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RESEARCH ARTICLES

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Colour vision can contribute to fast corrections of arm movements

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Abstract Can chromatic information be used for the fast on-line control of action? In order to find out we asked subjects to tap a red square as quickly as possible. In half of the trials the red square's position changed as soon as the subject's hand started to move. We examined how quickly subjects could adjust their movements to this change. In half of the trials there was also a green square of the same luminance as the red one. If there was a green square, and the red square's position changed, the change consisted of the two squares exchanging places, so that all that really changed was the squares' colours. In such cases subjects could not have adjusted their movements without having analysed the colour. Nevertheless, subjects could respond adequately within as little as 120 ms. This was even so if the squares' luminances changed considerably at the moment that the subject's hand started to move. Thus, chromatic information can be used for the fast on-line control of action

Keywords Colour · Human · Motor control · On-line · Reaction time

Introduction

A compelling visualisation of the existence of multiple independent visual pathways in the brain is that motion perception is much poorer when based on colour contrast than when based on luminance contrast. This phenomenon can readily be related to the presence of different cell groups within the retina and lateral geniculate nucleus (LGN) that each combine the signals from the rods and cones in different ways, so that they are each best suited for analysing certain visible properties. Such early specialisation has obvious advantages, but separating the processing into separate pathways also has consequences that could be disadvantageous. One such consequence is that motion perception is largely indifferent to colour (Gegenfurtner and Hawken 1996). However, normally this does not matter because it is only important when moving coloured objects are exactly the same luminance as their surroundings, which is only likely to happen in carefully designed experiments.

Certain aspects of our actions probably also depend on specialised pathways. One such aspect is the quick adjustments that we make to our movements if the target of the movement is suddenly displaced (Brenner and Smeets 1997; Goodale et al. 1986; Pélisson et al. 1986; Prablanc and Martin 1992). There is neurological evidence that a posterior parietal visual pathway is involved in this (Pisella et al. 2000). The evidence that this is a specialised pathway for correcting ongoing movements is that transcranial magnetic stimulation of the posterior parietal cortex disrupts the adjustments, although it does not disrupt the movement itself (Desmurget et al. 1999). If this pathway is responsible for the fast adjustments to target perturbations, then we should find poor responses to purely chromatic information because this pathway gets most of its input from the Magno-cellular layers of the LGN (van Essen et al. 1992; Merigan and Maunsell 1993).

Pisella et al. (1998) tested this hypothesis by comparing responses to a change in colour with ones to a change in position. They found that stopping a movement in response to a change in the target's colour takes more than 50 ms longer than adjusting the movement in response to a change in the same target's position. They interpreted this latency difference as evidence that people cannot respond quickly to changes in colour, and attributed this to poor colour processing within the parietal pathway. We tested the same hypothesis using targets that are only visible to the Parvo-cellular pathway (Brenner and Smeets 2003), and found that it took people only slightly longer to respond to perturbations of such targets than to respond to perturbations of other targets. We attributed the small time difference to the difference between the latencies in Magno-cellular and Parvo-cellular input to the parietal cortex (Maunsell et al. 1999;

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Schmolesky et al. 1998). Thus, we proposed that responses to chromatic information take slightly longer because the required visual processing takes slightly longer, but that they were otherwise just as readily available for guiding our actions. Why did we reach such different conclusions?

There are two important differences between the two studies, apart from whether the emphasis was on the initial response or the outcome. The first is that we (Brenner and Smeets 2003) examined the response to the *position* of a target defined by colour, whereas Pisella et al. (1998) examined responses to the *colour* itself. It is possible that the position of chromatic borders is passed on to the pathway that is responsible for fast adjustments, while the chromatic signal itself is not (see Heywood et al. 1998). The second difference is that aborting a movement may not be a task that can be done quickly (Smeets et al. 1995). Pisella et al. (1998) realised this and showed that subjects could stop quickly in response to a change in target position. However, this may not be a good control for two reasons: firstly, because in that case the target towards which one is moving disappears, which it does not if it changes colour and, secondly, because their method does not distinguish between actually stopping and diverting the movement to the new position (despite not being instructed to do so).

In order to determine which of the two above-mentioned differences is critical, we decided to repeat our own study in a manner that would force subjects to respond to the colour itself. In the critical condition there were two squares, a green one and a red one. Subjects had to tap the red one as quickly as possible. As soon as their finger started moving the luminance of both the squares changed. On some trials the squares also swapped positions (i.e. colours) at that moment. We determined how quickly subjects adjusted their movements to such a change in colour.

Methods

Subjects stood in front of a large, slightly inclined surface onto which stimuli could be back-projected at 120 Hz and a resolution of 800×600 pixels with the help of a Sony (VPH 1271 QM) CRT projector. The near edge of the surface was 120 cm from the floor. Together with the inclination of 20° this gave a large comfortable surface for tapping movements (see Fig. 1a). The position of the subject's index finger was recorded at 1,000 Hz and a high spatial resolution with an Optotrak 3020 (Northern Digital Inc.).

Subjects

This study is part of an ongoing research program that has been approved by the local ethics committee. Twelve people volunteered to take part in the study after being informed about what they would be required to do. Two were the authors. The other ten were colleagues who were unaware of the hypothesis that was being tested. Each subject made 160 tapping movements in each of two sessions. The order in which they performed the two sessions was counterbalanced across subjects.

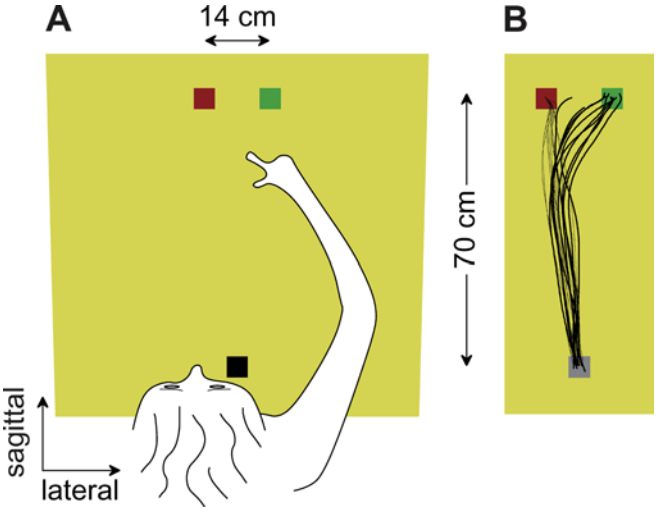

Fig. 1a, b The task. **a** Subjects stood in front of a large slightly inclined plane onto which the stimuli were back-projected. Each trial started with the subject putting his or her index finger on the black square at the near side of the screen. After some time a red square (the target) appeared at one of two possible locations further away. In half of the trials the target was accompanied by a green square at the other location (as shown). The subject's task was to tap the target as quickly as possible. On half of the trials the target 'jumped' to the other position as soon as the subject's hand started to move, switching positions with the green square if there was one. **b** Subject RB's movement paths for the trials in which a bright red square initially appeared on the left, and a bright green one on the right. These paths are from the session in which the luminance did not change. The black square is shown in grey so that the beginnings of the movements are visible. The *thin curves* show the paths on trials in which the target position did not change. The *thick curves* show the paths when it did, in which case the red square was obviously on the right and the green one on the left during most of the movement

Stimuli

The display consisted of several 32×32 pixel squares (sides of 4.2 cm) that were either brighter or darker than the yellow background (2 cd/m^2). The starting point was a black square, close to the near edge of the screen. The target was a red square, with a luminance of either 1.2 or 2.8 cd/m^2. On half of the trials there was also an irrelevant green square, of the same size and luminance as the red one (as measured with a Minolta LS-110 luminance meter). These squares were 70 cm from the starting point in the sagittal direction, and either 7 cm to the left or 7 cm to the right (see Fig. 1a).

Procedure

Subjects started each trial with their finger at the starting point. Some time after subjects placed their finger on this

black square, the target square appeared at one of its two possible positions. At the same time, on half the trials, a green square appeared at the other side. The task was always to tap the red square. As soon as the subject's finger started to move (velocity threshold of 1 m/s), the display could change in several ways.

One possible change was that the target could jump to the other position. If there was also a green square, then the latter jumped in the opposite direction, so that the two squares appeared to switch colours. The trials in which the green square was present formed the critical condition because in that case subjects must determine the colour of at least one square in order to know whether the target had switched location. Moreover, in that case there was still a square where the target had previously been.

In one of the two sessions the display also always changed at the moment that the subject's finger started to move: the luminance of the red target changed from being brighter than the background to being darker than the background, or vice versa. If there was a green square, its luminance changed in the same way as that of the target. In the other session the luminance did not change.

The trials in which there was no green square were included for comparison. They require no colour processing because the only square was the red target. There were no catch trials without a target. The session in which the luminance changed was included because although the red and green squares were always isoluminant for a "standard observer", they were not necessarily perfectly isoluminant for our observers. Perfect isoluminance is very difficult to achieve at the time of a change because one has to deal with a combination of chromatic and temporal properties. Thus, even if we had determined the isoluminance point for individual subjects, we would not be certain that our observers were not responding to a transient change in the effective luminance at the moment that the colour changes. By clearly changing the luminance at the time that the colour could change, we could be sure that subjects did not simply switch sides when they detected a change, without analysing the colour.

In each session there were 16 conditions. The conditions were obtained by taking all combinations of the number of squares (*target only* or *both target and green square*), the initial luminance (*higher* or *lower* than the background), the initial position of the red target (*left* or *right*), and whether or not the target changed position. There were ten repetitions of each kind of trial. The 160 trials were presented in random order. Subjects were instructed to tap the target as quickly as possible. They were rewarded for also being accurate by a tone that sounded if their movement ended on the target.

Analysis

Velocities were calculated by dividing the distance between two samples by the time interval between them (1 ms). This velocity was assigned to the moment between the two samples. A slightly smoothed acceleration was calculated by subtracting such a velocity from the velocity three samples later, and dividing this difference by the time interval between the two velocities (3 ms). This acceleration was assigned to the moment between the two velocities involved. Altogether this means that the two samples before and after each sample are used to determine the acceleration at the moment of that sample.

Synchronisation of the hand movements with the events on the screen was achieved by only connecting the red and green channels of the computer's image to the projector, but drawing some images with a blue component as well, and connecting the blue channel to the AD-input of the Optotrak. In this way we could determine when the target appeared, and when it jumped, with the 1-ms resolution with which the movement of the hand was recorded.

We defined the beginning of the tapping movement as the last interval before the hand's velocity reached its peak during which the finger moved at less than 0.1 m/s. The end of the tapping movement was defined as the first interval during which it fell below 0.1 m/s. The reaction time is the time between target onset and the beginning of the movement. The target changed position and luminance some time after what we consider to be the beginning of the movement because of inevitable delays in the presentation and because we used a higher threshold (1 m/s) during the experiment. This was necessary because we obviously could not work back from peak velocity on-line, and we had to be sure that the movement had really started before making the changes.

To determine how quickly subjects respond to a change in target position we determined the difference between the lateral acceleration of the finger when the target position did and when it did not change. When the target was initially on the left, rightward acceleration was considered positive. When it was initially on the right, leftward acceleration was considered positive. Thus, whenever the target position changed, acceleration in the direction of the new target position was considered positive. We call the difference between the lateral acceleration of the finger when the target position did and when it did not change the *additional lateral acceleration*.

In order to calculate this additional lateral acceleration we first synchronised all the trials relative to the moment that the target (would have) changed position. There were an equal number of trials in all conditions, and no trials were discarded, so any effect of initial target luminance (brighter or darker than the background) or initial position (left or right) is balanced across conditions. Thus, since we are not particularly interested in such potential effects, we can average the responses across these variables. This left us with four variables: whether or not the luminance changed (the two sessions) and whether or not there was an additional green target. The additional lateral acceleration for these four cases is calculated by simply subtracting the average lateral acceleration on the trials in which the target position did not change from the average lateral acceleration on trials in which it did.

For the trials on which the target did change position we also determined the peak lateral acceleration (in the direction of the change). Before looking for the peaks we smoothed the acceleration data by determining the weighted average for a time window of 80 ms (with the weight decreasing linearly from 20 to 1 from the centre of the window). We used these peaks to estimate the variability in the latency and intensity of the responses.

Results

The average reaction time was 313 ms. An analysis of variance on the subjects' mean reaction times, with the number of squares and the kind of session (one in which the luminance did or did not change) as factors, did not reveal any significant effects. The target changed position about 49 ms later. The average movement time was 474 ms when the target changed position and 446 ms when it did not. An analysis of variance on the subjects' mean movement times, with the number of squares, whether they changed position and the kind of session as factors, showed that this difference was the only significant effect (p =0.015).

Figure 1b shows the paths of a few typical movements. It is evident from these examples that the longer path when the target changed position can easily explain the longer movement time in this condition. We can also see that this subject sometimes stopped before reaching the target.

Figure 2 shows the average additional lateral acceleration of the hand in the presence (*thick curves*) and absence (*thin curves*) of the green square, both when the luminance changed (*red curves*) and when it did not (*black curves*). Each curve shows the difference in lateral acceleration between trials on which the target did and did not change position (see methods for details), averaged across the 12 subjects, two initial luminances and two initial positions of the red target. The main conclusion that we can draw from Fig. 2 is that people can respond to a change in target location within about 120 ms. They can do so even if only the squares' colours change, and even if the luminance changes quite dramatically at the same time, so it is very unlikely that their responses were based on residual luminance changes.

Although the response to a switch in target location seems to start at the same time in all four conditions, it is very clear that the average response was more vigorous when there was only a red square (*thin curves*) than when there was also a green one (*thick curves*). This could be because the lateral acceleration on individual responses was stronger when there was only one square, or because there was more variability in the timing of the responses when there were two squares. In order to distinguish between these two possibilities, or combinations of the two, we have to look at individual trials. For the trials in which the target position did change, we can do so if we assume that the peak in the lateral acceleration corresponds with the maximal response to the change.

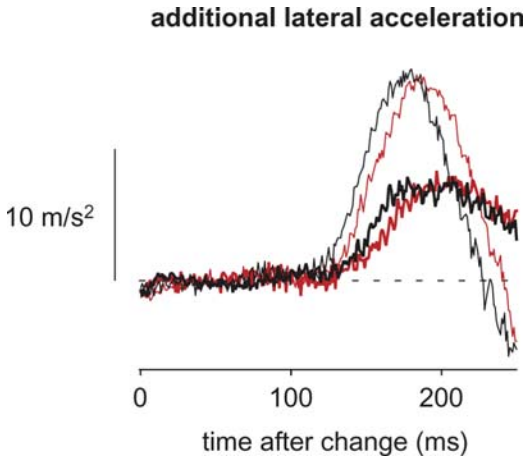

Fig. 2 The difference between the lateral acceleration of the hand when the target changed position and the lateral acceleration when it did not, as a function of the time after the change in position. Average of 12 subjects. A positive lateral acceleration is acceleration in the direction of the change in target position. The *red traces* are for the session in which the luminance changed and the *black traces* are for the session in which the luminance did not change. The *thin curves* are for trials in which the red target square was presented alone and the *thick traces* are for trials in which there was also a green square

Figure 3 shows the distribution of peak acceleration times for trials with only a red square (*red bars*) and trials with both a red and a green square (*black bars*). For the trials in which only the red target was present, the histogram has a clear peak at about 175 ms (*red bars* in Fig. 3). Since this is about the time of the peak in the average response on these trials (*thin curves* in Fig. 2), the assumption that the largest lateral acceleration corresponds with the maximal response to the change is probably correct. In an analysis of variance on the subjects' mean peak latencies, with the number of squares and the kind of session (one in which the luminance did or did not change) as factors, the effect of session and the interaction were not significant. The difference between trials with one and two squares was highly significant (p <0.0001). As we can see in Fig. 3, the earliest responses had the same latency in both cases, but the distribution of peak latencies was much wider when there were two squares. However, this does not answer our question because the wider distribution could be caused by more variability in the timing or by variability in the magnitude, and thus also the duration, of the response. In order to distinguish between these possibilities we have to look at the magnitude as well.

Figure 4 shows the average lateral acceleration when trials are synchronised with respect to the peak in their lateral acceleration rather than with respect to possible changes in the display. In this case we do not subtract the lateral acceleration on trials with no change because we cannot synchronise those accurately. It is clear from this figure that the magnitude of the response was the same for sessions in which the luminance changed as for ones in which it did not, and that the presence of a green square did not make a difference. This was confirmed by an analysis of variance on the mean amplitudes of subjects'

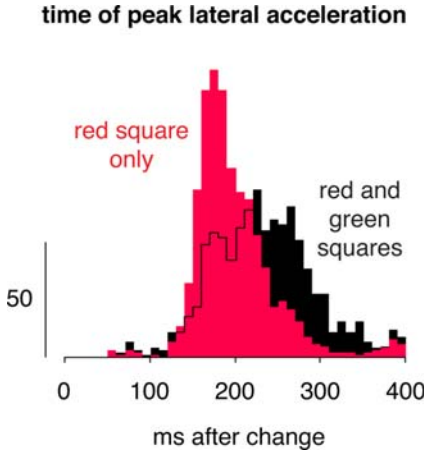

Fig. 3 Frequency histogram for the time of the peak lateral acceleration. The colour indicates whether the red target square was presented alone (*red bars*) or together with a green square (*black bars*). Pooled data from both sessions

peak lateral accelerations, with the number of targets and the kind of session as factors. Thus, we can conclude that the reason for the lower peaks when there were two targets in Fig. 2 is that the timing of the responses is more variable.

Discussion

Our main finding is that subjects can respond within about 120 ms to a change in colour, even if the luminance changes considerably at the same time. In Fig. 2 we isolated the response to the change in target position by comparing trials in which the target changed position with ones in which it did not. We could not use this procedure for Fig. 4 because we can obviously only synchronise trials with respect to the peak in the response when the target position changes (so that there is a response). The advantage of also considering trials in which the target's position does not change is that we can distinguish between lateral acceleration in response to the changed position and lateral acceleration due to systematic curvature in the hand's path. However, such systematic curvature is presumably the same for all four conditions, so it does not affect the comparisons within Fig. 4. Moreover, since we inverted the sign of the lateral acceleration for half the targets (to ensure that all responses in the direction of the change in position were positive) the influence of systematic curvature will largely be cancelled (assuming that it is similar for movements to the two target positions).

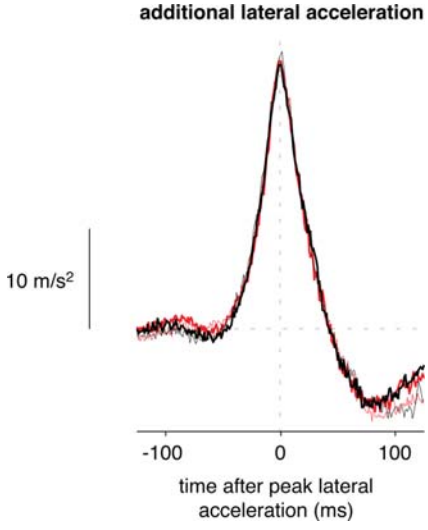

Fig. 4 The lateral acceleration of the hand as a function of the time after the peak lateral acceleration. Average of 12 subjects. A positive lateral acceleration is acceleration in the direction of the change in target position. The *red traces* are for the session in which the luminance changed and the *black traces* are for the session in which the luminance did not change. The *thin curves* are for trials in which the red target square was presented alone and the *thick traces* are for trials in which there was also a green square

The present study shows that fast corrections are possible on the basis of chromatic information. Schmidt (2002) reached a similar conclusion in a study in which he showed that undetected coloured primes could influence human movements. He used a pointing task that was somewhat similar to our trials with two targets and no change in luminance. When an inconsistent prime was presented just before the stimuli, subjects initially moved in the direction of the prime, but later adjusted the movement in the direction of the target. Schmidt did not explicitly try to determine how quickly subjects responded to the target being a different colour than the prime, but his Fig. 2 suggests that it takes at least 200 ms. Perhaps the reason for it taking so much longer in his study is that the prime was clearly different from the target, so that the subject could not rely on mechanisms that are intended to adjust an ongoing movement to a given target.

This explanation brings us back to the two studies that we mentioned in the introduction (Brenner and Smeets 2003; Pisella et al. 1998). It is now clear that having to determine the colour itself, rather than only using chromatic information to localise the target, was not the critical difference between those studies. Presumably the critical difference is that aborting a movement is a change in task, and that changing the task, like initiating a whole new movement, takes additional time. The subjects in our present study could quickly divert their movement to a second position when the target's position changed because the task remained to move towards the red target. When there were two squares, subjects needed to determine the colour before they could decide whether the target changed position, but the task did not change.

The responses often had longer latencies when there were two squares. This suggests that the fast on-line corrections do not always occur automatically. We propose that the longer latency is connected to the fact that the target square changed its colour to green rather than disappearing altogether. When planning a movement towards a target, various attributes could be used to specify that this is the target. Perhaps subjects sometimes initiate their movement towards a square at a certain

position, rather than towards one of a certain colour. When there is only one square, this makes no difference to the correction because if the target position changes, the nearest square to the specified position is also the one of the correct colour. However, when the two squares switch positions, there is still a square at the original position. It could be that when there are two squares and subjects direct their movements towards a position, they fail to respond quickly to the change and respond with a latency that is more like the reaction time that Pisella et al. (1998) found instead. Although this account is very speculative, it would explain the larger distribution of reaction times when there were two squares in the present study. It is also consistent with our impression that there are two groups of values in each of the histograms of the time of the peak latency (see Fig. 3). The difference is that almost all the peaks are within a group at about 175 ms if the target is presented alone (*red bars*), while most are at about 250 ms if there are two squares (*black bars*).

We designed the present experiment to be as simple as possible in order to make sure that no other factor than colour vision could be limiting our subjects' performance. The simplest case that we could think of was when two isoluminant targets of different colours swap places. As already mentioned, the problem with this condition is that subjects could simply switch targets as soon as they noticed anything happen. We showed that this is not what our subjects were doing by including a separate session in which the targets' luminances changed simultaneously by more than a factor of 2 (from being considerably brighter than the background to being considerably darker than the background, or vice versa) at the moment that the targets could swap places. Such changes will presumably also have masked the quick detection of any small (transient) differences in luminance (see Brenner and Smeets 2003). We could have made even more certain that subjects were using colour to perform the task by introducing independent changes in luminance and colour. However, that would mean that the precise appearance of the target is no longer predictable (our subjects could always know exactly what the target would look like at each stage of a trial). Whether this is important remains to be examined.

In the present study we show that people can respond to colour (almost) as quickly as to luminance contrast. The estimated latency of 120 ms is only slightly longer than the previously reported latency of about 110 ms for responding to displacements of luminance defined targets (Brenner and Smeets 1997; Prablanc and Martin 1992). Moreover, in our conditions with a single red square, in which subjects did not necessarily need to determine the colour, the fastest responses had about the same latency as in our conditions with two squares, in which subjects did need to determine the colour. The main difference between the conditions was that subjects *always* responded very fast when there was only one square, whereas they often took considerably longer (in the order of 50 ms) when there were two squares. Thus, some factor probably limited people's ability to make fast corrections to their movements during some of our trials in which there was a green as well as a red square, but this factor cannot be the need to process chromatic information because that was necessary on all such trials.

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