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Contrast induced changes in response latency depend on stimulus specificity

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ABSTRACT

Neurones in visual cortex show increasing response latency with decreasing stimulus contrast. Neurophysiological recordings from neurones in inferior temporal cortex (IT) and the superior temporal sulcus (STS), show that the increment in response latency with decreasing stimulus contrast is considerably greater in higher visual areas than that seen in primary visual cortex. This suggests that the majority of the latency change is not retinal or V1 in origin, instead each cortical processing area adds latency at low contrast. I show that, as in earlier visual areas, response latency is more strongly dependent on stimulus contrast than stimulus identity. There is large variation in the extent to which response latency increases with decreasing stimulus contrast. I show that this between cell variability is, at least in part, related to the stimulus specificity of the neurones: the increase in response latency as stimulus contrast decreases is greater for neurones that respond to few stimuli compared to neurones that respond to many stimuli.

1. Introduction

Neuronal response latency – the time when the stimulus elicited neuronal signal can first be detected – is an example of a neuronal code involving precisely timed spikes (see Oram et al., 2002 for review). Given the dissociation of response magnitude and response latency (Albrecht, 1995; Bair et al., 2002; Carandini and Heeger, 1994; Gawne et al., 1996; Reich et al., 2001a,b) it is not surprising that response latency of individual neurons in primary visual cortex convey information unavailable from the spike count (Gawne et al., 1996; Reich et al., 2001a,b). Indeed, it is has been speculated that changes in response latency are a potential source of the temporal code revealed by principal component and information theoretic analysis of spike waveforms (Optican and Richmond, 1987; Tovee et al., 1993). Thus, understanding factors that influence neuronal response latency may be relevant to studies examining the role of temporal variation in firing rate in visual processing (Eskandar et al., 1992; Heller et al., 1995; McClurkin et al., 1991; Optican and Richmond, 1987; Richmond and Optican, 1990) as well as shed light on the temporal precision of neuronal codes.

The latency of visually responsive neurones in the visual system increases with decreasing stimulus contrast in the retina (Shapley and ictor, 1978), LGN (Lee et al., 1981b), primary visual cortex (Albrecht, 1995; Carandini et al., 1997, 2002; Carandini and Heeger, 1994; Gawne et al., 1996; Movshon et al., 1978; Parker et al., 1982; Reich et al., 2001a,b; Wiener et al., 1998), area MT (Raiguel et al., 1999) and the anterior superior temporal sulcus (Oram et al., 2002; van Rossum et al., 2008). The increment in response latency with decreasing stimulus contrast is considerably greater in higher visual areas such as the anterior superior temporal sulcus (STSa) than that seen in primary visual cortex Fig. 1 and (Oram et al., 2002; van Rossum et al., 2008). Indeed, the average response latency in area STSa increases by 33 ± 3 ms for each halving of stimulus contrast compared to 8 ± 0.8 ms in V1 (van Rossum et al., 2008). The increasing dependency of neuronal response latency on stimulus contrast indicates that latency change is not retinal or V1 in origin, instead suggesting that each cortical processing area adds latency at low contrast (van Rossum et al., 2008).

Stimulus properties other than stimulus contrast influence response latency. For example, changes in spatial frequency influence both response magnitude and response latency of many V1 neurones (Bredfeldt and Ringach, 2002; Mazer et al., 2002). Position of moving gratings relative to the receptive field also influence response latency (Lee et al., 1981a), as does luminance of the stimulus (Maunsell and Gibson, 1992). On the other hand, changes in response magnitude do not necessarily influence latency in V1 (Albrecht et al., 2002; Gawne et al., 1996; Geisler and Albrecht, 1995; Opara and Worgotter, 1996; Reich et al., 2001a,b; Tolhurst and Heeger, 1997; Worgotter et al., 1996). Similarly, response latency of individual neurons in STSa show little dependency on response magnitude (Oram et al., 1993; Oram and Perrett, 1996, 1992) whereas changes in stimulus contrast cause large changes (>200 ms) in response latency (Oram et al., 2002; van Rossum et al., 2008; York et al., 2007).

In this article, I present data indicating that processing complexity may also influences neuronal response latency. Specifically,

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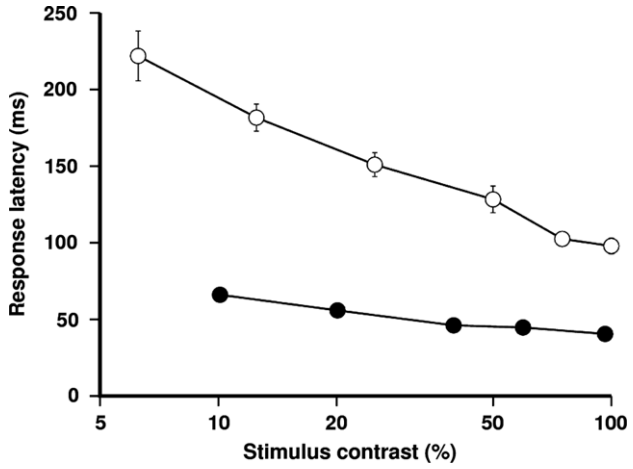

Fig. 1. Stimulus contrast influences response latency more in late visual areas than in early areas. Mean latency (±SEM) is plotted for primary visual cortex (V1, solid symbols, error bars lie under the symbol) and anterior superior temporal sulcus (STS, open symbols), adapted from van Rossum et al. (2008).

I show that the response latency of neurones that respond to a small number of stimuli is more sensitive to changes in stimulus contrast than neurones that respond in a less discriminative or selective fashion. The findings are discussed in terms of current models of visual processing.

2. Methods

The experimental protocols have been described before (Oram et al., 2002; van Rossum et al., 2008). Briefly, extra-cellular single-unit recordings were made using standard techniques from the upper and lower banks of the anterior part of the superior temporal sulcus (STSa) and the inferior temporal cortex of two male monkeys (Macaca mulatta) performing a visual fixation task. The subject received a drop of fruit juice reward every 500 ms of fixation (±3°) while static stimuli (10° by 12.5°) were displayed. During initial screening, images of different perspective views of monkey and human head, animals, fractal patterns, natural scenes, and everyday objects were presented for 110 ms. Visual inspection of on-line rasters and the post-stimulus time histogram (PSTH) to each visual stimulus allowed selection of stimuli that were effective (preferred) and non-effective (non-preferred) in eliciting a response from the recorded neuron.

2.1. Stimuli

Grey-scale images of the cell's preferred and non-preferred stimuli were presented for 333 ms with 333 ms inter-stimulus interval at different contrast levels in random order. Stimulus contrast was determined using foreground regions of the image. The 100% Michelson contrast $(L_{max} - L_{min})/(L_{max} + L_{min})$ was formed by normalising the foreground pixel values such that they occupied the monitor's full luminance range after adjusting the initial grey-scale image to have mid (50%) luminance. Other contrast versions (75%, 50%, 25%, 12.5%, and 6.25%) were achieved by systematically varying the width of the distribution of the foreground pixel values of the 100% contrast version while maintaining the average foreground luminance. Example stimuli are shown in Fig. 2. All manipulations were performed after correcting for the measured gamma function of the display monitor.

2.2. Data analysis

Spike density functions were computed by smoothing a 1 ms bin-width peri-stimulus time histogram with a Gaussian filter (s.d. = 10 ms) for each stimulus at each contrast. *Response magnitude* was taken as the average firing rate in the 333 ms following response latency. The *response latency* was extracted as the point at which the activity exceeded the baseline activity (estimated using the 200 ms before stimulus onset) by three standard deviations for a period of at least 20 ms. The latency was only accepted if the activity of the neuron in the 100 ms following the estimate was significantly ($p < 0.05$) above the baseline activity (paired t-test). *Population responses* were generated by normalising the spike density function of each cell to the most effective stimulus by setting the average of the 200 ms prior to stimulus onset to 0 and the peak of the spike density function to 1, average across neurons, and re-normalizing to the range 0–1 (Barraclough et al., 2005; Oram and Perrett, 1996, 1992).

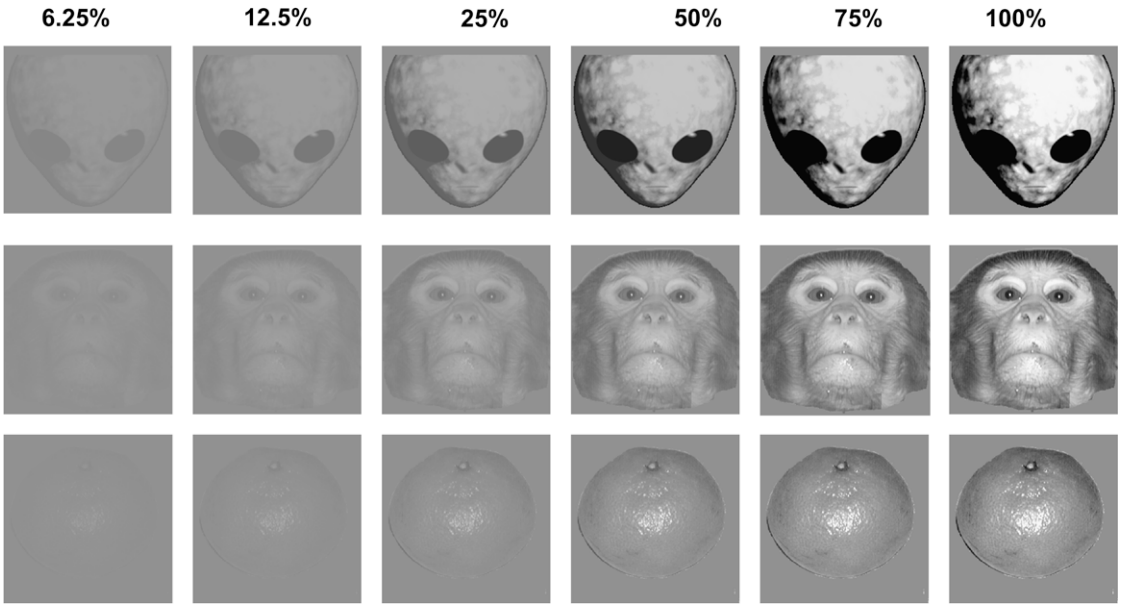

Fig. 2. Example stimuli at different contrasts.