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RESEARCH ARTICLE

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Perceptual requirements for fast manual responses

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Abstract The on-line visual control of human movements can be exceptionally fast. Whether it is fast depends on the kind of visual information that is involved. In the present study we examine whether fast on-line control is specific to the magnocellular visual pathway. Fast manual responses become evident when an ongoing movement has to be adjusted, for instance because the target is displaced. We examined whether the response to such perturbations is faster for stimuli that only activate the magnocellular pathway than for equally conspicuous stimuli that only activate the parvocellular pathway. The response was indeed about 35 ms faster for stimuli that activate the magnocellular pathway. However, we argue that the slower response to stimuli that only stimulate the parvocellular pathway is due to the properties of the neurones involved and the less direct connection to the motor areas, rather than to fast reactions being driven exclusively by magnocellular input.

Keywords Perceptual requirements · Fast manual responses · Visual control · Human movements · Magnocellular visual pathway · Parvocellular pathway

Introduction

Even if you do your best, it takes you almost 200 ms to release a button in response to a bright flash. If the target is difficult to detect, if you are only to respond to certain stimuli, or if you have to respond to different stimuli in different ways, it takes you longer. Yet, if a target is suddenly displaced while you are moving your hand towards it, it only takes you slightly more than 100 ms to respond in a goal-directed manner (Brenner and Smeets 1997; Pisella et al. 2000). This is even so if you do not notice the displacement (Goodale et al. 1986; Pélisson et al. 1986; Prablanc and Martin 1992). What makes us able to react so quickly in some cases? To answer this question we turn to the neuronal pathways that are likely to mediate these fast responses.

There is quite compelling evidence that the parietal visual pathway is involved in these fast responses (Milner and Goodale 1993). Parietal areas of the cortex are suitable for such a role because they are believed to process information about where things are (Mishkin et al. 1983), quickly taking into account any changes in the orientation of the eyes (Duhamel et al. 1992). Direct evidence for the parietal visual pathway being involved in fast responses is that a patient with a bilateral posterior parietal lesion was unable to make such quick responses (Pisella et al. 2000). Moreover, transcranial magnetic stimulation of the posterior parietal cortex disrupted such responses, although it did not disrupt movements toward targets that were not displaced (Desmurget et al. 1999).

The cells in the parietal pathway also have shorter visual response latencies than do cells in comparable areas in the temporal pathway (Bullier 2001; Schmolesky et al. 1998; review in Box 2 of Lamme and Roelfsema 2000). The shorter latency in the parietal cortex is probably at least partly a consequence of it getting most of its input from the magnocellular layers of the LGN, which respond faster than the parvocellular and koniocellular layers (Maunsell et al. 1999; Schmolesky et al. 1998). We therefore decided to examine whether fast responses are only possible for stimuli that stimulate the magnocellular pathway (van Essen et al. 1992; Lee 1996; Lee et al. 1990; Merigan and Maunsell 1993).

It is known that the properties of the magnocellular and parvocellular neurones are reflected in the reaction times to stimuli that selectively stimulate these cells (Burr and Corsale 2001; Plainis and Murray 2000; Schwartz 1992). We decided to examine whether the fast responses to target perturbations were only possible if the targets were visible to the magnocellular pathway. To do so we devised stimuli that would only be visible to the parvocellular pathway. We consider reactions to perturbations to be 'fast' if the latency to respond to them is clearly shorter than the latency to respond to target onset.

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Experiment 1: are fast reactions colour-blind?

Materials and 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 pointing movements (see Fig. 1). The position of the subject's index finger was recorded at 500 Hz and a high spatial resolution with an Optotrak 3010 (Northern Digital Inc.).

The stimuli

The main characteristics of the parvocellular pathway are a high spatial and chromatic resolution and a low temporal resolution. The stimulus that we designed to selectively stimulate the parvocellular pathway was an isoluminant red-green 8×8 checkerboard. Each field of the checkerboard was 4 by 4 pixels, corresponding from the subject's perspective with about 20 min of arc horizontally and 10 min of arc vertically (the difference is due to the orientation of the surface). The 21 cd/m^2 of the green fields was exclusively from the green gun of the projector. The 21 cd/m^2 of the red fields was a combination of the maximal output of the red gun and a modest contribution from the green gun. Careful calibration ensured that the average chromaticity of these two fields was identical to that of the surrounding, a 21 cd/m^2 yellow field (the average output of each gun, as measured with a Minolta LS-110 luminance meter, was identical). Thus this target could only be detected on the basis of its chromatic modulation, and this modulation had a reasonably high spatial frequency.

For comparison, we also designed a stimulus that would only stimulate the magnocellular pathway. This was a 32x32 pixel square defined by 30 Hz luminance flicker. Subjects saw two frames with a black square alternating with two frames with a 42 cd/m^2 yellow square. This stimulus can only be detected by a mechanism with a high temporal resolution. Note that for both stimuli the temporal and spatial average luminance and chromaticity of the target was identical to that of the surrounding (a 21 cd/m^2 yellow field), so that a pathway that does not detect the modulations will not detect any stimulus at all.

For comparison we also used targets defined by luminance decrements: maximal, 5% and 2% luminance contrast. The maximal contrast target was a black square. At 5% luminance contrast the target was about as conspicuous as the isoluminant and flickering ones. At 2% contrast the target was just visible clearly enough to give acceptable reaction times (Plainis and Murray 2000).

Procedure

Subjects started each trial with their finger on a target at the near edge of the screen (see Fig. 1). Some time after subjects placed their finger on this target the latter disappeared and a new target appeared at one of three positions 70 cm further away. There were five conditions. In three conditions subjects simply moved their finger to the new target (left, centre or right). In the other two the target that had appeared was the central one, but as soon as the finger started moving the central target disappeared and one of the other two appeared. The critical trials were these ones in which the target stepped laterally as soon as the subject started to move. We compared the lateral movement of the hand after the target stepped to the right, with its movement after the target stepped to the left. There were 10 trials for each of the 25 combinations of the 5 conditions and 5 kinds of target. Trials from all combinations were presented in random order. Subjects were explicitly instructed to move their finger to 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.

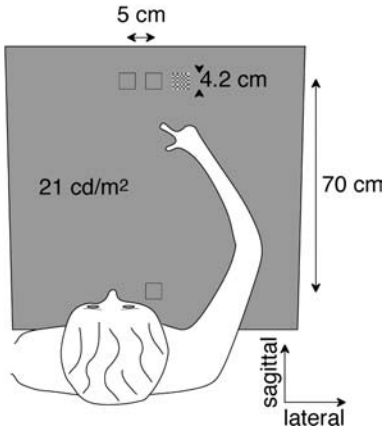

Fig. 1 The set-up. Subjects stood in front of a large slightly inclined plane onto which the stimuli were back-projected. The positions at which targets could appear are indicated by the *squares*. Only one was ever visible at a given moment. Each trial started with a target appearing at the position close to the subject. Some time after the subject put his or her finger on this target, the target jumped to one of the other three positions. On some of the trials in which the target jumped to the central position, it stepped to one of the lateral positions as soon as the subject's hand started to move

Subjective evaluation of how conspicuous the targets are

If fast responses are impossible for stimuli that only stimulate the parvocellular pathway then we expect the latency to be very much longer for such stimuli. However, decreasing the contrast is also likely to increase the latency of response (as it does for regular reaction times). In order to determine whether the stimulus that was designed to only stimulate the parvocellular pathway is simply less conspicuous than the one designed to only stimulate the magnocellular pathway we asked subject to indicate how conspicuous they felt that each was. They did so by moving it horizontally (by moving the computer mouse) to what they considered to be the appropriate position on a contrast scale formed by the three, luminance decrement targets (placed at equal distances).

Subjects

Seven colleagues volunteered to take part in this study after being informed about what they would be required to do. Two were the authors. The others were unaware of the hypothesis that was being tested. The research in this study is part of an ongoing research program that has been approved by the local ethics committee.

Analysis

All velocities were calculated by simply dividing the distance between two samples by the time interval between them. The resulting velocity was assigned to the moment between the two samples. Synchronisation with the targets 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 2 ms resolution with which the movement of the hand was recorded.

To determine how quickly subjects initially reacted to target onset we determined the average sagittal (see Fig. 1) velocity of the finger as a function of the time after the target appeared. All responses for each stimulus were first synchronised relative to the

first appearance of the target, then averaged for each subject, and finally averaged across subjects.

To determine how quickly subjects responded to the step change in target position we determined the difference between the average lateral velocity of the finger after a rightward and a leftward step. The responses in the two conditions with steps were first synchronised relative to the moment the target changed position, then averaged for each condition and subject, and finally the difference between the two conditions was determined and averaged across subjects.

The shape of an average response depends on the shape of the individual responses as well as on the variability. To determine whether differences between the responses to different kinds of targets were due to differences in the individual responses or to differences in the amount of variability between such responses we determined the average difference between the lateral velocity after a rightward and leftward step (as in the preceding paragraph), but now synchronised the responses relative to the peak lateral velocity rather than the change in target position.

Results

Figure 2 shows the seven subjects' impressions of how conspicuous the two targets are. Lines connect individual subjects' impressions for the two targets. All subjects considered the target that only stimulated the parvocellular pathway (Isoluminant) to be more conspicuous than the 5% luminance decrement. Most subjects considered the target that only stimulated the magnocellular pathway (Flickering) to be slightly less conspicuous. The larger variability between subjects for the flickering targets may have to do with differences in temporal sensitivity between the subjects or with the extent to which subjects made eye movements during the task (the two high-contrast components of the flickering target are separated on the retina during saccades).

About 4% of the movements were excluded from further analysis, either because subjects started moving less than 150 ms or more than 1500 ms after the target appeared, or for technical reasons (such as the infra-red light emitting diode attached to the finger not being visible to the cameras of the Optotrak during part of the movement). The average standard deviation in the movement endpoints was 0.84 cm. The variability was slightly larger when the target had stepped than when it had not, but was independent of the kind of target. The average movement time was 395 ms. It was about 5 ms longer when the target stepped than when it had not (t_{34}=2.1; p=0.04; t-test on data paired by subject and kind of target). This is probably because of the increased distance. The movement time did not depend on the kind of target.

Figure 3 shows the sagittal velocity at the beginning of the movement. As expected, the reaction time was about 200 ms. It was longer for low contrast targets than for high contrast targets (light and dark thin curves, respectively). The reaction to the flickering targets (light thick curve) was similar to that for the high contrast targets. The reaction to the isoluminant checkerboard (dark thick curve) was similar to that for the low contrast targets, despite this stimulus having subjectively been judged to

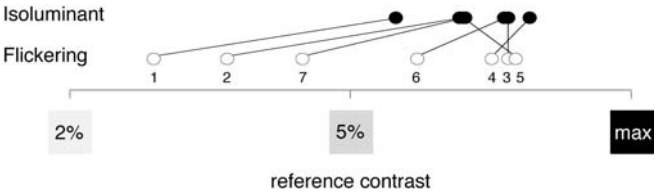

Fig. 2 Subjects' subjective impressions of how conspicuous the isoluminant (*solid symbols*) and flickering (*open symbols*) targets were in relation to the luminance decrements. The *numbers below the open symbols* correspond with the subject numbers in Table 1

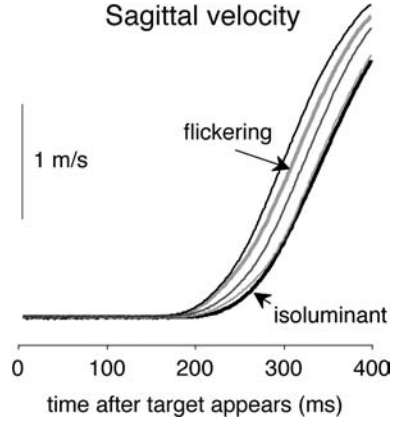

Fig. 3 The finger's sagittal velocity during the first part of the movement to each of the five kinds of targets. Average of all movements by all seven subjects. The *thin curves* are for luminance decrements, with lower contrast in the figure indicating a lower contrast of the target (maximal, 5% and 2% contrast). The *dark thick curve* is for the isoluminant checkerboard that selectively stimulates the parvocellular pathway. The *light thick curve* is for the 30 Hz flickering target that selectively stimulates the magnocellular pathway

be more conspicuous. The longer reaction time for the isoluminant targets is consistent with their detection being based on the slower, parvocellular pathway.

Figure 4 shows the difference between the lateral velocity of the hand after the target stepped to the right and its velocity after the target stepped to the left. The panel on the left shows this difference as a function of the time after the target appeared at the new position. This is shown for each of the five kinds of targets. For high contrast targets (darkest thin curve), subjects responded to the step in just over 100 ms. The latency to respond increased with decreasing target contrast (other two thin curves). The latency to respond to the isoluminant target (dark thick curve) was considerably longer than the latency to respond to even the lowest luminance contrast (lightest thin curve). Table 1 shows that this was so for all seven subjects.

The response to the flickering stimuli was fast (light thick curve in left panel of Fig. 4), but the shape of the average response was clearly different from that for the other targets. A simple explanation for this difference is that it is because the stimulus itself is temporally modulated. We did not synchronise the step to the phase

of the 30 Hz flicker. This presumably led to additional variability in the moment at which the displacement could be detected, and therefore in additional variability in the moment at which the response was initiated. Additional variability in the timing of the response leads to a lower and wider average response.

That temporal variability is responsible for the different shape of the response can be seen in the right panel of Fig. 4, which shows the same responses averaged with respect to the peak lateral velocity rather than the moment of the step. There is an almost perfect overlap between the responses for the flickering targets and those for the other four kinds of targets, indicating that the shape of individual responses was not affected. Note that the amplitude of the other responses is only about 40% larger when synchronised in this manner, indicating that the variability in response latency is small in those conditions.

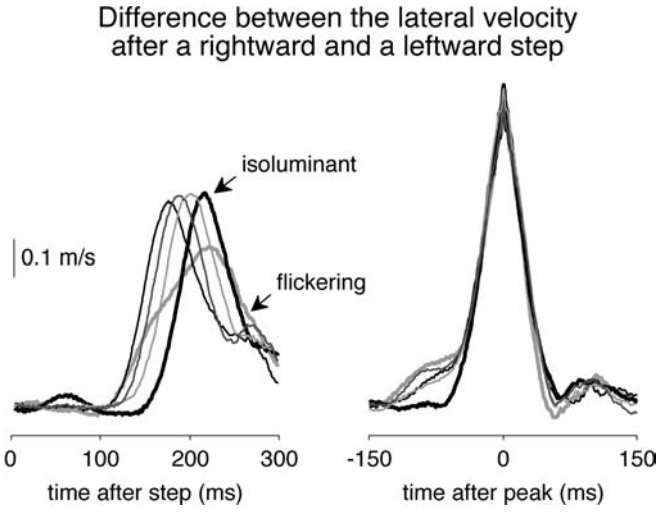

Fig. 4 Response to the step displacement for each of the five kinds of targets. Average of seven subjects. The *thin curves* are for luminance decrements, with lower contrast in the figure indicating a lower contrast of the target (maximal, 5% and 2% contrast). The *dark thick curve* is for the isoluminant checkerboard that selectively stimulates the *parvocellular* pathway. The *light thick curve* is for the 30 Hz flickering target that selectively stimulates the magnocellular pathway. In the *left panel* the lateral movements of the finger are synchronised relative to the moment that the target was displaced. In the *right panel* they are synchronised relative to the moment that the finger's lateral velocity was highest

Discussion

Subjects responded as quickly to step displacements of the flickering target as to step displacements of a high contrast target. It took them longer to respond to step displacements of the isoluminant checkerboard than to step displacements of a barely visible (2% contrast) luminance decrement target (left panel of Fig. 4). This difference does not reflect the subjects' subjective impression of how conspicuous each target is (Fig. 2). The relatively long latency to respond to isoluminant targets is also visible in the reaction time (Fig. 3), but there the difference is much less dramatic. These findings are consistent with the hypothesis that fast responses cannot be driven through the parvocellular pathway: the fast responses appear to be colour-blind. However, although step displacements of the isoluminant checkerboard took longer to respond to than step displacements of any other kind of target (left panel of Fig. 4), the responses were still faster than the normal reaction time (Fig. 3). Why is this?

One possibility is that our target was not *completely* invisible to the magnocellular pathway. We did not determine each subject's individual isoluminance values, so there is likely to be some residual luminance contrast for some subjects (at the spatial frequency of the fields of the checkerboard). Such residual luminance contrast could have activated the magnocellular pathway in these subjects. However, this is not the most likely explanation for a magnocellular contribution to the fast responses to the checkerboard because the same trend was found for all our subjects, as is evident from Table 1. It is more likely that the magnocellular pathway was stimulated by our checkerboard despite it being isoluminant (Lee et al. 1989). In order to be completely insensitive to chromatic modulation the input from the different types of cones to the magnocellular pathway would have to be perfectly matched. This is not the case for individual cells in area MT (Gegenfurtner and Hawken 1996) and there is no real reason to expect it to be the case in other areas.

An alternative possibility is that the responses to step displacements of the isoluminant checkerboard are driven through parvocellular pathways. Admittedly, the difference between the time that it takes to respond to isoluminant and flickering targets is larger than the difference between the time that it takes to activate the first stages of the parvocellular and magnocellular pathways (Maunsell et al. 1999; Schmolesky et al. 1998). However, assuming that areas in the posterior parietal cortex are involved, the additional difference may

Table 1 Latency with which the average *difference between the lateral velocity after a rightward and a leftward step* reached a threshold of 0.1 m/s for each subject and target type (ms). Latencies for the masked steps in Experiment 2 are shown *in brackets*

Subject	Maximal contrast	5% contrast	2% contrast	Flickering	Isoluminant
1	154 (175)	175 (206)	182 (220)	160 (227)	192 (211)
2	160 (152)	167 (191)	183 (221)	161 (193)	195 (190)
3	133 (122)	141 (168)	159 (216)	139 (130)	170 (170)
4	156 (204)	165 (221)	159 (250)	166 (200)	183 (221)
5	125	136	132	126	168
6	135	152	164	134	182
7	120	127	145	117	160

be because the magnocellular pathway provides its input more directly than does the parvocellular pathway (Van Essen et al. 1992), thereby increasing the difference in latency.

Experiment 2: disturbing the magnocellular pathway

Since we can never be completely sure of having only stimulated the parvocellular pathway, we decided to approach the remaining uncertainty by masking the transient in the displacement. Since the magnocellular pathway is presumably much more sensitive to such transients than the parvocellular pathway, such masking leads to different predictions for our two hypotheses. If residual magnocellular stimulation drives the responses, then we expect such responses to be severely disrupted by such masking. If the parvocellular pathway drives the responses, then we expect such masking to have little effect.

Materials and methods

The second experiment was identical to the first except that the whole screen was black (rather than yellow) for one frame when the target was displaced. Thus, on the trials in which the target was displaced, rather than having the target step as soon as the finger started to move, the screen went black for one frame and then the target appeared at the new position (on a 'new' yellow background) on the next frame. Obviously, the timing of the response was measured relative to the moment the new target appeared. Trials in which the target was not displaced were identical to those in experiment 1.

The analysis of the data was also identical to that in the first experiment. The only addition was that we used paired *t*-tests to evaluate whether the difference between the latency to respond to each kind of target in the two experiments was consistent across subjects. The subjects were four of the seven who had taken part in experiment 1 (including one of the authors).

Presenting a uniform black screen on one frame will mainly interfere with responses that are mediated by weak signals within the magnocellular pathway. Thus if the fast responses are normally driven by the magnocellular pathway, we expect a delay in the responses in the presence of the flash, and we expect this delay to increase with decreasing target contrast. We expect little delay for responses that are driven by the parvocellular pathway.

Results

On interrogation after the experiment only one of the three naïve subjects reported having noticed the black "flash". The left panel of Fig. 5 (no flash) shows a selection of the data from experiment 1. The curves show the difference in lateral velocity for each kind of target, for the four subjects who also took part in experiment 2. The dots indicate values at arbitrary positions near the beginning of the response. The right panel of Fig. 5 (flash at time of step) shows the difference in lateral velocity for each kind of target in experiment 2. The dots are at the same positions as on the left panel to facilitate a comparison of the response latency.

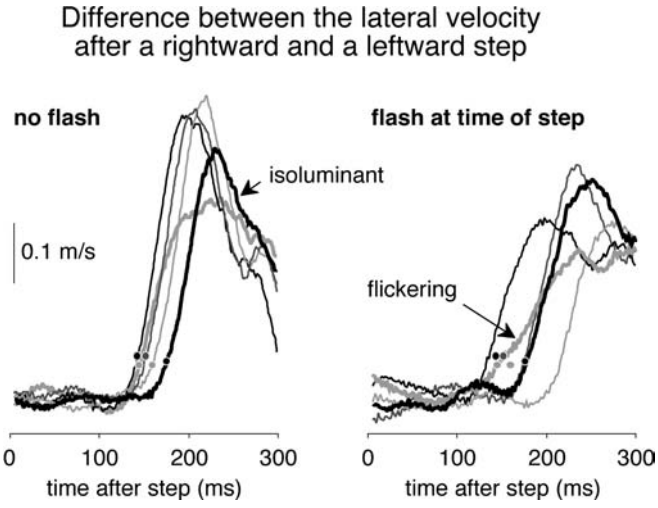

Fig. 5 Response to the step displacement for each of the five kinds of targets. Averages for the same four subjects in the two experiments: experiment 1 with *no flash* and experiment 2 with a *flash at the time of the step*. The *thin curves* are for luminance decrements, with lower contrast in the figure indicating a lower contrast of the target (maximal, 5% and 2% contrast). The *dark thick curve* is for the isoluminant checkerboard that selectively stimulates the parvocellular pathway. The *light thick curve* is for the 30 Hz flickering target that selectively stimulates the magnocellular pathway. The *dots on the initial part of the responses in the left panel* are reproduced at the same positions in the right panel to help compare the latencies

The positions of the dots relative to the curves in the right panel of Fig. 5 show that the black flash delayed the response to low luminance contrast targets considerably. This is what we predicted would happen because we expected these responses to be mediated by the magnocellular pathway. The response to the isoluminant checkerboard was hardly delayed. The response to the isoluminant checkerboard also hardly became weaker, in contrast to the response for several of the other targets, presumably because the flash introduced little additional variability in response latency for the isoluminant checkerboard.

The modest influence of the black flash on the latency of responses to step displacements of the isoluminant checkerboard was consistent across the four subjects. The numbers between brackets in Table 1 show the time it took for the finger to reach a difference in lateral velocity of 0.1 m/s (in the second experiment). The average increase in latency relative to that in the first experiment gives an indication of the masking effect of the "flash". This increase was 56 ms for the 2% contrast luminance decrement (t_3=4.5; p=0.020), 34.5 ms for the 5% contrast luminance decrement (t_3=4.7; p=0.018) and 31 ms for the flickering target (t_3=2.0; p=0.14). It was only 13 ms for the isoluminant checkerboard (t_3=1.3; p=0.28) and 12.5 ms for the maximal contrast luminance decrement (t_3=0.9; p=0.43). The implication of the response to the isoluminant checkerboard being unaffected by the flash is that the parvocellular pathway must be responsible for the

response, rather than residual, weak magnocellular stimulation.

General discussion

The conclusion from our experiments is that the parvocellular pathway can mediate fast responses to target perturbations. These responses take more time than ones mediated by the magnocellular pathway, but they are considerably faster than the initial responses to the target appearing. Fast responses are presumably normally used to correct movement errors that arise from misjudging the target's position or because the target moved. For such corrections to be of any use it is obviously essential that the visuomotor delay is very short.

There are many connections between the various pathways within the brain (Merigan and Maunsell 1993). Still the fact that fast responses can be mediated by information through the parvocellular pathway is not self-evident, because the various separate pathways presumably exist to ensure that the most efficient coding is used for each judgement. In order to be able to respond to stimuli with little luminance contrast, but substantial chromatic contrast, it would be enough to have cells within the magnocellular pathway that do not all respond to exactly the same balance of L, M and S cones (Calkins 2001; Gegenfurtner and Hawken 1996). However, if this were the origin of the responses to the isoluminant checkerboard then the "flash" in experiment 2 would have influenced the responses to these stimuli to the same extent as it did the response to low luminance contrast stimuli, which it did not.

We could not use colours that stimulate the S-cones to the same extent for our isoluminant checkerboard, because we used the blue channel of our stimulus signal to synchronise our equipment. Our checkerboard therefore also differentially stimulated S-cones. Assuming that subjects fixated the initial target, the spatial resolution at the eccentricity to which the target jumped is about 5 cycles per degree (Calkins 2001), so our checkerboard (about 3 cycles per degree vertically) could have been detected. However, the chromatic contrast and the spatial resolution were certainly more suitable for the parvocellular pathway. Moreover, the koniocellular pathway appears to be able to respond very fast (Morand et al. 2000), so we would expect a response based on S-cones to be exceptionally fast rather than relatively slow. We therefore consider it more likely that the parvocellular pathway is responsible for the fast responses to the isoluminant checkerboards.

There is also some evidence that subcortical pathways, such as that through the superior colliculus (Solomon et al. 1981; Stuphorn et al. 2000), can mediate fast responses (Day and Brown 2001; Perenin and Rossetti 1996). We consider it unlikely that our targets that were specially designed to only be visible to the parvocellular pathway will activate such subcortical pathways. Less is known about the visual properties of cells within subcortical pathways than about those within cortical pathways, but they probably have a much too low spatial and chromatic resolution to be activated by the isoluminant checkerboard, because they rely on a much more limited number of projections.

Our results may seem to be in conflict with those of Pisella et al. (1998), who found that stopping a movement in response to a change in the target's colour takes substantially more time than adjusting the movement in response to a change in the same target's position. We would like to point out that this is not a discrepancy. We examined the response to the *position* of a target defined by colour, whereas they examined responses to the *colour* itself. These are different issues that undoubtedly make use of some common (parvocellular) areas, but also involve quite different areas of the brain (Heywood et al. 1998).

The fact that the flash that we introduced in the second experiment did not influence the response to the isoluminant checkerboard is our main evidence that the parvocellular pathway mediates the response to such targets. Since faster reactions were found for flickering targets we must conclude that other pathways can also drive fast reactions. Thus fast responses can be driven by visual input through several pathways, including the parvocellular pathway.

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