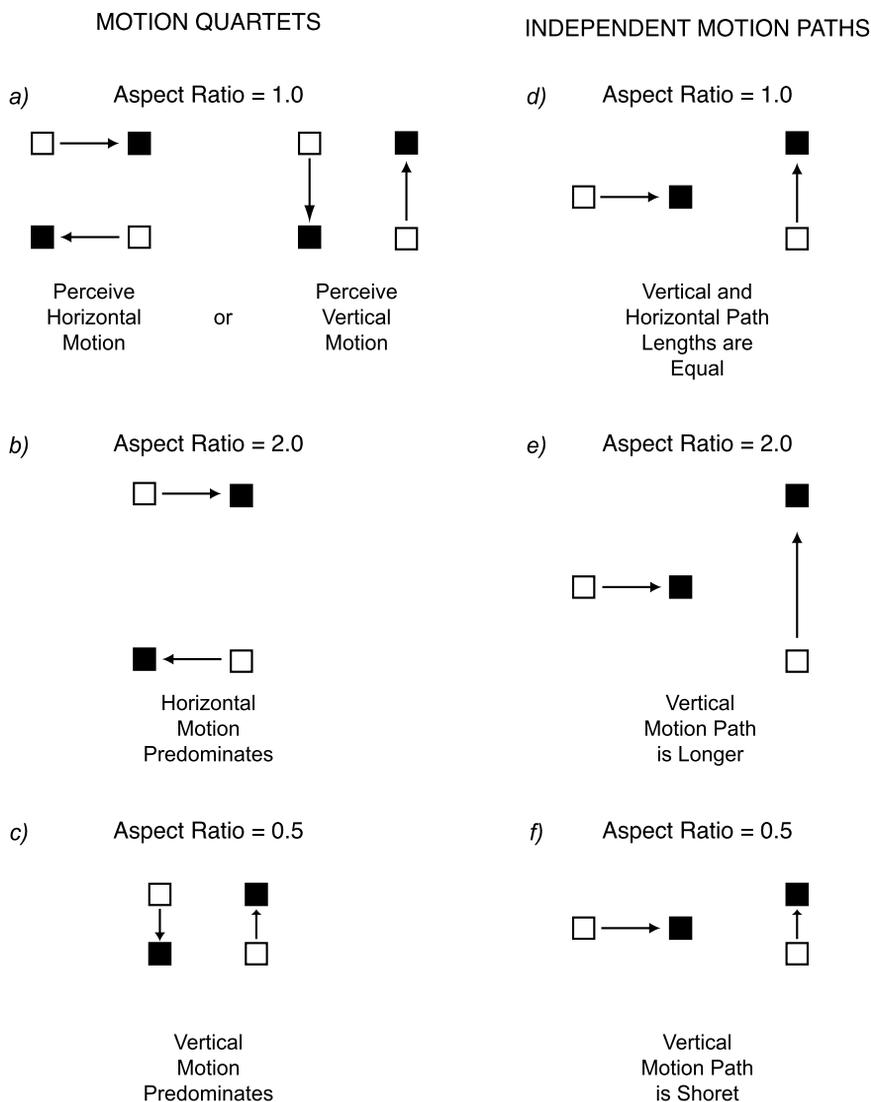
MOTION QUARTETS   INDEPENDENT MOTION PATHS

a)   Aspect Ratio = 1.0   *d)*   Aspect Ratio = 1.0

Perceive
Horizontal   or   Perceive
Motion   Vertical
Motion   Vertical and
Horizontal Path
Lengths are
Equal

b)   Aspect Ratio = 2.0   *e)*   Aspect Ratio = 2.0

Horizontal
Motion
Predominates   Vertical
Motion Path
is Longer

c)   Aspect Ratio = 0.5   *f)*   Aspect Ratio = 0.5

Vertical
Motion
Predominates   Vertical
Motion Path
is Shoret

Figure 1. (a–c) Illustration of the motion quartets used in the hysteresis experiments reported by Hock *et al.* (1993) and Hock *et al.* (2005). Either parallel-path vertical motion or parallel-path horizontal motion is perceived, depending on the aspect ratio of the motion quartet (the vertical divided by the horizontal path length). (d–f) Stimuli with independent vertical and horizontal motions that were matched in aspect ratio with the motion quartets in Hock *et al.* (2005).

whether their initial motion percept was horizontal or vertical, and then, whether or not there was a change to the alternative percept.)

The frequency with which the initial percept switched to the alternative percept was graphed as a function of the trial's end-point aspect ratio. The results for one of the participants in Experiment 2 of Hock *et al.* (1993) are presented in Fig. 2.

Table 1.

Twelve trials (one per row) that differ with respect to whether the sequences of motion quartet aspect ratios constituting each trial are ascending (starting with 0.5) or descending (starting with 2.0), and differ as well with respect to their end-point aspect ratio

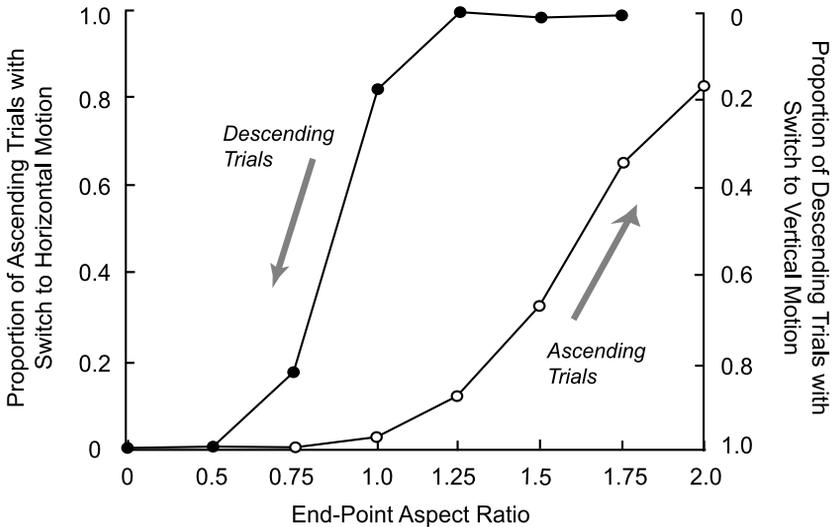| Ascending trials						
0.5	0.75					
0.5	0.75	1.0				
0.5	0.75	1.0	1.25			
0.5	0.75	1.0	1.25	1.5		
0.5	0.75	1.0	1.25	1.5	1.75	
0.5	0.75	1.0	1.25	1.5	1.75	2.0
Descending trials						
2.0	1.75					
2.0	1.75	1.5				
2.0	1.75	1.5	1.25			
2.0	1.75	1.5	1.25	1.0		
2.0	1.75	1.5	1.25	1.0	0.75	
2.0	1.75	1.5	1.25	1.0	0.75	0.5

Figure 2. Hysteresis effect observed by gradually increasing or gradually decreasing the aspect ratio of a motion quartet for a participant in Hock *et al.*'s (1993) second experiment. The proportion of trials with switches from horizontal to vertical motion, and *vice versa*, are graphed as a function of the aspect ratio at which each ascending or descending sequence of aspect ratios ends. (Note the inversion of the axis on the right.)

It can be seen that the frequency with which there were switches during trials with a particular end-point aspect ratio was different, depending on whether that aspect

ratio was preceded by an ascending sequence (the vertical axis on the left side of the graph) or by a descending sequence of aspect ratios (the *inverted* vertical axis on the right side of the graph). For example, when the end-point aspect ratio was 1.25, horizontal motion was perceived without a switch to vertical motion for all of the descending trials and vertical motion was perceived without a switch to horizontal motion for most of the ascending trials.

Perception therefore was *bistable* for the aspect ratio of 1.25 and other aspect ratios near it; both horizontal and vertical motion could be perceived for the same stimulus, the proportion of each depending on the direction of parameter change. As indicated above, this evidence for perceptual hysteresis was obtained under conditions in which potential artifacts of response perseveration and decision/response time were eliminated. Described next is an extension of the modified method of limits, which showed that the hysteresis effects obtained for motion quartets are not an artifact of judgment uncertainty.

5. Judgment Uncertainty

In most psychophysical procedures, observers are required to distinguish between two perceptual alternatives: "Do you perceive the attribute, or not?" or "Do you perceive attribute A or attribute B?" Judgment uncertainty would arise if the observer's percept does not clearly correspond to one of the alternatives.

Hock *et al.* (2005) addressed the issue of judgment uncertainty within the framework of the modified method of limits by comparing ascending and descending trials on the basis of two different response criteria. One criterion was the same as above; observers indicated after each trial whether or not there was a change from one of the specified perceptual alternatives to the other anytime during the trial. For the second criterion, they indicated whether or not their perception of the initial alternative was lost anytime during the trial. The idea was that judgment uncertainty would be indicated if there were an interval during a trial for which an observer's initial percept was replaced by an intermediate percept that could not be confidently judged to be the alternative to the initial percept. The modified method of limits is particularly well suited for this kind of determination. If judgment uncertainty were a factor, trials with a relatively small number of steps would reach parameter values for which the initial percept was lost, but trials with more steps would be required to reach parameter values for which there was a change to the alternate percept. The intermediate percept would occur during the intervening steps.

Hock *et al.* (2005) tested for judgment uncertainty with motion quartets and with stimuli for which observers were required to judge the relative length of independent horizontal and vertical motion paths (Fig. 1(d)–(f)). The variable-duration ascending and descending trials were constructed as in Table 1, with matching aspect ratios for the motion quartets and the stimuli with independent horizontal and vertical motions (the particular values of the aspect ratio were somewhat different than in Hock *et al.* 1993).

A participant's results for judgments of path length are presented separately for ascending and descending trials in Fig. 3(a) and 3(b). It can be seen for the ascending trials that the initial percept ("the horizontal path is longer") was lost for trials with smaller end-point aspect ratios compared with trials for which there was a change to the alternative percept ("the vertical path is longer"). For the descending trials, the initial percept ("the vertical path is longer") was lost for trials with larger end-point aspect ratios compared with trials for which there was a change to the alternative percept ("the horizontal path is longer"). The difference in aspect ratio between the loss of the initial percept and the emergence of the alternative percept indicated the range of aspect ratios for which there was an intermediate percept ("the motion paths are equal in length"), so judgments were uncertain with respect to the specified alternative percepts.

It can be seen in Fig. 3(c) and 3(d) that this was not the case for the motion quartets (all the results in Fig. 3 are for the same participant). Even though the two response criteria were tested during separate blocks of trials, the loss of the initial percept and the change to the alternative percept occurred for the same end-point aspect ratios. There were no aspect ratios for which participants were unsure whether the perceived motion pattern was vertical or horizontal, confirming that the hysteresis effect obtained for motion quartets was indicative of perceptual hysteresis, and was not an artifact of judgment uncertainty due to the occurrence of an intermediate percept (e.g., diagonal motion).

6. Inferences from Trial Duration and Single-Element Apparent Motion

Rather than a true change in perception, it might be argued that observers tested with the modified method of limits were basing their responses on inferences drawn from the duration of each trial ("the trial lasted long enough for the percept to have changed"). For example, they might never perceive switches between horizontal and vertical motion for motion quartets, but nonetheless report that they had occurred more frequently for long duration trials (many parameter steps) than for short duration trials (fewer parameter steps). This possibility has been addressed for motion quartets by Hock *et al.* (1993) and for single element apparent motion by Hock *et al.* (1997). We focus here on the latter because the single-element apparent motion paradigm is closer to the intent of threshold-measuring psychophysical procedures.

Hock *et al.*'s (1997) study was based on a generalized version of a single-element apparent motion stimulus that was similar to a stimulus that previously was described by Johansson (1950). In standard apparent motion, a visual element appears first at one location, and then is shifted discretely to another location (Fig. 4(a)). For generalized apparent motion, elements are simultaneously visible at both locations (Fig. 4(b)). Motion is perceived when luminance contrast decreases at one location and increases at the other. (Standard apparent motion is a special case of generalized apparent motion for which the lower luminance value at each element location corresponds to the luminance of the background.)
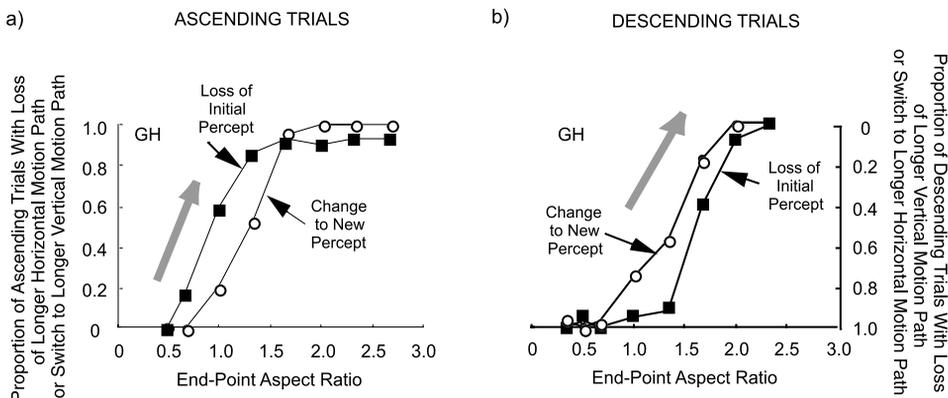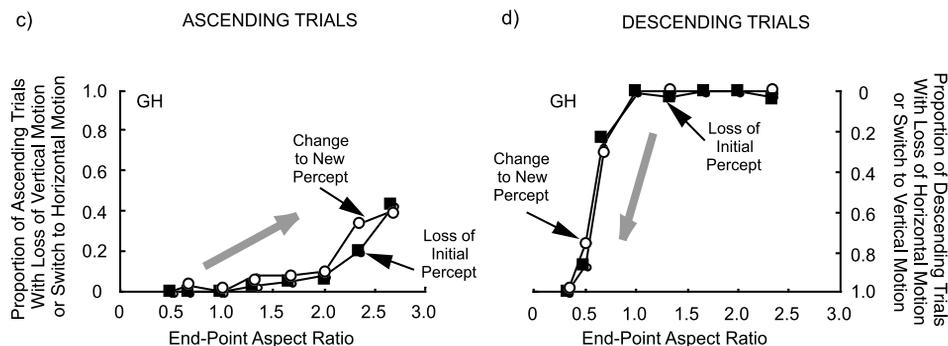
Independent Motion Paths

Figure 3. Results for one of the participants in Hock *et al.*'s (2005) comparison of hysteresis effects for motion quartets and for stimuli with independent vertical and horizontal motion paths. In separate blocks of trials, the participants reported whether or not they 'lost' their initial percept anytime during a trial, or whether or not there was a change to the alternative percept anytime during a trial. The results for these response criteria are reported separately for trials with ascending and trials with descending aspect ratios, for both independent motion paths, (a) and (b), and for motion quartets (c) and (d).

The parameter for the generalized apparent motion stimulus was the background-relative luminance contrast (BRLC), the change in luminance for each element divided by the difference between the element's average luminance and the luminance of the background: the larger the BRLC value, the greater the likelihood that motion will be perceived. Hock *et al.* (1997) created trials with ascending and descending BRLC steps, as per the modified method of limits. Ascending trials began with a BRLC value of 0.1, for which non-motion always was perceived. Descending trials began with a BRLC value of 0.9, for which motion always was perceived. BRLC values were then changed in steps of 0.1 for a variable number of steps. In Hock *et al.*'s (1997) third experiment, 'inferences from trial duration' were elimi-
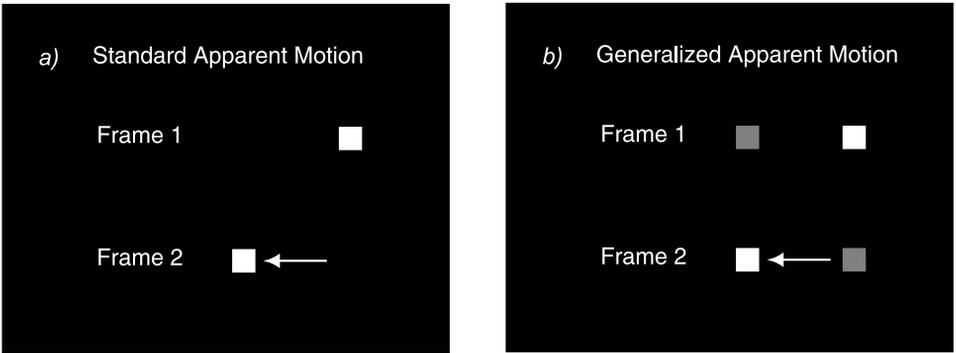
Figure 4. Examples of standard and generalized apparent motion stimuli.

Table 2.

Twelve trials that differ with respect to whether the BRLC values for sequences of single element apparent motion stimuli that are ascending or descending, and differ as well with respect to their end-point BRLC value

Ascending trials								
0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.2
0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.3
0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.3	0.4
0.1	0.1	0.1	0.1	0.1	0.2	0.3	0.4	0.5
0.1	0.1	0.1	0.1	0.2	0.3	0.4	0.5	0.6
0.1	0.1	0.1	0.2	0.3	0.4	0.5	0.6	0.7
0.1	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8
0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9

Descending trials								
0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.8
0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.8	0.7
0.9	0.9	0.9	0.9	0.9	0.9	0.8	0.7	0.6
0.9	0.9	0.9	0.9	0.9	0.8	0.7	0.6	0.5
0.9	0.9	0.9	0.9	0.8	0.7	0.6	0.5	0.4
0.9	0.9	0.9	0.8	0.7	0.6	0.5	0.4	0.3
0.9	0.9	0.8	0.7	0.6	0.5	0.4	0.3	0.2
0.9	0.8	0.7	0.6	0.5	0.4	0.3	0.2	0.1

nated as a potential artifact by constructing trials with equal duration but different end-point BRLC values. This was done by repeating the first BRLC value in the series an appropriate number of times, as indicated in Table 2.

The frequency with which the initial motion percept switched to non-motion (descending trials) and the initial non-motion percept switched to motion (ascending trials) was graphed as a function of each trial's end-point BRLC value. A participant's hysteresis effect is presented in Fig. 5. It can be seen that the frequency with
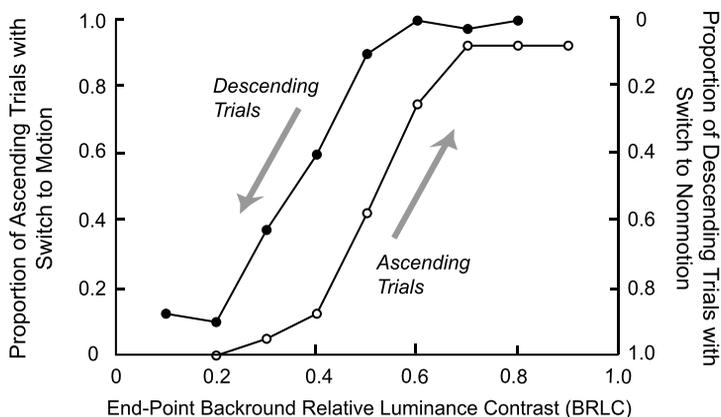
Figure 5. Hysteresis effect observed by gradually increasing or gradually decreasing the background relative luminance contrast (BRLC) for a participant in Hock *et al.*'s (1997) third experiment. The proportion of trials with switches from the perception of motion to the perception of nonmotion, and *vice versa*, are graphed as a function of the BRLC value at which each ascending or descending sequence of BRLC values ends. (Note the inversion of the axis on the right.)

which there were switches during trials with a particular end-point BRLC value was different, depending on whether that aspect ratio was preceded by an ascending (vertical axis on the left side of the graph) or a descending sequence of BRLC values (the *inverted* vertical axis on the right side of the graph). For example, when the end-point BRLC value was 0.5, motion continued to be perceived without a switch to non-motion for 90% of the descending trials, and non-motion continued to be perceived without a switch to motion for 58% of the ascending trials. Perception therefore was bistable for this BRLC value and other BRLC values near it; both motion and non-motion could be perceived for the same stimulus, the proportion of each depending on the direction of parameter change. It was thus confirmed that the hysteresis effect obtained for single-element apparent motion was indicative of perceptual hysteresis, and was not an artifact of 'inferences from trial duration'.

7. Near-Threshold Neural Dynamics

The perceptual hysteresis effect described above indicates that there are two stable activation states possible for the motion detectors stimulated by generalized apparent motion stimuli, one suprathreshold (motion is perceived) and the other subthreshold (motion is not perceived). Because of this stabilization of near-threshold activation, motion and non-motion percepts both can occur for the same stimulus (bistability), and both can resist random fluctuations and stimulus changes that would result in frequent switches between them.

7.1. Why Stabilization Is Necessary

Whether an individual detector is activated by a stimulus or not, a random perturbation will with equal probability increase or decrease its activation. Assume it

increases activation. The next and all following random perturbations will again with equal probability increase or decrease activation. For unconstrained sequences of perturbations that by chance resulted in more increases than decreases, activation would drift toward higher levels. Similarly, for unconstrained sequences of perturbations that by chance resulted in more decreases than increases in activation, activation would drift toward lower activation levels. Although the steady-state, mean activation would remain the same, the variance of the activation would increase indefinitely over time were it not constrained by stabilization mechanisms intrinsic to individual neurons. Such mechanisms would resist random changes in activation that would move activation away from the neuron's steady-state level by 'pushing' activation back toward the mean, steady-state value. The biophysics of ion flows through neural membranes provides a mechanism through which this stabilization of neural activation could be achieved (Trappenberg, 2002).

Nonetheless, neural stability does not guarantee perceptual stability. When an appropriate stimulus is presented, detector activation increases from no-stimulus, resting states toward stimulus-determined, steady-state values. The changing activation values are continuously stabilized by change-resistant neural mechanisms, as described above. If, however, activation settles at a value close to the read-out threshold (which determines whether or not there is sufficient detector activation for an attribute to be perceived), random fluctuations would rapidly shift activation back and forth across the threshold (Fig. 6(a)). This would render perception highly unstable and uncertain, despite the neural stabilization of activation. Such perceptual instability and uncertainty might occur for some stimulus attributes, but it does not occur for others. For example, either stable motion or stable non-motion is clearly perceived for generalized single-element apparent motion stimuli, with minimal uncertainty (Hock *et al.*, 1997).

7.2. Detection Instability

The stabilization of activation at suprathreshold levels for stimulus values that would otherwise have brought activation close to the read-out threshold is made possible by the connectivity of detectors, and in particular, by virtue of activation passing through a detection instability (Bicho *et al.* 2000; Johnson *et al.*, 2009; Schneegans and Schöner, 2008; Schöner, 2008). The principle is that when a stimulus is presented for which an ensemble of detectors with similar selectivity is responsive, the activation of the detectors rises from their no-stimulus resting level until a level is reached for which their activation is boosted by self-excitation; i.e., *via* mutual excitatory interactions within the ensemble, and/or excitatory feedback from higher-level detectors. Crossing such a self-excitation threshold results in detection instability; i.e., unstabilized, transient changes in activation that rapidly raise it to steady-state levels that are well above the read-out threshold (Fig. 6(b)). In signal detection terms (Green and Swets, 1966), the read-out threshold would correspond to the criterion, and the increased detector activation that results from passing through the detection instability would increase the detectability of a near-threshold
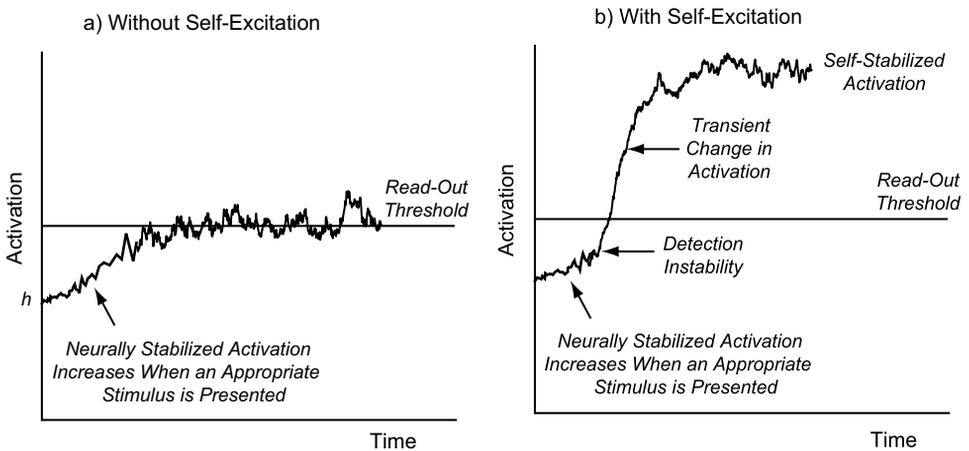
Figure 6. Illustration of detector activation increasing from its no-stimulus resting level (h) upon the presentation of a stimulus attribute to which it responds. The increasing activation is stabilized by intrinsic neural mechanisms. Panel (a) illustrates why perception would be unstable if the steady-state activation value were near the read-out threshold for the detector, which determines whether or not there is sufficient activation for the stimulus attribute to be perceived. Panel (b) illustrates the transient increase in detector activation (i.e., the detection instability) that would result from activation crossing a self-excitation threshold, with activation stabilizing at a level that is well above the read-out threshold.

attribute by decreasing the overlap of the signal-plus-noise with the noise-alone distribution.

7.3. A Dynamical Model

The effect of detection instability on near-threshold perception for generalized apparent motion is illustrated with a simplified feedforward/feedback model (Fig. 7). The stimulus, which was discussed in the preceding section, is depicted in Fig. 4(b). In the model, leftward and rightward motion detectors are alternately activated by the back-and-forth apparent motion stimulus. When activation for either reaches a threshold level, it feeds forward to a bidirectional 'horizontal motion' detector, which is activated by both leftward and rightward motion signals. (Cortical neurons with either unidirectional or bidirectional selectivity are found in Areas V1 and MT; Albright, 1984; Felleman and Kaas, 1984.) Excitatory feedback from the bidirectional horizontal detector closes the loop, adding activation to both the leftward and rightward motion detectors that boosts their activation well over the threshold level required for their perception (see Note 2).

The coupled dynamical equations that determine how activation evolves over time for the three detectors are presented in the Appendix. The equations for the leftward and rightward detectors indicate, at each moment in time, how their activation (u_L and u_R) will change in the immediate future, as determined by whether du_L/dt and du_R/dt are positive or negative. Whether activation will increase or decrease, and by how much, depends on the detectors' current level of activation,
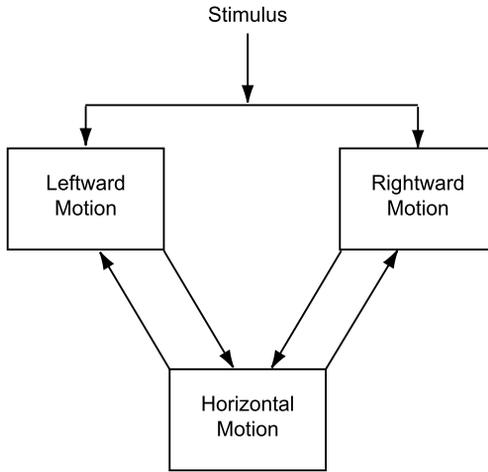
Figure 7. A feedforward/feedback model implementing detection instability. It is composed of unidirectional leftward and rightward motion detectors whose stimulus-initiated activation, if greater than 0, feeds forward to a bidirectional horizontal motion detector. Excitatory feedback from the horizontal to the leftward and rightward detectors boosts their activation.

the level of stimulus-initiated activation relative to their no-stimulus resting level, the feedback that is received from the bidirectional horizontal detector, and random noise. How the activation of the bidirectional horizontal detector (u_H) will change in the immediate future will likewise depend on whether du_H/dt is positive or negative, as determined by its current level of activation, the input it receives from the leftward and rightward motion detectors relative to its no-stimulus resting level, and random noise.

With these recursive increases and decreases, the activation levels of the three detecting units evolve over time until they settle at steady-state values for which all remaining changes in activation are due to random fluctuations. This occurs when du_L/dt, du_R/dt, and du_H/dt are approximately equal to 0. The model generates motion-perceived signals when the steady-state activation values for the leftward and rightward detectors exceed the read-out threshold, which is set at 2. Whether or not motion is perceived then depends on the extent to which activation exceeds this threshold relative to the level of noise in the decision process.

Feedforward from the leftward and rightward detectors to the bidirectional horizontal detector occurs in the model only when leftward or rightward activation is greater than the self-excitation threshold of 0. This nonlinear excitatory interaction is immediately followed by the feedback of excitation from the horizontal to the leftward and rightward detectors. The feedback also is nonlinear. It is implemented in the model with a Naka–Rushton equation (Naka and Rushton, 1966) that approximates a step function; i.e., there is no feedback when there is no feedforward activation, and the amount of feedback is the same for all input activation values greater than 0.1 (the latter prevented activation levels from soaring as a result of the closed feedforward/feedback loop being excitatory) (see Note 3).

In the four simulations that follow, the temporally evolving activation states for the leftward, rightward, and horizontal detectors were determined for trials composed of eight back-and-forth frames. With the exception of differences in the stimulus-initiated activation of the directionally selective leftward and rightward motion detectors, the model parameters were the same for all the simulations.

7.4. Simulations 1 and 2: Near-Threshold Perception without and with Feedback

The stimulus-initiated activation of the leftward and rightward detectors was $S = 10.5$ for Simulation 1, so with a no-stimulus resting level of $h = -8$, and in the absence of feedback, steady-state leftward and rightward activation values were reached at $u_L = u_R = S + h = 2.5$ (Fig. 8(a)). Although this stabilized activation is just above the read-out threshold of 2, low signal-to-noise ratios in the decision process would sometimes result in motion-perceived decisions and sometimes result in motion-not-perceived decisions.

Feedback was introduced in Simulation 2 (stimulus-initiated activation was the same as in Simulation 1). Because the stimulation of the leftward and rightward detectors was sufficient for their activation to exceed the self-excitation threshold of 0, the feedforward/feedback loop was engaged. The resulting detection instability led to the stabilization of activation for the leftward and rightward detectors at a steady-state value of 8.5 (the feedback excitation was 6), well above the read-out threshold level for perception (Fig. 8(b)). With the noise level in the decision process the same as in Simulation 1, the higher signal-to-noise ratio would much more consistently result in motion-perceived decisions.

7.5. Simulation 3: Bistability

The feedforward/feedback loop is activated when the activation of leftward or rightward detectors exceeds the self-excitation threshold, but because of random fluctuations in activation, crossing this threshold can occur for values of stimulus-initiated activation that would, without feedback, result in activation levels less than 0. Random changes in activation occur once every millisecond in the model, so for motion signals nominally lasting for 200 ms, there were 200 opportunities per frame for the occurrence of a threshold-crossing random fluctuation. When such a fluctuation occurs, the feedforward/feedback loop is engaged and activation is transiently boosted to values well above the read-out threshold for perception. When a sufficiently large fluctuation does not occur, the leftward and rightward motion detectors remain stabilized at an activation level that is subthreshold for perception.

This bistability was demonstrated in Simulation 3 for a stimulus-initiated activation of $S = 7$ (Fig. 9). Within the same trial, activation initially was stabilized below the read-out threshold at $u_L = u_R = -1$. Later in the trial, there was a random fluctuation large enough for activation to cross the self-excitation threshold, and there was a switch to activation levels that were well above the read-out threshold ($u_L = u_R = 5$).
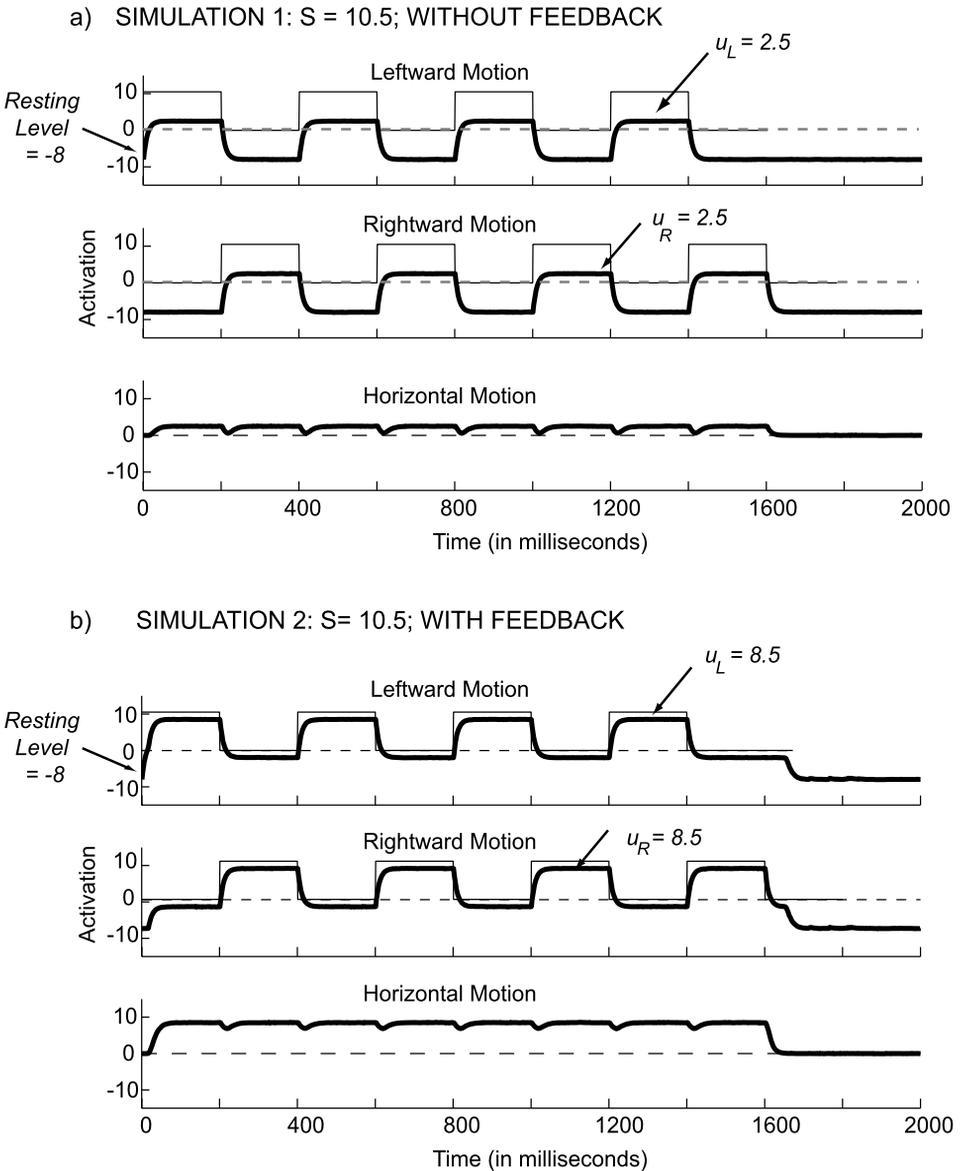
Figure 8. (a) Simulation 1: single trial simulation without feedback for stimulus-initiated activation ($S = 10.5$) that just exceeds the read-out threshold ($u = 2$), which determines whether there is sufficient detector activation to signal the perception of motion. (b) Simulation 2: single trial simulation for the same stimulus, but with feedback from the bidirectional horizontal motion detector boosting the activation of the unidirectional leftward or rightward motion detectors. This occurs when the stimulus-initiated activation of the leftward or rightward detectors is sufficient for activation to pass through a detection instability (the feedforward/feedback loop is engaged when the activation of the leftward or rightward detector exceeds the threshold for self-excitation ($u = 0$ in these simulations).
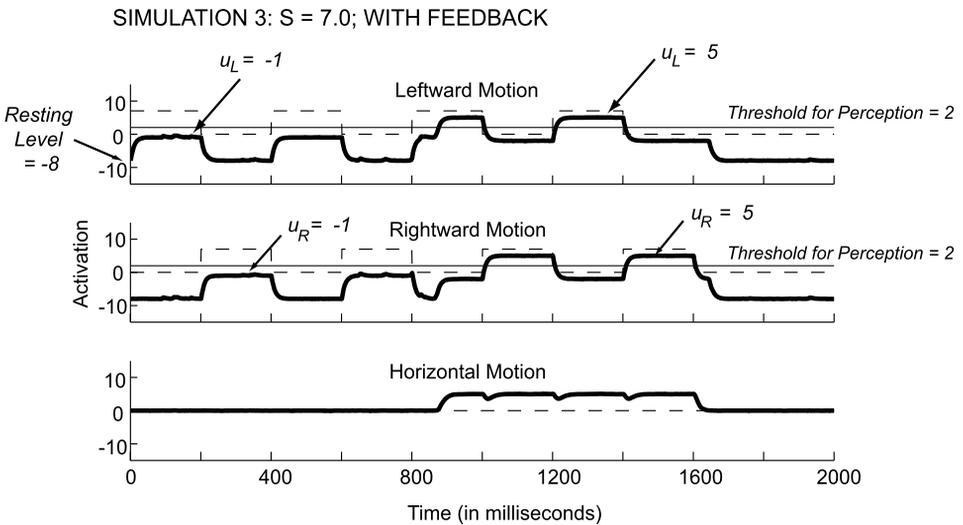
Figure 9. Simulation 3: single trial simulation for stimulus-initiated activation ($S = 7.0$) that would be insufficient to engage the feedforward/feedback loop (as was the case during the first part of the simulated trial) were it not for random fluctuations in activation that crossed the self-excitation threshold for a detection instability (as occurred during the second part of the simulated trial).

7.6. Simulation 4: Perceptual Hysteresis

The final simulation brings this article back to its beginning, where it was argued that the elimination of various artifacts in the classical method of limits could reveal the presence of perceptual hysteresis. Simulation 4 (Fig. 10) showed that neural feedback can produce perceptual hysteresis. Descending trials began with stimulus-initiated activation values that were well above and were gradually decreased to where they were well below the self-excitation threshold for the perception of motion. The opposite was the case for the ascending trials. The presence of hysteresis was indicated in the model by perception for stimulus-initiated activation values of $S = 5, 6$, and 7 depending on their immediately preceding perceptual history. That is, the perception of motion was signaled for these stimulus activation values when activation was above the self-excitation threshold during the preceding frames (descending trials), but not when activation was below the self-excitation threshold during the preceding frames (ascending trials).

8. Conclusion

When an attribute is presented for which an ensemble of detectors with similar selectivity is responsive, activation will increase for each detector at a rate determined by its intrinsic neural stabilization mechanism. It will settle at a steady-state level below the read-out threshold for weak attribute values and above the read-out threshold for strong attribute values. For intermediate values, steady-state activa-
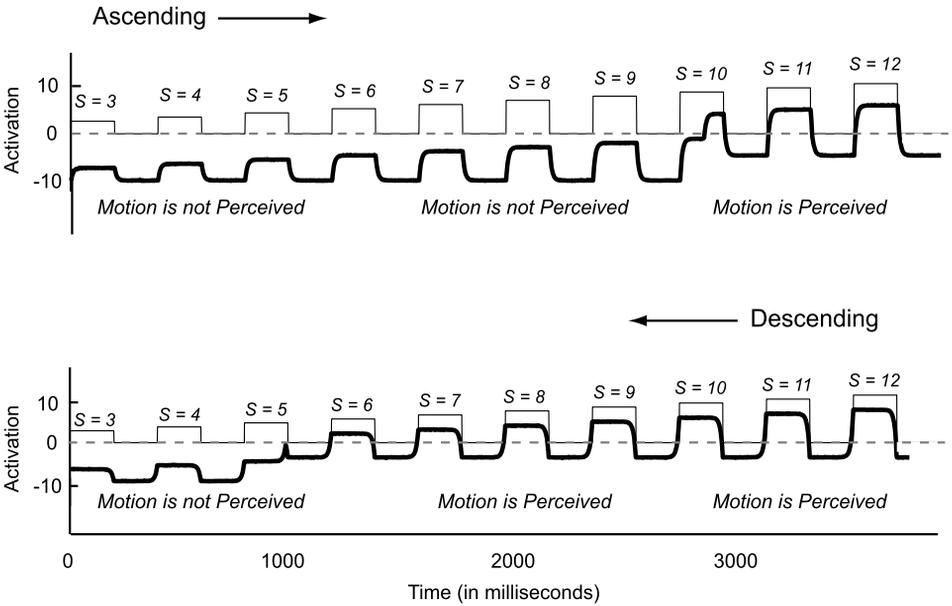
SIMULATION 4: WITH FEEDBACK

Figure 10. Simulation 4: single trial simulations for an ascending trial composed of a sequence of frames with increasing stimulus-initiated activation, and for a descending trial composed of a sequence of frames with decreasing stimulus-initiated activation. Hysteresis occurs when stimulus-initiated activation of the leftward or rightward detectors has crossed the self-excitation threshold of $u = 0$ and engages (ascending trials) or disengages (descending trials) the feedforward/feedback loop. It is indicated for end-point attribute values of $S = 6, 7, 8$ and 9. Whether motion or nonmotion is perceived for these attribute values depends on the activational history that precedes their presentation i.e., motion is perceived when these attribute values are encountered during descending trials, and nonmotion is perceived when these attribute values are encountered during ascending trials. This is shown only for the leftward motion. The same result is obtained for rightward motion, which is not shown.

tion will lie near the read-out threshold, where in the absence of a self-excitation induced detection instability, perception of the attribute is uncertain. This description is characteristic of classical psychophysics; detectors function independently and their cumulative effect is well characterized by signal detection theory (Green and Swets, 1966).

What sets the dynamical approach apart is what happens when stimulus-initiated activation reaches a level that engages excitatory feedforward/feedback loops and/or within-ensemble excitatory interactions. The stimulated detectors would then become functionally integrated, and each detector's activation would be transiently boosted to levels that exceed the read-out threshold. As a result of such detection instabilities, near-threshold perception can be clear and distinct, even for attribute values for which the alternatives are perceived equally frequently (motion and non-motion in our example), and non-artifactual perceptual hysteresis can be

observed for near-threshold attribute values when using the modified method of limits.

To be sure, there may be many stimuli for which the classical rather than the dynamical account pertains; e.g., the detection of dim light. For such stimuli, perceptual hysteresis would not be expected when potential artifacts due to response perseveration, decision/response time, and inferences from trial duration are eliminated by using the modified method of limits. In addition, evidence for judgment uncertainty would be expected for such stimuli, as per the 'two response criteria' methodology that could be used along with the modified method of limits.

In conclusion, there are two conceptually important implications of observing artifact-free perceptual hysteresis for near-threshold stimuli. The first is the indication it gives that individual detectors that would otherwise function independently can be organized into functional units when stimulus-initiated activation is sufficient to engage either feedforward/feedback loops or mutual excitatory interactions within ensembles of stimulated detectors. The second implication concerns the traditional definition of the threshold as a relatively arbitrary read-out criterion that determines whether or not there is sufficient detector activation for an attribute to be perceived. The neural dynamic account of perceptual hysteresis includes such a read-out threshold, but in addition, specifies a threshold for excitatory interaction that must be reached in order for feedforward/feedback loops and ensemble interactions to create an activational gap that enhances discrimination between alternative perceptual states. In contrast with the read-out threshold, or criterion, the self-excitation threshold is directly involved in the processing of near-threshold stimuli.

Notes

1. The parameter that is varied when using the method of limits need not correspond to the to-be-perceived attribute. For example, the size of the change in element luminance could be the varied parameter, and motion could be the to-be-perceived attribute, as illustrated for generalized apparent motion stimuli in Fig. 4(b).

2. A more complete model would include mutually inhibitory interactions among the leftward and rightward detectors to reflect the fact that they are generally not perceived simultaneously across the same space, as might occur (but does not) for counterphase sine gratings (Levinson and Sekuler, 1975). These interactions are not a factor in the current simulations because the opposing directions are never simultaneously stimulated.

3. Activation in a closed feedforward/feedback loop also can be prevented from soaring by the addition of delayed inhibitory interactions.

References

Albright, T. D. (1984). Direction and orientation selectivity of neurons in visual area MT of the macaque, *J. Neurophysiol.* **52**, 1106–1130.

Bicho, E., Mallet, P. and Schöner, G. (2000). Target representation on an autonomous vehicle with low-level sensors, *Intl J. Robotics Res.* **19**, 424–447.

Boring, E. G. (1942). *Sensation and Perception in the History of Experimental Psychology*. Appleton-Century-Crofts, New York, USA.

Braitenberg, V. (1978). Cortical architechtonics: general and areal, in: *IBRO Monograph Series, Architectonics of the Cerebral Cortex, 3*, Brazier, M. A. B. and Petsche, H. (Eds), pp. 443–466. Raven Press, New York, USA.

Fechner, G. T. (1860). *Elemente der Psychophysik (Elements of Psychophysics)*. Trans. Adler, H. E. Holt, Rinehart and Winston, New York, USA.

Felleman, D. J. and Kaas, J. H. (1984). Receptive field properties of neurons in middle temporal visual area (mt) of owl monkeys, *J. Neurophysiol.* **52**, 488–513.

Felleman, D. J. and Van Essen, D. C. (1991). Distributed hierarchical processing in primate visual cortex, *Cerebral Cortex* **1**, 1–47.

Fender, D. and Julesz, B. (1967). Extension of Panum's fusional area in binocularly stabilized vision, *J. Optic. Soc. Amer.* **57**, 819–830.

Girard, P., Húpe, J. M. and Bullier, J. (2001). Feedforward and feedback connections between areas V1 and V2 of the monkey have similar rapid conduction velocities, *J. Physiol.* **85**, 1328–1331.

Gori, S., Giora, E. and Pedersini, R. (2008). Perceptual multistability in figure-ground segregation using motion stimuli, *Acta Psychologica* **129**, 399–409.

Green, D. M. and Swets, J. A. (1966). *Signal Detection Theory and Psychophysics*. Wiley, New York, USA.

Hock, H. S., Bukowski, L., Nichols, D. F., Huisman, A. and Rivera, M. (2005). Dynamical *vs* judgmental comparison: hysteresis effects in motion perception, *Spatial Vision* **18**, 317–335.

Hock, H. S., Kelso, J. A. S. and Schöner, G. (1993). Bistability and hysteresis in the organization of apparent motion patterns, *J. Exper. Psychol.: Human Percept. Perform.* **19**, 63–80.

Hock, H. S., Kogan, K. and Espinoza, J. K. (1997). Dynamic, state-dependent thresholds for the perception of single-element apparent motion: bistability from local cooperativity, *Perception and Psychophysics* **59**, 1077–1088.

Hock, H. S. and Ploeger, A. (2006). Linking dynamical decisions at different levels of description in motion pattern formation: psychophysics, *Perception and Psychophysics* **68**, 505–514.

Hock, H. S. and Schöner, G. (2010). A neural basis for perceptual dynamics, in: *Nonlinear Dynamics in Human Behavior*, Jirsa, V. and Huys, R. (Eds). Springer Verlag, Berlin, Germany.

Hock, H. S., Schöner, G. and Giese, M. (2003). The dynamical foundations of motion pattern formation: stability, selective adaptation, and perceptual continuity, *Perception and Psychophysics* **65**, 429–457.

Johansson, G. (1950). *Configurations in Event Perception*. Almqvist and Wiksells Boktryckeri AB, Uppsala, Sweden.

Johnson, J. S., Spencer, J. P. and Schöner, G. (2009). A layered neural architecture for the consolidation, maintenance, and updating of representations in visual working memory, *Brain Research* **1299**, 17–32.

Kloeden, P. E. and Platen, E. (1992). *Numerical Solution of Stochastic Differential Equations*. Springer-Verlag, Berlin.

Levinson, E. and Sekuler, R. (1975). The independence of channels in human vision selective for direction of movement, *J. Physiol.* **250**, 347–366.

Movshon, J. A. and Newsome, W. T. (1996). Visual response properties of striate cortical neurons projecting to area MT in macaque monkeys, *J. Neurosci.* **16**, 7733–7741.

Naka, K. I. and Rushton, W. A. (1966). S-potentials from colour units in the retina of fish, *J. Physiol.* **185**, 584–599.

Schneegans, S. and Schöner, G. (2008). Dynamic field theory as a framework for understanding embodied cognition, in: *Handbook of Cognitive Science: An Embodied Approach*, Calvo, P. and Gomila, T. (Eds), pp. 241–271. Elsevier, The Netherlands.

Schöner, G. (2008). Dynamical systems approaches to cognition, in: *Cambridge Handbook of Computational Cognitive Modeling*, R. Sun (Ed.), pp. 101–126. Cambridge University Press, Cambridge, UK.

Trappenberg, T. P. (2002). *Fundamentals of Computational Neuroscience*. Oxford University Press, Oxford, UK.

Williams, D., Phillips, G. and Sekuler, R. (1986). Hysteresis in the perception of motion direction as evidence for neural cooperativity, *Nature* **324**, 253–255.

Wilson, H. R. (1999). *Spikes, Decisions and Actions: Dynamical Foundations of Neuroscience*. Oxford University Press, Oxford, UK.

Woodworth, R. S. and Schlosberg, H. (1938). *Experimental Psychology*. Holt, Rhinehart and Winston, New York, USA.

Appendix

The dynamical model for the perception of single-element apparent motion is composed of three coupled stochastic differential equations representing the activational states for the unidirectional leftward and rightward detectors (u_L and u_R), and the bidirectional horizontal detector (u_H). The equations are as follows:

$$\tau \frac{\mathrm{d}u_L}{\mathrm{d}t} = -u_L + h_{uni} + S_L(t) + \omega \cdot \sigma(u_H) + q \cdot \xi(t),$$

$$\tau \frac{\mathrm{d}u_R}{\mathrm{d}t} = -u_R + h_{uni} + S_R(t) + \omega \cdot \sigma(u_H) + q \cdot \xi(t),$$

$$\tau \frac{\mathrm{d}u_H}{\mathrm{d}t} = -u_H + h_{bi} + \Gamma(u_L) + \Gamma(u_R) + q \cdot \xi(t),$$

where τ determines the time scale of activation change, h_{uni} is the no-stimulus resting level of the unidirectional detectors, h_{bi} is the resting level of the bidirectional detector, and q is the strength of the additive Gaussian white noise, $\xi(t)$. The above equations are written somewhat differently by mathematicians. 'dt' is shifted to the right side of the equations and $\xi(t)$ is replaced by 'dW', where 'W' denotes a Wiener process; i.e., Brownian motion. Its differentiation leads to white noise stochastic perturbations.

The stimulus-initiated activation is $S_L(t)$ for leftward motion, and alternating with it, $S_R(t)$ for rightward motion. Feedback from the bidirectional horizontal detector to the unidirectional detectors is $\omega \cdot \sigma(u_H)$, where ω denotes the maximum strength of the excitatory feedback and $\sigma(u_H)$ denotes a Naka–Rushton equation

(Naka and Rushton, 1966) approximating a step function that begins at the self-excitation threshold of 0:

$$\sigma(u_H) = \frac{(u_H - 0)^4}{(0 - 0.05)^4 + (u - 0.05)^4} \quad \text{for } u \geqslant 0; \qquad \sigma(u_H) = 0 \quad \text{for } u < 0.$$

The feedforward input from the leftward and rightward motion detectors to the bidirectional horizontal detector is determined by ramp functions restricted to positive activation levels, as follows:

$$\Gamma(u_L) = u_L \quad \text{and} \quad \Gamma(u_R) = u_R \quad \text{for } u_L \geqslant 0 \text{ and } u_R \geqslant 0;$$

$$\Gamma(u_L) = \Gamma(u_R) = 0 \quad \text{for } u_L < 0 \text{ and } u_R < 0.$$

The time varying stimulus-initiated activations for the leftward and rightward motion detectors (S_L and S_R) are present during alternating 200 millisecond frames. In Simulations 1 and 2, $S_L = S_R = 10.5$. In Simulation 3, $S_L = S_R = 7.0$. In Simulation 4, the ascending trial begins with $S_L = S_R = 3$ and increases in steps of 1 until $S_L = S_R = 12$. The reverse is the case for the descending trial. All simulations are otherwise based on the same set of parameters: $\tau = 10$ ms, $h_{uni} = -8$, $h_{bi} = -2$, and $q = 0.008$. The excitatory strength for the feedback is $\omega = 6$, except when feedback is excluded in Simulation 1 (when $\omega = 0$). The read-out threshold is 2. Motion is signaled when the activation of the leftward or rightward motion detectors exceeds this value.

The numerical integration used the forward Euler procedure for stochastic differential equations (see Kloeden and Platen (1992), chapter 10).