

# Dynamic Effects in Real-Time Responses of Motion Sensitive Neurones

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## 1. Adaptation to motion

Bialek et al. (1991) put the theme of the present part on encoding dynamic information very succinctly: "Traditional approaches to neural coding characterize the encoding of known stimuli in average neural responses. Organisms face nearly the opposite task-extracting information about an unknown time-dependent stimulus from short segments of a spike train". Warzecha and Egelhaaf review their elegant experiments dealing with these difficult and topical issues. This article is intended to complement their efforts by reviewing literature and ideas that their work has made important again with a particular focus on adaptive effects.

Neural systems adapt, changing their behaviour according to the recent stimulus history. In the human it is clear that adaptive gain control mechanisms are at work. For example, human observers show a Weber fraction of about 5 to 7% for discriminating image velocity and this is maintained even in the face of quite large random fluctuations of image contrast and temporal frequency (McKee et al. 1986). That is to say in this process gain is regulated to maintain a just noticeable difference of about 5% of the mean velocity. Cats display a similar characteristic of velocity discrimination, albeit with larger Weber fractions (Vandenbussche et al. 1986).

The H1 neurone of flies shows large adaptive changes in the gain, and temporal resolution for the processing of image oscillations. The rate at which new adapted states are obtained is primarily determined by the temporal frequency content of moving images rather than the contrast of the images or their velocity (Maddess and Laughlin 1985), although at low speeds velocity may be more important (de Ruyter van Steveninck et al. 1986). Similar results are found for the human adaptation to image motion (Lorenceau 1987), in cat striate visual cortex (Maddess et al. 1988; Maddess and Vidyasagar 1992; Giaschi et al. 1993), in

optomotor neurones of wallabies (Ibbotson et al. 1998) and butterflies (Maddess et al. 1991). Insect optomotor responses also show adaptive gain control effects (Kirschfeld 1989) as do human ocular following responses (Maddess and Ibbotson 1992; Ibbotson and Maddess 1994).

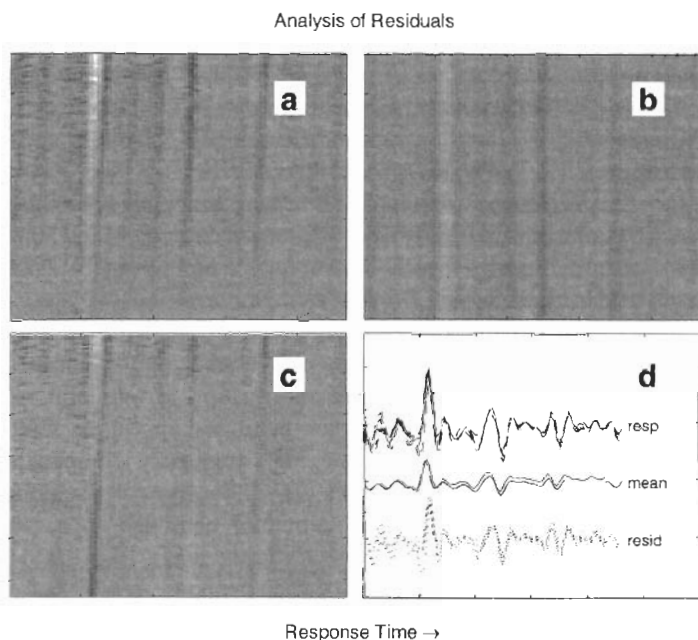
The lack of dependence shown by most of the motion adapting mechanisms mentioned above upon variables such as luminance contrast and response rate is understandable: changes of motion sensitivity should not be based upon information that cannot be reliably attributed to image motion. Low-level biological motion computation is believed to be based on cross-correlation between samples along a baseline (Reichardt 1961; Emerson et al. 1992), a computation that does not yield velocity per se. Thus, the best such a system could do perhaps is to base its adaptation upon signals within an ecologically interesting range of flicker frequencies induced by image motion.

## 2. Real-time assessment of neural responses

Warzecha and Egelhaaf (this volume) introduce several interesting ways of assessing real-time neuronal responses. Extracting the spike variance as a function of mean spike count within a narrow window (their Fig. 4) indicates that the spike process that is modulated by image motion is non-Poisson. Previous authors have reported H1 responses to less natural stimuli to be not independent of stimulus history (Mastebroek 1974; Gestri et al. 1980). Warzecha and Egelhaaf use an ideal observer model looking at spike rates to assess the neurone's ability to recognize a step in retinal slip and the time needed to detect motion, and to determine the number of stimulus states that can be discriminated by the neuronal response (their Fig. 8). Bruckstein et al. (1983) have shown that decoding the motion signal from the response was greatly improved when prior knowledge about the dynamics of changes in the modulated spike process is included. Evolution could have given the fly optomotor system that is post-synaptic to H1 such knowledge, so that the estimated performance of H1 and H2 as assessed by the ideal observer models of Warzecha and Egelhaaf may represent a lower bound on actual performance.

A third innovation is what Warzecha and Egelhaaf term the Stimulus Induced Response (SIR). Their SIR is the mean neuronal response obtained to many repeated presentations of the same velocity modulation. The authors subtract the SIR from the responses to each trial and describe the resultant residuals as the noise in the system (their Fig. 6). The mean response, however, may not in all cases be a good model of the neuronal response. For example the spike generation process itself may be changing as a function of response rate (see also Mastebroek 1974; Gestri et al. 1980). Even in a stationary system the median response for each time bin might be a better indicator of central tendency than the mean, if the distribution of spike intervals is non-Gaussian.

Figure 1 illustrates another example in which the mean SIR model would not be suitable. Figure 1a shows model responses of an elementary motion detector based on a conventional correlation mechanism (Reichardt 1961). The model has a DC component in one of its two inputs, giving a mixture of response components at the fundamental and second harmonic of the input drift frequency, that have been found experimentally (Ibbotson et al. 1991). Independent noise is added to both inputs. Horizontal slices across figure 1a represent responses to single presentations. A simple exponential adaptive process is included where the time constant of a low pass filter located after the motion computation stage decreases linearly over time. Thus, the response to a velocity impulse declines rapidly at first and then more slowly on subsequent trials. The change in filter characteristics also results in phase shifts shown as a tilt away from the vertical in the stripes of figure 1a. It is worth noting that the only critical feature for the present demonstration is the adaptation: the noise, the DC response component and the phase shifts are only introduced to make the model responses more realistic.



**Fig. 1** Analysis of the residuals from a mean SIR model. **a** Model responses of an H1 neurone to a moving periodic grating pattern. The moving grating stimulus is repeated many times (top to bottom) and the responses to each repeated stimulus are shown as horizontal image rows. Brighter regions indicate higher spike (response) rates. Responses slowly decline with stimulus repetition due to adaptation. The abscissa, ordinate and grey scale are the same in **b**, showing the mean response of the SIR model (see text), and **c** showing considerable response components rather than just noise in the residuals from the SIR model. **d** (*resp*) The first 5 response rows from the top of (a); (*mean*) the mean across trials in (a) used to create (b); (*resid*) the first 5 rows of the residuals of (c). The three sets of waveforms are displaced vertically by arbitrary amounts to aid viewing but are otherwise at the same scale.

Figure 1b is the mean of the responses across trials of figure 1a, reproduced repeatedly (vertically) to illustrate what an unchanging SIR would be like. Figure 1c shows the residuals obtained by subtracting figure 1b from figure 1a. Clearly the residuals in this case are not merely noise but contain a considerable amount of the response.

Such an effect may be modest in the data of Warzecha and Egelhaaf given that they interposed rest periods within each trial of their repeated 2.5 to 5 s motion stimuli but the actual adaptation rate will depend on the particular stimulus. Clearly, these types of issues will need to be addressed for continuous stimulation: long term changes in gain having been described even in the earliest recordings from motion sensitive insect neurones (Collett and Blest 1966). It has been demonstrated formally for the H1 neurone that consideration of epochs around 8 s (McCann 1974) is required to characterize adaptive changes.

This adaptation to image motion that changes not only the gain but also the temporal frequency tuning of neurones is indicated by responses to velocity impulses in H1 of flies (Zaagman et al. 1983; Maddess and Laughlin 1985; de Ruyter van Steveninck et al. 1986; Borst and Egelhaaf 1987) and those of visual interneurones in other insects (Maddess et al. 1991). When highly adapted the cells not only encode progressively higher image oscillation frequencies, but may also shift to encoding acceleration rather than velocity (Maddess and Laughlin 1985; Maddess et al. 1991; see also Shi and Horridge 1991).

The prospect of adapted optomotor neurones encoding something akin to acceleration is also foreshadowed by the comment of Warzecha and Egelhaaf that H1 responses contain higher temporal derivatives of the input (see also Egelhaaf and Reichardt 1987; Egelhaaf and Borst 1989). Nonlinear control systems generally have to deal with higher temporal derivatives (e.g. Dunstan and McRuer 1961). This may seem at odds with the data of Warzecha and Egelhaaf indicating that fly responses do not contain reliable information at temporal frequencies much above 30 Hz because, as optomotor neurones appear to shift towards encoding acceleration with adaptation, the high frequency components of the response are relatively larger (Maddess et al. 1991). For example, velocity impulse responses from some adapted butterfly optomotor neurones appear to encode information about image oscillation frequencies in the range 10 to 100 Hz. When unadapted the same neurones have most of their response power below 10 Hz. Overall, it would be surprising if flying insects did not make use of the 200 Hz bandwidth of their photoreceptors (Howard et al. 1984) to control their flight. Warzecha and Egelhaaf use conventional Fourier analyses where the average frequency content over the whole signal epoch is computed. A wavelet-like approach (e.g. Gabor 1946) might reveal significant short periods of high frequency response fluctuations. Such approaches permit short bursts of high frequency activity to be quantified where a normal Fourier approach, that looks at average frequency content, generates misleading results.

At the same time it should be recalled that Warzecha and Egelhaaf found that above 30 Hz the signal power was less than that of the noise under their test

conditions. We did not examine the signal to noise ratio measured in highly adapted conditions where average responses appear to encode acceleration (Maddess and Laughlin 1985; Maddess et al. 1991). As stated at the outset animals do not get the chance to examine their average response to hundreds of presentations when navigating in the visual environment. Thus, our data should not be taken as refuting the findings of Warzecha and Egelhaaf, and more experiments are needed to determine the exact effects of adaptation and its significance to real-time behaviour.

So far our experiments on frequency response dynamics have been crude in that they have only used lengthy adaptation times but there is precedent for very rapid changes in tuning of visual systems. For example the contrast gain control system of vertebrate retinal ganglion cells regulates these cells' frequency response on a time scale of 15 ms (Victor 1988) giving them their transient character. This "contrast" gain control system is strongly spatial and temporal frequency dependent. Figures 1b,d of Warzecha and Egelhaaf indicate that H1's response is sometimes a nonlinear, and sometimes quite transient, function of the stimulus. Thus, a similar contrast gain control system may precede motion processing by H1, at times amplifying higher frequencies. Such rapid changes in frequency response may explain apparent discrepancies between the results of Harris et al. (1999), who examined impulse responses of motion sensitive neurones after full adaptation, and experiments with continuous velocity fluctuations. The presence of a gain control preceding motion computation as in Y-cells would lead to the prediction that the impulse responses would be biphasic, which is actually observed (Harris et al. 1999), and would show contrast dependent transients, which is observed in wallaby motion sensitive neurones (Ibbotson personal communication). For continuous stimuli the velocity impulse response would partially reflect the frequency response of the presynaptic units with rapid contrast adaptation.

### 3. Low image speeds and afterimage effects

So far we have considered the impact of adaptation and non-stationarity of the spike generating process upon potential methods for assessing real-time performance of optomotor neurones. Another effect may be relevant when average image slip speeds are low: the so-called afterimage-like effect (Maddess 1985, 1986). Perhaps the best demonstration of this phenomenon is obtained by briefly placing a low contrast stationary bar in the receptive field of an H1 neurone. If the receptive field is probed a second or more later with a thin moving line, an imprint in the sensitivity profile of the H1 cell receptive field is observed where the bar was. This is clearly not a light adaptation effect given that a dark adapting bar can produce a depression of sensitivity to a moving bright line, and that there is markedly different processing of ON and OFF responses (Maddess 1986). When a

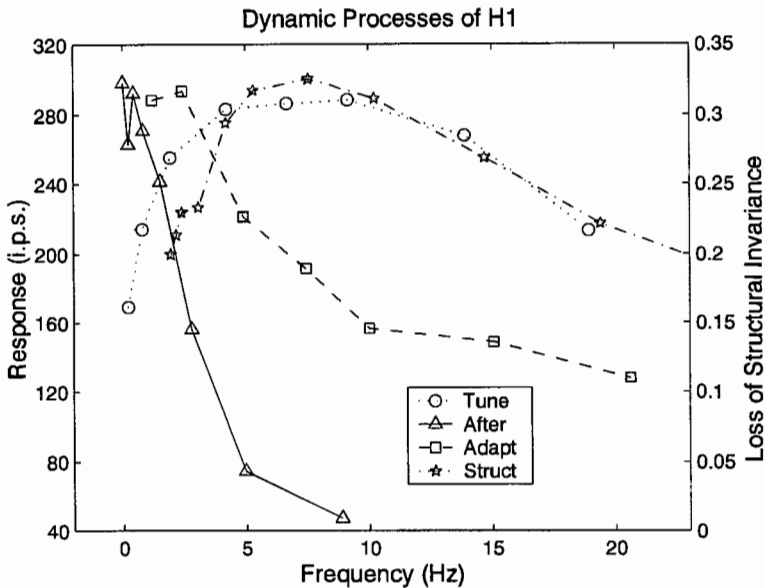
stationary grating is presented for 200 ms or more, a very deep modulation of the response can be observed once the grating begins to move. Afterimage effects for gratings moving at up to 100 %s have also been demonstrated with gratings that had a spatial frequency of 0.1  $c^\circ$  that are about optimal for flies (Maddess 1985). Hence the underlying mechanism is low pass with a corner frequency around 2 Hz (Fig. 2).

#### 4. Summary and suggestions

Figure 2 summarizes the temporal frequency characteristics of a number of dynamic processes that might be considered in any real-time analysis of motion processing in the fly. The overall unadapted temporal frequency tuning curve for H1 responses to drifting grating stimuli (Fig. 2, "Tune", Maddess and Laughlin 1985) is presented to provide a reference. The relative modulation depth of sensitivity changes produced by the afterimage-like effect in response to slowly drifting gratings is also provided (Fig. 2, "After", Maddess 1985) together with the time constant describing the rate of the previously described gain change with adaptation to motion (Fig. 2, "Adapt", Maddess and Laughlin 1985). I have also plotted (Fig. 2, "Struct") a parameter describing the loss of structural invariance that was introduced by Mastebroek (1974). This parameter provides a measure of the magnitude of the temporal frequency dependent change in the spike process, i.e. a loss of stationarity, in response to flashed stimuli. Similar effects have been shown for drifting gratings (Gestri et al. 1980). Clearly a number of effects determine the dynamics of the H1 response and these operate within the band of frequencies of interest to the cell. Thus, as illustrated by figure 1, slowly changing adaptation can cause contamination the residuals from mean SIR models with signal rather than noise, which can affect estimates of noise structure and amplitude. Lack of stationarity can lead to differences in the suitability of measures of central-tendency, such as the mean, for different parts of a response.

Experiments by McCann (1974) where fly visual neurones were characterized by estimating Wiener kernels (e.g. Marmarelis and McCann 1973; James 1992) may suggest a way to characterize adapting real time responses. The Wiener kernel expansion provides improvements over the velocity impulse response method (Maddess and Laughlin 1985; Maddess et al. 1991) because in the Wiener expansion linear, quadratic, cubic and higher order response interactions are each quantified by separate kernels. The full nonlinear SIR (or the linear and nonlinear parts separately) can be easily computed from the kernels, complete with long term adaptive dynamics if desired. For example, McCann (1974) showed that the first and second order kernels computed with a memory length of 8 s formally captured the long term adaptive character of H1. Another benefit is that the stimuli used can be less repetitive and are thus more like natural visual stimuli. Interaction

kernels, quantifying linear and nonlinear interactions between cells or between parts of a cell's receptive field, can also be computed.



**Fig. 2** Frequency dependent effects altering the response gain and dynamics of the fly H1 neurone. The following descriptions are labelled as in the figure legend. *Tune*: the overall unadapted tuning curve of H1 in response to image motion in the preferred direction, units (impulses per second) as for the left ordinate. *After*: the frequency tuning of the afterimage-like effect for afterimages induced by gratings moving in the preferred direction at the indicated contrast frequencies. The left ordinate units divided by 6 indicate the modulation depth in the H1 receptive field produced by the afterimage of a  $0.1\ c^\circ$  grating. The change in receptive field sensitivity is determined by moving a thin bar through the receptive field after presenting the moving grating, the thin bar producing a response of about 60 i.p.s. *Adapt*: the time constant of the change in gain of H1 neurones in response to motion of gratings in the preferred direction as a function of contrast frequency. The time constant in seconds has 30 times the units on the right ordinate. *Struct*: the "loss of structural invariance" described by Mastebroek (1974). This parameter indicates the magnitude of the change in the stochastic spike generation mechanism modulated by the neuronal response as a function of flicker frequency.

The Wiener method is not without problems, however, and methods modelling the changes in the velocity impulse response parametrically might be more parsimonious. Wiener models are non-parametric models where each point in every kernel is treated as a coefficient to be fitted. Thus, as the number and the dimension of the kernels is increased, there is an explosion in the number of coefficients to be estimated and so too in the number of data points required, since at least one datum per coefficient is needed. Parametric models can have many fewer coefficients. For example, Dubois (1993) demonstrated that the velocity impulse

responses of butterfly optomotor neurones can be modelled by a third-order filter (i.e. having 3 coefficients) and that the dynamics can in turn be modelled by changes to just one stage (coefficient) of the filter. Interestingly, the changes to the third order filter provide the system with response dynamics characterized by a constant damping ratio.

In summary, better characterization of stimulus dependent changes in the spike generation process, and tests that assume prior knowledge (e.g. Bruckstein et al. 1983) in interpreting or decoding the spike signals should be considered in future.

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