



The temporal order of binding visual attributes

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Abstract

The brain processes distinct attributes such as colour and motion in anatomically largely segregated systems. Moreover, these two attributes are perceived with different latencies. Here, we show that the time required to bind these two attributes differs too. In psychophysical experiments, we determined minimal presentation times required to perceptually pair spatially separate pairs of stimuli consisting of colour or motion. Binding two colours required longer presentation times than binding the directions of two moving stimuli. Cross-attribute binding between colour and motion took longer than within-attribute binding. This was so even when the relative perceptual delay between colour and motion was compensated for, which accelerated colour–motion binding. Moreover, stimuli could be discriminated but not bound at fast presentation rates. Our results thus show that spatial binding is an attribute-specific process and faster within the same than across different attributes. Furthermore, the time required to bind attributes is independent of that required to process them, since colour is perceived before motion but requires longer time for binding. Finally, our results suggest that binding acts on attribute-specific neural representations of the stimuli at a late, perceptually explicit stage. These results lead us to conclude that spatial binding is separate from, and subsequent to, stimulus processing and that it is an attribute-dependent and post-conscious process.

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1. Introduction

The visual system is organized according to the principle of functional specialization, in that different visual attributes such as colour and motion are processed by anatomically segregated systems (Livingstone & Hubel, 1988; Zeki et al., 1991; Zeki, 1978). Colour is processed predominantly by cells in the blobs of V1, the thin stripes of V2 and the V4-complex, while the motion processing pathway extends from cells of layer 4B in V1 to the thick stripes in V2 and to area V5 (Livingstone & Hubel, 1987; Shipp & Zeki, 1985b; Sincich & Horton, 2005; Zeki & Shipp, 1988). It is important to note that the two systems have direct yet sparse connections (Shipp & Zeki, 1995) and both receive input from the M- and P-systems, thus allowing for some interaction

between them as is reflected in the capacity of a fraction of motion selective cells to respond, even if grudgingly, to isoluminant colour stimuli (Logothetis, Schiller, Charles, & Hurlbert, 1990; Sincich & Horton, 2002). The two systems nevertheless differ systematically in their conduction velocities and signal arrival times, which is probably a consequence of the differential myelination of their axonal connections (Beckers & Zeki, 1995; Flechsig, 1901; Schmolesky et al., 1998). A perceptual correlate of this segregation is that different attributes are also perceived with different delays, with the consequence that for a stimulus changing in both colour and motion to be perceived in synchrony, changes in colour have to lag behind changes in motion (Arnold, Clifford, & Wenderoth, 2001; Bedell, Chung, Ogmen, & Patel, 2003; Moutoussis & Zeki, 1997; Nishida & Johnston, 2002; Viviani & Aymoz, 2001). These findings, together with patient and imaging data, have led us to propose that the relative perceptual delay between colour and motion reflects directly neuronal processing delays within the distinct systems involved, and that neural

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activity in them accounts directly for the (conscious) percepts of the features processed (Bartels & Zeki, 1998; Zeki & Bartels, 1998). This view is supported by several elegant psychophysical experiments, all suggesting that the time course of perceptual experience correlates directly with that of neural activity (Arnold, 2005; Arnold & Clifford, 2002; Arnold et al., 2001; Bedell et al., 2003; Clifford, Spehar, & Pearson, 2004). For example, the relative perceptual delay of a motion stimulus is reduced as a function of the angle of the direction change: motion direction changes of 180° lead to longer perceptual delays than direction changes of smaller angles, in direct accord with the degree of inhibition and thus latency for the direction selective neurons of V5 (Arnold & Clifford, 2002; Bedell et al., 2003). Similarly, when transients of neuronal inhibition in the motion system are reduced through motion transparency the relative delay of motion can be much reduced (Clifford et al., 2004). The important point here is the existence of relative perceptual delays, even if their exact duration may be affected by the perceptual saliency or task conditions (Adams & Mamasian, 2004). Our view, supported by these findings, thus differs from that postulating ‘temporal markers.’ These have been proposed to render temporal aspects of perception independent of the neural activity underlying attribute-specific processing, such that physically simultaneously occurring events are also perceived in synchrony (Eagleman & Sejnowski, 2000; Johnston & Nishida, 2001; Nishida & Johnston, 2002). The psychophysical findings described above run counter to this, and have led us to propose that not only perception, but also perceptual binding occurs in a distributed fashion, thus allowing it to occur between any two neural stimulus representations (Bartels & Zeki, 1998). In the experiments described here we tested our prediction that the time required for binding differs depending on the attribute pairs to be bound, since partly distinct neural machineries would underlie the binding process.

In a series of psychophysical experiments we measured the time required to visually associate distinct attributes with each other. We used spatially separated stimuli as this allowed us to measure binding times both within an attribute (for example motion-with-motion or colour-with-colour) and across attributes (motion-with-colour). This form of binding across space is a necessary prerequisite for many visual functions, above all the recognition of objects and more generally for figure-background segregation based on constituent features, which may be non-contiguous due to occlusion.

Given that colour is perceived before motion, one would predict that colour would also be bound before motion. In fact, our results show exactly the reverse. In contrast to perceptual latencies, the time required for binding is consistent with the velocities of signal conduction within the cortical components of the distinct processing systems. The fibres of motion processing regions like V5 (as well as the fibres connecting the V5s of both hemispheres) are heavily myelinated while of those of V4 (as well as those linking the V4s) are not (Flechsig, 1901) (see also Section 4). Correspond-

ingly, we found that binding across attributes was slower than within attributes, consistent with the comparably sparser connections between the systems (Shipp & Zeki, 1995).

The results of our experiments show that, as in perception, the minimal time required for binding differs between attributes (but in a direction opposite to what might have been expected from relative perceptual delays), and that binding is slower across attributes than within them. Furthermore, binding of colour and motion seems to occur after stimulus processing is complete, leading us to conclude that spatial binding is an attribute-specific and post-conscious phenomenon.

2. Methods

Eight subjects (three females, age range 19–32) participated in total: all eight in Experiment 1 and four in Experiments 2–4. All but two (S.W. and A.B.) were naïve with regards to the purpose of the experiment. Cogent software (John Romaya, Vision Lab, UCL; www.vislab.ucl.ac.uk) running under Matlab (Mathworks) on a Windows PC was used for stimulus presentation on a Sony 21 in. CRT monitor operating at 85 Hz. Below we first describe the basic stimulus features and then the different experiments.

2.1. Basic stimulus features

Stimuli alternated between two states at a fixed frequency in each trial and were presented in two squares of 6.45 deg width on either side of the fixation cross, with an eccentricity of 6.45 deg to their midpoints. There were three trial types: both squares colour, both motion, or one colour and one motion (Fig. 1).

Colours alternated in two pairs, either red/cyan or green/magenta. Before the experiment pairs were adjusted such that they fused into gray at high flicker frequencies and were set to isoluminance (12.3 cd/m^2) for each subject using heterochromatic flicker photometry in the same configuration at 21 Hz (Kaiser, 1991). Their 1931 CIE (Commission Internationale de l'Éclairage) *xyz* chromaticity co-ordinates were as follows: red ($x = 0.400$, $y = 0.313$), green ($x = 0.297$, $y = 0.519$), cyan ($x = 0.208$, $y = 0.286$), magenta ($x = 0.292$, $y = 0.202$), isoluminant with gray ($x = 0.292$, $y = 0.295$, luminance = 12.3 cd/m^2) (measured using a PhotoResearch PR650 Spectrometer). In colour–colour trials different pairs of colours were used in the two squares, and correspondingly orthogonal directions

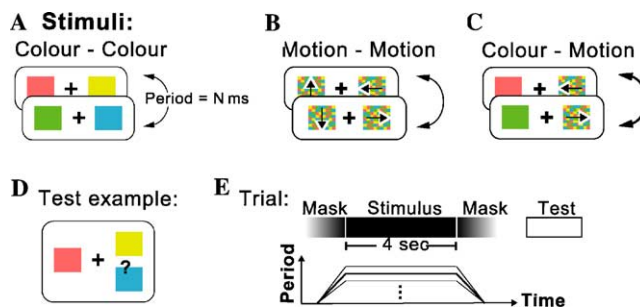


Fig. 1. Stimuli and trial timeline used in the experiment. (A–C) Each trial consisted of a stimulus pair (one attribute to either side of the fixation cross), which oscillated in their states, as shown in (A–C) for colour–colour, motion–motion, and colour–motion pairs. Motion stimuli were derived from the same isoluminant colours used in the colour stimuli. (D) Each trial ended with a 2AFC test prompt (randomized in side and identity in every trial) to indicate the correct pairing. (E) Trials lasted 4 s or until interrupted by the subject and were flanked by masks during which the oscillation frequency was ramped up or down from maximal to the trial oscillation frequency or vice versa, followed by the test prompt.

of motion in motion–motion trials. Motion was derived from a checkerboard of randomly assembled patches of the above colours (0.26 deg width) that moved behind the square, either up/down or left/right at a velocity of 5.5 deg/s. Isoluminant colours constitute a suboptimal stimulus for the motion pathway, thus providing a conservative motion stimulus given our hypothesis that integration time for motion would be shorter. If anything, our stimuli would thus have reduced the effect of our expected finding. The subjective experience of the stimuli was really that of two separate stimuli—in particular, it is important to note that the motion stimuli were in no instance perceived as belonging to a ‘global motion vector.’ Our choice of a horizontal (or vertical) stimulus arrangement with orthogonal motion directions and fixation in the middle was such that it would be physically inconsistent with a single solid object moving, rotating or expanding behind two apertures. Instead, the nearest mental image one could make of the stimulus if urged to do so would be that of two separate objects that pull each other through a rope that runs around a 90 deg corner, which is in our view thus quite far from the perception of a ‘global’ motion vector.

2.2. Task conditions

2.2.1. Experiment 1

This was the main experiment, designed to determine the temporal limit of spatial binding for three attribute pairs (colour–colour, motion–motion, and colour–motion). In detail, the subject would fixate a central fixation cross, while the attributes in the squares to its left and right would alternate between two states, simultaneously and with a fixed frequency. For example, in a colour–colour trial, the left square may alternate between red and cyan, while the right square may alternate (simultaneously with the left) between green and magenta. In this example, the only two possible states of the complete stimulus would be either red (left) and green (right) or cyan (left) and magenta (right). The task of the subject was to determine which of the colours were paired (i.e., appeared simultaneously) on the left and right. In the ensuing two alternatives forced choice (2AFC) task one of the two colours of one of the two squares would be shown, with the other square in grey (a neutral prompt). For example, the left square would be displayed in red and the right in grey. By pressing keys on the computer keyboard the subject then had to set the colour of the right square (in this example) either to green (correct) or magenta (incorrect). Motion–motion trials or colour–motion trials were organized analogous to this example with the corresponding attributes. Trials of all three binding types were presented in random order in each session, with systematically varying but randomly ordered stimulus alternation rates across trials. Trials were flanked by masks of gradually decreasing or increasing stimulus alternation frequencies. The (unmasked) trial lasted for four seconds or until button-press when subjects indicated their choice of the perceived pairing in the 2AFC task. To avoid attentional biases the ‘side’ and ‘identity’ of the 2AFC prompt (e.g. with which colour on the left (= ‘side’) was red (= ‘identity’) paired) was changed randomly with every trial. Correspondingly, all possible stimulus configurations were presented in a random and frequency balanced order. On the example of colour–colour trials: red/cyan would equally often alternate on the left as on the right (= ‘side’); red in one square would be equally often paired simultaneously with green or with magenta in the other square (= ‘identity’); and finally a trial would equally often begin with red and with cyan (= ‘face’). There were thus $2^3 = 8$ configurations for each of the three binding trial types. In each session trials of the same binding type and period were thus repeated eight times, leading to a typical number of about 240 trials per session for 10 alternation frequencies. Subjects performed eight to twenty sessions each, the initial sessions were discarded as training sessions. Four subjects performed the experiment for both a horizontal and a vertical stimulus configuration.

2.2.2. Experiment 2

This experiment served to determine the relative perceptual delay between colour and motion (see Moutoussis & Zeki, 1997, for details). The general structure of this experiment was similar to that of the first experiment. In contrast to it, all trials were performed at a fixed alternation fre-

quency, namely for each subject at its critical alternation period (75% correct) as determined in Experiment 1. Instead, across trials the change in colour was systematically delayed with respect to that in motion covering 0–360 deg phase shifts in steps of two to three frames, typically leading to about 20 different phase shifts. Like in Experiment 1, the subject had to decide in each trial on the correct pairing of the two stimuli in a 2AFC task. Subjects performed five sessions each with four trials per phase shift in each session. At every phase the rate with which the subject paired the motion direction that would be paired with the colour at 0 deg phase was measured. The resulting mean vector indicated the relative delay of this subjects’ motion percept (see Fig. 3). Randomizations, masks, etc. were as in Experiment 1.

2.2.3. Experiment 3

This was a replication of Experiment 1, but with trial types consisting of colour–colour, colour–motion with zero phase shift, and colour–motion with a phase shift as determined in Experiment 2 for each subject.

2.2.4. Experiment 4

This experiment served to confirm whether at high oscillation rates the features of the stimuli (identities of colours, directions of motion) could be perceived but not bound. First, subjects adjusted the oscillation period of colour–colour or motion–motion stimulus pairs until they could just confidently discriminate the stimulus features (eight repeats per subject). Subsequently subjects were tested at the determined mean oscillation period for their ability to (a) discriminate the stimuli (in a 2AFC task requiring them to indicate e.g. which colour was presented on which side of the display) and (b) to spatially associate the stimulus pairs like in Experiment 1, each in 24 trials.

2.3. Analysis

The critical alternation period necessary to allow spatial binding was defined as the point where subjects performed with a 75% success rate in the 2AFC task (50% = chance). For every session and each trial type psychometric functions were fitted to the logistic function using the `psignifit` toolbox for Matlab version 2.5.6 (<http://www.bootstrap-software.com>), which implements the maximum-likelihood method described by Wichmann and Hill (2001a). (Note that it uses the 75% point of the normalized fitted curve (and not the absolute 75% point), as it treats the variable lapse rate of maximal performance as a nuisance parameter). Two independent statistical tests were performed in each subject. Firstly, a one-way (repeated measures) ANOVA with the critical alternation period of the three trial types as factors across all sessions (between 8 and 20) was performed for each subject separately. Differences between all three pairs of the three trial types were assessed using a two-sided Newman–Keuls corrected post hoc test. Secondly, differences between psychometric functions of each type (pooled across sessions) were tested using `psignifit` by Monte-Carlo simulations testing the null hypothesis that the functions can be generated from a binomial process of a single function (Wichmann & Hill, 2001b). Both methods gave consistent results, and we report only results that reached significance in both the corrected ANOVA post hoc test and the Monte-Carlo test (with at least $p < .05$).

3. Results

3.1. Binding times depend on attributes to be bound

In the first and main experiment we determined the time required to associate pairs of separate stimuli belonging either to the same (motion–motion, or colour–colour) or to two different (motion–colour) attributes, with each other (see Fig. 1 and Section 2). The time required for binding was assessed in eight subjects in a 2AFC task as a function of the alternation period. In all eight, there was a consistent temporal difference in performance depending upon the

pairs of attributes to be bound. The shortest critical binding period was for motion–motion (period = 0.269 s \pm 0.033 SD, $n=8$), followed by colour–colour (0.328 s \pm 0.031 SD), followed by colour–motion (0.544 s \pm 0.142 SD) (Fig. 2A). In each subject colour–motion binding differed significantly from both within-attribute binding pairs ($p < .001$ for both Monte-Carlo and ANOVA across sessions) and in six out of eight subjects the difference between motion–motion and colour–colour was significant ($p < .05$ for both tests). Figs. 2B–E show psychometric data along with fitted curves of four subjects. In four subjects, sessions with a vertical and a horizontal stimulus arrangement had been alternated. Both arrangements led in every subject to the same sequence of critical binding periods as reported above.

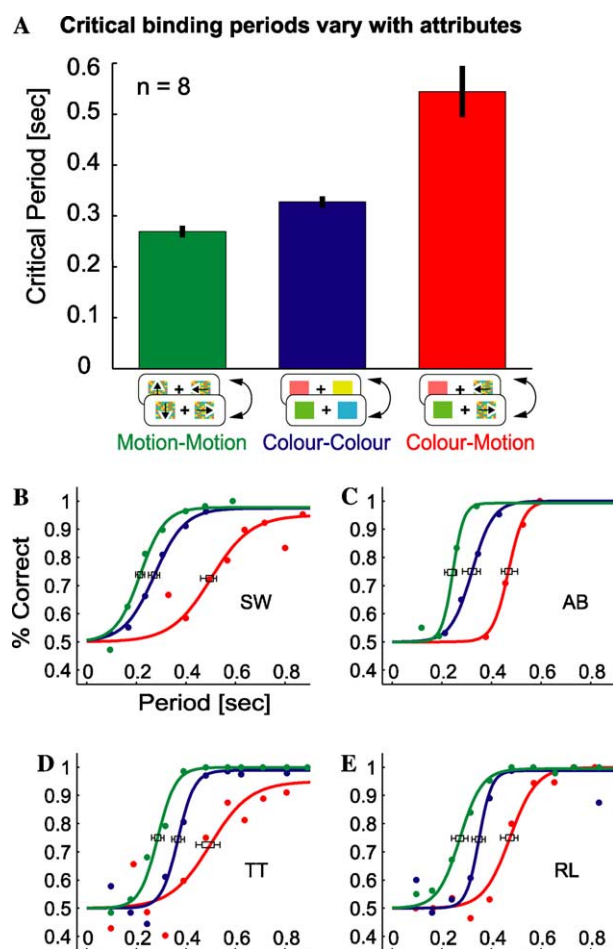


Fig. 2. Minimal stimulus integration times for spatial binding differ between attributes. Motion–motion can be bound at the fastest oscillation period, followed by colour–colour, followed by colour–motion. (A) Attribute-specific critical stimulus alternation periods (at 75% correct in a 2AFC task) for spatial binding averaged over all eight subjects, \pm SEM. (B–E) Single subject examples of four from eight subjects. Plotted are session-averaged psychometrical data (dots) and fitted logistic curves (continuous lines) for binding performance as a function of stimulus oscillation period. In each subject integration times of different attributes differed consistently (motion–motion < colour–colour < colour–motion) and significantly as assessed using corrected ANOVA across sessions and Monte-Carlo simulations ($p < .05$). Bars and whiskers indicate confidence levels corresponding to 1 and 2 SD at 75% performance according to 4999 psignif BCa bootstrap simulations (Wichmann & Hill, 2001b).

3.2. Perceptual delays affect binding times but do only partly account for slower across-attribute binding

One reason for the longer critical period for across-feature binding may be the previously reported differential latency between colour and motion perception. If binding occurs subsequent to perception, then one would expect that the relative lag between the perception of colour and motion to be reflected in binding the two non-synchronous signals: if the neural signals used for binding are not simultaneously available, binding would either fail or have to ‘wait’ until both signals are available and therefore be less efficient. We thus conducted two follow-up experiments to test whether the slow across-feature binding integration times may in part be accounted for by differential perceptual latencies between colour and motion. First we determined the relative perceptual lag of motion relative to colour at the critical alternation frequency in four subjects,

Perceptual asynchrony affects critical binding period

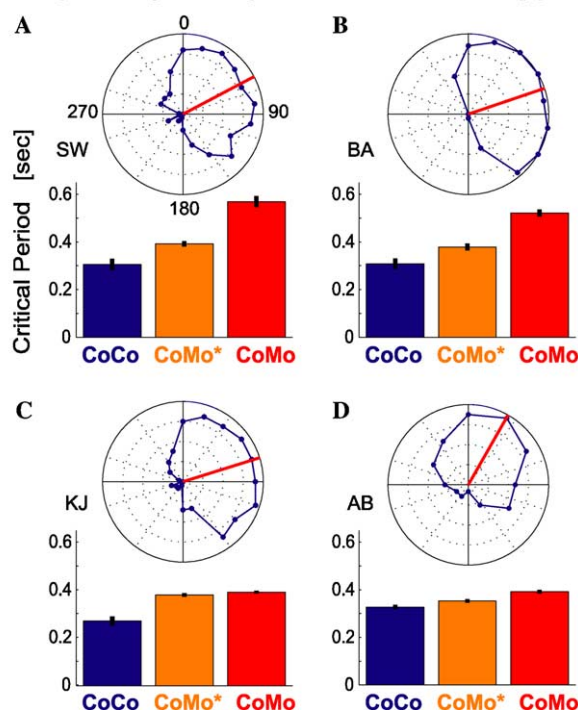


Fig. 3. Relative perceptual delays and their effect on the critical period of binding colour with motion in four subjects. (A–D) The critical period for colour–motion binding could be reduced by taking into account the relative perceptual delays between colour and motion ($p < .05$, same tests as in Fig. 2), but in every subject cross-attribute binding remained slower than within-attribute binding ($p < .05$). Top (Experiment 2): Polar plot indicating the relative perceptual delay between colour and motion for each subject. The average vector (red) indicates the physical delay (expressed as phase relative to oscillation period) with which colour needs to be shown relative to motion in order to achieve perceptual synchrony between colour and motion (for each subject determined at their critical oscillation frequency as determined in Experiment 1). Bottom (Experiment 3): Critical periods of binding colour–colour (CoCo), colour–motion with the phase shift determined above (CoMo*), and colour–motion with zero phase shift (CoMo). Errorbars: SEM (For references of colour in this figure the reader is referred to the web version of the article).

using the method introduced by Moutoussis and Zeki (1997). On average, colour had to be presented with $0.086\text{ s} \pm 0.038\text{ SD}$ ($n=4$ subjects) delay relative to motion for the two to be perceived synchronously (at an average alternation period of $0.512\text{ s} \pm 0.091\text{ SD}$, $n=4$ subjects) (see polar plots in Fig. 3). We then determined the critical binding times for colour–motion again, for stimuli with zero phase shift and ones with the phase shift as determined above for each subject such that the relative perceptual lag of motion would be compensated for. Colour–colour critical periods were determined again in the same session as a standard for the slowest within-attribute pair. In all four subjects the critical time for binding phase-shifted colour–motion was reduced (period = $0.380\text{ s} \pm 0.016\text{ SD}$, $n=4$ subjects) compared to zero-phase-shift colour–motion (period = $0.472\text{ s} \pm 0.084\text{ SD}$), yet colour–colour binding was still faster (period = $0.303\text{ s} \pm 0.025\text{ SD}$), as in the first experiment (see bar graphs Fig. 3). These findings were significant in each of the four subjects tested ($p < 0.05$, for both ANOVA across sessions and Monte-Carlo tests) (Fig. 3).

3.3. Discrimination without binding

The final experiment demonstrated what was perceptually evident in the ‘fast’ trials of the previous experiments, namely that at high alternation frequencies the distinct attributes (e.g. colour identities or motion directions) could easily be discriminated (near 100% correct), while it was impossible to associate the spatially separated stimuli to each other (chance level performance at 50% correct) (Fig. 4). This was true even at infinite trial lengths. These tests had been performed at oscillation periods adjusted such that subjects could confidently perceive the constituent features of each stimulus, for motion–motion at a mean period of $0.111\text{ s} \pm 0.036\text{ SD}$ and for colour–colour at $0.167\text{ s} \pm 0.072\text{ SD}$.

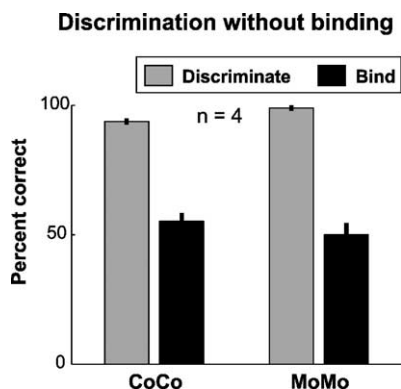


Fig. 4. Perceptual discrimination without binding at high oscillation frequencies. Shown is the mean performance for stimulus discrimination and binding across subjects (\pm SEM) at a fixed oscillation period. The oscillation period was set prior to the experiment to a level at which the subject could confidently discriminate attributes (motion–motion stimuli: $0.111\text{ s} \pm 0.018\text{ SEM}$; colour–colour stimuli: $0.167\text{ s} \pm 0.036$). While subjects could easily discriminate the constituent attributes making up the stimuli near 100% correct, they performed at chance level in spatially binding these attributes.

4. Discussion

In this study, we tried to determine the minimal stimulus presentation time necessary for associating spatially separate visual features with each other in a perceptual task. We found that: the integration time for binding varies with the attributes to be bound; binding motion to motion is significantly faster than binding colour to colour; furthermore, binding across attributes, i.e., colour to motion, is slower than binding within attributes; only a part of this longer cross-attribute binding time is due to perceptual asynchrony between colour and motion. Once relative perceptual delays were compensated for, binding time for colour–motion was significantly reduced, yet still longer than within-attribute binding. Finally we demonstrated that the presentation time that was necessary to perceive and discriminate attributes was considerably shorter than that required to bind them across space.

4.1. Attribute-specific binding and processing

The attribute-specific binding times are in line with our knowledge of the organization of the visual system, where colour and motion are processed in largely segregated systems (Livingstone & Hubel, 1987; Shipp & Zeki, 1985a; Shipp & Zeki, 1985b; Sincich & Horton, 2005; Zeki & Shipp, 1988; Zeki, 1978). We acknowledge that psychophysical evidence can only provide hints about anatomical organization, though ones which are powerful enough to be worth considering. In particular, our findings are consistent with the faster signal conduction times, due to heavier myelination, of the cortical components of the motion system, including area V5, compared to the slower conduction times in regions involved in colour processing like area V4. In particular, these differences in myelination also concern long-range connections at the same hierarchical level within a pathway that connect neurons representing different parts of the visual field. To give an example, the fibres connecting V5 of the right hemisphere with V5 of the left hemisphere are much more heavily myelinated than corresponding fibres connecting the two V4s (Flechsig, 1901). Thus, if the neural processing involved in spatial binding relies on these specialized systems (at any level), one would expect binding to be more efficient in the motion pathway than in the colour pathway, which is what we found. This leads us to suggest that spatial binding may be done at least partially within the specialized cortical components that also process the attributes. Isoluminant colours are known to be particularly ineffective motion stimuli. The fact that despite our conservative choice of isoluminant stimuli motion–motion binding was faster than colour–colour binding provides considerable reassurance of the general validity of our finding. Nevertheless, we acknowledge that the particular stimulus parameters may affect the binding times observed for within-attribute binding, as has been shown for perceptual latencies (Adams & Mamassian, 2004). Our finding that binding across attributes was generally slower than binding

within attributes shows that additional time is required for across-attribute binding that cannot be accounted for by the time constants involved in binding the individual attributes. This comparably slow across-attribute binding time is indicative of a comparably less efficient communication between the cortical components of the two systems than within. This may be a direct consequence of the comparably sparse connections between the colour and motion processing pathways (Shipp & Zeki, 1995).

4.2. *Perceptual lags and binding times*

It is important to note here that the time required to spatially associate stimuli seems entirely independent of the time required to process the stimuli per se. Our experiments here, as well as many previous ones, have consistently shown a substantial relative perceptual delay of motion relative to colour. This delay can be manipulated in ways that are entirely consistent with neuronal processing delays and thus seems to directly reflect neuronal processing delays in the two systems (Arnold & Clifford, 2002; Arnold et al., 2001; Clifford et al., 2004; Moutoussis & Zeki, 1997; Viviani & Aymoz, 2001; Zeki & Bartels, 1998). Despite this, the generally faster signal conduction times of the motion pathway seem at first sight inconsistent with the longer perceptual delay for motion relative to colour. One purely speculative interpretation of these divergent time constants for signal conduction and perception may be that the heavier myelination (and thus faster signal conduction velocity) may be the result of evolutionary pressure to reduce relative perceptual delays, as motion processing may inherently require longer processing. In contrast to perceptual delays, we found the time constants for binding to be compatible with those of the likely anatomical substrates as discussed above.

The difference in time constants for perceptual delays and for spatial binding suggests that the two constitute separate processes, and our results suggest that binding acts on neural representations of the stimuli after they have been perceived, that is after their processing is complete. Direct evidence for this comes from our comparison of binding times for colour–motion stimuli that were shown either in physical synchrony or in asynchrony that led to perceptual synchrony. Critically, binding required less time for perceptually than for physically synchronous stimuli. This can only be explained through the notion that spatial binding acts at neural stages that are at or subsequent to the stage that accounts for relative perceptual delays. A very recent study by Arnold (2005) also demonstrated faster binding for colour–motion stimuli presented with a generic colour-lag of 120 ms for every subject for spatially superimposed colour and motion. Our study thus confirms this finding and extends it to spatially separated stimuli.

Of key importance with respect to the main finding of this study was however that within-attribute binding (colour–colour, i.e., the attribute with the slowest binding time) was still faster than across-attribute binding, even when the

relative perceptual delay between colour and motion was compensated for. Taken together, the results of our experiments show that across-attribute binding is less efficient than within-attribute binding, even if we account for one of the factors contributing to this, namely asynchronous processing of the distinct attributes per se. In other words, even when the neural signals to be bound are synchronized, binding is less efficient across distinct attributes. This leads us to suggest that the communication between processing nodes that is a necessary step for binding can vary in efficiency, and in particular that it is less efficient across specialized systems than within.

4.3. *Post-conscious binding*

The final experiment showed that times for spatial binding are inherently longer than those for the mere stimulus processing necessary for discrimination. This allowed us to create stimuli that can be seen perfectly well, but whose constituent attributes could not be associated. This is a direct demonstration that binding across visual space is not required for the processing or the generation of a conscious percept of the visual components in it, and therefore that spatial binding is a process that can be separated from both processing and the generation of a conscious percept of visual attributes. We point this out here since it has been proposed that the very process of binding is what renders neural activity conscious (Engel, Fries, Konig, Brecht, & Singer, 1999). If this were so, asynchronous stimulus processing would pose a major limitation for the conscious perception of stimuli consisting of more than one attribute. Instead, our results confirm our earlier proposition that binding across space as well as across features occurs after completion of visual processing of the features per se. This is also implicit in the findings of Holcombe and Cavanagh (2001), who showed that spatially superimposed colour and orientation can be bound (and thus perceived) at extremely high oscillation rates, while binding spatially separate stimuli required more time, leading them to suggest that binding of spatially superimposed colour and orientation can happen locally. Arnold (2005) showed that this is not generally true for superimposed stimuli, as binding of superimposed colour and motion is slow and depends on their relative perceptual delays.

Our results finally demonstrate that the time required for binding spatially separate features depends on the feature combinations to be bound, which is likely to reflect the different neural pathways involved in the binding process, and that the time constants are compatible with the specific cortical components of the pathways processing the features concerned. Furthermore, the results show that binding is independent of stimulus processing, and that it happens at a stage after the stimuli have been perceived. These findings thus lead us to suggest that spatial binding is a stimulus-specific process that occurs after the generation of a conscious percept of the constituent attributes, thus fortifying our previous suggestion that binding is a

distributed and post-conscious process (Bartels & Zeki, 1998; Zeki & Bartels, 1999).

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References

- Adams, W. J., & Mamassian, P. (2004). The effects of task and saliency on latencies for colour and motion processing. *Proceedings of Biological Sciences*, 271(1535), 139–146.
- Arnold, D. H. (2005). Perceptual pairing of colour and motion. *Vision Research*.
- Arnold, D. H., & Clifford, C. W. (2002). Determinants of asynchronous processing in vision. *Proceedings of the Royal Society of London. Series B. Biological Sciences*, 269(1491), 579–583.
- Arnold, D. H., Clifford, C. W. G., & Wenderoth, P. (2001). Asynchronous processing in vision: Color leads motion. *Current Biology*, 11(8), 596–600.
- Bartels, A., & Zeki, S. (1998). The theory of multi-stage integration in the visual brain. *Proceedings of the Royal Society of London. Series B*, 265, 2327–2332.
- Beckers, G., & Zeki, S. (1995). The consequences of inactivating areas V1 and V5 on visual-motion perception. *Brain*, 118(1), 49–60.
- Bedell, H. E., Chung, S. T., Ogmen, H., & Patel, S. S. (2003). Color and motion: Which is the tortoise and which is the hare? *Vision Research*, 43(23), 2403–2412.
- Clifford, C. W., Spehar, B., & Pearson, J. (2004). Motion transparency promotes synchronous perceptual binding. *Vision Research*, 44(26), 3073–3080.
- Eagleman, D. M., & Sejnowski, T. J. (2000). Motion integration and post-diction in visual awareness. *Science*, 287(5460), 2036–2038.
- Engel, A. K., Fries, P., Konig, P., Brecht, M., & Singer, W. (1999). Temporal binding, binocular rivalry, and consciousness. *Conscious Cognition*, 8(2), 128–151.
- Flechsig, P. (1901). Developmental (myelogenetic) localisation of the cerebral cortex in the human subject. *Lancet*, 2, 1027–1029.
- Holcombe, A. O., & Cavanagh, P. (2001). Early binding of feature pairs for visual perception. *Nature Neuroscience*, 4(2), 127–128.
- Johnston, A., & Nishida, S. (2001). Time perception: Brain time or event time? *Current Biology*, 11(11), R427–R430.
- Kaiser, P. K. (1991). Flicker as a function of wavelength and heterochromatic flicker photometry. In J. J. Kulikowski, V. Walsh, & I. J. Murray (Eds.), *Limits of Vision* (pp. 171–190). Basingstoke: MacMillan.
- Livingstone, M. S., & Hubel, D. H. (1987). Connections between layer 4B of area 17 and the thick cytochrome oxidase stripes of area 18 in the squirrel monkey. *Journal of Neuroscience*, 7(11), 3371–3377.
- Livingstone, M. S., & Hubel, D. H. (1988). Segregation of form, color, movement, and depth: Anatomy, physiology, and perception. *Science*, 240, 740–749.
- Logothetis, N. K., Schiller, P. H., Charles, E. R., & Hurlbert, A. C. (1990). Perceptual deficits and the activity of the color-opponent and broad-band pathways at isoluminance. *Science*, 247(4939), 214–217.
- Moutoussis, K., & Zeki, S. (1997). A direct demonstration of perceptual asynchrony in vision. *Proceedings of the Royal Society of London. Series B*, 264(1380), 393–399.
- Nishida, S., & Johnston, A. (2002). Marker correspondence, not processing latency, determines temporal binding of visual attributes. *Current Biology*, 12(5), 359–368.
- Schmolesky, M. T., Wang, Y., Hanes, D. P., Thompson, K. G., Leutgeb, S., Schall, J. D., & Leventhal, A. G. (1998). Signal timing across the macaque visual system. *Journal of Neurophysiology*, 79(6), 3272–3278.
- Shipp, S., & Zeki, S. (1985a). Segregated output to area V5 from layer 4b of macaque monkey striate cortex. *Journal of Physiology—London*, 369(DEC), 32.
- Shipp, S., & Zeki, S. (1985b). Segregation of pathways leading from area V2 to areas V4 and V5 of macaque monkey visual cortex. *Nature*, 315, 322–325.
- Shipp, S., & Zeki, S. (1995). Segregation and convergence of specialized pathways in macaque monkey visual cortex. *Journal of Anatomy*, 187(Pt. 3), 547–562.
- Sincich, L. C., & Horton, J. C. (2002). Divided by cytochrome oxidase: A map of the projections from V1 to V2 in macaques. *Science*, 295(5560), 1734–1737.
- Sincich, L. C., & Horton, J. C. (2005). Input to V2 thin stripes arises from V1 cytochrome oxidase patches. *Journal of Neuroscience*, 25(44), 10087–10093.
- Viviani, P., & Aymoz, C. (2001). Colour, form and movement are not perceived simultaneously. *Vision Research*, 41(22), 2909–2918.
- Wichmann, F. A., & Hill, N. J. (2001a). The psychometric function: I. Fitting, sampling, and goodness of fit. *Perception Psychophysics*, 63(8), 1293–1313.
- Wichmann, F. A., & Hill, N. J. (2001b). The psychometric function: II. Bootstrap-based confidence intervals and sampling. *Perception Psychophysics*, 63(8), 1314–1329.
- Zeki, S. M. (1978). Functional specialization in the visual cortex of the monkey. *Nature*, 274, 423–428.
- Zeki, S., & Bartels, A. (1998). The asynchrony of consciousness. *Proceedings of the Royal Society of London. Series B*, 265, 1583–1585.
- Zeki, S., & Bartels, A. (1999). Toward a theory of visual consciousness. *Consciousness and Cognition*, 8, 225–259.
- Zeki, S., & Shipp, S. (1988). The functional logic of cortical connections. *Nature*, 335, 311–317.
- Zeki, S., Watson, J. D. G., Lueck, C. J., Friston, K. J., Kennard, C., & Frackowiak, R. S. J. (1991). A direct demonstration of functional specialization in human visual cortex. *Journal of Neuroscience*, 11, 641–649.