Masking within and across visual dimensions: Psychophysical evidence for perceptual segregation of colour and motion

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Abstract

Visual masking can result from the interference of perceptual signals. According to the principle of functional specialization, interference should be greatest when signal and mask belong to the same visual attribute (e.g. colour or motion) and least when they belong to different ones. We provide evidence to support this view, and show that the time-course of masking is visual attribute specific. Firstly, we show that a colour target is masked most effectively by colour (homogeneous target-mask pair) and least effectively by motion (heterogeneous pair), and vice versa for a motion target. Secondly, we show that the time at which the mask is most effective depends strongly on the target-mask pairing. Heterogeneous masking is strongest when the mask is presented before the target (forward masking) but this is not true of homogeneous masking. This finding supports a delayed cross-feature interaction due to segregated processing sites. Thirdly, lengthening the stimulus onset asynchrony (SOA) between target and mask leads to a faster improvement in colour than in motion detectability, lending support for a faster colour processing system and consistent with reports of perceptual asynchrony in vision. In summary we present three lines of psychophysical evidence all of which support a segregated neural coding scheme for colour and motion in the human brain.

Keywords: Functional specialization, visual masking, psychophysics

Introduction

Our seemingly effortless ability to perceive a world in which all the different visual attributes are in apparently precise temporal and spatial registration belies a complex cortical machinery which decomposes the visual image into constituents such as form, colour and motion, and processes them in separate and specialized visual areas. The evidence for this functional specialization in the primate visual brain comes from anatomical, electrophysiological (Zeki, 1978, DeYoe & van Essen 1988, Livingstone & Hubel 1988, Zeki & Shipp, 1988), and human imaging and clinical studies studies (Zeki, 1990, 1991; Zeki et al., 1991; Zihl et al., 1991; Meadows, 1974). This functional specialization has, moreover, temporal consequences, since we perceive different attributes at different times, colour taking temporal precedence over orientation, and orientation over motion (Moutoussis & Zeki 1997a & b; Zeki & Moutoussis, 1997; Arnold et al., 2001; Barbur et al., 1998).

Of all the visual attributes, perhaps the easiest to separate both physiologically and perceptually are colour and motion, colour being associated with activity of the V4 complex, and motion with activity of a separate system, based primarily on the area V5 (Zeki, 1978; Livingstone & Hubel, 1988; Zeki et al., 1991). The evidence in favour of the separation of motion and colour also comes from psychophysical experiments which show that motion detection is impaired under conditions of equiluminance (Ramachandran & Gregory, 1978; Cavanagh et al., 1984), indicating that the motion system, although sensitive to chromatic signals, does not contain neurons tuned to specific hues (Dobkins & Albright, 1994; Gouras & Kruger, 1979). Additional psychophysical evidence is consistent with functional specialization for other visual dimensions (Krumhansl, 1984; Theeuwes, 1992; Livingston & Hubel, 1987, Hong & Blake, 2009; Hong & Shevell, 2006).

In the study reported here, we investigate functional specialization psychophysically using a visual masking paradigm, by examining the strength of interference between two perceptual signals, either arising from the same visual attribute (homogenous target-mask pairs) or from different ones (heterogeneous target-mask pairs). Masking refers to the impaired detectability of a target stimulus when immediately preceded or succeeded by a task irrelevant visual input, referred to as the mask (Breitmeyer & Ogmen, 2006). Visual temporal masking has been reported in both the motion (Braddick, 1973, Ferrera & Wilson, 1987) and the colour domain (Schmidt, 2002; Breitmeyer et al., 2004), but not across the two. Moreover, although masking of a target colour with a colour mask has been reported in two studies (Schmidt, 2002; Breitmeyer et al 2004) both employed a meta-contrast masking technique, in which the target and mask regions were non-spatially overlapping. Because this type of masking has been hypothesised to rely on a form of ‘motion de-blurring’ (Ansorge et al., 2007), rather than direct interference between target and mask signals, we chose to use the simplified backwards masking technique in which the target and the mask overlap in space. This alone would enable us to draw conclusions regarding a functional specialization.

In our study, we manipulated the relationship between the target and mask, such that the target-mask pairing was either homogeneous (e.g. colour target & colour mask) or heterogeneous (e.g. colour target & motion mask). If regions or cells in the visual system are non-specialised and respond to multiple visual features (integrated representations) mask strength should remain constant across conditions (Fig. 1, Panel B). If cortical representations are exclusively integrated it should be impossible to selectively mask one feature (e.g. colour) whilst sparing the other (e.g. motion). This would not be true if the demonstrated functional specialization in the cortex is perceptually potent, i.e., if signals from target and mask are processed in separate cortical sites, or by different cells, when competition or interference will take place over a different time course, and is likely to be weaker (Fig 1, Panel B).

Our study is divided into three experiments. In the first we report the effect of homogeneous and heterogeneous target mask pairs at both short and long stimulus onset asynchronies (SOAs); Functional specialization predicts weaker masking in the case of heterogeneous pairs. In the second experiment we investigate the time course of homogeneous pair masking in more detail, with the aim of exposing perceptual asynchronies between the visual features of colour and motion. In the third section, we test the prediction that heterogeneous masking only occurs when the mask is given sufficient processing time (i.e. when the mask occurs prior to the target).

Our results constitute a psychophysical demonstration of functional specialization for the processing of colour and motion in the human visual system.

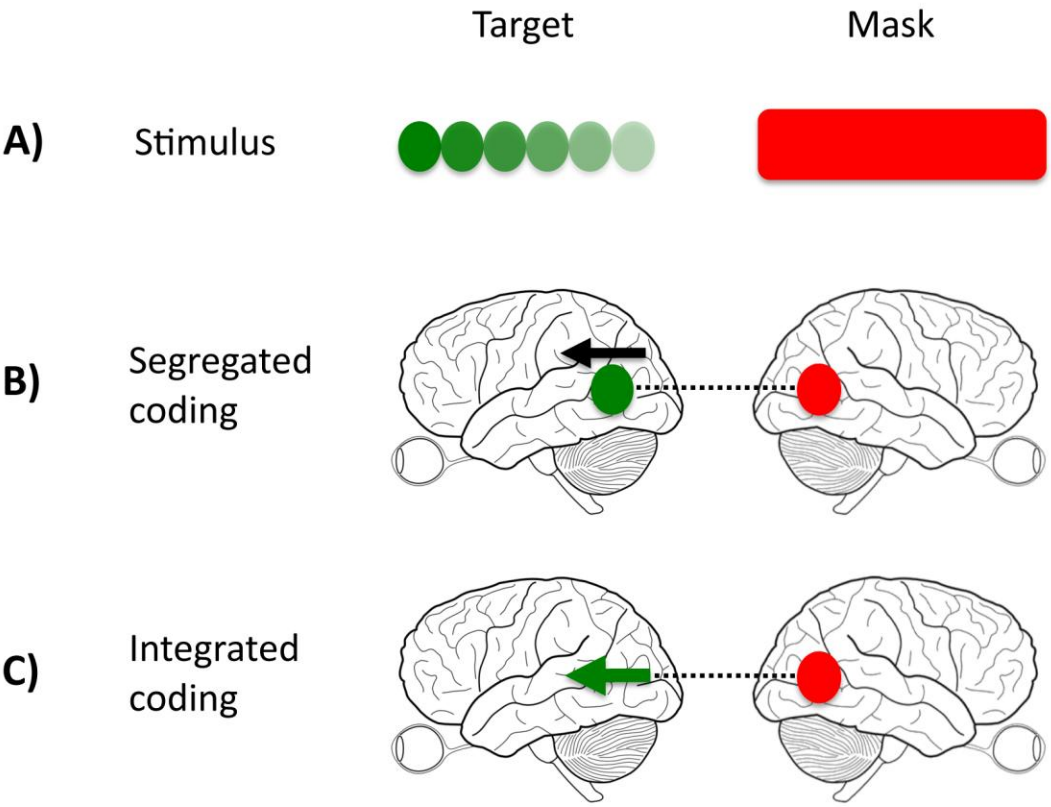

Figure 1. Interaction of target and mask signals. A) illustrates the physical stimulus, comprised of target and mask. B) and C) illustrate two possible ways in which the visual cortex may represent the target and mask. In the case of a segregated representation (B) colour and motion activate distinct and separate nodes (signified by the separate black arrow and green dot), whereas in the integrated case (C) both direction of motion and colour are represented within the same node (signified by the green arrow). A colour specific masking effect would support the existence of distinct processing nodes, because the interference produced by the mask (dashed black line) acts only on the target colour node.

Experiment 1: Feature selective masking

Method

Apparatus

For all experiments stimuli were displayed on a Sony Trinitron Multi-scan E450 monitor (refresh rate of 140Hz) and generated using the Cogent toolbox for MatLab on a windows XP machine.

Stimuli & Procedure

The target stimulus contained both colour and motion, while the mask featured only a single attribute[1]. Stimuli were presented on a grey background (6.9 cd/m^2). The target was a fast moving (145 deg sec^{-1};left or right) circle coloured red or green (Fig 2). It was presented for 35 ms and covered a region of 5.1^o. Two types of mask were tested, a colour mask which consisted of a uniformly coloured bar (10.2 x 5.1^o; 200ms duration; Fig 3A), and a motion mask generated from the horizontal cyclic left-right motion of two fast moving white circles (Fig 3B), covering the target region. The target colours were green and yellow while the mask colours were red and blue[2]. Therefore, the target and mask colours could either be opponent or non-opponent pairs. Figure 2 shows the four target mask colour pairs.

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[1] Salience was maximised for one visual feature dimension, and minimised for the other. Motion was maximised by presenting a moving achromatic stimulus. Colour was maximised by presenting a stationary chromatic stimulus.

[2] Colour settings: green (X=4.97, Y=9.95, Z=3.62), yellow (X=7.24, Y=9.66, Z=3.4), red (X=11.7, Y=6.79, Z=64.7) and blue (X=1.26, Y=6.52, Z=64.7), and grey background (X=6.75, Y=7.39, Z=13.3).

In the first experiment, one short and one long SOA condition was tested (0-21ms[3] and 504ms respectively). The long SOA is useful in ruling out confounding factors that could account for poor discrimination performance, such as general task difficulty or response confusion arising from the integration of target / mask information. 80 trials per SOA were tested for each subject.

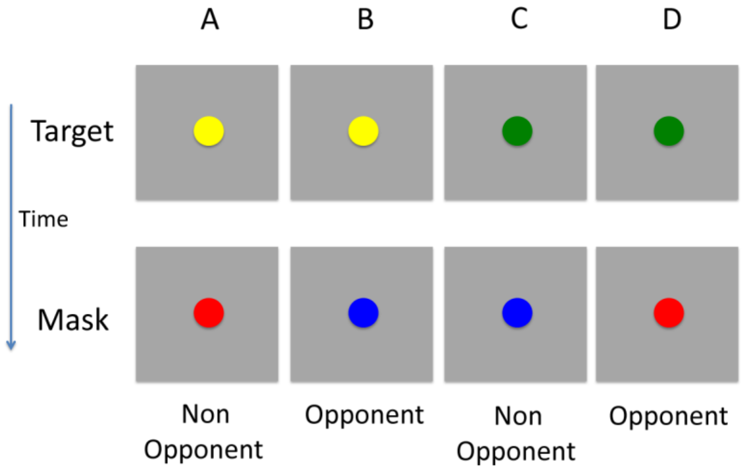

Figure 2. Illustration of the different target and mask colour pairs. The target was either yellow or green, and the mask either red or blue. There the pairs consisted of either opponent or non-opponent colours. Note that the motion component of the stimulus is not shown.

Observers

Ten subjects (average age 29; 7 female) were tested on the initial version containing two different SOAs. All had normal or corrected to normal vision.

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[3] Between subjects performance at short SOAs was highly variable. To maintain a constant task difficulty, the short SOA was set on an individual subject basis, based on the results of 3 practise blocks (40 trials each) where SOA was set to either 7, 14, 21ms.
140Hz corresponds to a frame duration of 7.14ms. For reasons of clarity we report SOAs rounded to the nearest millisecond.

Procedure

Observers were instructed to report either the colour or direction of motion (separate sessions) of the target, and to ignore all features of the mask. The experiment used a 2 alternative forced choice design, and was performed in four sessions, run in a counterbalanced order. Each session was composed of blocks of 40 trials, with a break given after each. Observers completed a single practice block for each new task.

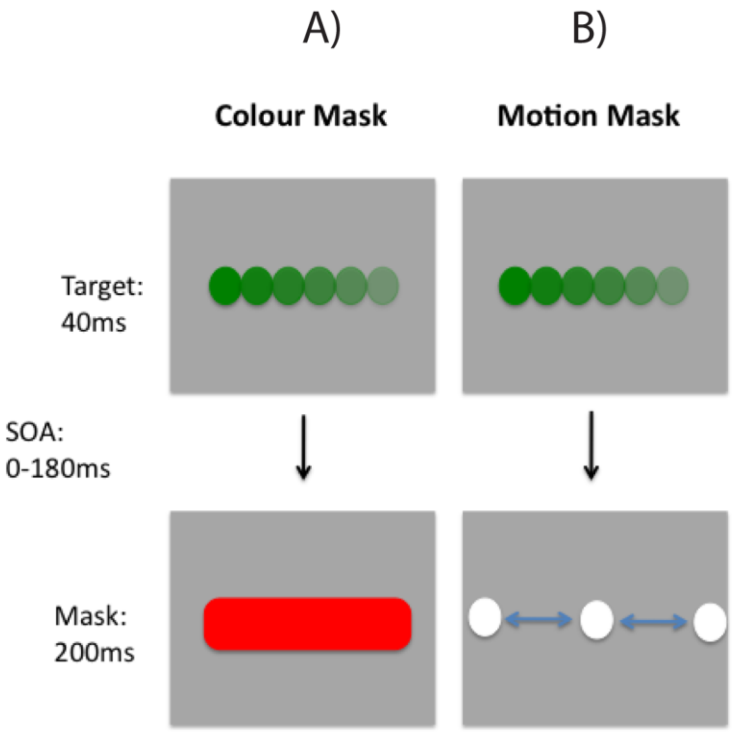

Figure 3. Schematic illustration of stimulus and task used in Experiment 2. In the examples A and B the target is identical in both cases; a rightward moving green dot. A) Colour masking stimulus, consisting of a red rectangle. B) Motion masking stimulus, consisting of horizontal motion

generated by achromatic white dots. For each display condition observers were run on separate blocks in which they had to report the colour or motion direction of the target.

Results

Figure 4A displays proportion correct results for all conditions when a motion mask is used. At short SOAs motion judgments are impaired (mean=60%), but this is not true of colour judgements (mean=95%) where performance is at ceiling. A reversed pattern is shown in the complementary condition, employing a colour mask (Fig 4B).

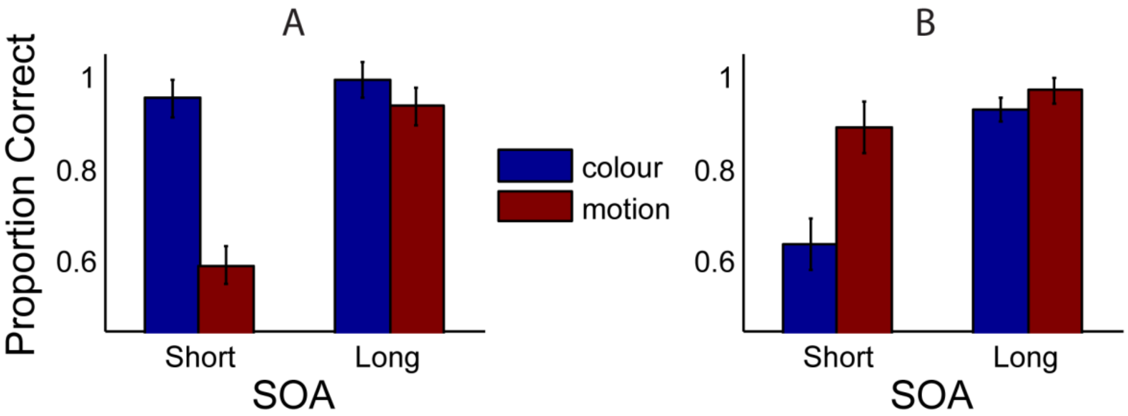

Figure 4. Proportion correct for all observers (n=12) for two SOA conditions (short and long) and two difference judgements (motion or colour). Panel A displays the case where a motion mask is used. Panel B displays the case where a colour mask is used. Error bars represent 1 SE (within subjects).

Statistical comparison reveals a significant difference at short SOAs for both mask types (Motion mask: t(11)=8.86, p<.001, Colour mask: t(11)=4.63, p<.001), thus demonstrating a feature selective masking effect. Conversely, there is no significant difference in scores for the long SOA conditions (Motion mask: t(11)=1.48, p=.166, Colour mask: t(11)=1.65, p=.13), for which masking was predicted to be minimal. Crucially, masking is not only significantly stronger within a visual dimension, but is also weak or absent across dimensions. For judgments of colour, the motion mask had little or no effect; performance remained at ceiling (95%). Similarly, for judgments of motion the colour mask appears relatively ineffectual, although performance in this condition drops slightly (< 90%). Thus, for the display settings used in this experiment, it is possible to strongly mask one feature, whilst having no effect on the other.

In a separate analysis of the colour masking data, we segregated trials into those containing opponent and non-opponent colour pairs. The results failed to show a greater masking effect for opponent colour pairs, t(9)=1.7, p=.13.

Experiment 2: Time course of the homogeneous masking effect

Feature selectivity of visual masking, as demonstrated in Experiment 1, lends clear support to the idea of segregated colour and motion processing. Another method to investigate this separation is to examine differences in the masking *time-course.* Previous studies, using a different paradigm, have argued for a faster colour processing system than for motion, resulting in the generation of a colour percept 70-80ms before that of motion (Moutoussis & Zeki, 1997a). Can this perceptual asynchrony be revealed using a masking paradigm? More specifically, is detectability of colour greater than that of motion at the same SOA, for masks of equal strength? In this experiment we measure colour and motion detectability, for homogeneous target mask pairs, using a range of different target and mask intervals (SOAs).

Method

Observers

Nine subjects (mean age of 26; 5 female) were tested. All had normal or corrected to normal vision.

Procedure

Using the within dimension stimuli described in Experiment 1, ten different SOAs, from 7 to 142ms (step size ~=15ms)[4] were tested (48 trials per SOA). In order for a meaningful comparison of colour and motion time-courses to be made it was important to first establish a benchmark at which the colour and motion masks were equally effective. For each subject, using masked stimuli with a constant SOA of 21ms, mask strength yielding 60% correct was established through the use of an adaptive staircase procedure. Mask strength was varied by increasing or decreasing the luminance of the mask. This was done for both types of homogeneous target-mask pairs (colour-colour and motion-motion). Each subject’s mask luminance values were then transferred to the main program measuring detectability at multiple SOAs.

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[4] The SOA values are accurate to within +-3ms due to MatLab/Cogent display limitations.

Results

Figure 5 shows detectability of the target feature (colour or motion) as a function of SOA (target – mask interval) for an individual subject (Fig 5a), and averaged across subjects (Fig 5b). Performance for the second SOA value (21ms) is approximately equal for colour and motion conditions, indicating that mask strength has been successfully equalised (see method for details). The idealised psychometric function fitted to the data (Fig 5a) demonstrates that colour detectability increases more rapidly than motion detectability, Colour detectability plateaus at ceiling level by 150ms SOA, while motion detectability continues to increase. Collapsed across the two longest SOA conditions of the group data (Fig 5c), there is a significant difference between colour and motion detectability, $t(8)=3.85$, $p<.01$. This difference is not present at short SOAs, $t(8)=.06$, $p >.5$. These time-course differences support a segregated processing scheme for colour and motion, with colour being processed more rapidly.

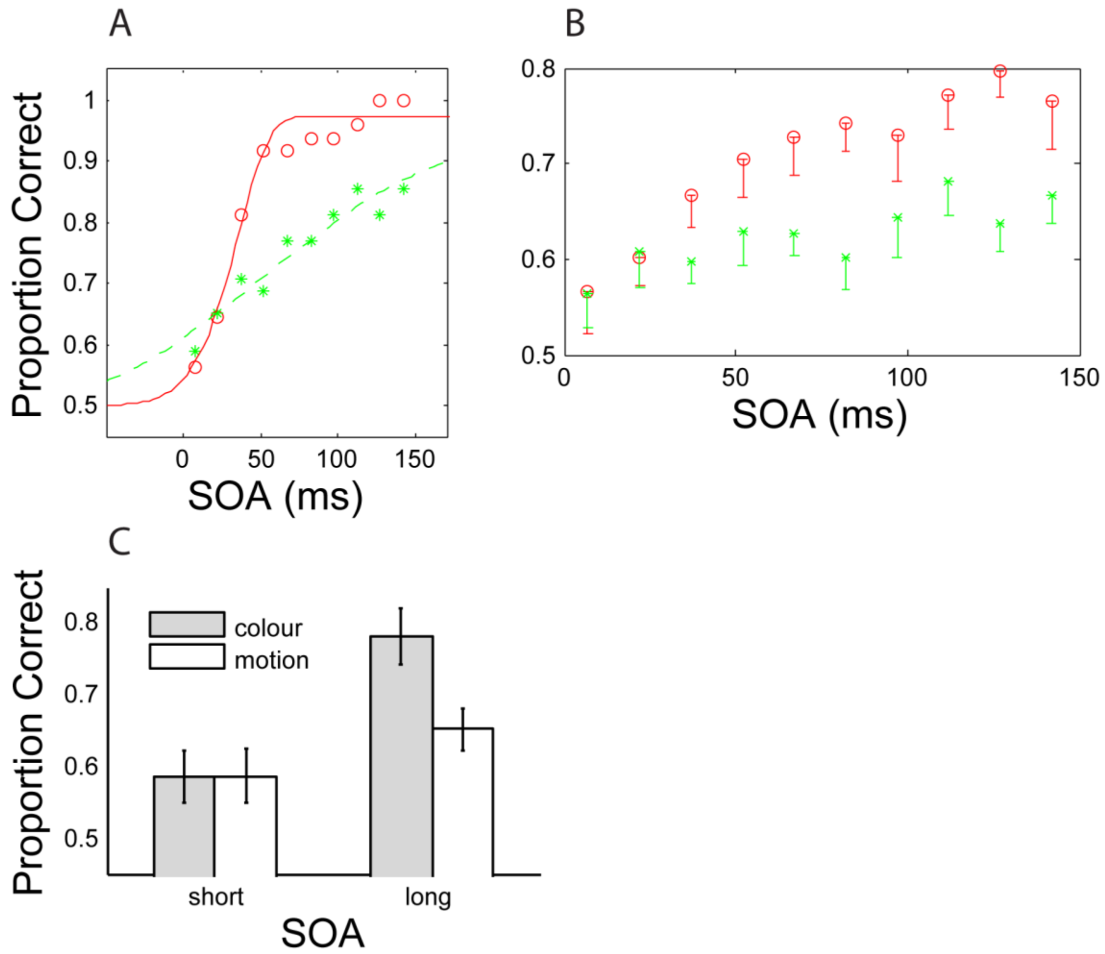

Figure 5. Time-course of heterogeneous masking for both colour (red circles) and motion (green stars). 5a displays the data of a typical subject fitted with an idealised psychometric curve (Weibull function; Wichmann & Hill, 2001). 5b display mean data averaged across all subjects (n=9). Error bars denote 1 standard error. 5c shows detectability of the colour or motion target at both *short* and *long* SOAs. The *short* condition was generated by collapsing across the two shortest SOA conditions, and the *long* condition was generated by collapsing across the two longest SOA conditions.

Experiment 3: Extending the time course: forward and backward masking

Experiment 1 demonstrated the existence of feature selective masking using a backwards masking paradigm. In the experiment 3 we wanted to learn if this pattern also applies to conditions when the mask is presented before the target (forward masking). Because binding requires more time when the signals to be bound are of a different type (e.g. colour and motion; Bartels & Zeki, 2006) we predicted that different target mask types will require longer to interact and that we will therefore see a strong cross dimensional masking effect when the mask appears before, but not after, the target.

Method

Observers

5 observers (mean age of 28; 1 female) were tested. All had normal or corrected to normal vision.

Procedure

In order to achieve greater flexibility in the temporal relationship between target and mask, and to test a finer scaled range of SOAs, the duration of the mask was decreased from 200ms to 100ms. Observers were tested on two forward masking and two backward masking SOA conditions. In the forward masking conditions the mask offset preceded the target by either 100ms (*Forward Long: FL*), or 7ms (*Forward Short: FS*). In the backward masking conditions the mask onset succeeded the target by either 100ms (*Backwards Long: BL*), or 7ms (*Backwards Short: FS*). For each of these SOAs observers were tested on all four colour –motion target-mask combinations (see Exp 1 for details), using identical stimuli to Experiment 1. In total each observer completed 80 trials per single condition.

Results

Figure 6 displays overall proportion correct scores for all conditions, averaged across the 5 observers. The outer bars illustrate scores for the conditions in which the mask and target had the greatest temporal separation. For these conditions it was expected that masking would be minimal. The central two grey bars (conditions *FS* & *BS*) represent the cases in which the target is immediately preceded or succeeded by the mask.

Heterogeneous masking

When target and mask were of different features (Fig 6 A & B), performance for the longest SOAs (outer bars) approaches ceiling level (90%), and masking is weak or absent. For the short SOAs, there is a large masking effect when the mask immediately precedes that target (*FS*); performance is significantly reduced in the forward (*FS*) vs. backward masking condition (*BS*), for both the colour mask - motion judgement ($t(4)=5.7$, $p<.001$), and motion mask - colour judgement ($t(4)=2.5$, $p<.05$) conditions.

Homogeneous masking

Overall performance for within dimension masking (69%) is less than that for across dimension masking (85%), consistent with the results of Experiment 1. In common with the cross dimension conditions, higher performance is seen for the longest SOAs (Fig 6 C

& D, outer bars). In contrast to the cross dimension conditions, there is no significant difference between the short SOA conditions (*FS* & *BS*) for the colour mask – colour judgement condition, t(4) = 1.04, p=.35 and for the motion mask – motion judgement, condition t(4) = .97, p=.39.

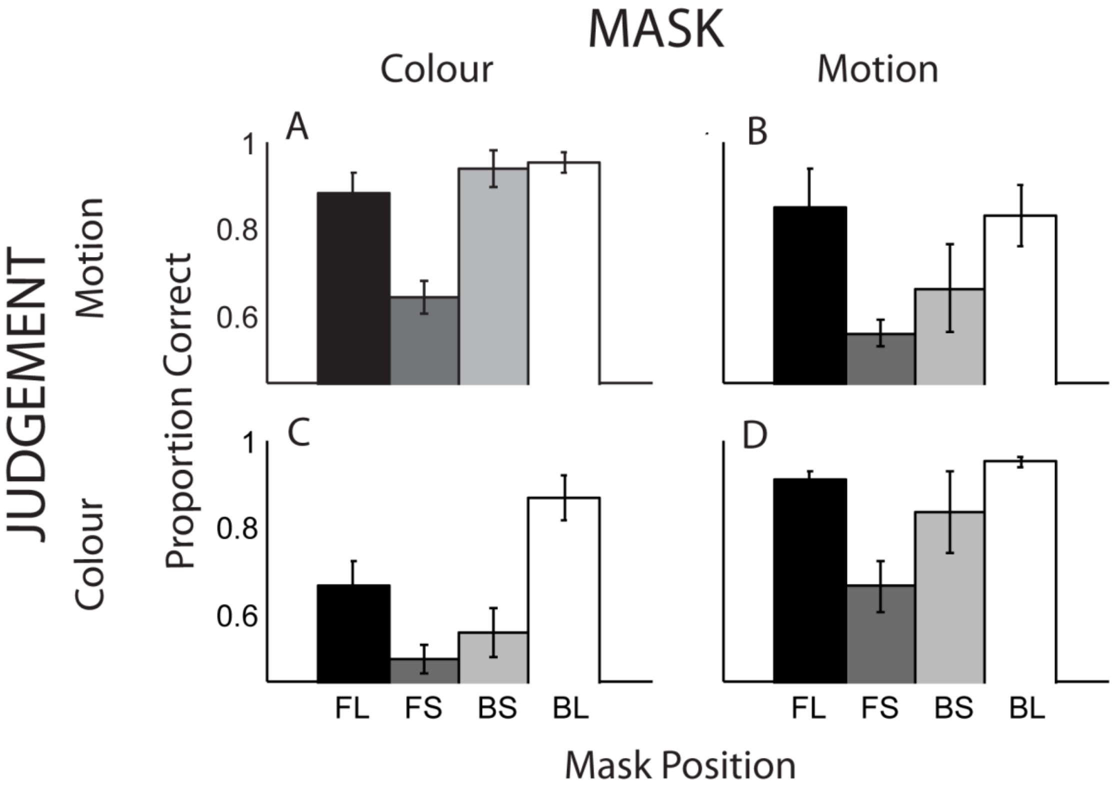

Figure 6. Proportion correct for detection of either the colour or direction of motion of a masked target. Each graph displays the four SOA conditions of FL, FS, BS and BL (see main text for details). A) motion mask - colour judgement, B) colour mask - motion judgement , C), colour mask – colour judgement , D) motion mask - motion judgement.

A significant interaction between mask position (using the short SOA conditions of *FS* & *BS*) and target-mask relationship (either across or within dimensions) provides strong evidence for dissociable masking time-courses, F(1,4) = 17.0, p=.015. These results indicate that when the target and mask are of different features, presentation of the mask prior to the target is optimal for maximising the strength of the mask. When the mask is presented subsequent to the target, the masking effect is weak. This finding is in agreement with the results of Experiments 1 and 2, which showed weak or absent heterogeneous backwards masking.

Discussion

Three variations on the visual masking paradigm have provided converging psychophysical support for the existence of functionally specialised colour and motion systems in the human visual brain. It has been shown that 1) masking is feature selective, 2) colour and motion recover at different rates from mask interference, and 3) the optimal temporal position of the mask is dependent on the feature relation of the target-mask pair. All three lines of evidence point towards a segregated coding scheme for colour and motion in the human visual system.

Although feature selective visual masking is a logical consequence of functionally specialised colour and motion systems, this separation has not been extensively explored with psychophysical techniques before. This was the main focus of Experiment 1 in which we show that when a colour mask is presented, colour judgments are impaired, while motion judgments are spared. When a motion mask is presented the reverse is true. The selective masking effect is apparent only when the mask is presented subsequently to the target (backwards masking), is significant only at short SOAs, and disappears by 500ms, consistent with previous masking results (Breitmeyer & Ogmen, 2006), and ruling out the influence of other factors such as response confusion or memory limitations. A more in-depth examination of the time-course of the masking effect was carried out in Experiments 2 and 3. The finding that detectability of the target colour increases more rapidly than for motion (Exp 2) is consistent with a shorter perceptual processing time for colour compared to motion (Moutoussis & Zeki, 1997a), and therefore a shorter time-window in which interference from the mask signal is effective.

Unequal processing times for colour and motion imply that their perceptual encoding is accomplished by different neurons in the visual system. Forward masking is not feature selective but takes place with any combination of target and mask (Exp 3). This implies that heterogeneous masking can be effective, but the target and mask signals may require more time to interact. This account fits well with the known functional segregation of the visual system, and is also supported by evidence that binding across feature dimensions requires more time (Bartels & Zeki, 2006). Additionally we found that masking strength does not depend on opponent / non-opponent target-mask colour pairs.

The results of these experiments add to previous evidence demonstrating functional specialization in the vision system (Zeki, 1978; DeYoe & van Essen, 1988; Livingstone & Hubel, 1988). They do not rule out the existence of cells in the visual system that respond to multiple properties, as has been reported for colour and form (Friedman et al., 2003), and for colour and motion (Seymour et al., 2009; Leventhal et al., 1995) but only that such units, assuming them to exist, do not display their perceptual potency in these experiments. Therefore, although these results point to the importance of separate processing streams, they are not in themselves at odds with the existence of conjunction detectors for separate visual properties, as previously reported for colour and form (Lovegrove & Over, 1973; Lovegrove & Badcock, 1981; Clifford et al., 2003) and colour and motion (Seymour et al., 2009). The observation that there was little or no carry over effect (colour masking motion, or vice versa) indicates that any conjunction selective cells contribute only weakly to perception, if at all. This of course raises the question of what the role of such putative conjunction selective cells may be.

It is worth noting that for heterogeneous masking (Exp 3), the type of target-mask pair made no difference. Regardless of whether colour masked motion, or motion masked colour, the largest effect was found when the mask preceded that target by 100ms. It is possible, therefore, that the processing latency differences for colour and motion (Moutoussis & Zeki, 1997a) relate only to the development of conscious percepts. Interference from the mask may take place before conscious percepts are generated.

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