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Visual processing levels revealed by response latencies to changes in different visual attributes

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Visual latencies, and their variation with stimulus attributes, can provide information about the level in the visual system at which different attributes of the image are analysed, and decisions about them made. A change in the colour, structure or movement of a visual stimulus brings about a highly reproducible transient constriction of the pupil that probably depends on visual cortical mechanisms. We measured this transient response to changes in several attributes of visual stimuli, and also measured manual reaction times to the same stimulus changes. Through analysis of latencies, we hoped to establish whether changes in different stimulus attributes were processed by mechanisms at the same or different levels in the visual pathway. Pupil responses to a change in spatial structure or colour are almost identical, but both are *ca.* 40 ms slower than those to a change in light flux, which are thought to depend largely on subcortical pathways. Manual reaction times to a change in spatial structure or colour, or to the onset of coherent movement, differ reliably, and all are longer than the reaction time to a change in light flux. On average, observers take 184 ms to detect a change in light flux, 6 ms more to detect the onset of a grating, 30 ms more to detect a change in colour, and 37 ms more to detect the onset of coherent motion. The pattern of latency variation for pupil responses and reaction times suggests that the mechanisms that trigger the responses lie at different levels in cortex. Given our present knowledge of visual cortical organization, the long reaction time to the change in motion is surprising. The range of reaction times across different stimuli is consistent with decisions about the onset of a grating being made in V1 and decisions about the change in colour or change in motion being made in V4.

Keywords: image attributes; pupil constriction; reaction time; visual latency; visual pathway

1. INTRODUCTION

In primates, the pupil's response to increments or decrements in retinal light flux depends principally on a subcortical projection through the pretectum to the Edinger–Westphal nucleus (Gamlin *et al.* 1984; Pierson & Carpenter 1974). Changes in the colour (Barbur 1991; Kohn & Clynes 1969; Saini & Cohen 1979; Young & Alpern 1980), spatial structure (Barbur & Forsyth 1986; Slooter & van Norren 1980; Ukai 1985) and movement (Barbur *et al.* 1992*a*) of visual stimuli can bring about transient constrictions of the pupil, even when they cause no overall change in, or actually reduce, average retinal illuminance. Such transient constrictions are absent or greatly reduced in people with damage to primary visual cortex (Barbur 1995). If cortical pathways are responsible for this transient constriction, we might expect its latency to exceed the latency of the pupil's normal light-reflex response. Moreover, because the transient constriction is not subject to voluntary control, and is highly reproducible, its latency might provide a sensitive indicator of the level in the visual pathway at which different stimulus attributes are analysed.

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In this paper we describe some new measurements of the pupil's responses to changes in several attributes of visual stimuli. If variations in the latency of response reflect the activity of analysing mechanisms at different levels in the cortical pathway, broadly similar trends ought to be evident in conventional measures of reaction time. We have therefore also examined manual reaction times to the same stimuli. Our results show that both pupil latencies and reactions times are longer when stimulus changes presumably engage cortical pathways, although the two kinds of latency measure show trends that differ in some respects.

2. METHODS

(a) *Subjects*

Four adults (age range 19–67 years) with normal vision served as observers. All the tests were non-invasive and involved only measurements of manual reaction time and pupil response.

(b) *Apparatus and methods*

Visual stimuli were generated by, and pupil responses and manual reaction times were measured with, the P_SCAN system (Barbur *et al.* 1987). This system sampled pupil size at

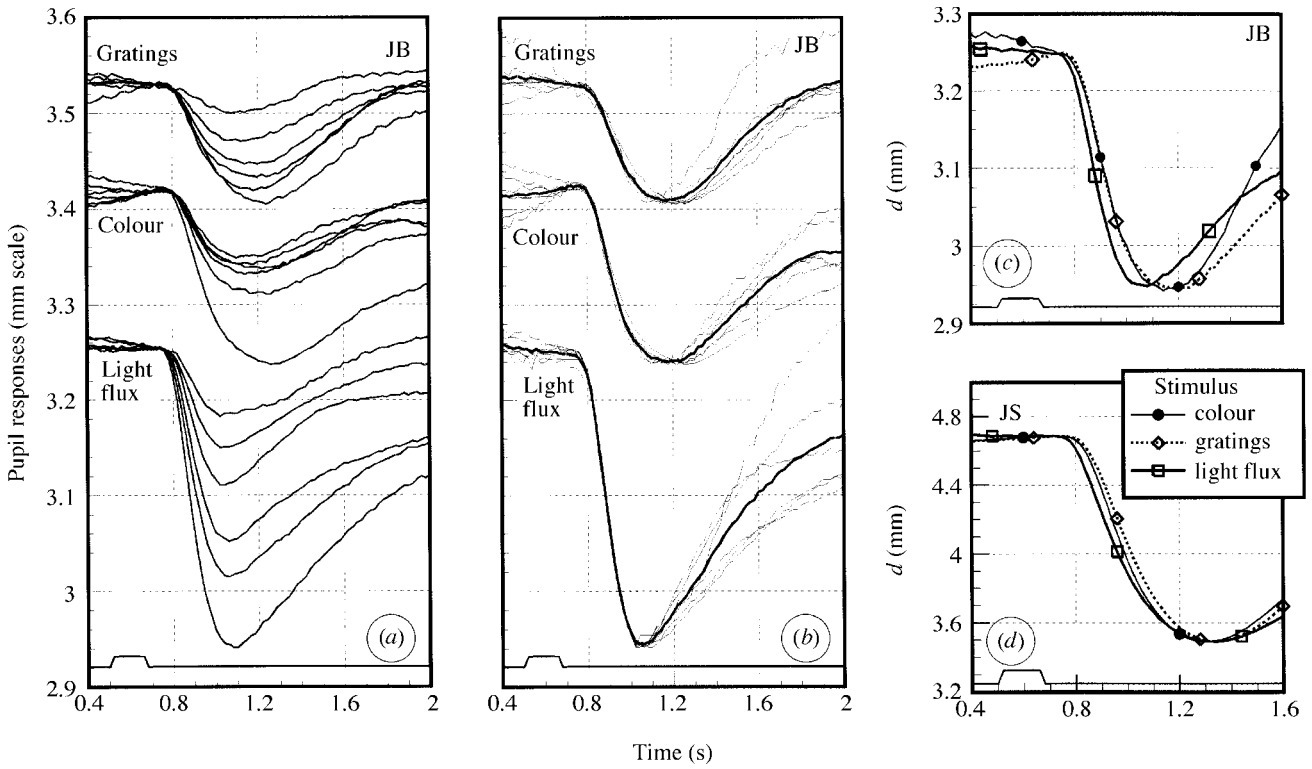

Figure 1. Pupil responses elicited by light-flux increments, a change from an achromatic uniform field to an isoluminant chromatic stimulus, and change from an achromatic uniform field to a grating of the same space-average luminance. The absolute pupil size is that shown for grating stimuli. The remaining sets were then shifted vertically for clarity. The rectangular trace plotted close to the abscissa shows stimulus time. (*a*) The change with time in pupil diameter following the onsets of gratings of various contrasts (0.08, 0.16, 0.32, 0.48, 0.75, 0.95) at 4.5 c deg^{-1}; uniform fields of various chromatic saturations (0.03, 0.045, 0.06, 0.09, 0.12, 0.16 with each number specifying the chromatic displacement (CD) of the test stimulus away from background chromaticity on the CIE–(*x*, *y*) chromaticity diagram); and luminance increments of varying contrasts ($\delta L/L_b$=0.3, 0.6, 0.9, 1.2, 1.5, 2.15). Each trace represents the average of 48 measurements. (*b*) Measurements from (*a*) scaled for equal peak amplitude of pupil constriction. The scaling procedure involves measurement of the peak response amplitude for each trace, multiplication by the appropriate scaling parameter and subtraction of a constant term so as to align the traces horizontally before the start of the constriction. The heavier line among each set of traces represents the mean of all traces in that group. (*c*) Means of pupil responses stretched for equal amplitude (from (*b*)). (*d*) Average traces (as for (*c*)) obtained for subject JS.

50 Hz, with a precision of 0.01 mm. It recorded manual reaction times (via button press with the index finger) with a precision of 1 ms. Visual stimuli resembled those shown in figure 1 of Gamlin *et al.* (1998) and were generated on a television display. The observer fixated a small cross in the centre of a rectangular field of luminance 24 cd m^{-2} and angular subtense *ca.* 26°×21°. To trigger a pupillary response or a manual reaction, a central region 6° in diameter changed briefly (typically for 164 ms) in luminance, colour, structure (onset of a grating) or movement (from incoherent to coherent). This change in the stimulus occurred after the onset of a circular field of achromatic square checks (each subtending *ca.* 13 min arc). The luminance of each element was modulated at 25 Hz by assigning it a value, selected randomly, within a range specified as a percentage of background luminance. This caused dynamic, random luminance contrast (LC) noise. The LC noise amplitude employed was typically 6% and served several purposes: (1) it defined the region, within the larger field visible on the television screen, where the stimulus would appear; (2) its onset provided a cue to the start of each trial, after which the stimulus appeared; (3) it provided, in the measurements that involved colour change, a mask for any luminance contrast potentially present for individual observers as a result of our using the CIE luminosity function as the basis of our luminance calibration (Barbur *et al.* 1992*b*, 1994). Preliminary observations (Freedman *et al.* 1997) showed that this noise has no significant effect on reaction times to chromatic stimuli, but a substantial effect on reaction times to achromatic stimuli.

For each kind of stimulus, we chose parameters that would minimize the probable contribution from early stages of visual processing (and therefore make more prominent variations due to central factors), and would also elicit sizeable changes in pupil diameter. *Sinusoidal gratings* were presented at a frequency of 4.5 c deg^{-1} and had the same mean luminance as the background; we examined how pupil latencies and reaction times varied with contrast. *Chromatic stimuli* were defined by an isoluminant excursion from the background (*x*, *y*: 0.305, 0.323) parallel to the *x*-axis of the chromaticity diagram, towards the red region of the spectrum locus; we examined how pupil latencies and reaction times varied with saturation. *Coherently moving stimuli* were defined by imposing coherent motion on a set of incoherently moving square-check elements similar to those used to provide the random noise mask. The first frame at the onset of coherent motion was spatially coherent with the last frame in the random motion sequence. Because the detection of a motion signal requires a minimum of two discrete frames, the duration of the first frame in the coherent motion sequence was subtracted from the measured reaction times. We examined how

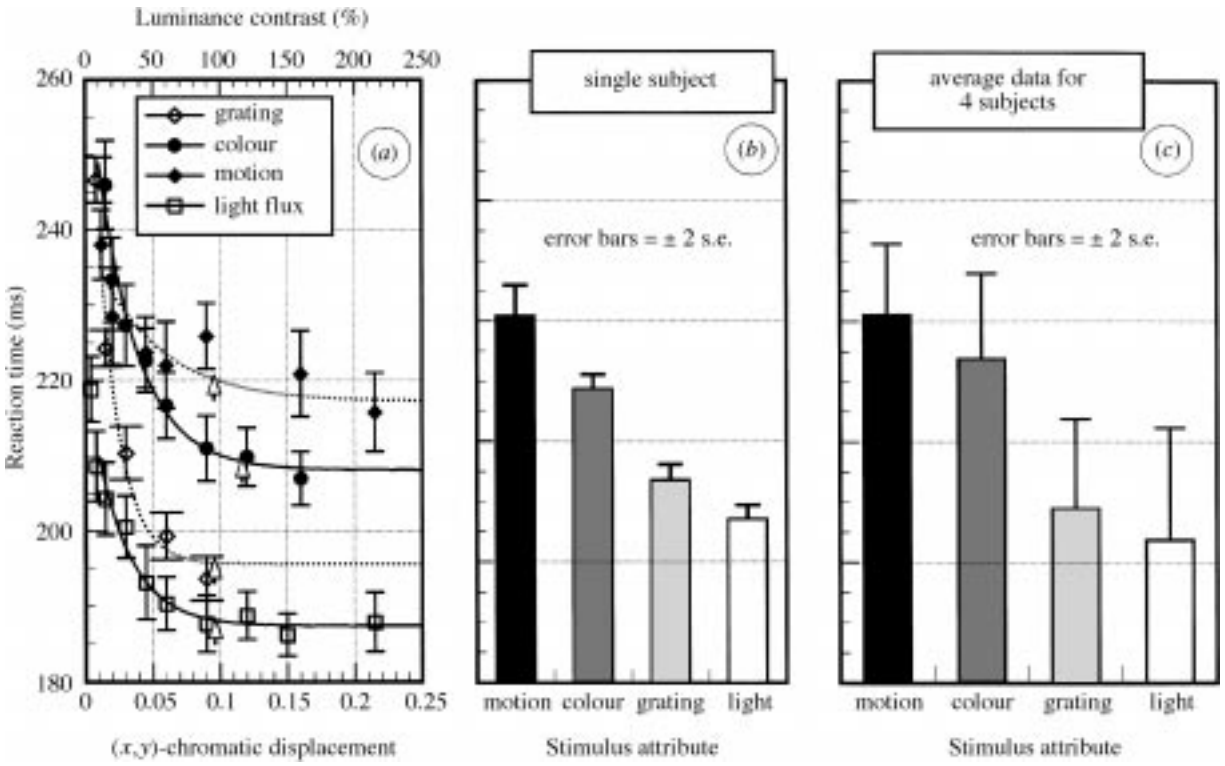

Figure 2. Manual reaction times to changes in four different attributes of the visual stimulus: light-flux increments, a change from an achromatic uniform field to an isoluminant chromatic stimulus, a change from an achromatic uniform field to a grating of the same space-average luminance, and a change from incoherent to coherent movement of random elements. (*a*) Variation in reaction time with stimulus strength. Each point represents the average of *ca*. 64 measurements; error bars represent ± 2 s.e.m. The speed of coherent movement was in the range 4.5–9° s^{-1}. The smooth curves drawn through the points are the best-fitting solutions of the simple model described in the text. All the measurements characterized by one curve were obtained in a single session. These curves and their associated points are aligned vertically with the open arrows, which represent dense measurements of reaction time made in a single session to one value of each stimulus attribute. These reaction times and associated error bars for a single observer are shown in (*b*). (*c*) Asymptotic reaction times to changes in stimulus attributes, averaged over four observers. Error bars show ± 2 s.e.m.

reaction times varied with the luminance contrast of the square checks that formed the stimulus.

(c) *Measurement procedure*

Pupil responses and manual reaction times (to identical sets of stimuli) were measured in separate sessions. In preliminary experiments we tried to measure both together, but this proved impracticable. Pupil measurements required relatively few lengthy trials, and reaction-time measurements required many brief trials. Combining these restrictions and the need to maintain steady head position during pupil measurements resulted in long sessions in which observers became tired, and their reaction-time performance variable.

At the start of each trial, random spatio-temporal luminance noise appeared on the screen and remained visible throughout. After a randomly varying time between 1.5 and 2 s the stimulus appeared for 160 ms, although greater values have also been used; the noise background continued for a further 2.14 s to the end of the trial. Pupil size was measured continuously from 500 ms before the trial until the trial ended.

3. RESULTS

(a) *Pupil response latencies*

Figure 1 (*a*) shows sets of pupil responses to stimuli of different strengths, elicited by a change in light flux, or the onset of a coloured patch or a grating (see figure 1 legend). Response amplitude increases systematically with the strength of the stimulus. Measures of latency obtained from graphs of this kind are difficult to interpret because latency (taken as the time at which the pupil changes size by a criterion amount) appears to decrease with the amplitude of pupil constriction (Alexandridis 1995). One can obtain more useful measures of the latency of the underlying response by exploiting the fact that, to a particular class of stimulus, all pupil responses have the same time-course to peak, and match perfectly when scaled to the same peak amplitude. Figure 1 (*b*) shows this for the response traces from figure 1 (*a*). To a single class of stimulus the normalized responses are identical; across different kinds of stimuli the normalized responses are not identical to peak, but their early phases follow almost exactly the same time-courses, and so permit a comparison of latencies that is robust to the choice of criterion amplitude. Figure 1 (*c*,*d*) shows, for two subjects, the mean normalized traces of responses to light-flux increments, to colour changes, and to gratings. These plots make clear that latencies of responses to the onset of a grating or a colour change are significantly longer (by about 40 ms) than the latency of response to a light-flux increment. Relative latencies of responses to different stimuli can be estimated precisely by measuring

the horizontal separation of the straight descending segments of the traces in figure 1(*c*). This separation was measured where the normalized trace was at one-third of peak amplitude. The absolute latency of the pupil response was taken as the point at which the trace first departed from the baseline.

(b) *Manual reaction times*

Figure 2(*a*) shows the change with stimulus strength in the reaction times to: an increment in uniform light flux, the onset of a grating (without change in space-average luminance), an isoluminant colour change buried in dynamic luminance contrast noise, and the change from random to coherent motion of spatially random checks. Each point represents the average of *ca.* 64 measurements and the error bars represent ± 2 s.e.m. For each kind of stimulus, data for all values were collected in a single session, and trials for the different values were interleaved randomly. An iterative procedure was used to eliminate from a set any individual reaction time that did not fall within $\pm$ 2.2 s.d. Reaction times to changes in different stimulus attributes were measured in different sessions; we took account of session-to-session variability by a procedure described below.

For each stimulus attribute, reaction time declined with increasing stimulus strength, as would be expected. Reaction times could not be reduced significantly by increasing either stimulus size or presentation duration. For each attribute the variation in reaction time with stimulus strength can be well characterised by a simple descriptive model with three parameters:

$$\mathrm{RT} = c_1 \mathrm{e}^{-x \cdot c_2} + c_3,$$

where RT stands for reaction time and x represents stimulus strength (e.g. luminance contrast or chromatic saturation). Two parameters determine the initial amplitude and rate of exponential decay in reaction time with increasing stimulus strength; a third parameter determines the asymptotic reaction time. We use this as a convenient way of comparing performance across conditions.

Reaction times from the same subject and for the same stimulus varied significantly from session to session. To permit us to discount these session-to-session variations in comparing reaction times to the different stimulus attributes, we measured reaction times in a single session in which we presented just four randomly interleaved stimuli, one for each stimulus attribute, each 128 times. The stimuli were chosen to elicit almost asymptotically fast reaction times. Figure 2(*b*) shows, for one observer, the mean reaction times obtained from these measurements. These values were then used to pin the curves and corresponding data sets in figure 2(*a*) (open arrows). Having pinned the curves, we used the asymptotic reaction times (figure 2*a*) in comparing performance across conditions. Figure 2(*c*) shows these asymptotic values averaged over four normal observers, and points to substantial differences in the speed with which different attributes of visual stimuli are processed. The shortest reaction time is elicited by a light-flux increment. Reaction times to changes in the other three stimulus attributes are longer by 6 ms for gratings, by 30 ms for colour and by 37 ms for coherent motion.

4. DISCUSSION

We have shown that when pupil responses are scaled for equal amplitude, the corresponding latencies show no significant variation with either luminance contrast or chromatic saturation. The only requirement is that the state of light adaptation of the retina remains unchanged. These observations make it possible to extract and compare latencies of responses of inherently different amplitude. When the amplitude difference is discounted, pupil responses to a colour change or the onset of a grating are of equal latency, but both are *ca.* 40 ms longer than the *ca.* 240 ms latency of the response to a change in light flux. Pupil responses in the rhesus monkey investigated with almost identical stimuli reveal similar differences in response latency (Gamlin *et al.* 1998). This suggests that the neural pathways that drive the pupil response are similarly organized in monkeys and humans.

The longer latencies of the transient constrictions to colour change or grating onset probably reflect processing delays that arise in the cortex, but the cortical pathways involved are evidently not the same ones (or at least not wholly the same ones) as those that determine the perceptual reaction time. Unlike the pupillary response, manual reaction times show a substantial, and in some ways surprising, dependence on the visual attribute that is changed. We might expect variation with stimulus attribute if decisions about different attributes were made by machinery at different levels of the cortical hierarchy. In a normal visual cortex the synaptic delay is probably close to 10 ms (Maunsell & Gibson 1992), so the differences across reaction times represented by the means in figure 2 reflect perhaps three synapses. Each stage in the cortical hierarchy is likely to involve more than one synapse (there is, for example, a 20 ms difference in the average latency of response of V1 neurons and V2 neurons in anaesthetized monkeys (Schmolesky *et al.* 1998)), so the performance of observers on the tasks studied here probably cannot rest on decisions from areas that are much separated in the hierarchy.

The surprising and in some ways most interesting finding is that the reaction time to the onset of coherent movement is reliably the longest among the attributes studied. As far as colour is concerned this finding is consistent with results of other psychophysical studies, which suggest that colour is perceived before motion (Zeki & Moutoussis 1997). Area MT has been associated with the analysis of visual information about movement, and in some cases decisions about movement (Britten *et al.* 1996). Visual latencies of MT neurons are only slightly longer than those of V1, as would be expected from the connections to V1 and the relatively large fibres through which they are made (Schmolesky *et al.* 1998). It therefore appears unlikely that area MT, or indeed any immediately succeeding area, could be responsible for the perceptual decision about coherent motion. On the other hand, the latency differences are consistent with, for example, a decision about grating onset being made in V1, and a decision about colour change or about coherence of motion being made in V4.

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