Slow and fast visual motion channels have independent binocular-rivalry stages

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We have previously reported a transparent motion after-effect indicating that the human visual system comprises separate slow and fast motion channels. Here, we report that the presentation of a fast motion in one eye and a slow motion in the other eye does not result in binocular rivalry but in a clear percept of transparent motion. We call this new visual phenomenon 'dichoptic motion transparency' (DMT). So far only the DMT phenomenon and the two motion after-effects (the 'classical' motion after-effect, seen after motion adaptation on a static test pattern, and the dynamic motion after-effect, seen on a dynamic-noise test pattern) appear to isolate the channels completely. The speed ranges of the slow and fast channels overlap strongly and are observer dependent. A model is presented that links after-effect durations of an observer to the probability of rivalry or DMT as a function of dichoptic velocity combinations. Model results support the assumption of two highly independent channels showing only within-channel rivalry, and no rivalry or after-effect interactions between the channels. The finding of two independent motion vision channels, each with a separate rivalry stage and a private line to conscious perception, might be helpful in visualizing or analysing pathways to consciousness.

Keywords: rivalry; motion; transparency; channels; consciousness

1. TWO MOTION CHANNELS AND BINOCULAR RIVALRY

Evidence for separate low- and high-speed global-motion channels has been obtained by various methods (Anderson & Burr 1985; Edwards *et al.* 1998; Gegenfurtner & Hawken 1996). One straightforward paradigm that we have used involved motion after-effects. The classical motion after-effect, or waterfall illusion (Mather *et al.* 1998; Wade 1994), occurs after viewing translational motion, such as a waterfall, for a while and then looking at a static scene. One then perceives (somewhat paradoxically) overall motion in a direction opposite to the adaptation direction. This classical version of the illusion is called the 'static' motion after-effect, since it is seen on a static test pattern. The static motion after-effect only occurs, however, for relatively low adaptation velocities, up to about 20–$30° s^{-1}$. Why do clearly visible high-velocity patterns (faster than 20–$30° s^{-1}$) fail to evoke a classical motion after-effect? One possibility is that low-speed and high-speed motions stimulate different processing streams, with different temporal properties. Indeed, one can generate a motion after-effect for high-velocity patterns, but only if the test stimulus is dynamic, e.g. noise or 'snow' (Verstraten *et al.* 1998). This is called the 'dynamic' motion after-effect (see also Hiris & Blake 1992). It is generally assumed that motion after-effects are due to the relatively slow restoration of some automatic gain control mechanism in, or just after, the elementary cortical motion sensors (e.g. Grunewald & Lankheet 1996). Motion after-effects apparently enable us

to selectively read out the automatic gain control of the high-speed channel with a dynamic test stimulus, and of the low-speed channel with a static test pattern. Using a test pattern consisting of a mixture of static and dynamic noise results in a transparent motion after-effect (Van der Smagt *et al.* 1999), that is, both after-effects are seen transparently at the same time and in the same place. This perceptual segregation is not based on motion direction differences, since it occurs even if the inducing directions are the same (Van der Smagt *et al.* 1999). In contradistinction, after-effects for adaptation patterns of similar (low or high) velocities do not segregate.

If there are indeed two independent motion channels, one for low velocities (temporal frequencies below *ca.* $20 Hz$) and one for high velocities (temporal frequencies above *ca.* $20 Hz$; Van der Smagt *et al.* 1999), what would be expected for a dichoptic stimulation of the two channels through different eyes? We did not expect the same binocular rivalry or suppression that one finds if the eyes are confronted with slow motion independent patterns covering corresponding retinal regions (Blake *et al.* 1985; Wade *et al.* 1984). In fact, we now report that it results in motion transparency, regardless of the motion directions of the slow and fast patterns. This 'dichoptic motion transparency' (DMT) is an unexplored and, to our knowledge, new phenomenon in binocular-vision studies. An analogous phenomenal segregation has previously been reported for the dichoptic combination of static gratings of very low and very high spatial frequencies (Yang *et al.* 1992). On this basis, Yang *et al.* have already proposed 'transparency' as a new category of dichoptic percepts but they did not consider motion transparency. Usually only the following three binocular perceptual categories are mentioned (for a review, see Fox 1991): first, binocular rivalry, which consists of dominance of either the left or

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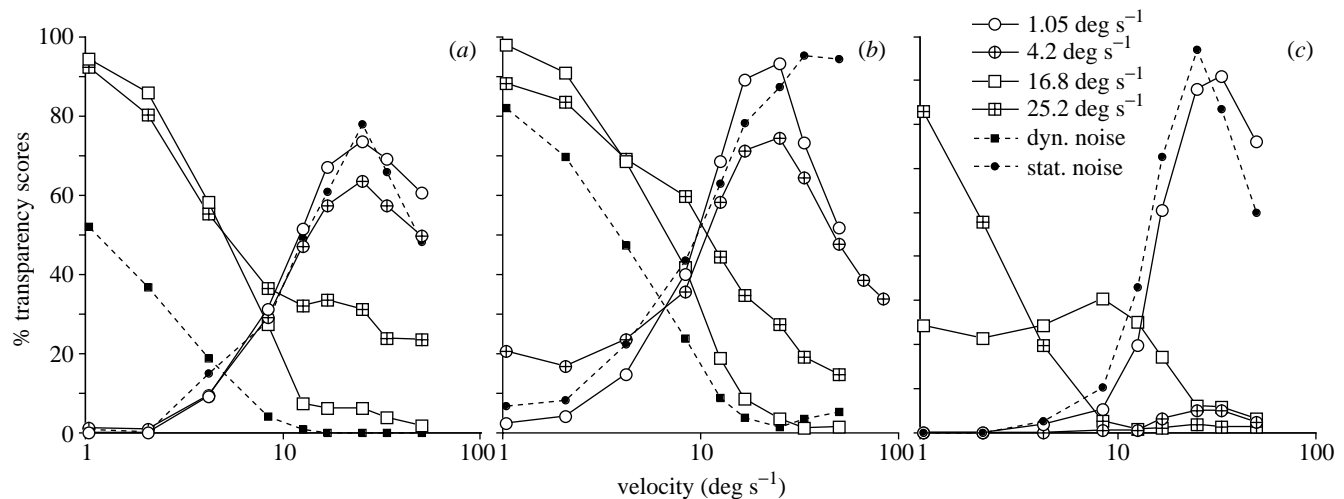
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Figure 1. Percentage transparent-motion scores as a function of speed for four values of the reference speed, V_{ref}, and three observers ((a) W.G., (b) P.H. and (c) B.B.). V_{ref} values are given in the inset. Opposite motion directions were used and presentations were of 1 s duration. For high reference velocities ($16.8° s^{-1}$ and $25.2° s^{-1}$) in one eye the percentage transparency scores are high for low velocities in the other eye (square symbols). For low reference velocities ($1.05° s^{-1}$ and $4.2° s^{-1}$) in one eye the percentage transparency scores are high for high velocities in the other eye (circles). Data based on 100 presentations per condition. The average standard errors of the mean were 5.5 for W.G., 6 for B.B. and 8 for P.H. The curves were smoothed with a standard three-point running average. Similar results were obtained for perpendicular motion directions (45° and 135°) and for two other observers (F.V. and M.S.).

the right eye's pattern (while the other is completely suppressed) or of a piecemeal mixture of the two; second, binocular fusion and stereopsis; and third, pattern superposition, which occurs mainly for very brief presentations (Wolfe 1983) or low contrast (Liu *et al.* 1990). (For other reports on linear and nonlinear pattern combination see Baitch & Levi (1989), Badcock *et al.* (1991) and Badcock & Derrington (1987).)

Apparently a fourth category is needed as proposed by Yang *et al.* (1992): unfused depth segregation or 'transparency'. Under this perceptual category we now propose to include the new phenomenon of DMT as described here. DMT should be distinguished from 'normal' motion transparency, where both motion stimuli are viewed by one or both eyes simultaneously. In §5 we will consider the difference between 'normal' transparency and DMT in some detail.

The idea of two separate motion channels immediately suggested the dichoptic experiments described below. We hypothesized that binocular rivalry occurs only within the channels not between them. In testing this hypothesis DMT was discovered. After describing the psychophysical results, we show with a model calculation that our results on binocular motion rivalry and DMT support the inference of the absence of rivalry between the slow and fast motion channels. The model provides a simple and natural link between the strengths of the motion aftereffect and of the binocular motion rivalry. The results therefore underpin the suggestion of a direct connection between the transparent motion after-effect and DMT, since both phenomena appear to be based on the independence of a low-velocity (low temporal frequency) channel and a high-velocity (high temporal frequency) channel. As explained in §5, we think these findings might also be helpful in consciousness studies.

2. METHODS

Moving random pixel arrays ('Julesz patterns') of 70% root-mean-square contrast and an average luminance of $50 \, cd \, m^{-2}$ were presented separately to each eye at a viewing distance of 135 cm. At this distance the pixel diameter was 1.4 arcmin. Each eye viewed a separate monitor via an adjustable mirror arrangement. The random pixel patterns moved behind a fixed square window of 256×256 pixels, which they filled completely. A central fixation point in each window was binocularly fused, but the uncorrelated moving textures would normally be expected to rival. The moving random pixel patterns were generated with custom-made hardware and displayed on multisync monitors at 90 frames s^{-1}. A speed of $2.1° s^{-1}$ is obtained for one pixel shift per frame, so this and higher velocities all have the same step rate (temporal frequency 90 Hz). Only the lowest speed used in these experiments had a lower step rate of one pixel shift per two frames (45 Hz).

The five observers were all experienced in similar experiments, but at the time of the experiments two of them (B.B. and P.H.) were naive as to the purpose of the experiments. A chin rest with forehead support was used and the observer's task was to classify, by pressing a button, his/her percept of each stimulus presentation as either rivalry or transparency. For each condition 100 presentations were scored, the conditions were intermixed in quasi-random fashion so that one seldom had more than a few sequential presentations with the same parameter settings. A typical run lasted about 1 h. Except for one experiment in which we studied the influence of presentation duration, all presentations lasted 1 s. It has been shown that this is long enough to judge the occurrence of rivalry (Fox 1991) and our control experiment, with a variable presentation duration, confirms this (see §4). For three of our observers we used both opposite and perpendicular (45° and 135°) motion directions in the two eyes. Since we found no significant differences between
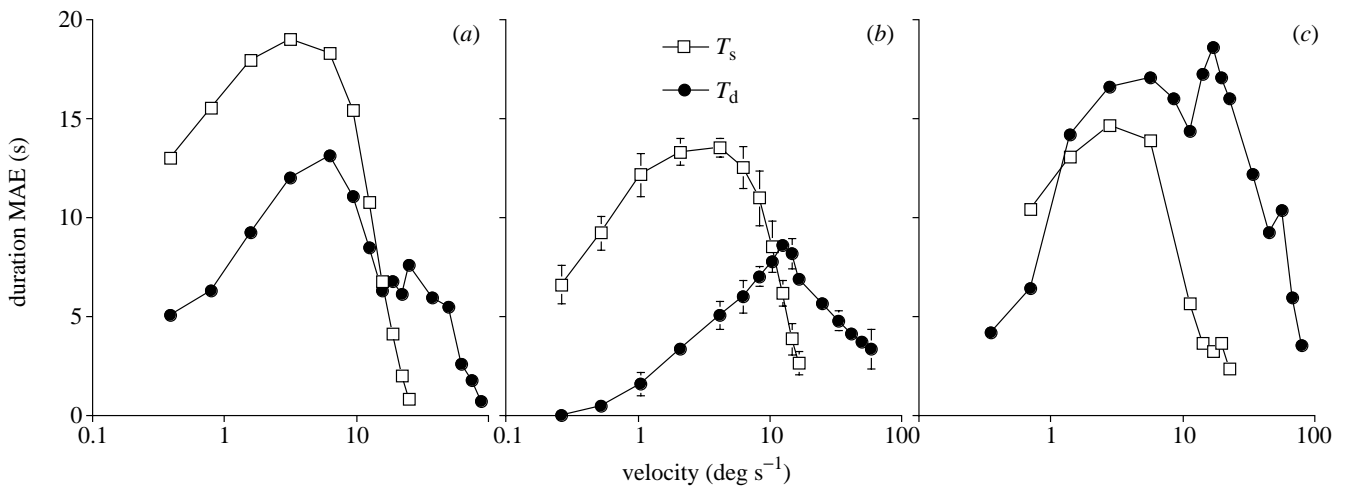
Figure 2. Duration of the motion after-effect as tested with a static test pattern (T_s, open squares) or with a dynamic noise pattern (T_d, filled circles) as a function of adaptation velocity for the same three observers as in figure 1. Two other observers (F.V. and M.S.) gave similar results. One of them (M.S.) gave results somewhat more like those of (*c*) B.B. with a low 'cross-over speed' (the speed where $T_d = T_s$). Observer B.B. has the lowest crossover speed out of our five observers. For (*a*) W.G., F.V. and (*b*) P.H. the crossover speed is about $12°\,s^{-1}$, for M.S. it is about $4°\,s^{-1}$ and for B.B. it is about $1°\,s^{-1}$. Vertical bars in (*b*) give the standard error of the mean for the eight duration measurements per point. These standard-error values were similar for all our observers. Data in (*a*) and (*b*) are smoothed by a three-point running average method; however, the s.e.m. values in (*b*) are those of the original data (unsmoothed). The curves in (*c*) are not smoothed. The average s.e.m. was 0.62 for the static and 1.2 for the dynamic motion after-effect data of B.B. The smoothing in (*a*) and (*b*) was applied to eliminate very fine and potentially confusing detail in densely sampled regions of the curves, but does not affect their overall shape.

3. RESULTS

In the basic experiment, one stimulus has a fixed speed, V_{ref}, while the contralateral stimulus moves with any of a range of speeds, V. The pattern with reference speed V_{ref} is randomly presented to the left or right eye. Formal measurements were carried out on five observers (including the authors) and six others confirmed the phenomena qualitatively. Figure 1 shows the percentage of trials in which three of the observers (W.G., P.H. and B.B.) reported transparency, as a function of the variable speed, V, for four choices of the reference speed, V_{ref}. In addition, we used reference stimuli with zero velocity, namely a static spatial noise (Julesz) pattern, for all three observers, and a dynamic spatial noise sequence (snow) for two observers (W.G. and P.H.).

For V_{ref} values of 0 (static pattern), $1.05°\,s^{-1}$ and $4.2°\,s^{-1}$, we find mostly rivalry for V values in the low-speed range. This is the well-known motion rivalry that has been studied previously (Blake *et al.* 1985; Wade *et al.* 1984). However, for the same V_{ref} values we find mostly transparency if V is in the high-speed range (an exception is observer B.B. at $V_{ref} = 4.2°\,s^{-1}$ and we will return to this below). If V_{ref} is a relatively high speed ($16.8°\,s^{-1}$ or $25.2°\,s^{-1}$) the situation is reversed and one gets mostly transparency if V is below, say, $12-16°\,s^{-1}$ and mostly rivalry or suppression if V is in the high-speed range. For an intermediate value of V_{ref} (data not shown) we find a mixture of results, indicating overlap of the channels. In this case, the further the two speeds are apart the less they influence each other (Blake *et al.* 1985). Note in figure 1 that for a low V_{ref} and very high V values the

these two conditions, we only used opposite directions for the other two observers. Here, we report results only for opposite motion directions in the two eyes.

transparency scores decrease again. This is due to the general decrease of visibility of the comparison stimulus with increasing V, so that transparency becomes unlikely since only V_{ref} will be visible.

The results of W.G. and P.H. look very similar and those of one other observer (F.V.) are like these. Our fifth observer (M.S.) had results somewhere in between those of B.B. and P.H., so it suffices to try to understand the deviations of B.B. from the more common pattern of W.G., P.H. and F.V. Why are the results of B.B. so different? For example, in the case of $V_{ref} = 16.8°\,s^{-1}$ and a low comparison speed such as $1.05°\,s^{-1}$ most of our observers had transparency scores in the range 75–100%, but B.B. only reached 25%. He reported that the faster stimulus usually masked the slower stimulus in these presentations, which suggests that his fast channel is stronger than his slow channel over a wider range of speeds than for the other observers. To check this we can look at the durations of his static and dynamic motion after-effects.

The durations of the motion after-effects seen on dynamic (T_d) and static (T_s) test patterns, have been measured, in a separate experiment, as a function of velocity for our five observers and at a viewing distance of 1 m. Three observers (F.V., W.G. and P.H.) showed a crossover from low-speed channel dominance ($T_s > T_d$) to high-speed channel dominance ($T_d > T_s$) at around $12°\,s^{-1}$. The other two observers (M.S. and B.B.) had much lower crossover speeds of $4°\,s^{-1}$ and $1°\,s^{-1}$, respectively. Results for F.V. and M.S. can be found in Verstraten *et al.* (1998). Data for the other three observers are given in figure 2.

Speed-tuning curves for the two motion after-effects have similar forms for all five observers but differ in their vertical positions, which represent the absolute after-effect durations. For observer B.B. the curve for the

dynamic motion after-effect is shifted upwards relative to that for the static motion after-effect as compared to most other observers. This leads to a lower crossover speed and a stronger dominance of the dynamic motion after-effect. The same holds, to a somewhat lesser extent, for M.S. (Verstraten *et al.* 1998). Given the results shown in figure 2, one prediction is that for an observer like B.B. a pattern of $V_{ref} = 4.2° \, s^{-1}$ would stimulate the fast and slow channels about equally, quite unlike the situation for the other observers. This means that for B.B. we would expect more rivalry at this V_{ref} value. Figure 1 shows that this is exactly what happens. Only patterns with $V_{ref} = 1.05° \, s^{-1}$ are slow enough for B.B. to prevent rivalry in the fast channel.

The individual differences thus support the thesis that there is a direct relationship between the 'channels' as indicated by the two kinds of motion after-effect and as suggested by the dichoptic rivalry–transparency switch. We will use this idea in §4 in a mathematical model to test whether we can deduce results such as those in figure 1 from motion after-effect data such as those in figure 2. If this can be done, we will have a direct qualitative and quantitative link between motion after-effects and dichoptic motion rivalry.

Before turning to the model calculations we summarize the above empirical findings.

(i) For a suitably chosen dichoptic combination of a low-speed and a high-speed kinematogram stimulus, rivalry gives way to DMT. What constitutes a 'low' and what a 'high' speed is observer dependent but can be determined from duration measurements of the static and dynamic motion after-effects. Under DMT conditions a low-speed and a high-speed kinematogram can be seen simultaneously and fully segregated (transparent) in the same direction in visual space.

(ii) A zero-velocity static-spatial-noise pattern appears to 'belong to' (stimulate) the low-speed channel and a zero-velocity dynamic-noise pattern appears to 'belong to' (stimulate) the high-speed channel (figure 1). This dovetails with our previous finding that the former stimulus can read out the static motion after-effect, and the latter stimulus can read out the dynamic motion after-effect (Van der Smagt *et al.* 1999).

4. MODEL CALCULATIONS

The question we want to answer next is whether the rivalry phenomena and DMT of figure 1 are compatible with the hypothesis that there is only rivalry within the channels not between them. To answer this question we first assume that there are two channels, as isolated by the motion after-effects, and that binocular rivalry occurs only within these channels not between them. If we can describe the data in figure 1 with this model then we accept the hypothesis (at least for now), if not then the channel-independence hypothesis is falsified as far as rivalry processes are concerned. Figure 3 illustrates this starting point.

We define dominance factors, *D*, for each channel, which simply give the contrast between the two inputs:
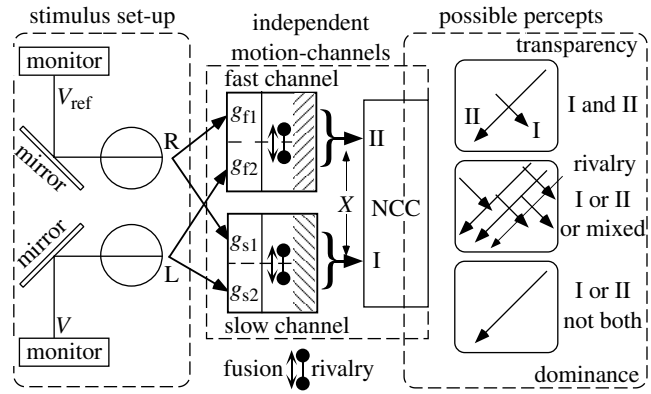
Figure 3. Model of motion-information processing in two independent channels, one for fast motion and one for slow motion. We assume that binocular rivalry and fusion are only possible within each channel and that the channels do not influence each other. The 'neural correlate of consciousness' (NCC) allows strong outputs from the two channels to be seen transparently (at the same time and in the same place). If *V* approaches V_{ref} then rivalry occurs in and from one channel (either the slow or the fast channel depending on the value of V_{ref}). No, or a very weak, response results from the other channel. If *V* and V_{ref} are far apart, one of them (and thus one eye) dominates one channel and the other motion stimulus (and eye) dominates the other channel, resulting in dichoptic motion transparency. From this model we calculate the frequency-of-transparency curves in figure 1 under the assumption that the gain factors are proportional to their corresponding motion after-effect durations (see §4).

$$D_f = (g_{f1}(V_{ref}) - g_{f2}(V))/(g_{f1}(V_{ref}) + g_{f2}(V)), \qquad (1)$$

$$D_s = (g_{s2}(V) - g_{s1}(V_{ref}))/(g_{s2}(V) + g_{s1}(V_{ref})), \qquad (2)$$

where g_{f1}, g_{f2} and g_{s1}, g_{s2} are speed-specific gain factors for the fast and slow channels, respectively.

If $D_f \gg 0$, V_{ref} dominates the fast channel and if, simultaneously, $D_s \gg 0$ then *V* dominates the slow channel, so we can expect dichoptic transparency. Similarly, if both these dominance factors are simultaneously $\ll 0$ we also expect transparency because then *V* dominates the fast channel and V_{ref} the slow channel. Transparency would not occur for unequal signs of the dominance factors, so the precondition for transparency is that $D_f \times D_s > 0$. Therefore, we define the transparency factor as the geometric mean of the dominance factors:

$$Tr = \sqrt{D_f \times D_s}. \qquad (3)$$

These formulae allow us to calculate the dimensionless 'transparency factor', Tr, if we know the four gain (g) factors in equations (1) and (2). This is the point where we propose to couple the motion after-effect data with the rivalry data. The duration of the dynamic motion after-effect, T_d, for V_{ref}, or $T_d(V_{ref})$, is assumed to reflect the mass activity set up by V_{ref} in the fast channel during adaptation, so we take:

$$g_{f1}(V_{ref}) = c_d \times T_d(V_{ref}), \qquad (4a)$$

where c_d is a proportionality constant. This 'constant' reflects the influence of the dynamic test pattern on the after-effect duration and might depend on the adaptation
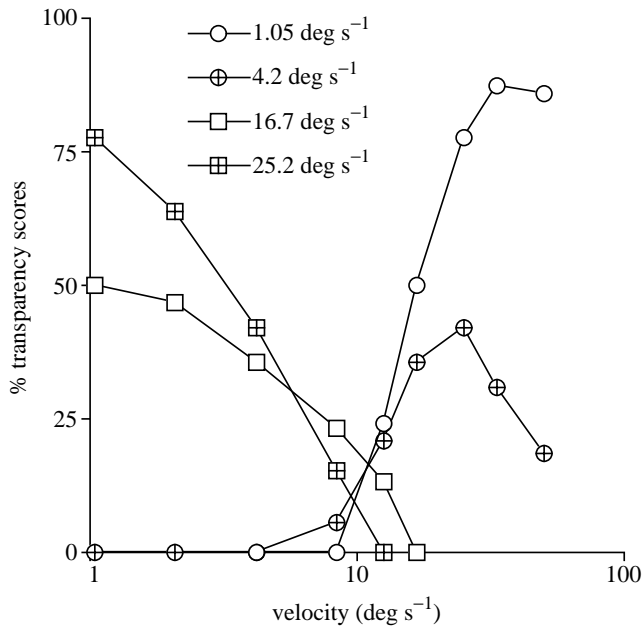
Figure 4. Transparency scores for observer P.H. as calculated from the model described in figure 3 and equations (1)–(4), as explained in §4. These theoretical results should be compared to the experimental findings in figure 1*b*. Input data of the model are exclusively after-effect durations, so it is remarkable that the model predicts the qualitative course of the gradual change from binocular motion rivalry to dichoptic motion transparency so well. The quantitative fit cannot be expected to be perfect for the reasons outlined in §4. In particular, the model does not take presentation duration into account and the results in figure 5 show that this variable has a quantitatively significant influence.

speed (V_{ref}) for which the after-effect duration is measured. As a first guess we assume that the dynamic test pattern influences all neurones in the high-velocity channel equally. Similarly we take

$$g_{\mathrm{f2}}(V) = c_{\mathrm{d}} \times T_{\mathrm{d}}(V), \tag{4b}$$

$$g_{\mathrm{s1}}(V_{\mathrm{ref}}) = c_{\mathrm{s}} \times T_{\mathrm{s}}(V_{\mathrm{ref}}), \tag{4c}$$

$$g_{\mathrm{s2}}(V) = c_{\mathrm{s}} \times T_{\mathrm{s}}(V). \tag{4d}$$

Here, c_{s} is a proportionality constant for a test of the slow channel's motion after-effect with a static-spatial-noise pattern. Again, c_{s} might actually vary with the adaptation velocity but we neglect this in our first guess. With these equations we can calculate the DMT strength, Tr, for all combinations of V and V_{ref} from the corresponding after-effect durations. It can be seen that the constants c_{d} and c_{s} immediately drop out of equations (1) and (2). This would not occur if we made them functions of the adaptation velocity. However, in such a model refinement we would be able to optimize the fit to the data. This is not what we want. We want to know how well the simplest version of the model (without any free parameters to improve the fit) describes the findings in figure 1. The results in figure 4 show that it describes them rather well.

Figure 4 presents the results of the model calculation for observer P.H., and should be compared to the middle panel of figure 1. Since Tr, by its definition, varies between

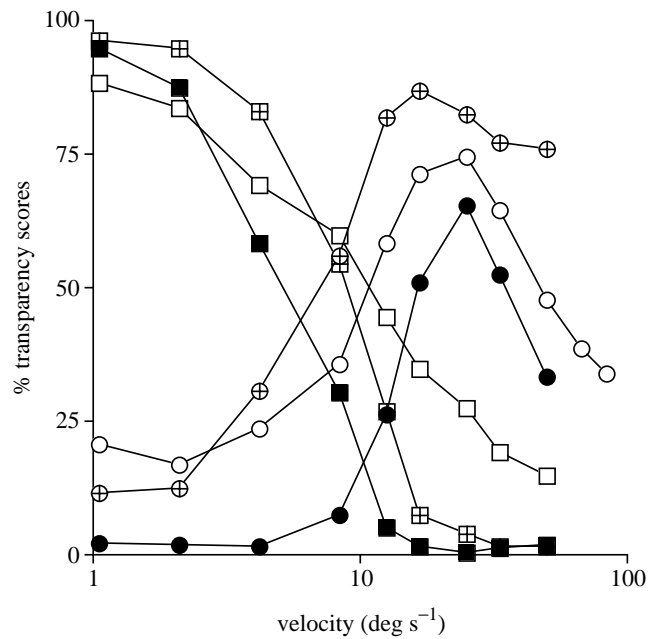Figure 5. Results of an experiment in which the presentation duration of the dichoptic motion stimuli was varied for two speeds, $4.2°\,\mathrm{s}^{-1}$ (circles) and $25.2°\,\mathrm{s}^{-1}$ (squares). The durations were 0.5 s (closed symbols), 1 s (open symbols) and 2 s (crossed symbols). These presentation durations give the same qualitative results but the curves tend to move slightly upwards for longer durations. Observer P.H.

0 and 1, it can be interpreted as an estimate of the probability of seeing transparency. This probability estimate is shown as a percentage in figure 4. Equations (1)–(4) thus lead us from the after-effect data in figure 2 (central panel, observer P.H.) to the DMT/rivalry data in figure 1 and provide the first link that we know of between after-effect data and rivalry results. The correspondence between the theoretical and the experimental curves for the other two observers was similar. This good qualitative likeness supports the hypothesis of an exclusively 'within-channel' rivalry. Now, one might object that the model results are only qualitatively similar to the experimental results and do not predict them in every quantitative detail. However, this is due to the absence of a completely worked-out model. As mentioned above, it would be possible to improve the quantitative fit by making the 'constants' c_{d} and c_{s} functions of the adaptation velocity.

A more serious shortcoming of this simple model is that we did not in any way specify the possible influence of the presentation duration. In figure 5 we present DMT/rivalry data for the same observer (P.H.) for a range of presentation durations (0.5, 1 and 2 s) and two speeds ($4.2°\,\mathrm{s}^{-1}$ and $25.2°\,\mathrm{s}^{-1}$). It is clear from these data that the presentation duration does not influence the results qualitatively but it has a non-negligible quantitative effect.

Figure 5 illustrates one reason why our preliminary model cannot be expected to predict DMT/rivalry data in quantitative detail. It is not *a priori* clear which of the curves in figure 5 should be picked to describe with the model. A complete model should at least include the dynamic characteristics of the rivalry process and this is beyond the scope of this paper. Suffice it to conclude that our model results support the two-channel hypothesis, including the idea that each of the channels has its own

rivalry mechanism. This simple model provides the first conceptual link between motion after-effects and binocular-rivalry processes.

5. DISCUSSION

Our main psychophysical finding is that binocular motion rivalry gives way to DMT if one eye's stimulus motion is in the high-velocity range while the other eye views low-velocity motion. Moreover, the two speed ranges overlap strongly and have observer-dependent optima. In these respects DMT appears to behave like the transparent motion after-effect described by Van der Smagt *et al.* (1999). One way in which these phenomena can be tied together is through the assumption that they both signify the presence of independent low-velocity–low temporal frequency ('slow') and high-velocity–high temporal frequency ('fast') channels in human motion vision. Such a two-channel assumption is, in itself, not original to us (see below). New are the findings that binocular rivalry appears to occur exclusively within these channels and not between them, so that dichoptic stimulation of the slow and fast channels through separate eyes leads to DMT. Moreover, the transparent motion after-effect of Van der Smagt *et al.* (1999) shows that the static and dynamic motion after-effects are also channel specific and highly independent of each other. The static motion after-effect can be read out with a static noise pattern and the dynamic motion after-effect can be read out with a dynamic noise test pattern. In this study we have found that a static spatial noise pattern behaves like a low-velocity kinematogram and a dynamic noise stimulus like a high-velocity kinematogram as far as dichoptic motion rivalry or transparency is concerned. It therefore seems parsimonious to assume that DMT and the transparent motion after-effect have a common mechanistic basis.

Our findings do not prove that the functional slow and fast channels are also anatomically separated but we think such an assumption is not unreasonable. One might tentatively identify the two channels with the ventral (mainly parvocellular) pathway for relatively low-speed motion processing and the dorsal (mainly magnocellular) pathway for relatively high-speed motion processing. The range of speeds to which the slow channel responds (as indicated by the classical motion after-effect; figure 2) is virtually identical to the range of speeds of pursuit eye movements (Carpenter 1977, e.g. p. 39) and of three-dimensional-shape-from-motion processes (which is easily checked with stereokinetic effects; W. A. van de Grind, unpublished results). Both of these processes break down at the higher speeds that exclusively stimulate the fast channel. These high velocities might mainly play a role in navigational processes, such as braking and steering. One should not forget, however, that the fast channel as isolated in our experiments (like the dorsal pathway) also contains relatively low-speed motion sensors. It only fails for the lowest visible speeds, which appear to be signalled exclusively by the slow channel. The slow channel in its turn only fails for the highest visible speeds. Figure 2 might be a useful reminder of this state of affairs. Motion sensors in the overlap speed range apparently come in two types for each and every velocity. One type has a gain control mechanism that can only be read out during the motion after-effect with a static test pattern, whereas the gain control of the other type can only be read out with dynamic noise. This is a good reason for assuming that they are physiologically different cells (such as parvo and magno cells). Moreover, if sensors of these two types are stimulated simultaneously with uncorrelated patterns through different eyes, they do not rival. Instead, they each support their own conscious percept of a moving texture, so that two layers are seen to move transparently. This complete independence is a good reason for assuming that the outputs of the two cell types are not intermingled.

Note that the above reasoning does not hold for just any kind of motion transparency. The well-studied 'normal' motion transparency phenomenon (reviewed by Snowden & Verstraten 1999), for example, leads to a unidirectional motion after-effect after adaptation to a bi-vectorial stimulus (Verstraten *et al.* 1994). The information that a stimulus is bi-vectorial can, in principle, be implicit in a population code, as has recently been shown for MT neurones (Treue *et al.* 2000). Since such cells give a uni-directional after-effect, there needs to be some coupling of their automatic gain controls, as in the model by Grunewald & Lankheet (1996). Therefore, it is reasonable to expect that these cells form part of one anatomical structure. One needs the trick of selective read-out of the motion after-effects with static and dynamic noise to see which proportion of the stimulated cells is in the slow or the fast channel. Similarly, two motions of equal speed (fast or slow) but sufficiently different directions are seen transparently if viewed by the same eye(s) but rival if each is presented to a different eye. This mutual rivalry again suggests that they form one closely knit anatomical module. Therefore, we propose that the hypothesis of two anatomically separate channels should be rejected for bi-vectorial motion stimuli, despite their motion transparency, if their after-effects merge or if they rival when viewed dichoptically. The hypothesis of independent slow and fast channels passes both these tests, making it a serious proposition. Moreover, the idea fits with a lot of independent evidence. Kulikowski (1971) (see also Kulikowski & Tolhurst 1973) was probably the first to propose explicitly that sustained cells form a 'pattern' channel and transient cells form a 'motion' channel. Since transient cells have higher temporal cut-off frequencies than sustained cells at the same eccentricity (Van de Grind *et al.* 1973), our present proposal is in line with these early suggestions. Supporting evidence was later presented by many others (e.g. Breitmeyer & Ganz 1976; Todd & Van Gelder 1979; Burbeck 1981; Anderson & Burr 1985; Snowden 1989; Wolf & Lusty 1994; Gegenfurtner & Hawken 1996; Edwards *et al.* 1998).

The study of bistable visual percepts has been recommended for investigating conscious perception (Crick & Koch 1998). If the input is constant but the percept changes, one can study the behaviour of neurons in the visual system that correlate with either the changing percept or the constant retinal stimulus. This provides valuable insight into the question of which neurons or brain regions might be part of the neural correlate of consciousness and which are not. The idea was used in studies of binocular rivalry (reviewed by Logothetis 1998) showing that neurons in visual cortices V1 and V2 mainly

follow the retinal stimulation, whereas in higher cortical areas many (in V4 and V5) or most (in superior temporal sulcus and inferior temporal cortex) neurons follow the awake monkey's percept, which was signified by key presses. Figure 1 shows that the switch from rivalry to transparency can be rather abrupt for a modest change in speed of one of the dichoptic patterns. This adds an extra dimension to the use of motion rivalry. By changing the speed of one or both the rivalling patterns, one might change the locus of maximal rivalry from the dorsal pathway to the ventral pathway or vice versa. If the speeds of the dichoptic pair are made sufficiently different, we predict the absence of rivalry in both pathways. The resulting DMT also suggests a simple method of localizing the neural correlate of consciousness (Crick & Koch 1998). If this correlate is a clearly localizable neural centre, it should be found at the final crossing of the low- and high-speed channels. An alternative suggestion by Zeki & Bartels (1998) is that consciousness is itself modular. In that case it should be possible in functional magnetic resonance imaging studies to pinpoint two loci of consciousness during DMT, which might differ from the two loci of activity generated by low-speed and by high-speed binocular rivalry.

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