



Colour, form, and movement are not perceived simultaneously

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Received 26 February 2001; received in revised form 29 May 2001

Abstract

Behavioural, neuro-anatomical and clinical evidence suggests that different aspects of the visual scene are processed separately, but the extent to which the processing is carried out along segregated and independent parallel pathways is still debated. Moreover, it is also unclear whether these aspects are processed at the same rate, and their neural correlates reach consciousness at the *same time*. An experiment investigated this issue in the case of three attributes of 2D displays: colour, form, and movement. There were three conditions, one for each possible pairing of these attributes. Stimuli were combinations of two values for each attribute (red/green, circle/square, fixed/moving). In each condition the stimuli changed twice in close temporal succession, each attribute switching asynchronously between the two possible values. The observer's task was to report which change had occurred first. Response probabilities were computed for 13 values of the asynchrony, and transformed into estimates of perception time with the help of a psychophysical model. The results showed that colour and form are processed almost simultaneously. By contrast, movement perception is delayed by about 50 ms. The implications of these findings vis à vis the so-called perceptual binding problem are discussed. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Asynchrony; Colour; Form; Motion; Perception

1. Introduction

Phenomenally, colour, form, and movement appear to us as distinct attributes of the visual scene insofar as they can be easily discriminated and identified, both in isolation and in any combination. Distinctiveness does not imply independence, however. Movement has a somewhat special status because being in motion is a visual attribute that can be added or subtracted to an object without affecting much its form and colour. By contrast, colour and form are more tangled: outside the laboratory, colour is always associated to an object, which always has a specific form. One cannot imagine subtracting the form attribute from an object while retaining its colour. Conversely, real objects normally have a specific colour.

The architecture of the visual system offers some analogies with the phenomenological picture. One view, originally put forward by Hubel and Livingstone,

(1987), emphasises the anatomical distinction among the magnocellular, parvocellular interblob, and parvocellular blob pathways. On the basis of the contrasting functional properties of the three pathways, these authors suggested that the mechanisms involved in motion detection are fed mostly by the first pathway, and are clearly segregated from those responsible for perceiving colour and form. Moreover, the parvocellular blob pathway has been assigned a major role in colour perception. A connection between colour and form perception is suggested by the fact that both involve V4 in area 19 where wavelength-sensitive neurons are intertwined with orientation-sensitive neurons, which presumably contribute to form identification. However, according to Livingstone and Hubel (1988), cells subserving colour, form and motion are segregated in layers 2 and 3 of area 17. Leventhal, Thompson, Liu, Zhou, and Ault, (1995) have questioned this widely accepted view by showing that most cells in these layers are selective concomitantly for aspects of colour, form, and motion. Furthermore, recent psychophysical data

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(Gegenfurtner & Hawken, 1996) are also inconsistent with the notion of a single motion pathway that would be insensitive to colour. Rather, they support the hypothesis of two functional streams each of which carries both colour and motion information with different temporal properties.

Clinical data provide further insights into the relationship among visual attributes. Cerebral achromatopsia—the partial or global failure to discriminate hues in the absence of other visual impairments—suggests that the mechanism responsible for colour perception has a certain degree of functional autonomy (Zeki, 1990). More specifically, it demonstrates the existence of at least one crucial processing step in the colour system that is not shared by functional modules subserving different functions. The conclusion is reinforced further by those clinical cases in which colour vision is selectively spared (Wechsler, 1933). A similar pattern emerges also for movement. Although rare, there are well-documented cases in which the perception of visual motion is either selectively impaired (akinetopsia; Zihl, von Cramon, & Mai, 1983) or selectively spared (cf. Zeki, 1991). Finally, apperceptive visual agnosia—the inability to recognise familiar forms while retaining normal colour discrimination and sensitivity to motion (Farah, 1990; De Renzi, 1999)—demonstrates that the synthesis of shapes is carried out by dedicated modules that can be selectively disrupted without affecting the perception of other visual attributes. However, apperceptive agnosia does not seem to have its obverse, i.e. the selective sparing of form perception.

These behavioural, neurophysiological and clinical data provide the basis for the so-called modular doctrine of vision (Zeki & Bartels, 1998a,b; Aleksander & Dunmall, 2000) which holds that (1) the visual brain consists of many distributed perceptual systems, each responsible for the processing of diverse visual attributes, and (2) that visual consciousness reflects the basic modularity of the perceptual systems and is itself modular. An open question within this framework is whether or not the duty cycles of the various processing modules have the same duration. Indeed, just as different sensory channels may have different processing rates (e.g. auditory messages are processed faster than visual ones), similar differences could be present also in the various sub-components of the visual modality.

The question has been addressed both with physiological and psychophysical methods. Physiological evidence (reviewed by Moutoussis & Zeki, 1997a) indicates without exception that the magnocellular pathway has a faster processing rate than the parvocellular one. In series of psychophysical experiments on colour, form, depth and movement perception, Livingstone and Hubel (1987) compared the fastest rate at

which one can follow the alternations between two stimuli differing in just one visual attribute. From their results the authors concluded that ‘the system or systems underlying movement [...] can follow more rapid events than the systems subserving colour and form’ (p. 3459). More recently, however, two experiments have challenged this conclusion (Moutoussis & Zeki, 1997a,b). In the first study perceptual synchrony was tested by showing moving squares whose colour and direction alternated in a square-wave fashion. The authors estimated the asynchrony between the moment each attribute change was perceived by controlling the phase relationship between alternations, and recording the perceived coupling between attributes. Surprisingly, it turned out that colour is perceived between 78 and 84 ms *before* movement. The second study added form as an additional variable, and considered all two-way comparisons (form-colour, colour-movement, form-movement). Again, colour was found to outpace movement by 118 ms. Moreover, it also preceded form by 63 ms. In its turn, form preceded movement by 52 ms.

In summary, there is clear disagreement between Moutoussis and Zeki’s results on the one side, and Livingstone and Hubel’s results on the other. Furthermore, the considerable delay with which movement is perceived with respect to the other two attributes appears to be inconsistent with the reputation of the magnocellular channel for being the fastest one. Here we report an attempt to adjudge the matter by a new psychophysical method. Colour, form, and movement were again pitted against each other in pair-wise comparisons. However, unlike the experiments summarised before, the stimuli were not periodical. Moreover, the form attribute consisted of different geometrical shapes, not simple orientations as in Moutoussis and Zeki’s two studies.

2. Method

2.1. Participants

Twenty University of Geneva students (15 female, 5 male) participated in the experiments. All participants reported normal or corrected-to-normal visual acuity and no deficiency in colour perception. Participants were paid for their services. A minimum of 20 SF was paid in all cases; an additional sum was granted on the basis of the performance, up to a total maximum of 40 SF. Informed consent was obtained from all participants who remained naive, however, as to the expected effects of the experimental manipulations. The experimental protocol was approved by the Ethical Committee of the University of Geneva.

2.2. Apparatus and stimuli

Participants were seated in a quiet room kept in dim light at a distance of about 50 cm from a computer monitor (HP mod. D8901; resolution: 800×600 pixels; vertical refresh rate: 84 Hz; CIE chromatic coordinates: red [$x = 0.6116$, $y = 0.3418$], green [$x = 0.2922$, $y = 0.5974$], blue [$x = 0.1456$, $y = 0.0688$]). The generation of the stimuli and the recording of the responses were controlled by a standard graphic software. The forms to be tested were two solid geometrical figures with the same area: a square (side = 8.8 cm) and a circle (radius = 4.96 cm; at the adopted viewing distance, 1 cm subtends approximately 1° of visual angle). Figures were defined only by their colour, which could be either red or green (no outlines). Stimuli were made isoluminant with the help of a DPT92 Monitor Calibrator (X-Rite Inc. Grandville, MI). The CIE X , Y , Z coordinates of the red and green stimuli were ($X = 32.69$, $Y = 18.17$, $Z = 3.09$) and ($X = 9.86$, $Y = 18.94$, $Z = 4.32$), respectively. Stimuli were presented against a brighter, grey background ($X = 28.15$, $Y = 30.33$, $Z = 44.88$).

In some trials (see below) the figures remained at the centre of the screen throughout the trial; in other trials they eventually moved from the centre toward the upper right corner of the screen with a constant velocity of 9.5 cm/s. In each trial we displayed in fast temporal succession three of the eight combinations of the two possible values of the attributes (colour [C]: red/green; form [F]: circle/square; movement [M]: fixed/moving).

2.3. Experimental conditions, procedure and task

There were three conditions, one for each pairing of the stimulus attributes: form/colour (FC), colour/movement (CM), and form/movement (FM). Trials always began with the display of a central fixation point (a

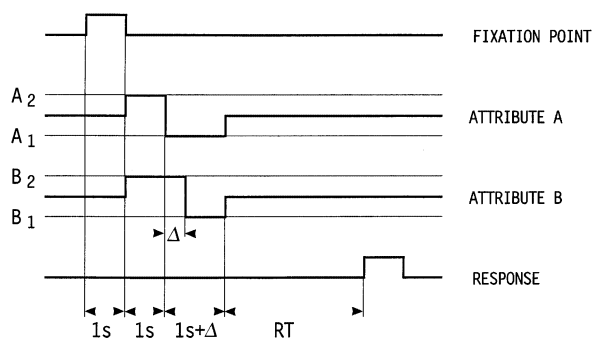


Fig. 1. Timing of the events within trials. A_1 and A_2 (B_1 and B_2) are the two possible values of the stimulus attributes A and B. In this example, the initial stimulus (A_2B_2) lasts for 1 s, changes into the intermediate stimulus (A_1B_2) which lasts for Δ ms (SOA), and is finally transformed into the final stimulus (A_1B_1) which lasts 1 s. Participants had to indicate which attribute changed first.

solid black circle 1 cm in diameter) lasting 1 s. Immediately after the disappearance of the fixation point, one of the two figures in one of the two colours (the *initial stimulus*) was displayed at the centre of the screen. One of the two attributes selected for comparison maintained its original value for 1 s, then switched to the other one. The other attribute also switched between its two possible values, but the change occurred after the first one, the asynchrony Δ (SOA) varying between 0 ms and 300 ms in steps of 50 ms. Thus, during the interval Δ an *intermediate stimulus* was displayed sharing only one attribute with the initial stimulus. The *final stimulus* resulting from the second change remained visible for an additional second, making the entire sequence last $2000 + \Delta$ ms (Fig. 1). Thereafter, the screen was filled with the background and remained so until the participant initiated a new trial by entering the response. By convention, the sign of the asynchrony interval Δ was set as positive when form changed before colour in condition FC, when colour changed before movement in condition CM, and when form changed before the movement in condition FM. The sign was set to be negative in the complementary cases. The participant's task was to indicate (forced-choice) which attribute had changed first in the transition from the initial to the final stimulus by using three keys in the upper row of the keyboard (F5 for answer C, Esc for answer F, and F10 for answer M).

In condition FC the initial stimulus was one of the 4 combinations of the colour and form attribute (e.g. *red square*), and the final stimulus was the corresponding complementary combination (e.g. *green circle*). Each transition from the initial to the final stimulus could have two intermediate stages (e.g. *red circle* or *green square*), depending on which attribute changed first. Thus, there were eight possible sequences of stimuli. Conditions CM and FM were slightly different because we wanted the transitions to occur always near the centre of the screen. Therefore, movement changed only in the transition between the intermediate and the final stimulus. However, by combining also the irrelevant attribute (form for CM, and colour for FM) in the definition of the initial stimulus, we considered four additional combinations and four possible transitions (Table 1). Thus, the sample size for computing individual response frequencies was 40 for $\Delta \neq 0$, and 80 for $\Delta = 0$.

In each condition there were 4 [transitions] \times 13 [SOA] = 52 different sequences. Each sequence was presented ten times for a total of 560 trials (sequences with $\Delta = 0$ were presented twice). The order of presentation of the sequences was randomised for each participant. Conditions were blocked and administered in separate sessions lasting approximately 30 min. The order in which conditions were tested was counterbalanced across participants. Each session was preceded by a

Table 1
Three-step sequences of attribute values in the three experimental conditions

	FC (form/colour)	CM (colour/movement)	FM (form/movement)
$\Delta = -300, -250, -200, -150, -100, -50, 0$ (ms)			
1	SRF → SGF → CGF	SRF → SRM → SGM	SRF → SRM → CRM
2	SGF → SRF → CRF	SGF → SGM → SRM	SGF → SGM → CGM
3	CRF → CGF → SGF	CRF → CRM → CGM	CRF → CRM → SRM
4	CGF → CRF → SRF	CGF → CGM → CRM	CGF → CGM → SGM
$\Delta = 0, 50, 100, 150, 200, 250, 300$ (ms)			
5	SRF → CRF → CGF	SRF → SGF → SGM	SRF → CRF → CRM
6	SGF → CGF → CRF	SGF → SRF → SRM	SGF → CGF → CGM
7	CRF → SRF → SGF	CRF → CGF → CGM	CRF → SRF → SRM
8	CGF → SGF → SRF	CGF → CRF → CRM	CGF → SGF → SGM

Note—S, square; C, circle; R, red; G, green; F, fixed; M, moving. Values of irrelevant attributes in each transition are in italic. Each transition in the two blocks was paired with the indicated seven values of the asynchrony Δ between the first and the second attribute change. By convention, SOAs are negative (positive) in the first (second) block. Each combination of transition and SOA was repeated ten times in randomised order. Responses for equivalent transitions (i.e. conditions [1, 2, 3, 4] for $\Delta < 0$ and [5, 6, 7, 8]) for $\Delta > 0$ were pooled (sample size = 40). For $\Delta = 0$ the sample size was 80.

period of adaptation to the dim ambient light, a verbal description of the task, and a familiarisation phase of 10 trials.

3. Results

The results are presented in the form of psychometric functions which, for any two attributes A and B, describe the relationship between the SOA (Δ), and the relative frequency $p(A)$ with which the change of attribute A is perceived before the change of attribute B. Following the convention introduced above, the SOA is taken to be positive (negative) when A changes before (after) B, and zero when A and B change simultaneously. For all participants, response frequencies increased as a function of the SOA. The lower panels in Fig. 2 show the psychometric functions for the three comparisons FC, CM, and FM (smoothed averages over all participants). There were no ceiling effects. Actually, the response distributions for two comparisons involving movement were incomplete. Even in those trials when either colour or form changed 300 ms before motion onset, movement was perceived first in about 10% of the cases, suggesting that, for some reason, the processing of colour and form was occasionally delayed by an abnormal amount. To avoid the contaminating effect of these outliers, perceptual asynchrony was measured by robust estimators (see later).

The distribution of the response frequencies depended on the attributes being compared. Statistical significance of the differences (Table 2) was tested by considering the five middle values of the SOA ($-100 \leq \Delta \leq 100$ ms), and applying the variance-stabilising arcsin transformation to the response frequencies (two-way ANOVA, 5 [SOA] \times 3 [comparison], treatment-by-treatment-by-participant design). For each

participant and each comparison, Table 3 reports two estimates of the perceptual biases, namely the response frequency at $\Delta = 0$ (P_0) and the Δ value for which responses were at chance level ($\Delta_{P=0.50}$, linear interpolation). The table reports also the differential limen estimated by the semi-interquartile range $SIR = (\Delta_{P=0.75} - \Delta_{P=0.25})/2$ (linear interpolation). The results suggest a temporal hierarchy common to all participants: movement perception was delayed with respect to both colour and form perception. Colour and form changes were instead perceived almost simultaneously. The shape of the distributions differed also. Fig. 3 shows the z -transform of the raw (un-smoothed) response frequencies for the three comparisons. The data for condition FC could be fit quite accurately by a linear regression indicating that the frequency distribution is very nearly a cumulative Gaussian function. By contrast, the data for the two conditions involving movement show a significant departure from the Gaussian model.

The biases reported in Table 3 reflect an underlying difference in the speed at which stimulus attributes are processed. The smoothed response frequencies (Fig. 2) were used to estimate the relative duration of perceptual processing. The estimation involves a number of assumptions schematised in Fig. 4. The first assumption is that the two attributes of the stimuli defining the experimental condition are processed independently (upper panel). When attribute A switches from one value to the other, the delay before perceiving the change is a random variable t_A with probability density function (pdf) d_A . Likewise, a random delay t_B with pdf d_B characterises the processing of attribute B. The relative position of the pdf's d_A and d_B depends jointly on the SOA, and on the average processing times μ_A and μ_B . The response of the participant is supposed to follow a simple deterministic rule: if $t_A < t_B \rightarrow$ answer

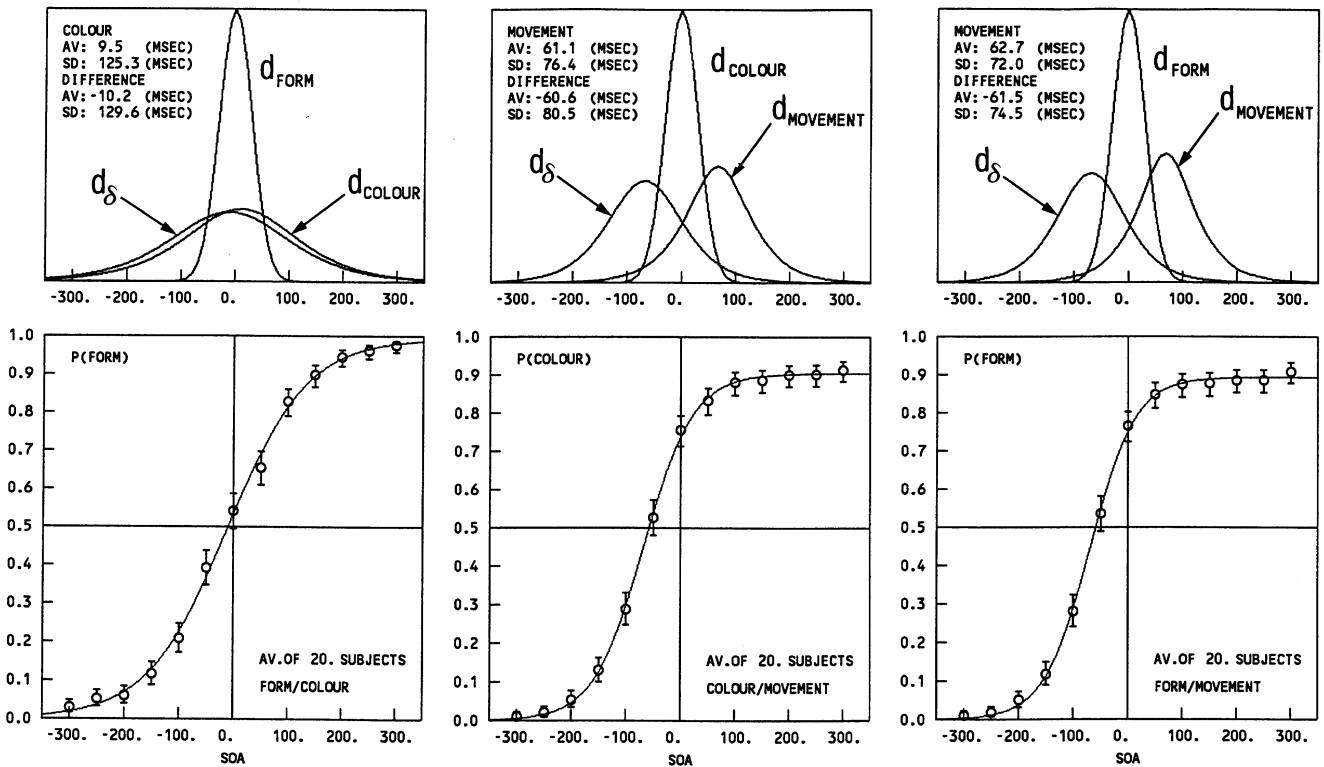


Fig. 2. Lower panels: response frequencies as a function of the asynchrony (SOA) between the first and the second attribute change of the stimuli (psychometric functions). Data pooled over all participants for the indicated conditions. Average frequencies smoothed by a double exponential numerical filter. Bars around data points are the 0.99 confidence intervals (exact binomial model). The continuous lines through the data points were fit by a running average method with a gaussian kernel. Upper panels: probability density functions (pdf) of the total processing times for the indicated attributes and pdf of the difference between the total processing times. The distributions were computed from the interpolations of the corresponding psychometric functions (see Fig. 4).

‘A’; if $t_A > t_B \rightarrow$ answer ‘B’. Thus, response probabilities are dictated by the pdf d_{δ} of the difference $\delta = t_B - t_A$, i.e. the convolution of $d_A(-t)$ and $d_B(t)$. Because d_A and d_B depend only on the nature of the attributes, the effect of varying the SOA is simply to shift d_{δ} along the time axis (lower left panel). The final assumption, therefore, is that the function relating the response probabilities to the SOA is the cumulative distribution of d_{δ} . The lower right panel of Fig. 4 illustrates three such functions corresponding to a positive, zero and negative value of $\mu_B - \mu_A$.

For a given pdf d_{δ} , there is an infinite number of pairs d_A and d_B such that the criterion variable $t_B - t_A$ is distributed as d_{δ} . Because of the independence assumption, however, the average μ_{δ} is always equal to the difference $\mu_B - \mu_A$ between the average processing times. Moreover, if d_A is specified, the corresponding d_B is uniquely defined by d_{δ} . For each pair of attributes, we assumed the fastest processing time to have a normal distribution with zero average and a standard deviation of 30 ms, and we estimated the distribution of the slowest processing time by solving the convolution equation $d_{\delta}(t) = d_A(-t) * d_B(t)$. The results for each comparison are reported in the upper panels of Fig. 2,

which show the pdf of δ , the assumed gaussian pdf of t_A , and the computed pdf of t_B . Finally, the average of t_B relative to t_A and its standard deviation (shown inset) were computed from the estimated d_B . This analysis confirmed the results of Table 3 by indicating that the processing times for colour and form attributes are roughly equivalent, whereas processing movement requires an additional 50 ms.

4. Discussion

We addressed the question of whether colour, form, and movement attributes of the visual scene are processed asynchronously, and, in this case, whether the

Table 2
Summary of the analysis of variance

Factors	F	df	MS	P
Condition	14.262	2	1.099	<0.001
SOA	225.228	4	7.617	<0.001
Interaction	13.334	8	0.241	<0.001

Table 3
Constant errors and differential limina for each participant

Participant	$\Delta_{P=0.50}$			$P_{\Delta=0}$			JND		
	FC	CM	FM	FC	CM	FM	FC	CM	FM
1	-0.035	-0.023	-0.060	0.783	0.825	0.625	0.041	0.018	0.079
2	0.071	-0.123	-0.116	0.400	1.00	1.00	0.117	0.018	0.029
3	-0.012	-0.034	-0.029	0.538	0.863	0.800	0.074	0.027	0.025
4	0.042	-0.047	-0.032	0.363	0.875	0.762	0.083	0.029	0.031
5	-0.015	-0.047	-0.039	0.613	0.863	0.925	0.059	0.040	0.038
6	-0.036	-0.075	-0.070	0.563	0.913	0.950	0.069	0.037	0.036
7	0.063	-0.024	-0.041	0.450	0.688	0.850	0.139	0.043	0.030
8	-0.025	-0.095	-0.084	0.625	0.975	0.988	0.122	0.047	0.021
9	-0.002	-0.074	-0.065	0.512	0.988	0.962	0.064	0.015	0.021
10	-0.050	-0.094	-0.097	0.613	0.887	0.962	0.075	0.037	0.034
11	-0.030	-0.114	-0.084	0.688	0.975	1.00	0.083	0.031	0.025
12	-0.057	-0.032	-0.041	0.500	0.962	0.950	0.075	0.018	0.025
13	-0.043	-0.055	-0.042	0.663	0.950	0.875	0.064	0.027	0.028
14	0.017	-0.030	-0.055	0.425	0.887	0.938	0.076	0.020	0.039
15	-0.038	-0.044	-0.103	0.663	0.887	0.938	0.082	0.049	0.057
16	-0.043	-0.080	-0.075	0.950	0.950	0.988	0.030	0.015	0.034
17	-0.064	-0.017	-0.025	0.488	0.688	0.775	0.084	0.117	0.023
18	0.005	-0.032	-0.033	0.488	0.762	0.837	0.070	0.039	0.028
19	-0.053	-0.033	-0.039	0.412	0.900	0.863	0.073	0.024	0.030
20	-0.046	-0.060	-0.075	0.775	0.850	0.825	0.038	0.057	0.057
Average	-0.018	-0.057	-0.060	0.573	0.884	0.891	0.076	0.035	0.034

Note— $\Delta_{P=0.50}$, asynchrony for which responses were at chance level (linear interpolation); $P_{\Delta=0}$, response probability when both attributes changed simultaneously; JND, just noticeable difference estimated by the semi-interquartile range (linear interpolation).

order of priority is the one indicated by Moutoussis and Zeki (1997a,b), or the different one suggested by Livingstone and Hubel (1987). Our results were mixed. In qualitative agreement with Moutoussis and Zeki, we found that movement onset is perceived after colour and form changes. The asynchrony, however, was smaller (50 ms) than both estimates provided by these authors (81 and 118 ms). By contrast, the experiment did not confirm the existence of a difference between the processing rates of colour and form. On this point, our results were instead in keeping with Livingstone and Hubel who reported that the maximum alternation rate at which changes can be perceived is the same for both colour and orientation (Livingstone & Hubel, 1987, Table 6).

This mixed pattern calls for comments. Livingstone and Hubel's conclusion that the channel involved in motion detection should be faster than the chromatic channel was based on a single experimental condition in which they measured the highest frequency at which the observer could still detect to-and-fro step displacements of an illusory contour. Both our experiment and those reported by Moutoussis and Zeki involved instead smooth displacements of real contours, that is, a more realistic approximation to actual moving objects. In addition, our estimate of the delay with which movement is detected was based on explicit categorical judgements on the timing of single events. These two important methodological differences may well account

for the discrepancy with respect to Livingstone and Hubel's results. The finding that movement perception is relatively slow seems at odds both with the known physiology of the magnocellular pathway (cf introductory remarks), and with the important role that perceived motion has in preserving the continuity of object identity across time and space (Cavanagh, 1993). However, as already stressed by Moutoussis and Zeki, the relationship between cell response latencies and temporal integration periods on the one side, and perceptual awareness on the other side need not to be a simple one, particularly when one compares locally definable attributes such as colour, and cinematic attributes that must be derived from at least two measures. Indeed, the fact that the magnocellular channel can follow more rapidly alternating stimuli than the parvocellular one does not imply per se that the latency with which stimuli reach the central brain processes along the first pathway is shorter than the latency along the second pathway. Also, the difference in the velocity at which action potentials are conveyed along the magno- and parvocellular pathways is too short to account for the differential processing delays (cf. Lennie, 1980, pp. 570–571).

Two reasons may be considered to explain why colour and form changes were perceived before movement onset. First, it could be that, instead of reacting to the relevant attribute changes, participants were actually reacting to some sort of perceptual flash associated

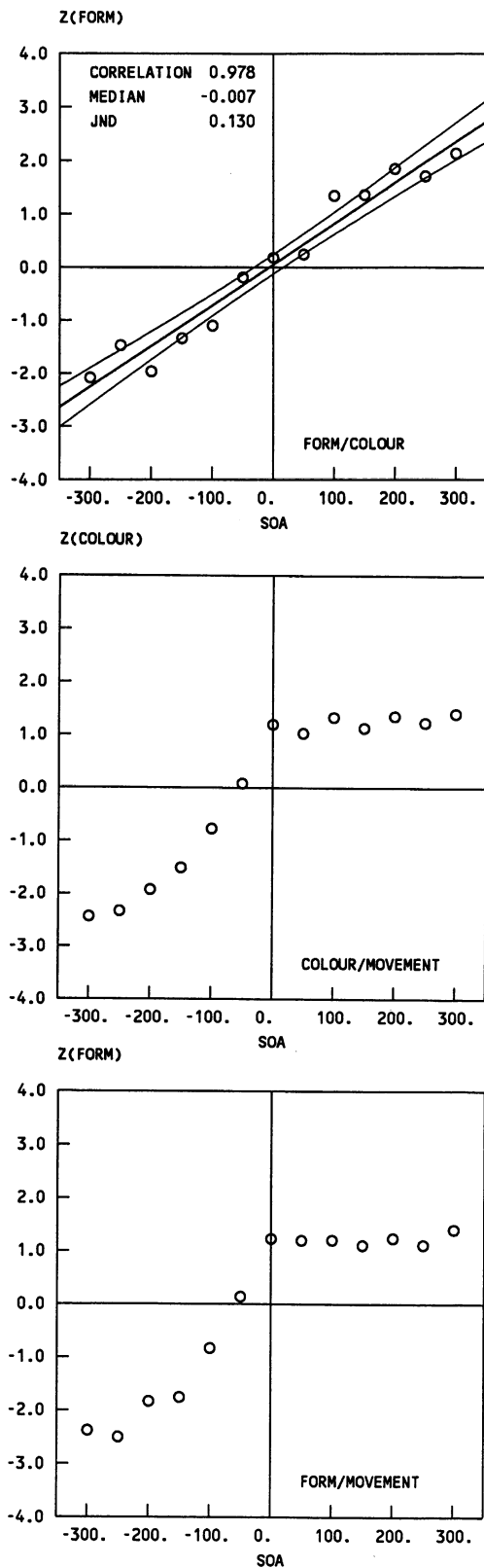


Fig. 3. Z-transform of the psychometric functions for the three indicated conditions. Raw (unsmoothed) data. The data points for the form/colour condition are well interpolated by a linear regression (heavy line and associated 0.95 confidence parabola) indicating that the psychometric function is very nearly a cumulative Gaussian distribution. No such fit is possible for the other two conditions.

to these changes. If so, one could then argue that such an unstructured stimulus is actually processed faster than movement onset, i.e. a second-order change. Evidence against this hypothesis has been provided by a recent study (Whitney, Murakami, & Cavanagh, 2000) of the flash-lag effect (a stimulus flashed adjacent to a moving bar is perceived to lag behind the bar). By showing that alternative accounts are not satisfactory, the authors argue that the effect results from a differential neural delay, with the moving bar being actually perceived some 45 ms *before* the flash.

Alternatively, it may be argued that, at movement onset, the effective stimulus is a mixture of acceleration and velocity signals. Evidence suggests that the perceptual correlate of acceleration is not derived directly from the time derivative of velocity, but rather via a two-stage processing of the cinematic variables (Werkhoven, Snippe, & Toet, 1992). If so, the relatively long delay with which movement is perceived would partly be a consequence of the fact that one component of the stimulus is extracted in an indirect, time-consuming manner. Note that this explanation would not detract from the interest of our findings inasmuch as they make reference to perceptual events that may take place even under more naturalistic circumstances.

Our estimate of the asynchrony between colour and movement perception (50 ms) is in the same direction but somewhat shorter than those reported by Moutoussis and Zeki (1997a,b) (78–84 and 118 ms, respectively). Methodological differences may be responsible for this quantitative discrepancy. One such difference is the background against which stimuli were presented. We made the background grey and 70% brighter than the stimuli (see Section 2), whereas Moutoussis and Zeki used a dark background. If anything, however, this should have resulted in the opposite discrepancy, because experiments with moving grating (Campbell & Maffei, 1981; Thompson, 1982; Cavanagh, Tyler, & Favreau, 1984; Burr, Fiorentini, & Morrone, 1998) and kinematograms (Cavanagh, Boeglin, & Favreau, 1985) have shown that the perceived velocity of equiluminous stimuli is substantially slower than the velocity of stimuli differing in brightness. Thus, the brightness difference in this case being smaller than the one adopted by Moutoussis and Zeki, movement should have been less salient in our experimental condition. Note, however, that equating salience with velocity may be unwarranted because the relationship between perceived velocity and luminance contrast is not linear.

The other, perhaps more crucial difference was in the nature of the stimuli (repetitive vs. single change), and the type of judgement required from the observers. A recent unpublished experiment (Nishida & Johnston, 1999) found that repetitive changes of colour and movement give rise to the same perceptual asynchrony found by Moutoussis and Zeki (about 100 ms), whereas

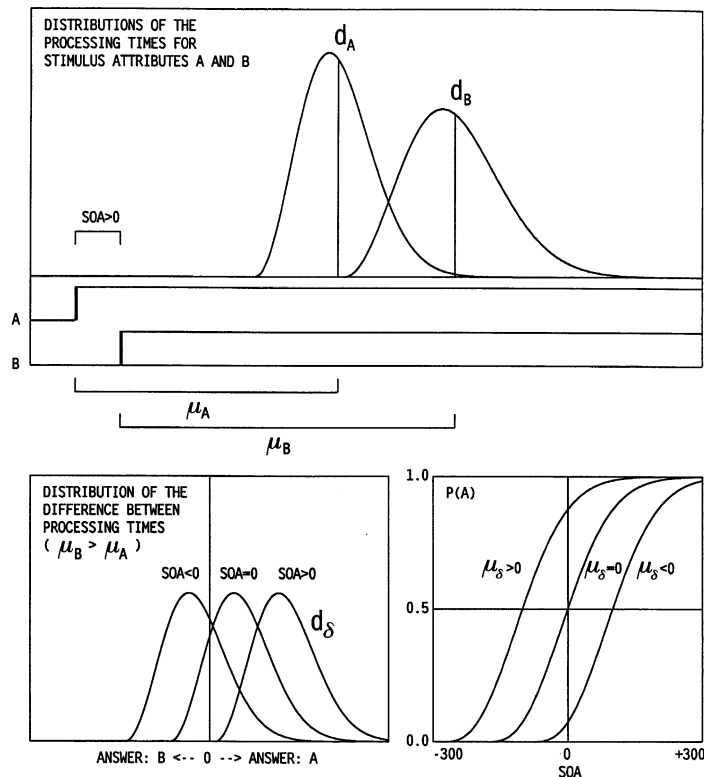


Fig. 4. Scheme for transforming the response into an estimate of the processing times. Upper panel: the transition between the two possible values of the attributes is perceived only after completing a processing requiring a random amount of time. The probability density functions (pdf) of the processing times may be different. In this example the mean processing time is longer for aspect B than for aspect A ($\mu_A < \mu_B$), and aspect B changes after aspect A ($SOA > 0$). Lower left panel: three hypothetical distributions of the difference between the pdf for B and the pdf for A. Participant answers A (B) when the difference is positive (negative). Because $\mu_A < \mu_B$, the probability of answer 'A' is greater than that of answer 'B' even at $SOA = 0$. Lower right panel: Psychometric functions relating the probability of answer 'A' as a function of SOA for three values of the mean difference μ_δ

single changes are perceived simultaneously. Although the single-change method did not suppress the asynchrony, the fact that we found smaller values (50 ms) is in keeping with the hypothesis that movement interferes with a process that sets aspect changes in one single time frame. It is also possible that processing a temporal succession of single events is intrinsically faster than processing the relative phase of periodic stimuli. At any rate, it may be argued that our estimates computed from psychometric functions (13 response probabilities, Fig. 2) are more robust than those obtained from the best-fit 'red/green reversal lines' (Moutoussis & Zeki, 1997a, Fig. 3).

The asynchronies in the conditions CM and FM were quite similar. As expected, no consistent asynchrony was found in the condition FC. In contrast, Moutoussis and Zeki (1997b) reported that colour perception precedes orientation perception by 63 ms. The discrepancy, however, need not to be real provided that one does not equate orientation discrimination with form discrimination, as these authors occasionally do. Arguably, discriminating the orientation of edges is one step towards the perceptual synthesis of a complete form such a

triangle, but this does not imply that the latter process is necessarily longer than the former. A triangle turning into a square (or vice-versa) generates a richer array of coherent changes than a single segment switching from one orientation to another (Moutoussis and Zeki's conditions b and c). It is possible that the parallel activation of several orientation-detecting processes has a faster perceptual outcome than the activation of just a single process. It should be noted, however, that the finding that the detection of colour changes is at least as fast as the detection of form changes is inconsistent with the impulse-response data reported by Burr and Morrone (1993).

The fact that movement onset is not perceived at the same time as either colour or form changes is directly relevant to the so-called *binding problem* (Treisman, 1986, 1996). Ever since evidence has accumulated that different—albeit partly overlapping—networks are responsible for extracting chromatic, figural and cinematic information from the visual scene (cf. Livingstone & Hubel, 1988; Zeki, 1993), physiologists and cognitive scientists alike have been wondering how distributed information is ultimately integrated into a coherent

representational state. One view (e.g. Singer, 1993; Roelfsema, Engel, König, & Singer, 1996; Engel, Fries, König, Brecht, & Singer, 1999) is that integration is achieved by synchronisation: neurons which, in different networks, respond to different attributes of the same object would nevertheless discharge in temporal synchrony in the millisecond range. No such synchrony would instead be present among cells activated by different objects. On the basis of the evidence summarised in the introduction, Zeki and his collaborators take issue with the synchronisation hypothesis and actually defend the opposite view that ‘when two attributes (e.g. colour and orientation) are presented simultaneously, they will be perceived at *different times* if the percepts are created by the activity of cells at *different sites*. Conversely, they will be perceived at the same time if the percepts are created by the activity of cells at the *same site*. [...] Consciousness is not the consequence of binding the activities of cells at different sites; rather it is the micro-consciousnesses [generated by each specialised network] that are generated at *different sites* that require binding’ (Zeki & Bartels, 1998b, p. 1584, our emphasis). Dennet and Klinsbourne (1992) go one step further along the same line of thinking by arguing that the generation of a unitary perceptual experience does not even require a master process that ultimately sets the outputs of the processing modules into a time register. It should also be noted that the need for a late binding process has been questioned by a recent study (Holcombe & Cavanagh, 2001) showing that the rate at which brightness, orientation, and colour can be reliably paired in rapidly alternating stimuli is much higher when the features are spatially superimposed than when they are spatially separated. Thus, spatially superimposed features of any given object may be assessed in combination from early levels of visual processing.

Clearly, our results are more in keeping with the Zeki’s modular doctrine than with the notion of temporal binding. It is an open question whether some form of highly accurate synchronisation of the neural activity is achieved and, if so, what purpose it may serve. Whatever the reason why we did not detect an asynchrony between colour and form perception, we confirmed that both attributes are perceived well before movement. Thus, the process that binds together the different attributes of an object does not seem to be fastidious about asynchronies of the order of 50 ms which can be detected by carefully contrived experimental strategies, but may well go unnoticed in daily life.

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